Douglas-fir

The Genus *Pseudotsuga*

Denis P. Lavender and Richard K. Hermann

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Oregon State
UNIVERSITY

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Forest Research Laboratory

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Abstract

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Douglas-fir (*Pseudotsuga menziesii*) has a wide distribution in North America and is one of the tree species most widely distributed outside its natural range. The species has been introduced to Europe, New Zealand, South America, and elsewhere around the world. At present, Douglas-fir is an accepted and integral part of forest management in many countries because of its economic importance and its reputation as a species that may be able to deal with climate change.

This book provides an overview of research activities and findings that highlight unique aspects of Douglas-fir physiology, genetics, and other related issues. It begins with the evolutionary history and distribution of Douglas-fir and provides a detailed description of introductions of Douglas-fir to other countries, including information about initial plantings, provenance trials, and genetic tree improvement activities.

The sections about life history, drawn from extensive research and teaching experiences, include detailed descriptions of flowering, seeds, root, and seedling physiology, followed by sections about mycorrhizae and insects, diseases, and other biotic factors. It discusses research that demonstrates some of the unique aspects of Douglas-fir physiology, for example: (1) Douglas-fir has an annual growth cycle that includes a cold period in the late fall or early winter. Failure to experience these low temperatures results in a substantial loss of vigor; (2) the reproductive system of the stem is stimulated by material from the roots; and (3) the root system plays a supportive role. Nutrient and moisture uptake are mediated by mycorrhizae.

This book is intended as a resource for everyone interested in understanding the opportunities and challenges of managing Douglas-fir in a variety of regions and settings. It provides information for historians and social scientists investigating forestry trends; researchers, educators, and managers looking for detailed information in areas such as genetics and regeneration practices; and all others interested in the beautiful trees we call Douglas-fir.

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Foreword

Experience is the mother of knowledge. —English proverb

Denis Lavender and Richard Hermann combine more than 60 years of forestry research experience each in completing this synthesis about Douglas-fir. This monumental work is an extremely valuable contribution to our understanding of this beautiful and valuable genus. In current times, when researchers are pressured to increase their publication list and H-indices, summarizing our understanding about *Pseudotsuga*, as done here by the authors, is not likely to happen. We are grateful that Denny and Dick maintained a commitment to its completion during their retirement.

The compendium includes an invaluable collection of study descriptions and results, supported by citations and references, many of which are only available through paper copies. By synthesizing this information and making it available on a digital, searchable platform, the authors have assured that this tremendous body of knowledge will remain an extremely useful resource for future generations of researchers and practitioners.

One impressive aspect of the book is its global coverage of *Pseudotsuga*. This was only made possible by the authors' global reputations and network of colleagues around the world from whom they were able to obtain information, and by their ability to read publications in numerous languages.

The book has an impressive scope and covers more than a century of research results and management experience. It thus provides a historical timeline that highlights how challenges and information needs changed over time and how research activities were centered around relevant issues. Obviously, the authors relied heavily on their own work and experience, and the literature coverage is especially detailed for the period from the 1960s to 1990s. Even as new knowledge becomes available, their groundbreaking work as scientists and their synthesis efforts in writing this book will stand the test of time. Their careers and work are a source of great pride for Oregon State University, and this book will further strengthen the reputation of the College of Forestry as a premier research and teaching institution.

On behalf of College of Forestry faculty, students, alumni, and also all scientists and forest managers who stand to benefit from this book, the Dean and Deans Emeriti thank Denny and Dick for this very significant contribution to the field of forestry.

Thomas Maness, Dean, College of Forestry, 2012 – present
Hal Salwasser, Dean, College of Forestry, 2000 – 2012
George W. Brown, Dean, College of Forestry, 1990 – 2000

Preface

Pseudotsuga menziesii is distributed more widely outside its natural range than any other species of American forest tree, with the exception of *Pinus radiata.* Its successful introduction beyond its natural habitat into many parts of the temperate regions of the northern and southern hemisphere is all the more remarkable because of the early ignorance of, or disregard for, the importance of provenance.

The introduction of Douglas-fir went through various phases. Initially the species was introduced through individual tree plantings in Europe and elsewhere around the world. Successes were mostly dependent on the seed sources, and setbacks were due to the occurrence of diseases, especially *Rhabdocline pseudotsugae* and *Phaeocryptopus gaeumannii.* Over time, seed source problems and diseases were overcome through genetic selection and silvicultural practices that allowed for wider establishment, including monoculture stands. Social issues influencing such phases included trade barriers, e.g., during war time, but more influential were the political discussions about the introduction of non-native species. The proportion of Douglas-fir is often limited because of concerns about its ecological impacts; for example Forest Stewardship Certification standards in Germany limit non-native species to 20% stocking in management units.

Douglas-fir is nevertheless presently an accepted and integral part of forest management in many countries because of its economic importance, as well as its perceived reputation as a species that may be better able to withstand some aspects of climate change, especially given its drought resistance. But despite its unique characteristics and potential, Douglas-fir may also suffer from potentially detrimental effects of a changing climate, such as warmer temperatures that may not provide the critically important cooling period needed for flowering. Indeed, a primary impetus for the development of this book came from our research showing definitely negative effects of changing temperature that may negatively impact Douglas-fir—making this “a species in peril.”

This book discusses research that demonstrates some of the unique aspects of Douglas-fir physiology. In it, we provide an overview of research activities and findings that highlight unique aspects of Douglas-fir physiology, genetics, and other related issues. The book begins with the evolutionary history and distribution of Douglas-fir and provides a detailed description of introductions of Douglas-fir to other countries, including information about initial plantings, provenance trials, and genetic tree improvement activities. The sections about life history, drawn from extensive research and teaching experiences, include detailed descriptions of flowering, seeds, root, and seedling physiology, followed by sections about mycorrhizae and insects, diseases, and other biotic factors.

This book is intended as a resource for everyone interested in understanding the opportunities and challenges of managing Douglas-fir in a variety of regions and settings. It provides information for historians and social scientists investigating forestry trends; researchers, educators, and managers looking for detailed information in areas such as genetics and regeneration practices; and all others interested in the beautiful trees we call Douglas-fir.

About the Authors

Denis P. Lavender is Professor Emeritus of Forest Science at Oregon State University and former head of the Forest Science Department at the University of British Columbia. He earned a bachelor's degree in Forest Management from the University of Washington, where he was named Outstanding Freshman Forestry, 1944; a master's in forest science from Oregon State College in 1958; and a doctorate in botany from Oregon State University in 1962.

After retiring as a professor in the OSU Forest Science Department in 1984, Lavender went on to serve as head of the Forest Science Department at the University of British Columbia from 1985 until 1992. While in Canada, Lavender and several colleagues established the Silvicultural Institute of British Columbia.

He is also a Co-founder Forest Biology Workshop. Lavender has served as president, executive secretary, and interim director of the Northwest Scientific Association, which named him an honorary life member. He joined the Society of American Foresters (SAF) as a member of the Willamette Chapter, where he served as chairman, vice chairman, and secretary. Lavender is a member of the Xi Sigma Pi Forestry Honor Society, the Phi Sigma Biological Sciences Honor Society, and the Sigma Xi Scientific Research Society.

One noteworthy outcome of Lavender's research in silviculture and plant physiology over many decades is the creation of a methodology for the storage and planting of seedlings that has increased conifer survival rate by 20%.

Richard K. Hermann is Professor Emeritus of Forest Resources at Oregon State University. He earned a Diplom Forstwirt from Ludwig-Maximilians-Universität München in 1951; and was awarded a full tuition scholarship to Yale University in 1954, where he earned a master's in forest soils science in 1956. At Oregon State University, Hermann earned a doctorate in forest ecology in 1960. He was awarded an honorary doctorate in silviculture from Georg-August-Universität Göttingen, Germany, in 1979.

Hermann was a scientist in an exchange program between the U.S. National Academy of Sciences and the Polish Academy of Science in 1971. In 1978, he held a fellowship from the Institut National de la Recherche Agronomique (INRA) of France at the Station d'amélioration des arbres forestiers, Centre d'Orléans. He was guest professor in forestry at Georg-August-Universität Göttingen in 1982 and 1989.

He has served as the leader of several working parties in the International Union of Forest Research Organizations (IUFRO) Division 1 (1965–1981); as Coordinator, Division 1 (1981–1986); and as a member of the IUFRO Executive Board (1981–1986). Hermann was named Corresponding Member of L'Accademia Italiana di Scienze Forestali (Italian Academy of Forest Sciences) in 1982; an Oregon SAF Fellow by the Society of American Foresters in 1991; and an Honorary Member of IUFRO in 1992. He is a member of SAF, the Ecological Society of America, the NW Scientific Association, and the Sigma Xi Scientific Research Society.

Hermann's familiarity with both Douglas-fir in its native range and the silvicultural practices in countries into which the species has been introduced have enabled him to help his colleagues find solutions to problems they have encountered in planting Douglas-fir, whether in the Pacific Northwest or around the world.

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The authors would like to acknowledge Martha Brookes, who edited early drafts of the manuscript; Gretchen Bracher and Tristan Bahr, who created most of the illustrations; student Alexa Pinckard, who typed much of the reference section; and Bryan Bernart, who coordinated the project during interim stages, edited chapters, and provided the cover photograph. Special thanks go to our editor, Caryn M. Davis, who toiled tirelessly to enable the publication of this book, and to Klaus Puettmann, who coordinated the review process.

Richard Hermann would like to acknowledge the contribution of Freya Hermann, whose support made the completion of this book possible.

1. Evolutionary History

Richard K. Hermann

A voluminous body of literature scattered through a multitude of publications in many languages covers the genus *Pseudotsuga*. The tremendous proliferation of literature makes an overall review of existing knowledge increasingly difficult. Our book attempts to bring together what is known about the genus *Pseudotsuga*.

The present distribution of the genus *Pseudotsuga* is strongly discontinuous: it is confined to western North America, Mexico, and eastern Asia. The genus includes eight to twelve species of which two are indigenous to the United States and Canada (Little 1979), four of questionable status to Mexico (Martinez 1963), four to mainland China, one to Taiwan (Li 1975), and one to Japan (Ohwi et al. 1965).

The Genus *Pseudotsuga*

Douglas-fir belongs to the family Pinaceae, but is unique among the Pinaceae in having a diploid chromosome number of 26. All other species in the Pinaceae, including big-cone Douglas-fir and the Asian Douglas-firs, have a diploid chromosome number of 24 (Doerksen and Ching 1972). As in most other conifers, Douglas-fir's nuclear genome (O'Brien et al. 1996) is large and complex (3.7×10^{10} BP); chloroplast DNA is inherited paternally (Neale et al. 1986) and mitochondrial DNA is inherited maternally (Marshall and Neale 1992). Douglas-fir is monoceous and has a mixed mating system (selfing and out-crossing) but it mostly outcrosses.

The fossil record suggests that intergeneric divergence in the Pinaceae, on average, took place 135 million years ago in the Neocomian Epoch of the Lower Cretaceous (Florin 1963). Fossil remains of the genus *Pseudotsuga* from pre-Cenozoic times have been reported from Russia and Mexico. Malyavkina (1958) designated pollen from Lower Cretaceous deposits of the Eastern-Gobi depression in eastern Mongolia as *Pseudotsuga punctata*. Alvarez (1994) stated that 23 different kinds of fossil coniferous pollen, including those of the genera *Abies*, *Picea*, *Pinus*, *Larix*, and *Pseudotsuga*, were found in deposits from the Turonian Epoch (90–84 million years BP) of the Upper Cretaceous in the Mexican State of Coahuila. These assignments of fossil pollen to the genus *Pseudotsuga*, however, are not substantiated by megafossils. By the time *Pseudotsuga* appears in the Tertiary fossil record, it clearly resembles the modern genus. Thus, we lack a record of most of the evolutionary history of the genus *Pseudotsuga;* all we have are hypotheses based on phylogenetic studies.

On the basis of morphological, anatomical, and cytological studies, two principal hypotheses have been advanced about the phylogenetic position of *Pseudotsuga* in the family Pinaceae. One theory holds that *Pseudotsuga* and *Larix* branched from a common lineage to *Pinus* (Boureau 1938, Ferré and Gaussen 1945, Gaussen 1955). The other hypothesis is that *Pseudotsuga* descended from *Larix* which, in turn, supposedly descended from *Pinus* (Flous 1936, Campo-Duplan 1950, Gaussen 1966). The close relation between *Pseudotsuga* and *Larix* had already been pointed out in 1918 by Doyle, who called attention to the striking similarities between the two genera. They include anatomy of wood, nonsaccate pollen, and structure of the female gametophyte.

Results of immunological studies conducted half a century later (Praeger et al. 1976, Price et al. 1987, Price 1989) indicate that the close phylogenetic relation between *Larix* and *Pseudotsuga* proteins is consistent with morphological evidence. Because the two lineages diverged, however, major phenotypic changes arose between them. For example, *Larix* became deciduous but *Pseudotsuga* remained evergreen.

Sziklai et al. (1987) used cytological techniques to provide some insight into the phylogeny of *Pseudotsuga*. Based on the assumption that karyotype differentiation of *Pseudotsuga menziesii* is the result of a misdivision of a metacentric chromosome and the production of stable telocentrics, they attempted to reconstruct the 12 chromosomes thought to be present in the ancestral Douglas-fir. This hypothetical karyotype was used for numerical studies of similarities among species in the genus, except for the Asian *Pseudotsuga brevifolia*. Their results of canonical variates analyses of chromosome arm lengths suggest that *Pseudotsuga menziesii* is more closely related to *Pseudotsuga macrocarpa* than to any of the six Asian species. In addition, their data show that the karyotype of *Pseudotsuga gausseni* is the most discrete of the Asian species and is also the most similar of the Asian species to *Pseudotsuga menziesii*.

In an effort to shed more light on the evolutionary origins of the genus *Pseudotsuga,* Strauss et al. (1990) used restriction fragment analysis of chloroplast, nuclear, and mitochondrial DNA to study its phylogeny. Five species of the genus, *Pseudotsuga menziesii* (Mirb.) Franco, *P. macrocarpa* (Vasey) Mayr, *P. japonica* (Shiras.) Beissn., *P. wilsoniana* Hayata, *P. sinensis* Dode, and *Larix occidentalis* Nutt., were included in the study. These authors concluded on the basis of their analysis that *Pseudotsuga* evolved first in North America and then migrated around the continental rim into Asia. They found that genetic similarities declined with migration distance around the Pacific Rim.

The model for the origin of *Pseudotsuga* and subsequent migration to Asia is consistent with the fossil record. Fossils both mega- and micro- of *Pseudotsuga* are represented in western North America since about 50 million years ago, and in Japan since about 15 million years ago (Hermann 1985). Mid-Tertiary fossils have been reported (Wolfe 1969) from Homer, Alaska, near the northernmost point of the migration route by way of the Bering land bridge (Florin 1963). If some of the fossil pollen of Upper Cretaceous age found in Coahuila indeed represent *Pseudotsuga*, that too would support the hypothesis that the genus evolved first in America. Alvarez (1994) considered the fossil *Pseudotsuga* reported from Coahuila to be the oldest known in America, which, in his opinion, raised the possibility that the state of Coahuila is the center of origin of the genus.

Strauss et al. (1990) noted that their data suggest two principal hypotheses for evolution within the genus. The first hypothesis is that the bulk of the genus may have been derived from a *Pseudotsuga macrocarpa*-like ancestor, which then gave rise to a *P. menziesii*-like line from which the migrants to Asia were derived. The second hypothesis would imply that a lineage containing the future Asian migrant may have split from the common ancestor of the genus in North America before speciation of the progenitors of present-day *Pseudotsuga menziesii* and *Pseudotsuga macrocarpa*. According to Strauss et al. (1990), for the first hypothesis to be true, the 13-chromosome karyotype of *P. menziesii* "would have to have either (i) evolved after the split of the Asian stock from it, (ii) remained polymorphic within ancestral pre-*Pseudotsuga menziesii*, eventually become fixed in *P. menziesii* and lost in the Asian line, or (iii) been present but subsequently lost in the Asian derivatives. Because of the similarity of the Asian species' karyotypes to that of *Pseudotsuga macrocarpa* such a loss or reversion is unlikely. Finally, and most important, unless rates of evolution in these lineages vary widely, an early split between the North American species suggests that they would have accumulated a greater genetic distance between them in comparison to the Asian species. This is not the case. The actin-derived distance of 17.57 between *P. menziesii* and *P. macrocarpa* was equivalent to that between *P. japonica* and *P. sinensis* (18%) (Strauss et al. 1990, Table 2).

Both the studies by Strauss et al. (1990) and Sziklai et al. (1987) show that the North American and Asian species form well-differentiated monophyletic groups. Where these authors differ is in their assignment of the relation of two of the Asian species to *Pseudotsuga menziesii*. Strauss et al. concluded that *Pseudotsuga japonica* is the Asian species closest to the North American species, and Sziklai et al. suggested that *Pseudotsuga gausseni* is the Asian species most similar to *Pseudotsuga menziesii*. The geographic location of the range of *P. gausseni*, however, appears to make such a relation unlikely.

The few studies about the evolutionary origins of the genus *Pseudotsuga* have contributed to a better knowledge of the taxonomic relationships within the genus but provide no answers as to when speciation of modern *Pseudotsuga menziesii* occurred. Morphological characteristics of North American Douglas-fir little changed since its appearance in the fossil record about 50 million years ago. The karyotype of fossil Douglas-fir is unknown and leaves us with the question had Eocene *Pseudotsuga sonomenis*, the ancestral Douglas-fir, already a haploid chromosome complement of 13, or evolved the n = 13 species some time later in the Tertiary from a progenitor with a complement of n = 12. Although the evolutionary history of the modern *Pseudotsuga menziesii* remains obscure, the suggestion that karyotype reduction and fragmentation has been an evolutionary trend in *Pseudotsuga* (Sziklai et al. 1987) would indicate that *Pseudotsuga menziesii* is the most recent species of the genus because *P. menziesii* has the smallest chromosomes of all *Pseudotsuga* species.

The fossil record appears also to lend support to the assumption that *P. menziesii* is of rather recent origin. In contrast to the Tertiary, *Pseudotsuga* is often abundantly represented in Quaternary mega- and microfossil assemblages. This would indicate that Douglas-fir assumed its dominant role in the forests of northwestern America in the Quaternary. Wolfe (1969) emphasized that Early Pleistocene assemblages still have low amounts of Douglas-fir pollen whereas interglacial deposits begin to show large quantities of pollen of this genus. Therefore, he concluded that today's dominance of *Pseudotsuga* throughout much of the conifer forest of western northwestern North America was attained during the Middle or Late Pleistocene. That change in the status of Douglas-fir as a member of northwestern forests suggests that a new species had evolved during the repeated glacial cycles that could adapt to a wide range of climates and site conditions.

Differentiation into varieties

Douglas-fir is one of several western conifers that illustrate an advanced stage of subspecies evolution. Its geographic races differ conspicuously and have been recognized as the coastal variety, *menziesii*, and the interior variety, *glauca*, or Rocky Mountain Douglas-fir. These races appear to have evolved during repeated long periods of geographic isolation, alternating with short flushes of gene exchange like the present (Critchfield 1984).

Several hypotheses have been advanced about when the two varieties of Douglas-fir evolved. Axelrod (1980, pp. 72–73) proposed that they had already originated during the Tertiary. According to him, fossil evidence indicates that the two varieties may have evolved as early as the Oligocene and were definitely in existence by the Miocene. The Late-Oligocene flora of Creede, Colorado, dated 27 million years BP, included Douglas-fir with small cones characteristic of the interior variety. Both varieties were supposedly represented in floras of 13 million years ago. Douglas-fir in the Purple Mountain flora of western Nevada had small cones (Axelrod 1980), but Douglas-fir in the Trout Creek flora of southeastern Oregon had large cones (Arnold 1935). The two varieties came into contact with each other in central British Columbia, northern Idaho, and north-central and northeastern Washington about 7,000 years ago, after their Late-Quaternary migrations from their respective glacial refugia (Tsukada 1982).

Galoux (1956) suggested that both varieties descended from a common ancestor in Mid-Pliocene. In his opinion, the variety *glauca* originated as the result of eastward migration across the Great Basin and subsequent adaptation to the environment of the Rocky Mountains. He based his theory on the observation that the Pacific floral elements most closely related to woody species in the Rocky Mountains occur in the southern Cascades and in the Sierra Nevada. An argument against Galoux's thesis is the statement by Sziklai et al. (1987) that the smaller size of chromosomes in the variety *menziesii* suggests that it is a more recently derived lineage than the variety *glauca*.

Halliday and Brown (1943), as well as Heusser (1968), assumed a more recent evolution of the two varieties. They proposed that the varieties evolved sometime in the Late Pleistocene, during the Wisconsin glaciation (100,000–10,000 years BP) in glacial refugia, one in the Pacific Coast region, and the other in the southern Rocky Mountains.

Perhaps the best available estimate of the time since divergence between the coastal and interior variety was provided by Li and Adams (1989). They suggested, based on their determination of the average genetic distance between 103 populations distributed over the entire range of the species, that the two varieties have been in existence for at least half a million years, and that they may have diverged during the Middle Pleistocene, much later than the Pliocene but well before the Wisconsin glaciation. The differentiation of Douglas-fir into varieties may have been influenced by large-scale climate change (Gugger and Sugita 2010).

Figure 1.1 Frothingham's (1990) division of the range of Douglas-fir into five growing regions.

Intraspecific variation

The validity of recognizing two varieties of *Pseudotsuga menziesii* has been questioned by Silen as recently as 1978 with the statement, "The clinal nature of both morphological and chemical traits over the range of Douglas-fir and the variability of types in a locality still raises doubts about the logic of varieties or subspecies within the species." Nonetheless, Douglas-fir from the western and eastern parts of the species' range show sufficient differences in their traits to make a case for a taxonomic division into a coastal and interior variety.

The differences in size and form of *P. menziesii* within its range led, already at the beginning of the 20th century, to the realization that the division of the species into a coastal and interior variety did not account adequately for its variability. Frothingham (1909), based on his detailed review of Douglas-fir, divided its range into five growing regions (Figure 1.1) in an attempt to go beyond purely taxonomic classification. Although he arrived at the delineation of these regions without the benefit of modern biochemical and molecular genetic tools,[1] his scheme showed a remarkable degree of insight into the regional differentiation of the species. Ascherson and Graebner (1913) acknowledged the existence of intermediates between coastal and interior populations and designated these intermediates as variety *caesia*. That taxonomic designation was quickly accepted in Europe, in spite of the lack of clearly distinguishable morphological characteristics. Schenck (1939) distinguished a coastal (var. *viridis*) and two inland varieties, var. *caesia* north, and var. *glauca* south of lat 39° N. That

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[1] Molecular genetic markers are those derived from direct analyses of genetic polymorphism in DNA sequences. Biochemical markers are those derived from study of the chemical products of gene expression, such as protein sequences or net charges, and composition of secondary chemicals such as terpenoids.

geographic delineation of a northern and southern inland variety comes close to the line of division between a northern and southern inland chemical race that was made more than three decades later by Zavarin and Snajberk (1973). Flöhr (1958) with reference to Munns (1938) and Schenck (1939) considered a relatively small area in north-central Washington and south-central British Columbia along the Frazer River south of lat 50°30′ N as the area of transition between the varieties *menziesii* and *caesia*. He assigned all population west of that area of transition to the variety *menziesii* and east of it to the variety *caesia*, and those south of lat 41° N and east of long 109° W to the variety *glauca*. The region west of long 109° W and north of lat 27° N, up to a line running northeast from lat 45° N to long 111° W, was designated as one that contained populations of both variety *glauca* and *caesia*.

Morphological, anatomical, cytological, and physiological studies during the 1960s and 1970s gradually increased knowledge of intraspecific variation patterns of *Pseudotsuga menziesii*. Allen (1960b) and two of his students (Robinson 1963, Dunlap 1964) demonstrated that the two varieties of the species can be distinguished by the shape of their seed. But they noted also that differences become less distinct in the transitional zone from the coastal to the drier interior region, pointing to the existence of intermediate forms. Tusco (1963), who had sampled 43 populations from coastal British Columbia to the Porcupine Hills of Alberta, has argued for the recognition of subspecific taxa in *Pseudotsuga menziesii* within British Columbia based on the interpretation of his data. Tusko's interpretation, however, has been challenged. Chen et al. (1986), in a study of morphological variation of Douglas-fir in southwestern British Columbia, concluded that most of it was within the chosen 46 populations. Hence, these authors proposed that recognition of subspecific taxa in this portion of the species' range is inappropriate. Similar results were obtained by Scagel et al. (1987), who investigated the variation of cone and seed morphology in 89 populations from west and east of the Cascade Range in British Columbia, Washington, and Oregon. They suggested, however, that a latitudinal cline may exist, a suggestion previously made by Sziklai (1969) and Chen et al. (1986). A growth chamber study involving 16 coastal and 12 interior provenances (Nicholson 1963) had shown different growth responses to short-day photoperiods between coastal and interior provenances, and also between provenances from the northern and southern part of the interior variety's range.

A study by Lavender and Overton (1972), on the effects of a range of thermoperiods and soil temperatures on the growth of Douglas-fir seedlings raised from Vancouver Island, western Washington, western Oregon, northern Montana, and New Mexico seed sources, demonstrated distinct physiological differences between the coastal and interior provenances. Seedlings representing populations from the northern and the central portion of the coastal variety did not differ conspicuously in their growth responses, but seedlings from a southern Oregon seed source exhibited a growth response that more closely resembled the interior variety than the coastal.

In a study of intraspecific variability of seed weight that used all 189 provenances from the 1966-1969 IUFRO seed collections, Birot (1972) distinguished a northern coastal group (British Columbia, Washington, and northern Oregon); an east of the Cascades group (east side of Cascades in British Columbia, Washington, and Oregon); a southern coastal group (southern Oregon and California); and an interior group (New Mexico, Arizona, Colorado, and Utah). Except for the fact that the range of the interior variety is not separated into a northern and southern part, Birot's grouping is very similar to that of Frothingham (1909).

Two studies (El-Lakany and Sziklai 1971, 1973) of variation in nuclear volume and relative DNA content in 27 coastal and 25 interior provenances from the 1966-1969 IUFRO seed collection revealed that coastal provenances have larger nuclear volumes and greater relative amounts of DNA than the inland provenances, and that a gradient exists between coastal and interior populations. De Vescovi and Sziklai (1975) were able to show distinct differences. Values were significantly lower for the inland than the coastal provenances.

Studies of wood properties of Douglas-fir (Griffin 1919, Miller 1961, Miller and Graham 1963, Bramhall 1966) also provided evidence of large variability within the range of the species. They demonstrated higher permeability of the wood of coastal Douglas-fir than for interior Douglas-fir after preservation treatments. Logs of eastern Washington and central-south British Columbia origin showed intermediate degrees of permeability. Although wood of Douglas-fir from California does not reach the low permeability values of variety glauca, Miller and Graham's (1963) investigations indicate the existence of a coastal California gradient with less permeable wood in the south and more permeable wood towards the Oregon border. Sierra Nevada material from Plumas and Nevada counties gave the lowest permeability values for logs from California. Differences in size and arrangement of tracheids and position of the torus within the bordered pit cavity between coastal and interior populations and their intermediates are probably responsible for the differences in permeability.

Figure 1.2 Chemical races of Douglas-fir distinguished by Rudloff (1973a) based on leaf oil terpenes. The broken line denotes the line of division between coastal and interior Douglas-fir as based on terpene patterns.

Drew (1957) concluded that northern and southern wood property types could be distinguished in the inland Douglas-fir. The wood of the northern type is considerably more dense and is stronger than that of the southern type. The distinction made by Drew between a northern and a southern inland type was supported in the following decades by the results of terpene and allozyme analyses of materials from the range of the variety *glauca*.

Terpenes

An important step towards more detailed knowledge of intraspecific variation of *Pseudotsuga menziesii* was made with a series of chemo-systematic studies. Von Rudloff (1972, 1973a, 1973b, 1975) demonstrated that analysis of leaf oil terpenes permits not only a clear-cut qualitative and quantitative distinction between the two recognized varieties of Douglas-fir but also a convenient quantitative description of interior and coastal intermediates. He emphasized that this is possible because of the presence of distinctly different patterns of terpene distribution and the relatively small tree-to-tree variations within populations of the two varieties. Several chemical races (Rudloff 1973a) differing quantitatively in certain monoterpenes, appear to exist in each variety (Figure 1.2).

In a later paper, von Rudloff and Rehfeldt (1980) described possible biosynthetic pathways, geographic variation, and inheritance of terpenes in Douglas-fir from southwestern Canada and the northwestern United States. Hypothetical biosynthetic pathways imply that geographic variation in 17 monoterpenes of the leaf oil can be represented by three or four biogenetic pathways. Therefore, geographic variation between the coastal and the interior variety can be described by the relative percentages of β-pinene, the terpinene-sabinene group of terpenes, the camphene group, and perhaps limonene. An abrupt transition between coastal and interior varieties was found for terpenes of the camphene group. An explanation for this kind of transition is suggested by the results of progeny tests with F_1 intervarietal hybrids, which indicated that high percentages of the camphene group are controlled by a single dominant gene. Conversely, relatively broad zones of introgression developing from gradual changes in gene frequencies appear to accompany geographic variation in β-pinene, terpenes of the terpinene-sabinene group, and possibly limonene. Such a pattern is to be expected, if quantitative inheritance is involved, again indicated from results with F_1 intervarietal hybrids. Von Rudloff and Rehfeldt (1980) cautioned that the problem of constraint inherent in the use of relative percentages imposes limitations on the evaluation of genetic aspects. Nonetheless, their findings with these intervarietal hybrids suggest that the intermediate terpene percentages found in most trees in the zones of overlap are indeed a measure of intermixing of the two varieties of Douglas-fir.

Zavarin and Snajberk (1973, 1975, 1976) used cortical monoterpenes to study geographic differentiation of Douglas-fir throughout its range except for Mexico. They distinguished four chemical races (Figure 1.3): a coastal range in western Oregon, western Washington, and western British Columbia; a northern inland race in the Rocky Mountains of Canada and the United States north of the Snake River Basin (lat 42°30′ N); a southern inland race in the United States south of the Snake River Basin; and a Sierra Nevada race in the central Sierra Nevada of California (Zavarin and Snajberk 1973). They found that the northern inland and the coastal race intergrade extensively in central British Columbia, northeastern Washington, and northern Idaho. Some intergradation occurs also in the mountains of central and east-central Oregon. California Sierra Nevada populations are chemically different from pure coastal and interior populations, but show closer affinity with the interior than the coastal variety. Southern Oregon and coastal California populations exhibit a chemically intermediate status between variety *menziesii* and the Sierra Nevada race (Figure 1.3; Zavarin and Snajberk 1973).

Zavarin et al. (1977) suggested that the differentiation of *Pseudotsuga menziesii* into its southern and northern inland races was apparently brought about by the geologic history of the Snake River basin. In the Oligocene, an east-to-west trough, the ancestor of the present day Snake River basin, formed in central Idaho. This trough widened and deepened in time, and thus separated from each other the populations of coniferous species growing in that area. The evolution of the Sierra Nevada race is explained by Zavarin and Snajberk (1975) as a result of the emergence of the Great Basin arid regions during the Pliocene-Pleistocene epochs that disjoined western Douglas-fir populations from their eastern, inland counterparts.

Critchfield (1984) summarized the results of the studies by Zavarin and Snajberk and von Rudloff and Rehfeldt (1980) as follows,

> The most conspicuous feature of terpene variation in Douglas-fir is the uniformity of the coastal race west of the crest of the Cascades and north of the California border. Stands in this region do not vary at all in a 3-carene, or terpinolene. The uniformity ends abruptly at the Siskiyou Mountains along the Oregon-California border. The gradient connecting coastal and interior races varies in width and steepness, depending on the terpene. The sharpest distinction is in the frequency of trees with high levels of camphene-group terpenes, none in most coastal stands and 100% throughout the northern interior. Douglas-fir is highly variable in terpenes throughout its California range with a complex pattern of variation that may have evolved over a long period under relatively stable conditions. The interior region differs from the Pacific region in lacking comparable discontinuities.

By contrast, analysis of cortical terpenes from samples collected in the northern, central, and southern parts of the range of big-cone Douglas-fir indicated insignificant intraspecific variability in that species (Zavarin and Snajberk 1976). In addition, that study did not provide any evidence of gene exchange between *Pseudotsuga menziesii* and *Pseudotsuga macrocarpa* and corroborated the work of Latling and Scora (1974) who had shown good chemical separation between the two species.

Enzymes

Electrophoresis has become a more widely used tool than terpene analysis for assessments of the extent and pattern of genetic variation in Douglas-fir. As gene markers, isozymes are useful for describing

Figure 1.3 Geographic differentiation of Douglas-fir based on cortical monoterpenes; extent of Wisconsin glaciation colored dark (from Zavarin and Snajberk 1977).

genetic differentiation within and between taxa, and for verification of hybridity. Allozyme (allelic isozyme) analysis permits description of variation patterns in terms of direct measures of genetic diversity (Adams 1981). Several allozyme studies of Douglas-fir (Bergmann 1973, Muhs 1974, Yang et al. 1977, Yeh and O'Malley 1980, Adams 1981, Hamrick et al. 1981) centering mainly on its coastal variety demonstrated that the species has a great genetic diversity at enzyme loci. As in other conifers, most genic variation (95%) appears to be maintained within populations, which may reflect the species' ecological amplitude, its breeding system, and the lack of effective barriers to gene flow between subpopulations (Yeh and O'Malley 1980).

Results of some of the allozyme studies indicate that northern and southern populations differ markedly in variability at isozyme loci. Critchfield (1984) considered climatic conditions during the Pleistocene to be responsible for these differences because coastal and transitional populations of Douglas-fir averaged 0.15 in heterozygosity (Yeh and O'Malley 1980) and interior populations 0.18 (Yeh 1981) in glaciated British Columbia. Much higher levels were found by other investigators far south beyond the boundary of the Wisconsin Ice Front: 0.33 in coastal California (Morris cited by Hamrick et al. 1981) and 0.26 in eastern Colorado (Hamrick et al. 1981). Although some weak clines in gene frequency over environmental transects have been reported among populations (Bergmann 1975, Mejnartowicz 1976, Yang et al. 1977, Yeh and O'Malley 1980), other investigations (Merkle and Adams 1987; Moran and Adams 1989) did not show any association between allozyme diversity and geographic variables in intensive sampling of Douglas-fir in southwestern Oregon, a geographically restricted but environmentally diverse region of the coastal variety.

A remarkable insight into the geograpical patterns of genetic variation of Douglas-fir comes from an allozyme study by Li and Adams (1989), which used seeds from 104 sources distributed over the entire natural range of the species (Figure 1.4). The racial patterns of allozyme variation found by these investigators conform closely to patterns determined earlier from studies of terpenes and quantitative traits,

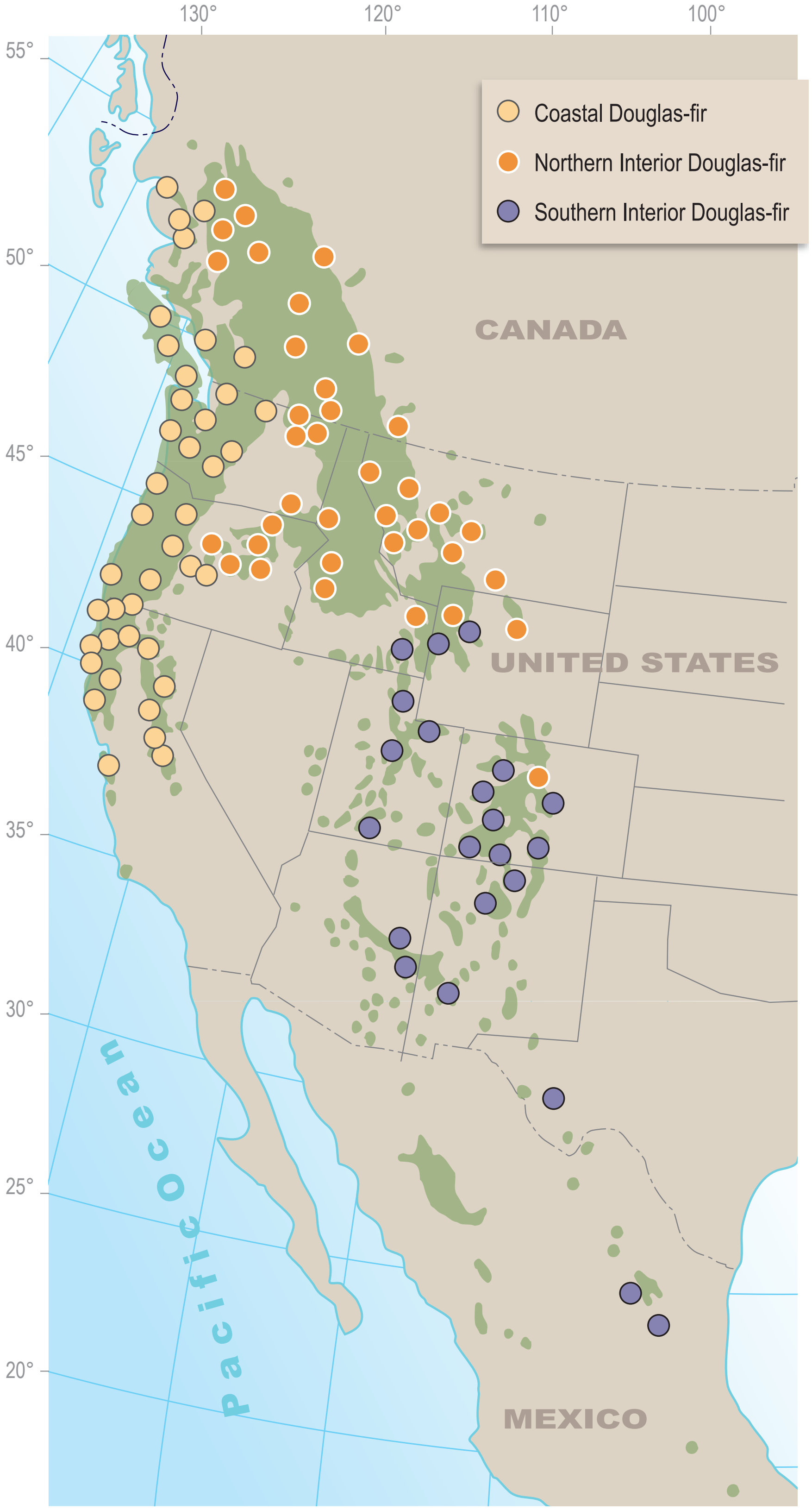

Figure 1.4 Locations of seed from 104 sources used by Li and Adams (1989) in their allozyme study.

but they give a far more detailed picture of genetic variation in the species than heretofore available. Cluster analysis based on genetic distances between all pairwise combinations of the 104 populations show that they clustered into two groups corresponding to the recognized coastal and interior varieties, except for one (no. 103) of the two Mexican provenances included in the study (Figure 1.5).

The finding that Mexican population 103 from Coahuila appears to differ genetically from all other populations (Figure 1.5) may shed new light on the taxonomic position of Mexican *Pseudotsuga*. The large genetic distance (0.123) between population 103 and the rest of the species implies that the view that all of Mexican Douglas-fir is part of variety *glauca*, held by North American dendrologists (Harlow and Harrar 1969, Little 1979), probably needs revision. Incidentally, Alvarez (1994) pointed out that population 103 came from the vicinity of General Cepeda, which is near the locality where fossil Douglas-fir pollen was found in an upper Cretaceous formation. The interior populations separated into a northern subgroup (British Columbia, Alberta, Idaho, Montana, and northern Wyoming) and a southern subgroup (central and southern Wyoming, Utah, Colorado, Arizona, New Mexico, and Mexico) at around lat 44° N.

Genetic structure of populations turned out to differ substantially among the three major subdivisions. The coastal variety and northern subgroup of the interior variety show considerable genetic variation within populations but little variation between them. By contrast, populations in the southern interior subgroup are far more genetically differentiated but have only about one half the genetic diversity observed in coastal and northern interior populations.

Although range-wide patterns of genetic variation reported by Li and Adams agree in general with those found in previous studies of quantitative traits and terpenes, they differ from them in some details. Results of the allozyme analyses place zones of transition between the coastal and interior variety into south central British Columbia, north central Washington, and central Oregon as did those of earlier studies (Rudloff 1973a, Zavarin and Snajberk 1973). The terpene analyses indicated rather broad zones of transition except for terpenes of the camphene group (Rudloff and Rehfeldt 1980), but the data of Li and Adams suggest an abrupt transition regardless of whether the two varieties are geographically separated as in central Oregon and north central Washington, or are contiguous as in British Columbia. Li and Adams speculated that their inability to identify intermediate populations in British Columbia might reflect insufficient sampling. They also considered the possibility that gene flow between the varieties is not as intensive in this region as was once assumed, but that genes coding terpene variants may have spread more rapidly because of selective advantage.

The findings of Li and Adams (1989) support separation of the interior variety into a northern and southern subgroup as proposed by Zavarin and Snajberk (1973) on the basis of cortical terpene analysis. They placed the break between the two subgroups at lat 42°30′ N but Li and Adams set it farther north at 44° N. Li and Adams emphasized, however, that separation between the subgroups seems actually to be a gradual transition over at least three to four degrees of latitude rather than an abrupt change. The racial differentiation shown by Li and Adams with allozyme analysis differs in one major respect from that found by Zavarin and Snajberk (1973). Li and Adams did not identify a California Sierra Nevada race with genetic affinity closer to the southern race of the interior variety than to the coastal variety. Their findings indicate a close alignment of the Sierra Nevada population with those of the coastal variety. They pointed out, however, that this difference in racial patterning is not necessarily conflicting because different traits may respond differently to selection pressures. The deviation in terpene composition of the Sierra Nevada population from the rest of the population of the coastal variety may be related to differential selection pressures imposed by insects. As an example, Li and Adams cite work by Stephan (1987) who found that Douglas-fir provenances from north coastal California, which is the intergradation zone between the Sierra Nevada and coastal terpene races identified by Zavarin and Snajberk (1975), were more resistant to attack by the Cooley spruce gall adelgid (*Adleges* [*Gilletteella*] *cooleyi*) than coastal provenances farther north in Oregon, Washington, and British Columbia.

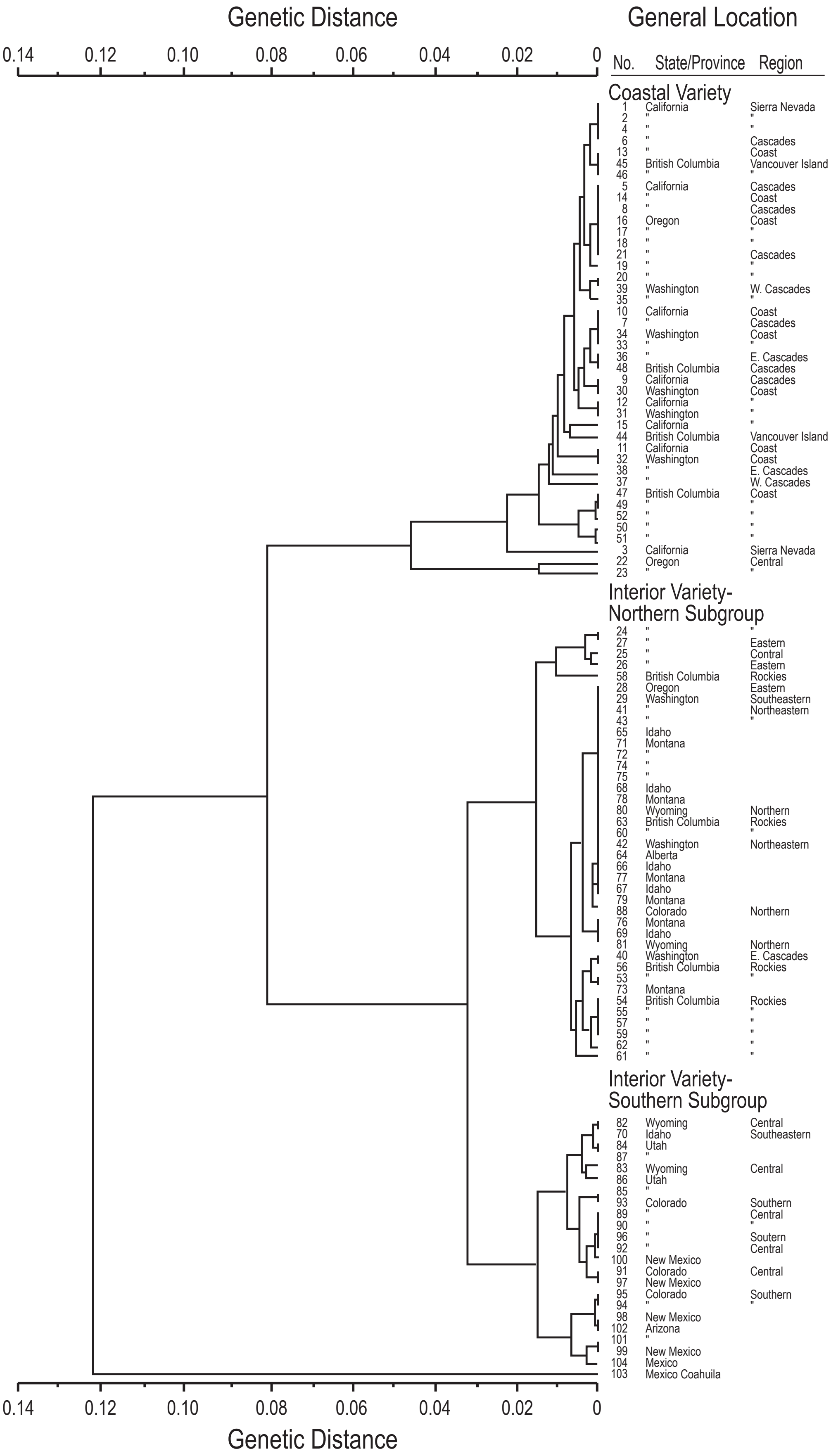

Figure 1.5 Genetic distances between provenances used for the range-wide allozyme study (from Li and Adams 1989, modified).

Random amplified polymorphic DNA

The use of random amplified polymorphic DNA (RAPDs) is the most recent technique applied to the investigation of genetic variation in Douglas-fir. Aagaard et al. (1995) studied racial differentiation and genetic variability between and within the coastal, north interior, and south interior races of Douglas-fir by means of RAPD and allozyme markers. Seed samples of the coastal variety and the north interior race of the interior variety came from 20 locations along an east-west transect from just west of the Cascade summit to eastern Idaho. That transect, which crosses the putative transition zone between the two varieties in central Oregon, is essentially the same used earlier by Sorensen (1979) for a common garden study. Seeds of the southern interior race of the interior variety stemmed from three locations in Utah, two in Arizona, and four in New Mexico. For a comparison of genetic differentiation and diversity between RAPDs and allozymes, Aagaard et al. (1995) matched their 29 seed sources with 31 populations from Li and Adams' (1989) range-wide allozyme study of Douglas-fir (Figure 1.6) and re-analyzed data from these 31 populations.

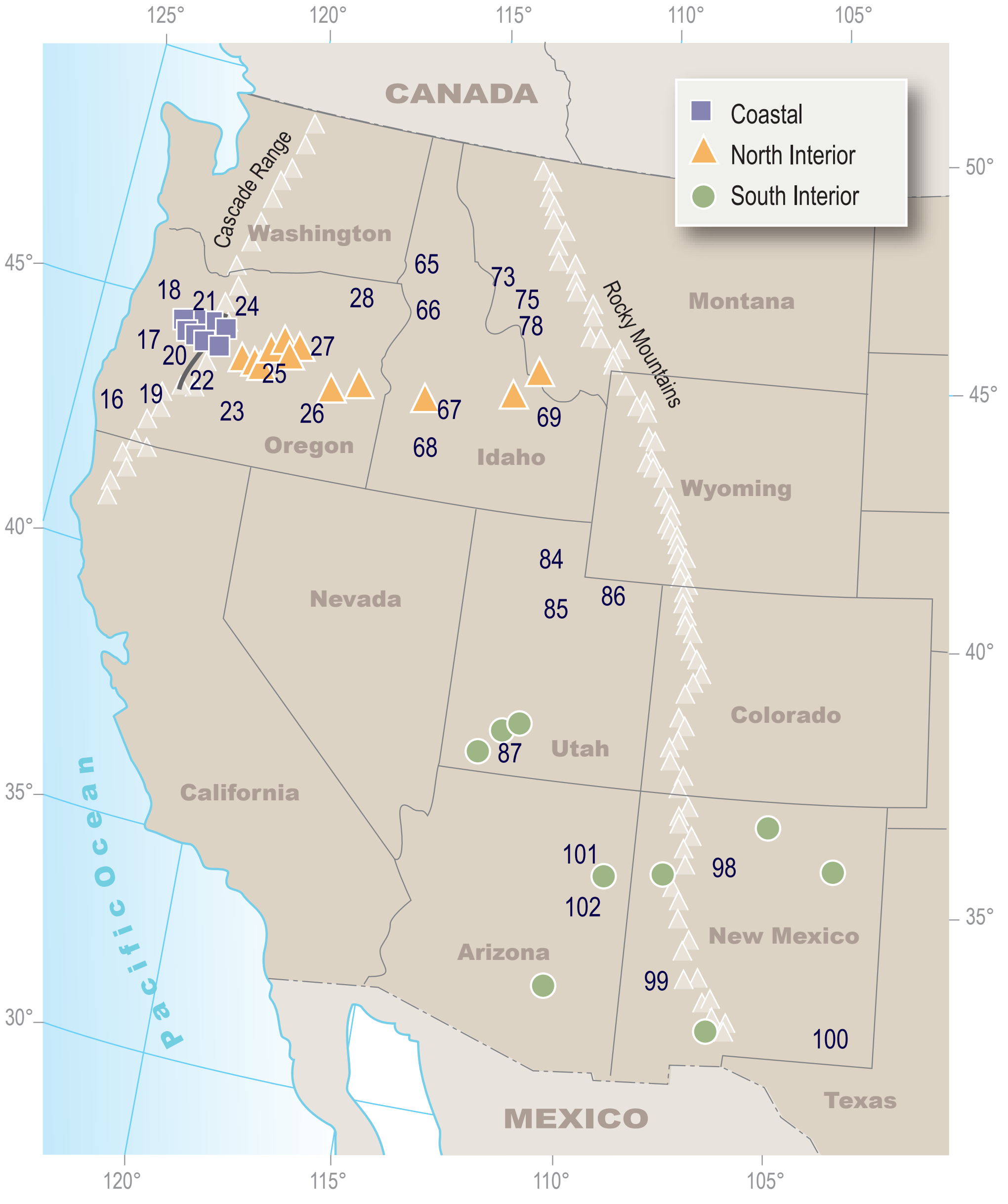

Figure 1.6 The 29 seed sources matched with 31 populations from Li and Adams (1989)range-wide allozyme study.

Table 1.1 Racial differentiation, genetic distances, and genic and allelic diversity based on RAPDs and allozymes between or within races of the coastal and interior varieties of Douglas-fir. Standard errors are calculated for G_{ST} from variance among locus-specific estimates.

	RAPDs	Allozymes
Differentiation (G_{ST}) between races		
Coastal × north interior × south interior	0.73 ± 0.09	0.26 ± 0.03
Coastal × north interior	0.76 ± 0.12	0.21 ± 0.03
Coastal × south interior	0.82 ± 0.09	0.36 ± 0.04
North interior × south interior	0.52 ± 0.11	0.19 ± 0.03
Gene diversity (H_S) calculated within races		
Coastal	0.07 ± 0.04	0.21 ± 0.04
North interior	0.15 ± 0.05	0.17 ± 0.05
South interior	0.18 ± 0.05	0.09 ± 0.04
Mean gene diversity (H_T) averaged over races	0.13 ± 0.03	0.16 ± 0.03
Total gene diversity	0.49 ± 0.05	0.21 ± 0.05

Results of the RAPD study revealed striking contrasts between estimates of racial differentiation and diversity with RAPD and allozyme markers (Table 1.1). Differentiation between races of Douglas-fir based on RAPD analysis accounted for more than 70% of the total diversity observed (G_{ST}= 0.73; Aargard 1995). Conversely, of the total genetic variability found for allozyme data, less than 30% (G_{ST} = 0.26) was attributed to racial differentiation. Furthermore, allelic and genic diversities between races were inverted for RAPDs relative to that for allozymes. Gene diversity for RAPDs was highest in the south interior race (H_S = 0.18) and lowest in the coastal race, but the reverse was true for allozymes (Table 1.1). The observed number of alleles per locus paralleled these trends, with the highest values in the south interior race (1.44) and the lowest in the coastal race (1.25).

Results of the study of RAPD phenotypes pointed to a sharp boundary between the coastal and north interior races. The break occurred between the lowest elevation Santiam population (915 m; lat 44°25′ N, long 121°38′ W) and the Grizzly population (1,555 m; lat 44°26′ N, long 120°57′ W), which are separated by a mere 55 km. That finding supports the suggestion by Li and Adams (1989) of an abrupt transition between the coastal and northern interior races, although their allozyme study indicated the possibility of a narrow transition zone between these races. The abrupt transition between the coastal and interior varieties found by Zavarin and Snajberk (1973) for terpenes of the camphene group agrees most closely with the RAPD data by suggesting

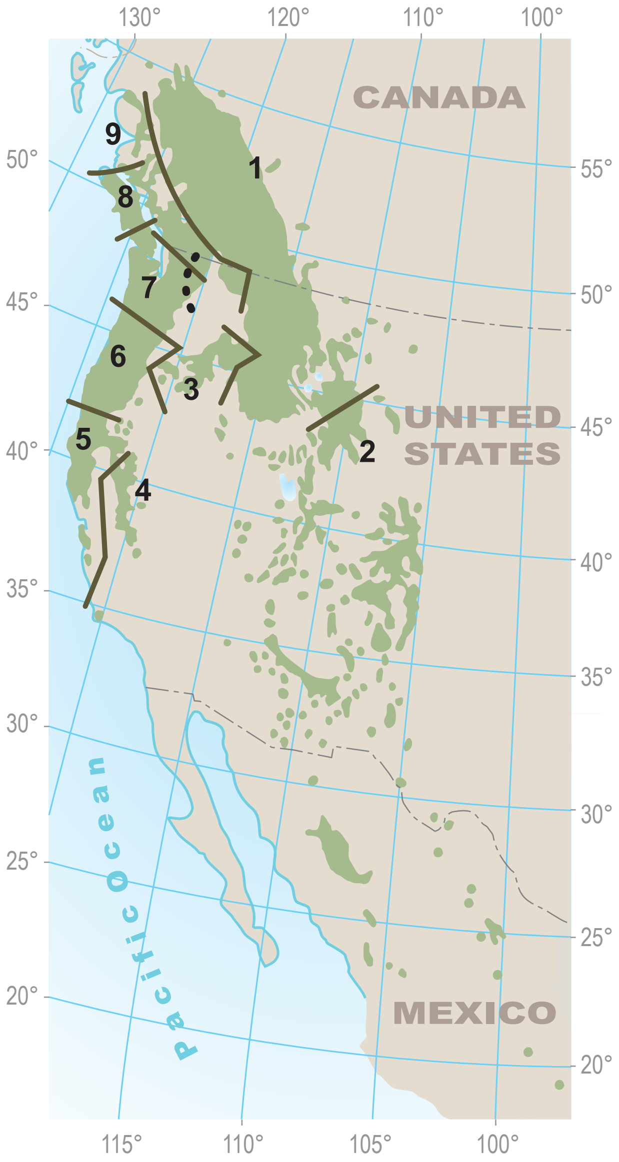

Figure 1.7 Ecotypes of Douglas-fir based on geographic variation of allelic structures (from Klumpp 1999).

a distinct racial boundary in nearby populations. Aagaard et al. (1995) pointed out that intervarietal hybrids of Douglas-fir are known to readily occur in zones of contact, and gene flow through pollen and seed dispersal is extensive in conifers. From that information, they inferred that the close proximity of coastal and interior varieties in central Oregon may have come about in recent geologic time. Aagaard et al. (1995) summed up their comparison of RAPD and allozyme markers as follows: "RAPDs appear to provide greater sensitivity than allozymes for the detection of genetic differentiation, at least for long-isolated gene pools such as races of Douglas-fir."

The results of an isozyme study by Klumpp (1999), based on commercial seed from 27 sources within the natural range of *Pseudotsuga menziesii* and buds from 11 populations in German provenance trials, are essentially in agreement with those of Li and Adams (1989). Klumpp recognized three major forms of the species, coastal, northern, and southern inland Douglas-fir. But he went one step further than Li and Adams (1989) and distinguished nine ecotypes (Figure 1.7) on the basis of the geographic variation of allelic structures. Klumpp, however, considered these additional subdivisions as provisional in view of his limited sample size.

2. Natural Range

Richard K. Hermann

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco growing on the moist Pacific slopes from British Columbia to California, commonly referred to as the Douglas-fir region, is the commercially most important tree species in western North America. In its drier interior range the species has been rapidly gaining in commercial importance since the middle of the 20th century (Hermann and Lavender 1990). Douglas-fir has been a major component of the forests of western North America since the middle-Pleistocene (Hermann 1985). Although the fossil record indicates that the native range of the species has never extended beyond western North America, it has been successfully introduced into many regions with a temperate climate since the mid-19th century (Hermann and Lavender 1999). The introduction of Douglas-fir into temperate zones of both hemispheres has been expanding in the 20th century because appropriate provenances often outgrow the native conifers on suitable sites (Hermann 1987).

History

Douglas-fir was discovered by Archibald Menzies (1754-1842) on the west coast of Vancouver Island. Menzies, who accompanied Captain Vancouver on journey to northwest America as ship surgeon on board the *Discovery*, did not mention the tree in his journal (Menzies 1923). He brought back, however, a specimen of Douglas-fir which the British botanist Lambert had described in 1803 as *Pinus taxifolia*. For his original description, Lambert (1803) did not have cones; however, he included them in an illustration for the 1832 edition (Figure 2.1). Douglas-fir underwent several changes in its scientific name in the next 150 years (Hermann 1982). The Portuguese botanist Franco (1954) proposed *Pseudotsuga menziesii* (Mirb.) Franco as the valid scientific name that has won universal acceptance.

Varieties of *Pseudotsuga menziesii*

The British botanist Murray was the first to recognize two geographically distinct groups of Douglas-fir in 1869 (Little 1952). They are now recognized in North America as the coastal variety (*Pseudotsuga menzie-*

Figure 2.1 Lambert's (1832) botanical illustration of Douglas-fir.

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1. The International Code of Botanical Nomenclature specifies that the variety that includes the type specimen of the species must bear the same epithet as the species without citation of author (Little 1952).

sii var. *menziesii*)[1] and interior variety (*Pseudotsuga menziesii* var. *glauca* Beissn. (Franco) (Little 1979). The two varieties intergrade in areas of contact from the northern half of Oregon northward into central British Columbia (Rudloff 1972, Sorensen 1979). In contrast RAPD markers amplified from mitochondrial DNA showed a rather abrupt genetic discontinuity in this area (Aagard et al. 1995). The varieties are morphologically, physiologically, and chemically distinct (Silen 1978). Needles of the coastal variety are green; presumably that is why the variety was referred to in the older European literature as var. *viridis* (Latin for green). Needles of the interior variety are blueish. Either color of foliage is occasionally displayed by both varieties. Structure of their cones differs also. Cones of coastal Douglas-fir have straight, flat bracts while those of the interior variety have exserted and strongly reflected bracts. In general, coastal Douglas-fir lives longer and reaches greater height, diameter, and volume than interior Douglas-fir (Table 2.1). The data in Table 2.1 were compiled from second- and third-growth stands and, thus, do not show dimensions known to have been attained by old growth Douglas-fir.

Coastal Douglas-fir commonly reaches ages of 750 years (Franklin and Dyrness 1973) but may live longer. The oldest coastal Douglas-fir on record was found near Mount Vernon, Washington. The age count was made on a section about 12 m above the stump. The age at that point was 1,375 years. Since at least 25 years were required to reach the height at which the age count was made, the tree must have been over 1,400 years old when cut in 1913 (McArdle and Meyer 1949). On the best sites, coastal Douglas-fir can become huge; the tallest on record was cut in 1895 in the Capillano Valley near Vancouver, British Columbia. It measured 127.1 m from ground level to the tip of the leading shoot. That is, 15.8 m taller than the tallest then-known *Sequoia sempervirens* in California (Edlin 1965). A 1,022-year-old coastal Douglas-fir cut in 1924 near Mineral, Washington was 119.3 m tall, with a diameter of 4.9 m and a volume of 249 m^3 (O'Brian 1994). The Mineral tree was 9 m taller than the 110 m-tall coast redwood at Dyerville, California (Bronaugh 1992). Interior Douglas-fir rarely grows older than about 400 years (Frothingham 1909). The oldest living interior Douglas-fir ever reported was found on

Table 2.1 Individual tree characteristics for Douglas-fir in the western United States (modified from Van Hooser et al. 1991).

	Diameter at breast height (cm)		Height (m)		Volume (m^3)	
	Mean	Max	Mean	Max	Mean	Max
Interior Douglas-fir region/ Northern Rocky Mountains						
Idaho	34.5	204.7	19.5	61.0	1.08	24.5
Montana	28.7	120.7	15.8	54.3	0.62	14.4
Wyoming	28.7	107.2	13.1	32.3	0.65	6.4
Interior Douglas-fir region/ Southern Rocky Mountains						
Arizona	18.5	38.6	10.4	21.6	0.14	0.7
Colorado	27.4	106.4	12.5	38.7	0.59	6.3
New Mexico	23.6	84.8	11.9	32.0	0.51	4.7
Utah	31.5	113.5	14.9	38.1	0.82	8.5
Pine subregion						
Eastern Oregon	25.4	129.0	16.7	51.5	0.42	11.7
Eastern Washington	25.4	192.8	18.3	70.7	0.48	36.9
Coastal Douglas-fir region						
Western Oregon	27.2	195.6	20.1	78.9	0.71	43.6
Western Washington	27.7	192.5	22.6	78.3	0.79	45.2
California	28.9	186.0	18.9	71.3	0.96	48.0

the Bandera lava flows in the El Malpais National Monument, New Mexico (Swetnam and Brown 1992). It has a pith date of CE 1062. Compared to coastal Douglas-fir, the interior variety tends to be slower-growing, more cold hardy, more drought hardy, more shade tolerant, and more susceptible to Swiss needle cast (*Phaeocryptopus gaeumannii*).

Figure 2.2 Natural range of Douglas-fir (from Little 1971).

Range

Early botanical explorers of the American west, such as David Douglas, were already aware of the extensive range of Douglas-fir. Hooker (1838) wrote in his Flora Borealis-Americana: "Mr. Douglas observes that the principal part of the gloomy forests of Northwest America, in the valleys of the Rocky Mountains, and throughout the interior skirting those mountains, is composed of this species." Nearly a century would pass, however, between the discovery of Douglas-fir by Archibald Menzies in 1792 at Nootka Sound and the first comprehensive description of its natural range by Sargent (1884). Frothingham (1909) published the first distribution map of *Pseudotsuga menziesii*, including both the coastal and interior varieties. Subsequently, this map was revised by Sudworth (1918), Munns (1938), Fowells (1965), and Little (1971). The latitudinal range of Douglas-fir (Figure 2.2) is the greatest of any commercial conifer of western North America. The range resembles an inverted V with uneven sides. From the apex in central British Columbia, the western half extends along the Pacific mountain ranges into California for about 2,200 km. The eastern half stretches along the Rocky Mountains of Canada and the United States into the mountains of central Mexico over a distance of nearly 4,500 km. The western half is considered as representing the range of *Pseudotsuga menziesii* var. *menziesii*, and the eastern half the range of *Pseudotsuga menziesii* var. *glauca*.

Sargent's statement, "The line which marks the northern limits of its distribution as now known is curiously irregular" is still valid (Figure 2.3). The most northerly record of living Douglas-fir in the Prince George Forest District is Tudyah Lake, lat 55°05′ N, long 123°00′ W. The species reaches farther northward, to 55°30′ N at Babina Lake and Takla Lake (Garman 1963, Revel 1966, unpublished paper) in the eastern part of Prince Rupert Forest District. From there, its boundary runs in a general south-southeasterly direction to the headwaters

Figure 2.3 Line designates the northern limit of Douglas-fir in British Columbia (Schmidt 1965, unpublished paper).

of the Nazko River, then in a west-southwesterly direction to the headwaters of the Klinaklini River. From here, the line follows a generally northwesterly direction to Bella Coola, and finally turns south, proceeding to the coast. From Bella Coola, a small tongue extends northward and then divides, Douglas-fir reaching up the Dean River Valley in an easterly direction, and the other half extending in a northwesterly direction into the vicinity of Kemano (lat 53°30′ N). The presence of Douglas-fir on the Skeena River (lat 54°20′ N) is mentioned by several authors (Sargent 1898, Sudworth 1908, Frothingham 1909) and is shown as an "insular" occurrence on all range maps of Douglas-fir published, except that by Krajina et al. (1982). The older maps are in error. Neither R.L. Schmidt[2] (personal communication) nor P.G. Haddock[3] (personal communication) could confirm an outpost of Douglas-fir on the Skeena River.

An interesting point was made by Schmidt (1960) about the northern limit of Douglas-fir in coastal British Columbia. He argues that the present northern boundary of the range of coastal Douglas-fir reflects low fire frequency rather than climatic control as postulated by Henry and Flood (1920, p. 71). Schmidt (1960) saw supporting evidence for his claim in a comparison of the altitudinal and latitudinal limits of Douglas-fir and its principal associates:

> Within its range Douglas fir is able to grow to altitudes as great or greater than western red cedar, and reaches within a few hundred feet of western hemlock. It would be reasonable to expect that the upper altitudinal limits of these species are primarily controlled by factors associated with decreasing temperatures occurring with increasing altitude. It would also be reasonable to expect that the northern latitudinal limits would come under the control of temperature; and therefore, the order of species limits should be the same latitudinally as altitudinally. However, this is not the case. The northern limit of Douglas fir stops almost 480 km south of western red cedar and nearly 1,120 km south of western hemlock. These anomalies support the view that northward migration of Douglas fir has been halted by a low fire hazard barrier, whereas red cedar and western hemlock have successfully colonized their entire potential range by virtue of their capacity to reproduce in shade as well as on denuded areas. (Schmidt 1960, pp. 156–57)

Little's (1971) map indicates a discontinuity of the range of Douglas-fir in the area of the Seymour-Neechanze Rivers. The inventory data of the British Columbia Forest Service, however, suggest continuous distribution of Douglas-fir along these drainages. Little's map further shows absence of Douglas-fir in a continuous strip in the Coast Range of British Columbia extending southeastward from about lat 53° N to slightly below lat 50°N. Actually, the distribution of Douglas-fir is continuous through the Coast Range along several corridors. North, east, and south of Haylmore is a large enclave without Douglas-fir. The boundaries of Douglas-fir in the area delineated by long 122°30′ W and 124°10′ W and by lat 51° N and 51°50′ N are uncertain (R.L. Schmidt, personal communication). The species is absent from the northern tip of Vancouver Island and the coastal archipelago. Douglas-fir ranges continuously through western Washington and western Oregon. The eastern slopes of the Cascades form the eastern boundary. Sudworth's (1908) report that the species is absent from the east side of the Cascade Range south of lat 45° N is incorrect. Douglas-fir continues along the upper east-side slopes and stops short of the Oregon-California line (Franklin and Dyrness 1973). The range forks in northern California between lat 40° N and 41° N.

In the West, Douglas-fir extends along the California Coast Ranges into the northern end of Sonoma County. From here on southward, the range becomes discontinuous. The largest discontinuous area of the species is in the Santa Cruz Mountains

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[2] R. L. Schmidt, British Columbia Forest Service.

[3] Philip G. Haddock, University of British Columbia.

between San Francisco and Monterey Bay. A stand along Salmon Creek south of Los Burros in the Santa Lucia Mountains was the most southerly known (Langenheim and Durham 1963) until 1964. That year Griffin reported the discovery of a grove of *Pseudotsuga menziesii* in a deep, narrow canyon in the Purisima Hills (lat 34°44′ N, long 120°25′ W) near Lompoc, 145 km southeast of Salmon Creek. He considered this stand a Pleistocene relict but did not dismiss entirely the possibility that the trees had been planted. Analysis of cortical monoterpenes (Zavarin and Snajberk 1975) from trees of the Lompoc stand, however, indicated that the stand belongs to their Sierra Nevada chemical race and fits exceedingly well into the south-to-north chemical gradient along the coast, which lends strong support to the idea that the Lompoc stand represents a Pleistocene relict.

The eastern half of the range in California extends continuously in a south-southeasterly direction through the Sierra Nevada into the southern part of Yosemite National Park. The southern limit in the Sierra Nevada is at Big Creek (lat 37°11′ N, long 119°15′ W; elevation 1490 m) about halfway between Yosemite and Kings Canyon national park's boundaries (Zavarin and Snajberk 1975). The stand at Big Creek is limited in extent and isolated from the main distributional range of the species. The species is found on the east side of the Sierra Nevada, although it is extremely rare there (Frothingham 1909).

Beginning again at the northernmost occurrence of Douglas-fir is the starting point for the description of the eastern half of its range. The northern boundary runs from Takla Lake east southeast to McLeod. There, the boundary of Douglas-fir turns in a southeasterly direction representing the eastern limit along the Continental Divide to the Canada-United States line.

Reports on the northern limit of the species between Takla and McLeod are at variance. Little's map shows an outlier, which according to R.L. Schmidt (personal communication) is not separate from the main distribution shown by the range map of Douglas-fir in British Columbia (Figure 2.4). Douglas-fir is reliably reported from Tudyah Lake (P.C. Haddock, personal communication), barely over the lat 55° N line and closely adjacent to the Hart Highway leading north from Prince George to the Peace River. The boundary line is difficult to draw in that area because small groves of Douglas-fir and individual trees that survived fires are scattered in the region north of Prince George to about lat 55° N. None of the reports cited above confirms the statement by Halliday and Brown (1943) that the northern limit of Douglas-fir is near the Finlay Forks on the 56th parallel.

Another mapping problem is posed by the grassland areas in central British Columbia. Douglas-fir is scattered throughout these areas, but Little (1971) mapped these areas as not containing Douglas-fir. Contrary to older descriptions, such as that of Sudworth (1908), the species is represented in the Caribou Range and high elevations in the Gold and Selkirk Mountains (Figure 2.4; J. Revel,[4] P.G. Haddock, personal communication). Douglas-fir is abundant in the Porcupine Hills, and Bow, Kananaskis, and Oldman River valleys south and west of Calgary (Moss 1944, Bird and Hong 1969). Elsewhere in Alberta, Douglas-fir forests are common only in the Athabasca and Miette River valleys around Jasper town. Small groves and isolated trees occur sporadically in the foothills and upper North Saskatchewan River Valley. The northern recorded limit of Douglas-fir in Alberta is near Brule Lake (53°15′ N, 117°50′ W) (Stringer and LaRoi 1970).

The range of Douglas-fir is fairly continuous through northern Idaho, western Montana, and northwestern Wyoming. A large area containing Douglas-fir extends southwestward from central Idaho into the Wallowa and Blue Mountains of Oregon. Several outliers of Douglas-fir are present in Alberta, Montana, and Wyoming, the largest in the Bighorn Mountains. From southern Idaho southward through the mountains of Utah, Colorado, New Mexico, and Arizona, the distribution becomes discontinuous. "The species is absent or rare in the dry interior basins, and on the semiarid plateaus and minor mountain spurs lying between the principal ranges, especially toward the southern and eastern limits of its range" (Frothingham 1909). Distribution in the Rocky Mountain region has now been more accurately mapped, although minor revisions may still become necessary. Thus, Critchfield and Allenbaugh

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[4] J. Revel, British Columbia Forest Service.

Figure 2.4 Range map of Douglas-fir in British Columbia (from Revel 1966).

(1969) pointed out that Douglas-fir extends northwestward from the Wasatch Range into the Raft River (Preece 1950) and Albion Mountains. The species stops short of the South Hills of southern Idaho but is mapped there by Johnson (1961) and Fowells (1965). Critchfield and Allenbaugh (1969) also doubted the occurrence of Douglas-fir in the mountains of Elko County in northeastern Nevada as reported by Little (1956). In addition, they recorded two sizable but previously unreported outliers of Douglas-fir in the Owyhee Range of southwestern Idaho.

The most southerly occurrence of Douglas-fir in the United States is in extreme western Texas. The tree is present in the Guadalupe Mountains which extend from southeastern Arizona into Texas, in the Sierra Vieja, and farthest south in the Chisos Mountains (lat 29°13′ N).

In Mexico, Douglas-fir extends discontinuously along the Sierra Madre Occidental and is present in Sonora, Chihuahua, Durango, and Zacatecas. In the Sierra Madre Oriental, the species is reported from Coahuila, Nuevo Leon, Tamaulipas, Hidalgo, and Puebla (Figure 2.5). The description of the range of Douglas-fir in Mexico by Martinez (1949) agrees in general with Little's (1971) map, except that Little does not show the species to be present in Tamaulipas. Martinez's account that it "then extends from Tamaulipas toward the south through the central and eastern region to the north of Puebla" could be interpreted to mean that Douglas-fir in Mexico does not form large stands (Blanco 1941) and usually is a minor component of the forest. Until 1994, lat 19° N in Puebla was the known southern limit of Douglas-fir. The discovery of Douglas-fir in the state of Oaxaca has extended the known distribution of the genus *Pseudotsuga* to 16°22′ N, 96°06′ W, 110 km southeast of the town of Oaxaca. The locations of three isolated stands, each of about 2–3 ha, have been reported so far from Oaxaca (Debreczy and Racz 1995).

Altitudinal distribution

Altitudinal distribution of both varieties of Douglas-fir increases from north to south reflecting climatic control over distribution of the species. The principal limiting factors are temperature in the north, and moisture in the south of the range. As a general rule, the interior variety grows at considerably higher altitudes than the coastal variety at the corresponding latitude. For example, at lat 45° N, Douglas-fir occurs up to an elevation of about 1,220 m in the Coast Ranges, and up to 2,440 m in the Rocky Mountains. Whether this distribution is a genetic adaptation or reflects climatic differences is unclear (Silen 1978).

Altitudinal limit for Douglas-fir in central British Columbia is about 760 m but rises to 1,250 m on Vancouver Island (Heusser 1960). In Washington and Oregon, the species ranges from sea level to 1,524 m, although locally it may occur higher. On Mount Hood, Douglas-fir extends to an altitude of 2,195 m according to U.S. Forest Service inventory records. In the southern Oregon Cascades and in the Sierra Nevada, the altitudinal range is generally between 610 m and 1,829 m. In river valleys and canyon bottoms, the species may occasionally descend to elevations of 244 to 274 m. Below 610 m, however, Douglas-fir is infrequent and is scrubby in appearance. Near the southern limit of its range, in the Sierra Nevada, the species will grow to elevations of 2,286 m according to Frothingham (1909). Sudworth (1908) listed the highest altitude at which Douglas-fir occurs in the Sierra Nevada as 2,225 m at Glacier Point in Yosemite National Park. In the Santa Cruz and Santa Lucia Mountains, the lower altitudinal limit for Douglas-fir is 762 m. Elevation of the southernmost stand of the coastal variety in the Purisima Hills is 213 m (Griffin 1964).

The inland variety grows at altitudes from 549 to 2,438 m in the northern part of its range (Kirkwood 1922). In Jasper and Banff national parks, the upper altitudinal limit for the species is at 1,372 m (Heusser

Figure 2.5 Range of Douglas-fir in Mexico (modified from Martinez 1963).

1968) and increases gradually to 2,438 m in Montana, Idaho, and northern Wyoming.

According to Hall[5] (personal communication), the lower altitudinal limit of Douglas-fir in the Blue Mountains of northeastern Oregon is at 518 m, and the upper limit is at 2,134 m. In the central Rocky Mountains the species is mostly found at elevations between 1,830 m and 2,592 m (Bates 1924, Costello 1954), and in the southern Rocky Mountains between 2,440 m and 2,898 m (Pearson 1931). The lower elevational limits in the central and southern Rocky Mountains vary more from place to place than do the upper limits (J.R. Jones,[6] personal communication). In northern Colorado, absolute lower limits lie at about 1,769 m on steep, north-facing slopes in the lower foothills of the Front Range. Here, young Douglas-fir forms dense stands on north-facing slopes as low as 1,830 m. In some localities in southern and central Arizona, Douglas-fir descends to 1,830 m on north-facing slopes, and may occur as low as 1,555 m in canyon bottoms. But, in general, Douglas-fir is rarely found below 2,440 m in the Southwest.

In central Colorado, the species occurs as high as 2,958 m on the rim of Coffee Pot Mesa; adjacent vegetation is sagebrush and fescue with aspen groves. On the Frazer Experimental Forest in northern Colorado (lat 40° N), a few overmature Douglas-firs are scattered through a stand of lodgepole pine with an understory of Engelmann spruce and subalpine fir at an elevation of 2,267 m. In the White Mountains of east-central Arizona, Douglas-fir is represented in Engelmann spruce/corkbark fir stands up to 3,050 m elevation. According to J.R. Jones (personal communication), the highest elevation at which Douglas-fir occurs in the Southwest is at 3,264 m on the crest of Mt. Graham in southeastern Arizona.

In Mexico, Douglas-fir grows at altitudes of 2,000 to 3,200 m. Stands of Douglas-fir are present largely in the Sierra Madre Occidental, from Sonora and Chihuahua as far as Zacatecas, in some mountainous area of Coahuila and Nuevo León, in the highest part of the Sierra de Pachuca, Hidalgo, and in a small area in the center of the state of Puebla (Rzedowski and Huerta 1978).

Area occupied by Douglas-fir

The area occupied by Douglas-fir in the United States was listed as 14.4 million ha in 1989—or 7.3% of the country's 195.7 million ha of non-reserved timberland (Waddell et al. 1989). The data on acreage of forest types dominated by Douglas-fir have changed over time (Table 2.2). They show a decline of 3.6 million ha in the area of coastal Douglas-fir from 1936 to 1977, and then an increase of 0.5 million ha by 1987. For interior Douglas-fir, the data indicate a decrease of 1.8 million ha from 1936 to 1952, followed by an increase of 3.3 million ha in the next 35 years. To what extent these changes represent actual increases or decreases in acreage, and how much of the changes reported reflect different inventory procedures is open to question.

A breakdown of the area occupied by Douglas-fir according to region and productivity class (Table 2.3) indicates that the acreage of Douglas-fir in the Pacific Coast region exceeds that of Douglas-fir in the Rocky Mountain region by 1.8 million ha. The largest share of Douglas-fir in the Pacific Coast region is concentrated in the Pacific Northwest Douglas-fir Subregion, which comprises western Oregon and western Washington. Western Oregon contains roughly two-thirds, and western Washington one-third of the Douglas-fir acreage in the Pacific Northwest Douglas-fir Subregion. Moreover, that subregion has also the largest share of acreage in the two highest productivity classes.

The area occupied by Douglas-fir in Canada, about 4.5 million ha is slightly less than one-third of that in the United States. According to the 1968 inventory data (British Columbia Forest Service 1968), Douglas-fir occupied 1.1 million ha in the coastal region of British Columbia. The 1984 inventory data (British Columbia Ministry of Forests 1984) show a decline of 15.2% in that acreage to 900 million ha. Douglas-fir in interior British Columbia occupied 3.6 million ha in 1968.

In 1987, the Pacific Northwest Douglas-fir Subregion contained slightly more than half of all standing Douglas-fir timber (Waddell et al. 1989). Oswald et al. (1986) listed the timber volume in the

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[5] Frederick C. Hall, USDA Forest Service, Region 6.

[6] John R. Jones, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station.

Table 2.2 Area of Douglas-fir in the United States by variety and date of inventory.

	Coastal variety [a] (thousand) ha	Interior variety [b] (thousand) ha	Total (thousand) ha	Source
1936	11,209	4,681	15,890	Mattoon 1936
1952	9,927	2,920	12,847	USDA 1958
1977	7,562	4,947	12,509	USDA 1982
1987	8,091	6,260	14,351	Waddell et al. 1989

a. Data from California, Oregon, and Washington.
b. Data from the Rocky Mountain region.

Table 2.3 Area occupied by Douglas-fir 1987 in the United States by region and productivity class (from Waddell et al. 1989).

	Area (thousand ha)				
Productivity class	Pacific Northwest Douglas-fir subregion	Pacific Southwest	Ponderosa pine subregion	Rocky Mountains	Totals
120+	3,033	191	108	325	3,657
85-120	1,731	267	226	851	3,075
50-85	805	127	538	2,275	3,745
20-50	103	49	633	1,935	2,720
0-20	137	6	137	874	1,154
Totals	5,809	640	1,642	6,260	14,351

Table 2.4 Volume of standing Douglas-fir timber in the United States (Waddell et al. 1989).

	Million		
	m^3	ft^3	%
Pacific Northwest	1,337	47,225	51.9
Pacific Southwest	360	12,701	13.9
Ponderosa pine subregion	242	8,570	9.4
Rocky Mountains	639	22,566	24.8
Total	2,578	91,062	100.0

Douglas-fir type of the Pacific Northwest Douglas-fir Subregion as 1.7 billion cubic meters. That is, 328 million cubic meters (11.6 billion cubic feet) more than given in the 1987 inventory data by Waddell et al. (1989) (Table 2.4). According to Oswald et al. (1986), the volume of coastal Douglas-fir in British Columbia amounted to 240 million cubic meters in 1984. In 1992, the combined volume for coastal and interior Douglas-fir was 687.6 million cubic meters for pure stands and 24.4 million cubic meters in mixed stands (Macklin and Manning 1992).

Climate

Douglas-fir grows under a wide variety of climatic conditions (Table 2.5). The coastal region of the Pacific Northwest has a truly maritime climate characterized by mild wet winters and cool, relatively dry summers, and long growing seasons. The climate becomes increasingly continental toward the east. The major environmental gradients within the region are associated with distance from the ocean, latitude, and elevation. The Klamath area in southern Oregon and northern California are particularly hot and dry, whereas more northern areas on Vancouver Island, British Columbia, and the Olympic Peninsula of Washington include temperate rainforests with up to 4,445 mm of rain a year. Most of the precipitation occurs in winter as rain although snow is prevalent at higher elevations particularly in the Cascade Range and the Sierra Nevada.

Table 2.5 Climatic data for five subdivisions of the range of Douglas-fir.

	Pacific Northwest		Rocky Mountains		
Climatic data	Coastal	Mountainous	Northern	Central	Southern
Mean temperatures (°C)					
July	20–27	22–30	14–20	14–21	7–11
January	−2.5 to 2.5	−9.0 to −2.5	−7.0 to −2.5	−9.0 to −6.0	0 to 2.0
Frost-free period (d)	195–260	80–180	60–120	65–130	50–110
Precipitation (cm)					
Mean annual	76–300	60–300	56–102	36–61	41–76
Snowfall	0–60	10–300	41–584	50–460	180–300

In the northern Rocky Mountains, Douglas-fir grows in a climate with a marked maritime influence, except for a dry period in midsummer. In the central Rocky Mountains, Douglas-fir experiences a continental climate. Winters are long and severe; summers are hot, and, in some parts of the region, very dry. Annual precipitation, which is higher on the western sides of the mountains, is mainly snow. Rainfall patterns for the southern Rocky Mountains generally show low winter precipitation east of the Continental Divide, but high precipitation during the growing season. West of the Continental Divide, the rainfall is more evenly divided between winter and summer. Frost may occur in any month in the northern part of the range. The length of the frost-free period, however, varies within the central and southern Rocky Mountain regions, even at the same elevations.

Soils

The coastal variety of Douglas-fir reaches its best growth on well aerated soils with a pH range from 5 to 5.5. It will not thrive on poorly drained or compacted soils. Soils in the coastal belt of northern California, Oregon and Washington originated chiefly from marine sandstones with scattered igneous intrusions. These rocks have weathered deeply to fine-textured, well-drained soils under the mild, humid climate of the coast. Surface soils are in general moderately acid, high in organic matter and total nitrogen, and low in base saturation. Soils in the Puget Sound area and in southwestern British Columbia are almost entirely of glacial origin (Tarrant 1956). Podzolization is the dominant soil-forming process but is not intensive in the mild, moist climate. Inceptisols (Sols Bruns Acides) of the order Inceptisols have formed on the younger glacial landscapes. Alfisols (Gray Brown Podzolic soils) and Ultisols (Red-Yellow Podzolic soils) are found on older surfaces. Because cooler and wetter climates at higher elevations promote podsolization, Spodosols (Podzols) are found. Soils farther inland within the range of the coastal variety are derived from a wide variety of parent materials. They include metamporphosed sedimentary material in the northern Cascades and igneous rocks and formations of volcanic origin in the central and southern Cascades.

Depth of soils ranges from very shallow, on steep slopes and ridgetops, to deep, where deposits of volcanic origin and residual and colluvial materials are found. Texture varies from gravelly sand to clays. Organic matter content ranges from moderate in the Cascade Range to high in parts of the Coast Range and Olympic Peninsula. Total N content varies considerably but is usually low in soils of glacial origin.

Great soils groups characteristic of the range of Douglas-fir include Haplohumults (reddish Brown Lateritics) of the order Ultisols, Dystrochrepts Brown Lateritics), Haplumbrepts (Sols Bruns Acides) of the order Inceptisols, Haplorthodes (Western Brown FVorest Soils) of the order Spodosols, Xerumbrepts (Brown Podzolic soils), and Bitrandepts (Regosols) (Heilman et al. 1979).

Soils influenced by volcanic ash (Andepts) occur throughout the Cascades of Washington and Oregon. An extensive area of such soils is on the east side of the Cascade Range in southern Oregon. Along the Pacific coast and in southwestern Oregon, except at high altitudes, older landscapes and a warmer climate give rise to Ultisols (Reddish-Brown Lateritic soils). East of the Cascade Range where a more severe and arid climate prevails, Alfisols (Brown Forest soils and Gray Wooded soils) are common except for some higher elevations where Spodosols have developed. Farther east, Alfisols grade into Mollisols (Chernozems, Rendzinas) which cover the extensive arid areas of interior Washington and Oregon.

Soils within the range of the interior variety of Douglas-fir also originated from a considerable array of parent materials. In south-central British Columbia, eastern Washington, and northern Idaho, soils vary from basaltic talus, to deep loess with volcanic ash, to thin residual soils over granitic or sedimentary rocks. They are mostly Vitrandepths and Xerochrepts. Parent materials in Montana and Wyoming consist of both igneous and sedimentary rocks, and locally of glacial moraines. Soils derived from noncalcareous substrates are variable in texture but are consistently gravelly and acidic. A significant portion of the sedimentary rock is limestone, which gives rise to neutral or alkaline soils ranging in texture from gravelly loams to gravelly silts. Limestones often weather into soils that are excessively well drained. Soils are Cryoboralfs of the order Alfisols, and Cryandepts and Cryochrepts of the order Inceptisols. Soils in the central and southern Rocky Mountains are very complex. They developed from glacial deposits, crystalline granitic rocks, conglomerates, sandstones, and, in the Southwest, limestones. These soils are Alfisols (Gray Wooded soils), Mollisols (Brwon Forest soils), Spodosols (Brown Podzolic soils, Podzols), and Entisols (Alexander 1974, Pfister et al. 1977).

Associated forest cover

Douglas-fir grows together with other conifers and hardwoods throughout its natural range. The kinds of species mixture are listed by the Society of American Foresters as forest cover types (Eyre 1980). Coastal Douglas-fir is the dominant component of type 229 (Pacific Douglas-fir). This type is restricted in the United States to areas west of the Cascade Range in Washington and Oregon, and to a more limited area in northwestern California. Periodic recurrence of catastrophic wildfires created vast almost pure stands of Douglas-fir throughout its range north of the Umpqua River in Oregon. Although logging has mainly eliminated the extensive original old-growth forest, clearcutting combined with slash burning has helped maintain Douglas-fir as the major component in second-growth stands (Hermann and Lavender 1990). Toward the fog belt of the Pacific coast, Douglas-fir gives way to types 230 (western hemlock), 223 (Sitka spruce), 228 (western red cedar) but remains a common component of these types. Douglas-fir is usually an early seral component of forests. Large continuous stands are succeeded by more shade-tolerant species, especially western hemlock, that regenerate and grow better below the canopy of mature Douglas-fir, unless natural catastrophes, such as wildfire and windthrow, intervene.

South of type 229 (Pacific Douglas-fir), there is a transition to types 234 (Douglas-fir-tanoak-Pacific madrone) and 244 (Pacific ponderosa pine-Douglas-fir, the mixed conifers and hardwoods of southwestern Oregon. Mixed conifer forests occupy nearly half of the area of southwest Oregon. They extend from the Calapooya Mountains (143°30′ N) south into northwestern California, and from the western slopes of the Cascade Range to the Pacific Ocean (Minore and Kingsley 1983). The mixed-conifer forests of southwestern Oregon vary in composition, but two or more of the following species are always present: Douglas-fir, incense cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), white fir (*Abies concolor*), and ponderosa pine (*Pinus ponderosa*). Hardwoods often associated with mixed conifers include giant chinkapin (*Chrysolepis chrysophylla*), California black oak (*Quercus kelloggii*), Oregon white oak (*Quercus garryana*), canyon live oak (*Quercus chrysolepis*), and bigleaf maple (*Acer macrophyllum*). In the past, wildfires tended to perpetuate seral species, such as Douglas-fir, ponderosa pine, incense cedar, and Pacific madrone (*Arbutus menziesii*) throughout southwestern Oregon. Under modern fire prevention practices, however, natural stands slowly convert to more shade-tolerant species, such as white fir, Port Orford cedar (*Chamaecyparis lawsoniana*), and tanoak (*Lithocarpus densiflorus*) (McDonald et al. 1983).

Douglas-fir is a component of Sierra Nevada mixed conifers (Type 243). Five conifers define Type 243: California white fir, Pacific ponderosa pine, sugar pine, incense cedar, coastal Douglas-fir, and black oak. Douglas-fir dominates the mix in the north, but is absent south of the Merced River (Laacke and Fisk 1983).

Douglas-fir is the principal component of forest cover type 210 (interior Douglas-fir), apart from grand fir (*Abies grandis*), ponderosa pine, lodgepole pine (*Pinus contorta*), and western larch (*Larix occidentalis*), of forests in most of eastern Oregon, eastern Washington, and adjacent British Columbia. Douglas-fir is the climax species in these forests north of the Entiat River in Washington. Both Douglas-fir and grand fir form climax forests on the east side of the Cascade Range in Washington south of the Entiat River. Grand fir is the usual climax species in Oregon (Franklin and Dyrness 1973). Stand structure and species composition of the stands formed by Douglas-fir and its associates in eastern Washington and eastern Oregon are extremely variable, depending upon site, past management practices, and fire history.

Douglas-fir grows in extensive pure stands, either even- or uneven-aged, or in mixtures with ponderosa pine, western larch, grand fir and lodgepole pine, in southern Idaho, northern Utah, and western Montana. These forests are represented by forest cover types 210 (interior Douglas-fir, 237 (interior ponderosa pine) 212 (western larch) and 213 (grand fir). Wherever Douglas-fir grows in mixture with other species, the proportion may vary greatly, depending upon elevation, aspect, soil, and especially fire history. That is particularly true of the mixed conifer stands in the central and southern Rocky Mountains (Alexander 1974). While some stands may consist of only two species, others may be composed of as many as seven additional associates, along with Douglas-fir: ponderosa pine, white fir, Engelmann spruce (*Picea engelmannii*), southwestern white pine (*Pinus strobiformis*), corkbark fir (*Abies lasiocarpa*), blue spruce (*Picea pungens*), and quaking aspen (*Populus tremuloides*). Stands are often multistoried, with Douglas-fir and interior ponderosa pine in the overstory (Muldavin et al. 1996, Hoffman and Alexander 1983, Moir and Ludwig 1979).

Pseudotsuga macrocarpa

The distribution of bigcone Douglas-fir, *Pseudotsuga macrocarpa* (Vasey) Mayer, is restricted to southern California. Its discontinuous range forms an arc extending from the Figueroa and San Emigdio Mountains southward to its type locality in Banner Canyon at the southern end of the Volcan Mountains in San Diego County (Figure 2.6). Bigcone Douglas-fir occurs in all mountain ranges, except for the Hot Springs, Santa Rosa, and northern San Jacinto Mountains, which are relatively arid, owing partly to rain shadows from the Cuyumaca, Palomar, and Santa Ana Mountains to the west (Minnich 1982). According to McDonald (1990), the northern limits of the range of the species are near Mt. Pinos in Kern County, and the headwaters of Labrea Creek in Santa Barbara County. As westernmost limits, he indicates Mission Canyon in the Santa Ynez Mountains, and Zaca Peak in the San Rafael Mountains.

Some older publications (Bergen 1904, Sudworth 1908, Standley 1920-26, Davidson and Moxley 1923, Bowers 1942, Dallimore and Jackson 1948) contain references to the presence of *Pseudotsuga macrocarpa* in Baja California, Mexico. Both Munns (1938) and Gause (1966) mapped bigcone Douglas-fir in the Sierra de Juárez and the Sierra de San Pedro Mártir of Baja California south to lat 31° N—that is, about two degrees farther south than Banner Canyon.

Doubts about a Mexican distribution of the species have long existed. Martinez (1949) emphasized that he had not encountered bigcone Douglas-fir in Baja California or any other region of Mexico. The question of whether *P. macrocarpa* is present in Baja California appears to have been conclusively answered by Minnich (1982). His search for the tree in Baja California, both on the ground and by means of aerial photographs, was unsuccessful. Although he conceded that absolutely disproving the occurrence of bigcone Douglas-fir in such inaccessible country is impossible, he provided additional arguments for the absence of the species in Mexico. One is the likelihood that Sudworth's (1908) account of bigcone Douglas-fir in Baja California is based on either a misinterpretation of a geographic name or reliance on an ambiguous report by North (1907) on conifers in the Sierra de San Pedro Mártir; this set off a chain reaction of erroneous references. The second and even more compelling argument is that the physical environment of northern Baja California appears to be unsuitable for members of the evergreen mixed forest, such as *P. macrocarpa,* that have mesic temperature requirements.

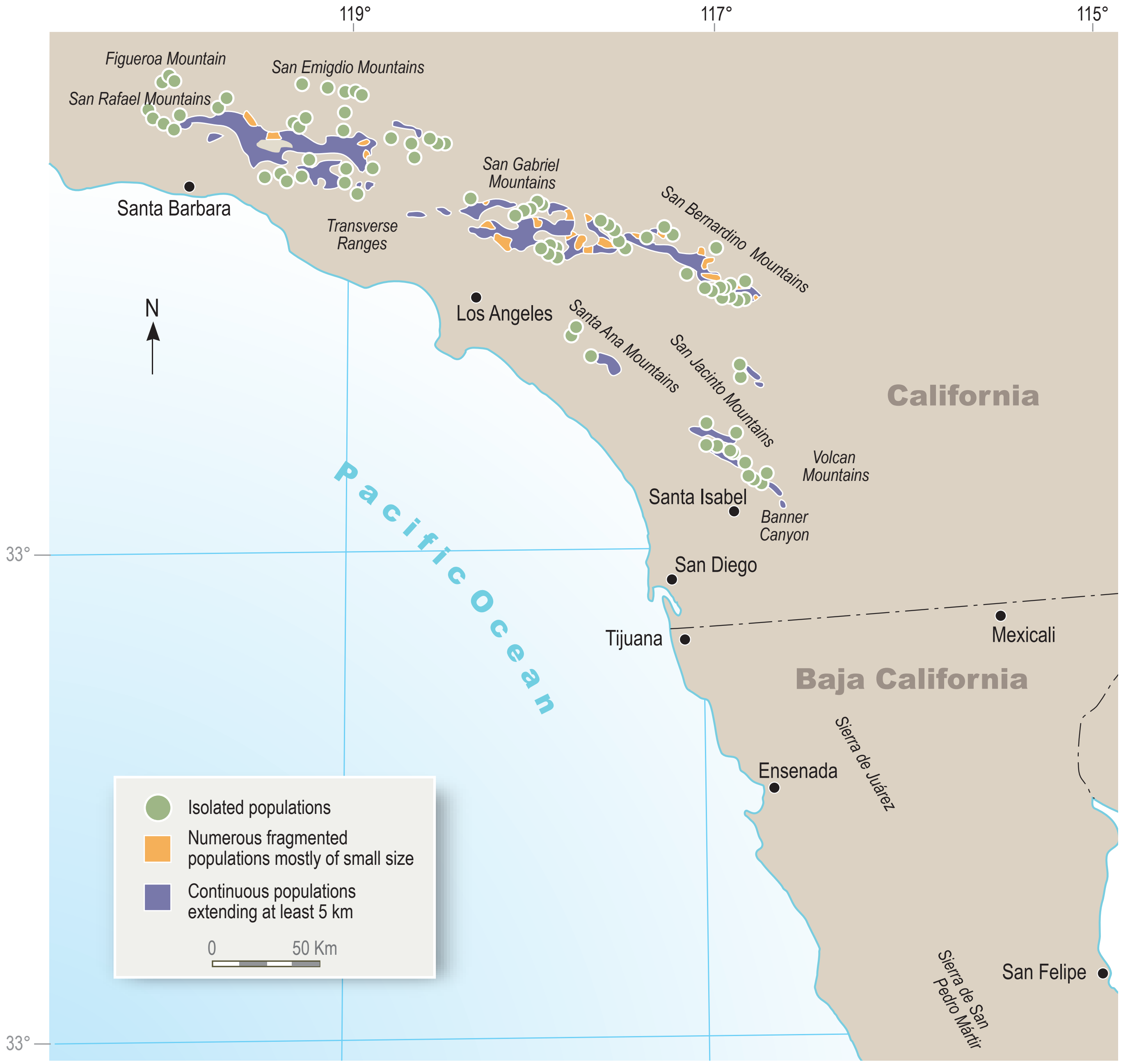

Figure 2.6 Range of Pseudotsuga macrocarpa (from Minnich 1982).

The altitudinal distribution ranges from 275 m on cool, moist north slopes of canyon bottoms to 2,400 m on warm south-facing plateaus (McDonald 1990). In the Transverse Ranges, larger stands are found from 915 m to 1,650 m on southwest through north slopes, mainly in the upper canyons. Vigorous stands occur in the Coastal and Peninsular Ranges in westerly canyons from 730 m to 1,525 m, apparently because of the year-round influx of marine air. Above 1,830 m, bigcone Douglas-fir grows in open stands in mixture with *Pinus ponderosa, Pinus jeffreyi, Pinus lambertiana,* and *Calocedrus decurrens* (Gause 1966).

Pseudotsuga japonica

The distribution of Japanese Douglas-fir, *Pseudotsuga japonica* (Shinas.) Beissn., is limited to Japan. The species occurs on the Kii Peninsula of southern Honshu and on Shikoku (Figure 2.7). Hayata (1915) pointed

Figure 2.7 Range of Pseudotsuga japonica Beissn. (from Hayashi 1952).

out that he and other botanists had erroneously regarded *P. japonica* and *P. wilsoniana* as identical, which explains why he indicated earlier (1905) the presence of *P. japonica* on Taiwan.

The Japanese Douglas-fir is a rare tree whose range is highly discontinuous (Hayashi 1952). The northern limit of the species is on Mt. Kunimi at lat 32°22′ N, longitude 136°10′E. The range extends southwestward through Mie, Nara, and Wakayama Prefectures on the Kii Peninsula. The tree occupies only a small area in the southeastern part of Shikoku Island. Its western limit is about longitude 134°05′E; the southernmost occurrence is on Mt. Senbon in Kochi Prefecture at lat 33°26′N. Vertical distribution extends from 400 m to 1,000 m on Shikoku Island and to 1,100 m on the Kii Peninsula. Most of the trees, however, grow at elevations between 500 m and 900 m (Ohwi et al. 1965).

The Chinese Douglas-firs

Descriptions of the ranges of the Chinese Douglas-firs may not be entirely accurate because the literature contains conflicting statements about taxonomic status and distribution.

Pseudotsuga wilsoniana

The Formosan Douglas-fir, *Pseudotsuga wilsoniana* (Hayata), is limited to Taiwan and a few locations in China (Figure 2.8). In Taiwan, the species extends north-south from about lat 24°41′ N to 23°03′ N, and east-west from about long 122°24′ E to 121°24′ E (Liu 1966). The tree is rare (Li 1950) and is restricted to a belt between 800 and 1500 m in steep, mountainous terrain (Lin et al. 1953). Li (1975) cites 2,500 m as the upper altitudinal limit of the species. Liu (1966) listed *P. wilsoniana* as endemic in Formosa. According to Wang (1961), however, a few relicts of the species exist in the southern part of Fujian province in China. Most of the forest in this province has been cleared, and only remnants of the former forest still exist. At higher elevations, these remnants supposedly contain Formosan Douglas-fir.

The island of Taiwan was separated from the Chinese mainland during the Pleistocene 200,000 to

400,000 years ago (Liu 1966). The proximity of Fujian and Taiwan suggests that the Formosan Douglas-fir may once have formed a continuous range in the two regions.

Pseudotsuga sinensis

Wang (1961) wrote that the Chinese Douglas-fir, *Pseudotsuga sinensis* (Dode), extends over a distance of nearly 2,000 km along the Yangtze Valley from the Pacific coast to western Sichuan. But according to Chengde (1981), the species is limited to the upper Yangtze region. He described the distribution (Figure 2.8) as "widely scattered in west Hupeh [Hubei], northwest and south Hunan, northeast Kweichow [Guizhou] and southeast Szechuan [Sichuan] at an elevation of 800 to 1,200 m. In southwest Szechuan, central and northeast Yunnan, the tree occurs at 1,500 to 2,800 m altitude."

Pseudotsuga gaussenii

Eastern Chinese yellow fir, recognized by Chinese botanists as a species separate from *Pseudotsuga*

Figure 2.8 Range of Pseudotsuga in China (after Chengde 1981).

sinensis, grows in the lower Yangtze region (Figure 2.8). Wang (1961), who still called the Douglas-fir of that region *P. sinensis*, listed it as occurring in northern Zhejiang, southern Anhui, and northern Jiangxi. Chengde (1981) described the distribution of *P. gaussenii* as "only scattered in south Anhwei [Anhui], and west and south Chekiang [Zhejiang] at 600 to 1,500 m altitude." Cheng and Fu (1978) reported that *P. gaussenii* occurred also in the province of Guangdong.

Pseudotsuga forrestii

Until the publication of the keys to Chinese Douglas-firs by Cheng and Fu (1978), the only available records on the distribution of the Mekong yellow fir were comments on herbarium sheets of specimens collected in 1914 by Forrest (Craib 1919) in the Mekong-Salween watershed of northwestern Yunnan at lat 27°40′ N, and in 1922 by Maire (Wilson 1926) in southeastern Tibet at lat 28°25′ N. Chengde (1981), apparently following Cheng and Fu (1978), gave the range of *Pseudotsuga forrestii* Craib as including northwest Yunnan, southeast Tibet, and southwest Sichuan, at elevations of 2,400 to 3,300 m.

Pseudotsuga brevifolia

Shortleaf yellow fir has a limited distribution in Longzhou and Jingxi counties of southwest Guangxi at altitudes of about 1,250 m (Chengde 1981) on south slopes or near peaks (Cheng and Fu 1978).

3. Areas of Introduction

Richard K. Hermann

Pseudotsuga menziesii is distributed more widely outside its natural range than any other species of American forest tree, with the exception of *Pinus radiata*. Its successful introduction beyond its natural habitat into many parts of the temperate regions of the northern and southern hemisphere is all the more remarkable because of the ignorance of, or disregard for, the importance of provenance variation until lately.

The introduction of Douglas-fir went through various phases. Initially the species was introduced through individual tree plantings in Europe and elsewhere around the world. Successes were mostly dependent on the seed sources and setbacks were due to the occurrence of diseases, especially *Rhabdocline pseudotsugae* and *Phaocryptopus gaeumannii*. Over time, seed source problems and diseases were overcome through genetic selection and silvicultural practices that allowed for wider establishment, including monoculture stands. Social issues influencing such phases included trade barriers, e.g., during war time, but more influential were the political discussions about the introduction of non-native species. The following chapter describes this development until the mid-1990s.

At present, Douglas-fir is an accepted and integral part of forest management in many countries because of its economic importance and its reputation as a species that may be better able to deal with climate change, especially with its drought resistance. However, the proportion of Douglas-fir is often limited because of concerns about its ecological impacts; for example Forest Stewardship Certification standards in Germany limit non-native species to 20% stocking in management units.

Northern Hemisphere

The principal region of introduction of Douglas-fir to the northern hemisphere is Europe. By comparison, the extent of introduction to regions in North America outside the natural range of the species is minor.

Western North America

Alaska

The current range of *P. menziesii* var. *menziesii* does not extend into Alaska although fossil evidence indicates that Douglas-fir grew there in the Miocene (Wolfe 1969) and Pleistocene (Hopkins and Benninghoff 1953). A few small plantations with *Pseudotsuga menziesii* var. *menziesii* were established, one as early as 1927, in southeast Alaska (Harris 1971) from 208 km to 352 km north of the coastal variety's northern natural limit. Although experience with Douglas-fir in Alaska is limited, Harris stated that, "under present climatic conditions the species is capable of germinating, becoming established, making excellent growth, and producing viable seed far north of its present northern coastal natural limit."

Hawaii

The compilation of "forest plantings in Hawaii by genera, 1908-1960" (Nelson 1965) lists the numbers of Douglas-fir planted as 1,835 trees, but does not provide exact dates and locations of plantings. Included in that number is probably a small plantation established by L.W. Bryan, a former Territorial Deputy Forester for Hawaii. He planted 50 seedlings of coastal Douglas-fir in 1934 near the 1,829 m level on the northeast slope of majestic Mauna Kea as a monument to David Douglas. At this spot in 1834, Douglas met a violent death in a wild bullock pit. Of the 50 trees planted in 1934, some were uprooted by wild pigs and others smothered by vines. In 1976, the largest of the surviving trees had a height of 37 m and a dbh of 76 cm. Coastal Douglas-fir in that grove, situated at about lat. 10°30′N, represents trees of the variety *menziesii* growing closest to the equator (Nelson 1976). In 1984, on the 50th anniversary of the original planting of Douglas-fir at that site, a second planting of coastal Douglas-fir took place nearby (Anonymous 1985).

Central and Eastern North America

Attempts to grow the coastal variety east of the Rocky Mountains have mostly failed. Jäger and Beissner (1884) mentioned a communication from A. Strauch, Superintendent of Spring Grove Cemetery in Cincinnati, Ohio, to the effect that coastal Douglas-fir would do extremely poorly in the central and eastern United States. Sargent (1898) wrote: "Early attempts to introduce it into the eastern United States by means of plants obtained in England and raised from seeds gathered in Oregon, or from trees which had grown in Europe, were generally unsuccessful, the young plants soon succumbing to the heat and dryness of the eastern summers or to the cold of eastern winters."

C.A. Schenck established a small plantation of Douglas-fir with 4-year-old plants in 1896 on the Vanderbilt estate near Biltmore, North Carolina. Trees were 5.5 to 7.3 m high with diameters breast high of 8.9 to 12.7 cm at age 32 from seed. The plantation did not thrive, however, because of infection with *Polyporus schweinitzii* (Hedgcock et al. 1925).

None of the Douglas-firs in a plantation established in 1919 in Mahoning County, Ohio, survived (Aughanbaugh 1960), but Douglas-fir planted 1928 at Cloquet in northeastern Minnesota about 30 km (18 mi) west of Lake Superior had 90% survival at age 20, and 83% at age 41 (Alm et al. 1972). Grigsby (1969) reported on performance of non-native species under planting conditions in southern Arkansas and northern Louisiana. Among species that failed completely was *P. menziesii* of California origin.

To explore the feasibility of growing Douglas-fir as Christmas trees in Pennsylvania, a series of plantings were made at eight locations in the state beginning in 1952 (Bramble and Byrnes 1952). Of the 19 coastal and interior provenances used in the study, those from the Pacific Northwest suffered severe winter injury. After six years, 55% of the coastal Douglas-firs had died (Byrnes et al. 1958).

In an effort to find Douglas-fir provenances suitable for Christmas tree plantations, shelterbelts, and ornamental plantings in the Midwest, a major study was initiated in 1961 (Wright et al. 1971). Trees for the study were grown in a nursery near East Lansing, Michigan, from seed collected in 128 locations throughout the natural range of the species in the United States and Canada. Subsequently, seedlings were distributed to participants in the study to establish test plantations in Nebraska, Michigan, and Pennsylvania. Seedlings of *P. menziesii* var. *menziesii* had already suffered extreme winter injury in the East Lansing nursery, and many of them died in the nursery. Gerhold (1966), who tested 67 of the provenances from the Wright collection in a nursery near Potters Mills, Pennsylvania, also reported severe damage by winter cold to seedlings from west coast seed sources. Of the trees of 14 west coast provenances from the Wright collection grown in a Nebraska test plantation, all from 12 of the 14 provenances died in the first three years after outplanting. Read and Sprackling (1976) concluded that trees of the coastal variety of Douglas-fir cannot survive Nebraska winters, and hence, should not be planted there.

Pseudotsuga menziesii var. *glauca* has been grown as an ornamental tree for more than 100 years in the eastern United States. Sargent (1898) wrote:

> In 1862 Dr. C. C. Parry found the Douglas Spruce on the outer ranges of the Rocky Mountains of Colorado, and the following year sent seeds to the Botanic Garden of Harvard College. The plants raised from these seeds have proved perfectly hardy and have grown rapidly and vigorously in the neighborhood of Boston, and now give promise of surpassing all other exotic conifers in permanent beauty and usefulness; and in recent years the Douglas Spruce, raised from seeds gathered at high altitudes in Colorado, has been planted in considerable numbers in the northern states.

Results from the test plantations established with trees of the interior variety from the Wright provenance collection have pointed to various degrees of adaptability between provenances to growing conditions outside their natural range. In a 12-year-old plantation at Kellogg, Michigan, provenances from Arizona, New Mexico, and Colorado proved to be highly susceptible to late spring frost injury, whereas provenances from the northern Rocky Mountains in Montana and Idaho were not susceptible (Steiner and Wright 1975). Van Haverbeke (1987), summarizing the 20-year-performance results of interior provenances at the Plattsmouth plantation in eastern Nebraska, found that they were in close accord with those reported at age 11 by Reed and Sprackling (1976). More of the trees from southern Rocky Mountain provenances survived and were taller after 20 years than those from central and northern Rocky Mountain provenances. The good showing of the trees of southern Rocky Mountain origin is remarkable because they suffered heavily from repeated dieback of terminal shoots in successive winters caused by cold injury. Superior performance of New Mexico provenances over those from the central and northern Rocky Mountains had also been noted in earlier trials in New Hampshire (Baldwin and Murphy 1956) and Iowa (Erdmann 1969). Douglas-fir in a mixed conifer plantation established 1960 in Newfoundland (Singh 1970) and in a small plantation made in 1941 on Prince Edward Island (Peterson 1964) are the easternmost introductions in North America on record. Whether these trees belonged to the coastal or interior variety of Douglas-fir was not indicated.

Experience over the span of a century clearly shows that the coastal variety of Douglas-fir is unsuitable for planting in North America east of the variety's natural range because they lack frost hardiness. Trees of the interior variety can better adapt to climatic conditions in central and eastern North America, although their potential for survival and growth varies considerably between provenances. A serious threat, especially in the northeastern United States, to cultivation of the variety *glauca* is its great susceptibility to infection by the fungus *Phaeocryptopus gaeumannii*, which causes needle cast.

Europe

Weck (1949) wrote, "Currently more pure stands of Douglas-fir, introduced to Europe around 1700, exist than any other introduced species."[1] Volk (1969) claimed that Douglas-fir was brought to Germany at the end of the 18th century by Baron von Wangenheim, a Hessian officer sent to America to fight for the British in the Revolutionary War. Both these accounts of the introduction of Douglas-fir to Europe are erroneous.

The event that marked the introduction of *P. menziesii* to Europe was the arrival in early 1827 of the Douglas-fir seed shipped to Great Britain by David Douglas. In the nearly 200 years since arrival of the first shipment of seed, Douglas-fir has become more widely distributed in Europe than any other North American conifer (Figure 3.1).

Both varieties of *P. menziesii* have been planted in Europe, but the coastal variety turned out to be far better suited to cultivation in most European forest regions than has the interior variety. Based on an analysis of climate and physiography, Schwarz in 1933 concluded that the potential range for cultivating Douglas-fir in Europe would include the southernmost parts of Norway and Sweden, Denmark, Germany, western Poland, parts of northern Austria, northern Switzerland, Belgium, Holland, Great Britain, Ireland, northern Spain, Portugal, and France exclusive of its Mediterranean region. His assessment of conditions for growth of coastal Douglas-fir in various parts of Europe, although founded mainly on theoretical considerations, was proven to be largely correct by more than a century of experience with the cultivation of Douglas-fir.

Great Britain

That the introduction of Douglas-fir to Europe began in the British Isles is probably more than just a historical accident. As noted by Macdonald (1957), exotic trees play a more important role in Britain than in other European countries because of the poverty

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[1] Translated from the original: "Fuer die bereits um 1700 nach Europa gebrachte Douglasie liegen gegenwärtig mehr Einzelanbauflächen vor als für jede andere eingeführte Holzart" (Weck 1949, p. 20).

Figure 3.1 Areas ocupied by Douglas-fir in Europe, in hectares (modified from De Champs 1997b). Some smaller stands or plantings may not be shown on this map, but may b ediscussed in the text or may appear on individual country maps.

of its native arboreal flora. That is particularly true of conifers whose sole indigenous representatives are Scots pine (*Pinus sylvestris*), English yew (*Taxus baccata*), and juniper (*Juniperus communis*). The acquisition of colonies in different parts of the world favored acquaintance with foreign plants and their subsequent import. By the time Douglas-fir came to Britain, people of that country had considerable experience with exotics, and displayed none of the resistance to their introduction sometimes encountered on the continent.

The first Douglas-firs grown in Britain arose from seed sent by David Douglas in the fall of 1826. The exact source of that seed is unknown, although a common assumption is that the seed was from collections Douglas made near his base at Fort Vancouver on the Washington side of the Columbia. Booth (1890, p. 47) reasoned as follows: "Because he arrived on August 31 at Fort Vancouver, and, according to his diary, sent already on September 1 his boxes on board of the ship that left that same day for England; his diary entries from 2 to 9 September 'laid in specimens of *Pinus taxifolia* with fine cones' lead to the conclusion that he could have collected these only in southern Washington on the border to Oregon after he had sent off his collection from northern Washington on the border to Oregon. Until proof to the contrary, I state on the basis of Douglas' diaries that the trees from the year 1826 described by me earlier must have originated from the seed collected near Vancouver at the border to Oregon."

The Royal Horticultural Society, sponsor of Douglas' expedition, distributed the seed from his 1826 shipment among its members. Trees raised from that seed were planted in the parks of numerous estates. Hutchison (1873) lists sites of early plantings of Douglas-fir and remarks in that context "the tree at Raith, near Kirkcaldy, in Fife, planted by Douglas himself is now a splendid specimen." Details on locations of early plantings are also provided by A. Murray (1884), Elwes and Henry (1909), and Anderson (1967). Many of these trees still existed in the 1950s (Edwards 1957, Streets 1962), some in 1980 (Zander 1980), and others still in 1993.[2]

Other early introductions were from seed collected in the late 1840s by Sir William Douglas Stewart in California (Booth 1890), in 1846/47 by Hartweg in the Santa Cruz Mountains of California, and from collections for the Oregon Association made by William Lobb and John Jeffrey in 1852/53 (Edwards 1957). Lobb who had come to California in the summer of 1849 made an excursion three years later to the Columbia River and Oregon, where he succeeded in obtaining seeds of Douglas-fir (Dallimore 1932). Some of the seed obtained by Lobb may have come from locations not far from those of the Douglas collections. The origin of the Douglas-fir seed sent by Jeffrey is unknown. Most likely, the seed came from stands in California because he is not known to have made collections farther to the north.

Trees from Douglas' original seed grew so well that they excited considerable interest, and when they began to bear cones, seed was collected from them. Loudon (1838, p. 2321) wrote: "The tree bore cones for the first time in England, at Dropmore (Buckinghamshire) in 1835, when the plant there already mentioned produced one cone. This year (1837) it has above a dozen; so that in all probability, there soon will be an abundance of seeds of this species, from which extensive plantations may be raised, and the value of the species as a timber tree proved."

The most famous, however, are two trees at Lynedoch, Scone Estate in Perthshire, planted in 1834; one of them was a particularly heavy cone bearer. The first cones were harvested from these trees in 1844. In the next 30 years, the two trees yielded about 200,000 cones from which about 4 million plants were raised (Booth 1877, p. 63). They are known to be the source of many stands in Perthshire and some in Argyll (Lines 1987), and are still in existence.[3] The seed lots sent by Hartweg and Lobb produced many specimen trees but did not produce such vigorous progeny as the seed of Douglas (Matthews 1953). Booth (1890, p. 43) mentions that he saw about 50 splendid Douglas-fir at Murthly Castle raised from the seed collected by Stewart at the end of the 1840s in California. In 1871, seed worth 75 pound sterling was collected from these trees. Booth emphasized

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[2] Letter from Dr. D.C. Malcolm, University of Edinburgh, dated 7 December 1993.

[3] Alan Fletcher, British Forestry Commission, personal communication.

that plantations established from that seed were better than those from imported seed.

British land owners became interested in Douglas-fir as a forest tree relatively early. Douglas-fir, like other exotics, had been tried first on fertile, sheltered sites where it had displayed rapid growth (Anderson 1967). The vigorous growth of the species in parks and arboreta prompted some estate owners to plant it under forest conditions in small plots. The remarkable performance of Douglas-fir on such trial plots led to establishing a 2.4 ha plantation in 1858 on the estate of the Duke of Montrose in Buchanan, Stirlingshire (Anderson 1967). Another, and perhaps the best known of the early Douglas-fir plantations, is the one at Taymount on the former Mansfield estate in Perthshire. William McCorquodale (1880), who worked as wood surveyor on the Mansfield estate, gives the following account of the plantation's establishment: "Again in 1860, 8 acres were enclosed with rabbit-proof wire netting on the estate of Taymount, alongside the Highland Railway, and planted with Douglas firs at 9 feet apart for the permanent crop, and the intermediate spaces were filled up with larch as nurses. This plantation is now 20 years of age, and the nurses are all thinned out. It now stands a pure Douglas fir plantation, in prime condition, and is the admiration of all who see it."

R.M. Gorrie (1965), who was forester on the Mansfield estate in 1919, stated that "the various written accounts give 1860 as the date of planting, but Lord Mansfield himself verified from records that it was in fact 1858." Booth (1890) mentions 1857 as the year of establishment. The discrepancies between accounts probably stem from the fact that authors did not distinguish clearly between the Taymount plantation and a 13-acre plantation established in 1857 at Scone (Hutchison 1879, McCorquodale 1880). The seed source for these plantations were trees at Lynedoch that Scone grew from the seed sent by David Douglas in 1826.

The Taymount plantation was thinned in 1887 to 499 trees per ha. In 1896, all trees were pruned to a height of 10 to 12 m (Somerville 1904). Schlich (1888) estimated the volume of the plantation to be 206.8 cm/ha at age 28 years. In 1900, at age 40, volume had increased to 339 cubic meter/ha (Crozier 1908). Subsequent growth of the plantation appears to have slowed. Robinson (1914), after a 1913 survey of Douglas-fir plantations, states: "The Taymount plantation which by its volume production first drew general attention to the Douglas fir, now proves to be the least vigorous of the woods examined." According to Gorrie (1965), data of standing timber were not recorded after 1913, and no record exists of the felling or disposal of the felled crop. He believes that the trees of the Taymount plantation were probably cut about 1920, shortly before the estate was sold by Lord Mansfield in 1921. Matthews (1983), without citing a source, gives 1923 as the year when the trees of the Taymount plantation were felled.

The Taymount plantation became a showpiece of Douglas-fir, and this was an important factor in extending the planting of the species throughout Great Britain (Edwards 1957). Numerous plantations of Douglas-fir had been established in the last quarter of the 19th century (Macdonald 1952), and thousands of Douglas-firs had been planted as solitary trees to fill vacant spots in existing plantations (McCorquodale 1880). Undoubtedly, many of the 19th-century plantations resulted from home collections, but not all. From 1870 to 1880, the firm of C.H. Manning of Roy, Washington, supplied seed, at first from near the lower Columbia River and later from northwestern Washington. Seed was also probably imported in the late 19th century from British Columbia (Lines 1987). In general, these early seed imports were made up of provenances well suited for the British Isles, although not always. Henry and Flood had already written in 1920 that the interior variety had been tested in numerous localities but was invariably a failure. Kay and Anderson (1928) also pointed out that several plantations had been grown from unsuitable seed, giving rise to poor-quality stands.

Cultivation of the species declined after the turn of the century when the first enthusiasm for the tree had waned. Creation of the Forestry Commission in 1919, and the large forestation program initiated by that organization, led to renewed interest in the planting of Douglas-fir. Lines (1987) gives the following account of seed procurement from 1920 to 1980:

> The first seed imported by the Forestry Commission in 1921 was 913 lbs, reputed to be from Washington. The following year 4,000 lbs came from the lower Fraser

> River. Thereafter most seed up to the 1950s came from both these sources. Small amounts came from the Shuswap Lake area in the interior of British Columbia, from Oregon or from undefined sources in 'USA' or 'BC'. During the next 30 years a few seedlots came from Vancouver Island and Oregon, but the bulk was from Washington. Of the total of 50,747 lbs imported, 77 percent came from the USA and 23 percent from British Columbia.

The predisposition of interior British Columbia provenances to *Rhabdocline pseudotsugae* has led to them not being recommended for use in Great Britain (Alan Fletcher, personal communication).

Douglas-fir seems to have lost some of its appeal to woodland owners in the second quarter of the 20th century. Scott (1931) noted a reduction in the area planted to Douglas-fir on account of prejudice against the wood of the species. Macdonald (1952) states that Douglas-fir had begun to lose favor with private land owners, and Wood (1955) mentions that the species lost favor in southeastern England because of its disappointing lack of vigor, adding "It is not at all clear how far the troubles which have rendered it unpopular are specific, or how far race has entered into the matter." A factor in the decline in its use was the widespread occurrence of infestation by the Cooley spruce gall adelgid (*Adelges* [*Gilletteella*] *cooleyi*), which made the trees look sickly and slowed growth for a period.[4]

A reversal of that trend took place in mid-century. The data from the latest woodland census (Locke

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[4] Letter from Dr. D.C. Malcolm, University of Edinburgh, dated 7 December 1993.

Table 3.1 Area stocked with Douglas-fir, according to census of woodlands in 1947 and 1982. Percentages are percent of all conifers (from Edwards 1957, Locke 1987).

		England		Scotland		Wales		Great Britain	
Year		ha	%	ha	%	ha	%	ha	%
1947	Private woodlands	2917	4	2202	2	747	9	5866	3
	Forestry commission	4251	6	2320	3	2861	9	9432	5
	Total	7168	5	4522	2	3608	9	15298	4
1982	Private woodlands	12144	7	5190	2	3159	8	20493	4
	Forestry commission	12919	6	6438	1	7549	6	26906	3
	Total	25063	6	11628	2	10708	6	47399	4

Table 3.2 Area and standing volume of Douglas-fir in Great Britain by planting year classes (From Locke 1987).

Planting year class	Private woodlands (ha)	Forestry commission	Total	All woodland ownerships (thousand m^3 with bark)
Pre-1861	158	41	199	91.0
1861–1900	299	36	335	172.5
1901–1910	193	51	244	107.1
1911–1920	490	96	586	224.9
1921–1930	1260	2896	4156	1494.3
1931–1940	1031	1503	2534	773.3
1941–1950	1041	1786	2827	593.4
1951–1960	5116	9100	14216	1749.5
1961–1970	7499	8306	15805	879.5
1971–1980	3406	3091	6497	—
TOTAL	20493	26906	47399	6085.9

1987) show that the area occupied by Douglas-fir increased between 1947 and 1982 by a total of 32,101 ha, of which 17,474 ha were on Forestry Commission lands and 14,627 ha on private woodlands. In 1982 Douglas-fir formed 3% (26,906 ha) of the total area of private coniferous woodlands. The largest share of land stocked with Douglas-fir was in England, followed by Scotland and Wales (Table 3.1). A breakdown of the area in Douglas-fir by planting-year classes (Table 3.2) shows a similar pattern of periodic increases and decreases in area planted to Douglas-fir for both Forestry Commission and private woodlands that appears to reflect changes in the popularity of the species. Data for the area planted to Douglas-fir before 1900 do not truly represent that period. Macdonald's (1952) remark, "Numerous fine plantations were created throughout the last century such as the celebrated stand at Taymount in Perthshire, but most of them have now disappeared," indicates that more land was planted to Douglas-fir than shown by these data. By contrast, the data for the years 1971 to 1980 reflect an actual trend of reduced planting of Douglas-fir after a peak in the preceding decade. The area occupied by the species has shrunk somewhat since the 1982 census because of its reduction from 26,906 ha to 25,400 ha on Forestry Commission lands by 1987 (Lines 1987). However, the amount of land stocked with Douglas-fir on private holdings did not change. The standing volume of Douglas-fir in Great Britain amounted in 1982 to slightly more than 6 million cubic meters. The 20- to 30-year, and 50- to 60-year-age classes contained the largest shares of standing volume (Table 3.2). The largest percentage of standing volume was in pole-sized timber, and the smallest in saw timber (Table 3.3).

Table 3.3 Standing volume of Douglas-fir in Great Britain by size classes (from Locke 1987).

Size class (dbh)	Thousands m^3 with bark	Percent
7 to 20 cm	2525.0	41.5
21 to 30 cm	984.4	16.2
31 to 50 cm	1858.8	30.5
>50 cm	717.7	11.8
Total	6085.9	100.0

Climate permits growth of Douglas-fir throughout much of the British Isles. Limits of temperature and precipitation for growth of the species in Great Britain are not clearly defined, however (Wood 1955). Although the mild and humid climate in the western parts of the country provides highly favorable growing conditions, the species is also capable of making a satisfactory but slower growing crop in the lower rainfall and more continental climate of eastern and southeastern England (Day 1955, Streets 1962). Mitchell (1983a) reported outstanding growth of trees native to the Pacific Northwest in Scotland, prompting him to write, "Scotland is incomparable in its wealth of immense conifers and is the Oregon/California of Europe." He found a Douglas-fir in Craigvincan that measured 60 m in height, which makes it probably the tallest Douglas-fir on record in Great Britain. That tree was still growing at a rate of 0.3–0.5 m per year in 1993 (D.C. Malcolm, 1993, personal communication).

The most favorable sites for growth are in the wet and moderately wet coastal areas on well-drained loams and sandy loams of intermediate fertility. But the sensitivity of Douglas-fir to constant wind exposure to wind restricts the species to sheltered sites for best growth. Anderson (1961) considered Douglas-fir to be a species for the middle-hill slopes rather than the valley bottoms and higher reaches. Cultivation of the tree is not necessarily confined to low elevations, however. Douglas-fir has been grown successfully at altitudes of 305 m in Scotland (Macdonald 1952) and up to 408 m in Wales (Bennett and Long 1919), but because of the high risk of top damage in wind-exposed areas, it is best kept below 250 m.[5]

Silvicultural practices have influenced the distribution of Douglas-fir aside from environmental factors. The species has been much used for restocking poor scrub areas of oak and birch. As a result, the distribution is to some extent governed by the situation of oak and birch scrub, which has been converted to high forest (Edwards 1957). Thus, in Scotland, the greatest concentrations of sites stocked with Douglas-fir are in Kirkcudbright, Argyll, Perth and Inverness because of the frequent use of Douglas-fir to rehabilitate scrub lands (Anderson 1967).

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[5] Ibid.

Compared to two other western-American species, Sitka spruce and lodgepole pine, which accounted in 1982 for 40% and 10%, respectively, of the total area stocked with conifers in Great Britain (Locke 1987), Douglas-fir held a relatively small share, 4%. That share may increase in the future, however, according to Lines (1987): "In view of its high timber value, rapid growth and resistance to butt rot it is likely to be used on an increasing scale as the emphasis swings away from afforestation of bare ground to replanting of more sheltered valley sites, e.g. those carrying better quality Scots pine or larch."

Ireland

Douglas-fir was introduced to Ireland shortly after 1850 (Fitzpatrick 1966). The first plantings consisted of solitaires or small groups in arboreta and selected spots in open woodland. Professor Tom Clear wrote in 1951,

> The results of this type of planting are to be seen in many parts of Ireland, particularly in desmenes like Powerscourt, Carton, etc. The growth of the specimens thus planted at Kilruddery was most remarkable and by the beginning of the present century Douglas-fir was well on the way to becoming a firm favourite in the race for pride of place among the newer exotics. After seeing the giants at Powerscourt and Carton one can well understand the superoptimism that prevailed with regard to this species some 40 or 50 years ago.

The tallest Douglas-fir in Ireland stands at Powerscourt Demesne, County Wicklow. Its height was measured at 53.14 m in 1991, and its age was about 125 years. By 2013, its height was measured at 61.5 m, and it was officially recognized as not only the tallest Douglas-fir, but the tallest tree in Ireland since recordkeeping began.[6]

The use of Douglas-fir as a forest tree coincided with the advent of State Forestry in Ireland (Clear 1951). The species' history of planting is reflected by area occupied according to age class (Table 3.4). Many of the early plantations were on old woodland sites and usually in mixture with *Picea abies* and *Larix europea*. Planting of Douglas-fir ceased almost completely in World War I and was not resumed on any appreciable scale until 1921. The early 1920s saw the establishment of extensive monocultures with Douglas-fir on sites favorable for the species. With further extension of planting programs, site requirements of Douglas-fir received less attention. As Clear (1951) phrased it "This departure from sound selection of sites could have but one result-poor crops." In addition, appearance of the Cooley spruce gall adelgid (*Adelges [Gilletteella] cooleyi*) and the Swiss needle cast disease (*Phaeocryptopus gaeumannii*) contributed to stagnation of growth in plantations. All of these problems led to a decline in popularity of Douglas-fir and, by 1940, planting of it had virtually come to a halt. Moreover, existing stands were regarded as being without future because of their stagnant and debilitated appearance (McEvoy 1943), and a policy of replacing unsatisfactory stands of Douglas-fir was instituted (Clear 1951).

Table 3.4 Area occupied by Douglas-fir and mean yield class in state plantations in Ireland by age class.

Age class	Area (ha)	Mean yield class
Pre 1920	9	14.4
1920 - 1929	165	14.4
1930 - 1939	208	13.7
1940 - 1949	23	12.4
1950 - 1959	483	13.2
1960 - 1969	2206	15.4
1970 - 1979	1874	17.7
1980 - 1989	2104	17.6*
1990 - 1993	701	17.5*

* Projection

Note: yield class = 1 m^3/ha/y. Source: Data provided by A. Pfeifer, Irish Forest and Wildlife Service.

Heavy thinnings during and after World War II dramatically improved the remaining stands and led Irish foresters to reassess the value of Douglas-fir. The most notable plantations saved by these rigorous stand openings are in the Suir Valley, between Carrick and Clonmel, and on Slievenamon, as well as in the glens of County Wicklow (Fitzpatrick 1966). The interest in Douglas-fir to Irish forestry lies in the high returns that may be obtained in the lucrative market for transmission poles (O'Driscoll 1978). Expected rotations in state forests are from 40 to 60 years.

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[6] Mr. Alistair Pfeifer, Forestry & Wildlife Service, Bray, Ireland, letter of 16 February 1994; "Ireland's tallest tree - a 200ft Douglas Fir," Breaking News, Ireland, 05/11/2013, http://www.breakingnews.ie/ireland/irelands-tallest-tree-a-200ft-douglas-fir-612237.html.

Douglas-fir does well on sheltered sites with deep, moist, and well-drained soil. It grows poorly on exposed sites, on peat, and on lime soils, all conditions common in Ireland. Thus, the species is restricted, to the lower slopes of the mountains in Counties Louth, Tipperary, Waterford, Wexford, and Wicklow (Fitzpatrick 1966).

Only the coastal variety of Douglas-fir is suitable for Irish conditions. Much of the seed imported in the past apparently represented provenances from the coastal regions of Washington. Early results from Irish participation in the IUFRO international provenance trials indicate that coastal provenances from Washington hold considerable promise for use in Ireland (O'Driscoll 1978, Pfeifer 1988).

The 1958 woodland census in the Irish Republic recorded nearly 1,375 ha of pure stands of Douglas-fir with a volume of 274,096 m^3, or an average of 199 m^3/ha, the highest for any species in Ireland (Fitzpatrick 1966). In the 1968 woodland census (O'Flanagan 1968), Douglas-fir represented only 3% of the total afforested area, and had a yield class range from 2 to 24, with the weighted average of 14. In 1993, Douglas-fir occupied 7,772 ha in the Irish State Forests. The area occupied by Douglas-fir plantations in the private sector is very small, amounting to about 500 ha.[7] That Douglas-fir assumes a minor role in the species composition of Irish forests reflects the fact that its planting range is limited by the availability of suitable sites. Although Douglas-fir is regarded as the premier conifer in Ireland, many foresters shy away from it because of difficulties with its establishment, and they plant Sitka spruce (*Picea sitchensis*) instead.[8]

Western Central Europe

Germany

Douglas-fir was introduced to Germany shortly after it had come to Great Britain. John Richmond Booth (1800-1847), a nurseryman in Flottbeck near Hamburg, was a member of the Royal Horticultural Society. He received some of the Douglas-fir seed collected by David Douglas when it was distributed to members of the Society (Kremser 1974). In 1829, Booth planted a 2-year-old seedling raised from the seed collected by David Douglas in his arboretum, which was then the largest in Europe, next to that of the Duke of Bedford at Woburn Abbey. That seedling was probably the first Douglas-fir ever planted in Germany (Booth, 1877). It developed into a tree that was felled in 1882 by John Cornelius Booth,[9] son of John Richmond, to demonstrate the quality of Douglas-fir wood grown in Germany (J. Booth 1882).

The elder Booth was a strong advocate for introducing of North American tree species to Germany. In an address to the Society of German Agronomists and Foresters at its meeting in 1841 at Doberan, Mecklenburg, he told his audience that Douglas-fir grows well under the climatic conditions of Germany, and recommended trials with that species (J.R. Booth 1841, p. 51-52). J.R. Booth's efforts were not entirely without success. An inventory of foreign tree species planted in Germany before 1880 (Weise 1882) recorded Douglas-firs in many parts of Germany, although their numbers were very small.

In 1988, the oldest still-standing Douglas-firs, one at Jaegerhof in Pommerania, the other at the Barneführerholz near Oldenburg, had come from the Booth Nursery in Klein-Flottbeck. The Jaegerhof tree had been planted as a 4-year-old seedling in 1842. The planting date for the Barneführerholz tree is 1843, but information is lacking about its age at time of planting (Rothkirch and Struthoff 1989). J. Booth (1907a) emphasized that both trees are of the «green» variety and had been grown from seed that had come from the American Northwest. That the seed had been part of the original David Douglas collection, as suggested by Rothkirch and Struthoff (1988), is unlikely because 11-year-old seed would scarcely have been viable without the availability of cold storage facilities.

A «Kommission für die Douglas-fichte» was established at the 1878 meeting of the Brandenburg Forestry Association (Märkischer Forstverein) at Neubrandenburg, marking the beginning of wider interest in the species. That Douglas-fir commission, consisting of six men with Count Willamowitz-Moellendorf as chairman, began its work by dis-

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[7] Ibid.

[8] Ibid.

[9] John Cornelius Booth did not use his middle name in his numerous publications and in the literature is usually referred to as John Booth.

tributing Douglas-firs to interested forest owners in spring of 1879. The seed was supplied by J. Booth, and came from the northernmost part of the range of Douglas-fir (Booth 1882, p. 34)

Booth (1880) delivered a paper on exotic tree species at the meeting of the Union of German Forest Experiment Stations in September 1880 in Baden-Baden at the request of the Prussian Forest Experiment Station. In that paper, Booth outlined the advantages to be gained by introducing exotic tree species into the forests of Germany. His presentation must have been convincing because the members of the Union decided to initiate systematic trials with North American and East Asian broadleaves and conifers. The working plan for these trials, which was agreed upon by the members of the Union at their meeting in August 1881 at Braunschweig, included Douglas-fir among the conifers selected for the trials (Ganghofer 1884).

The testing program of the Prussian Forest Experiment Station spanned an area from the Eifel Mountains in the west to East-Prussia in the east. That provided the opportunity to observe the performance of Douglas-fir under climates ranging from mild oceanic to harsh continental. Bernhard Danckelmann, head of the Prussian Forest Experiment Station, reported in 1884 that plots of Douglas-fir totaled 87 ha; by 1890, that number had expanded to nearly 140 ha (Schwappach 1891). Danckelmann's successor, Adam Schwappach, already concluded after the first decade of trials in 1891 that Douglas-fir should be introduced into the Prussian forests. He reiterated that conclusion in subsequent reports (1901, 1911) and stated in his final report (1920) that Douglas-fir was particularly suited for the sandy soils of northern Germany, where Norway spruce (*Picea abies*) is a common, but off-site tree. He was not alone in his assessment. Already in 1904, at the meeting of the Society of East- and West-Prussian Foresters, participants had expressed the opinion that Douglas-fir was suitable for use in East-Prussia (Anonymous 1904). Additional accounts of performance of Douglas-fir were published by Reichenau (1911) for West-Prussia, and by Böhm (1922) for East-Prussia. These early assessments of the suitability of Douglas-fir for use in East-Prussia were shown to be correct by a report on 4 plantations of *P.* var. *menziesii* established 1889, 1906, 1914, and 1916 in the Kaliningrad (formerly Königsberg, East-Prussia) region of Russia (Fedorov 1981). In 1981, the oldest of these plantations had a standing volume of 1,160 m^3/ha. Trees in the plantations are hardy and flower every 3 or 4 years, producing seed of good quality.

Most of the seed used in the Prussian State Forests before 1890 was probably supplied by J. Booth. From 1891 to 1895, the U.S. Bureau of Forestry shipped about 145 kg of Douglas-fir seed to Prussia. The origin of that seed is unknown. Beginning in 1896, purchase of seed was at the discretion of State Forest Districts, who usually bought it from the least expensive sources. Since about 1909, seed procurement for the Prussian State Forests was handled by the German Dendrological Society. The Society collected seed of the var. *menziesii* primarily in the Cascade Range of Washington and Oregon (Kanzow 1937).

The Brunswick Forest Experiment Station established small trial plantations in 1876 with 3-year-old Douglas-fir seedlings. Puchert (1954) presumed that the seed from which these seedlings were raised came from British mother trees established from seed brought by David Douglas. In 1880, the Experiment Station bought seed from three firms—Appel, Nungesser, and Trumpff—that represented unsuitable provenances and led to plantation failures. By contrast, seed obtained from J. Booth in the years 1881 to 1888 gave such good results that the Experiment Station encouraged operational planting of Douglas-fir as early as 1899 (Puchert 1954). The origin of the seed supplied by Booth is unknown, as is that of seed lots obtained from a dozen different seed dealers from 1886 to 1910 (Grundner 1921). After World War II, Brunswick became part of the state of Lower Saxony, which in 1950 had 1,850 ha of Douglas-fir (Borchers 1951). From 1950 to 1992, the acreage of Douglas-fir in Lower Saxony increased to about 15,000 ha.[10]

The first plantings of Douglas-fir in the then kingdom of Saxony were made in 1878 in the Tharandt District of the Saxon State Forests, and in the Plauen City Forest (Zacharias 1931). Plantations of the spe-

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[10] Dr. H.J. Otto, Lower Saxon Ministry of Nutrition, Agriculture and Forestry, letter dated 29 July 1993.

cies were established in state and municipal forests in the next 25 years on a very small scale, with seedlings of the variety *menziesii*. Most of the seed appears to have been supplied by J. Booth. The initial results were sufficiently encouraging that Nobbe (1895) recommended wider use of Douglas-fir. But not until 1904 did the Saxon Forest Experiment Station begin systematic trials with both the coastal and interior varieties of the species. Neger (1914), who reported on trials located at elevations of 100 m in the lowlands to 1,000 m in the Erzgebirge (Ore Mountains), stated that the coastal variety had performed well in the lowlands and the interior variety had grown better at high elevations. A detailed review of the distribution of Douglas-fir after World War I in Saxony by Zacharias (1931) showed that of the 87 State Forest Districts, 47 contained Douglas-fir in 1928. The area occupied by stands of Douglas-fir was small, namely 88 ha or 0.05% of all state-owned forests. Apparently, the area occupied by Douglas-fir did not increase greatly in the next 50 years. M. Hartig (1980) listed 1,394 ha stocked with Douglas-fir for a region that covered the major part of the former state of Saxony.

The first plantings of Douglas-fir in the State of Hesse were made in 1858 in the Darmstadt City Forest (Walther 1911), although systematic trials with the species did not begin until 1884. With few exceptions, like the Büdingen City Forest where 70 ha were planted to Douglas-fir from 1898 to 1917 (Spengler 1925), introduction of the species proceeded rather slowly. By 1945, only 722 ha of Douglas-fir plantations existed. Then, the pace of planting Douglas-fir accelerated. By 1967, about 5,000 ha, or 0.6% of the total forest area of Hesse were stocked with Douglas-fir (Groos 1968). By 1980, the acreage of Douglas-fir had increased to about 15,000 ha (37,050 acres) (Riebeling 1979, Weissgerber 1980[11]). Based on percentage, the increase was largest in private and communal ownerships where the share of Douglas-fir constituted 2.3% in each of these two ownership categories, but it was only 1.2% in the State Forests.

Douglas-firs up to 20 years of age existed in Bavaria by 1880, but they were too few to permit any conclusions about their value as forest trees (Ganghofer 1884). The Bavarian Forest Experiment Station began with systematic trials of Douglas-fir in the decade 1881 to 1891. These first trials were conducted on a small scale, that is, planting of no more than 50,000 trees. Seed used in these trials was obtained through J. Booth; Prof. C.S. Sargent; and the seed dealers Robert Douglas in Waukegan, Wisconsin; Keller in Darmstadt; and Steingaesser in Miltenberg (R. Hartig 1892).

Encouraged by initial success, nearly one million trees were planted in State Forests from 1891 to 1904 (Mayr 1907). A questionnaire sent to 156 forest districts in 1905 about the performance of Douglas-fir provided mostly positive responses, and led to increased planting of Douglas-fir until 1913. Planting of Douglas-fir nearly ceased during the next 10 years because seed imports stopped during World War I and during the first 5 years after the war. A census of foreign trees by the Bavarian Forest Service in 1923 showed that 157 ha were stocked with Douglas-fir. The inventory was incomplete, but the total area occupied by Douglas-fir was unlikely to be more than 200 ha, indicating considerable losses of Douglas-fir plantations. Harrer (1925) attributed these failures to disregard for provenance and insufficient knowledge of the silvical characteristics of the species.

The next census of Douglas-fir in the Bavarian State Forests was undertaken almost half a century later in 1969 (Bayerische Staatsministerium für Ernährung, Landwirtschaft und Forsten 1970). The results showed the existence of 1,248 ha of Douglas-fir plantations, of which 66% had been established after 1950. Since 1970, the acreage of Douglas-fir in Bavaria has increased considerably. According to a questionnaire addressed to forest owners, the annual area planted to Douglas-fir averaged 600 ha (Huss and Siebert 1976). Först (1980) mentions 2,000 ha of Douglas-fir stands just in Lower Franconia in 1980, but figures for all of Bavaria in 1980 or afterwards are lacking in the literature.

The oldest known plantings of Douglas-fir in the former grand duchy of Baden date back to 1860 in the forest district of Oberweiler, and to 1865 in the city forests of Heidelberg and Freiburg. By 1880, Douglas-fir had been planted in 20 localities (Wimmer 1909). The early trials between 1870

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[11] Dr. H. Weissgerber, Hesse Forest Experiment Station, letter 10 March 1980.

and 1880 were largely failures because of frost kill (Mörmann 1956). Although Baden was among the first German states that participated in the trials initiated by the German Union of Forest Experiment Stations in 1880, the Grandducal Forest Directorate issued a directive in 1884 that limited the cultivation of Douglas-fir to forest districts designated as trial participants. That directive remained in force until 1899 (Klumpp and Gürth 1988). Results of the trials begun after 1880 were summarized in a report by Alten (1898) that was distributed to all Baden State Forest Districts. His favorable assessment of the performance of Douglas-fir provided the impetus for increased cultivation of Douglas-fir in Baden.

A total of 53 kg of Douglas-fir seed had been distributed to State Forest Districts in Baden from 1883-1899 (Wimmer 1909). The seed, presumably of Washington and Oregon origin, was supplied by the firms of J. Booth and Sons and G. J. Steingässer. Between 1898 and 1910, seed was obtained from seed dealers in Victoria, British Columbia, and Roy, Washington (Klumpp and Gürth 1988). Plantations established between 1880 and 1910 developed into stands of high quality. By some fortunate circumstance, seed from which these trees were grown came from provenances well suited for this part of Germany. Later imports of seed, especially those directly from the Long Bell Company in Washington in the years 1927-1935, often contained unsuitable provenances and resulted in poorly growing stands (Mörmann 1956b).

In spite of the efforts of many foresters to plant Douglas-fir (Oeschger 1975), the area occupied by the species in publicly owned forests remained small for decades. Baden had 112 ha, stocked with Douglas-fir in 1906 (Wimmer 1909), 150 ha in 1920 (Hausrath 1921), 505 ha in 1930 (Killius 1931). After World War II, the pace of planting Douglas-fir quickened, and in 1960 about 4,000 ha were stocked with Douglas-fir in public forests (Scheifele 1965). Douglas-fir stands are not evenly distributed throughout Baden but are concentrated in the Odenwald and the west slope of the Black Forest (Behler 1980, Weidenbach 1980). Public forests in the Upper-Rhine region already contained 7,065 ha of Douglas-fir in 1975 (Schülli 1986). That amounts to 8% of the total forest area of that region.

Special mention must be made of the Freiburg City Forest. Here, Douglas-fir has been planted since 1901. In 1948, the Freiburg City Forest contained about 220 ha (543 acres) stocked with Douglas-fir. At that time, that was probably the largest area of Douglas-fir in a single forest in Germany (Seibert 1951). The Freiburg City Forest and the nearby Kandern and Sulzburg State Forest Districts belong to the best Douglas-fir areas in Germany. Nearly all are in site class I and stands have a mean annual increment at age 100 of 15-18 m^3 (Volk 1959).

In Wuerttemberg, Prof. Lorey, Head of the Royal Wuerttemberg Forest Experiment Station, initiated the first trials with Douglas-fir in the years 1882 to 1892. By 1890, 21 trial plots with a total area of 3.87 ha had been established (Lorey 1890). In a follow-up report to his 1890 paper, Lorey (1897) indicated that between 1891 and 1895, 62 kg of seed of the coastal variety, and 10 kg of seed of the interior variety, had been distributed to State Forest Districts by the Royal Forest Directorate. In 1896, Douglas-fir was represented in 18 State Forest Districts. An additional 257 kg of seed of the variety *menziesii* was distributed until 1908, and by 1911, 67 ha of Douglas-fir plantations had been established (Holland 1912). The next four decades saw only a small increase in the share of Douglas-fir in the state forests of Württemberg. In 1950, only 368 ha were stocked with Douglas-fir (Zimmerle 1952).

Following World War II, Baden and Württemberg were combined into one state, and recent statistical data on the area stocked with Douglas-fir do not provide a breakdown between the former two states. Between 1960 and 1970, planting of Douglas-fir increased considerably. By the end of the decade, the area occupied by Douglas-fir was assumed to be in excess of 10,000 ha (Volk 1969). By 1984, the area stocked with Douglas-fir had grown to about 20,000 ha. The annual harvest of Douglas-fir in publicly owned forests in Baden-Wuerttemberg amounted to about 25,000 m^3.

The State of Rhineland-Palatinate (Rheinland-Pfalz) created after World War II from lands belonging before the war to Bavaria and Prussia, has perhaps the largest concentration of Douglas-fir stands in Germany. In 1986, the species occupied 29,400 ha in both private and public ownerships, or

6% of the total forest area of Rhineland-Palatinate (Petri 1986).

Beginning as early as 1865, some private forest owners also began to introduce Douglas-fir into their forests with notable success. The most famous are the Douglas-fir plantations in the Sachsenwald estate of Prince Bismarck in Schleswig-Holstein (Titze 1906, 1920), and the former estate of Count Wilamowitz in the northern Elbe River region (Wilamowitz-Möllendorf 1907, Zeidler 1956). The seed, of the coastal variety of Douglas-fir, was supplied by the firm of J. Booth and Sons. The area of Douglas-fir at Gadow increased from 17 ha in 1920 to 131 ha in 1949. Since 1922, only seed from Douglas-fir mother trees at Gadow was used for establishing new plantations (Adolph 1936, 1949).

Foremost among the advocates of Douglas-fir was J. Booth, who worked for the introduction of the species with the zeal of a crusader (1877, 1880, 1882, 1890, 1896, 1903, 1904, 1907a,b) and later Carl Alwin Schenck (1928, 1939). But not everybody shared that enthusiasm for introducing Douglas-fir. Reuss (1885) cautioned that a valid judgement of the species' merits in Germany would be possible only after 100 to 150 years of experience. Boden (1902) argued that Douglas-fir was actually inferior to native European conifers, typical of an opinion apparently held by a few practicing foresters in Germany at that time. However, few seem to have gone as far as a "Forstmeister" who purposely left Douglas-fir raised by his predecessor in the nursery beds, and after a few years, simply disposed of the young trees as too old for transplanting (Mayr 1907).

Planting of Douglas-fir declined sharply from 1914–1924 because World War I, and the ensuing period of monetary instability in Germany interrupted the import of seeds from North America. A further setback to cultivating Douglas-fir occurred when the rapid spread of the Swiss needle cast pathogen (*Phaeocryptopus gaeumannii*) assumed epidemic proportions in the late 1930s. As a result, planting of Douglas-fir was discouraged or outright prohibited, as in Württemberg in 1940 (Merkle 1951). Increasing knowledge of the biology of the fungus showed the conditions under which Douglas-fir could be grown without excessive risks, and Douglas-fir planting was resumed in the 1950s on a scale larger than before.

The Federal Republic of Germany had about 6,000 ha of Douglas-fir in 1950 and, based on Knell's (1960) estimate of an annual rate of increase of 1,250 ha per year, had about 31,000 ha stocked with the species by 1970. In 1987, the Federal Republic of Germany, (excluding the German Democratic Republic, had about 80,000 ha of Douglas-fir. Forest planning programs allotted to Douglas-fir 10% to 20% of the total forested area in the Federal Republic of Germany.

Statistics on Douglas-fir covering all of the former German Democratic Republic (GDR) have not been published. According to a letter of August 10, 1970 by, Landforstmeister Vonhof, Douglas-fir occupied between 10,000 and 14,000 ha, or about 0.5% of the total forest area of the GDR, at that time. Apparently, the area stocked with Douglas-fir did not increase substantially in subsequent years. Nearly 20 years later, Braun and Weissleder (1986) pointed out that the goal was to increase the area occupied by Douglas-fir in the lowlands of the GDR from less than 1% to 7.6%, and, in the highlands, from 0.16% to about 3%. Based on the above data, the assumption that the area of Douglas-fir in 1990 approached 100,000 ha in the united Germany seems justified.

Nearly all of the Douglas-fir in Germany belongs to the coastal variety of the species. Stands established in the last quarter of the 19th century with seed of the variety *menziesii* showed exceptional growth, and prompted repeated attempts in the second half of the 20th century to trace the origin of these early seed imports. All such efforts remained unsuccessful, for two reasons: (1) designation of seed origin was not customary when seed was shipped and (2) records that may have provided relevant information are long lost.

Seed of the variety *glauca* came first to Germany between 1891 and 1895 (Heyder 1986). Its origin is also unknown. Seed from interior British Columbia, designated as variety *caesia* in Germany, was imported regularly from 1902 to 1912 (Fürstenberg 1923). The generally poor growth of the inland form of Douglas-fir, and its susceptibility to *Rhabdocline pseudotsugae* and *Phaeocryptopus gaeumannii* soon discouraged further cultivation of the interior variety. A directive issued by the Bavarian Forest Service in 1932 led to the systematic removal of trees of the interior variety in existing stands (Foerst 1980).

A recommendation was made again in 1950 to eliminate all stands of interior Douglas-fir by cutting them as soon as they start to flower (Schippel 1950). The experience with interior Douglas-fir, however, has not been negative everywhere. Hartig (1997) assessed the performance of coastal and interior Douglas-fir in three stands in the Saxon Ore Mountains (Sächsische Erzgebirge). These stands had been established in 1905, 1909, and 1936, with var. *menziesii* and var. *glauca* planting stock. Trees that belonged to var. *menziesii* had succumbed to frost injury soon after planting, and those that belonged to the southern subgroup of var. *glauca* died after infection with needle cast fungi. By contrast, growth of the trees that belonged to the northern subgroup of var. *glauca* was equal or better than that of Norway spruce, and their tolerance of SO_2 emissions was far superior to that of spruce. Cone crops of these Douglas-firs provided enough seed to permit establishing several small plantations totaling about 25 ha from 1960 to 1984. This second generation progeny grew vigorously and showed resistance to frost and SO_2 injury.

Growth of Douglas-fir, with mean annual increment (m.a.i.) of 100 years as the criterion, decreases from the south to the north, and from the west to the east of Germany (Jahn 1959). The best growth is in the Black Forest region of southwestern Germany and the poorest growth is in the diluvial plains of northeastern Germany. But even where Douglas-fir is doing poorly, its growth is often better than that of native species on the same site.

The Netherlands

The indigenous forests of the Netherlands are mixtures of oak (*Quercus robur*) and birch (*Betula* spp.) and, on the better sites, oak and hornbeam. The financial yield from the native forest is low, and thus considerable efforts have been made to obtain higher returns by introducing conifers (Van Soest 1956). Of the exotic conifers used in Dutch silviculture, Douglas-fir has long been considered the most important.

One of the earliest plantings of Douglas-fir in the Netherlands dates to 1848, when J.H. Schober of Amsterdam established a plantation of exotics that included Douglas-fir on dune land unsuitable for agricultural purposes. Booth (1907a) cites an article in the November 6, 1895 issue of Garden and Forest, which indicated that the largest Douglas-fir in the 47 years since planting had reached a height of 18.5 m and a dbh of 49 cm, a remarkable performance on poor dune sand. Hacke-Oudemans and Oudemans (1955) attempted to trace the origin of Douglas-firs planted before 1870. They concluded that these trees apparently came from three different sources. Some were progeny of the original David Douglas trees in Scotland, but others were raised from seed obtained from Canada. A document in the Gelderland Archives states "Through Mr. Eduard Hamp of Victoria, British Columbia, seed has been shipped to the Dutch Government from Douglas-firs 300 feet tall and over 9 feet in diameter." The seed from which the trees of the Schober plantation were raised stemmed from another but unknown location in northwestern America. The oldest, still existing Douglas-firs, planted in 1857 (Veen 1951) are in the park of the royal palace "Het Loo." The tree had been used in plantations, but with varying degrees of success.

In 1899, the Dutch "Heidemaatschappij" (society for the reclamation of uncultivated land) instituted the "Committee for the Study of Exotic Coniferous Trees." To learn more about the potential of Douglas-fir for Dutch forestry, the committee commissioned a comprehensive study of Douglas-fir in the Netherlands that covered 29 stands ranging in age from 19 to 67 years. Results of the investigation (De Hoogh 1924) led to the conclusion that Douglas-fir would be of considerable advantage to Dutch silviculture, but that more knowledge of the species was needed, especially about the question of provenance. Probably on the basis of that report, a Douglas-fir provenance study was begun in Holland as early as 1923.

The area occupied by Douglas-fir in Dutch forests remained fairly small until the 1940s. At the end of World War II, several hundred hectares were stocked with Douglas-fir (Fovernied 1946). Five years later, Veen (1951) estimated that Douglas-fir occupied about 4,000 ha. The share of the species increased between 1939 and 1959 to nearly 30% of the plantations in the 1- to 40-year age classes (Van Soest 1959). The 1969 census lumped *Pseudotsuga* and

Larix together, and listed the area occupied as 32,000 ha. The area was about evenly divided between the two species (Wolterson, personal communication).

Results of the IUFRO Douglas-fir provenance study, begun in 1967 (Kriek 1974), will help in the selection of provenances best suited to growing conditions in the Netherlands. Of a total forested area of 342,000 ha in the country, some 18,399 ha were stocked in 1996 with Douglas-fir.

Belgium

The planting of 50 seedlings of Douglas-fir in 1872 on the estate of Count Visart at Sibret near Bastogne in the Ardennes (Visart and Bommer 1909) was probably the first introduction of the species into Belgium. The results were so encouraging that Count Visart planted another 30,000 Douglas-firs between 1878 and 1909. The interior variety was also tested at Sibret but grew very poorly. Unfortunately, the Douglas-firs of Sibret were destroyed in World War I (Hickel 1922). Another early introduction is a grove of Douglas-firs planted about 1880 on a private estate in Antwerp Province (Geelhand 1954). The species was not widely planted during the next 50 years, however. The age-class distribution of Douglas-fir stands in Belgium, listed in the 1958 general census of Belgian forests, indicated that Douglas-fir occupied about 200 ha in 1930 (Ministère de l'Agriculture 1958). By 1950, the area covered by Douglas-fir had increased to about 1,500 ha (Gathy 1956) and, in the next 10 years, doubled to nearly 3,100 ha.[12] The area stocked with Douglas-fir continued to grow, and in 1970, had attained 7,200 ha, amounting to 1.2% of the total forested area in Belgium (Nanson 1978). According to an estimate by Nanson,[13] the species currently occupies between 10,000 and 15,000 ha.

Climate in all parts of Belgium, from the coast to the high plateaus of the Ardennes, permits growth of Douglas-fir. The species grows best on soils with good drainage, such as the "sols bruns acides."[14] The Ardennes offer the best conditions for cultivation of Douglas-fir (Galoux 1952). Rates of failure used to be rather high in plantations above 500 m (1,640 feet) elevation (Delvaux 1964). But that is no longer the case because the use of more suitable provenances has eliminated the problem.[15]

Only the variety *menziesii* is suitable for planting in Belgian forests. Washington provenances from the region between Darrington and Hoquiam are best for planting in Belgium (Nanson 1978). Today, Belgian foresters consider Douglas-fir to be the most promising species for timber production in Belgium, which is understandable in view of its performance. A stand at Mésy (Ardennes) produced 1,297 m^3/ha that includes volume removed by thinning, and a mai of 23 m^3/ha (Poncelet 1963). These values rank among the highest documented. The growth rates of the species compare very favorably with those of other productive species. At the end of the rotation, which varies from 60 to 80 years, production of Douglas-fir stands varies between 12 and 24 m^3/ha/year depending on provenance and site quality. To put that in proper perspective, average production of Belgian forests amounts to about 5 m^3/ha/year, while that of Norway spruce, the most profitable species in the past, averages 12 to 13 m^3/ha/year (Nanson 1978).

The trend toward rising importance of Douglas-fir in Belgian forestry continues. That is reflected by the fact that Douglas-fir represents 20 to 25% of the species utilized in the current annual plantation establishment in Belgium ranging from 5,000 to 10,000 ha.

Luxembourg

Douglas-fir was introduced to Luxembourg in 1850, when it was planted at the "Jardin Linden" in Limpertsberg (Modert 1965). A tree planted in 1865 in the inner courtyard of Meysemburg castle was, in 1965, the oldest existing Douglas-fir in Luxembourg. At that time, the tree was 32 m high and had a dbh of 29 cm. Several small stands of Douglas-fir established in subsequent years near Meysemburg were cut during World War II, and no records exist about their performance. A Douglas-fir plantation from the year 1883 in the communal forest of Grevenmacher

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[12] J. Delvaux, Station de Recherches des Eaux et Forêts, Groenendaal, Belgium, letter of 11 May 1970.

[13] A. Nanson, Station de Recherches Forestieres, Gembloux, Belgium, letter of 22 July, 1993.

[14] Corresponds approximately to inceptisols.

[15] Nanson, Station de Recherches Forestires, Gembloux, Belgium, letter of 22 July 1993.

was the oldest existing stand in 1965. It was a remnant of a much larger stand, which was so heavily damaged during World War II that a large portion of it had to be cut (Decker 1965).

The state acquired an abandoned farm in 1902 and began experimental planting of exotic conifers, including both coastal and interior Douglas-fir (Modert 1965). The Douglas-fir seed was obtained from the firm of J. Booth in Hamburg, Germany. Data are not available on the area planted to Douglas-fir in the following years; all that remains is a statement that World War I caused a reduction in planting of the species and that planting ceased completely in the 1930s (Decker 1965).

Interest in the species was apparently renewed after World War II. Because records on origin and performance of Douglas-fir in Luxembourg were nonexistent, Decker (1965) made an inventory, and took growth measurements of all the Douglas-fir stands older than 30 years (Figure 3.2) in Luxembourg. He concluded that Douglas-fir is probably the most desirable exotic species for cultivation in Luxembourg. Particularly on south and southwest exposures, the species grows better than Norway spruce. Although the seed origin of the stands inventoried by Decker is unknown, he presumed that coastal provenances from western Washington are probably best for use in Luxembourg. The area stocked with Douglas-fir in 1991 amounted to 1,674 ha, according to Edmond Lies, Directeur des Eaux et Forêts of the Grand Duchy of Luxembourg, as cited by De Champs (1997).

France

Two dates appear in the literature for the introduction of Douglas-fir to France. The statement of Fourchy (1954) that the species was brought to France in 1827 is questionable because no records are known of distribution of the original Douglas seed by the Royal Horticultural Society to someone in France. More likely in accordance with the facts is the account by E. A. Carrière, cited by Hickel (1922), that Monsieur Gautier-Lachase made the first planting of Douglas-fir in 1842 at a place called Pré de l'Aulne (alder meadow) in the vicinity of Louvigné-le Désert (Dept. Ille-et-Vilaine) in the Bretagne. Apparently, he planted several trees because Hickel mentioned that the last of those planted in 1842 was still alive in 1922.

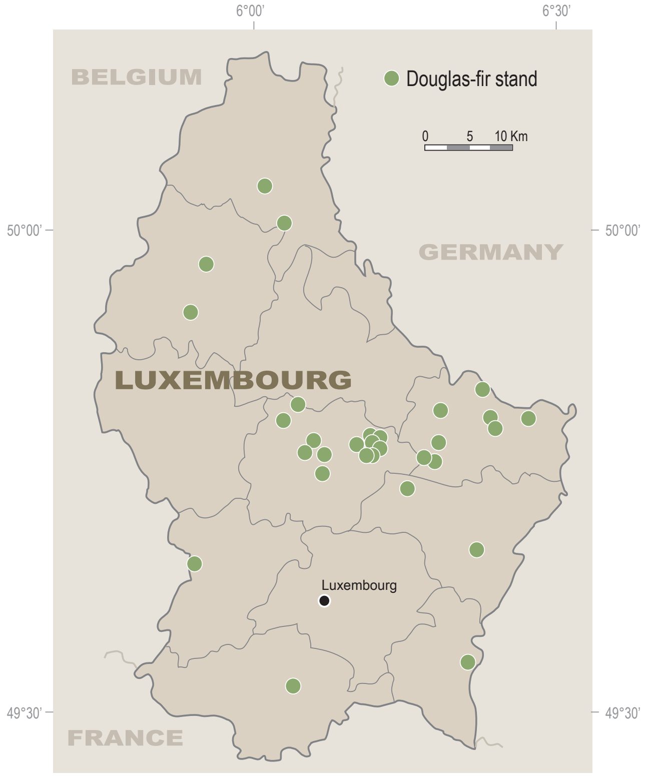

Figure 3.2 Douglas-fir stands in Luxembourg (from Decker 1965).

In 1844, shortly after that first planting, the Marquis de Vibraye introduced Douglas-fir into his park at Cheverny (Dept. Loir-et-Cher). Carrière reported that these trees have produced viable seed since 1851. Another of these early introductions is a group of 30 Douglas-firs planted between 1842 and 1844 at Bord, the property of the Vicomtesse de Sèze, near the village of St. Priest-Taurion (Dept. Haut-Vienne). Slightly more recent are the plantations in the Park of Harcourt (Dept. Eure), belonging to the National Academy of Agriculture, made from 1852 on by Monsieur Pépin.

David Cannon began to plant Douglas-fir about 1875 at his estate at Vaux not far from Salbris in the Sologne. He was so impressed with the performance of the species that he wrote in 1909, "I believe that Douglas-fir is by now the best acclimatized of exotic conifers everywhere it has been planted."[16]

At first, plantings were made mostly in parks and along highways. Only since 1890 has Douglas-fir been considered for planting in forests. These early

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[16] Translated from the original: *L'Abies Douglasii* est, jusqu'à présent et partout, je crois, ou il a été planté, le triomphe de l'acclimatation des conifères exotiques" (Cannon 1909).

forest plantations are mainly in the Beaujolais.[17] Although small plantations of Douglas-fir existed in at least some 30 of France's 97 departments by 1920, the total area occupied by the species had remained small because of the lack of interest in Douglas-fir by the country's Forest Administration (Hickel 1922).

World War I, during which about 650,000 ha of French forests were destroyed, temporarily interrupted reforestation activities. Several hundred kilograms of Douglas-fir seed shipped to France immediately after the war provided some of the planting stock for rehabilitation of these forest lands (Podhorsky 1927). These seed shipments may well have consisted of unsuitable provenances because few Douglas-firs are present in the stands planted right after World War I.[18] Notwithstanding seed problems, the area planted to Douglas-fir gradually increased between the two world wars, especially in the western part of the Massif Central (Limousin, Plateau des Millevaches), but also in other parts of France. By 1937, the area occupied by the species had grown to about 4,000 ha. A detailed account of the locations where these plantations had been established and their size is given by Sornay (1937).

Establishment of the Fonds Forestier National (FFN) resulted in the availability of large funds for reforestation, a development that was instrumental in bringing about the rapid growth of the area stocked with Douglas-fir. By 1956, the area had increased to more than 10,000 ha (Pardé 1956), and by 1970, was estimated to have risen to between 100,000 and 150,000 ha. Data collected by the French National Forest Inventory showed 220,000 ha of Douglas-fir stands (Bouchon 1984). In 1993, the area stocked with Douglas-fir had grown to 333,000 ha, an area larger than anywhere else in Europe (De Champs 1997a). The greatest concentration of the species is in the Massif Central including the Morvan. Considerable areas are also occupied by Douglas-fir in the northeast and northwest of the country, but the species is sparsely represented in the southeast and southwest of France (Figure 3.3). Of the lands stocked with Douglas-fir, 82% are private and only 18% public.

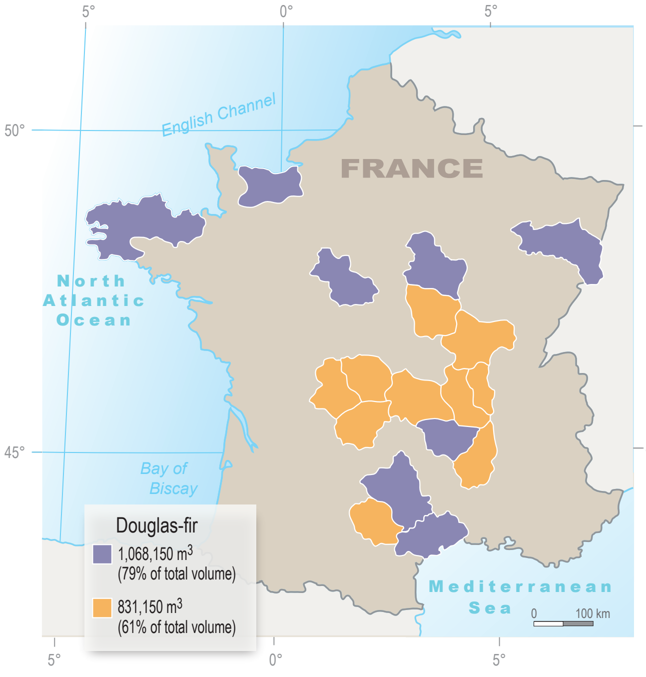

Figure 3.3 Standing volume (m^3) of Douglas-fir in France (from De Champs 1997a).

About 312,000 ha—that is, nearly 94% of the total area stocked with Douglas-fir in 1993, contained stands younger than 35 years. That age-class distribution reflects the annual rate of about 10,000 ha for planting of Douglas-fir from 1960 to 1980. That rate has markedly decreased since 1980, as did the reforestation efforts supported by the F.F.N. But even with the reduction of the area annually planted to conifers, the proportion of Douglas-fir in coniferous plantations established since 1980 remained nearly constant, with an average of about 30% (De Champs 1997b), until the end of the millenium.

The first Douglas-fir plantations financed by the FFN were made with seed purchased from American firms, but practically without control of origin. These imports of seed of uncontrolled origin continued until 1966, the year the EEC issued directives aimed at controlling the origin of imported seed. Establishment of 90 ha of Douglas-fir seed orchards between 1974 and 1990 will provide an important source of seed of known origin.

Douglas-fir finds its best development in regions with a warm Atlantic climate as in the Bretagne, and at low and medium elevations up to 800 m in the west and southwest of the Massif Central. But it also

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[17] Letter from P. Bouvarel, Centre de Recherches INRA de Nancy, dated May 5, 1970.

[18] Letter from J.-Ch. Bastien, INRA Centre des Recherches d'Orléans of 7 August 1992.

performs well in other parts of the country, as for example in the Cevennes and the Beaujolais. The species is now planted throughout France except for the Mediterranean region in the south, and the Massif Landais in the southwest. Only the variety *menziesii* is considered suitable for planting in France.

In the words of J.-Ch. Bastien,[19] "The reason for the success of Douglas-fir in France are: its rapid and sustained growth, its high production (13 m^3/ha/yr), its plasticity, the absence of parasites or serious pests, and the mechanical qualities of its wood little changed by fast growth. Its only fault is its great attractivness to roe deer."

Switzerland

In 1861, the Swiss Forestry Association formed the "Kommission für Anbauversuche mit exotischen Holzarten" (commission for trials with exotic tree species) (Charbon 1991). The first plantings of Douglas-fir in Switzerland were perhaps made shortly after the commission was established. In any event, its seed inventory of 1865 lists Douglas-fir under the name *Abies Douglasii* Lindl. (Schwager 1979). Based on the age of the oldest Douglas-fir in the country, Hans Burger (undated, cited by Schwager 1979, p. 91) presumed that the species was introduced to Switzerland between 1860 and 1870.

The oldest forest plantings of Douglas-fir on record were made on privately owned land in the period 1874-1876 near Küssnacht. They were mixed plantations of Douglas-fir, eastern white pine and Norway spruce. A pure stand of Douglas-fir (0.53 ha) was established by the same owner in the spring of 1888 with 2-2 seedlings (Coaz 1897). They had been grown from seed of unknown provenance purchased in Erfurt, Germany (Krutina 1927). That stand, situated at 630 m elevation, grew so well that Dr. Coaz of Bern made special reference to it in a 1905 speech before the German Dendrological Society. Two small plantations of Douglas-fir were established in the City Forest of Biel in 1886 and 1893 with 2–2 and 2–1 stock, respectively. In 1926, Badoux reported on the development of these three stands, and pointed out that their volume production was superior to that of Norway spruce on comparable sites. The two oldest Douglas-fir plantations in the French part of Switzerland were established 1886 near Lausanne (Charbon 1991). Interim reports on their development already appeared at the beginning of the 20th century (Curchod 1901, Buchet 1913).

Trees in all these plantations belong to the variety *menziesii* but their provenance is unknown. In an effort to learn more about the seed origin of early plantations, Berney (1972) used regressions of relative DNA content of embryo cells on latitude to analyse samples from a stand at Boesingen near Biel. On the basis of that analysis, he concluded that the Boesingen stand came from parents situated between lat 44° N and 47° N in the coast ranges of Oregon and Washington.

Although Douglas-fir appeared to hold much promise for use in Swiss silviculture, planting of the species was greatly reduced from about 1930 to the early 1970s because of concerns about the presence of *Rhabdocline pseudotsugae* and *Phaeocryptopus gaeumannii*, first noticed in 1914 and 1925, respectively. In spite of that setback, coastal Douglas-fir has become the most important introduced tree species in the country. *Pseudotsuga* represented 43% of exotic tree species in Swiss forests in 1986. Its role is modest, however, because estimates indicate that Douglas-fir occupies less than 0.1% of Switzerland's forested area. Notwithstanding its marginal importance, Douglas-fir has been increasingly planted by Swiss foresters since the 1970s. In 1986, nearly half of all Douglas-fir plantations were in the 1- to 20-year age class, and most of the other half were in the 60+ age classes (Bürgi and Diez 1986).

Douglas-fir plays an important silvicultural role by the conversion of coppice forests on the south side of the Alps, which is a consequence of its relatively rapid juvenile growth, its high volume increment, and the fact that Douglas-fir can be planted successfully on drier sites for which a dearth of suitable indigenous species exists (Buffi 1987).

Few Swiss studies have been concerned with the productivity of Douglas-fir and its relation to site characteristics. However, recent investigations (Diez and Bürgi 1991, Begin 1992) have shown that Douglas-fir performs well overall on the best sites and also on poorer sites. Diez and Bürgi believe that provenances from elevations 500 to 700 m in the

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[19] Ibid.

Washington Cascades are probably best suited for Switzerland. The trials at Copera in the Ticino show general superiority by Washington over Oregon provenances (Buffi 1987).

Austria

The oldest Douglas-firs on record in Austria are in the City Forest of Bregenz, Vorarlberg. They were planted in 1876 in an abandoned nursery during a training session for forest guards (Rannert 1959a). Soon thereafter, the Austrian Forest Experiment Station, largely through the initiative of Adolf Cieslar, began to undertake systematic trials with foreign tree species, including Douglas-fir. Cieslar obtained Douglas-fir seed directly from G. B. Sudworth of the Forestry Department, U.S. Department of Agriculture (Rannert 1979), and later from commercial sources. The origin of the seed is unknown, except for the fact that shipments included seed belonging to both the coastal and interior varieties.

Cieslar subscribed to the idea that establishing many small plantations distributed throughout the country would provide more useful information than a few large plantations because of the diversity of the Austrian landscape. The first plantations, dating back to 1886, were concentrated in the Alps and the northwestern part of Austria. Cieslar (1898) attributed the surprisingly satisfactory growth on his trial plots to high amounts of precipitation, high relative humidity, and good soils. Douglas-fir performed well even in higher elevations of the Austrian Limestone Alps (Oesterreichische Kalkalpen), although the rate of growth was slower than at low altitudes. At the turn of the century 89 plots existed throughout the former Austrian-Hungarian Monarchy encompassing elevations from 120 m near the Adriatic Sea to over 1,600 m in the Tyrolian Alps (Cieslar 1901). The report by Zederbauer (1919) on the Austrian trials with exotic trees shows that in 1916, a total of 142,497 Douglas-firs had been planted on 134 plots.

The end of World War I resulted in the dissolution of the Austro-Hungarian Empire. Thus, only 43 Douglas-fir plots remained in the Republic of Austria (Rannert 1979). But with one notable exception, a one-hectare stand in the Reindlmühl District of the Forest Administration Ort near Gmunden, recordkeeping of the plots was discontinued and many were subsequently lost. Planting of Douglas-fir almost ceased until the 1950s, although Cieslar (1920) had argued that enough evidence existed to conclude that the climatic conditions of Austria would permit satisfactory growth of the species. Another advocate of Douglas-fir was Schwarz (1932a,b) who, based on a study of site conditions within the range of coastal Douglas-fir, distinguished three climatic growth regions for the cultivation of Douglas-fir in Austria: the Vorarlberg region, Ober- und Niederösterreich region, and the Burgenland-Steiermark region. He emphasized that only the coastal variety should be considered for planting in Austria.

Renewed interest in Douglas-fir began with the attempt by the Austrian Forest Experiment Station in 1956 to salvage what was left of the plots with foreign tree species established by Cieslar. In a survey of exotic trees that covered all of Austria over a period of 14 years (Rannert 1958, 1959a, 1959b, 1960; Minelli 1967; Rannert 1973, 1979) the data showed that Douglas-fir occupied 108 ha in 266 localities. The largest concentration of Douglas-fir (52 ha) was in Niederösterreich. The majority of the trees (37%) were in the age class 1–20, and those in the age classes 61–80 and 81–100 amounted to only 6%. Information provided by the survey demonstrated that coastal Douglas-fir shows excellent growth when planted on suitable sites. That was demonstrated by long-term growth trials with coastal Douglas-fir with unknown provenances in eastern and north-central Austria. The mean annual increment at age 70 was 18.5 m^3/ha (Kristöfel 2003). The interior variety, on the other hand, performed poorly and is unlikely to be planted in the future. An extensive program of provenance trials (Günzl 1987) that began at the end of the 1970s was designed to provide a basis for a much wider use of Douglas-fir in the forests of Austria than in the past.

Northern Europe

Denmark

Douglas-fir has been planted in Danish parks since 1851. Trees planted in 1851 to 1863 had been imported from German nurseries (Holm 1940). Introduction of the species into Danish forests began in 1866. The area stocked with Douglas-fir amounted to

3.7 ha in 1882. That area grew to 10.1 ha by 1892, to 27.1 ha by 1902, to 72.2 ha by 1912, and to 154.5 ha by 1922 (Fabricius 1926). Planting in the next 25 years increased the area of Douglas-fir to 1,550 ha. Included in this figure are probably not more than 10 ha stocked with interior Douglas-fir (Thulin 1949). Madsen[20] estimated that the area occupied by the species has remained about at the 1947 level. That estimate appears to be corroborated by an estimate of 20,000 m^3 for the annual cut of Douglas-fir in Denmark (Moltesen 1988).

Origin of the oldest Douglas-firs in Denmark is unknown. Trees for the 1866 plantings were obtained from Scotland and probably represented progeny of trees grown from the seed shipped in 1826 by David Douglas. Holm (1940) cited excerpts from a 1911 letter by the Danish seed dealer Johannes Rafn, in which he expresses his belief that the early Danish Douglas-fir plantations were established with seeds from stands in California and Oregon. Rafn based that belief on the fact that early seed shipments came from the firm Sonntag & Co. in San Francisco. But that assumption is open to question. Some of the seed supplied by Sonntag & Co. may also have come from Washington. Rafn himself made contact in 1902 with a seed dealer in Washington from whom he purchased 100 kg seed in 1902, 150 kg in 1903, 250 kg in 1905, 500 kg in 1906, and 800 kg in 1909. Thus, many of the Douglas-fir plantations established in the early part of the 20th century in Denmark most likely represent Washington provenances.

Performance of Douglas-fir in the early plantations was so satisfactory that Oppermann wrote in 1922, "About the year 1900 cultivation of the green Douglas-fir was as yet in its experimental stage. Since then the species has attained a secure position in our forestry and the reason for enlarging its cultivation are strong." That view was challenged by the appearance of *Phaeocryptopus gaeumannii* in Douglas-fir stands throughout the country (Buchwald 1940). Larsen (1940), however, considered pessimistic predictions about the future of Douglas-fir in Denmark to be unjustified. He contended that selecting of unsuitable sites and improper silvicultural practices were probably the primary causes for the spread of the disease. Later developments proved him to be correct. Although Douglas-fir has found serious competitors in Sitka spruce and grand fir, it seems to have the edge in the driest parts of Denmark, the Jutland heath region, with annual precipitation of 500-550 mm (Henrickson 1956, Oksbjerg 1965).

Norway

Single Douglas-firs have been planted in western Norway since about 1870 (Nedkvitne 1964). Heiberg (1978) listed location, height, and diameter of 27 solitaires planted from 1879 to 1925. The tallest, planted in 1883, was 40 m high. The tree with the largest dbh, 118 cm, had been planted about 1880.

Plantations have been established since the turn of the century, but data on the area stocked with Douglas-fir are not available. Børtnes (1970) gave the following figures on numbers of Douglas-fir planted in western Norway: before 1928, 34,030; 1928-1939, 130,080; 1940-1949, 76,180; 1950-59, 20,000; 1960-69, 260,000. Heiberg (1978) examined 102 plantations in 1976 and 1978, ranging in age from 12 to 80 years, throughout Norway south of lat 63° N (Figure 3.4). Most of the plantations were small and of unknown provenance. Many were in steep and remote country

Figure 3.4 Locations of Douglas-fir stands in Norway (from Heiberg 1978).

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[20] Letter dated 4 November 1993 from S.F. Madsen, Danish Forest and Landscape Research Institute, Lynby

and had not received any subsequent silvicultural treatment.

Successful plantations appear to belong mainly to provenances from the northern end of the coastal variety's range. The interior variety is growing too slowly in Norway to be of value as a forest tree (Hagem 1931). The same conclusion was reached by Robak (1967) after more than 30 years of nursery studies in western Norway. He recommended against the use of provenances from interior British Columbia because of their slow growth and great susceptibility to *Rhabdocline pseudotsugae* and *Phaeocryptopus gaeumannii* after outplanting in the field. Moreover, in nurseries where frost heaving is a problem, the small size of seedlings from interior British Columbia provenances makes them particularly prone to damage. Twenty-year results of a trial by the Norwegian Forest Research Institute with provenances from British Columbia showed best growth for those from coastal sources, such as Babine Range, and poorest performance for those from interior sources, such as Prince George (Heiberg 1978).

In general, Douglas-fir has performed best in the southern coastal region and the western coastal region northward to about lat 61° N. Heiberg believed failures have been more common than successes with Douglas-fir, and that the principal cause of failure was absence of suitable strains of mycorrhizae, rather than frost damage or diseases. Both *Phaeocryptopus gaeumannii* and *Rhabdocline pseudotsugae*, however, have caused severe damage to plantations (Nedkvitne 1964). A statement made by Heiberg in 1975 is probably still valid: "Even though Douglas-fir seems to be a promising tree in the successful plantations, it has been capricious in our trials, and its introduction is still in the trial and error stage. Several more years and plantations are needed before we may be able to decide if it has a future as a commercial tree at these latitudes."

Sweden

The first Douglas-firs were planted in Sweden about the middle of the 19th century. The first actual stand of Douglas-fir was established in 1880 on the Rössjöholms estate (Refn 1965). An inventory of Douglas-fir in Sweden by Lemoine and Wirten (1988) shows that small stands of the species had been established throughout the next 100 years. The plantations range from Jämtland in the north to Skåne in the south (Figure 3.5). The northernmost plantations, Muråsen and Avardo, are at Frostviken, lat 64°30′ N. The inventory lists 96 stands covering 99.85 ha. The total area occupied by the species, however, may be somewhat larger. Lemoine and Wirten cautioned that their inventory should not be considered as a complete catalogue because additional stands are likely to be discovered on private forest lands.

Figure 3.5 Douglas-fir stands in Sweden, totaling 100 ha (from La Moine and Wirten 1988).

Lemoine and Wirten established permanent sample plots in 13 of the 96 stands and control plots in nearby Norway spruce stands. Stands ranged in age from 10 to 60 years when plots were established.

After remeasurement of the plots in 1992, Eriksson and Widerlund (1992) concluded that the results did not permit a generally valid comparison between volume production of Douglas-fir and Norway spruce. Some of the Douglas-fir plantations have shown remarkable growth with a total production of slightly more than 650 m^3/ha of stemwood in 60 years.

Sweden's climate severely limits choice of provenances suitable for that country. Experience has shown that provenances from the major part of the range of the variety *menziesii* will not survive, or they grow very poorly. Some of the old stands that seem to be well adapted to growing conditions in central and southern Sweden originate from southern British Columbia seed sources, or are progeny from Douglas-fir grown in Denmark (Martinsson 1990). Performance of these old stands and initial results from recent provenance trials (Martinsson and Kollenmark 1993) suggest that provenances from the northern part of the range of Douglas-fir are those that offer the most promise for successful cultivation in Sweden.

Finland

The oldest plantation of Douglas-fir in Finland was established in 1905 in the Mustila Arboretum. The seed source of trees in that plantation is indicated as Quesnel, British Columbia. Subsequently, trial plantations of Douglas-fir were established at Solböle (1924, 1926, 1927, 1937). Ruotsynkylä (1924, 1927, 1942), Aulanko (1927) and Punkaharja (1926, 1927, 1938). The locations of these trial plantations between lat 60° N and 62° N are several degrees above the northern limit of the natural range of the species (Figure 3.6).

All surviving trees in 1980 belonged to provenances from interior British Columbia and Alberta, except for one from Washington (Lähde et al. 1984). Early growth of Douglas-fir appears to have been rather poor. In 1956, Heikinheimo published a list of Douglas-fir stands in Finland, and wrote in a later publication (Heikinheimo 1957) that growth of these stands was not very promising. Most of these interior provenances are clearly maladapted to the semi-maritime climate of Finland and tend to become stagnant at ages of more than 30 years (Tigerstedt 1990).

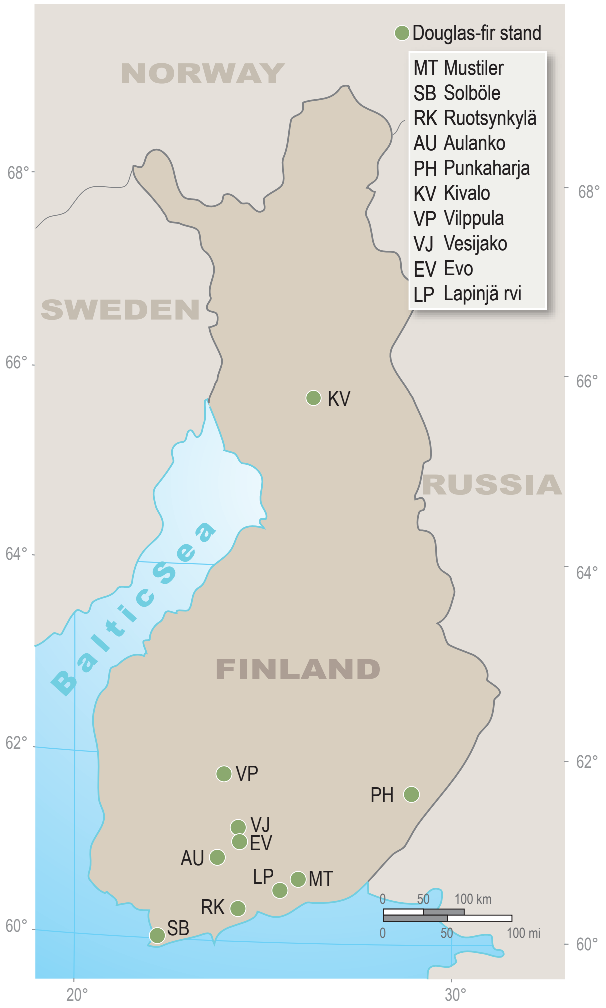

Figure 3.6 Douglas-fir stands in Finland (from Lähde et al. 1984).

The survey of Finnish Douglas-fir stands by Lähde et al. (1984) indicated that volume production by age 55 years may approach that of the native *Pinus sylvestris* and *Picea abies* on good sites, but the quality of Douglas-fir is poorer. Crooked, bowed and leaning stems are common in all Douglas-fir stands. At age 75, the stand at Mustila had 780 m^3/ha, with a dominant height of 28 m, and a dominant dbh of 38 cm. At an early age, the second northernmost of the surviving provenances was already considered to be the best (Cajander 1926, Ilvessalo 1926). Mean volume production of the 5 most productive stands ranging in age from 50 to 55 years was 400 m^3/ha.

In Finland, Douglas-fir suffers from frost and *Rhabdocline pseudotsugae*. Lähde et al. (1984) concluded Douglas-fir "is a species which has received much interest but recent measurements indicate that Douglas-fir cannot be recommended for widescale commercial use in Finland."

Mediterranean Europe

Portugal

A single Douglas-fir planted on the slope of the Castelo dos Mouros, another next to the Fonte dos Passarinhos, and a third tree of a *P. menziesii* var. *glauca*, mark the introduction of the species into Portugal (Gomes and Raposo 1939). The oldest of these trees, the one near the Castelo dos Mouros, was planted sometime between 1844 and 1849. As to the origin of the Castelo dos Mouros and Fonte dos Passarinhos trees, Gomes and Raposo suggested that they were progeny of trees raised in Scotland from the seed shipped by David Douglas. Other early introductions are Douglas-firs planted 1871 in the Forest of Buçaco (Peres 1964), and several trees dating to about 1876 in the Pedras Salgades Park (Coutinho 1936, Gaussen 1944).

The first forest plantations of Douglas-fir were established by the Forest Service in the Serra da Estrella in 1904 (Freitas 1989), and in the Serra do Gerês in 1906 (Coutinho 1936). But in general, little use was made of Douglas-fir until the last quarter of the 20th century, except for individual trees planted in parks and gardens, and small plantations established by the Portuguese Forest Service (Carvalho 1965).

In 1976, the area of Douglas-fir plantations was less than 300 ha (Goes 1991). A few large plantations were established in the late 1970s and early 1980s at Bornes and Malcata, increasing the area of Douglas-fir to 4,200 ha.

Through the "Fundo de Fomento Florestal (Forest Development Fund) a large afforestation program was initiated at the beginning of the 1970s. For that program various exotic conifers were used, notably Douglas-fir (Luis 1989). As a result of that program, Douglas-fir occupied about 7,000 ha in 1989. Forecasts were that the area planted to Douglas-fir would have increased as a result of the "Programa de Acçáo Forestal" (forest action Program) to more than 15,000 ha by 1997 (Rego and Alvares 1988).

The fast growth of Douglas-fir, its ability to grow under a wide variety of conditions, and to regenerate naturally, has shown its great potential for planting in the mountains of central and northern Portugal (Goes 1991, Louro and Cabrita 1989, Luis 1989, Diniz 1969). Although that potential is recognized, the species represents only about 0.1% of the country's total forest cover. Fontes et al. (2003) investigated the environmental factors affecting Douglas-fir productivity and, based on these factors, modeled Douglas-fir productivity to provide information for future afforestation projects. They estimated that an area of 250,000 ha exists where Douglas-fir trees could be planted and will exceed 17 m dominant height at age 30 years. This would correspond to 8% of the existing Portuguese forest area. The best sites for Douglas-fir growth are those in the north coastal to central regions at altitudes between 500 m and 1,000 m, and with a moisture deficit (precipitation minus evapotranspiration) above 1,000 mm. Areas with acceptable sites for Douglas-fir growth are in the north and center of Portugal at 700 to 1,000 m elevation, and with a moisture deficit above 400 mm.

Spain

Single Douglas-firs planted in the Province of Vizcaya in the Basque country shortly before and after the turn of the century probably represent the first introductions of the species to Spain. Pellon (1962) refers to a 74-year-old Douglas-fir with a height of 45 m and a dbh of 72 cm, and in 1966, to another solitary Douglas-fir tree that had attained a height of more than 40 m at age 60. He noted, however, that forest plantations dating to the turn of the century do not exist in Vizcaya.

The oldest plantations of Douglas-fir appear to be in the province of Gerona in northeastern Catalonia on three private ownerships. One of these plantations, on the Serrat estate, dates to 1926. Plantations on the Mas-Joan Garolera estates were established in the 1950s. Arenas (1962), who gave a detailed account of the Douglas-fir plantations on these estates, estimated that yields of 500 to 600 m^3/ha may be expected with rotations of 45 to 60 years on sites of medium fertility.

Overcutting and forest fires have led to the disappearance of much of the native forest, degradation of sites, and development of scrublands in the mountains of northern Spain (Arenas 1962). Douglas-fir is considered to be a promising species for rehabilitating such sites, as well as for abandoned agricultural lands at sites above 600 m that are unsuitable for the economically more profitable plantations of

Monterey pine and *Eucalyptus globulus*. Estimates of the extent of land available for planting Douglas-fir range from 300,000 ha (García,[21] Vega 1990) to 550,000 ha.[22]

The early trials resulted in far less satisfactory results with the interior than the coastal variety of Douglas-fir (Arenas 1962). Provenance trials with coastal Douglas-fir initiated in 1978 are intended to identify seed sources best suited for use in Spain (Vega 1990).

About 5,000 ha of Douglas-fir plantations existed in Spain in 1993 distributed through Catalonia, Rioja, Navarra, the Basque country, and Galicia.[23] By contrast, De Champs (1997), based on information received in 1993 from G. Vega of the Centro de Investigaciones Forestales at Louridan Pontevedra, puts the acreage for Douglas-fir in Spain far higher than 5,000 ha. According to Vega, the area covered by Douglas-fir is estimated to be 30,000 ha of which 21,000 ha are in public and 9,000 ha in private ownership. The annual area planted to Douglas-fir in the 1980s was about 800 ha. Lack of an adequate supply of seed has been an impediment to more extensive planting of the species (Vega 1990).

Italy

A single Douglas-fir planted 1858 in Tuscany in the parks of Moncioni southwest of Montevarchi, and one or two at Brolio northeast of Siena represent the earliest known introduction of the species to Italy (Bernetti 1987). The tree at Moncioni was 16 m high and had a dbh of 33 cm in 1883 at age 25 (Booth 1907). In 1918, at age 60 that tree was 26 m high with a dbh of 78 cm (Hickel 1922). The first actual plantations were established between 1885 and 1890 at Vallombrosa, followed by others at Masseto and Bivigliano near Florence (Ciancio et al. 1980).

In general, however, foresters showed little interest in Douglas-fir until the extensive work with the species by Aldo Pavari, Professor of Silviculture at Florence University. He established 98 experimental plantations of Douglas-fir in the Alps; the northern, central, and southern Apennines; and the Mediterranean region between 1922 and 1938. These trials demonstrated that a variety of sites in central and northern Italy is suitable for the species (Pavari and de Philippis 1941, Pavari 1958).

Allegri's (1962) perhaps somewhat exuberant statement, "We can claim that Douglas-fir has now victoriously found its way into Italian silviculture,"[24] apparently reflected the growing interest for the species stimulated by the results of Pavari's trials. The view, however, that Douglas-fir had a place in Italian silviculture was not universally shared. Giacobbe argued in a series of papers (1942, 1963, 1967) that the tree's liability to damage from climatic agents and disease, notably *Rhabdocline pseudotsugae* and *Phaeocryptopus gaeumannii,* would preclude it from general cultivation in Italy. Merendi (1956, 1965) disputed the case against planting of Douglas-fir and stated that the risk of disease had been exaggerated.

The view in favor of Douglas-fir has apparently prevailed because planting it has continued. The tree has proved to be particularly useful for two purposes. One is afforestation of abandoned agricultural land in mountainous regions to prevent erosion and to keep the land productive. The other is the conversion of forests of low production to higher production (Morandini 1968). Increased production is made possible by the growth rate of Douglas-fir, which enables it to outproduce both native conifers and broadleaves (Susmel 1962, Ciancio et al. 1980). For instance, Cristofolini (1968) reported mean annual increment of 11.7 m^3/ha, and current annual increment of 17.3 m^3/ha for 22-year-old Douglas-fir in Liguria. Morandini (1961) noted that on good sites in the Apennines, Douglas-fir can attain volumes of 500 m^3/ha at age 30.

The Castanetum and the Fagetum are phytoclimatic zones best suited for planting Douglas-fir with optima in the cool subzone of the Castanetum and the warm subzone of the Fagetum (Pavari 1958). Upper altitudinal limits for cultivating Douglas-fir are given by Susmel (1962), as follows: 500 m in the eastern Alps, 800 m in the central and western Alps, 1,200 m in the central Apennines, and 1,400 m in the southern Apennines.

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[21] Letter from José García Salmerón, Instituto Forestal de Investigaciones y Experiencias, Madrid, dated 15 September 1970.

[22] Letter from Dr. Ramon Elena, Instituto Forestal de Investigaciones y Experiencias, Madrid, dated 27 October 1993.

[23] Ibid.

[24] Translated from the original: "Possiamo affermare che la Douglasia e ormai entrata vittoriosamente nella selvicoltura italiana" (Allegri 1962).

Only the coastal variety of Douglas-fir is suitable for cultivation in Italy. Initial experience indicates that Oregon and northern California provenances hold the most promise, although some southern Washington provenances also perform well (Morandini 1968). The largest concentration of plantations is in the northern Apennines, especially in Tuscany, with about 4,000 ha (Bernetti 1987). Most of the stands were established between 1950 and 1970. More recently, reforestation activities declined in general. Douglas-fir is planted only on a limited scale, mainly to replace degraded silver fir (*Abies alba*) stands in the Apennines.[25]

According to statistics of the Italian Forest Service, 429 stands of Douglas-fir occupied 1,315 ha in 1963. By 1980, the area planted to Douglas-fir was estimated by Ciancio et al. (1980) to be somewhat in excess of 10,000 ha. The Italian National Forest Inventory of 1985 lumped Douglas-fir together with other exotic conifers. Thus only estimates are available, which place the area stocked with Douglas-fir still at slightly over 10,000 ha.

Croatia

Douglas-fir is important in Croatia for increases in timber yield through amelioration of degraded forests (Pavle 1967). That applies particularly to rehabilitation of degraded sites in the Karst region (Piškorić 1960).

Planting of Douglas-fir must have already taken place in about 1890 in Croatia because Klepac (1962) mentions a 70-year-old stand with a standing volume of 678 m^3/ha in the River Valley of the Gorski Kotar region. Apparently, Croatia has more Douglas-fir stands than any of the other republics of the former Yugoslavia, but actual figures for the area occupied by the species in Croatia are unavailable. Klepac (1962) pointed out that productivity in Croatian Douglas-fir stands is less than that given in British (Hummel and Christie 1953) and German (Schober 1955) yield tables. He attributed the lower productivity of Croatian Douglas-fir stands to unfortunate choice of planting sites, poor silvicultural practices, and other unspecified causes. Use of provenances suitable for Croatia (Pintarić 1967) may help to obtain higher yields from Douglas-fir.

Slovenia

The earliest plantings of Douglas-fir, in about 1890, were made when Slovenia was still part of the Austro-Hungarian Empire (Miklavzic 1951). These plantings, however, were either solitary trees or very small plantations. In 1926, Douglas-fir occupied 16 hectares. Nearly all of these were in the Maribor district with the exception of 0.3 ha in the Ljubljana district (Urbas 1926). More Douglas-fir has been planted since but mostly in mixture with Norway spruce, European silver fir and eastern white pine (Cokl 1965). Statistics on area currently occupied by the species in Slovenia are unavailable.

Greece

The 1919 planting of Douglas-fir in the arboretum of Vitina in the Peloponnesus marks its introduction to Greece. Since 1960, some trial plantations have been established with the species. A current annual increment of 15 m^3/ha between ages 16 and 20 was recorded at Pertouli in central Greece and of 17 m^3/ha at Chalkidike in eastern Greece. But, aside from these trial plantations Douglas-fir was planted only on an extremely small scale and covers probably not more than 100 ha (De Champs 1997b).

Turkey

The introduction of Douglas-fir to Turkey dates to the years after World War II. The favorable results of a few small plantations near the Black Sea coast suggested that Douglas-fir might be a valuable tree species for the country's reforestation program in that region (Simsek 1977). A comprehensive provenance trial was initiated in 1971 to identify potential seed sources suitable for Turkey.

Cyprus

A small plantation of coastal Douglas-fir has been established in a sheltered stream bed at about 762 m altitude on this island in the eastern Mediterranean Sea. The trees were healthy, but their growth had been slow (Streets 1962).

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[25] S. Nocentini, University of Florence, letter of January 17, 1994.

Eastern Europe

Czech Republic

The history of the introduction of Douglas-fir up to 1919 in the Czech Republic, made up of Bohemia and Moravia, has been described in detail by Nozicka (1963). Interest in Douglas-fir began as early as 1828 when F.G. Rietsch of Zbraslav near Prague discussed the tree in the journal "Forst- und Jagdneuigkeiten." The oldest Douglas-fir on record in the Czech Republic was planted in 1843, as a 2- or 3-year-old seedling in the American Garden of the Chudenice Arboretum in western Bohemia near Klatovy. That seedling was part of a shipment of exotic trees from the Booth Nursery in Flottbeck, Germany. Another record of an early planting is from Gross-Skall (Hruba Scala) Estate near Wartenberg. Here, two 5-year-old Douglas-firs were planted in its Bukovina Park. The two trees came from the Booth Sons Nursery in Flottbeck (Anger 1879). Hofman (1964) lists several locations where Douglas-fir presumably had been planted in the period 1850-1870, but details are lacking.

Although the earliest plantings of Douglas-fir consisted only of solitary trees, small plantations of the species in forests began to be made in the late 1860s. An inventory of Douglas-fir stands published by Hofman and Heger in 1958 indicated establishment of 36 stands from 1868 to 1878, and of 95 stands between 1878 and 1888. Planting of the species attained a first peak in the decade 1908-1918 and a second peak in the years 1928-1938. This peak was followed by a decline in planting of the tree until 1954. That year marked the beginning of renewed planting activities with Douglas-fir (Hofman 1962).

The first attempt at an inventory of Douglas-fir in what was then Czechoslovakia was made by Polansky (1934) by means of questionnaires sent to forest districts throughout the country. He recorded 24 ha of pure stands and 78 ha of stands where Douglas-fir was mixed with other species. Polansky doubted that responses to the questionnaires provided accurate figures, however, and suspected that the actual area stocked with Douglas-fir was two or three times greater than shown by returned questionnaires. The next inventory covered only stands older than 10 years by 1953 in both the Czech and Slovak parts of the country (Hofman and Heger 1958). It showed 447 stands in the Czech Republic, with an area of 120.5 ha. But even that inventory apparently failed to include all existing stands of Douglas-fir. Sika (1979), in a later inventory restricted to the Czech Republic, found that the area occupied by Douglas-fir older than 60 years (i.e., for plantations established before World War I), amounted to 245 ha. The total area stocked with Douglas-fir in 1976 was 1,990 ha. On nearly half of that area stood plantations in the 1- to 10-year age-class. Stands are small, ranging in size from 0.07 ha to about 2 ha with an average size of 0.15 ha. In 1982, plantations less than 10 years old occupied 1,125 ha, those in the 11- to 60- year age-class 774 ha, and stands in the 60+ age-classes 621 ha (Sika 1983).

More recent data on forest tree species in the Czech Republic[26] show an increase from 2,520 ha stocked with Douglas-fir to 3,800 ha at the end of 1991. Distribution by age classes had also shifted, with 990 ha in the 10-year class, 2,252 ha in the 11- to 60-year classes, and 558 ha in the 61- to 130-year age-classes. The largest concentration of Douglas-fir is in southwestern Bohemia (Figure 3.7). Standing volume of Douglas-fir in the Czech Republic in 1991 was nearly 370,000 m^3.

The first Douglas-firs planted in Bohemian forests were raised from seed purchased from C. Geyer, a forester turned seed dealer in Karlshafen on the Weser River in Germany. Afterwards, seeds were directly imported from the USA (Hofman 1962). Information on the amount and origin of seed purchased before 1910 is not available. Between that year and 1948, 961 kg of seed were imported and 120 kg were obtained from Douglas-fir stands in Czechoslovakia. A large amount of seed (4,635 kg) was imported in the years 1955-1957, at the beginning of a 10-year plan aimed at establishing 20,000 ha of Douglas-fir plantations, equivalent to 0.5% of former Czechoslovakia's forested land.

Hofman (1962) pointed out that the 1,081 kg of imported and domestic seed should have been sufficient to establish at least 1,000 ha of plantations.

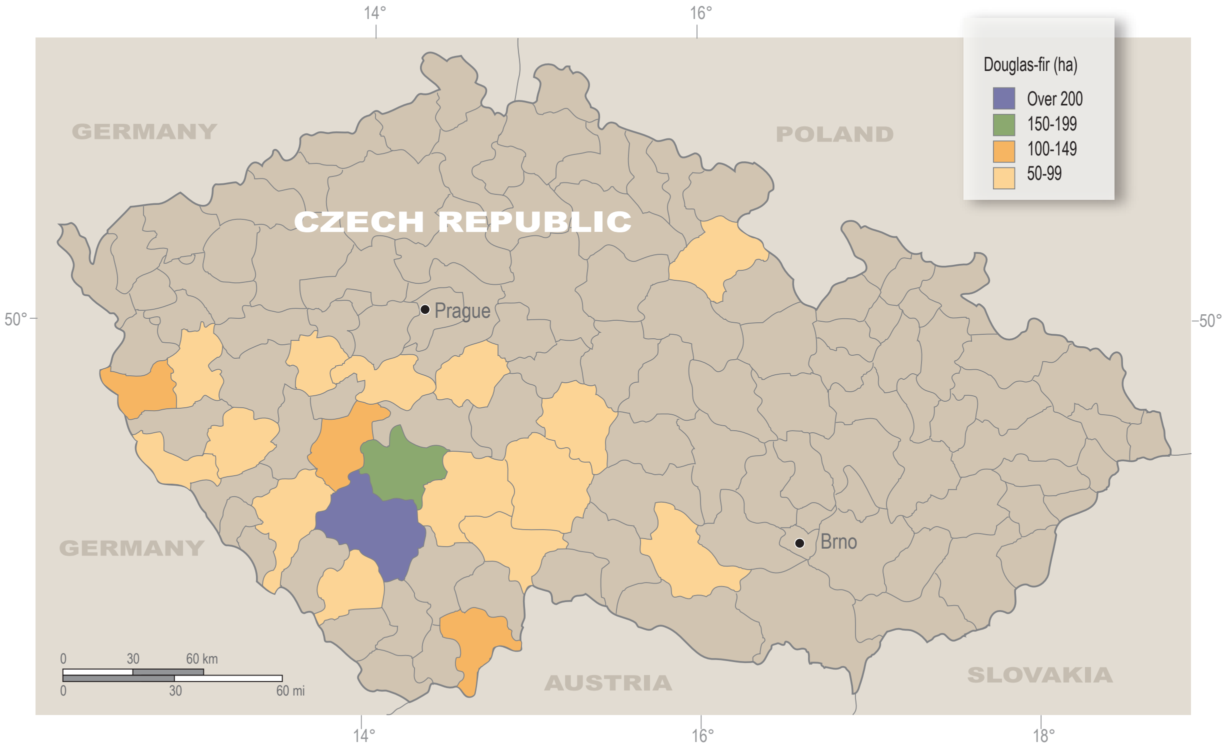

Figure 3.7 Area stocked with Douglas-fir in Czech Republic (from Vancura 1993).

But, according to him, only 196 ha of stands older than 10 years existed in 1953 in Czechoslovakia. Likewise, the fulfillment of the 1956 ten-year plan fell far short of its goal of 20,000 ha of Douglas-fir plantations by 1966, at least judging by the results of the 1976 inventory. The reasons for this are poor quality seed, unsuitable provenances, poor choice of planting sites, lack of proper silvicultural treatment, and insufficient protection against wildlife damage (Hofman 1962, Sika 1979).

Studies of the growth of Douglas-fir in Bohemia date back to the last quarter of the 19th century, and the beginning of the 20th century. The Imperial Austrian Forest Research Institute Mariabrunn established experimental plots in Bohemia, then still a part of the Austro-Hungarian Empire. These were established in 1883 (Hofman 1962), 1902, and 1905 (Žabka 1946). These and later investigations by the Czech Forest Research Institute at Zbraslav indicated that Douglas-fir can be grown successfully, particularly in the rolling hill country of the Czech Republic (Sika 1979). Early plantations included both the interior and the coastal varieties of Douglas-fir (Hejtmanek 1952), but only the latter performed satisfactorily. Trials are under way to identify provenances particularly suited for use in Czech forests (Hofman et al. 1964, Sika 1982). Hofman (1962) noted that the growth of Douglas-fir in the Czech Republic and Slovakia is comparable to that of the species in other countries of central and western Europe, an indication that very favorable conditions exist for increased planting of the species in both countries. Apparently, efforts were made to plant more Douglas-fir, with the ultimate goal of having 120,000 ha in the Czech Republic—that is 5% of all its forested land—stocked with Douglas-fir (Sika 1981).

Slovakia

Douglas-fir was introduced to Slovakia[27] as an ornamental tree about 1830, when the country was still part of the Austro-Hungarian Empire. Use of the species as a forest tree began toward the end of the 19th century, when professors at the Mining Academy in Banka Stiavnica established trial plots in forest stands. These early plantings were made with

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[26] Copy received February 8, 1993 from K. Vancura, Czech Forest Research Institute Zbraslav.

[27] The account of Douglas-fir in Slovakia is based on the letter of Sept. 1, 1993, from Dr. Peter Tavoda, Forest Research Institute, Zvolen, Slovakia.

Figure 3.8 Location of oldest Douglas-fir stands in Hungary (from Harkai 1975).

trees of unknown provenances, some of which were unsuitable, and plantings failed soon after establishment. Other provenances used in the early trials adapted well to the new environment and grew vigorously. The oldest existing stands in 1993 were 100 years old.

In 1993, Douglas-fir covered about 1,200 ha (0.18% of Slovakia's forest lands) and the number of pure stands was small. Usually, Douglas-fir is mixed with Norway spruce, European silver fir, or European larch, and sometimes with Scots pine and grand fir. Most of these stands are younger than 50 years, and the proportion of Douglas-fir generally ranges from 10% to 30%. The species has been planted throughout Slovakia at altitudes from 200 to 1,000 m, but the best growing conditions are found at elevations between 400 and 600 m. Stands on the best sites have reached heights of 43 to 45 m.

In general, experience with Douglas-fir in Slovakia has been favorable and it may be expected that its use will be continued in Slovac forests on a modest scale.

Hungary

In 1877, Pausinger suggested considering the introduction of Douglas-fir as a means of increasing the yield in some Hungarian forests. Shortly afterwards, Bedö (1878) recommended trials with Douglas-fir. He appeared to have been influenced by Booth's (1877) book, in which that author extolled the merits of Douglas-fir. The introduction of the species into Hungary began with the procurement of several kilograms of seed in the years 1880-1882 by the Hungarian National Forestry Association (Harkai 1975). Guidelines for trials with Douglas-fir were drawn up shortly afterwards (Dietz 1885, Marosi 1885).

The oldest Douglas-fir stands in the forests of present-day Hungary,[28] near Haromhuta in northeastern Hungary, and in Iharosbereny and Zalaegerszeg in western Hungary (Figure 3.8) stem from around the turn of the 19th century. Their provenance is unknown. Interest in the species appeared to have waned in the first half of the 20th century, but increased after World War II because of the government policy to solve the softwood shortage through conifer plantations. That discussion was reflected by the establishment of numerous trial plots of Douglas-fir until 1970 (Harkai 1975). Nonetheless, the area stocked with Douglas-fir has remained small. In 1961, Papp published a list of Douglas-fir stands in Hungary, most of which were less than one hectare. The total area occupied by the species was given as 37 ha. That area has increased only moderately since 1961. It amounted to 353 ha in 1990.[29]

That Douglas-fir occupies only such a small area is surprising in view of the fact that the species finds favorable growing conditions on sites with brown forest soils[30] where precipitation is above 600 mm (Papp 1961, Szöny 1963, Harkai 1971). These are sites

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[28] 28. Hungary lost nearly 90% of its forest lands to other countries after World War I. As a result, the initial plantations of Douglas-fir established by the Hungarian Forest Service are now outside the territory of present-day Hungary.

[29] 29. Letter of Sept. 13, 1993 by Dr. Mátyás Csaba, Univ. of Sopron, Hungary.

[30] 30. Corresponds approximately to mollisols.

where the yield of Douglas-fir is considerably higher than that of native conifers (Bano 1963). Inventories have shown 60-year-old stands of coastal Douglas-fir with standing volumes ranging from 800 to 1,000 m^3/ha (Szönyi and Nagy 1968). In a comparative trial at the Budafa Arboretum in southwestern Hungary, Douglas-fir reached a mean annual increment of 22 m^3/ha at age 20, which is twice the m.a.i. of traditionally planted Scots pine (Gergacz and Csaba 1993). Under field conditions, 250-350 m^3/ha of standing volume has been measured at age 40 in the same region depending upon initial spacing (Harkai 1987).

Although the yield potential and the range of sites suitable for Douglas-fir are sufficiently well known, the species has not been planted more widely for several reasons. Parts of the country have a combination of semiarid climate and soils that result in site conditions where native conifers and broadleaves show much better growth than Douglas-fir (Majer 1980, Gergacz and Csaba 1993). Even on sites favorable to the growth of Douglas-fir, the rate of initial mortality in plantations is high because of the frequency of spring droughts. In general, more than 50% of seedlings in a plantation are replanted.[31]

Fencing of plantations is necessary for at least 20-25 years. Damage by deer through stripping the bark with their antlers threatens the existence of unprotected stands. In the inadequately protected comparative test of conifers at Zalaerdod, Douglas-fir proved to be the most susceptible to game damage and, thus, the least productive (Harkai 1981).

Serbia

The share of conifers amounted to slightly more than 7% in the forests of Serbia in 1962. Plans were made to increase that share and to include Douglas-fir with the species considered for planting (Marić 1962).

Douglas-fir represented a miniscule part of Serbian coniferous woodlands. Petrović listed six small stands of Douglas-fir known to him. One of those stands in the Avala State Forest near Belgrade was established in 1911 when the Serbian Forest Service converted oak coppice to conifers (Marković 1951). The performance at Avala State Forest prompted Radulovi (1960) to advocate wider use of the species. Development of Douglas-fir plantations established at that time in central and eastern Serbia were described in 1973 by Stamenković and Miscević. Information on provenance of Serbian Douglas-fir stands is probably unknown because it is not mentioned by those authors. However, one of the initial stands is of such quality that it was selected as a seed stand (Marić 1962). Information about the current status of Douglas-fir in Serbia is unavailable.

Bosnia and Herzegovina

Professor Konrad Pintarić of the faculty of Forestry, University of Sarajevo, initiated an experiment in 1963 with provenances from the Pacific Northwest. Seedlings were outplanted in 1966 at Batalovo, about 20 km west of Sarajevo. In 1997, the standing volume projected to per hectare, ranged from 125 to 235 m^3 (Ballian et al. 2003). Additional trials were established at Crna Lokva (44° 51′ N, 16°51′ E), elevation 665 m (Pintarić 1989, Godevar et al. 2003); Gostovic (44°23′ N 18°08′ E) elevation 411 m; and Blinje (43°50′ N, 18°03′ E), elevation 951 m. The performance of Douglas-fir in these limited trials suggests good potential for introduction to Bosnia and Herzegovina (see additional information in chapter 4).

Bulgaria

A review by Petkova (2004) of the history and performance of Douglas-fir in Bulgaria indicates that it has become well adapted to site conditions in that country. The French forester Felix Wogeli established the first Douglas-fir plantation in 1906 with seed of unknown origin at 700 m elevation in the Stara Planina mountain range. Other early plantings in parks in Sofia, Koprivschtitza, and the Rila monastery region constituted mixtures of Douglas-fir with hardwood and other softwood species.

Planting of Douglas-fir ceased during the period 1930–1956, but recommenced after the beginning of renewed seed imports in 1956. Bulgaria imported 12,949 kg of Douglas-fir seed between 1956 and 1969. Most of the seed originated from sources in western Washington. The remainder stemmed from British Columbia. Data on the amounts of seed imported since 1970 were not given. Petkova's review merely indicates that several provenances from western

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[31] Letter of Sept. 13, 1993 by Dr. Csaba Mátyás, University of Sopron, Hungary.

Washington and a single provenance from Oregon (Forest Grove) were used for plantings in the period 1970–1985.

In addition to imported seed, domestic seed has already been used. Cone crops of the oldest Douglas-fir stand in the Kazanluk Forest District have yielded sufficient amounts of seed permitting the establishment of second-generation plantations.

Douglas-fir has shown good growth, especially at elevations between 800 and 1,200 m in the Stara Planina Range. Inventories of 43 plantations in this mountain range indicated that 20-year-old Douglas-fir trees on moist sites with northern exposures had a mean annual increment between 15 and 18 m^3/ha. But m.a.i. at that age was much lower, 6 to 8 m^3/ha, on dry, warm sites.

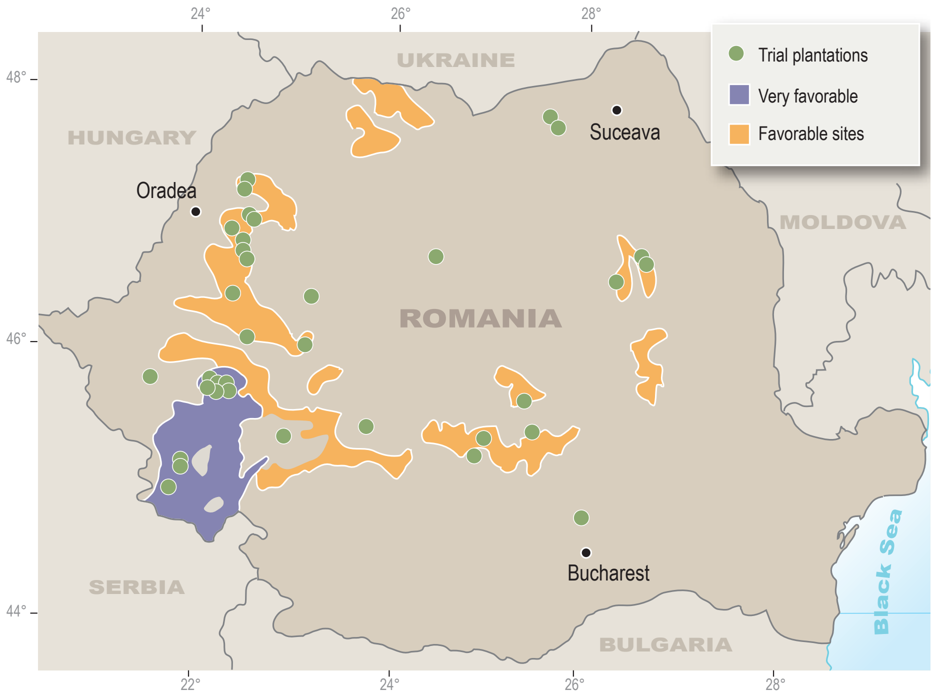

Figure 3.9 Douglas-fir stands in Romania. Dots denote location of stands: dark areas = sites very favorable for planting; lighter marked areas = sites favorable for planting.

Petkova stated that the total area of Douglas-fir plantations amounted to 12,664 ha in 1985, but gave no source for that figure. Inventory data of the Bulgarian Forest Service cited by her indicated that Douglas-fir was found on 6,792 ha in 2000. She did not explain the large decrease in the area occupied by the species, however. Large increases in the population of roe deer in the second half of the 20th century, and drought conditions in the decade 1983-1993, may have resulted in considerable losses of trees, but these events are unlikely the sole reasons for a reduction of nearly 6,000 ha stocked with Douglas-fir over a relatively short span of time.

Romania

Douglas-fir was introduced into Romania in the period 1870-1880, as plants or seeds of unknown provenance. All that is known about that early introduction is the fact that the plant material came from Austria (Lazarescu and Ionescu 1964). Planting of Douglas-fir continued on a very limited scale until about 1950.

From 1959 to 1962, Ionescu and Lazarescu (1966) inventoried and studied stands throughout Romania that contained Douglas-fir. The coastal variety of the species was represented in 41 stands covering a total of 59 ha, the interior variety in 8 stands on about 7 ha. Nearly all stands were mixed, with the share of Douglas-fir varying between 10% and 90%. Coastal Douglas-fir was represented in all age-classes from 15 to 70 years. Based on the findings from their study, Ionescu and Lazarescu identified regions suitable for cultivating the coastal variety in Romania (Figure 3.9). The best growing conditions exist in the southwestern part of the country at elevations between 300 and 1,000 m.

By chance, many of the early plantings were made with provenances of the coastal variety that is well suited for growing conditions in Romania. After the encouraging performance of coastal Douglas-fir in these early plantings, 23,382 ha of plantations were established between 1960 and 1970 with seed imported from a dealer in the Pacific Northwest (Violeta Enescu 1979). Unfortunately, many of these plantations failed, and in 1993, only about 13,000 ha stocked with Douglas-fir were left. The imported seed was presumably of unsuitable provenance and, thus, became a major contributing factor to the planting failures.[32]

To reduce the chance of such failures in the future, provenance trials have been initiated (Violeta Enescu 1984). However, the need for imports of seed is greatly reduced because seed can be harvested in sufficient amounts from existing Douglas-fir stands of good quality in Romania. Additionally, seed can be obtained from 37 ha of seed orchards, and raising planting stock through vegetative propagation seems possible.[33]

The Romanian Institute of Forest Tree Improvement recommends planting coastal Douglas-fir on sites that have at least 750 mm of annual precipitation and a mean annual temperature of 7–9°C, and avoiding sites with stagnant air or excessive drought in the spring. The interior variety of Douglas-fir has grown satisfactorily in parts of Romania where a continental climate prevents cultivation of the coastal variety (Haralamb 1971). But any future use of the interior variety is likely to be on a miniscule scale.

Currently many silviculturists are oriented toward the use of indigenous species even if they are less productive than Douglas-fir. Researchers will need to demonstrate that Douglas-fir is a remarkable species that should have a place in Romanian silviculture.

Poland

Douglas-fir was first introduced to Poland in 1833 by Count Stanislaw Wodzicki, who had it planted as an ornamental on his estate in Niedwiec near Cracow.[34] The oldest stands of the species were established in three waves, 1879–1880, 1891–1895, and 1907–1910. Most of these stands are in territories formerly under Prussian and Austrian administration in the western part of the country and in south-central Poland, respectively (Bialobok 1959). Seed origins of the stands are unknown. Maciejowski (1950) presumed that they were established with seed obtained by Schwappach from British Columbia, Washington, and Great Britain.

The first paper on the introduction of Douglas-fir to Poland appeared before the turn of the century (Tyniecki 1891), and as early as 1912, Sokolowski reported that yield of coastal Douglas-fir was superior to native conifers of the same age on similar sites. In 1926, Suchocki remeasured plots of coastal Douglas-fir established by Schwappach in three forest districts in western Poland. The results indicated that volume production of these stands was equal to that of British Douglas-fir stands of the same age. Suchocki noted that performance of the interior variety was unsatisfactory, and recommended against its planting. Bieler (1935) reported a total yield of 626 m^3/ha for a 54-year-old stand planted in 1881 in the Poznan region, a yield that according to him is produced there by European silver fir at age 62, and by Norway spruce only at age 72.

Maciejowski (1950, 1951) concluded, after a comprehensive review of experience with Douglas-fir in European forests, that its potential for use in Polish forests had been underestimated. He believed that Douglas-fir could play a role rehabilitating the country's forests ravaged in World War II. However, he made a strong plea that Douglas-fir should not be planted in Bialowieska and parts of Bialystok and Augustowo Forests to preserve the unique character of these forests.

Stands of exotics, as well as files of pertinent information, had been destroyed in many instances during World War II. In 1959, Bialobok published an inventory of foreign tree species made in the post-war years in an effort to determine and salvage those that had remained. He mapped and described 103 stands of Douglas-fir covering 191 ha. He pointed out, however, that his list was probably incomplete. A few years later, an update of the original exotics inventory was published (Bialobok and Chylarecki 1965). It showed the existence of 1,169 stands of Douglas-fir (Figure 3.10) comprising a total area of 1,405 ha.

An excellent account of Douglas-fir in Poland is provided by Chylarecki's (1976) study of 84 stands selected from 1,136 sites throughout Poland. His data show that Douglas-fir grows best in the coastal region along the Baltic Sea with its oceanic

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[32] Valeru Enescu, Romanian Institute of Forest Tree Improvement, Bucharest, letter of 23 February 1993.

[33] Ibid.

[34] L. Meynartowicz, Polish Academy of Science, Institute of Dendrology, Kórnik, letter of 15 June 1993.

climate and annual precipitation between 600 and 700 mm. Other regions where Douglas-fir grows well are the lower elevations in the Sudeten Mountains, Silesian Beskide Mountains, and Carpathian Mountains. Volume yield surpasses that of almost all the indigenous conifers. At age 80, mean stand volume is 640 m^3/ha, which corresponds to the volume of the best Norway spruce stands and exceeds yield obtainable from Scots pine stands by nearly 40%. The maximal yield of Douglas-fir of 850 m^3/ha is close to the productivity of the best stands of European silver fir. An updated and enlarged version of the 1976 study was published in German (Chylarecki 2005).

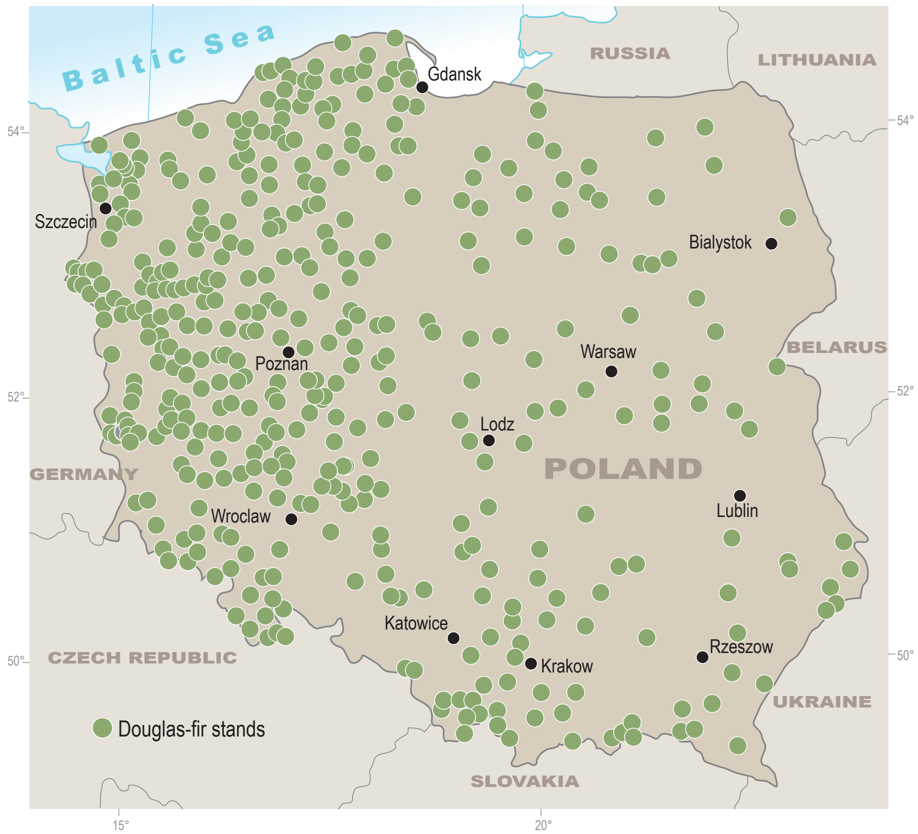

Figure 3.10 Douglas-fir stands in Poland (from Bialobok and Chylarecki 1965).

Tumilowicz (1967) recommended that coastal Douglas-fir should even be grown in the western and central Masurian Lake region of northeastern Poland. Only in the eastern part of the region are temperatures in winter too low for survival of the coastal variety. Tumilowicz based his conclusions on an inventory of Douglas-fir stands older than 30 years in 24 forest districts in the Masurian Lake region. Stands established in the years 1884-1897 had standing volumes that would fall between site classes III and IV of the McArdle and Meyer yield tables.

Dominik's (1963) statement, "Douglas-fir is little known by our foresters while lovers of our nature protection are ardent opponents of it," is probably not applicable anymore, at least in regard to the first part of the statement. Polish foresters have become more knowledgeable about the species, and Polish participation in the IUFRO international Douglas-fir provenance trial (Mejnartowicz 1976) is a clear sign of interest for future use of Douglas-fir in Poland. L. Mejnartowicz (letter of July 10, 1993) indicates that in 1993 about 1,000 ha were stocked with Douglas-fir, and that opposition by environmentalists is unlikely to prevent future use of the species in Polish forests.

Baltic States

Lithuania

A map from Jankauskas (1951) shows 27 locations throughout Lithuania where stands of Douglas-fir are situated (Figure 3.11). The oldest of these stands were established in 1900 to 1910. Most of the existing plantations appear to belong to the interior variety, which is considered to be completely acclimatized in Lithuania (Navasajtis 1966).

Latvia

Douglas-fir has been planted in Latvian parks since the middle of the 19th century. The first forest plantations were established between 1900 and 1902 (Pirags 1990). In 1968, 10 stands of Douglas-fir of unspecified size existed in the forest districts Talsi, Rezekne, Ogre, Dobele, and Dangavpils, as well as numerous groups and solitary trees in other districts and parks (Pirags 1968). The area occupied by Douglas-fir older than 20 years was very small, but new plantations have been established since 1965 (Pirags 1979).

Figure 3.11 Douglas-fir in Lithuania (from Jankauskas 1951).

Both the interior and coastal variety have been planted in Latvia, the latter being the more productive one under Latvian growing conditions. Douglas-fir is outperforming both Norway spruce and Scots pine, with a m.a.i. of 11 m^3/ha at age 60 (Pirags 1979).

Estonia

The earliest attempt to grow Douglas-fir in Estonia, situated between lat 57°30′ and 59°40′ N, long 21°45′ and 28°15′E, was made in 1880 in the environs of Tallinn. That initial attempt was unsuccessful, probably because of unsuitable seed (Margus 1961). First efforts to find suitable seed sources were made by Count Berg, a private forest owner, and Mr. M. Sievers, chairman of the Baltic Forestry Association (Baltischer Forstverein). In spite, of the encouraging results of a few small plantations established early in the 20th century, the species received little attention until 1954. That year, H. Taimre kindled renewed interest in Douglas-fir through a paper about a stand of *Pseudotsuga* in Kaarepere Forest District.

In 1958, small stands covered about 6 ha in seven forest districts. In 1963, groups of Douglas-fir of unspecified size stood 15 forest districts and in several arboreta and parks (Margus 1961, 1963). By 1978, the area occupied by the species had increased to about 25 ha. Trees on 5 of the 25 ha stemmed from domestic seed collections. Domestic seed crops are fairly good. Douglas-fir begins to produce seed at about age 20,, and continues to produce cone crops at 2- to 3-year intervals (Laas 1967). Etverk (1978) attributed the small area covered by Douglas-fir to a shortage of seed and lack of systematic provenance experiments. The oldest stand in 1978 was about 70 years old. Nearly all stands belonged to the interior variety, referred to as either variety *glauca* or variety *caesia*. The interior variety is considered to be suitable for all of Estonia, but the coastal variety is only suitable for the western part of the country (Laas 1967).

Former Soviet Union

Belarus

Following a survey of the performance of conifers introduced into Belarus, Ivanova (1963) recommended *Pseudotsuga menziesii* var. *glauca* for use in forest plantations. Skutko (1966) evaluated the performance of several provenances of the interior variety, which he referred to as varieties *caesia* and *glauca*, in plantations where they grew mixed with Siberian larch, Norway spruce, and scots pine. He noted that trees of variety *glauca* were inferior to them and thus should not be considered for use in forest plantations.

Ukraine

Both the coastal and the interior variety, as well as some cultivars of Douglas-fir, are grown in Ukrainian gardens and parks (Lipa 1940), but only the variety *menziesii* is used in forest plantations. The excellent growth of Douglas-fir in the western Ukraine prompted Brodovich (1964) to recommend collecting seed from stands of the species in the Ukraine to

Table 3.5 Growth and productivity data of Douglas-fir in the Ukraine (from Brodovich 1967).

Age (y)	Mean Height (m)	Mean Diameter (cm)	Number of stems/ha	Basal area (cm^2)	Form factors (0.001)	Standing volume (cm^3/ha)	Volume increment (cm^3) Mean (annual)	Volume increment (cm^3) Current (annual)
10	4,6	4,7			641			
20	14,1	14,3	2136	34,3	492	238	11,9	27,0
30	22,8	22,5	1258	50,0	478	545	18,2	32,0
40	29,2	29,4	862	58,5	475	810	20,2	24,8
50	34,1	34,8	664	63,2	473	1018	20,3	18,6
60	37,8	38,8	555	65,6	473	1167	19,5	12,8

establish more Douglas-fir plantations. He wrote in 1976, "Almost 70-year-long trials in acclimatization and propagation of Douglas-fir in the Soviet Union proved that the green Douglas-fir[35] in the western Ukraine is one of the most rapidly growing, valuable and promising forestry species." Data on growth and productivity of Douglas-fir in the Ukraine reported by Brodovich (1967) are reproduced in Table 3.5.

Douglas-fir has been grown in plantations in the Carpathian region of the Ukraine since 1906 and, in 1985, covered 1,555 ha (Rudenko and Derzhanovskaja 1985). The best sites for Douglas-fir in the western Ukraine are north, northeast, and northwest slopes. Natural regeneration is abundant under favorable site conditions ranging from 20,000 seedlings per hectare (Brodovich 1978) to 70,000 to 100,000 plants per hectare (Rudenko and Derzhanovskaja (1985)). According to Brodovich (1978), Douglas-fir has completely adapted to conditions in the western Ukraine and is far more productive than the native Norway spruce.

Russia

As elsewhere in Europe, arboreta were the first places where Douglas-fir was planted. The oldest Douglas-firs in the Nikitsky Botanical Garden in the Crimea are thought to have been raised from seed brought between 1830 and 1840 from the former Russian colony at Fort Ross in California (Wulff 1926). In 1914, the Moscow Botanical Garden contained several Douglas-firs planted about 1880 (Meyer 1914).

The history of the introduction of Douglas-fir and other exotic conifers in tsarist Russia, and subsequently in the Soviet Union was reviewed by Kalutskii et al. (1981). The Central Research Institute for Forest Genetics, Breeding, and Selection, established at Voronezh in 1971 paid particular attention to the introduction of Douglas-fir and other fast-growing exotic conifers in the western regions of the former USSR. A map prepared by that institute shows a division of the country into 6 zones according to suitability for growth of introduced species. Zones are numbered consecutively 1 to 6 from north to south. Planting of Douglas-fir is recommended for zones 3, 4, and 5. According to Tkatchenko (1958), W. Sievers had suggested the line Leningrad – Moscow – Saratov as the eastern boundary for cultivating Douglas-fir in Russia.

Plantations of Douglas-fir have been established in European Russia since the last decade of the 19th century. Reports on Douglas-fir in the forest-steppe region (Vehov and Vehov 1962, Akimockin 1964, Lukin 1966, Biryukov 1971) indicate that the species shows good growth. In the south-central part of Russia, growth and productivity of Douglas-fir exceed those of most native and introduced species. Dudetskaja and Lukin (1977) emphasized that the species has survived the severest winters there.

The Black Sea coastal zone of the Caucasus and the Crimea are important resort areas where exotic conifers have been introduced primarily for aesthetic reasons (Dusha 1977). But the species also has great potential for timber production in that region (Sud'ev 1980), as is apparent from the performance of a plantation of Douglas-fir about 5 km from the Black Sea coast. At age 32, it had a standing volume of 602 m^3/ha (Dudarev et al. 1975).

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[35] "Green Douglas-fir" = *Pseudotsuga menziesii* var. *menziesii*.

Asia

India

A trial in the Punjab on a hot, bare, and rocky hillside at 2,134 m elevation with exotic species included 100 Douglas-firs. By 1951, only three trees had survived. Das and Chand (1958) attributed the failure of Douglas-fir to the mismatch between species and site.

Sri Lanka

Douglas-fir was planted in the 1920s in Sri Lanka (formerly Ceylon) at elevations between 1,219 and 1,829 m. Troup, in 1932, described the results as "unpromising."

Southern Hemisphere

The areas of introduction of Douglas-fir in the southern hemisphere are New Zealand, Australia, Chile, Argentina, and eastern and southern Africa. Except for Africa, the areas of introduction in the southern hemisphere all have parts where the species has been grown successfully.

Southwestern Pacific

New Zealand and Australia are the regions of earliest introduction of Douglas-fir to the southern hemisphere. Aside from France, Germany, and the United Kingdom, New Zealand has by far the largest acreage of that species outside its natural range. In Australia, planting of Douglas-fir has remained limited. Lack of suitable sites and climatic limitations are probably the principal reasons that the tree has not found wider use in Australian forestry.

New Zealand

Douglas-fir was introduced to New Zealand in 1859 by J. B. Acland of Canterbury (Anonymous 1994). From about 1870, the species was planted as an ornamental and shade tree on farms in the South Island (Streets 1962). Planting of Douglas-fir in State forests began in 1897, when it was among the species used in the first trials of exotic trees on the Kaingaroa Plains in central North Island (Kirkland 1969). The area planted to Douglas-fir was small until 1917: 450 ha (Spurr 1961). By 1940, the area of Douglas-fir plantations had increased by almost 16,000 ha. Nearly double that area was planted to Douglas-fir between 1940 and 1974, reaching a total of 47,126 ha (Table 3.6). Most of that area, 90.8% was in State forests. In 1964, Rotorua Conservancy, with 26,188 ha, contained 55.6% of the country's Douglas-fir resource. At that time, somewhat more than two-thirds of New Zealand's Douglas-fir stands were on the North Island, most of them concentrated in the Rotorua Conservancy. In 1974, there were about 27,000 ha of Douglas-fir plantations less than 20 years old. Of these plantations, those on more than 11,000 ha (almost all in State forests) had been established between 1966 and 1970. The peak of planting Douglas-fir in that 5-year period was followed by a marked decline in the following years (Fraser 1978).

It is unlikely that these 1974 figures reflect the extent of previous planting because some plantations failed. For instance, of the more than 18,000 ha of Douglas-fir planted between 1920 and 1936 in Kaingaroa Forest, a third of these plantations failed (Kirkland 1969). Another example comes from the Westland Conservancy. In the 1950s, Douglas-fir was planted in State forests at an annual rate of 100 to 200 ha, and that was increased to 600 to 700 ha in the 1960s (Allan 1978). However, only 461 ha of Douglas-fir were recorded for the State forests of the Westland Conservancy in 1974.

The New Zealand Ministry of Forests annually publishes, "A National Exotic Forest Description" (Neumann 1993), which includes data on stocked areas and age-class distributions for Douglas-fir for all 78 districts in the country. The data for 1990 and 1991 are contained in Table 3.7. These data cover only

Table 3.6 Number of hectares stocked with Douglas-fir in New Zealand in 1974 (From Fraser 1978).

	Up to 1940 (ha)	Post 1940 (ha)	Mixed-age classes (ha)	Total (ha)
North Island				
Auckland	17	2,055	–	2.072
Rotorua	13,974	12,214	–	26,188
Wellington	429	5,677	–	6,106
South Island				
Nelson	771	4,883	–	5,654
Westland	7	454	–	461
Canterbury	457	2,610	26	3,093
Southland	764	2,788		3,552
	16,419	30,681	26	47,126

Table 3.7 Number of hectares stocked with Douglas-fir in New Zealand, 1940 to 1991.

		1940[1]	1974[1]	1990[2]	1991[2]
Auckland[3]	Northern[4]	17	2,072	5	2
Rotorua	Central	13,974	26,188	36,309	31,571
Wellington	Southern	429	6,106	1,614	1,587
	North Island	14,420	34,366	37,928	33,160
		87,8%	72,9%	57,2%	55,9%
Nelson/Marlborough		771	5,654	11,583	11,439
Westland		7	461	556	556
Canterbury		457	3,093	5,292	4,663
Otago/Southland		764	3,552	10,936	9,473
	South Island	1,999	12,760	28,367	26,131
		12,2%	27,1%	42,8%	44,1%
	New Zealand Totals	16,419	47,126	66,295	59,291

1. Fraser 1978.
2. Neumann 1993.
3. As listed by Fraser 1978.
4. As listed by Neumann 1993.

Table 3.8 Douglas-fir age class distribution in New Zealand as of April 1, 1991 (from Neumann 1993).

Age class (y)	1–10	11–20	21–30	31–40	41–50	51–60	61–80
Hectares	15,661	13,047	16,909	5,673	859	2,944	4,198
Percent	26.4	22.0	28.5	9.6	1.4	5.0	7.1

about 90% of the total area occupied by Douglas-fir, however, because the forest survey does not include holdings of less than 100 hectares. If these areas are included, the total area stocked with Douglas-fir for all of New Zealand was 71,066 ha in 1990, and 65,478 ha in 1991.[36]

The data in Table 3.7 show a substantial increase in the area stocked with Douglas-fir from 1974 to 1990, particularly in the central North Island region, and in Nelson/Marlborough, Canterbury, and Otaga/Southland. They also demonstrate that the area occupied by Douglas-fir decreased, the result of increased harvesting to supply the booming log export industry.[37] A breakdown of Douglas-fir stands by age (Table 3.8) shows that most stands (76.9%) were less than 30 years old.

Douglas-fir can be grown successfully in many parts of the country, provided that appropriate sites are chosen. In general, altitudinal limits for the species are 900 m in the North Island and 750 m in the South Island (Kirkland 1971). Wind exposure is a major limitation to survival and satisfactory growth at all altitudes. Because New Zealand is a relatively narrow country oriented at right angles to the prevailing west to southwesterly air flows, many localities experience, strong, desiccating or salt-carrying winds. Lack of sufficient precipitation is not a limiting factor, except for parts of Canterbury and Southland (Prior et al. 1963, Revell 1978).

Douglas-fir has been grown in New Zealand since the second half of the 19th century, but records of seed origin were not kept until 1927. The 6,650 ha of Douglas-fir planted from 1915 to 1928 in the northern part of Kaingaroa Forest are presumably from western Washington seed sources. The New Zealand Forest Service imported 3,223 kg of seed from 1927 to 1974 (Table 3.9). During that same period 8,381 kg were obtained from Douglas-fir stands in New Zealand (Wilcox 1978; Table 3.10). Imports ceased in 1930; seed supplies from 1931 to 1964 were obtained entirely from New Zealand stands. Major local seed sources have been Kangaroa, Whaka, Golden Downs,

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[36] Dr. Colin O'Loughlin, Forest Consultant, Wadestown, Wellington, letter of April 21, 1993.

[37] Ibid.

Table 3.9 Imports of Douglas-fir seed to New Zealand since 1926 (from Wilcox 1978).

Year	Origin	Quantity (kg)
1927	Southern Washington	308
	Salmon Arm, British Columbia	62
1928	Washington	27
	Washington	163
	Washington	78
1929	Coast Range, Oregon	91
	Coast Range, Washington	32
	Washington	322
	Washington	54
	Southwest Washington	272
1930	Cowlitz County, Washington	705
	West of Cascades, British Columbia	17
1956	Caspar, California	18
1965	Pierce County, Washington, 150 m	227
1966	Pierce County, Washington, 150 m	204
	Humboldt County, California, 360 m	5
1967	Meyer's Flat, California 460 m	7
1968	Deadwood, Oregon	302
	Bandon, Oregon	35
	Langlois, Oregon	39
	Langlois, Oregon	11
	Snoqualmie, Washington	32
	Snoqualmie, Washington	14
	Snoqualmie, Washington	6
	Tahkenitch, Oregon, 240 m	6
	Mt. Rainier National Forest, Washington	97
	Pecwan, California, 240 m	11
	Pecwan, California, 200 m	10
1970	Swanton, California, 80 m	10
1972	Korbel, California, 80 m	13
1974	Coquille River, Oregon, 200 m	45
Total imports		3,223

Tapawera, Coalgate and Queenstown. Kaingaroa Forest alone was the source of 3,377 kg, an amount slightly higher than that of all imported seed. From 1927 to 1930, 2,131 kg of seed were imported, mainly from Washington. Central and southern stands in Kaingaroa planted in 1930 to 1936, amounting to 5,600 ha, are from these Washington seed lots (Wilcox, 1978). Some of the oldest stands in Golden Downs Forest originated from Washington seed. Most of the Golden Downs stands, however, originated from seed collected from old shelterbelts in the Stoke, Tapawera, Tadmor, and Motupiko districts. These shelterbelts in turn are thought to be progeny of the Mararewa Cemetery plantings made about 1875 by John Stanley who brought the seed from England. In general, the Douglas-fir in Golden Downs has a much narrower genetic base than the stands in Kaingaroa (Wilcox 1978). Further large imports of Washington seed were made in 1965-66, and again in 1968 when J. Spiers procured an assortment of seedlots from Washington, Oregon, and California. Some coastal Californian seed was imported in 1970 and 1972 as a direct result of the observation that low-elevation Californian Douglas-fir was performing exceptionally well in provenance trials in New Zealand. Experience has shown that provenances of Douglas-fir from Oregon and California were the best performers in New Zealand.[38]

The future role of Douglas-fir in New Zealand forestry is to some degree a matter of contention. Of concern is the presence of *Phaeocryptopus gaeumannii*, first detected in New Zealand in the 1960s. That fungus is thought to be largely responsible for the severe decline of growth in stands established before 1940. But other factors, such as insects, a series of dry summers, unsuitable sites, and insufficient care of stands, may have been contributory causes (Groome 1978, James and Bunn 1978).

But economics is what weighs most heavily against the planting of Douglas-fir. Fenton stated in 1976 that in the context of national forest planning, the planting of Douglas-fir implies a delay in attaining production targets and a reduction in profitability because the species takes considerably longer than Monterey pine to reach merchantable size (Fenton 1978). Because most of New Zealand's State Forests have been privatized, there is no overall policy within the forest sector about Douglas-fir.[39]

Past experience suggests that the potential is greater for Douglas-fir than for Monterey pine at elevations above 650 m in the North Island and above 500 m in the South Island (Revell 1978). The greatest potential for expanding the Douglas-fir estate in New Zealand exists in the hills and high country of the South Island, where annual rainfall exceeds 800

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[38] Ibid.

[39] Ibid.

Table 3.10 Sources and quantities of Douglas-fir seed used in New Zealand 1926-1974 in kg (from Wilcox 1978).

Source	1926-34	1935-44	1945-54	1955-64	1965-74	Total
Imports	2,131	0	18	18	1,074	3,223
Kaingaroa	0	102	490	1,330	1,455	3,377
Whaka	166	110	121	37	11	445
Karioi	0	0	168	76	0	244
Golden Downs	11	10	122	293	543	979
Tapawera	197	122	162	186	138	805
Hanmer	0	2	271	154	149	576
Ashley	0	0	0	0	164	164
Coalgate	0	0	0	154	271	425
Palmside	0	0	0	37	37	74
Wanaka	0	0	0	35	54	89
Queenstown	0	0	22	32	359	413
Naseby	0	0	12	19	88	119
Tapanui	0	0	161	0	0	161
Dusky	0	0	39	69	81	189
Other sources	46	1	60	115	99	321
Total	2,551	347	1,628	2,555	4,523	11,604

mm. Ledgard and Belton (1985) and Belton (1991) have shown that Douglas-fir grows extremely well, at rates of between 20 and 32 m^3/ha/yr for fully stocked stands before age 50 in high country areas below 900 m elevation and with precipitation of more than 800 mm per year. The eastern high country of the South Island has about 200,000 ha of land physically suited to forestry. Much of that land is partly or severely degraded under the present pastoral land use. In any future large-scale afforestation projects in the South Island high country, Douglas-fir would undoubtedly be an important, if not the most important component of the forest scheme.[40]

The future prospects for New Zealand-grown Douglas-fir have received a boost because the declining supply of Douglas-fir from the United States has raised the price of Douglas-fir wood in international markets, thus improving the economics of growing Douglas-fir in New Zealand. A sign of confidence in the future of the species in New Zealand was the fact that the New Zealand Forest Research Institute at Rotorua set up a Douglas-fir Research Cooperative in 1993 with the aim to foster continued research into the silviculture, genetics, and use of Douglas-fir in New Zealand.

Australia

Statistics for Douglas-fir in Australia are not as complete as for New Zealand. Available data indicate a total area of about 2,665 ha in State Forests (Griffin and Matheson 1978). Apparently few, if any, Douglas-fir plantations are on privately owned land. Nearly all Douglas-fir plantations are located in the southeastern part of Australia. The species has been planted on a trial basis in the Mount Lofty Range of South Australia and in Western Australia (Troup 1932, Streets 1962).

Douglas-fir was one of the secondary species in the planting program for the upper elevations of the Southern Table Lands in New South Wales (Streets 1962). According to Fenton (1967), 67 ha were planted to Douglas-fir between 1920 and 1960, and 437 ha between 1961 and 1965. An anonymous article in the Australian Timber Journal (1965) cited by Fenton (1967) reported plans for planting about 200 ha per annum in New South Wales. Margules (1968) wrote that about 101 ha are planted annually to Douglas-fir on the Bago State Forest and that, in general, Douglas-fir is likely to become one of the major species at altitudes of 762 to 1,219 m in the Tumut and Bombala districts. That forecast was unrealistic. Griffin and Matheson (1978) gave the area stocked with Douglas-fir as 1,350 ha, and added that New

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[40] Ibid.

South Wales has no current planting program. In the Capital Territory, Douglas-fir grows vigorously in the Cotter Valley at elevations between 762 and 1,463 m. The species does not thrive, however, at lower elevations in the vicinity of Canberra (Streets 1962).

Douglas-fir was introduced to Victoria about 1902 (Troup 1932), but was not planted on State land until 1920. The Forests Commission planted the tree on favorable sites in areas such as Beechworth and the Air Valley (Margules 1968). In 1962, Victoria had about 809 ha of Douglas-fir plantations, of which 381 ha were in one block. Most of the plantations were established between 1936 and 1942 at elevations between 457 and 914 m with seedlings of unknown provenance. Mean annual precipitation for the planting sites ranges from 889 mm to 1,905 mm. Growth is best where fog and low clouds are common and rainfall is light but frequent. Shelter is essential for good growth. Exposure to wind results in reduced height growth but little blowdown (Streets 1962). The Forests Commission of Victoria announced in 1957 that Douglas-fir would not be planted anymore. The Forests Commission reversed that decision 5 years later when it indicated that the species would be considered for suitable sites. The planting of Douglas-fir reached a second peak in the years 1965 to 1975. The emphasis was on higher elevation sites where Monterey pine suffers snow damage. Planting was again suspended when the presence of *Phaeocryptopus gaeumannii* was discovered. In 1978, Douglas-fir occupied 1,250 ha (3,088 acres) (Griffin and Matheson 1978).

In Tasmania, Douglas-fir was probably introduced during the gold rush of the 1850s. The tree was planted as an ornamental until the Forest Service in 1936 established Douglas-fir plantations at Warrentina (Streets 1962). Annual precipitation on planting sites ranges from 1,016 to 1,524 mm. Natural vegetation on these sites is eucalypt forest dominated by *Eucalyptus regnans* and *E. obliqua*. By 1956, the area planted to Douglas-fir amounted to 94 ha (Fenton 1967). Streets (1962) mentions that the extension of Douglas-fir plantings was planned at the rate of 20 ha per year. These plans were not realized because plantations of Douglas-fir occupied only 65 ha in 1978 (Griffin and Matheson 1978). Insect pests of economic importance have not been observed on Douglas-fir in Australia. In Victoria, wallabies have frequently damaged trees to age 6 or 7 years (Streets 1962).

Douglas-fir in Australia belongs almost exclusively to the coastal variety of unknown provenance, except for trees in nine provenance plantations established in 1972/1973. Spurr (1961) suggested that provenances from the central Sierra Nevada of California might be suitable for Australian conditions and should be tested at higher elevations in New South Wales and Victoria. Preliminary results from 40 seedlots of the IUFRO Douglas-fir collection under test in New South Wales, Victoria, and Tasmania, however, indicated that provenances from higher elevations in California are highly susceptible to *Phaeocryptopus gaeumannii*. Provenances from the coastal fog belt of northern California and southern Oregon appear to be best suited for use in Australia.

The only report of the existence of a plantation with trees of the interior variety is from Tasmania; 1.2 ha were planted at Stoodley Forests in 1940 with trees raised from seed imported from Colorado. The interior variety was judged unsuitable, and has not been used again (Streets 1962).

In all likelihood, Douglas-fir is going to remain an insignificant component of Australian forests. The prospects for future use of Douglas-fir have been evaluated by Fenton (1967) as follows:

> On end-use considerations only, there is little need for Australia to plant Douglas-fir, as equivalent timber is potentially available from radiata pine and the object of expanded afforestation is to replace imports. To do this by growing Douglas fir instead of radiata pine as an exotic would take from 20 to 30 years longer, and market preference for the species would have to be sustained by imports during this period to benefit from its current market reputation. Apart from sites which present limitations for radiata pine, there is no compelling reason why afforestation of Douglas-fir should be extended in Australia.

Although the areas suitable for large-scale commercial planting of Douglas-fir are limited, the tree has use for shelterbelt and ornamental planting. According to Margules (1962) few species are more suitable for single-row shelterbelt planting than Douglas-fir because it has numerous small branches which, in the open, are retained to ground level and carry vigorous foliage to an advanced age.

South America

In contrast to the Southwest Pacific region, Douglas-fir had been planted on a relatively small scale in South America in the 1990s. That scale will probably change as the depletion of the indigenous forest resource progresses, and reforestation efforts will be helped with accelerated planting of fast-growing exotic species.

Chile

Douglas-fir was introduced to Chile as an ornamental tree about 1895 (Rocuant 1967). A 67-year-old Douglas-fir cut for stem analysis in 1962 came from a park near Valdivia (Brun 1963). The first plantation of Douglas-fir was established in 1914 by Hugo Weber on his estate, Bellavista, near Traiguen (Weber and Gothe 1954). At age 50, trees in that plantation had reached heights of 35 m and diameters at breast height of 63.5 cm (Rocuant 1967). Another early trial with the species was made by the Caja Agraria, with the successful establishment of several Douglas-fir plantations between 1939 and 1944 on its property near Loncoche (Weber and Gothe 1954). In spite of encouraging results in these early trials, use of Douglas-fir as a plantation tree increased only slowly until the 1960s. By 1967, Douglas-fir occupied between 2,000 and 2,500 ha. The major share (1,500 ha) or about 60% of the total area covered by Douglas-fir at that time in Chile, was concentrated in four estates (Rocuant 1967). By 1977, the area covered by Douglas-fir had increased to 5,449 ha (Diaz-Vaz and Ojeda 1980), and to 9,000 ha by 1985 (Instituto Forestal 1986).

Existing plantations are in a part of Chile that extends from lat 35° S in the north to about lat 42° S in the south. Growth studies carried out in 1966/67 by Rocuant (1967) and Contreras and Smith (1973) indicated impressive growth of Douglas-fir. Based on his findings, Rocuant recommended the area from lat 35° S to lat 43° S for growing of Douglas-fir. But because of differences in growth patterns of the species found in his 1966/67 study, he suggested a distinction between two regions: region I from lat 35° S to 38°30′ S, which includes the provinces of Maule and Malleco, and region II from lat 38°30′ to 43° S, which encompasses the provinces of Cautin and Chiloe. In the coastal and Andean Cordilleras of region I, rotations of 60-68 years will be necessary to cut trees with a dbh of 51 cm. In the plains, rotations would probably have to exceed 80 years because Douglas-fir grows more slowly there. In region II, a dimension of 51 cm is probably obtainable with 40- to 50-year rotations.

Drawing on results from a series of experimental plantations installed by the Instituto Forestal in 1962, and reports of the studies by Rocuant (1967), Contreras and Smith (1973), and Contreras and Peters (1982), the Instituto Forestal produced a map of potential volume growth of Douglas-fir according to homogenous edapho-climatic units in the areas recommended for planting of Douglas-fir (Figure 3.12). A note of caution was added, however, by pointing out that predictions of growth behavior under local conditions will be difficult because of the extent of the edapho-climatic units.

Provenance is undoubtedly another source of variation in growth patterns. Seed being used in Chile has come primarily from seed dealers in the

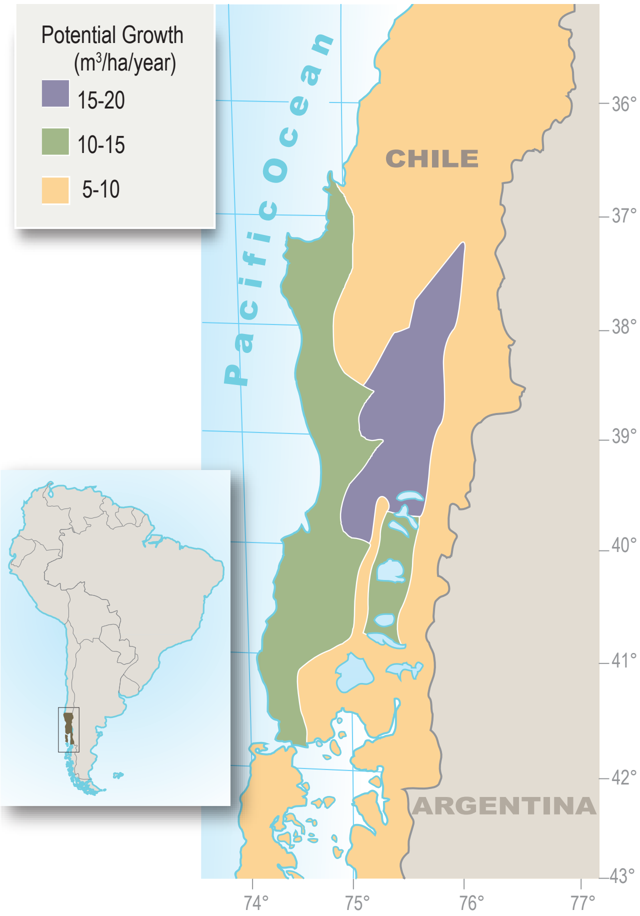

Figure 3.12 Potential volume growth of Douglas-fir in areas of Chile recommended for planting the species (from Instituto Forestal 1986).

United States. Carrasco (1954) mentions that plantations in the pre-Cordilleran zones of Valdivia province were established with seed harvested in the fog belt zone of southern Washington and northern Oregon, supplied by Manning Seed Company in Roy, Washington. In general, information about the origin of seed appears to be non-existent, and provenance tests have been of limited scope. In a test of 14 provenances initiated by Rocuant in 1965, the best results were obtained with provenances from the coastal region of southwestern Oregon (Lopez 1973). Droppelmann (1986) analysed the performance of 17-year-old Douglas-firs from 10 provenances in a trial near Valdivia. He found that "near coast provenances" were superior to other provenances in increment at the test site.

Planting of Douglas-fir is likely to increase in the future because it adapts well to the climate in Chile, shows good growth, and produces wood whose quality is considered equal or better than that of Monterey pine (Weber 1953; Diaz-Vaz and Ojeda 1980). Some of Douglas-fir's silvical characteristics contribute also to its growing popularity. The species can withstand extended periods of drought without major injury. Unlike Monterey pine, it is much less likely to suffer from snow breakage at sites where that is a problem (Buch 1965). Douglas-fir has also been shown to have potential for rehabilitating sites degraded by certain agricultural practices (Buch 1978).

Argentina

In one of the first published accounts of Douglas-fir in Argentina, Rodriguez (1960) mentions the existence of several small plantations of the species throughout the Andean-Patagonian forest region, and of experimental plots in the National Parks Nahuel Huapi (Isla Victoria) and Lanin. Rodriguez stated that these plantations, roughly situated between lat 38° and 42° S and long 71° and 72° W, were thriving and growing rapidly. Information on the age of the plantations was not given. Data on growth are available for young stands only. A 20-year-old plantation near the northern fringe of Lake Lacar about 20 km west of San Martin de los Andes had a standing volume of 634 m^3/ha and a mean height of 18 m (Fernandez 1964). A 13-year-old plantation in the Cordilleran region in the northwest of the province of Chubut had a mean height of 15 m (Miglioli and Rozados 1972).

The performance of the plantation near Lake Lakar is remarkable. The trees were not damaged by temperatures as low as −13°C, and did not suffer from snow breakage. A layer of volcanic ash, rich in iron and aluminum oxides, was deposited on May 22, 1960, but did not harm the plantation (Fernandez 1964).

Douglas-fir has been used for rehabilitating *Notofagus antarctica* scrubland in the southern Cordillera of Rio Negro territory (Gomis 1974) and is considered suitable for conversion of *Berberis* scrubland in the Patagonian Andes (Seibert 1979). The planting of 6,200 ha had been projected according to a national development plan in the early 1970s (Yakubson 1973). Nothing in the available literature indicates whether or not that goal was attained.

Africa

Repeated attempts have been made to introduce Douglas-fir to Africa, but this has resulted mostly in failure, as in Kenya (Troup 1932) and Zimbabwe, formerly Rhodesia (Streets 1962).

Republic of South Africa

Foresters in the Republic of South Africa initiated trials with both the coastal and interior varieties of Douglas-fir around the turn of the 19th century. Troup (1932) mentioned plantations of Douglas-fir in silvicultural subdivisions A (mountains of southwestern Cape Province), D (area between Great Brak and Kromme Rivers), and H (highlands of eastern Cape Province, Natal, Transvaal, and eastern and central Orange Free State). These three subdivisions have annual precipitation of more than 635 mm. Legat (1932) considered Douglas-fir as unsuited for South Africa, and cited as proof repeated failures of plantations. He asserted that the intensely dry atmosphere of South Africa, combined with long periods of drought, is mainly responsible for the failures of Douglas-fir. Streets (1962) mentioned only a single plantation of Douglas-fir in subdivision H at 1,615 m altitude. Trees belonged to the interior variety of Douglas-fir. Their mean height and dbh at age 51 years were 9.75 m and 19.8 cm, respectively.

4. Provenance Trials

Richard K. Hermann

Provenance trials are designed to study the performance of seeds from different stands of trees, which may either be native to their place of growth or are introduced from elsewhere (Edwards 1956). Usually, provenance trials are established on several sites to assess both the genetic variability of the provenances tested and the interactions between genotype and environment. Such trials, also referred to as common garden studies, have made important contributions to the knowledge of genetic variation in Douglas-fir. Although some were conducted as nursery studies, the majority were initiated as long-term field trials. The need for long-term trials is clearly expressed by Silen's (1978) statement that, "Meaningful expression of genetic variation can occur early for some traits but requires many decades for several that are commercially important."

Pacific Northwest Studies

Questions arose as to the consequences of seed movements with the beginning of artificial regeneration in the National Forests of the Pacific Northwest. Because of the economic importance of Douglas-fir, a provenance study was initiated by Raphael Zon in 1912 (Munger and Morris 1936).

That first common garden experiment with *Pseudotsuga menziesii* var. *menziesii* was started with collections of seed from 120 open-pollinated parent trees, 15 to 600 years of age, in the fall of 1912 at altitudes that ranged from 90 m to 1,170 m. The 13 localities where seed was collected are situated between 44°and 49°lat. N in western Oregon and Washington (Figure 4.1).

Progeny from each parent were planted in 1915 and 1916 as 1–1 stock in four localities: the northern Washington Cascades on the Snoqualmie NF at 610 m; the southern Washington Cascades on the Gifford Pinchot (formerly Columbia) NF at 335 m; the northern Oregon Coast Range on the Siuslaw NF at 600 m; and the northern Oregon Cascades on the Mt. Hood NF at 853 m and 1,402 m. In the Mt. Hood NF, six test plantations were established at three different sites that differed in altitude. The 1915 and 1916 plantings at the third site were destroyed by fire in 1917. In the Snoqualmie, Gifford Pinchot, and Siuslaw National Forests, only one site was used for the test plantations. Unfortunately, the 1915 plantings on the Snoqualmie NF and the 1916 plantings on the Siuslaw NF had also to be abandoned shortly after establishment because of animal damage in the former, and poor survival in the latter.

Notwithstanding some shortcomings in its experimental design (that is, individual tree progenies were not replicated and were planted in the same sequence in all plantings), the 1912 provenance study has provided some valuable answers as to the value of a local seed source in regeneration.

Records of the performance of the 13 seed sources over a period of 60 years, summarized by Silen (1965, 1966b, 1978), demonstrate that seed source and genotype by environment interactions were mostly of minor consequences at age 17, but had become large at age 60 for both families and seed sources. With more than 80% of live trees on all five sites, survival did not differ greatly near the end of the second decade. That pattern had changed drastically by the end of the sixth decade. Then, survival varied from 24% to 64%. Exposure of site turned out to be a significant factor in relation to survival. In the Mount Hood plantation B, at the highest elevation (1,402 m) and most severe site, progeny from some low-elevation races suffered heavy losses during the first decade. By age 60, only progeny from three of the high elevation sources had enough survivors to form a stand. In plantations at lower elevations (335 m and 610 m), but exposed sites, mortality was high in maladapted races after age 30. At age 60, several of the 13 sources displayed poor stocking and growth on these sites. By contrast, all but two races had full stocking at that age on a sheltered site at 853 m altitude. Decimation of these two occurred mostly in the fifth decade after establishment.

Perhaps the most important result of the 1912 Douglas-fir heredity study was the demonstration that seed movement can involve risks of unacceptable mortality, but a long time may pass before it becomes apparent. As Silen (1978) stated, however, "The results suggest also that these risks may be reduced by shorter rotations, by seed movements involving only minor environmental changes, or by choice of sheltered sites."

Concerning the Wind River test site and the then 80-year-old 1912 provenance study, Silen and Olson (1992) concluded that

- understocking is the primary symptom of maladaptation;
- inherent growth rates are stable over time; and
- yields are initially related to growth rate but become increasingly related to survival.

This last point is very important as some provenances that had good growth rates for the first 20 years suffered considerable damage and mortality from some extreme climatic event such as the November 1956 freeze that damaged and killed some mature trees.

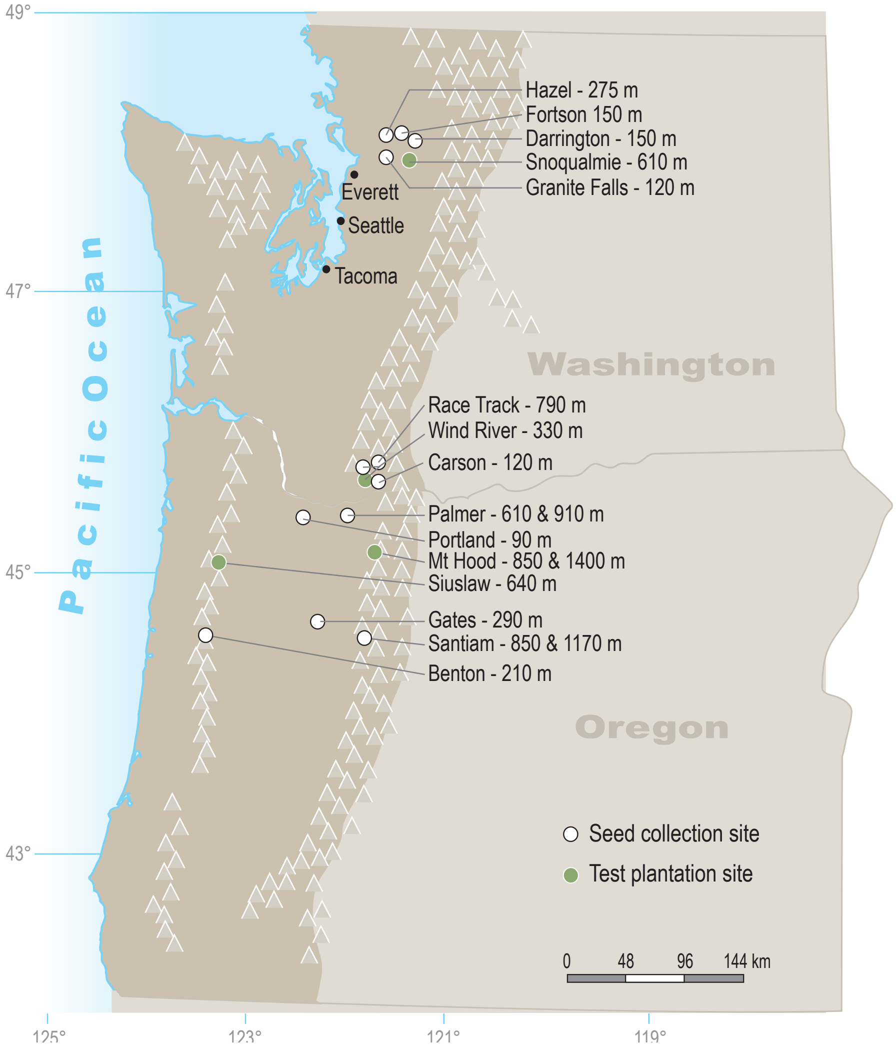

Figure 4.1 Seed collection and planting sites of 1912 Douglas-fir heredity study (from Munger and Morris 1936).

The 1954 Oregon State University provenance study

Forty-two years after initiation of the 1912 Douglas-fir provenance study, a second provenance trial was initiated at Oregon State University (Ching and Bever 1960). Like the 1912 study, the 1954 trial was limited to seed sources from the coastal variety. It included 16 different provenances from Vancouver Island to southwestern Oregon in 16 reciprocal outplantings of two plantations each, at or near the locations of seed collection. In addition, a single plantation that contained the 16 provenances was established in northern California. Assessments of the performance of provenances were made at ages 3 (Ching 1965), 9 (Rowe and Ching 1973), 20 (Ching and Hinz 1978), and 25 years (White and Ching 1985). The study showed only small differences at age 25 in the relative performance of the different provenances, and none among eight low-elevation seed sources. There was little evidence for interactions between provenances and planting location. These findings appear to conflict with those of seedling tests that indicated tight adaptation of Douglas-fir in the Pacific Northwest to local environments (Hermann and Lavender 1968, Campbell and Sorensen 1978, Campbell 1979, White et al. 1981). A possible explanation for these seemingly contradictory results may be that a broad genetic mix of families within each provenance of the 1954 trial tended to reduce, or even eliminate, provenance x location interactions. Furthermore, most of the plantations were on fertile sites with mild climates, and did not experience extreme climatic disturbances. On such sites, expression of provenance differences and provenance x location interactions may require unusual climatic events.

Also in 1954, another provenance trial commenced in British Columbia, but it was restricted to just one planting site at Haney, British Columbia (Haddock et al. 1967). The trial was established with commercial seed lots representing nine coastal provenances from British Columbia, Washington, Oregon, and California, with six interior provenances from British Columbia, Montana, and Colorado. Differences in height growth among the provenances apparent in the nursery phase remained essentially the same at age 11. The provenances Ashford, Washington and Surrey, British Columbia ranked consistently at the top from ages 2 to 11. Data on ranking at later ages are not available.

Compared to Haddock et al. (1967), a far more comprehensive study of geographic variation was begun in 1957 by Irgens-Møller (1963). He established a rangewide source archive containing well over 600 individual parent trees or stands. The collections included open-pollinated seed and occasional live seedlings from 10 western states and parts of Canada and Mexico.

Growth and survival measurements, coupled with a complete inventory of the archives plantation in 1989, provided a rare opportunity to assess geographic patterns of genetic variation in a three-decades-old plantation of Douglas-fir (Gamble et al. 1996). Analysis of the plantings made in 1961 and 1987 revealed that (1) local and other low-elevation coastal provenances had the fastest growth and highest survival in the archives plantation; (2) high-elevation provenances from the Cascade Range also had high survival, but significantly smaller diameters at breast height; (3) southern interior provenances from Arizona and New Mexico had the smallest diameters and lowest survival; and (4) the northern interior provenances from Montana and Idaho were intermediate in survival and diameter. These results match a pattern found by Li and Adams (1989) in a rangewide allozyme study of Douglas-fir, which led them to distinguish between three groups, namely coastal, northern, and southern interior populations. The striking differences in growth and survival between coastal and interior provenances found in the archives plantation support the distinction of two varieties within *P. menziesii*.

The British Columbia Forest Service study

The British Columbia Forest Service initiated a comprehensive provenance experiment in 1966 whose principal objective was to develop biologically sound seed transfer rules for British Columbia (Schmidt 1973). That year, the British Columbia Forest Service collected seed from 76 stands in British Columbia, 7 in Washington, and 5 in Oregon (Figure 4.2). Of these 88 seed lots, 26 were included among the IUFRO collection. Seed lots represented variety *menziesii*, except for 10 lots from interior British Columbia, which belonged to variety *glauca*. Each lot comprised a bulked seed sample from at least 10 parent trees spaced widely apart to reduce the likelihood of family relations (Illingworth and St. Pierre 1975).

From 1968 to 1975, provenance plantations were established with 1–1 bare-root transplants at 36 locations throughout British Columbia's Douglas-fir zone (Illingworth and St. Pierre 1975). The provenance study was divided into four series (Figure 4.3) in order to

- screen provenances in five coastal climatic zones (88 at Sooke and Lookout Mountain; 77, 58, 52 at Port Renfrew, 77; 58 at Kemano, and 52 at Mud Bay, respectively;
- test the feasibility of seed transfer across altitudinal gradients (10 provenances at 6 sites);
- probe genotype environment interactions by the response of five standard provenances and a local provenance at 22 sites; and

Figure 4.2 Collection sites for 1966 British Columbia Forest Service provenance study (from Schmidt 1973).

Figure 4.3 Sites of a series of four provenance plantations established 1968 to 1975 (from Illingworth and St. Pierre 1975).

- compare three representative coastal and four representative inland provenances at three high-elevation sites on Vancouver Island.

In his summary of 6-year results, Illingworth (1978) stated that they confirmed the remarkable variability of Douglas-fir populations, not only in their ability to survive and grow on a particular site, but also in their responses to different environments. The data did not demonstrate a pattern of variation in relation to geographic variables.

Trees from the coast-interior transition zone and north-mainland populations were generally shorter, suggesting a relationship between latitude or elevation of population origin. However, in the extensive region between the Coast and Cascade Ranges and the mountains of Vancouver Island and the Olympic Peninsula, there was no clear relationship between vigor and these variables. Moreover, at most sites within that region, the performance of local populations was inferior to that of introduced populations.

The sites where local provenances grew best were located in the Coastal Western Hemlock subzone a (CWHa),[1] the drier of the two CWH subzones. The most vigorous populations originated from within the Coastal Western Hemlock zone (CWH), and they invariably outgrew populations from the Coastal Douglas-fir zone (CDF), especially when planted in that zone. Geographically, the CDF encompasses the islands and lowlands rimming the Strait of Georgia and Puget Sound.

The results also indicated that populations can be transferred up or down in elevation without serious consequences within the CWH zone. But in the high-elevation Mountain Hemlock zone (MH), or

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[1] Zonal classification by Krajina (1969).

in the mainland valleys of the central coast, high-elevation or north-coast populations appeared hardiest. Although they were less vigorous, they are preferable for use in these locations.

At plantation age 20, the patterns observed had not changed from those observed at earlier ages (Ying 1990). The provenances belonging to variety *menziesii* continued to exhibit broad regional differentiation corresponding to the major climatic regions of their origin. Provenances from the moist maritime zone maintained their superiority over those from the dry lowland and the cold coast-interior transition zone. Elevational differentiation was not apparent, however, and regional differences accounted for about 50% of the among-provenance variation.

The results at age 20 appear to lend support to Illingworth (1978), who inferred tentatively from the 6-year results that, "Douglas-fir varies ecotypically throughout a considerable part of its coastal distribution, a primary ecotype being a zone of optimum growth." The substantial variation between provenances in that zone still awaits an explanation, however.

The University of British Columbia trial

Oscar Sziklai, Professor of Forest Genetics at the University of British Columbia, established a Douglas-fir provenance test in 1971 at the UBC Research Forest at Haney, lat 49°16′ N, long 122°34′ W, elevation 145 m, with 102 provenances from the 1966 and 1968 IUFRO seed collections. Seedlings were planted as 1+1 plugs in 1971. The objectives of the study were to estimate the degree of genetic variation among and within provenances under a specific local condition, the magnitude of genetic control over growth characteristics, and the strength of juvenile-mature correlations (Fashler et al. 1987).

Height measurements of trees in 348 families from 11 British Columbia, 16 Washington, 15 Oregon, and 6 California provenances were made in 1972, 1975, and 1978, and then analyzed by grouping provenances according to four seed zones. Three of the seed zones represented coastal and the fourth zone interior provenances. Results of the height measurements demonstrated significant variation in height growth among and within seed zones. The observed large range in seed zone and provenance means indicated considerable genetic variation. This finding suggested that substantial gains were achievable by selecting the most desirable provenances. Ranking of provenances according to mean 1975 and 1978 total height for all provenances showed little change in the ranking of the best 25% of the provenances, which suggested good reliability in the selection of the best provenances at age 5.

Sziklai (1990) wrote that, "Even after 16 growing seasons only the extreme families show a certain consistent performance but the large majority of the families standing between the best and poorest performers still alter their position year after year." Of the five tallest provenances after 16 growing seasons at Haney, four originated from Washington and only one from British Columbia. The most southerly of the four Washington provenances came from Naselle (2°54′ south of Haney). As to the question of which provenances are best suited to a specific site, and how long a wait is necessary to be certain of the right choice, Sziklai (1990) concluded that, after 16 growing seasons, the question can be answered with more certainty than before.

Short-term seedling tests

Short-term seedling tests of coastal Douglas-fir in outdoor nurseries, greenhouses, and growth chambers typically involve a detailed assessment of adaptive traits in the first one to three years, whereas long-term field tests measure overall tree growth over a much longer period of time (Howe et al. 2006.)

Seedling tests in common garden environments and allozyme studies have indicated genetic variation of the variety *menziesii* on a macrogeographic scale that appears to follow gradients (clines) described by latitude, elevation, and distance from the ocean. Some tests have shown that microgeographic factors—aspect for instance—may modify patterns of variation in quantitative traits.

A steep east-west genetic gradient of coastal Douglas-fir in its central range was reported by Campbell and Sorensen (1978). They sampled 40 populations from elevations ranging from 6 to 1,400 m between lat 42°00′ and 48°15′ N. The differential response to soil and air temperatures by these populations was attributed to differences in their genetic makeup.

An investigation of microgeographic variation of Douglas-fir populations was conducted by Campbell (1979). He estimated genetic values of 193 parent trees throughout a 6,100 ha watershed in west-central Oregon from progeny grown in a common garden through three growing seasons. Variation was partitioned into components attributable to parent tree location and differences among trees within locations. Campbell described the large within-location variation as being homogenous within the watershed because variation of traits among trees within locations did not differ among locations. By contrast, virtually all variation could be accounted for by the location of parent trees. The variation patterns in the watershed suggest a three-dimensional cline in which trait values are a function of elevation and north-south or east-west location, the function varying somewhat for each trait. He concluded that topoclinal variation in traits, as well as the large within-location variation, are the consequences of high selection intensities in the seedling stage, the former to selection by average environmental differences along gradients, the latter to microenvironmental heterogeneity.

That the majority of seedling tests in common garden environments concerned with the coastal variety has focused on Douglas-fir from southwest Oregon and northwest California seems to reflect the fact that these are regions of great vegetational, edaphic, topographic, and climatic complexity. In some areas in these two regions, Douglas-fir displays many of the characteristics of a species near its adaptional limits—that is, difficult regeneration, a distribution influenced by topography, and all-aged stands of a species that, in the central parts of its range, is commonly represented by even-aged stands. To maintain fitness in such a heterogenous environment, Douglas-fir, in the opinion of Campbell (1987), has generated many genotypes and a large amount of genetic variability.

A common garden study by Hermann and Lavender (1968) in southwest Oregon provides evidence that microgeographic factors may modify patterns of phenotypic variation along individual mountain slopes. They collected open-pollinated cones from south- and north-facing aspects at 150-m intervals along a transect from 450 to 1,500 m elevation on the western slope of the Cascade Range between lat 42°00′ and 43°12′ N. The progeny were grown for two years in two nurseries, one in southern, and the other in northern Oregon. They were also grown in growth rooms under six combinations of thermoperiod and photoperiod. Trends of variation in traits with elevation were shown to depend partly on slope and aspect.

A geographically broader study (White et al. 1981), intended to represent the range of sites on which Douglas-fir grows in southwest Oregon, involved samples of wind-pollinated seed from two parent trees at 36 locations between lat 42°00′ and 43°12′ N. Elevation of collection sites ranged from 475 to 1,630 m, 61 to 162 km inland from the Pacific Ocean. Seedlings were grown in three test environments (growth room, nursery, and greenhouse) to assess environmental influences on genetic variation of first-year height growth. In all three test environments, mean first-year population height growth correlated most strongly with elevation of place of origin. Seed collected at higher elevations—that is farther inland—produced shorter seedlings.

Subsequently, Campbell (1986) described patterns of genetic variation based on 135 parent trees from 80 locations in southwest Oregon. The area he sampled is nearly square with west and east boundaries about 60 and 190 km from the Pacific Ocean. The southern boundary is on the border with California, and the northern boundary is along the 43°N parallel. Campbell estimated genetic values for 13 traits from the open-pollinated progeny grown in nursery beds. The pronounced east-west gradients shown in this experiment followed trends of steep east-west gradients farther north at high elevations in western Oregon and Washington demonstrated by his earlier work (Campbell and Sorensen 1978), and those reported by Griffin (1978) for the Coastal Ranges of northwest California, and by Sorensen (1983) for the western Siskiyou Mountains.

Sorensen's (1983) study of genetic differentiation of Douglas-fir in the lower Rogue River watershed of southwest Oregon between lat 42°20′ and 42°40′ N provided evidence of steeper genetic clines (elevational and latitudinal) along the coast than farther inland. The investigation of seed and seedling traits was based on a collection of open-pollinated seed made at four elevations between 150 and 1,065 m on west- and east-facing slopes on the first two ridges inland from the Pacific Ocean. Trait differences were generally greater between the west and east aspects of the coastal ridge than between the two aspects of the inland ridge. This pattern of variation appeared to be determined by adaptation to local moisture and temperature regimes.

A comparison of the genetic structure of Douglas-fir from different habitats in southwest Oregon in a common garden seedling study (Hamlin 1990) included eight populations, two each from four major conifer zones: the *Tsuga heterophylla* zones in the Coast Range and the western Cascade Range, the mixed-evergreen zone in the Siskiyou Mountains, and the mixed-conifer zone in the South Cascades-Klamath Range. Measurements of 19 traits over two growing seasons indicated that differences in genetic structure did not vary randomly, but were associated with the extent of habitat divergence.

A nursery study of 18 wind-pollinated families from the North Coast Ranges and Klamath Mountains of northwestern California (Griffin and Ching 1977, Griffin 1978) included progeny from 85 stands at 9 locations within an area extending from lat 37°08′ N, long 122°11′ W to lat 41°47′, long 124°00′ W. At each location, the altitudinal range of Douglas-fir had been sampled by spacing seed collections at 76-m intervals. All assessed traits varied geographically. With the exception of time of budburst, the most significant contrast was between populations from the coastal fog belt and those from the interior ranges. Coastal seed was smaller and germinated more slowly than seed from the interior ranges. Coastal seedlings had fewer cotelydons but greater epicotyl growth, grew for a longer period before setting buds, showed less capacity to set buds in response to moisture stress, and were less cold hardy than those from the interior ranges. But in spite of broad similarities in variation patterns, distribution of variation among sampling levels was not the same for all traits. Griffin and Ching concluded: "The most satisfactory concept of the northern California Douglas-fir population is that of a single gene pool within which a complex spectrum of selection pressure gradients have differentiated sub-populations expressing a comparable range of character combinations."

A later study by Kitzmiller (1990) of genetic variation among northwestern California Douglas-fir was based on height growth of 675 open-pollinated families planted in 1980 in native locales. The investigation included also allozyme analyses of seed from 315 parent trees. His findings indicated the association of a substantial amount of genetic variation with latitude, longitude, and elevation of seed source. Seed weight patterns followed a northwest to southeast cline of increasing seed weight. The main factors associated with changes of seed weight were distance from the ocean and mean annual precipitation. The lightest seeds came from an area 13–16 km distant from the ocean and the heaviest seeds from 40–48 km inland.

Specific gravity of wood exhibited a different pattern. Apparently wood densities of coastal and Klamath Mountains populations are similar at similar elevations, but major differences occur locally between low and high elevation populations. Allozyme patterns, just like those of seed weight, change from northwest to southeast, and with elevation. They separated trees into 8 groups, which formed four geographical zones in a longitudinal direction: coastal, west central, east central, and eastern, subdivided further into two elevational bands.

In marked contrast to variation in the quantitative characters found in seedling common garden studies, results of allozyme studies of coastal Douglas-fir, except one by Kitzmiller (1990), did not indicate associations between allozyme variation and environmental variables. Merkle and Adams (1987) studied the distribution of allozyme diversity among 22 breeding zones in southwestern Oregon based on the electrophoretic analysis of haploid megagametophytes from 1,230 parent trees. These 22 breeding zones provide elevational transects in each of seven breeding units,[2] west-east from the coast inland, and north-south along the coast and inland. Climate differs widely along these transects. Mean annual precipitation decreases rapidly west to

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[2] Southwest Oregon has been subdivided into 38 Douglas-fir breeding zones within 13 geographically designated areas called breeding units. Breeding zones are elevational bands, each of which spans an altitudinal range of < 300 m and is generally smaller than 60,000 ha. They were established in regional Douglas-fir tree improvement programs (Silen and Wheat 1979).

east, and minimum winter temperatures decrease with distance east from the coast and with increasing elevation. Merkle and Adams reported that less than 1% of the variation could be attributed to differences among zones. The lack of a relation between allozyme variation and geographic variables was in striking contrast to a companion common garden study that, although based on the same material, revealed significant clinal patterns of genetic variation for quantitative traits (Loopstra 1984, Loopstra and Adams 1989). Use of a different technique, multivariate analysis of allozyme variation patterns to describe the distribution of genotypic variation among and within these 22 southwest Oregon breeding zones also failed to provide evidence that allozyme variation is adaptive in the coastal Douglas-fir breeding zones studied (Merkle et al. 1988).

In another attempt to ascertain whether a similar adaptive differentiation for allozyme variation exists in the same heterogenous environments as has been shown for quantitative traits, stands of Douglas-fir on nearby south- and north-facing slopes were genetically compared in two of the breeding zones in southwest Oregon (Moran and Adams 1989). Samples for the study consisted of 60 trees from each of 12 stands. Dormant buds (as well as needle tissue in one stand) were used for enzyme analyses. These analyses indicated that the proportion of total genetic diversity that resulted from differences among stands was only 1.8%, a percentage close to that attributed to differences in the distribution of allozyme diversity among 22 breeding zones in southwest Oregon (Merkle and Adams 1987). The obvious conclusion is that abrupt changes in slope aspect or steep elevational gradients within breeding zones in southwest Oregon appear to have little influence on the genetic structure of Douglas-fir as shown by allozymes.

Results of the allozyme studies in southwest Oregon agree with those of an earlier study in southwest British Columbia (El-Kassaby and Sziklai 1982). That investigation described genic patterns at 27 different allozyme loci in a natural stand of Douglas-fir along an elevational transect divided into four elevational segments, as well as the pattern of variation for seven different quantitative traits. Only 7% of the total genetic diversity was attributed to differentiation among the elevational segments; the remaining 93% resided within segments. The traits studied showed the same general trend of variation in the different elevational segments ranging from 94% to 100%.

Common garden studies: variety *glauca*

Except for the rangewide source archive plantation established in 1957 by Irgens-Møller (Gamble et al. 1996), reports of observations extending over several decades have not been published for any of the common garden studies of variety *glauca* in North America. Wright et al. (1971) initiated a comprehensive study in 1961 to determine geographic variation patterns in interior populations of Douglas-fir, and to identify suitable provenances for Christmas tree and ornamental use in the north-central states. The study included 74 provenances belonging to the northern subgroup and 33 provenances from the southern subgroup of inland Douglas-fir, as well as 21 provenances of the variety *menziesii*. The tallest seedlings were outplanted as 1-2 stock in 1965, the remaining ones as 1-2-2 stock in 1967, in three locations in southern Michigan. Five-year results indicated that Arizona and New Mexico provenances grew rapidly enough to be harvested as Christmas trees 6 to 8 years after planting, but those from the central and northern Rocky mountains grew considerably slower. By contrast, the pattern for cold and frost hardiness was just the opposite: the slower growing northern provenances were hardier than the faster growing southern provenances.

A provenance test begun 1965 in Plattsmouth in eastern Nebraska (Read and Sprackling 1976) included seedlings of 26 provenances from the northern subgroup and 15 provenances from the southern subgroup of inland Douglas-fir. Seedlings came from the collection made for the Michigan study by Wright et al. (1971). Data that covered performance for the first 11 years in the plantation showed that growth rates of provenances were inversely related to their latitude of origin. Progeny of populations from Arizona, New Mexico, and southern Colorado grew two or three times as fast as those from populations belonging to the northern subgroup of interior Douglas-fir. But the former incurred more frost damage and winter injury than the latter. By age

22, this pattern had essentially remained the same (Van Haverbeke 1987).

In 1966, the British Columbia Forest Service collected seed lots from 64 stands distributed over the entire natural range of variety *glauca* for a provenance trial. Each seed lot consisted of bulked, open-pollinated seed from a minimum of 10 dominant or codominant trees per population. The trial had as its objective to determine broad patterns of geographic variation in interior Douglas-fir and to generate information about growth and adaptability for a broad spectrum of var. *glauca* populations in the southern interior of British Columbia (Jaquish 1990).

The seeds were sown in spring 1972 at the Cowichan Lake nursery. The resulting seedlings were planted in fall 1975 in a replicated experiment at the Trinity Valley Tree Breeding site near Enderby in southern interior British Columbia. The site is at 600 m elevation in the cool, moist Interior Cedar Hemlock (ICH) biogeoclimatic zone.[3] After 10 growing seasons, survival for the entire plantation was 87%. Survival of provenances ranged from 0 and 1% for the two Mexican provenances to 100% for five provenances that belonged to the northern subgroup of var. *glauca*.

Provenances varied tremendously in height at age 13 from seed, with a range from 130 to 472 cm. Most provenances—that is 21 out of 23—that belonged to the southern subgroup ranked in the lower half, below 300 cm, of the height range. Of the 13 tallest provenances, 7 originated from the low to middle elevations of the interior wet belt (ICH) zone, and 6 came from the dry subzones of the east slopes of the Coast mountains and Cascade range (Coast Interior Transition zone). Provenances from the Shuswap Lake and North Thompson River areas were the tallest among the provenances from the ICH zone. These findings indicated strong racial differences in height growth of interior Douglas-fir and, in particular, between its northern and southern subgroup in height growth patterns. But the results are at variance with those from provenance tests by Wright et al. (1971) and Van Haverbeke (1987), who found that provenances from the southern subgroup grew much more rapidly than those that belonged to the northern subgroup. Maladaptation of the southern provenances to the Trinity Valley environment may account for the slow growth at that site. Jaquish (1990) concluded that, "On mild, low elevation sites within the ICH biogeoclimatic zone of the southern Interior, seedlings from most provenances belonging to the northern race can be established and expected to survive; however, major differences in productivity can be expected among provenances. To maximize productivity in plantations on these sites, provenances originating from the Shuswap Lake/North Thompson River area are recommended for planting."

A series of seedling common garden studies by Rehfeldt (1974a, 1974b, 1978, 1979a, 1979b, 1982, 1983a, 1988) have provided by far the best insight into the reasons for the variability of quantitative traits in the northern subgroup of variety *glauca*. These experiments, which compared populations throughout the range of the northern subgroup of variety *glauca*, showed steep adaptive clines for inland Douglas-fir in northern Idaho and western Montana. Rehfeldt (1989) summarized patterns of genetic variation in interior Douglas-fir across 250,000 km^2 of forested lands in the northern Rocky Mountains, based on results from four of his common garden studies. He used data from 228 populations included in these tests to show the extent of genetic variation within four physiographic provinces; in northern Washington and northern Idaho (Rehfeldt 1979b); northwestern Montana (Rehfeldt 1982); central Idaho (Rehfeldt 1983a); and southwestern Montana and Idaho, near the Continental Divide (Rehfeldt 1988).

For each of these studies, seeds were collected from open-pollinated trees in natural stands. Their progeny were grown for three years in two of the same common gardens at elevations of 762 m and 1, 524 m near Priest River in northern Idaho. Comparisons of the seedling populations were based on several traits that reflected growth, development, and frost tolerance. Rehfeldt used third-year height to index adaptive differentiation because this variable was the only trait common to all studies but was also the most strongly correlated with other traits. Populations from elevationally or geographically mild sites were tall but had low freezing tolerance, and populations from harsh sites were short and

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[3] Zonal classification by Pojar et al. (1987).

cold hardy. Rehfeldt (1991) constructed a model of genetic variation from the data provided by these studies that produced elevational clines of the same shape for all locations. The slope of the elevational clines varied geographically, however. For instance, the elevational cline is steepest in northern Idaho and northeastern Washington, where Douglas-fir grows at the lowest elevations but is nearly flat in southwestern Montana where the species occurs only at high elevations.

Models are invariably subject to errors and require verification with independent data. A strong validation of this model of genetic variation resulted from a study that attempted to answer the question of how much variation in site index is associated with genetic variation. Monserud and Rehfeldt (1990) correlated the genetic variability predicted by Rehfeldt's (1989) model with the mean 50-year height of three trees in each of 135 natural stands in northern Idaho and western Montana. The genetic variability predicted by the model accounted for 42% of the variation in 50-year dominant height among these 135 stands. Rehfeldt (1991) concluded that the variability of the northern subgroup of interior Douglas-fir has been brought about by environmental selection to produce populations physiologically adapted to specific segments of the various environmental gradients. Nonetheless, substantial genetic variation exists within populations.

The IUFRO International Douglas-fir Provenance Study

The introduction of *P. menziesii* into the temperate zones of the southern and northern hemisphere, outside of North America, led to numerous provenance trials of the species in various countries during the first half of the 20th century. Most of these trials suffered from two shortcomings, however. One was lack of precise information about the geographic location of the seed sources and the method of seed collection, and the other was very limited coverage of the natural range of Douglas-fir.

The project of a range-wide seed collection initiated by the former Section 22 of the International Union of Forest Research Organizations (IUFRO) in 1965 provided an opportunity for institutions not only to obtain seed of exactly known origin but also the prospect of comparing results later with others who conducted provenance tests with the same material. The IUFRO seed collection was organized by H. Barner of the Danish State Forestry Tree Improvement Station in Humlebaek, Denmark. A total of 326 kg of Douglas-fir seed was collected from 182 stands in the years 1966/68/69/70. To facilitate revisits for additional collections, the exact location of each of the 182 seed sources was marked on a large-scale map (Fletcher and Barner 1987). To eliminate any inbreeding effects, cones were harvested in each stand from 15 to 20 dominant and codominant trees distributed equally throughout the stand within a distance of about 100 m from each other. Seeds were kept separate for each tree, so that single-tree samples could be provided for institutions that requested them. The remaining seeds from each provenance were bulked before distribution to participants in the IUFRO International Douglas-fir provenance study. By 1973, samples had been distributed to 45 institutions in 30 countries (Barner 1973) in both the northern and southern hemispheres. Published findings that pertain to the IUFRO International Douglas-fir provenance study are covered after the discussion of earlier European provenance trials.

Pre-IUFRO European Studies

Douglas-fir was introduced into Europe in the 19th century with seed of the variety *menziesii,* but the location of the mother stands is unknown. Trees from these early plantings adapted well to the environment and often surpassed the growth of native European conifers. The early plantings had been on a small scale and little thought had been given to the origin of seed. That changed as some European foresters advocated larger use of Douglas-fir in forest plantings and realized the need for more knowledge about suitable seed sources. Consequently, numerous provenance tests were initiated in Europe in the 20th century.

German provenance trials

The 1904–1911 Fürstenberg trial

Baron von Fürstenberg established six test plantations between 1904 and 1911 on his estates in

Westphalia. Kanzow (1937) referred to that undertaking as the "*caesia* provenance trial of Fürstenberg," although it would hardly qualify as a provenance test by present-day standards. The Fürstenberg trial is included here, however, because it represents the first recorded attempt to test the growth of Douglas-fir from the transition zone between the coastal and inland variety in Germany. Apparently, some of the trees in his test plantations originated from seed Fürstenberg had collected during his travels in British Columbia in 1903 and 1904. He did not indicate as to how many stands his collections represented, merely that they came from areas in the vicinity of Field and Quesnel, British Columbia (Fürstenberg 1923).

Fürstenberg did not plant any coastal provenances for comparison. But Kanzow compared mean height of trees in Fürstenberg's plantations with his yield tables (Kanzow 1937) for coastal Douglas-fir. He found that growth of Fürstenberg's trees was intermediate between his site class I and II for coastal Douglas-fir, at least until age 33. Information about the subsequent development of the Fürstenberg plantations was not found.

The 1910 Schwappach trial

Shipments of seed of inland Douglas-fir to Germany by the U.S. Bureau of Forestry from 1891 to1895 led eventually to the initiation of a provenance trial by the former Prussian Forest Experiment Station. Adam Schwappach, its director from 1899 to 1925, had noticed what he conceived to be geographic variability in progeny from these seed imports and decided to investigate the importance of seed source for future procurements of seed (Schwappach 1907).

He established a provenance test at Chorin, Brandenburg, in spring 1910 with seed from the 1909 cone crop obtained through the help of Raphael Zon of the US Bureau of Forestry (Schwappach 1914). The first good seed year after the crop failures in 1907 and 1908 was in 1909 (Schwappach 1909). The seed collection consisted of 19 provenances, 12 from the northern and 2 from the southern subgroup of variety *glauca*, and 5 of the variety *menziesii*. Three of the coastal provenances were from California and two from the Snoqualmie area in Washington. That only two western Washington provenances were included in the collection sent to Schwappach is surprising in view of the fact that Zon had told Schwappach (1911) that seed from the western slopes of the Cascades between lat 45°and 50°N would be best suited for use in Germany.

Trees in the Chorin plantation were measured at ages 5, 18, 25, and 44 from seed (Schwappach 1914; Kanzow 1936, 1937; Flöhr 1954). Growth ranking remained essentially the same from age 5 to 44. The two Snoqualmie provenances were the best performers and had reached heights of 27 and 26 m and diameters breast height of 31 and 29 cm, respectively. Height of the three California provenances was 4 to 6 m less, and that of the surviving inland provenances was from 8 to 14 m lower.

Infection with *Rhabdocline pseudotsugae*, first observed in 1930, caused serious damage to the inland provenances in the following year but remained without noticeable effects on the coastal provenances (Liese 1932, 1935, 1936). Flöhr (1954) reported that, by 1953, 5 of the 14 inland provenances had been practically eliminated and the remaining 9 showed low vigor.

The 1912 Kaiserslautern trial

Ernst Münch, Professor of Forest Botany at Ludwig-Maximilian University in Munich, established a parallel test with 10 of the 19 provenances in the Chorin trial, during his tenure as supervisor of the former Kaiserslautern-Ost Forest District in Rhineland-Palatinate. Schwappach had sent Münch 8,000 two-year-old seedlings which were planted in spring of 1912 in the northern Pfälzerwald mountain range. The test plantation is located at lat. 49°25'N, long. 7°40'E. Seedlings belonged to one var. *menziesii* provenance from northwest Washington and to nine var. *glauca* provenances, four from the variety's southern subgroup and five from its northern subgroup.

Performance of provenances in this trial has been followed for 88 years, which is probably the longest period of observation for any of the European provenance tests. Assessments made during that span of time were published by Münch (1923, 1924, 1928), Kanzow (1937), Boiselle (1953), Rohmeder (1956), Stimm (1995), and Stimm and Dong (2001). The earlier assessments, as well as the last at age 90 from seed, showed that Snoqualmie, the only var.

menziesii provenance in the trial, was consistently the best performer throughout the length of the trial. The total cumulative yield at age 90 was 1, 958 m^3/ha with bark. The MAI at that age was 21.8 m^3/ha. The volume production of the three surviving var. *glauca* provenances reached not even half of that of the var. *menziesii* provenance. The provenance Bitterroot from western Montana, which ranked second in volume production, had only a total cumulative yield of 847 m^3/ha and a MAI of 9.4 m^3/ha.

Trees remained free of diseases until 1932 when Münch observed infection with *Rhabdocline pseudotsugae* on two of the provenances. In subsequent years, the disease spread to all inland provenances. *Phaeocryptopus gaeumannii* appeared in the plantation in 1939. By 1967, nearly all trees of six of the var. *glauca* provenances had succumbed to the needle cast fungi. Infection with both *Adelopus* and *Phaeocryptopus gaeumannii* was first noticed in trees of the provenance Snoqualmie in 1951. The infections were never so severe as to have a major effect on growth.

The 1930s trials

In spite of the shortcomings of the first German provenance tests of Douglas-fir (that is, very limited coverage of the species' range and lack of replications), they yielded one important result. The tests demonstrated that var. *glauca* is poorly suited for planting under most forest conditions in Germany because of its slow growth and its susceptibility to severe infection with *Rhabdocline pseudotsugae*. The realization that var. *menziesii* was inadequately represented in the initial provenance tests led to initiating several provenance tests mainly with coastal Douglas-fir in the 1930s. The good Douglas-fir cone crop of 1929 in many parts of the Pacific Northwest, which made seed readily available, seems to account for the fact that these tests were begun at about the same time.

The 1932–1933 Wiedemann trials

The most comprehensive of these trials was due to the initiative of Eilhard Wiedemann, Director of the former Prussian Forest Experiment Station (Schober 1954). His test included 19 provenances, 15 from the Pacific Northwest, 1 from Colorado, and 3 from German stands of coastal Douglas-fir of unknown origin. Some of the American provenances had identical geographic designations, but they may have differed somewhat by elevation of seed source. The seed was bought in 1932 from the Long-Bell Lumber Company in Longview, Washington. Wiedemann had secured the cooperation of 12 forest districts in various parts of Germany and of the Danish and Hungarian Forest Experiment Stations to establish test plantations to compare the performance of provenances under different growing conditions. He divided the 19 provenances into two series with the assignment of 8 of the provenances to 7 German forest districts, and 11 of the provenances to 5 German forest districts and to the Danish and Hungarian cooperators (Tables 4.1 and 4.2).

Wiedemann's choice of locations for the test plantations represented a cross section of the major climatic provinces of Germany. Although 10 of the test plantations have been destroyed or have met with an unknown fate, those that have remained available for observation are in regions of contrasting climates. The Danish and Rosengarten plantations are on low-elevation sites with a pronounced oceanic climate. The Braunlage plantation represents

Table 4.1 Provenances and test locations in the 1932 to 1933 Wiedemann trials (modified from Schober 1954), Series I.

Provenance	Elevation (m)
Salmon Arm, British Columbia	900
Stella, Washington	60
Ryderwood, Washington	250
Spirit Lake, Washington	1100
St. Helens, Washington	2000
Lebanon, Oregon	550
Sweet Home, Oregon	900
Kleinengstigen, Würtemberg	?
Plantation location	
Korpele, Poland (formerly East Prussia)*	160
Eberswalde, Brandenburg**	30
Freienwalde (section 151), Brandenburg*	95
Rosengarten, Lower Saxony (formerly Harburg)	40
Namslau, Lower Silesia, Poland***	121
Schönlanke, Pommerania***	75
Kirchzarten, Black Forest	1300
Braunlage	600

* Destroyed by frost

** Destroyed by fire

*** Fate unknown

Table 4.2 Provenances and test locations in the 1932 to 1933 Wiedemann trials (modified from Schober 1954), Series II.

Provenance location	Elevation
Kamloops, British Columbia	800
Salmon Arm, British Columbia	100
Elma, Washington	60
Ryderwood, Washington	200
Spirit Lake, Washington	1100
Snoqualmie, Washington	1650
Lebanon, Oregon	500
Cascadia, Oregon	900
Gaildorf, Württemberg	329
Lauterbach, Hesse	370
Plantation location	
Freienwalde Brandenburg (section 171)	95
Krasiejów, Upper Silesia***	189
Pfeil, East Prussia*	132
Braunlage, Lower Saxony (formerly Hohegeiss)	560
Giessen, Hesse*	200
Nødebo, Denmark	9
Kompedal, Denmark	65
Hungary***	

* Destroyed by frost
** Destroyed by fire
*** Fate unknown

a medium elevation site in the transition zone from an oceanic to a continental climate. The Freienwalde plantation is subject to the continental climate of the northeast German plains, and the one at Kirchzarten has the harsh climate typical of high elevations in the mountains of southwestern Germany.

Kanzow (1937) reported on the initial phases of the plantations in the Wiedemann study. Schober (1954) reviewed available information on plantations of Series I and II at age 24 from seed and analyzed in detail development of the plantations at Kirchzarten and Braunlage. The following year Schober and Meyer (1955) reported on the plantation at Rosengarten; it had been presumed a war loss but it and the papers containing the layout of plots were relocated in the early 1950s. Erteld (1948), Dittmar (1954), and Dittmar and Knapp (1967) provided accounts of the state of the Freienwalde compartment 171 plantation.

The best growth performers at age 24 from seed were provenances from low and medium elevations of the western slope of the Washington Cascades, except on the sites with a continental or harsh high-elevation climate. Provenances from sources in the Cascades above 1,000 m had excellent growth at the 1,300 m site in the Black Forest (Kirchzarten District), but they performed marginally elsewhere, as did the Oregon provenances in all test plantations. The British Columbia provenances from the northern subgroup of var. *glauca* grew rather poorly in the maritime climate of the coastal region of northwest Germany but they exhibited good growth in the continental climate of the northeast German plains. That rate of growth is shown by measurements at age 37 in the Freienwalde plantation where the two inland provenances from British Columbia retained their leading position in total volume growth. The Colorado provenance, however, was a complete failure at Freienwalde, as in all other test plantations. Performance of the progeny from German Douglas-fir stands was equal to that of the best American provenances.

The Kirchzarten plantation, elevation 1,300 m was remeasured in 1981 at age 52. The low-elevation provenances from the Washington Coast Range showed the best growth, but the superiority of the high-elevation provenances from the Washington Cascades observed in 1952 had not been maintained. Estimates based on the 1956 yield tables for Douglas-fir by Schober indicated an M.A.I. at age 75 of 2 to 5 m^3/ha. That estimate pointed to poor prospects for Douglas-fir at high elevation sites in the Black Forest (Kenk and Thren 1984b).

The Wiedemann study suffered several shortcomings quite common in early provenance studies. Provenances were not replicated in the test plantations. The condition of seedlings at outplanting in the field appears to have differed significantly between plantations. First- and second-year survival was highest, 88%, at Rosengarten, the site nearest to the Halstenbeck nursery where all the seedlings for the experiment had been raised. It was lowest, 55%, at the sites in East-Prussia and Upper Silesia farthest away from the Halstenbeck nursery. All plantations, except the one at Rosengarten, were established on large clearings. The consequence was heavy damage by early and late frosts. At the Rosengarten site, seedlings were planted under the shelter of 85-year old Scots pines that prevented frost damage. Subsequently, however, competition from the pine overstory and establishment of natural regeneration of pine affected the growth of Douglas-fir.

In spite of all these shortcomings, a broad picture of differences in provenance performance did emerge. Coastal provenances from low elevations in Washington grew best in the coastal region of northwestern Germany and at low elevations in the montane regions of central Germany. Provenances from interior southwestern British Columbia showed their best performance in the northeast German plains and at high elevation sites in central and south German mountain ranges.

The 1930 Geyr von Schweppenburg trial

The test was established with 13 provenances in a single plantation at an elevation of 360 m in the Gahrenberg forest district in Lower Saxony by Geyr von Schweppenburg, Professor at Georg-August University at Göttingen. Five of the provenances belonged to var. *menziesii,* four to the northern subgroup, and three to the southern subgroup of the var. *glauca*. Except for two of the inland provenances obtained from the Danish seed firm Rafn, all other seed came from the Long Bell Lumber Company and probably from seed sources geographically close to those used in the Wiedemann trials. The 1953 measurements at Gahrenberg by Schober (1954) gave results similar to those reported from the Braunlage and Freienwalde plantations—that is, the highest volume production by the Salmon Arm, Kamloops, and low- and medium-elevation Washington provenances, and marginal growth by the Oregon and high-elevation Washington provenances.

The 1930 Fabricius trial

Professor Ludwig Fabricius, former Director of the Bavarian Forest Research Institute, established a provenance trial with test plantations in 23 Bavarian forest districts (Rohmeder 1954). The provenances included five from the western slope of the Washington Cascades, one from the Siskiyou Mountains, and one from Mexico. The Washington provenances were not identified by geographic location but only by a letter code, based on the five elevational spans. Each of the five Washington provenances represented one of these elevational spans: <100 m, 100-300 m, 300-600 m, 600-900 m, 900-1,500 m. The seed stemmed from a 1929 shipment by the Longbell Lumber Company. The Longbell Lumber Company used letter codes to indicate elevation of seed source and the corresponding number of frost-free days (Table 4.3).

The objective of the trial was to learn more about potential seed sources specifically for use in Bavaria. Presumably, limited availability of planting stock permitted planting of all 7 provenances solely at the Grafrath test plantation. Plantations in the other 22 districts contained just one or two of the provenances. At the time of measurements in 1951, test plantations were left in only 12 of the districts. Performance in regard to total volume production at age 21 from seed is shown in Table 4.4.

Phaeocryptopus gaeumannii, the Swiss needle cast pathogen, was present in all plantations, but provenance e was less affected by the disease than any of the others. That circumstance may have been a contributory factor to provenance e's superior volume production. In spite of its shortcomings, the Fabricius trial pointed to seed from low and medium elevations in western Washington as a good choice for planting on medium elevation sites in Bavaria.

The 1954/1958 Lower Saxony Forest Experiment Station trials

Renewed interest after World War II in finding suitable seed sources of Douglas-fir for planting in Germany led to the initiation of a provenance trial in four Lower Saxon forest districts in 1954

Table 4.3 Letter codes used by Longbell Lumber Company to indicate elevation of seed source and the corresponding number of frost-free days.

Code	Elevation (m)	Frost-free days
a	<100	<270
e	100-300	180-270
i	300-600	150-180
o	600-900	110-150
u	900-1,500	60-110
y	>1,500	>60

Table 4.4 Performance of seed in test plantations in 23 Bavarian forest districts in regard to total volume production at age 21.

Provenance	a	e	i	o	u	Siskiyou Mountains	Mexico
MAI m^3/ha	4.7	7.3	4.3	3.2	2.5	1.7	1.0

through the initiative of Ernst Pein, owner of a large forest-tree nursery near Hamburg. The trial included 19 provenances from Washington and Oregon. A complement to that trial consisted of establishing test plantations in eight more forest districts by the Lower Saxon Forest Experiment Station in 1958 with four Washington, one Oregon and two British Columbia provenances. Seed for the trials came from commercial sources.

In both the 1954 and 1958 tests, the Washington provenances grew better than those from Oregon, and low-elevation provenances grew better than those from higher elevations. Of the two British Columbia provenances, Salmon Arm grew better than the Vancouver Island provenance (Dong 1970). Mortality and severity of frost damage was significantly less in the Washington provenances than in those from Oregon. Lowest mortality and frost damage occurred in Washington provenances from elevations below 600 m and in the Salmon Arm provenance. The southern Oregon provenances incurred the heaviest losses (Dong 1973).

The 1955/1958 Baden-Wuerttemberg trials

Aside from the provenance plantation at Kirchzarten—established in 1932 on an extreme site—no other existed in Baden-Wuerttemberg before 1955. This region has some excellent stands of Douglas-fir, but they can provide only a fraction of the amount of needed seed. The initiation of 4 provenance tests on 16 sites throughout Baden-Wuerttemberg from 1955 to 1961 represents an effort to provide some basis for selecting suitable seed sources (Kenk and Thren 1984a).

The 1955 test established by Professor Mitscherlich of Ludwig Albert University Freiburg and Mr. Kirschner, a retired forest service officer, included 9 Washington and 10 Oregon provenances. The seed stemmed from collections by the USDA Forest Service and was obtained by Ernst Pein of the Pein & Pein Forest Tree Nurseries during a visit to the Pacific Northwest. Information about site and quality of mother stands was provided by Charles Rindt, former silviculturist of Region 6 of the USDA Forest Service.

The second 1955 trial, with two British Columbia and three Washington provenances with commercial seed of loosely defined origin, was established by the Stuttgart Forest Directorate. Professor Mitscherlich initiated a third test in 1958 with four provenances from Washington and one from Oregon. The seed purchased from the Manning Seed Company in Washington was a composite from several stands.

A fourth trial was established 1961 at 10 locations in Baden-Wuerttemberg through the initiative of Prof. Schober (Kenk and Thren 1984a). The 11 North American provenances, 4 from British Columbia, 4 from Washington, and 3 from Oregon in this test stemmed from seed collections made for the 1958 provenance trial in northwest Germany (Schober et al. 1983). Progeny from 4 Douglas-fir stands in the Black Forest and the Suabian Alb was planted, in addition to the North American provenances.

Kenk and Thren (1984b) concluded that after 22 years of observation of test plantations in the 16 localities preliminary judgments were possible as to the suitability of seed sources for cultivation in Baden-Wuerttemberg. Washington provenances from elevations between 300 and 600 m, as well as progeny from German stands, appear to be best suited because they performed extremely well on all test sites. Poorly suited seed sources are from interior British Columbia, the Oregon Cascades, and the Klamath Mountains because of their unsatisfactory growth.

The 1958 Schober trial

Members of the Section Mensuration in the German Union of Forest Research Institutes decided in 1954 to initiate a Douglas-fir provenance trial because of the need for more extensive testing of provenances of exactly known origin. The task fell to Reinhard Schober, Professor at Georg-August University Göttingen, who, in conjunction with the Lower-Saxon Forest Experiment Station, organized the establishment of an experiment with 39 provenances on 14 sites in northern and western Germany (Schober et al. 1983, 1984).

The trial includes seed from 37 documented sources in British Columbia, Washington, Oregon, and two German stands. Because of spotty cone crops, seed collection took from 1955 to 1958. Trees were outplanted as 1+2s in 1961. Measurements were taken at ages 11, 16, and 21 from seed.

The results confirmed those of earlier trials but revealed something less apparent in earlier tests. The provenances from Vancouver Island, and especially those from interior British Columbia, decreased growth with increasing age. Secondly, provenances from the coastal region of northwestern Oregon showed surprisingly good growth, equal to that of those from the Washington Cascades and the Olympic Peninsula. Differences in growth between provenances were considerable, although the trial covered only that part of the species' natural range of interest for procuring seed to be used in Germany. Provenances ranged from site class I to III in total volume production.

The 1958 Hessian Forest Experiment Station trial

The Hessian Forest Experiment Station initiated a Douglas-fir provenance test in 1958, with 30 of the 39 provenances used in the 1958 Schober trial. The material used in the Hessian test stemmed from 5 British Columbia, 17 Washington, 7 Oregon, and 6 additional German seed sources, 5 of which came from the Odenwald and one from the Vogelsberg area (Rau 1985). Seedlings were outplanted in 1961 as 1-2s in seven Hessian forest districts. Height, diameter, and stem form were recorded at age 23 from seed.

The best provenance for growth was Humptulips from the Olympic Peninsula. Most provenances from the west slope of the Washington Cascades, especially those from the Darrington area, likewise showed excellent growth. The performance of the two interior provenances from British Columbia was poor, and growth of those from Vancouver Island and the western half of the Oregon Cascades was only slightly better. Progeny of German stands, particularly those from the Odenwald, was generally superior in growth to nearly all the North American provenances. Results of the Hessian test generally agreed with those of the 1958 Schober trial, in spite of differences in experimental design and site conditions.

The 1962–1963 trial of the Schmalenbeck Institute of Forest Genetics and Forest Tree Breeding

Klaus Stern, Professor of Forest Genetics at Georg-August University, Göttingen, initiated a trial in the Forest District Nordhorn as part of the Emsland reforestation project in northwest Germany (Herrmann 1973). The test included 81 provenances from throughout the range of the species including one from Mexico at lat 25°17 N. The seed stemmed from collections made by North American forest research institutions.

Height measurements at age 10 and 11 years showed the provenances from the coastal regions of Washington and northern Oregon to be the best performers (Stern et al. 1974, Hattemer and König 1975). The growth of the provenances belonging to the interior variety was moderate or poor. Three provenances from New Mexico which ranked right behind the best Washington and Oregon provenances made up a notable exception. Perhaps mention ought to be made here that the only New Mexico provenance in the Schwappach 1910 trial showed far better growth than any of the other interior provenances in that test until infection with *Rhabdocline pseudotsugae* in 1930.

The 1961 German Democratic Republic trial

The Forest Sciences Institute at Eberswalde established six plantations in 1961 with 1+2 seedlings across the former German Democratic Republic from the Baltic Sea coast to the mountains in the south of the country (Dittmar et al. 1985). The experiment included 26 provenances, 2 from interior British Columbia (Salmon Arm area), 4 from the east side of Vancouver Island, 14 from Washington, and 6 from Oregon.

The experiment demonstrated relatively small differences between provenances at plantation age 20. That finding was a surprise because the provenances represented only that part of the species' natural range shown in earlier provenance tests to contain the optimal seed sources for its cultivation in central Europe. The results, however, narrowed the choice of seed sources apparently best suited for the northeast German lowlands, referred to as "Pleistozän", to the west slope of the Washington Cascades, the Washington Coast Range, and the Cascade Range of northwest Oregon. Vancouver Island, the north side of the Olympic Mountains, and the Oregon Cascades were judged to contain less desirable seed sources. Seed sources in the Shuswap Lake area and the west slope of the Washington Cascades were considered to be the most appropriate for the mountainous region in the south of the country.

The IUFRO Trials

As noted, the provenance tests of the first seven decades of the 20th century had covered the vast range of Douglas-fir in a rather spotty fashion; thus, their results had provided a limited basis for selecting seed sources suitable for use in the pre-1989 Federal Republic of Germany. In addition, insufficient or even complete lack of information about the exact geographic origin of many provenances in the tests diminished the utility of their results. To alleviate these shortcomings, the tree breeding institutes of the states of Baden-Württemberg, Bavaria, Hesse, and Lower Saxony decided to participate in the IUFRO international Douglas-fir provenance study. The four tree-breeding institutes planned a joint experiment with 111 provenances from the IUFRO collections, 9 non-IUFRO provenances from British Columbia, and seed from 4 German stands (Kleinschmit et al. 1974). Seed from the IUFRO collections consisted of 38 provenances from the northern subgroup of the inland variety and 72 provenances of the coastal variety, and one Mexican provenance whose taxonomic status within the genus *Pseudotsuga* is still open to question. Provenances from the southern subgroup of the inland variety were not included in the experiment because results of older trials (Kleinschmit 1973) had indicated their poor suitability for cultivation in Germany.

The experiment was divided into two parts. For part one, all 124 provenances were sown 1970 in each of three nurseries located in northwest, southwest, and southeast Germany. The objective of part one was producing seedlings for establishing plantations to be observed for 20 years, and to make a first selection at the end of the nursery phase. Part two of the experiment consisted of a sowing in 1973 of the best one-third provenances from the 1970 sowing selected on the basis of height growth and frost hardiness. Performance of seedlings raised for part two of the experiment was supposed to be followed for 40 years in the field (Kleinschmit et al. 1974).

In spring of 1973, 16 plantations, distributed throughout the pre-1989 Federal Republic of Germany at elevations ranging from 20 to 600 m, were established with seedlings from the 1970 sowing. Their performance in 7 of the 16 plantations was reported at age 9 from seed (Kleinschmit et al. 1979). Provenances displayed distinct differences in their ability to adapt to site conditions at the 7 plantations. Provenances from the coastal region and the North Cascades of Washington displayed the greatest adaptability, if it is defined as superior growth combined with a high rate of survival. Those from Vancouver Island, the central Cascades in Washington, and the coastal region of northern Oregon ranked next; they had good growth but a lower rate of survival. Provenances from coastal British Columbia, the southern Washington Cascades, and the Cascades in Oregon adapted poorly to the test sites. Their growth was very uneven and their rate of mortality was extremely high. The unsatisfactory performance of the provenances from the southern Washington Cascades contrasted with the findings of a study by Racz and Kleinschmit (1978), which included 18 provenances from that region with satisfactory performance. Provenances from Oregon south of lat 45° N and California were judged to be unsuitable for cultivation in Germany because of poor growth and a high rate of mortality. Provenances belonging to the interior variety had a very low rate of mortality, but their growth was too low to recommend them for use in Germany.

Performance of provenances in six of the plantations at age 14 (Kleinschmit et al. 1987) and age 20 (Kleinschmit et al. 1990) followed essentially the pattern observed at age 9. Provenances from the western part of the Olympic Peninsula and the western slope of the northern Washington Cascades continued to display the best overall performance, and those from the Puget Sound region, southern Oregon, and California the poorest.

Seedlings representing 50 provenances selected for part two of the German participation in the international IUFRO provenance test were outplanted in 1975 in 12 plantations (Kleinschmit 1978). Results have not yet been published.

The 1970 Hesse trial

Aside from its participation in the IUFRO provenance test jointly by the four German forest breeding institutes, the Hessian Forest Breeding Institute initiated an additional provenance experiment in 1970, designed to narrow the choice of seed sources for use in Hesse (Jestaedt 1980). The experiment includes 118 provenances, 25 belong to the northern subgroup of the interior variety and 93 to the coastal variety from the IUFRO collection, 9 provenances from commercial sources, and progeny from 4 German stands in Baden, the Palatinate Forest (Pfälzer Wald), the Eifel mountains, and Lower Saxony. Added to the experiment was progeny of 91 single-tree selections from 6 Douglas-fir stands in the Eifel Mountains. At the time of cone collection in 1968, the 6 stands ranged in age from 32 to 86 years. As in the collections made by IUFRO in 1966-1968, cones were collected from 8 to 20 trees in each of the 6 stands (Rau 1987). Test plantations were established in 1973 with 1+2 seedlings in 13 locations throughout Hesse.

Measurements of several quantitative and qualitative traits during the nursery phase and in the field provided, as early as age 8, useful criteria for judging provenances (Jestaedt 1980). Provenances from the lower elevations of the western slope of the North-Washington Cascades and the Olympic Peninsula were by far the best performers. Next in growth ranked the provenances from the east side of Vancouver Island, the lower elevations of the west side of the Cascades in southern Washington, the Coast range in northwest Oregon, and progeny from the 4 German stands. Provenances that belong to the inland variety and coastal provenances from the southern part of their range had the poorest growth. Measurements at age 14 did not significantly change rankings (Rau 1987).

Results of the 1970 trial largely agreed with those from the 1958 provenance test in Hesse, which led Jestaedt (1980) to recommend use in Hesse of seed from the following regions:

- the area between the coast and west slope of the Cascades in northern Washington and southwest British Columbia between the Frazer River and lat 47° N, up to about 700 m elevation
- the southern and southwestern part of the Olympic Peninsula, to about 700 m elevation
- the east side of Vancouver Island, to about 600 m elevation

Height and diameter growth, phenological characteristics, and frost resistance of progeny from the single-tree selections in the 6 Eifel Mountain stands were recorded at ages 8 (Jestaedt 1980), 14 (Rau 1987), and 20 (Hesse FVA 1993). Growth of these trees matched that of the best IUFRO provenances. Although marked differences in the measured traits were found between progeny from individual trees of each of the six stands, mean values for progeny from each of the stands varied little. Jestaedt (1980) stated that the range in age of the six mother stands justifies the assumption that they come from different seed sources and that the homogeneity of their progeny represents a process of adaptation towards a "land race," as defined by de Vecchi (1969).

The GDR IUFRO Trial

Another German IUFRO provenance test was initiated in 1970 in the former German Democratic Republic by the Forest Sciences Institute at Eberswalde (Braun 1985). The experiment included 139 IUFRO provenances and progeny of 5 East German Douglas-fir stands. Seedlings were outplanted in 1973 near Stralsund in the northeast German low lands. The objective of the experiment was to test the ability of these provenances to grow in open areas without the benefit of any kind of shelter.

Height and survival was recorded at age 13 from seed. The best performers were provenances from northwestern Washington because of good growth coupled and an acceptable rate of survival. Provenances from interior British Columbia had the highest rate of survival (77-90%) but only moderate growth. Heavy losses, primarily caused by frost, accounted for the low rate of survival (34%).

Seed sources for Germany

The German Douglas-fir provenance trials demonstrated that the best seed sources for that country are to be found in northwestern Oregon, western Washington, and southwestern British Columbia at elevations up to about 600 m. For high elevation sites in German mountain ranges, however, some seed sources in the range of the northwestern subgroup of var. *glauca* appear to be better suited than any var. *menziesii* seed sources. Var. *menziesii* progeny from German Douglas-fir stands performed in provenance tests as well, or even better, than the best North American var. *menziesii* provenances. Unfortunately, seed production from German Douglas-fir stands is insufficient to meet demand, and probably will remain so for years. Therefore, the former GDR will continue to depend on seed imports for the foreseeable future.

International Studies

British provenance trials

Douglas-fir has grown in Britain since 1828, but not until 1928, a century later, did the provenance trials begin. The next 44 years saw the establishment of 11 experiments with 82 provenances in Scotland and northern England, and of 19 experiments with 118 provenances in southern England and Wales (Lines 1987). Among these are two main series, one planted in 1953/54 and another in 1970-1972. The 1953/54 series constituted the first large-scale British provenance trial. The seed was obtained from the Manning Seed Company and consisted of 14 Washington and 3 Oregon provenances. The establishment of two plantations at Laiken (Nairn) and Glentress (Peebles) in 1953 was followed, in 1954, by a third planting at Sunart (Argyll) to include a site with the typical high rainfall and mild winter of western Scotland (Lines 1957). The 1953 planting at Glentress also included two provenances from interior British Columbia (Salmon Arm and Prince George) and three from Vancouver Island (Lines 1956).

In 1954, plantations were established at three sites in England (Mortimer, Herfordshire; St. Clement, Cornwall; Shouldham, Norfolk) and on a site in Wales (Rheidol, Cardiganshire). A first assessment at the end of the third growing season showed a considerable difference in growth between the Washington and Oregon provenances, the Oregon provenances being rather poor (Wood et al. 1960). At plantation age 12, the Washington provenances had maintained their superiority over the Oregon provenances at the four English and Welsh sites. As a follow up to the 1954 trial and to extend it to a wider range of seed sources, 15 provenances were planted in March 1968 at the New Forest and the Forest of Dean besides a smaller trial at Helwill, Cornwall. The provenances included two from Vancouver Island, four from Washington coastal areas, and nine from along the Oregon coast to its southern end (Lines and Mitchell 1968).

Measurements of the 1953 (age 20) and 1954 (age 23) showed that differences in height between them were small but total volume differed considerably between provenances, with Elma outstanding at 314 m^3/ha = GYC 20 (Lines 1977).[4]

The second main series consists of plantations established in 1970-1972 with seed from the 1966 and 1968 IUFRO collections. The intent was to sample portions of the species' range not covered by earlier trials and to test different provenances from known regions of promise.

In 1970, three plantations were established in Scotland, one at Culloden Forest 32 km east of Inverness and two at Craigvinean (Dunkeld Forest) 24 km northwest of Perth. Each site contained six provenances from British Columbia, eight from Washington and six from Oregon. Seven more IUFRO provenances, three from British Columbia and four from Washington, together with two commercial seed lots from Elma were planted in 1972 at Craigvinean (Lines and Samuel 1987).

Survival and growth of provenances at Dunkeld Forest differed greatly 6 years after planting in the field. Little evidence was seen of clinal variation with latitude, elevation, or distance from the coast. The trial at Culloden Forest had to be abandoned because of severe losses from frost damage (Lines 1980).

The companion plantations in southwest England were established in 1972 at Bodmin Forest, Cornwall; Charmouth Forest, Devon; Forest of Dean, Gloucester; Quantock Forest, Somerset;[5] and Radnor Forest, Hereford. At Bodmin Forest, seedlings were planted on east; south- and north-facing slopes, which closely matched in physical and chemical soil properties. The provenances included in the English trials consisted of 44 IUFRO provenances from interior (8) and coastal (7) British Columbia, Washington (12), Oregon (9), and California (8), besides 2 commercial seed lots from Washington

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[4] General yield class (GYC) is defined as the maximum mean annual increment per hectare in m^3.

[5] Abandoned after 6 years.

(Elms and Hoodsport). Not all provenances were present on all sites, however, because only 31 provenances were planted on each site. At the end of the sixth growing season in the field, growth had varied between sites and aspects at Bodmin Forest. The relative performance between provenances was constant across the range of sites, and aspects, however. The best provenances were from a geographically narrow area of coastal Washington and coastal northern Oregon that has been traditionally used as a source of seed for use in Britain (Pearce 1980).

A report of height and diameter growth 10 years after planting at four English (Bodmin, Charmouth, Dean, Radnor) and one Scottish site (Craigvinean) showed little change in rank of height growth from that measured after 6 years since planting (Lines and Samuel 1987). Rank for diameter was closely correlated with rank for height.

Provenances from above lat 50° N and below lat 43° N, as well as high elevations, displayed a pattern of poor growth. Performance of provenances from Vancouver Island was only moderate. Best growth was mainly by provenances from sites under 305 m elevation in a U-shaped zone from Arlington southward along the west side of the Washington Cascades to the Columbia River and thence north to Forks on the Olympic Peninsula. Lines and Samuel (1987) pointed out that results of the IUFRO experiments indicate negligible interaction between provenances and site and concluded that selecting different seed sources for different parts of Britain is likely to be of minor importance.

Height, diameter, and branching characteristics (branch number, diameter, angle) were measured on 38 IUFRO provenances 16 years after planting at the Forest of Dean and Radnor Forest. In addition, measurements of dbh and basal area were recorded at Craigvinean 19 years after planting (Fletcher and Samuel 1990). The trials at Dean and Radnor contain 38 of the 44 seed sources with 26 of these common to both sites. Craigvinean contains 20 provenances 15 of which are present at either one or both of the Dean and Radnor sites.

In an earlier report (Lines and Samuel 1987), the 44 IUFRO seed lots were grouped in 12 zones based on geographic or climatic data; these zones have been modified and reduced to 10 (Figure 4.4). That change appears to be justified because, for all the traits measured, significant differences between zone means were found but rarely between provenances within zones.

The provenances from British Columbia (Zone I and II) were the poorest because of small diameter growth and low basal areas. They had superior branching characteristics and high survival but that

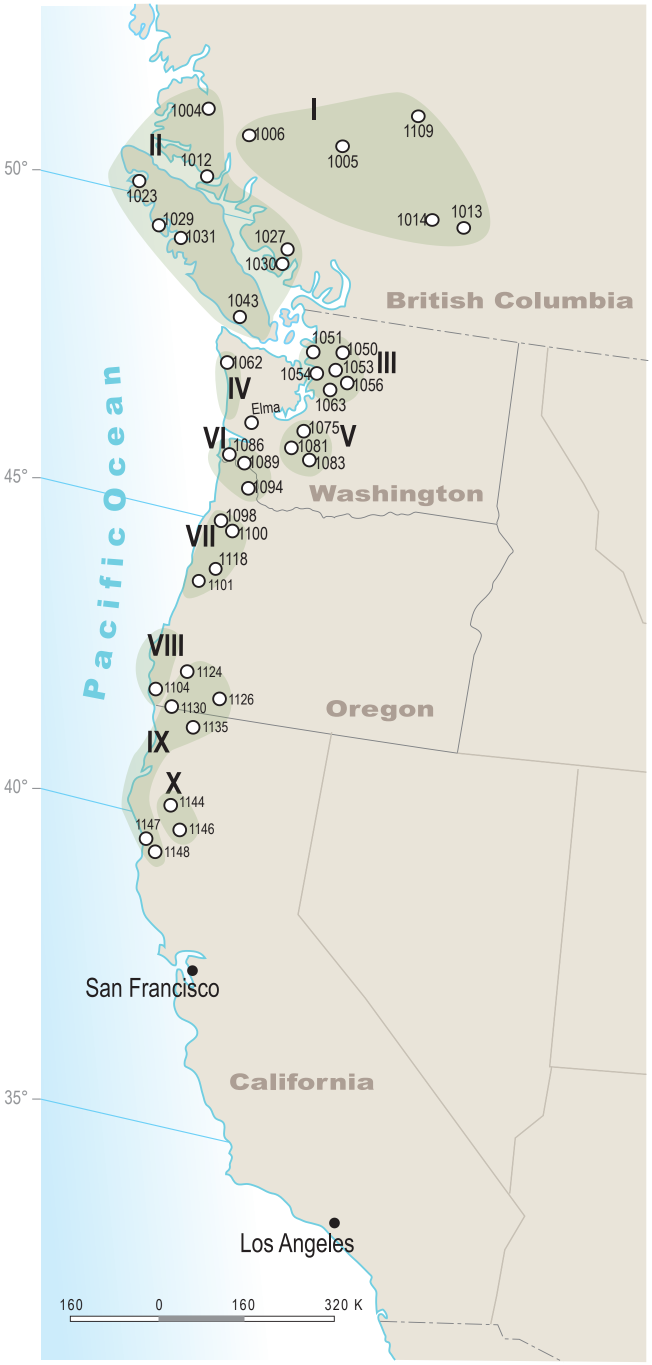

Figure 4.4 IUFRO seed lots used in British provenance trials grouped into 10 zones (from Lines and Samuel 1987).

would not offset the low volume production. By contrast, provenances from Washington (Zones III, IV, V, and VI) had high survival and, combined with above-average diameter, did produce the highest basal area. Although the provenances from southern Oregon and northern California had the largest individual tree diameters, the nature of their branch characteristics, a combination of high branch numbers and large branch diameters, negated the benefits of rapid diameter growth.

Results of the measurements at age 16 of progeny from zones III, IV, and V at these three sites confirmed predictions from earlier reports that the best sources of seed for use in Britain are to be found in a U-shaped area in Washington; to that can now be added the southwestern corner of Washington and the adjoining northwestern corner of Oregon. The areas considered to contain the best seed sources for Britain correspond to the Northwest Forest Tree Seed Council[6] zones 202, 403, 411, 412, 030 (northern half), 012, 041, and 052 at elevations below 500 m in all these zones (Fletcher and Samuel 1990).

A third series of noteworthy experiments was established to compare progeny from eight older stands of Douglas-fir, many of which derived from the David Douglas introduction to Lynedoch, Scone Estate, with five North American provenances. Seedlings were planted in 1959 at Elibank (Peebles-shire), Castle O'er (Dumfries-shire), and Thornthwaite (Cumberland) and in 1960 at the Forest of Dean (Gloucester). An assessment of height growth after six growing seasons indicated a rather disappointing performance of progeny from some of the eight Scottish stands. Many trees had poor growth and were malformed (Lines and Mitchell 1967, Lines et al. 1967). Progeny from the Scottish mother trees apparently show signs of inbreeding depression because of their extremely small genetic base. Seed had been collected from only one or two trees. Progeny from Scottish stands known to result from a large seed import did not show these features (Lines 1987).

Irish provenance trials

The decline in the amount of Douglas-fir planted in Ireland, after the period 1922 to 1927 when the species accounted for 32% of the annual planting program (O'Driscoll 1973), is a likely reason that provenance trials with Douglas-fir did not commence until the early 1960s. The first two trials were made with commercially collected seed. Results were of limited usefulness, however, because of lack of authenticity of seed sources. Availability of the 1966/68 IUFRO seed collection provided the Irish Forest and Wildlife Service with the opportunity to begin an experiment with seed of well-documented origin.

The trials with seed from commercial collections had shown that interior provenances were unsuitable. Emphasis was therefore placed on selecting var. *menziesii* provenances with preference to those from low elevations. The 32 seed lots from the 1966 IUFRO collection, received in l967, represented 13 provenances from British Columbia, 11 from Washington, and 8 from Oregon. Twenty-five of the provenances belonged to the var. *menziesii* and 7 to the northern subgroup of var. *glauca*.

Seeds were sown in 1968 and outplanted as 1+1+1 transplants in spring of 1971 on 5 different sites throughout Ireland (O'Driscoll 1978). At the year-3 height assessment in the nursery, an emerging trend showed that high elevation and more northerly provenances occupied lower rankings than those from low elevations and more southerly origin. The latter two kinds of provenances had a higher incidence of lammas growth than the former two kinds.

A sixth set of the 32 provenances was planted on the grounds of a former nursery at Glenealy, County Wicklow, to study the growth patterns of the different provenances. Ranking of provenances by height growth did not follow a clinal pattern. Three provenances, Coquille in southern Oregon's Coast Range, Granite Falls, and Sedro-Woolley in Washington's Puget Sound region were consistently in the top three ranks while the interior provenances were always at the bottom of the rankings. Provenances from southern Oregon were the best performers but their long period of growth increases their chance of injury by early frost. Provenances from the Puget Sound area appear to be more suitable for Irish Conditions as they combine vigorous growth with a shorter growth period (O'Driscoll 1978).

Provenances from coastal Washington, coastal Oregon, and the Puget Sound region were the best

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[6] Later the Western Forest Tree Seed Council.

in the IUFRO provenance trials 9 years after planting (Pfeifer 1988). He considered provenances from the north and central Washington coast (seed zone 012, 030) and the south Washington coast (seed zone 041) as preferable for Ireland, based on the results of the IUFRO trial.

Dutch provenance trials

Douglas-fir has been planted in the Netherlands since 1860 with varying success. The importance of seed source for the success of plantations was recognized in the beginning years of the 20th century. Because origin of the early seed imports was unknown, a series of provenance tests was begun in 1923, with 4 interior and 2 coastal provenances. Every year from 1925 to 1932, a few provenances were added to bring their total to 35. They consisted of 11 inland provenances: 10 from British Columbia and 1 from Washington; and 22 coastal provenances: 2 from British Columbia, 17 from Washington, 2 from Oregon, and 1 from California. Two of the 35 provenances came from Dutch Douglas-fir stands. Seeds were obtained from several providers, the seed dealer Katzenstein and Co., in Atlanta, Georgia; the "Associated Foresters" in Calgary, Alberta, the Long Bell Lumber Company in Washington, and the USDA Forest Experiment Station in Portland, Oregon. The provenances were used in establishing 27 test plantations in five Dutch provinces. Veen (1951), in his analysis of the performance of the 35 provenances, distinguished four groups—very good, good, medium, poor —based on height growth between 10 and 15 years of age. The best performers were Washington provenances from low elevations, and the worst were those from interior British Columbia and northeastern Washington. Veen (1951) concluded that inland and high-elevation coastal provenances are poorly suited for planting in the Netherlands. Both grow slowly, the inland provenances are highly susceptible to Rhabdocline needle cast, and coastal provenances from high elevations are highly prone to injury from late spring frosts because of their early flushing.

Thinnings in the test plantations began at age 20 and were continued for 12 years at 3-year intervals (de Vries 1961) The MAI_{30} for the three best provenances (Chilliwack, BC; middle WA, a composite of King, Lewis, Thurston, and Pierce Counties; and Pacific Coast, WA) ranged from 10.1 to 12.2 m^3/ha. The MAI_{30} for the two poorest provenances (northeast Washington—composite of Okanagan and Ferry Counties); and Salmon Arm, British Columbia) ranged from 3.5 to 5.9 m^3/ha. The measurements of volume growth provided essentially the same ranking of provenances as Veen's (1951) based on height growth.

Results of the provenance research begun in 1923 indicated that western Washington and southwestern British Columbia contained the most promising seed sources for use in the Netherlands. But the sampling had not been extensive enough to allow for a reliable delineation of seed collection areas for the Netherlands. Achieving that goal required more provenance research. The IUFRO seed collections provided a timely opportunity for testing many provenances from throughout the species range.

In 1971, a provenance test was begun with 57 provenances from the 1966/67 IUFRO seed collection (Kriek 1974). Twenty-five of the provenances came from British Columbia, 24 from Washington, and 8 from Oregon. All provenances belonged to the coastal variety. Seed was sown in two nurseries in December 1967, and seedlings were transplanted in spring 1969. Two plantations were established with the transplants, one in 1971 at Sleenerzand (52°50′ N lat.) in northeastern Holland, the other at Sprielderbos (52°14› N lat.) in the southwestern part of the country. Kriek (1974, 1978) reported on the development of the provenances up to age 10 from seed. Provenances from Washington performed best, but not equally well, throughout the areas sampled by IUFRO in that state. The best provenances came from the western slope of the northern half of the Cascades covering parts of seed zones 202, 403, and 412 at altitudes of 100–300 m, from along the western and southern flanks of the Olympic Mountains covering parts of seed zones 012 and 030, and Pacific County in the southwest corner of the state just north of the Columbia River, covering part of seed zone 041. Kriek (1974) remarked that the very best provenance imported into the Netherlands up to then came from Pacific County. That provenance "was tested in the 1923-1932 trial series and is known under the name Pacific Coast."

The measurements in 1987 up to age 20 from seed closely matched the results up to age 10 both at Sleenerzand and Sprielderbos. This outcome justifies, according to de Vries (1990), continuing to regard provenances from these three areas as the best sources of seed for the Netherlands.

In 1970, a second provenance study was initiated with 104 provenances, 58 of which came from individual trees, from the 1968/69 IUFRO collection. Twenty-five of the provenances—4 from Oregon and 21 from California—belonged to the coastal variety. The other provenances—19 from Colorado, 4 from Utah, 28 from Arizona, and 28 from New Mexico—were from the southern subgroup of the interior variety. By age 11 from seed, their performance already indicated that none of the areas where these provenances originated should be chosen as seed sources for use in the Netherlands (Research Institute for Forestry and Landscape Planning 1981, Kriek 1983).

In the late 1980s, two of the three plantations established with progeny from the 1968/1969 IUFRO collection were abandoned because of too many losses of trees. The third plantation has been maintained as a demonstration object for the consequences of planting provenances unable to adapt to sites in the Netherlands (de Vries 1990).

Belgian provenance trials

The first provenance tests in Belgium date to 1925 (Galoux 1956). They included provenances from the range of interior Douglas-fir and from throughout the range of coastal Douglas-fir. Their results indicated that interior Douglas-fir is unsuitable for use in Belgium because of inferior growth and high susceptibility to *Rhabdocline pseudotsugae*. The outcome of these first tests suggested that progeny from Douglas-fir in western Washington and southwestern British Columbia held the most promise for cultivation in Belgium.

To better identify provenances desirable for different parts of Belgium, the Forest Research Station at Groenendaal initiated, in 1951, a trial with 31 provenances, 22 from Washington and 9 from Oregon (Gathy 1961). The mother stands stocked at altitudes ranging from about 100 m to 500 m, except for two stands in Oregon at about 650 m. The seed was provided by two seed dealers, Manning Seed Co. and Wood Seed Co., in Washington.

Two plantations were established in 1954 with 3-year-old plants in the High Ardennes at 460 m and 515 m, respectively. Two more plantations were established in 1955 in central Belgium at 65 m and 75 m, respectively.

Washington provenances from elevations below 200 m showed the best growth and were also the most frost resistant. None of the Oregon provenances matched the Washington provenances in growth or frost resistance. That pattern had not changed significantly by age 22 from seed (Nanson 1978). The best provenances originated from a U-shaped area extending from Forks near the Pacific coast to Darrington. Trees from those seed sources grew best at both low and high elevations in Belgium; they flushed late and thus were least susceptible to injury by late frosts.

The Groenendaal Forest Research Station initiated in 1969 a provenance trial with 26 provenances: 5 from southwest British Columbia, 6 from Vancouver Island, 12 from western Washington, 2 from eastern Washington, and 1 from Oregon, with seed from the 1967/68 IUFRO collections. The trial included also progeny from 10 Belgian Douglas-fir stands in the Ardennes (Nanson 1973).

Performance in the nursery at age 3 from seed was best by provenances from western Washington, average for the Belgian Douglas-fir, and below average for the British Columbia and Vancouver Island provenances. The poorest provenances were those from eastern Washington and Oregon. The Brookings, Oregon, provenance suffered extreme injury from a fall frost. Nanson (1978) concluded that elevations below 500 m in western Washington—roughly covered by seed zones 030, 240, 232, 412, 411, 403, and 202—are most likely to contain the seed sources most suitable for use in Belgium.

French provenance trials

The rapid growth of the share of Douglas-fir in reforestation after World War II in France prompted the initiation of provenance trials with that species in the 1960s. The Institute of Forest Tree Improvement (Station d'Amélioration des Arbres forestiers), a branch of INRA (Centre National de la Recherche

Agronomique) established Douglas-fir provenance and progeny tests in 15 locations throughout France from 1965 to 1978 (Figure 4.5).

The first series of provenance plantations was established in the years 1965 to 1968. The locations of these provenance tests are Epinal in the northeast, Peyrat-le-Chateau and Besséde-Barade in the southwest, and St. Amans Valtoret, Sauclières and Le Treps in the south. Seed for these provenance tests came from commercial collections of coastal Douglas-fir in North America except for the test at Sauclières where all plants represent progeny from Douglas-fir stands in France.

The 1965 test plantation at Peyrat-le-Château contains 5 British Columbia, 15 Washington, and 5 Oregon provenances, as well as progeny from a 25-year-old French Douglas-fir stand in the southern Rhone region. Lacaze and Tomassone (1967) analyzed the nursery performance of these provenances. They concluded that the results pointed to Vancouver Island, the Olympic Peninsula, and the western slope of the Washington Cascades as the areas that contain the most suitable seed sources for eastern France.

Assessment of performance at age 18 from seed based on volume production, stem form, branch angle, and knottiness showed most of the Washington provenances as best performers but also surprisingly poor performance by the Vancouver Island provenances (Birot and Lanares 1980).

Rozenberg (1993) compared height growth of 12 (2 Vancouver Island, 7 Washington, 3 Oregon) of the 25 provenances to age 25 from seed. The comparison was based on 12 felled trees from each of the 12 provenances. He created height-age curves for each of the 144 trees, which indicated that changes in rank of provenances between age 10 and 25 were mostly minor. The best provenances, those from Washington, remained the best, and the poorest, those from Oregon, remained the poorest.

Figure 4.5 Locations of Douglas-fir provenance and progeny tests established by INRA in France; map compiled by Hermann (2012) from several literature sources.

The sites for the provenance trials aimed at identifying of seed sources suitable for the Mediterranean region of France are at Sauclières in the Cevennes, St. Amans Valtoret in the Monts de Lacaune, and Le Treps in the Massif des Maures at altitudes of 800, 700, and 600 m, respectively (Birot and Ferrandes 1980). The two plantations established in 1968 at le Treps in the Massif des Maures were to test 3 provenances from the California Coast Range, 2 from the Sierra Nevada, 1 from the extreme southern end of the Cascades, 1 from Washington, and progeny of a French Douglas-fir stand from the Beaujolais Mountains. A severe drought in 1970 showed the California provenances to be far more drought resistant than the Washington Granite Falls and French provenance. The survival rate of the 6 California provenances was 75%, compared to 50% for the latter two (Birot and Ferrandes 1972). An estimate of biomass at age 12 from seed by the summation of height of surviving trees indicated the superiority of the California populations. Birot and Ferrandes (1980) concluded, on the basis of their findings, that Douglas-fir from California seed sources shows promise for use in the French Mediterranean region.

A second series of trials was begun in 1970 with seed from the IUFRO collections and from several Douglas-fir stands in France. These trials contain provenances representative of much of the species› range. Fifteen plantations with varying numbers of coastal and interior provenances had been established throughout France by 1977 (Figure 4.5). The plantations with most provenances were at Peyrat-le-Chateau, Amance, and the Forêt d›Orléans.

Temporarily waterlogged soils at the Forêt d›Orléans and Amance led to such poor survival of the interior provenances that the experimental plots had to be abandoned. By contrast, the difference was slight in survival between interior and coastal provenances, 91% versus 97%, at Peyrat-le-Chateau 6 years after planting. In general, provenances of variety *menziesii* from western Washington outperformed those from other parts of the range of coastal Douglas-fir and the variety *glauca* provenances (Bastien et al. 1980).

In tests in the French Mediterranean region with provenances from the IUFRO collections, most belonged to variety *glauca* and the remainder to variety *menziesii* from southern Oregon and California. Results after the first decade after outplanting in the field showed higher survival and better growth by coastal than interior Douglas-fir, except on the most severe sites, namely Felines Minervois and St. André-les-Alpes (Bastien et al.1988). Incidentally, St. André-les-Alpes is the only site where survival in provenances from the southern subgroup of variety *glauca* was higher than in those from the northern subgroup: that is, 72% versus 51%. Within the southern subgroup, provenances from New Mexico and Arizona grew better than those from Utah and Colorado.

Figure 4.6 AFOCEL provenance test plantations established by AFOCEL in France (from Michaud 1987).

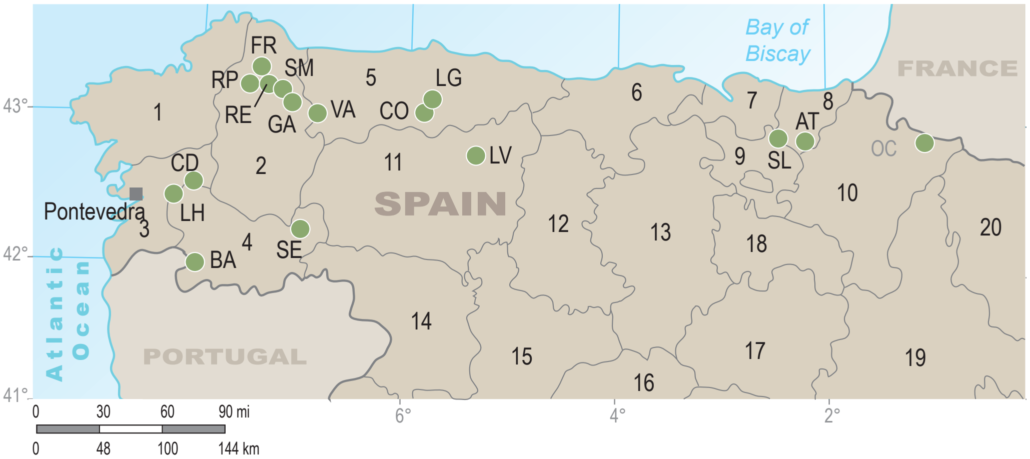
The performance of southern Oregon and California provenances from the IUFRO collection, at age 13 from seed, tend to support the conclusion drawn by Birot and Ferrandes (1980) from an earlier study that such provenances may be successfully grown in the French Mediterranean area. Although variety *glauca* may initially grow well at high elevations in the Mediterranean mountains because of its cold hardiness (Bastien et al. 1988), its susceptibility to severe infection by *Rhabdocline pseudotsugae* will most likely offset benefits derived from the cold hardiness.

The appearance of *Rhabdocline pseudotsugae* in the provenance plantations in the Mediterranean region led to a detailed study of the pattern of infection with the fungus at the St. André-les-Alpes test site, which contains 10 variety *menziesii* and 66 variety *glauca* provenances (Soutrenon 1986). Data collected each spring from 1984 to 1986, the 9th, 10th, and 11th years after planting in the field, demonstrated that the ranking of provenances in percentage of trees infected remained nearly the same from one year to the next. The percentage of infected trees was low in coastal Douglas-fir and the northern subgroup of the inland variety but high in its southern subgroup. The exception was Douglas-fir from Mexico, which apparently was not very susceptible to the disease.

The AFOCEL provenance tests

A French timber industry group, the Association Forêt-Cellulose (AFOCEL), began a program of provenance tests with the procurement of 186 seed lots, including 75 from the IUFRO collections, which covered nearly the entire natural range of Douglas-fir (Michaud 1978). The AFOCEL established a first series of test plantations in various parts of France (Figure 4.6) from 1977 to 1978. From 1978 to 1981, two additional series of tests were initiated, one with 82 provenances from Washington and the other with seed collected from French Douglas-fir stands.

A report on performance of provenances in seven of the plantations of the first series, measured by total height at age 8 after planting in the field, indicated that the most vigorous provenances came from the part of the species range between lat 44° N and 50° N west of the crest of the Cascades (Michaud 1987). Ranking of provenances remained nearly the same for all test sites. As in the INRA trials, lateness of flushing was positively correlated with growth.



Autonomy/Province	Map no.
Galicia	
La Coruña	1
Lugo	2
Pontevedra	3
Ourense	4
Asturias	5
Cantabria	6
Euskadi/País Vasco	
Bizkaia/Vizcaya	7
Araba/Álava	8
Gipuzkoa/Guipúzcoa	9
Navarra	10

Autonomy/Province	Map no.
Castilla y León	
León	11
Palencia	12
Burgos	13
Zamora	14
Valladolid	15
Segovia	16
Soria	17
La Rioja	18
Aragón	
Zaragoza	19
Huesca	20

Plantation ●		Elev. (m)
Principal tests		
LH	La Hermida	700
SE	Sierra del Eje	1360
Satellite tests		
BA	Bande	900
CD	Castro Dozón	750
RP	Rocha da Perdiz	520
FR	Fragavella	580
RE	Regavella	450
SM	Sierra de Meira	850
GA	Gamalleira	660
VA	Valdemadeiro	920
CO	Conforcal	850
LG	La Gallina	600
LV	La Vecilla	1160
SL	Salinas de Léniz	900
AT	Ataun	750
OC	Ochagavía	900

Figure 4.7 Location of Spanish Douglas-fir provenance tests (from Fernandez et al. 1993).

Recommendations based on provenance tests

Although provenance tests of Douglas-fir did not begin until the mid-1960s in France, recommendations for seed sources to be used in that country were already issued 30 years later based on the findings from these trials. The recommendations are contained in a publication of the French Ministry of Agriculture (Michaud 1997). They are for six regions by listing seed zones, established by the Northwest Forest Seed Council, which are considered to contain seed sources suitable for each of the regions. For the northwest and northeast of France, the Massif Central, and the foothills of the Pyrenees, all the recommended seed sources are in western Washington and northwest Oregon at elevations below 450 m. Only in the Mediterranean region are seed sources from California below 1,200 m and from southern Oregon below 450 m recommended.

Spanish provenance trials

The first provenance tests in Spain were installed in 1950 by Dr. Fernando Molina and served as the basis for the common-garden tests initiated in 1976 (Vega 1990). Of the provenances used in this test, 85 were from the 1966/68 IUFRO seed collections; 4 from a 1970 collection by the Institute of Forest Genetics (IFG) at Placerville, California; and 1 each from a 1961 and 1965 collection in the Sierra Madre Oriental of eastern Mexico (Fernandez et al. 1993). Both coastal and interior seed sources were included in these tests. Sixteen test plantations, 10 in northwest and 6 in north-central Spain, were established from May 1978 to April 1981 (Figure 4.7). The plantations at Carballa Blanca in the Sierra del Eje in the northeast and La Hermida in the northwest of Ourense province received all the IUFRO and IFG provenances obtained for the 1976 common-garden test. The two plantations are situated on sites of contrasting climates. Carballa Blanca has an inland climate with a short growing season and cold winters, but the climate of La Hermida is coastal with a longer growing season and milder winters. The other 14 plantations, referred to as “satellite tests,” arrayed from southwest Galicia to northeast Navarra

(Figure 4.7), were allocated subsets of the IUFRO and IFG provenances. The availability of planting stock and the nature of planting sites determined the allocations.

Assessment of growth 5 and 10 years after planting indicated that the best performing provenances came from areas between lat 44° N and 50° N at elevations below 700 m. Their mother stands are located in regions where climate is dominated by the Pacific Ocean air mass. These regions include maritime slopes along the Georgia Strait in southwest British Columbia, the Olympic Peninsula, and the Coast Ranges of Washington, Oregon, and northwest California. Inland, they include the lower slopes of the Olympic Mountains and the Coast and Cascade ranges facing the Puget Trough in western Washington and the Willamette Valley in Northwest Oregon.

The height measurements at plantation ages 5 and 10 demonstrated a definite effect of planting site on growth. It is well illustrated by the two major plantations of the 1976 common-garden test. At age 7 years from seed, mean plantation height at La Hermida was 69 cm and 39 cm at Carballa Blanca (Toval 1987). At age 12 from seed mean plantation height had increased to 233 cm at La Hermida and to 184 cm at Carballa Blanca (Vega 1990).

Seed source x planting site interaction was significant in several plantations. Pairings of test sites that have many provenances in common demonstrated them most clearly. Many of the best provenances showed consistently good growth on diverse planting sites some of the other best provenances grew well on one site and poorly on another (Hernandez et al. 1993). Unfortunately, future comparisons between the two principal plantations in the 1976 common-garden test will be impossible because the test site at La Hermida was destroyed by fire shortly after the measurements of growth 10 years after planting (Vega 1990).

The 10-year results have yielded valuable information where seed sources likely to provide progeny well suitable for planting in northwest and north-central Spain may be found (Vega 1990). The rapid, juvenile growth of nearly one-third the number of progenies tested indicated that coastal Douglas-fir, which originates from that part of its natural range where it shows optimal growth, can successfully adapt even to some of the rather harsh sites in the mountains of northern Spain. As Fernandez et al. (1993) stated, “The Pacific and interior valley climates of western Washington, western Oregon, and northern California match those of the Iberian Peninsula so closely that Douglas-fir may have greater potential in Spain and Portugal than in the rest of western Europe.”

Italian provenance trials

The experimental plantations established throughout Italy in the 1920s and 1930s by Pavari (1958) demonstrated that Douglas-fir could be grown successfully in the northern half of the country. The desire to identify seed sources best suited to Italian needs led to the initiation of a provenance trial by Pavari at Vallombrosa Forest, 30 km east of Florence, in 1951, and was followed by trials at Acquerino Pistoria Forest in 1954, at Vallombrosa Forest in 1957, and in Calabria in 1965 (Morandini 1968).

Pavari chose 10 provenances from Washington between lat 48°30′ and 45° N west of the crest of the Cascade Range and one from northwest Oregon (Vernonia), all purchased from the Manning Seed Company, for the 1951 trial. He had originally planned to compare provenances from north and south of the 46th parallel, but that was not feasible because seed dealers had made their 1949 and 1950 collections mainly in British Columbia and Washington. Although intended, progeny from Italian Douglas-fir stands could not be included in the trial because cone crops in the preceding years had been complete failures.

Seed was sown in spring 1951 in the Vallombrosa nursery, seedlings were transplanted in spring 1953 and planted as 2–1s in the last week of October 1953 at 700 m in the Vallombrosa Forest (lat. 43°40›N). Survival was very high for all provenances; it ranged from 97.5 to 99.5% at age 16 from seed. The 1967 measurements of height, dbh, and projections of basal area and volume to a per hectare basis showed less uniformity in growth than survival between provenances. Those from the east slope of the Coast Range in northwest Oregon (Vernonia) and southwest Washington (Castle Rock) performed best and those from San Juan Island and the Olympic

Peninsula were the least vigorous. The provenances from the Washington Cascades were intermediate, except for the provenance Palmer which belonged to the top performers.

Morandini (1968) noted that the excellent growth of the provenances Castle Rock and Vernonia confirmed Pavari›s opinion that seed sources in the Coast Range of southwest Washington and northwest Oregon are most likely to provide progeny that will adapt particularly well to the environment of the Apennines.

Another trial was begun in 1969 by the Istituto Sperimentale per la Selvicoltura in Arezzo, Tuscany, with 73 provenances from the 1966/67 IUFRO seed collection (Ducci and Tocci 1987). They comprised 54 provenances of var. *menziesii* from British Columbia, Washington, Oregon, and California and 20 of var. *glauca* from Utah, Colorado, Arizona, New Mexico, and Mexico. In addition, progeny from 9 Italian Douglas-fir stands were included in the experiment.

Seeds were sown in late spring of 1969 in the Vallombrosa nursery and seedlings transplanted in spring 1971. One group of 2-2 seedlings that contained all provenances was planted in 1973 in the Vallombrosa Forest. A second plantation was established in 1974 at Faltona near Arezzo with 2-3 seedlings that included half the number of provenances at the Vallombrosa site.

Measurements taken at ages 5, 7, 11, and 16 from seed in the Vallombrosa plantation indicated only minor changes in rank of the best and worst performing provenances of var. *menziesii* and the northern subgroup of var. *glauca* over the 16-year period. Provenances with the greatest height and largest dbh at age 16 came from southwest Washington (Castle Rock) and the western slope of the Oregon (Hebo, Coquille) and California (Gasquet, Willits, Lower Lake) Coast Range. Those with the least height and diameter growth originated from interior British Columbia (Merritt), the east slope of the Washington Cascades (Cle Elum) and the east slope of the California Coast Range (Big Bar, Weaverville).

Growth of the provenances from the southern subgroup of var. *glauca* was inferior to that of var. *menziesii*. Within the subgroup of var. *glauca*, provenances formed 3 distinct groups in growth performance. Those from Arizona and New Mexico were the best, followed by those from Colorado; Utah provenances were the poorest. The exception from this south to north clinal pattern was the Mexican provenance Saltillo, which showed the poorest growth of all provenances.

Provenances in the Faltona plantation underwent notable changes in rank during the first 7 to 9 years but that changed afterwards. Provenances from the west slope of the Cascade Range, and the Oregon and California Coast ranges had consistently the best height and diameter growth whereas those from British Columbia, the east slope of the Cascade Range and the Mt. Shasta region were always the poorest performers.

Based on the results from the provenance tests in the 2 locations, considered to represent the environmental conditions in the north-central Apennines, Ducci and Tocci (1987) concluded that seed sources between the coast and the crest of the Coast range in southwest Oregon, as well as in the northern California coast Range, appear to be particularly well suited for the north-central Apennines. Moreover, the satisfactory growth of provenances from the Washington and northwest Oregon Coast range and the west slope of the Washington and Oregon Cascade range indicate a broad area of seed origin optimal for introducing Douglas-fir to the north-central Apennines.

Another provenance experiment with seed from the 1966/67 IUFRO collection was initiated in 1969 by the National Institute for Woody Plants in Turin (de Vecchi 1973). The Institute established 3 plantations in the Piedmont in 1970 with 2-0 seedlings from 24 seed sources. They consisted of 15 var. *menziesii* provenances, 12 from Washington and 3 from British Columbia, and also 7 var. *glauca* provenances, 3 from Washington and 4 from British Columbia, and progeny from 2 Italian Douglas-fir stands.

Assessments made at ages 2, 6, and 12 from seed showed heavy losses from winter frost. They ranged for var. *menziesii* provenances from 33 to 63%, and for var. *glauca* provenances from 17% to 30%. In growth, the percentages were reversed. Growth of surviving coastal Douglas-fir was much better than that of interior Douglas-fir (Ferraris 1993).

By 1992, only the plantation at lat 45°05 N at 330 m elevation in the hills near Turin was left. The plantation at Brosso had been destroyed by fire, and the one at Voltaggio had to be abandoned because too few trees had survived. Even in the Turin plantation, survival had decreased to less than 50% for all provenances, and to less than 20% for 8 of the 15 var. *menziesii* provenances. The exceptions were the 2 Italian provenances and one var. *glauca* provenance, Revelstoke, from British Columbia, with survivals of 93%, 60%, and 67%, respectively.

The Turin plantation had apparently not been thinned because Ferraris (1993) attributed the extremely heavy losses between ages 12 and 22 to competition, winter frost, and physiological drought caused by a combination of frozen soil and exposure to solar radiation. De Vecchi (1978) had stated that the generally poor performance of the North American provenances was probably a consequence of the use of 2-0 seedlings instead of sturdier transplants. The good results with progeny from the Italian Douglas-fir stands which also were planted as 2-0 seedlings, suggests poor adaptability to site conditions in the northwest of Italy as a more likely reason for the poor performance of the IUFRO provenances in the Piedmont trial.

Austrian provenance trials

Participation in the international IUFRO provenance trial by the Federal Institute of Forest Research at Vienna marked the beginning of provenance tests in Austria. The first two test plantations were established in 1973 with 2+2 seedlings. They included 7 coastal and 8 inland provenances. Seven more plantations were installed with 44 IUFRO provenances in 1977 (Günzl 1981). The number of test plantations had increased to 53 by 1987 (Günzl 1987).

The observations from these tests (Günzl 1986) demonstrated that provenances from the west slope of the Washington Cascades, especially those that originated from elevations above 500 m, and the southern part of the Olympic Mountains were the best. Progeny from Austrian Douglas-fir stands included in some of the tests had also shown excellent growth. Inland provenances, however, grew slowly and suffered much from late frost.

Schultze and Raschka (2002) analyzed the performance of 177 North American provenances and progeny from 14 Douglas-fir stands in eastern Austria. The North American provenances stem from IUFRO collections, collections made by Austrian and German foresters, and seed dealers. Seedlings were raised in the Mariabrunn nursery of the Austrian Federal Forest Research Institute (FBVA) and planted during 1973 and 1993. Thirteen plantations were 20 to 25 years old, twelve were 15 years old, and five were 10 years old when measured.

Provenances with the best growth came from the western slopes of the Cascade Range in Washington and northern Oregon, the eastern part of seed zone 041 in the Coast Range in southern Washington, and of seed zone 052 in the Coast Range in northern Oregon. Provenances from British Columbia, most of the Coast Range in Washington and Oregon, and from the east slope of the Cascade Range in the two states performed poorly. The outstanding performance of provenances from the southern part of seed zone 652, the eastern edge of seed zone 652, and the northwest corner of seed zone 661, was an exception. The progeny of Douglas-fir stands in eastern Austria did as well as the best North American provenances or even better, except for progeny from mother trees of apparently interior origin.

Based on the trials' results, Schultze and Raschka recommended provenances from the SE seed zones (Figure 4.8) as best suited for eastern Austria.

Bulgarian provenance trials

A provenance trial was initiated in 1987 (Petkova 2004). It included 31 provenances of the variety *menziesii*, 22 of the northern and 2 of the southern subgroup of variety *glauca*. The provenances of coastal Douglas-fir came from the western slopes of the Washington and Oregon Cascades and coastal regions of the two states. The provenances which belong to the northern subgroup of interior Douglas-fir came from British Columbia, Washington, Oregon, and Montana. Those which belong to the southern subgroup of interior Douglas-fir stemmed from Arizona and New Mexico.

Provenance plantations were established in five locations in the western half of Bulgaria (Figure 4.9) in 1989 and 1990. At age 11 from seed, provenances from the western Cascades in Washington (seed zones 402,403,411) and from the coastal regions of Washington and Oregon (seed zones 012,053) had the best and provenances of interior Douglas-fir the poorest growth. These early results of the provenance trial point to western Washington and western Oregon as the best seed sources for Bulgaria as has also been shown by existing Douglas-fir stands in that country.

Bosnia and Herzegovina provenance trials

Professor Konrad Pintarić of the faculty of Forestry, University of Sarajevo, initiated an experiment in 1963 with five provenances from Washington (Joyce, Wishkah, Elma, Darrington, Palmer). The provenance Palmer is apparently mislabeled as from Multnomah County, Oregon, elevation 900 m. Pintarić reported in 1967 on their nursery performance. He outplanted 1-2 seedlings from these provenances in 1966 at Batalovo, about 20 km west of Sarajevo. The provenance Elma, however, had been replaced by one from Kamloops, British Columbia. Measurements in 1997 (Ballian et al. 2003) at age 34 from seed showed the standing volume of the four Washington provenances, projected to per hectare, ranged from 125 to 235 m^3. By contrast, the Kamloops provenance had produced much less volume at that age, namely 135 m^3/ha.

Pintarić continued trials with some var. *menziesii* provenances from the IUFRO seed collection with the establishment of several experimental plantations in 1972. One of the plantations is located at Crna Lokva (44° 51′ N, 16°51′ E) elevation 665 m. That plantation contains two provenances from Vancouver Island, British Columbia (91029 Thasis, 1036 Alberti), four from Washington (1060 Sequim, 1069 North Bend, 1090 Cougar, 1091 Yale), and two from Oregon (1099 Pine Grove, 1100 Grand Ronde). Results were reported

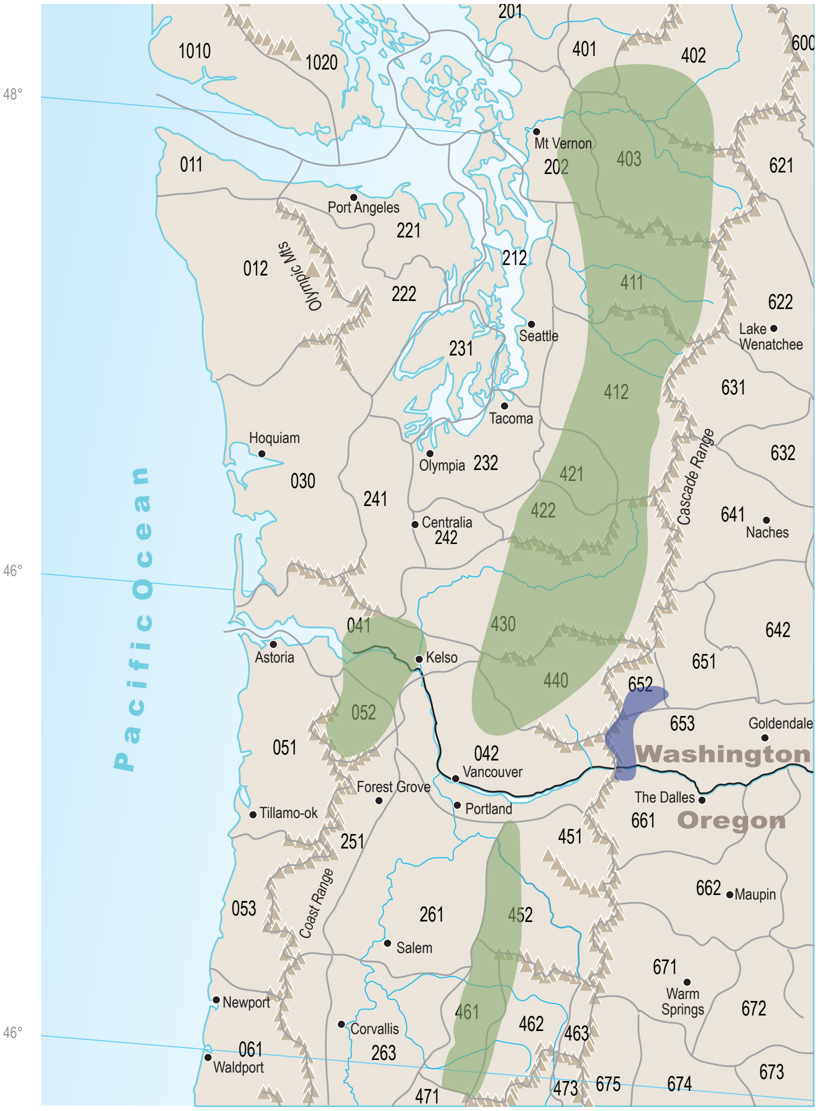


Figure 4.8 Seed zones with provenances recommended for Austria (from Schultze and Raschka 2002).

Figure 4.9 Location of Bulgarian provenance test plantations (squares) and cities (from Petcova 2004).

after 17 (Pintarić 1989) and 32 growing seasons (Govedar et al. 2003). Statistical analysis did not show significant differences in survival and volume production between the eight provenances. Govedar et al. (2003) showed how well these provenances had performed through a comparison of their data with those in the Schober (1987) yield tables for Douglas-fir. That comparison demonstrated that the volume production of the provenances in the Crna Lokva plantation exceeded that given for site I in the Schober table.

A second plantation is at Gostovic (44°23′ N 18°08′ E) elevation 411 m. Only six of the eight provenances planted at Crna Lokva were planted at Gostrovic. The two provenances not represented are 1069 North Bend and 1091 Yale. Results after 32 growing seasons were similar to those reported for survival and volume growth at Crna Lokva.

A third plantation at Blinje (43°50′ N, 18°03′ E), elevation 951 m contains only the two Vancouver Island (1029, 1036) and the two Oregon provenances (1099, 1100). At this location too, survival and volume growth did not differ significantly between provenances at age 32 after outplanting (Ballian et al. 2002).

Although the provenances tested contributed a very limited sample of coastal Douglas-fir, their performance suggests that progeny from seed sources in northern Oregon, Washington, and Vancouver Island is well suited for introduction to Bosnia and Herzegovina. The large intro-provenance variance observed in all three tests provides an opportunity for future selection of materials for the establishment of clone or seed orchards (Ballian et al. 2003).

Czech provenance trials

The first provenance trials with Douglas-fir in the Czech Republic were initiated between 1959 and 1961 in three forest districts with seed obtained from the Manning Seed Company in Washington (Hofman et al. 1964). Of the provenances tested, 4 came from west-central and southern Oregon, 5 from Washington, 1 from Vancouver Island, and 1 from interior British Columbia (Shuswap Lake). At plantation age 20, provenances from the western slopes of the Cascade Range showed the best growth and the fewest losses to winter injuries. The southern Oregon and Vancouver Island provenances were the poorest performers (Sika 1982).

A second set of provenance trials was established in 1961 and 1962, one in Bohemia and one in Moravia. These trials included 31 provenances, 5 of which came from Czech Douglas-fir stands. In these trials a provenance from Salmon Arm performed best, even better than the best Czech provenance (Zavadil and Sika 1978).

A third provenance experiment was initiated in 1968 with 25 provenances from the 1966 IUFRO seed collection (Sika 1981). They represented 11 British Columbia, 10 Washington, and 4 Oregon seed sources. Trees were outplanted in 1971 and 1972 in five Bohemian forest districts. Winter drying (physiological drought) and frost damage, mainly in the winters 1972/73 and 1975/76 caused the largest losses. Coastal provenances from Oregon and Washington suffered most, and provenances from interior British Columbia and upper elevations in the Washington Cascade Range were afflicted least from these types of climatic injury. Provenances from the west slope of the Cascade Range in northern Washington and interior British Columbia had attained significantly greater heights at plantation age 10 than those from coastal regions. The latter had shown a pronounced reduction in annual height increment after the severe 1972/73 and l975/76 winters. The reduction may have been too large for compensation by subsequent growth. Differences in height growth between some of the provenances in the 5 plantations also indicated significant seed source x planting site interaction. The ranking of provenances according to height growth had changed little by plantation age 11 in the IUFRO experiment and plantation age 20 in the two earlier sets of provenance trials (Sika 1982).

Sika (1981) concluded from the 10-year results of the IUFRO provenances experiment that 3 regions should be considered suitable as seed sources for the Czech Republic. In order of preference, they are the western slopes of the Cascade Range in northern Washington, the lower Frazer River Valley, and the southern inland of British Columbia. But he cautioned that high susceptibility of the interior variety of Douglas-fir to *Rhabdocline* and *Phaeocryptopus* needle cast may require reconsideration of the suitability of inland British/Columbia seed sources.

Slovac provenance trials

The Forest Research Institute at Zvolen initiated the first Douglas-fir provenance experiment in Slovakia with seed from one of the IUFRO collections (Tavoda 1991). Test plantations were established in 1972 at two locations. The Kmetova plantation received 21 var. *menziesii* provenances from British Columbia, Washington, and Oregon, as well as progeny from two Slovak Douglas-fir stands. Of the 13 provenances planted at the Velka Straz plantation, 11 belonged to var. *glauca* and only 2 to var. *menziesii*. The var. *glauca* provenances originated from Montana (1), Colorado (6), and British Columbia (4); the 2 var. *menziesii* provenances came from high elevations in the Washington and Oregon Cascade Range.

Based on the performance over 20 years in the field by these provenances, Tavoda (1991) provisionally recommended seed from the following regions for use in Slovakia:

- the west slopes of the Washington Cascades (Seed Zones 402, 412)
- the rainshadow of the Washington Coast Range (Seed Zone 221)
- the Frazer River Valley (Seed Zone 1050)
- the southern inland British Columbia (Seed Zone 2040)

Hungarian provenance trials

In 1969, the Hungarian Forest Research Institute initiated a provenance experiment with 44 IUFRO provenances, 3 from British Columbia, 25 from Washington, and 16 from Oregon (Harkai 1983). All Washington and Oregon provenances belonged to the var. *menziesii* and those from British Columbia to var. *glauca*. A plantation with seedlings of the 44 provenances was established in 1971 at Zalaerdöd.

Both the provenances from Washington and Oregon had given very satisfactory results by age 14 from seed. Mean height was 6.8 m and dbh 10.7 cm. The top performers from Washington were the provenances PeEll, Tenino, Ashford, and Randle. Those from Oregon were Vernonia and Estacada. These results suggested that the west slope of the Washington and northern Oregon Cascade Range as well as the southern Coast Range of Washington and the northern Coast Range of Oregon contain the most promising seed sources for use in Hungarian silviculture. The slow-growing provenances from interior British Columbia are considered suitable only for the culture of ornamental and Christmas trees (Harkai 1983).

Polish provenance trials

Polish provenance trials of northwest American conifers began in 1960 with an experiment initiated by Prof. Ilmurzynski of the Polish Research Institute at Warsaw, which included 5 Douglas-fir provenances from Washington, Idaho, New Mexico, and progeny from 2 Polish Douglas-fir stands (Bialobok and Mejnartowicz 1970). The institute commenced a second provenance trial in 1968 with 38 provenances from the 1966/67 IUFRO collection, 9 commercial Washington provenances bought from Silva Seed, and progeny from 9 Polish Douglas-fir stands. The 38 IUFRO provenances included 12 from British Columbia, 23 from Washington, and 3 from Oregon. Between 1971 and 1974 eleven plantations were established, but only one contained all 56 provenances (Burzynski and Gutowski 1973).

An assessment of the performance of the 56 provenances at age 20 from seed led Burzynski et al.(1990) to the conclusion that all of the provenances tested can be grown in the parts of Poland with a moderate climate except the provenance Brookings from southwest Oregon. Significant differences in growth and frost resistance between provenances became apparent, however. Although the interior British Columbia and eastside Washington provenances showed inferior growth, they did not suffer any frost damage. But only 14 of the 28 var. *menziesii* provenances from Washington were able to withstand the severe environmental conditions without appreciable cold injuries in the parts of the country with the most pronounced continental climate.

An interesting account of the relative performance of some IUFRO provenances was provided by Birot and Burzynski (1981). They compared the performance of the same 14 provenances, 5 from British Columbia, 6 from Washington, and 3 from Oregon, at a Polish and a French site 9 years after planting. The Polish plantation is at Dolice, lat. 53°14’N, 40 km southeast of Szczecin. The climate is continental with oceanic influences because of the vicinity to the

Baltic Sea. Average annual precipitation is 670 mm. The French plantation is at Peyrat-le-Chateau, lat. 45°49′N in the Limousin. The location is under the influence of an oceanic climate and has an average annual rainfall of 1,270 mm.

That comparison showed surprisingly similar performances of provenances at the French and Polish test plantation although growth was lower in the Polish test, which reflects the more severe climatic conditions at Dolice. Provenances from the foothills of the westside of the Washington Cascades were the most vigorous, and those from interior British Columbia the least vigorous. The only exception was the provenance Brookings from southwestern Oregon, which grew well at Peyrat-le-Chateau but poorly at Dolice.

The Institute of Dendrology of the Polish Academy of Sciences initiated a third trial in 1968 with seed from the 1966/67 IUFRO collection at Kornik in western Poland. That experiment initially included 104 provenances from British Columbia, Washington, and Oregon. Because excessive frost damage to 4 provenances left insufficient numbers of seedlings, only 100 provenances are represented in the test plantation established at Kornik, lat. 52°15′N, in 1971 with 3-year-old seedlings.(Mejnartowicz 1973). Performance at age 7 from seed already showed a distinct differences between provenances. The var. *glauca* provenances from British Columbia and Washington showed poor height and diameter increments but excellent cold hardiness. Var. *menziesii* provenances from coastal British Columbia, and especially Vancouver Island, varied remarkably in growth. But the advantage of good growth was offset by high susceptibility to cold injury. Mejnartowicz (1976) concluded on the basis of the 7-year results that the western slope of the northern Washington Cascades appears to contain the best seed sources for use in Poland.

To determine genetic variation and diversity of provenances in the Kornik plantation, Mejnartowicz and Lewandowski (1994) estimated the allozyme polymorphisms in wind-pollinated seeds collected from every of the 71 cone-bearing trees in the plantation. He considered one sample size to be sufficiently large to obtain a reliable estimate of allelic frequencies at the population scale in a stand. The trees were 23 years old and represented 41 provenances. Expected and observed heterozygosity, proportion of polymorphic loci, average and effective number of alleles per locus—indicators of genetic variation and diversity—were slightly higher than found by other investigators (Yeh and O'Malley 1980, Merkle and Adams 1987, Moran and Adams 1989, Li and Adams 1989) in natural stands of Douglas-fir. Mejnartowicz attributed the difference to the fact that the test plantation contains a compressed gene pool which comprises populations from a vast area within the natural range of the species. In such an artificial stand, the probability of mating among relatives is low. The high level of genetic polymorphism seems to indicate that genetic variety was not diminished in the artificial population.

Danish provenance trials

The first Danish provenance test of Douglas-fir owes its initiation to the Danish forest inspector S.M. Storm (1887-1918). He proposed to establish provenance trials with conifers from the American West after his return in 1914 from travels in North America. Shortly thereafter, with A. Oppermann, he asked Henry Graves of the U.S. Department of Agriculture for samples of seed. As a result of their request, they received, in 1915 and 1916, several lots of seed, together with information about the parent trees and their habitats. The shipment included 5 provenances from western Washington, 3 from western Oregon, 5 from California, 1 from eastern Washington, 2 from Idaho, and 2 from Montana.

Oppermann established, in 1918, test plantations with these provenances in mid-Jutland, Funen, south Seeland, and the isle of Bornholm. In addition, the plantations contained a Washington, Oregon, and California provenance obtained from the seed firm Johannes Rafn, as well as progeny from two Danish Douglas-fir stands. Oppermann reported on the 10-year performance of trees in the experiment. The provenances from western Washington turned out to be the best because of excellent growth and relatively high cold hardiness. The Oregon and California provenances grew well but suffered considerable winter injury in the unusually severe winter of 1923/24, in which temperatures dropped to a low of -27°C. The inland provenances were the hardiest but had the lowest rate of growth. Based on these results, Oppermann (1929) advocated the cultivation of Douglas-fir from western Washington seed sources but recommended against the use of seed of interior Douglas-fir as well as seed from Oregon and California sources. Performance at age 20 of the 1918 test plantations gave further credence to his opinion. The coastal provenances had attained heights that ranged from 9.75 to 11.9 m compared to 7.0 to 7.9 m for the inland provenances. Moreover, the inland provenances had become heavily infected with *Rhabdocline pseudotsugae* while the coastal provenances had remained healthy (Bornebusch 1939).

The 1918 Oppermann trial was followed by five successive trials initiated by the research branch of the Danish Forest Service between 1930 and 1968. They represent tests of 76 provenances in 17 locations throughout Denmark (Table 4.5). Providers of seed included the Longbell Lumber Company, the Manning Seed Company, and IUFRO. Detailed descriptions of seed sources and location of the test plantations are given by Lundberg (1957) and Larsen and Kromann (1983). Of the 31 provenances in the 1930 trial, 11 are the same as those in Series II of the Wiedemann trials in Germany (Table 4.2).

Most provenances tested in the five trials are from the coastal regions of British Columbia and Washington. Inland provenances were not included anymore after the 1930 trial, except for one in the 1958 trial and 1968 IUFRO trial because the early tests had already demonstrated that slow growth and vulnerability to *Rhabdocline* needle cast made inland Douglas-fir unsuitable for cultivation in Denmark.

Based on their analysis of the Danish provenance trials, Larsen and Kromann (1983) concluded that provenances from the coastal regions of British Columbia and Washington hold the greatest promise for successful cultivation. Within this part of the Pacific Northwest, provenances from the south and southwest of the Olympic Mountains were the best performers. They considered provenances from the western slope of the Cascades and the northern part of the Olympic Peninsula suitable too, but pointed out that they had shown greater variability in perfor-

Table 4.5 Provenances in five Danish trials from 1930 to 1968 (from Larsen and Kromann 1983).

Provenances	Germination	Year of plantation Establishment	Number of plantations	Seed provider
Colorado 1	1930	1933/1935	4	Longbell Lumber Co.
Montana 2				
Idaho 2				
Inland British Columbia 5				
Coastal British Columbia 3				
Washington 12				
Oregon 2				
California 1				
Denmark 1				
Germany 2				
Washington 5	1937	1940/41	3	USDA Forest Service
Oregon 2				Joh. Rafn
Coastal British Columbia 1	1956	1959	3	Manning Seed Co.
Vancouver Island 3				
Washington 3				
Denmark 2				
Inland British Columbia 1			2	Manning Seed Co.
Vancouver Island 4	1958	1961		
Inland British Columbia 1	1968	1971		IUFRO
Coastal British Columbia 11				
Washington 3				
Denmark 1				

mance than those from south and southwest of the Olympic Mountains. Larsen and Kromann recommended against the, use of provenances from the southernmost part of Vancouver Island because of high sensitivity to frost. As had already been noticed by Lundberg (1957), growth of progeny from Danish and German Douglas-fir stands included in the Danish trials was found to be on a level with the best American provenances (Larsen and Kromann 1983).

Norwegian provenance trials

Some of the earliest provenance experiments with Douglas-fir in Europe were carried out in Norway. Børre Giertsen began trials in 1901 in the Ekheng nursery with Douglas-fir from seed sources in Colorado but that work stopped with his death in 1905 (Hagem 1931). Resumption of provenance experiments was advocated by Hagem in 1915. He sent Anton Smitt in 1916 to British Columbia to make a seed collection for the Norwegian Forest Research Institute. Hagem tested 24 var. *menziesii* provenances from British Columbia and Washington, and 6 var. *glauca* provenances from British Columbia. Based on their performance in the field for 10 years, Hagem (1931) concluded that only the northernmost of the var. *menziesii* provenances appear to be suitable for cultivation in western Norway. Frost killed all trees from Washington seed sources. The more frosthardy var. *glauca* was deemed to be disadvantageous for western Norway because it grows slower than the native spruce. Hagem, however, considered Douglas-fir from the Frazer River area suitable for growth in eastern Norway.

Half a century after the initiation of the provenance trial by Hagem, the Norwegian Forest Research Institute in Bergen obtained 51 seed lots from the 1966 and 1968 IUFRO collections. The objective of the trial with these 51 provenances was to identify areas that contain seed sources suitable for West Norway (Magnesen 1973). The provenances chosen for the experiment were thought to have the potential for growth under the climatic conditions of West Norway. They included 17 var. *menziesii* provenances from British Columbia, 5 from Washington, and 8 from Oregon besides 14 var. *glauca* provenances from British Columbia and 7 from Washington.

Seeds were sown in spring 1969 in a forest tree nursery at the end of the Ulvik fjord, lat. 60°35′N, in Hardanger. A test plantation was established with 2-0 seedlings in the Mobergslien Research area in spring of 1971. The research area is 26 km south of Bergen at lat. 60°10N, long. 5°27›E, at about 100 m elevation. Annual precipitation in the area ranges from 1,800 - 2,000 mm.

An assessment of survival at age 9 from seed indicated that only 38% of the trees belonging to coastal provenances were still alive, in contrast to 53% of the inland provenances. Most of the losses had occurred during the extremely severe winter 1971/72 (Magnesen 1978). In 1981, at age 18 from seed, 34% of the var. *menziesii* and 48% of the var. *glauca* trees had survived (Magnesen 1987). Survival of var. *glauca* provenances from interior British Columbia above lat. 50°N was higher than that of all other provenances. Although these inland provenances had a small proportion of trees with sinuous stems and broad crowns and had been growing much slower than the coastal provenances, Magnesen (1987) concluded that they “may be the best choices for Norway after all.”

Swedish provenance trials

An initial provenance trial with seed from the 1966/70 IUFRO seed collection was apparently a failure. Most of the provenances originated from latitudes too far south to be able to adapt to growing conditions in Sweden. Consequently, seedlings died soon after planting (Martinsson 1990). As a follow-up, another provenance experiment was initiated to investigate the adaptability of provenances from the northern part of the species’ natural distribution.

In May 1984, Owe Martinsson of the Swedish Agricultural University at Umeå selected 13 stands in British Columbia and 2 in northern Washington (Figure 4.10) for cone collections. The cone collections and seed extractions were made in 1985 and 1986 by two local contractors. The collections in the Washington and 9 British Columbia stands were single-tree collections from 12 dominant trees. In 4 of the British Columbia stands, cone collections were made from squirrel caches. In addition, seed from bulk collections in 1 Danish and 2 Swedish Douglas-fir stands were included in the experiment.

Figure 4.10 Collection sites for Swedish provenance tests (open circles) and sites of test plantations (closed circles); from Martinsson and Kollenmark (1993).

Seedlings were raised in the Almfors tree nursery in Hälsingland and planted as 2-year-old seedlings in 3 test plantations in southern Sweden in 1990 and in 4 test plantations in central Sweden in 1991 (Figure 4.10). Survival of seedlings was recorded 2 years after planting in the southern plantations, and 1 year after planting on the sites in central Sweden (Martinsson and Kollenmark 1993). Survival ranged from 71% to 100% in southern Sweden, but coastal provenances had the lowest rates of survival in all three plantations. The survival rate was considerably lower in the central Swedish than in the south

Swedish plantations. Survival for the 10 best provenances, which excluded all coastal provenances, varied between 49% and 84%.

Although Martinsson and Kollenmark (1993) stated that 2 years in the field are too short a period for an evaluation of the seed sources in the experiment, they nevertheless pointed out that coastal provenances had such a low rate of survival that their use anywhere in Sweden would probably be doomed to failure. For introduction to central Sweden, only provenances from the northernmost part of the species' natural range or from high elevations in the interior of British Columbia should be considered. A look at the map (Figure 4.10) makes the reason for these recommendations very clear.

Finnish provenance trials

Small test plantations established in Finland during the first half of the 20th century had shown generally poor performance by both varieties of Douglas-fir. Some variety *glauca* provenances from interior British Columbia, especially the upper Frazer River valley (Heikinheimo 1956), were an exception. Because early trials lacked adequate replication, the Finnish Forest Research Institute decided to initiate another provenance trial with an up-to-date experimental design, when seed from the IUFRO collection became available. But in view of the earlier experience, their choice of provenances was limited to the 9 northernmost (IUFRO numbers 1001–1008) of the IUFRO collection in British Columbia (Hagman 1973).

Seeds were sown in May 1970 in a tree nursery on the island of Nagu (lat. 60°11′N) in southwest Finland. Frost in fall and winter of the first year in the nursery killed nearly all the seedlings from the 2 var. *menziesii* provenances in the experiment, but the 7 var. *glauca* provenances suffered far less dramatic losses. At the end of the third year in the nursery, survival of seedlings from the 7 interior provenances ranged from 48% to 65%.

Although the results of the trial with IUFRO provenances covered only 3 years in the nursery, they appeared to give credence to previous experience that the variety *menziesii* seems to be unable to adapt to Finnish conditions, even under such a mild climate as prevails in the country's southwestern archipelago. Hagman (1973) emphasized that the number of provenances in the IUFRO experiment is small but expressed the hope that it can give some guidelines for further selection.

Latvian provenance trials

The Latvian Research Institute for Forestry Problems has embarked on a large program of provenance trials. The trials involve 300 provenances, 125 of which are from the IUFRO collection. The other 175 provenances come mostly from second generation Douglas-fir stands in Russia, the Ukraine, Bulgaria, Poland, Hungary, Norway, Denmark, Germany, and the Netherlands (Pirags 1968, 1990). Initial results indicated that provenances suitable for Latvia come from the area between lat 45° and 55° N, and long 117° and 125° W. Progeny from stands in the Baltic region (Estonia, Latvia, Lithuania) did very well. Provenances from south of lat 43° N are absolutely unsuitable for Latvia (Pirags 1979, 1990).

Estonian provenance trials

Among the earliest provenance experiments in Europe is that of Count Berg, established on his estate in Sagnitz, Estonia. After disappointing results with seed purchased from European seed dealers, Berg was able to obtain 13 seed lots in 1909, and another 12 in 1910, of known origin from the US Bureau of Forestry. All were var. *glauca* provenances from New Mexico, Colorado, Montana, Idaho, and the east slope of the Washington Cascades, except for a Snoqualmie, Washington, and Lake Tahoe, California, provenance. Initial results suggested that var. *glauca* provenances would be more suitable for use in Estonia than would var. *menziesii* provenances (Berg 1912, Zon 1913). Some of the trees from this experiment were still alive in 1978, but records pertaining to the experiment are unfortunately lost (Etverk 1978). M. Sievers, chairman of the Baltic Forestry Association, bought seed of different provenances directly from North America in 1911 but records of plantations established with that seed are also lost (Margus 1961).

Several trials were begun during 1930 - 1932 by Prof. Mathiesen in the forest of Tartu (formerly Dorpat) University. Results confirmed the suitability of var. *glauca* seed sources from interior British Columbia for Estonia (Margus 1963). In the spring of

1973 a provenance test was begun in the state forest managed by the Estonian Academy of Agriculture at Järvselja. Provenances from northern interior British Columbia and Montana did not suffer frost damage in the first 5 years since germination but grew slower than progeny from Estonian Douglas-fir stands (Etverk 1978).

Initially, Estonia was unable to participate in the international IUFRO Douglas-fir provenance experiment. In spring 1978, however, H. Barner provided 23 lots of seed from British Columbia, Washington, and Oregon from the IUFRO seed collection. They were sown in the plastic greenhouses of the Estonian Forest Research Institute (Etverk 1978). Information about the progress of this experiment was not available to us.

Turkish provenance trials

Except for a few small Douglas-fir plantations established after World War II, experience with the species' adaptive ability to Turkish site conditions was lacking. To provide a basis for the selection of suitable seed sources, the Research Institute for Poplar and Fastgrowing Conifers at Ismit initiated a comprehensive provenance experiment in 1971, with 85 var. *menziesii* and 33 var. *glauca* provenances from the IUFRO seed collections (Simsek 1978).

Seeds were sown in 1972 in the Alendag nursery near Istanbul. Because 37 of the provenances had a low percentage of germination, only 81 provenances were available for establishing 9 plantations on ecologically different sites along the Black Sea coast in 1974. Latitude of the sites ranged from 40°44′ N to 41°23′ N, longitude from 29°48′ to 38°25 E, elevation from 25 m to 1,340 m.

An assessment of performance at age 6 from seed, based on survival, height, and diameter growth, showed provenances from elevations below 600 m of the west slope of the Washington and Oregon Cascade Range, and the east side of the California Coast Range, to be the best ones (Simsek 1978). Subsequent assessments at ages 9 and 11 from seed (Simsek 1980, 1982) revealed excellent growth by provenances from the Washington central Cascades and Coast Range between lat 47° and 48° N. Other var. *menziesii* provenances had begun to perform less satisfactorily. All var. *glauca* provenances had shown particularly poor growth and could be ruled out for further consideration for use in Turkey.

After 14 growing seasons in the field, marked changes in performance between var. *menziesii* provenances became apparent (Simsek 1987). Growth of British Columbia, Oregon, and California provenances had greatly slowed, and their rate of survival had decreased to unacceptably low. Simsek (1987) was confident that the performance of the provenances from the central Washington Cascades in both low- and high-elevation test plantations suggested that the central Washington Cascades contain the most promising seed sources for the Black Sea region. He justified his opinion with these words, "if adaptability of provenances is looked upon as optimization between good growth and a high rate of survival, than the provenances from the central Washington Cascades show the greatest adaptability, among the provenances tested."

Taiwan provenance trials

The Taiwan Forest Research Institute initiated a provenance experiment with *P. menziesii* to explore the possibility of successfully introducing the species to the island's forests in the early 1970s (Yang 1978). Seed collections were made in 14 stands in coast ranges of the Pacific Northwest: 9 in California, 3 in Oregon, 1 in Washington, and 1 on Vancouver Island

Seeds were sown in the Chi-tou and Chu-yun Shan nurseries. Growth of provenances from southern or lower elevation origins was consistently superior to that of provenances from northern or higher elevation origins. Based on their performance in the two nurseries, Yang considered four provenances from the fog belt of California to be the most adaptable to the environment of medium high elevations in Taiwan. The locations of origin of these four provenances are given in Table 4.6.

Table 4.6 Locations of the origin of four provenances used in Taiwan trials.

Provenance	Latitude N	Elevation (m)
A	37°13'	394
B	39°38'	380
D	40°23'	454
E	41°78'	563

New Zealand provenance trials

Second- and third-generation stands of Douglas-fir in New Zealand, in contrast to those in Europe, have provided far more seed than imports from North America. Location of the original seed sources of stands established before 1926 is uncertain but a record exists of site of seed origin used in plantings after that date (Wilcox 1978). Although seed source descriptions were available for the post-1926 imports, performance of their progeny was not evaluated by provenance tests.

Preparations for provenance trials commenced with collections from the 1955 cone crop in British Columbia, Washington, Oregon, and California made by American seed suppliers (Anonymous 1994). Plantations with seedlings from the North American collections were established at 10 locations on the North and South Island. Included in that trial were also progeny from New Zealand Douglas-fir stands at Dusky, Kaingaroa, Whaka, and Tapavera. After the sixth growing season in the field, Washington provenances from low altitudes were generally the tallest at all locations. The four New Zealand provenances were among the best at most sites (Wilcox 1978).

A second trial was begun with 44 provenances from Washington, Oregon, California, and a bulk seed lot collected at Kaingaroa Forest. The North American collections were made in 1956 by Egon Larsen (Figure 4.11) to fill out gaps in the first trial (Anonymous 1994). Most of his seed lots were from cone collections on at least 10 trees. Seedlings for the second trial were planted in 1959 at 19 locations in the North and South Island (Sweet 1964).

In the assessment of performance 13 years after outplanting nine traits (height, diameter, stem straightness, malformation, needle retention, branch diameter, wood density, heartwood percent, and survival) were measured or scored on 15 provenances in six plantations (Figure 4.12), and on all 44 provenances in three of the six plantations. The 15 provenances were the same ones already judged at age 5 in the field by Thulin (1967) as the most promising. Of the traits analyzed, height varied the most and gave the clearest separation of provenances. Genotype x environment interaction for all traits was small, indicating that the best provenances were the superior performers on all sites. The best provenances came from low elevations in the fog belt of northern California and southern Oregon. Washington provenances and those from the Sierra Nevada of California grew distinctly slower at all test sites than the provenances from the California and Oregon coast.

As a result of the 1959 trial, seven provenances (Table 4.7) were identified as those from whose sources of origin seed should be imported for use in New Zealand and on which a breeding program should be based (Wilcox 1974). Six of these seven provenances had ranked at the very top in height growth at age 5 in the field. In the words of Wilcox (1974), "This early assessment provided the information which led to the importation of several commercial seed lots from coastal Oregon and California. The 13-year assessment results confirm that these interim choices were substantially correct."

The New Zealand tree seed company PROSEED funded, in 1988, the selection of plus trees from the best coastal fog belt provenances in the 1959 trial. Because the test plantations had been thinned in 1976 only about 20 of the original 144 trees per plot were left. All trees in the best provenances were measured over six sites (Table 4.7) and the best tree per plot selected. The selected trees were grafted into a seed

Table 4.7 Superior Douglas-fir provenances selected for use in New Zealand (from Wilcox 1974).

Provenance	Origin	Characteristics
636	Oregon, Deadwood	Excellent form, and good needle retention, vigorous
641	Oregon, Four Mile (Bandon)	High wood density, vigorous
642	California, Berteleda (Gasquet)	Very vigorous and excellent form
647	California, Mad River (Korbel)	Very vigorous and high wood density
654	California, Caspar (Fort Bragg)	Vigorous
659	California, Stinson Beach	High wood density, vigorous and excellent form, prone to needle cast
660	California, Santa Cruz	Very vigorous, low wood density, prone to needle cast

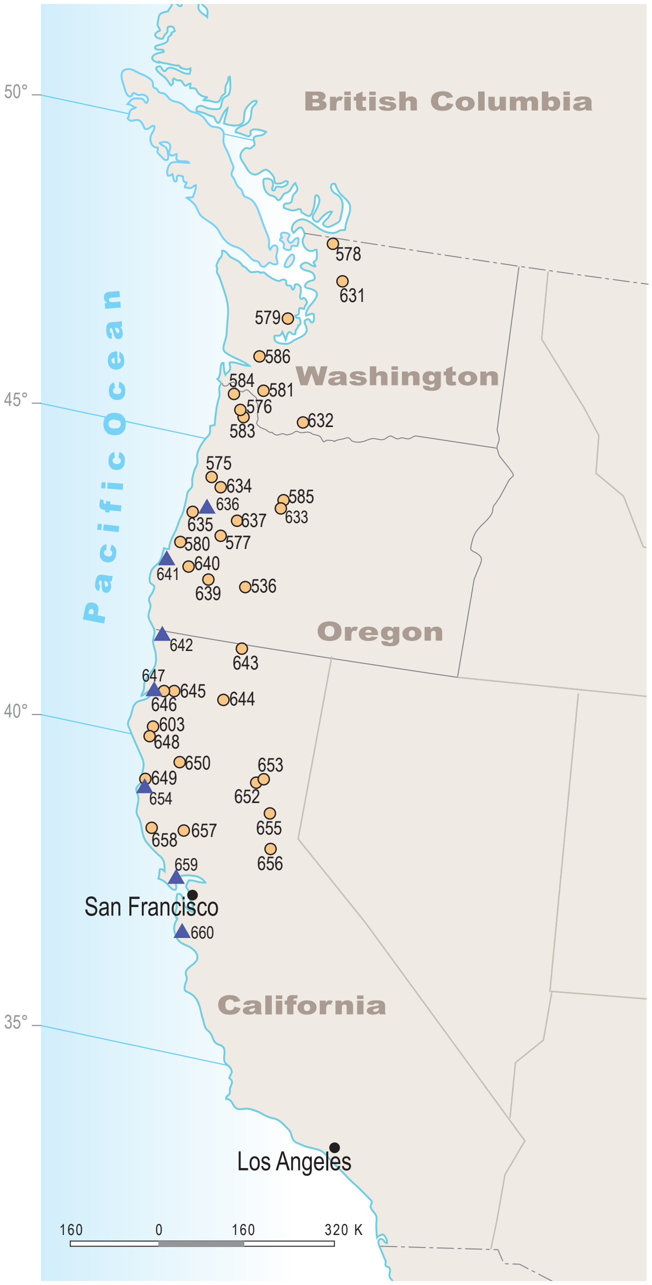


Figure 4.11 Sites of Egon Larsen seed collection (circles); provenances recommended for use in New Zealand based on performance 16 years after outplanting (triangles); from Wilcox (1974).

Figure 4.12 Location of six plantations of the 1959 provenance test in New Zealand (from Wilcox 1974).

orchard at Canterbury. In addition, PROSEED and the New Zealand Forest Research Institute funded a seed collection from southern coastal California and coastal Oregon with the primary objective of widening the genetic base to include previously untried provenances (Anonymous 1994, Miller and Knowles 1994).

A third provenance experiment was begun in 1967 with the establishment of test plantations at Kaingaroa, Rotorua, and Gwavas. That experiment included two Mexican Douglas-firs, *Pseudotsuga flahaulti* and *P. macrolepis,* a California provenance from Santa Cruz, and New Zealand Douglas-fir from Kaingaroa (Wilcox 1978). The assessment of the 7-year performance of the trees at the Rotorua site showed that the Santa Cruz provenance, with an average height of 4.6 m, was significantly taller than the New Zealand and Mexican Douglas-firs but had suffered loss of needles because of infection with *Phaeocryptopus gaeumannii. P. flahaulti,* with an average height of 3.7 m, was as vigorous as the 3.5-m-tall Kaingaroa provenance. The second Mexican Douglas-fir, *P. macrolepis,* had only attained a height of 2.6 m and showed poor vigor.

Additional provenance tests were established in 1971 and 1974 on numerous sites throughout New Zealand. Their results have led to the identification of distinct, superior local strains. A 1980 report of the New Zealand Forest Research Institute at Rotorua (1981) describes four such strains as follows:

Fort Bragg strain

The native provenance of this strain originated in Jackson State Forest close to Caspar, Fort Bragg, California (altitude 160 m). It is typical of the low-elevation coastal Californian provenances that have grown so well in provenance tests, particularly in the North Island. Seed stands at Rotoehu Forest and Golden Downs Forest have been formed in blocks planted in 1959 and so far 88 kg of seed have been collected. Compared to the widely used and more familiar Kangaroa strain of Douglas-fir (originally from Washington), the Fort Bragg strain is distinguished in the nursery by its exceptional vigor, comparatively early flushing in spring, and by its bright green color.

Ashley strain

This strain has proved to be a consistently good grower on both low- and higher altitude sites in the North and South Islands. A seed stand has been certified at Ashley Forest, and new second-generation seed stands are being developed at Golden Downs and Ashley. The Ashley strain originated from shelterbelts in the Tapawera district near Golden Downs Forest, Nelson. The native origin of these early introductions is not known; in flushing time, however, the Ashley strain (and other seedlots of Tapawera ancestry) is intermediate, similar to that of provenances from coastal localities in Oregon.

Figure 4.13 Australian Douglas-fir provenance plantations (from Griffin and Matheson 1978).

Beaumont strain

The origin of this strain (Beaumont Forest, Southland) can be traced to various stands of Douglas-fir in the Tapanui district, supposedly of Washington origin. The strain has not yet been performance-tested but is nonetheless expected to be reliable for planting in the South Island.

Kaingaroa strain

Most of the Douglas-fir in Kaingaroa Forest originated in the state of Washington. "Kaingaroa strain" refers to any of the larger seedlots collected from various compartments in the forest. It is a dependable, late-flushing strain, giving maximum protection against late frosts, but its growth rate is not exceptional.

Australian provenance trials

The CSIRO Division of Forest Research initiated in 1970 a provenance experiment with 40 seedlots from the 1966/69 IUFRO collection and some non-IUFRO seedlots from low-elevation sites in the California coastal region. The IUFRO seedlots included *Pseudotsuga menziesii* var. *menziesii* from British Columbia, Washington, Oregon, California, and Mexico (Griffin and Matheson 1978). Nine test plantations were established in 1972-73 in New South Wales, Victoria, and Tasmania on sites considered to have potential for the growth of Douglas-fir. These sites cover a latitudinal range from 31° to 41°S (Figure 4.13) and elevations from 180 to 1,200 m. Because a common design for all plantations was not attempted, only 11 of the 40 seedlots were planted at all 9 sites. With the exception of one Washington provenance (Cle Elum), the provenances represented in each of the test plantations originated from the southern Oregon and California coast ranges.

Measurements of height growth at plantation age 5 clearly demonstrated the faster growth of provenances from low elevations in the coastal regions of southern Oregon and northern California relative to those from comparatively short distances farther inland in the coast ranges. But Griffin and Matheson (1978) cautioned that these early results, "do not demonstrate clear superiority of any particular seed collection area within the low-elevation coastal areas of northern California, Oregon, and Washington, and it may be that traits other than growth potential per se would influence the final choice of provenances". They concluded, however, that—based on current evidence—seed from sources in the coastal fog belt of northern California and southern Oregon would be recommended for use in Australia.

What has been learned from provenance experiments?

Provenances experiments have shown that the variety *glauca,* with perhaps a few exceptions, is not desirable for introduction outside its natural range, mainly for two reasons: (1) the growth of inland Douglas-fir is inferior to that of the variety *menziesii*, and (2) inland Douglas-fir is highly susceptible to infection by *Phaeocryptopus gaeumannii* (the Swiss needle cast pathogen), which significantly reduces growth and frequently leads to premature death.

Because of the generally poor performance of variety *glauca* in areas of introduction, emphasis has focused on variety *menziesii* in provenance studies. "Studies initiated in the first half of the 20th century showed that the most promising seed sources for many parts of Europe may be found in western Washington and northwestern Oregon. The experience gained from these early studies also pointed to the need for a more accurate way to assess the performance of a given provenance in different geographic locations of introduction. That led to the decision by IUFRO Working Party S2.02-05 Douglas-fir provenances at its 1978 Vancouver, British Columbia, meeting, to create a database that would permit a valid comparison of the results of field tests obtained by participants in the international IUFRO Douglas-fir provenance experiment

The database was set up in France by INRA and AFOCEL in 1979 (Breidenstein et al. 1990). In September 1989, the base contained data from 108 test sites provided by 20 institutions in 14 European countries and Canada. Those data represented barely half of the 33 countries that had received seed from the IUFRO collections. Breidenstein et al. (1990) evaluated available data by arranging plantation sites into these ecological groups: (1) sites with continental climate in north-eastern Europe; (2) sites with a mild oceanic climate in northwestern Europe and southwestern British Columbia; (3) sites exposed to a relatively harsh oceanic climate with low mean annual temperatures in northwestern British Columbia, Norway, and a few locations in France and western Spain; (4) southern Europe south of lat 48° N. Provenances were separated into three groups designated as coastal, intermediate, and interior, based on broad geographic areas of origin: "coastal" indicated that provenances originated from the area between the Pacific shore and the crest of the Coast Range; "intermediate" that provenances came from the area between the crest of the Coast Range and the crest of the Cascade Range; and "interior" that provenances were from east of the crest of the Cascade Range. The database had been originally designed to compare performance of provenances based on assessment of three traits: survival, height growth, and time of budburst. Bud burst, however, had to be omitted from consideration because of insufficient data. Provenances belonging to the southern subgroup of variety *glauca* had to be excluded from analysis because they were tested in few of the sites.

Survival

Survival at or close to age 10 in the 108 test sites ranged from 70% to 85%. Provenances within groups 2 and 4 had higher rates of survival than those within groups 1 and 3, however, provenances originating from elevations above 1000 m had slightly higher survival than those from lower elevations. In group 1 sites, coastal provenances from southern Oregon had the lowest survival; in group 4 sites, provenances from interior British Columbia had the lowest survival. Provenances from low elevations in western Washington had consistently the highest survival on sites in groups 1,2, and 4.

Height growth

Analysis of the influence of latitude of origin showed a parabola-like pattern of variation of growth with latitude of origin for provenances from the coastal area. Growth of provenances from the intermediate area showed a linear increase with origin from lat 39° to 49° N. Height growth of interior provenances that came primarily from the northern part of their range failed to reveal a relation with latitude. The largest number of fast-growing provenances came from elevations below 600 m in Washington and Oregon. In contrast, provenances from low elevations in British Columbia had moderate height growth. IUFRO collected few provenances from low-elevation seed sources in California; they were planted in very few test sites. So, California is represented mainly by relatively slow growing provenances; that stem from elevations above 900 m.

The data submitted to the database may not have given an entirely unbiased picture because of differences in data collection and experimental procedures. Breidenstein et al. (1990) attributed the surprisingly high rate of survival to the choice of favorable test sites, focus on subsets of provenances deemed well adapted to the experimental site and submission of data to the base only from successful experiments. Whatever bias may have been involved in the data analysis, its results largely confirm the findings of provenance tests established before the international IUFRO Douglas-fir provenance experiment.

Southern hemisphere

Participants in the international IUFRO Douglas-fir provenance experiment from Australia and New Zealand did not provide results from their tests to the database set up by INRA together with AFOCEL. Although direct comparisons between the performance of individual provenances in the northern and southern hemisphere are therefore not possible, at least one notable difference is apparent. Provenances originating from the coastal regions of southern Oregon and northern California performed extremely well in Australia and New Zealand, in contrast to Europe, where these provenances were generally failures, except for a few locations in the Mediterranean region of France. Most Douglas-fir provenance studies have shown considerable variation not only between but also within populations. That may partially explain the broad adaptability of trees of many provenances (Kleinschmit and Bastien 1992). Individual trees can also have rather broad adaptability, but, considerable differences in individual adaptability may be explained by differences in heterozygosity. As Li and Adams (1989) have indicated, expected heterozygosity is highest in the Pacific coastal regions of northern Oregon, Washington, and Vancouver Island. Kleinschmit and Bastien (1992) suggested that might be an additional explanation for the broad adaptability of provenances from this part of the Pacific Northwest.

Progeny of introduced populations

Provenance experiments have shown that progeny of some introduced populations of Douglas-fir performed as well, or even better than the best native North American provenances. As the origin of most of the populations introduced before the second half of the 20th century is unknown, their progeny is sometimes referred to as “artificial stands” or “land races.” Attempts have been made to identify their provenance. Berney (1972) made probably the earliest of such attempts by using the DNA content of embryo cells to determine the origin of a Douglas-fir stand in Switzerland. In studies that tried to trace the North American parents of Douglas-fir stands in Switzerland (Stauffer and Adams 1993), France (Prat and Arnal 1994), and Germany (Klumpp 1999) isozymes were used as genetic markers. Rehfeldt and Gallo (2001) tried to determine the parentage of a Douglas-fir stand in Argentina by using quantitative traits because of their suitability for estimating genetic variances. Results of all these studies indicated broad rather than specific geographic locations from where the progenitors of the Douglas-fir land races had come from.

Conclusion

Since most of the classical questions of provenance research have been answered for Douglas-fir the focus is now on breeding and gene conservation.

5. Tree Breeding and Improvement

Richard K. Hermann

Jakob Roeser (1926) foresaw the need for tree improvement almost 90 years ago: "The improvement of forests by any mean whatever is at present so urgent, and a creative method makes so great an appeal to the American type of mind, that it is desirable to direct the attention of foresters generally to the possibilities of tree breeding." Genetic improvement in forest trees mostly comes from increasing vegetative growth, improving resistance to biotic or abiotic stresses, and enhancing wood and stem quality (Howe et al. 2006). Tree breeding efforts in western North America have centered on Douglas-fir in particular because of its great economic and ecological importance. The species exhibits high levels of genetic variation for all economic and adaptive traits studied, providing a rich foundation for genetic improvement (Howe et al. 2006).

The climate within the range of coastal Douglas-fir changes dramatically from west to east. A narrow coastal strip extending from San Francisco to northern Washington has an unusually long frost-free period and annual rainfall of up to 4400 mm (US Department of Commerce, Weather Bureau 1957). The change is due to mostly north-south mountain ranges where adiabatic cooling and rain-shadow drought effects interact. More climatic complexity is added each growing season by droughty summers in the Douglas-fir region, particularly below lat 42° N. Silen (1989) noted how changes in cold and drought with elevation and latitude affect growth patterns:

> Typically rain-shadow drought is most severe in valley bottoms and decreases with increasing elevation. This is the opposite in direction to the trend of decreasing growing season length with elevation caused by diabatic cooling. A typical situation in the mountains at the southern part of the region is for best growth of Douglas-fir to occur at middle elevations, with growth restricted by increased cold upward and by more intensive drought downward. Along the west slope of the Cascades, the corresponding elevation of maximal growth descends northward from mid-elevation in southern Oregon to about sea level in northern Washington, with a gradually narrowing band of droughtiness below and colder temperatures upward toward timber line. (Silen 1989)

For both varieties, low temperatures are the major limiting factor within the northern part of the range, whereas lack of moisture is the predominant limiting factor in the southern part.

Tree species occupying widely varying habitats can be subdivided into geographic races (Callaham 1970). Evidence has shown that these races are the result, in large part, of adaptation to the environments in which they are found (Adams 1981). The Douglas-fir yield tables of McArdle and Meyer (1930), for instance, indicate that feedback mechanisms are precise, probably template-like in matching genetics to environment (Silen 1989). McArdle and Meyer produced their tables in 1930, when the Douglas-fir region was mainly in natural forests. The tables give total yield by decade for stands indexed into 3-meter height classes. For example, dominant trees on best, average and poorest sites (site classes I, III, and V) attain 61, 43, and 24 m in height, respectively, at age 100. They sampled over 1,900 plots throughout the region, confining plots to pure stands of "Normal" stocking, which were dense-canopied in the self-thinning stage and generally almost devoid of other vegetation. Moreover, when analyzed decades later in terms of −3/2 power law of self-thinning, the data produced slopes with an exponent value of −1.5 the theoretical limiting value (Silen 1989):

> A frequently overlooked, but important point is that the 3/2 power law, which expresses average tree size over the range of spacing, has an interchangeable, alternate

> form, the law of constant final yield. That version uses the same data to express volume per unit area over spacing instead of average tree size over spacing, has an interchangeable, alternate form, the law of constant final yield. That version uses the same data to express volume per unit area over spacing instead of average tree size over spacing. If data from fully-stocked stands fit the theoretical -1.5 slope, it follows that a given site will also attain a constant final yield over a great range of initial densities. It is important to grasp that most fully-stocked stands in the sample must have approached theoretical maximum yields which occur at the theoretical -1.5 slope. To have such sampling accurately approximate theoretical yield maxima suggests that natural populations at each locale must be attuned phenologically to use the entire growing season. (Silen 1989)

Genecology of Douglas-fir

The term genecology was coined by the Swedish botanist Turesson in 1923. As cited by Langlet (1979, p. 657), Turesson wrote: "It seems appropriate for several reasons to denote the study of species-ecology by the term genecology (from the Greek 'genos,' race, and 'ecology') as distinct from the ecology of the individual organism, for which study the old term autecology seems to me to be the adequate expression." Turesson additionally defined genecology as "the study of the species and its hereditary habitat types from an ecological point of view" (Langlet 1979, p. 657).

The genecology of Douglas-fir has been studied at many scales, using wide ranging provenance tests (Wright et al. 1971) to studies of variation within a single watershed (Campbell 1979). Studies of genecology focus on "adaptive traits" – traits believed to be under strong natural selection because they confer adaption to the environment and enhance individual fitness (Howe et al. 2006). Studies of adaptive traits typically include survival, height growth, fall and spring frost hardiness, drought hardiness, vegetative bud phenology (the time of bud set in fall and budburst in spring) and the frequency of second flushing (Howe et al. 2006). Second flushing occurs when a tree stops elongating and sets a bud, then flushes a second time in the same growing season. Douglas-fir exhibits high levels of genetic variation for each of these adaptive traits within and among varieties, provenances, and populations (Silen 1978, Rehfeldt 1989).

Patterns of genetic variation in adaptive traits have been studied using long-term field tests and short-term experiments in outdoor nurseries, greenhouses and growth chambers. These studies have confirmed the overriding importance of temperature and moisture regimes in shaping genetic variation throughout the range of Douglas-fir. The species is particularly responsive to these selective forces, and is considered an adaptive specialist (Howe et al. 2006).

St. Claire et al. (2005) described and mapped patterns of genetic variation in adaptive traits in coastal Douglas-fir in western Oregon and Washington. They measured growth and phenology in seedlings grown from wind-pollinated seed of 1338 parents in naturally regenerated stands at 1048 locations. Seedlings were measured for traits of emergence, bud phenology, growth, and partitioning. The authors concluded that adaptation of Douglas-fir populations to Pacific Northwest environments appear to be largely a consequence of trade-offs between selection for traits to avoid exposure to cold and traits that confer high vigor in mild environments. Winter temperatures and frost dates are of great importance to population differentiation. Selection for drought avoidance by early budburst also appears to have resulted in population differentiation. The authors stated that an important question arising from their work remains unanswered: what specific genetic and epigenetic phenomena are responsible for geographic variation observed in adaptive traits? To address this fundamental question, parent trees from this study are currently being genotyped at candidate genes presumably involved in cold hardiness and drought tolerance.

Quantitative genetics and inheritance

As understanding of genetic and environmental variation is important for designing breeding strategies, picking suitable mating designs, designing field tests, and predicting genetic gains. Key pieces of information include relative amounts of additive vs. non-additive genetic variance, genetic and environmental variances, heritabilities, and genetic correlations (Namkoong and Kang 1990). Most information on quantitative genetic parameters is derived from analyses of wind-pollinated families collected from natural populations as compared to advanced-generation breeding populations (Howe et al. 2006).

Additive genetic variation, the variation associated with the additive gene action effects, is the main reason that progeny resemble their parents and the main determinant of population response to selection (Johnson 1988). Douglas-fir breeders are mainly interested in the additive genetic variance because most breeding strategies rely on improving populations via recurrent selection, and because most materials are produced via wind-pollinated seed orchards, which do not capture the non-additive component (Howe et al. 2006).

Heritabilities and amounts of genetic variation

One of the most important indicators of potential breeding success is heritability (h^2), a measure of the relative degree to which a character is influenced by heredity as compared to environment, that is the ratio of genetic variation to phenotypic variation. The higher the heritability, the more an individual's phenotype is indicative of its genotype (R Johnson 1998). Trait heritabilities have received much attention because they integrate information on genetic and environmental variation, and because they can be altered to increase genetic gains, primarily by reducing environmental variability in genetic tests and by increasing family size to increase family heritabilities (Howe et al. 2006). These authors compiled from 23 sources a list of mean heritabilities for common traits measured in Douglas-fir progeny tests under field conditions. They included only experiments in which trees were at least 4 years old.

The list shows that heritabilities for bud break, bud set, second flush, spring cold hardiness, branch angle and wood density (specific gravity) are moderate to high; and low to moderate for growth traits (height and diameter), fall cold hardiness, stem defects (ramicorn branches, forks and sinuosity). Traits vary, however, in their degree of genetic control (h^2) and the relative amount of genetic variation. Traits such as wood density have high heritabilities but low genetic variation whereas other traits such as height and diameter have low heritabilities but high levels of variation (Cornelius 1994). Douglas-fir breeding programs emphasize productivity which is measured as height and diameter. Because these are the mostly frequently measured traits, more is known about their heritabilities than for other traits. Heritabilities for growth traits typically range from 0.10 to 0.30. Because growth traits have low heritabilities, most breeding programs rely heavily on among family selections to obtain genetic gain. Heritabilities of family means tend to be much higher (0.60–0.90) because families are typically planted on 4 or more sites and are usually represented by more than 60 progeny (Howe et al. 2006). The added benefit of replicating families over multiple sites is the possibility to reduce the impact of genotype by environment interaction by finding families that perform well and are stable across a breeding zone (Stonecypher et al. 1996). Heritabilities must also be examined in the context of age because heritabilities for growth traits slowly increase with age (Johnson et al. 1997).

Genetic correlations

Genetic correlations are important because breeders may cause undesirable changes in some traits by selecting for other correlated traits. In Douglas-fir increased growth is associated with increased second flushing, late bud set, and increased cold injury in fall. These adverse relationships are stronger among than within populations. In contrast there is no consistent correlation between growth, cold injury in spring or bud burst (Howe et al. 2006). Wood density consistently shows an adverse genetic correlation with growth. This association is stronger for diameter than for height growth (King et al. 1988a, El-Kassaby and Park 1990, St. Claire 1994). Howe et al. (2006) cite two studies (King et al. 1988a, Vargas-Hernandez and Adams 1992) in which the adverse genetic correlation was strong, wood density decreased by 3 to 6.5% by selecting for increased growth using a selection intensity of 10%. One reason for their modest loss in wood density is that density has a high heritability, but a small coefficient of additive genetic variation (Howe et al. 2006).

Genetic correlations are valuable when they allow a breeder to use indirect selection. Although stem volume is the primary trait of interest, selection is usually based on height and diameter measurements. These traits are highly correlated, with genetic correlations usually 0.80 or higher (Yeh and Heaman 1982, Johnson et al. 1997), but lower correlations between height and diameter are sometimes found (e.g., 0.45 by King et al. 1988b). The timing of bud set in first-year seedlings, which have seasonally indeterminate growth, has a negative genetic correlation with fall frost hardiness, those that set bud early are more frost hardy. In saplings that have seasonally determinate growth, and set buds earlier in summer, the correlation with fall frost hardiness in weak (Li and Adams 1993). The positive correlation between bud break in spring and spring frost hardiness is stronger and less influenced by age. Trees that flush late in spring are more frost hardy. Correlations between cold hardiness in spring and fall seem to vary by population. Such correlations are not found in seedlings and saplings of a Cascade population or were weak to moderately negative in a coast population (O'Neill et al. 2000, 2001).

Estimates of genetic gain

Realized genetic gains may be determined by comparing the performance of genetically improved materials in genetic gain trials. Stoehr et al. (2010, 2011) established realized genetic gain trials in British Columbia on five low-elevation sites representing a range of site indices. Populations of three types of genetic quality were chosen as control unimproved (from a mix of wild stand seed lots); elite (by crossing the best nine parents to yield an average breeding value of 18 (that is should produce 18% more volume at rotation age than nonimproved populations; intermediate (obtained by mating of parents of somewhat lower ranking than the top parents yielding a breeding value of 10.

Seedlings were planted as 1-0 container stock in 1996 at four different planting spacings: 1.6 x 1.6 m, 2.3 x 2.3 m, 2.9 x 2.9 m, and 4.0 x 4.0 m; these yielded an equivalent of 3906, 1890, 1189, and 625 trees/ha, respectively. Sites were established with two replications each of 12 x 12-tree square plots (144 seedlings) per genetic level and spacing combination. Therefore, on each site a total of 3,456 seedlings were planted. Mortality was highest at the 1.6 x 1.6-m spacing compared to the three other spacings. The intermediate population suffered the highest mortality in all four spacings, while elite and control populations survived best. Overall mortality, however, was low. Realized gains at age 12 for the elite progeny were 48% for volume and 15% for height, compared to predicted genetic gains of 36% for volume and 18% for height. Realized gains for the intermediate progeny were 29% for volume and 10% for height, compared to predicted gains of 20% for volume and 10% for height. The realized gains were above control means across all sites and spacings.

The Northwest Tree Improvement Cooperative (NWTIC) and the Pacific Forest Research Station, initiated a realized genetic gain study along the west slopes of the northern Oregon Cascades in 1997 (Ye et al. 2010). Parents were selected from the first-generation Molalla breeding zone in the Cascade foothills southeast of Portland, Oregon. Populations of three kinds of genetic quality were chosen: elite (created by single pair matings of 20 top parents); intermediate (created by single pair matings of 20 parents of somewhat lower ranking than the top parents); unimproved (the unimproved population was a random selection of 50 trees selected from naturally regenerated stands well distributed throughout the breeding zone). One or two transplant seedlings of the elite, intermediate, and unimproved populations were planted in spring 1997 at five sites in the Molalla breeding zone. In each of the six replicates at each site seedlings of the three genetic quality types (elite, intermediate, unimproved) were planted at each of two stand densities: low density (3.6 x 3.6-m spacing, 772 trees/ha) and high density (1.8 x 1.8-m spacing, 3,086 trees/ha) using a split-plot design with planting density as the whole plot and genetic quality as the subplot. Each split-plot had 100 trees arranged in a 10 x 10-tree square.

The realized gains at age 15 averaged over both the elite and intermediate progeny were 17.2% for stand volume per hectare, 3.5% for height and 4.5% for diameter compared to predicted genetic gains of 16% for volume, 5.4% for height, and 6.4% for diameter. The results from the realized genetic gain trials in British Columbia and Oregon demonstrate that progress from selection and breeding of coastal Douglas-fir is achievable.

Breeding Goals and Objectives

The two main objectives of Douglas-fir breeding programs in western North America are to improve economic traits, that is, to achieve increased crop value, and to ensure that the resulting breeding populations are well adapted and have sufficient genetic variation for gains to continue in subsequent generations (Johnson 1998). Although the value of tree crops is determined on a per-hectare basis, the traits used for selection are usually measured on individual trees because it is difficult and expensive to measure the performance of many families on a per-hectare basis. Breeders, however, must be mindful of the assumption involved in defining breeding objectives on a per-tree basis when the real goal is to increase the value of the entire crop (Howe et al. 2006).

Primary breeding objectives

The two main breeding goals—increasing crop value and maintaining adaptability—are generally met in different ways. The most important adaptive traits are cold and drought hardiness. They are usually maintained through the use of appropriate breeding zones. The reason for that is three-fold (Howe et al. 2006). First, because severe frosts and droughts are rare, it is difficult to measure frost and drought hardiness under normal progeny test conditions. Secondly, how these rare events will affect production plantations is difficult to predict and thus the value of improving cold and drought hardiness. Thirdly, inexpensive artificial tests can be used to measure cold and drought hardiness (cf. chapters on frost and drought). Most of the parents in first-generation breeding populations were selected from the breeding zones in which they will be used; thus damage from cold and drought should be comparable to that in natural populations.

In contrast to adaptability, tree value is generally improved by selecting and breeding the most valuable genotypes within these well-adapted populations. Tree value is primarily determined by stem volume and secondarily by stem quality, and by wood properties such as density (Howe et al. 2006). Therefore, the primary breeding objective for Douglas-fir is to increase volume growth (Adams and Joyce 1990, Campbell 1964, Wheat and Silen 1977). Greater growth results in greater yields at harvest or permits shortening of rotations. The key traits used as predictors of rotation age are DBH and total height, usually measured anywhere at ages 5 to 20. In addition to increasing tree value, most breeding programs seek to maintain sufficient physiological adaptability and genetic variability. In fact, the existence of breeding programs to maintain adaptability is a hallmark of Douglas-fir breeding (Howe et al. 2006).

Secondary breeding objectives

Improvements in wood properties and stem quality are secondary in importance because their impact on tree volume is neither as great, nor as quantifiable, as it is for stem volume (Howe et al. 2006). The single most important wood property is wood specific gravity because dense wood is associated with wood strength as well as increased pulp yields. Important stem defects include forks and ramicorn branches. Forked stems are formed when the terminal leader is damaged or killed and two lateral branches subsequently assume equal dominance. Ramicorn branches are excessively large, upright branches. Forks and ramicorn branches tend to make a portion of the stem unmerchantable. Genotypes with many stem defects are unlikely to be included in future breeding populations. Selections for increased wood density are often made only among the fastest-growing genotypes in a two-stage selection.

Few insect and disease problems have risen to the level where they form key components of Douglas-fir breeding programs. The steadily increasing infection of Douglas-fir stands in coastal areas of Oregon, Washington, and British Columbia with the pathogen *Phaeocryptopus gaeumannii* in the last decades of the 20th century has become a matter of great concern. Hence, tolerance to Swiss needle cast has become a breeding objective. McDermott and Robinson (1989) demonstrated significant variation in resistance to the pathogen among nine provenances from California, Oregon, Washington, and British Columbia. Studies carried out within the framework of the Swiss Needle Cast Cooperative suggest that tolerance to Swiss needle cast can be improved via selection and breeding (Johnson 2002).

Steps in Tree Breeding Programs

Howe et al. (2006) listed four main steps for a typical tree-breeding program:

> The first step is to delineate breeding zones. The second step is to develop one or more breeding populations for each breeding zone. In the first generation, breeding populations may be selected from wild stands within each breeding zone, from superior non-local populations that have been identified based on provenance test, or from land races. The first approach is common for Douglas-fir in its native range, whereas the second approach has been used for Douglas-fir in Europe and the southern hemisphere. The third step is to field test the progeny of selected parents and pursue advanced-generation breeding within each breeding population. The fourth step is to produce genetically improved materials for outplanting. In most Douglas-fir programs, this involves establishing the best genotypes in separate wind-pollinated seed orchards.

Breeding zones

Breeding zones are used to manage the deployment of trees from breeding programs and wild seed collections, respectively. A breeding zone is a group of sites across which a breeding population can be planted and expected to perform well. Two vastly different approaches have been used to delineate breeding zones: 1. direct approaches based on long-term field tests of breeding materials, and 2. indirect approaches based on seedling tests of natural populations. A major disadvantage of the indirect approach is the unknown relationship between the genetic distance measured in indirect tests and the genotype by environment interactions measured in long-term field tests (Howe et al. 2006).

Selection

Because of the long rotations in forest trees, selections must be made long before harvest age. In Douglas-fir, final selections are commonly made when trees are about 10 to 15 years old (Howe et al. 2006). Based on age-age correlations from more than 51 progeny test sites in Oregon, Johnson et al. (1997) concluded that per-year gains are maximized when selection are made for height at age 10, and for diameter at age 13.

For improving tolerance of Douglas-fir to Swiss needle cast disease, early selection in the field at age 2 years was 25% to 100% as efficient as waiting until age 10 or 12 years (Temel et al. 2004, 2005).

Genetic Improvement Programs

North America

Woods (1993) and Lipow et al. (2003) described major Douglas-fir genetic improvement programs in North America. Their accounts were updated in 2006 by Howe et al. Most Douglas-fir improvement in North America is carried out by the Northwest Tree Improvement Cooperative (NWTIC), Inland Empire Tree Improvement Cooperative (IETIC), British Columbia Ministry of Forests (BCMoF), and Weyerhaeuser Company. These four organizations are responsible for developing improved materials planted by private companies, tribal governments, and public agencies in the USA and Canada.

Northwest Tree Improvement Program (NWTIC)

Douglas-fir tree improvement programs in the Pacific Northwest began in the 1950s when a small group of government agencies and timber companies began to select coastal Douglas-firs and established clonal seed orchards. The Industrial Forestry Association (IFA) was instrumental in these undertakings by hiring John Duffield, a forest geneticist, to guide their tree improvement efforts (Hagenstein 1966). Roy Silen, a USDA Forest Service geneticist, proposed in 1966 a “progressive tree improvement program” based on results from the 1912 Douglas-fir heredity study (Silen 1966a). His proposal was accepted the same year by the IFA. The name progressive infers incremental genetic gains with each succeeding seed crop as information about parent trees improves (Silen and Wheat 1979). The Progressive Tree Improvement Program was implemented by forming local, geographically based cooperatives to share the costs and benefits of tree improvement. The IFA Progressive Tree Improvement Program evolved into the Northwest Tree Improvement Cooperative (NWT1C) in 1986. As of 2004, the NWTIC, housed at Oregon State University, consisted of 27 member organizations, representing forest industries, tribal governments, state and federal agencies within the USA and Canada (Howe et al. 2006). Distinctive features of the Progressive Program included the assumption that local seed sources are best in the mountainous and environmentally heterogeneous Douglas-fir region, low-intensity selection of first-generation parents, use of many small breeding zones, and the use of very large breeding populations. This approach was intended to ensure adaptability of the first-generation breeding populations, which consisted of parents selected from natural stands within the breeding zone (Silen and Wheat 1979). Although breeding zones have been consolidated and breeding populations are being reduced, the NWTIC program is still one of the largest tree breeding programs in the world (Howe et al. 2006).

When the establishment of first-generation tests was completed in 1993, 21 first-generation cooperatives had been formed and the Douglas-fir zone west of the Cascades was blanketed with 109 breeding zones ranging from the Canadian border to northwest California. More than 26,000 first-generation parents have been evaluated based on more than three million progeny test trees (Lipow et al. 2003). The large number of breeding zones was recently reduced to eight second-generation zones and the number of parents used in advanced-generation breeding is expected to be about 2,000 (Howe et al. 2006).

Weyerhaeuser Company

Weyerhaeuser Company has managed a tree breeding program since 1963. One of their key assumptions was that rigorous phenotypic selection of superior trees in natural stands would produce genetic gain in growth. Therefore, the foundation of their program was an intensive plus-tree selection program in stands 25- to 80 years old. Some 3500 parents were selected in six breeding zones covering Weyerhaeuser lands in Washington and Oregon (Stonecypher et al. 1996). The primary objective of the first-generation program was to improve growth and stem quality. Selection, breeding, and testing of a large second-generation population are almost complete, and the third-generation of improvement is underway (Howe et al. 2006).

British Columbia Ministry of Forests (BCMP)

In Canada, first-generation testing began about I960 for coastal Douglas-fir and 1980 for interior Douglas-fir. Historically, tree improvement programs were coordinated by cooperative tree improvement councils, consisting of the BCMF, the Canadian Forest Service, private companies, and universities. A Plus Tree Board was formed in the 1960s, followed by the Coastal Tree Improvement Council in 1979, and the Interior Tree improvement Council in 1981. These two councils were later merged into the Forest Genetics Council of British Columbia (FGC) in 1998. In the coastal program, half diallel, factorial, and open-pollinated mating designs have been used to test about 660 parents in 130 field tests. In the interior program, an open-pollinated mating design was used to test about 1,600 parents in 32 field tests (Howe et al. 2006).

Inland Empire Tree Improvement Program (IETIC)

The IETIC was formed in 1968 to develop improved ponderosa pine for the Inland Empire, a region including eastern Washington, eastern Oregon, northern Idaho, and western Montana. The IETIC is housed at the University of Idaho and consists of 19 organizations, including federal and state agencies, private companies, tribal governments, and universities. A Douglas-fir species group was formed in 1974. In most of the 13 breeding zones, 200 to 300 trees were selected, and more than 2,500 first-generation parents have been field-tested to date. Compared to the Pacific Northwest, Douglas-fir is relatively less important in the Inland Empire. The area planted to Douglas-fir has declined in recent years because reliance on natural regeneration rather than on planting is now common. Consequently, the Douglas-fir breeding program in the Inland Empire is much less intensive than it is in the Pacific Northwest (Howe et al. 2006).

Europe

Interest in Douglas-fir improvement has grown in conjunction with the growing use of Douglas-fir in European forestry. Collaboration among forest research organizations in several European countries has led to the formation of a European Douglas-fir Improvement Research Cooperative (EUDIREC). Among its objectives are the development of a database for European gene resources, the building of a common breeding population, improving methods of seed production, and conservation of ex situ genetic resources of Douglas-fir in Europe. In 1986, the Federal Republic of Germany had 1,346 Douglas-fir stands covering 1,453 ha, certified as selected seed sources for Douglas-fir representing ex situ genetic resources of Douglas-fir in Germany (Ruetz et al. 1990). The number of such stands has probably grown since the reunification of Germany.

New Zealand

Douglas-fir is second only to Monterey pine as a plantation species in New Zealand. Large-scale planting of Douglas-fir began in New Zealand in the early 20th century. Large provenance trials were established in the mid-20th century, with provenances from seed collections in North America and from existing Douglas-fir stands in New Zealand (Ruetz et al. 1990; personal communication, HP Schmitt and W Ruetz, 1990). A Douglas-fir breeding program was begun in 1970 by M.D. Wilcox of the New Zealand Forest Research Institute.

6. Flowering

Denis P. Lavender

The initiation of reproductive structures in plants has been the subject of many studies (Evans 1971; Zeevaart 1976; Wareing 1980; Bernier 1981, 1988; Bernier et al. 1993). Most of these studies, however, have been about herbaceous annual plants. The reproductive phase of these plants differs significantly from that of woody, perennial plants in that (1) upon receipt of an external signal (such as a critical photoperiod), the annual plant can convert all apical meristems on the shoot to flower primordia, whereas the perennial plant must conserve many such meristems for future vegetative growth; and that (2) the mature perennial plant has what is called a "burden of history" that can affect the incidence of flower production in any given year.

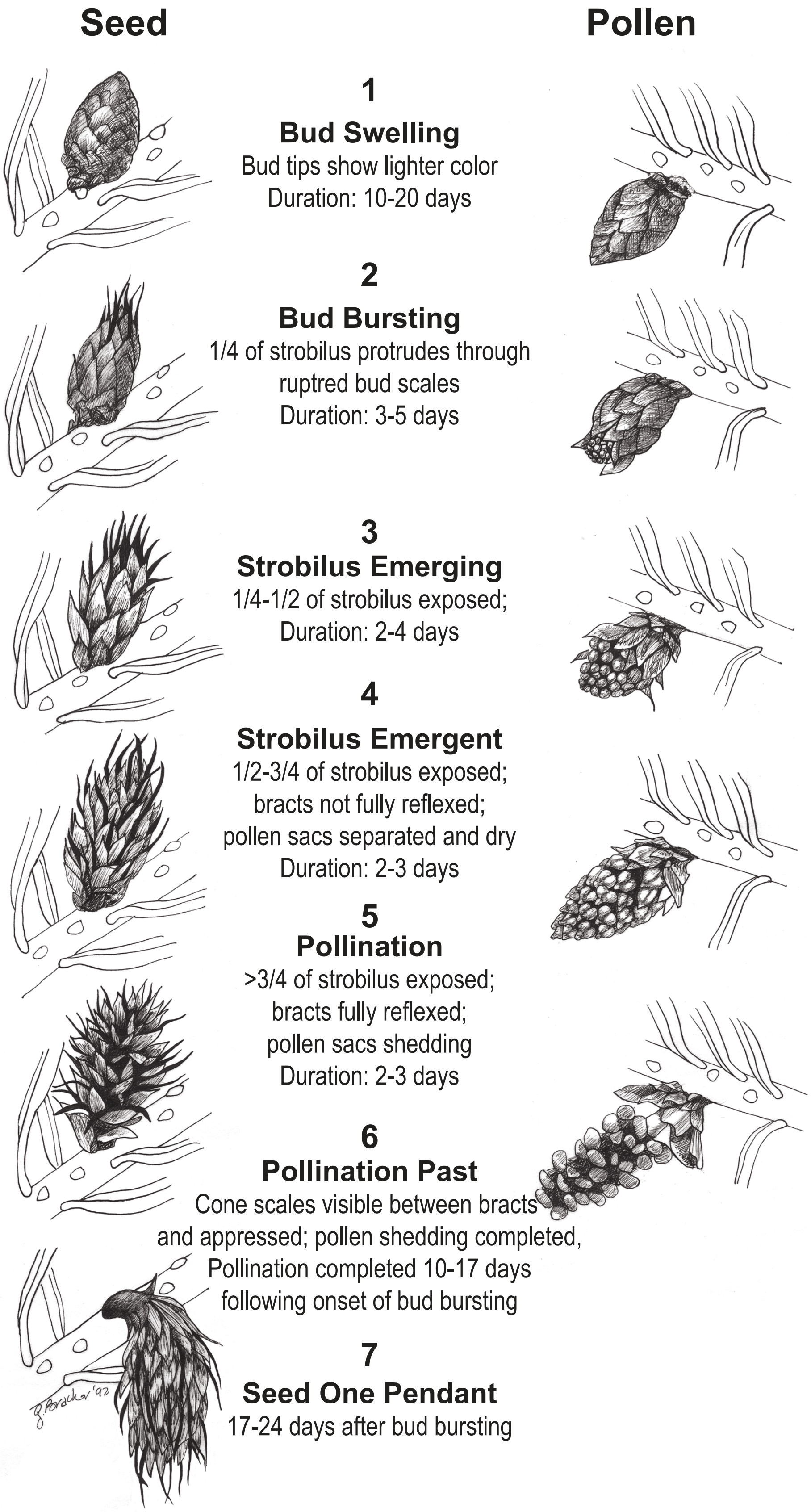
Previous reviews of the literature on flowering in angiospermous forest trees (Lavender 1984), for temperate zone woody plants (Jackson and Sweet 1972), and for temperate zone coniferous trees (Lavender and Zaerr 1985, Puritch 1972) demonstrated that relatively little research effort has been focused on flowering in large, woody perennial plants; that flowering may be stimulated by a range of cultural treatments; and that application of plant growth regulators may stimulate differentiation of reproductive structures. Evans (1971) noted that more than 1,200 papers on flowering had appeared in a 6-year period, and there have been many more since then. Although most were concerned with herbaceous angiosperms, enough discussed conifers and were sufficiently repetitious; therefore, it is most practical if we limit much of our discussion to material in the many review papers.

Three major topics important to flowering are the history and nomenclature of the reproductive structures of conifers, the role of juvenility and maturity in flowering, and the incidence of flowering and methods of eliminating the initiation of flowering.

History and Nomenclature

A flower has been defined as "a determinate axis with spore-bearing appendages (and, usually, sterile appendages) and short internodes occurring in the angiosperms" (Bold et al. 1980, p. 748). Douglas-fir reproductive structures, in common with those of other conifers, are frequently called "flowers," but they lack the calyx, corolla, stamens, and pistil common to the flowers of angiosperms, and they certainly do not qualify under the definition of Bold et al. (1980). They also do not meet the definition of "a determinate sporogenous shoot that bears carpels," as offered by Romberger and Gregory (1974, p. 138). Jackson and Sweet (1972), however, proposed a simplified definition of a flower as, "a determinate sporogenous shoot," which qualifies coniferous reproductive structures as "flowers." Actually, the staminate strobilus (male flower) consists of several spirally arranged microsporophylls, each of which bears two microsporangia on the lower surface. The ovulate strobilus (female flower) comprises a central axis that bears ovulate scales, each borne in the axis of a bract. Each scale has two ovules on the upper surface, each of which consists of an integument surrounding a megasporangium (Figure 6.1).

There has been some debate over the morphology of female reproductive shoots. Florin's classic monograph (1954) noted that the first three decades of the 20th century were dominated by discussions of the "Sachs-Eicher excrescence" (female of conifers as a simple flower) and brachybest (megasporophylls) florescences theories (pp. 380–384). By 1940, the brachybest theory was favored, although



1

Bud Swelling

Bud tips show lighter color
Duration: 10-20 days

2

Bud Bursting

1/4 of strobilus protrudes through
ruptred bud scales
Duration: 3-5 days

3

Strobilus Emerging

1/4-1/2 of strobilus exposed;
Duration: 2-4 days

4

Strobilus Emergent

1/2-3/4 of strobilus exposed;
bracts not fully reflexed;
pollen sacs separated and dry
Duration: 2-3 days

5

Pollination

>3/4 of strobilus exposed;
bracts fully reflexed;
pollen sacs shedding
Duration: 2-3 days

6

Pollination Past

Cone scales visible between bracts
and appressed; pollen shedding completed,
Pollination completed 10-17 days
following onset of bud bursting

7

Seed One Pendant

17-24 days after bud bursting

Figure 6.1 Seed and pollen development.

Florin argued that more research was necessary to precisely define the coniferous cone. He observed that the female "flower" of conifers has been of interest since 1950, and that early research on flowering was largely confined to the classification of megasporophylls. Florin also noted that "the taxads are accordingly regarded as forming a class of their own—Taxopsida—distinctly separate from the conifer opposites" (Florin 1954, p. 382). Conifers have and taxads have been considered an ancient and relic group and have been referred to as "living fossils" (Williams 2009, p. 3). Several researchers have listed both conifers and taxads under the order *Coniferophyta* (Gifford and Foster 1988, pp. 402–404; Bold et al. 1980, pp. 506–508).

The role of juvenility and maturity in flowering

Wareing's (1959) review of the literature concluded that juvenility and maturation each represent two stable states of the plant, and that aging describes the transitory states during the increase in size as the plant grows. Further, several morphological features change gradually with the change to maturity. The plant's capability to flower is perhaps the most notable. In his description of the general growth curve of a perennial plant, Wareing (1958) observed that the production of female flowers begins on the ascending limb of the curve and that male flowers are generally initiated on the descending limb. This relation between flowering and the reduced vigor holds not only for the whole plant, but for individual branches. Other important points are as follows:

- Plant size and duration of the juvenile period are roughly correlated.
- Plants in the juvenile stage generally root readily, but mature plants commonly do not.
- Nutrition is generally higher in juvenile than mature plants.
- The phase change between juvenile and mature plants is associated with size and complexity of the shoot and not with the number of annual cycles it has passed through.
- Both "juvenile" and "mature" status are stable.

According to Brink (1962):

> Phase change sometimes involves a relatively abrupt switch in potential of apical meristems in higher plants from a juvenile to an adult type of growth. The two growth forms are highly persistent in different parts of the same individual and in clonally propagated offspring. Reversion to the juvenile condition occasionally occurs in buds on adult-type shoots, and invariably takes place in sexual reproduction. It is pointed out that counterparts of phase change, expressed in a wide variety of ways, are common among both plants and animals; structures arise in the development of all organisms with characteristics that are not merely functional adaptations but are innate and self-maintaining in mitosis. Phase change is to be considered, therefore, as illustrating a general aspect of cell heredity and variation; it is singular only in the distinctness with which the alteration in type of growth may be phenotypically expressed. The mechanism whereby such characteristics are maintained and perpetuated in somatic cells is an unsolved problem. There is now limited evidence, some of it also indirect, suggesting that the chromosomes are the site of such discontinuous and potentially reversible onto-genetic changes. This evidence is briefly reviewed in terms of a hypothesis in which it is assumed that in addition to the genes, which are stable, the chromosomes also contain self-perpetuating accessory materials that undergo paramutation in an orderly way in somatic cells as an essential aspect of a nucleo-cytoplasmic system of morphogenetic determination. (Brink 1962, p. 1)

Romberger (1967, p. 2) asks:

> What is the state of our present knowledge of the control of flowering trees? In a very general way we can say that even on good sites young trees do not flower until they have attained a certain minimum size, complexity of branching, and "physiological age." Such a statement is not an explanation, but only an enumeration of conditions which usually, or sometimes, are prerequisites to the onset of flowering. It does not address itself to the problem of the means by which it is determined that a bud shall develop into a flower rather than a shoot. The physiologist who has attempted to analyze the problem of flowering in trees is apt to find unconvincing any general statement about its control. This is because of the diversity, or even contradiction, of actual observations and the paucity of data from well-designed experiments.
>
> Discussion of the problem of flowering with reference to the literature is difficult without involving concepts of "juvenility," "ripeness to flower," "maturity," or "physiological aging." These concepts are not amenable to precise definition, and they cannot be given much concrete content until our understanding penetrates much deeper than it yet has. Nevertheless, for the present, they are useful in spite of their lack of precision because they delineate comprehensible areas of concern from the vastness of developmental biology. Similar use of a term such as "epigenetic" should also be allowed.

Romberger (1967) believed that the knowledge of the physiology and development of flowering in trees is inadequate and therefore difficult, and that explaining contradictory results is also difficult: "The large and poorly defined area including juvenility, aging, apical dominance, gravimorphism, and growth habit also needs additional attention. Failure to flower is usually concurrent with the juvenile form, but the two may really be independent (p. 24)."

The concept of juvenility has been questioned, in that all attributes that are said to be a function of it are not expressed simultaneously, and that it does not fulfill the requirements of a systemic analysis (Borchert 1976). Therefore, as Borchert argues, "the existence of one uniform juvenile state must be seriously doubted based on the available evidence" (Borchert 1976, p. 22). Sussex (1956, p. 271) asked two questions: "Does the plant body attain some critical size and then signal the meristem to initiate the developmental phase-change response, or does the meristem behave independently of the remainder of the plant?" His review of papers by Wareing answer the first question affirmatively.

Schwabe (1976) noted that the juvenile stage may have an important role in a plant's survival, in that energy required for height growth will not be diverted to flowering until the plant has successfully competed with neighbors. Citing results of experiments with several plants, including trees, Schwabe hypothesized that flowering may be controlled by the distance a plant apex is from the roots or by root activity, and suggested that gibberellins (GAs) are the likely cause. Further, he noted that root disease frequently causes cones to form in Japanese larch and Sitka spruce (as it does in Douglas-fir).

For woody angiosperms plants, Wareing and Phillips (1970, p. 61) suggested that, "low gibberellin levels are a necessary but not sufficient condition for juvenile/adult transition." Ross (1976) reported flowering on Douglas-fir grafts of mature tissue, but not on equal-sized seedlings, concluding that the age of the meristem, not plant size, controlled the juvenile-to-adult phase change in this species. Longman (1976) argued that juvenile trees may be forced to flower and that basal girdling is a powerful tool for doing so.

In reviewing the literature on juvenility and maturity, Hackett (1985) noted:

> Attainment and maintenance of the ability or potential to flower is the only consistent criterion available to assess the termination of the juvenile period. Other characteristics known to change with development and/or age are not consistent from species to species, and none has been demonstrated to be causally related to sexual maturity . . . it is possible to show that there is a transitional phase of development during which flowering potential is increasing. (Hackett 1985, p. 111)

Plants grown in a low rainfall area of southern Vancouver Island started flowering at 6 to 10 years of age, whereas those grown 50 miles away in a cool, wet region started later. Pharis et al. (1980) concluded that "the best way to shorten the juvenile period is to grow the plant rapidly to a minimum size and then apply a flower inducing treatment, both appropriate for the given species":

> It is now not known why attainment of a minimum size is required for transition to the mature condition. The observations that the juvenile-to-mature phase change usually occurs at a predictable stage (size) in the development cycle of a plant and that changes occur at the shoot apical meristem raise questions about the organismal locus of the phase change: Does the plant body attain some critical size and then signal the meristem to initiate the developmental phase change response? Or does the meristem behave independently of the remainder of the plant? (Pharis et al. 1980, p. 120)

In one of his last papers, Wareing (1987) asserted the following:

> The properties of the apex are determined by the structure and organization of the apex as a whole, and the differences between the two phases (juvenile and adult) arise from the different organization of their apices. . . . There are intrinsic differences in the meristematic cells of the juvenile and adult apices, and the differences in their properties and structure arise from intrinsic differences in the cells. . . . It is suggested that phase change indicates the existence between cells with respect to gene expression, which can be transmitted through repeated cycles of cell division. Persistent differences in gene expression, without permanent changes in the genome, are said to be epigenetic. (Wareing 1987, pp. 85–86)

This hypothesis is supported by the fact that the DNA of apical meristems of juvenile and adult shoots in *Hedera helix* (English ivy, a plant frequently used to study phase transition) is the same. Finally, Wareing (1987) wrote,

> It has been argued that phase change must involve intrinsic differences in juvenile and adult apical meristems, but this does not exclude the possibility of influences from the mature parts of the plant, especially hormonal factors arising in the leaves or roots. In particular, influences from other parts of the plant may be important in promoting or inhibiting phase-change or its reversal, but phase-change is an inductive phenomenon and once it has taken place the conditions that promoted the change need not continue to operate. (Wareing 1987, p. 90)

Poethig (1990) summarized the role of phase and phase change in detail, using primarily genetic data:

- Six gene loci individually or collectively govern the transition from vegetative to reproductive state.
- Several anatomical and morphological states include foliage characteristics, phyllotaxy, plastochon, growth habit, aerial root rooting ability in much studied *Hedera helix* associated with juvenile and adult states that are regulated independently of flowering.
- The three phases are juvenile vegetative, adult vegetative, and an adult reproductive.
- Phase changes regulated by factors both intrinsic and extrinsic to the terminal meristem.
- The compound florigen's origin has not been isolated and probably will not be in the near future.
- Factors that increase growth generally tend to promote flowering; factors that reduce growth inhibit flowering.
- The whole concept of phase change represents an extremely complicated growth pattern.

In summary, "genetic, developmental, and molecular analyses of mutations that affect the expression of particular phases of shoot development are beginning to yield a clearer picture of the regulatory framework of shoot development" (Poethig 1990, p. 929).

Hackett and Murray (1992) suggested that the maturation process (phase transition) in woody plants is "a very dramatic and protracted example of determination and differentiation" of an array of phenotypic characteristics that may not be closely linked temporally or mechanistically (p. 197). Hackett et al. (1992) proposed that phase development, "is not fundamentally different from plant development in general but may have unique features that are particularly important to understand," and that "phase-related changes in phenotype are the result of subtle changes in the gene expression that overlay the fundamental patterns of gene expression that is common to both the juvenile and a mature plant body" (Hackett et al. 1992, pp. 84–85).

Greenwood (1992) noted that maturation "has received renewed attention over the last 10 years since, as maturation processes, the vegetative propagation of woody plants becomes increasingly difficult" (p. 19). This aspect of maturation has been of interest in Douglas-fir. It will be discussed further in the section on rooting. According to Greenwood (1992),

> The onset of the mature state is usually gradual. For example, grafting studies on loblolly pine and eastern larch have shown that maturational change is gradual for most traits, except for plagiotropism and branch frequency. But plantlets derived from buds induced on the cotyledons of mature embryos from several conifers exhibit mature characteristics immediately after they begin to grow . . .
>
> Maturation affects a wide variety of morphological, physiological, and biochemical traits, but these traits appear to vary independently of one another. Maturational traits are often persistent, and their maintenance is not always a function of tree size or proximity to roots. Differences in chlorophyll content, specific leaf weight, and xylem morphology among eastern larch scions from trees of different ages grafted at the same time persist for several years. On the other hand, anecdotal evidence suggests that mature morphological characteristics disappear quickly after grafting or rooting cuttings in *Populus* spp. and *Eucalyptus* spp.
>
> Evidence suggests that the cells of the apical meristem itself become determined in some woody plants. Grafted apices from mature plants of *Citrus* spp. or *Sequoia* spp. consisting of only the apical meristem, and one or two leaf primordial, grow out into plants with mature characteristics. (Greenwood 1992, p. 21)

Greenwood and Hutchinson (1993) observed that four major methods to maintain juvenility have been frequently studied: serial propagation, hedging, repeated subculture, and tissue storage. Hedging has failed with Douglas-fir. They also argued that reproductive competence is not a good measure of maturity. Studies with several species strongly suggest that male:female ratio is a better measure of maturity than is the presence of strobili alone. (This measure is true with Douglas-fir, according to numerous observations by Lavender: young seedlings produce more female flowers than male.) In concurrence with other researchers, Greenwood and Hutchinson (1993) argued that minimum size and minimum maturity are necessary for flowering; however, "experiments with grafted scions do not, in our opinion, indicate that the ability to flower is solely a function of increased size and complexity of the plant" (p. 24). They noted that information was lacking on "the relationship of gene expression to phase change in woody plants. Therefore, models for the role and the regulation of gene expression in maturity are more speculative than predictive." Additionally, some data suggest that, "genes play a role in the regulation of maturity," and that control of any one trail of maturity is independent of that for others (Greenwood and Hutchinson 1993, p. 26).

In a later paper on conifer juvenility and maturation, Greenwood (1995) offers this explanation:

> Maturation is an integral part of the life cycle of all vascular plants. Four phases of maturation have been recognized: (1) the embryonic phase, (2) the post-embryonic juvenile vegetative phase, (3) the adult vegetative phase, and (4) the adult reproductive phase. In woody plants, maturation is associated with decreased growth rates during phases 2-4 (which often persist in vegetative propagules), increased plagiotropism, and changes in reproductive competence, branching characteristics and foliar morphology. In addition to morphological changes, there are numerous physiological and biochemical changes that accompany the transition to the adult phase. . . .
>
> Maturation involves changes in the habitual behavior of meristems, where habit is defined as a behavior pattern that develops in response to a particular set of physiological inputs. By definition, habits tend to resist change, but nonetheless can be altered in response to varying environmental inputs. The earliest maturation event is the polarization of the embryo into roots and shoots, where each meristem, starting with the same genes, acquires unique habits adapted to different environments. In shoots, the meristems continue to develop new habits as the plant grows. Over time, the meristems of conifers change their behavior, losing regenerative potential and capacity for vegetative growth, but gaining reproductive competence and more massive leaves. (Greenwood 1995, p. 493)

The above survey, although admittedly brief, refers to most of the reports relating the juvenile and mature phases in woody coniferous plants to the incidence of flowering in these trees. None of the reports was concerned with Douglas-fir, although studies by Owens (1984a,b) related the effects of treatments that stimulate flowering on the anatomy of apical and lateral meristems with that of control trees (see also Owens and Blake 1985). Because the trees were all probably juvenile (10 years old), the data could not be interpreted in terms of potential differences between juvenile and mature shoots. Although some disagreements were described by Owens (1984a,b), the general conclusion remains the same as that found in an early review (Mathews 1963), which noted that flowering in conifers is associated with the adult state. Unfortunately, while subsequent work qualifies as basic research, carefully done, it does not identify the basic cause of the differentiation change resulting in flowering.

Romberger (1967) argued that flowering is a developmental phenomenon—a point with which later researchers agreed (McDaniel et al. 1987)—and concluded that "strenuous efforts should, I think, be made to collect, organize, and evaluate present information on development physiology in trees with full references to related information and thinking in other areas of biology" (p. 11).

Incidence of flowering

The work described above correlates the incidence of flowering strongly with the development of the adult phase, not surprisingly because the ability to flower often defines maturity, but does not identify the biochemical reasons for either. Similarly, several reports have noted that flowering in conifers is very erratic (Matthews 1963). Romberger and Gregory (1974) observed that "the subject of flowering in trees" is "vast, complex, and confusing. A subject of such breadth and importance needs a firm base of good detailed, descriptive, developmental and experimental studies. That base is now quite inadequate and it is not being enlarged very rapidly" (p. 132). For example, among 4,073 papers about trees published from January 1970 to June 1974, none were about flowering. As Romberger and Gregory (1974) explained, trees are inconvenient subjects for research. They differ from annual plants, in that flowering is not subject to one or several environmental factors because trees must conserve some buds for vegetative growth. Experiments on flowering focus on single observation dates, whereas trees have the burden of years of exposure to environments that may condition their response to current trials. Finally, trees have an extended developmental time scale: months may intervene between events that stimulate flowering and the evidence of it. According to Romberger and Gregory (1974), "numerous biochemical or physiological systems are involved in the control of flowering in every bud on the tree. For floral development to be 'evoked' or initiated, all systems must be 'permissive,' if any one system is 'non-permissive,' vegetative growth prevails."

In a previous paper, Romberger (1967) noted that, "flowering research to date is not capable of defining the basic cause of flower initiation. Romberger and Gregory (1974, p. 145) state, "Analytical morphogenesis offers a means of attaining a new level of understanding of the control of flowering in trees." Unfortunately, little in the literature suggests that this procedure has been followed—instead, several papers propose environmental factors, none of which allude to the basic cause of reproductive tissues.

Sweet (1975, p. 72) noted that both the time of flower bud initiation and the developmental period during which the bud becomes irrevocably programmed to produce a flower are important in studies of factors influencing cone production. He cites evidence that such a period may be lengthy in Douglas-fir.

Methodology of flower induction

Despite any remaining gaps in understanding, there are nevertheless significant contributions in the literature that describe the effects of several major techniques on the initiation of flowering in conifers including Douglas-fir. The following material outlines cultural techniques and environmental exposures which, singly or in combination, have resulted in increased flowering in many trees, including Douglas-fir.

Moisture stress

In a review of factors affecting seed production in trees, Matthews (1963) noted that moisture stress during the summer has long been associated with the production of flower buds. And, in western North America, several seed orchards have been in the rain shadow of the Olympic Mountains (Lavender and Zaerr 1985). Similarly, Jackson and Sweet (1972) observed that flowering is often reported to be associated with moisture stress, but they cautioned that timing may be important. Ebell (1967, 1970) correlated summer moisture stress with flowering Douglas-fir seedlings and suggested that the effect is mediated by high arginine levels. Ross (1988) noted that drying seedlings to a foliage moisture content of –2.0 MP (with intervening irrigation periods) stimulated flowering. But in their review, Owens and Blake (1985) argued that, at best, the relationship between moisture stress and flowering in trees is inconsistent. Reasons for this may be that moisture stress was frequently not measured and it may often have been too low to promote flower bud formation; Owens and Blake (1985) suggest that pre-dawn moisture stress of at least 12 to 20 bars is necessary to promote flowers. A drought period immediately before shoot formation may stimulate flowering, as Bonnet-Masimbert and Lanares (1978) suggest in a report describing flowers on lammas shoots of Douglas-fir. Additionally, however, excess moisture (periodic root flooding) has also been linked to enhanced flowering in 6-year-old Douglas-fir clones (Bonnet-Masimbert and Zaerr 1987). Although the data to date do not clearly define the role of moisture in flower initiation, one tenable hypothesis is that its effect is mediated through root physiology.

Lavender and Zaerr (1985) reviewed several papers that discussed the weak correlation between moisture stress and cone production for a range of species, but they indicated that evidence for a moisture-related cone crop is not clear. They did note that many seed orchards in the Pacific Northwest are sited in areas with pronounced summer drought. Puritch (1972) found that moisture supply is correlated with cone production, but that the response to moisture stress is variable and depends on both the species of tree and the time of year. Moisture stresses of –15 to –33 atm. have been shown to be effective in stimulating flowering in Douglas-fir. Researchers for Weyerhaeuser Company, working with measurements of internal moisture stress, reported correlations between moisture stress and increased flowering of conifers: where applied moisture stress had no positive effect on flowering, the treatment failed to produce increased moisture stress on the tree (see Schmidtling 1974). Owens (1991) reviewed several references that reported a correlation between moisture stress and flowering in Douglas-fir and pines, but noted that much of this work did not include the time of floral bud initiation.

Light intensity

Higher levels of light intensities generally favor formation of female flower buds in trees and lower light intensities may increase male bud formation, according to Matthews (1963) and Owens and Blake

(1985). Silen (1973) found that shading devices increased flowers of both sexes, but his shading devices raised the temperatures; thus, his results may have been mediated by temperature rather than light intensity alone. In their review, Bonnet-Masimbert and Zaerr (1987) cite unpublished material showing a strongly promotive effect of high light intensities on Douglas-fir flower initiation. Owens (1990) suggested that light intensity effects are indirect and related to the environment within the crown, proposing that the stimulus was perhaps from increased temperature associated with high light intensities, rather than the light itself. Finally, Masimbert and Zaerr (1987) reported that, "increased light intensity strongly stimulates both male and female flowering of Douglas-fir" (p. 19); and Winjum and Johnson (1964) noted that high light favors reproductive development in Douglas-fir.

Photoperiod

Although the fact that photoperiod affects the flowering of many annual plants is well known, little evidence of such control has been shown for woody perennials. One major reason for this difference is that annual plants can afford to convert all of their meristems from vegetative to reproductive uses, but perennial plants must reserve some meristems for vegetative growth the following year. Owens and Blake (1985) suggested that species (such as those in the Cupressaceae that form male and female buds at different times) may have the sex of their flowers determined by photoperiod. But there is no evidence of such an effect in Douglas-fir, which initiates both sexes simultaneously. Certainly the data of Bonnet-Masimbert (1978), which describes flowers initiated in the spring and other flowers on lammas shoots in late summer, are good evidence of the day-neutral nature of this species. Owens (1991) and Kozlowski et al. (1995) both noted that no evidence has been found indicating that photoperiod-related flowering exists in trees, as it does in herbaceous plants.

Fertilizers (mineral nutrition)

Numerous publications deal with the effects of fertilizer on conifer cone production. An early trial of effects of nitrogen on Douglas-fir is described by Stoate et al. (1961). They found that nitrate nitrogen was effective in the production of large cone crops when applied in the fall. And the same material stimulated more cone buds, both male and female, if applied at time of vegetative bud break. Ebell and McMullan (1970) and Ebell (1972) agreed with Stoate et al. (1961) in that nitrate nitrogen applied at bud break stimulated the greatest cone production. In the 1970 paper, Ebell and McMullan showed that nitrate N stimulated an increase in amino acids, but the size of the total free amino acid pool was not related to cone production. However, levels of the amino acid arginine and guanidine substances were raised more by nitrate and were associated with seed cone production. With the nitrate application, ammonia raised the soluble amino acid content, but not cone production. Trials on medium and productive sites resulted in greater responses than trials on a poor site. Ebell (1972) showed that the effect of added nitrate was greatest in years with a good crop of cones on the control trees and that the strongest responses were when a dry period followed fertilization. He hypothesizes (p. 636) that, "reproductive development is possibly enhanced by an abrupt properly timed change in nitrogen status," and noted that application of more than 897/kg/ha can lead to toxicity symptoms.

Irrigation can enhance the fertilizer effect, and a wide variety of pines have shown increased cone yields with fertilizer treatment under certain conditions. Thus, careful fertilizer application can apparently be expected to improve cone yield when soil fertility is the limiting factor in tree growth and vigor, which is true for most forest sites. Ebell (1972) noted that the strongest responses to fertilizer were followed by a dry period.

Several reviews (Owens 1991, Lavender and Zaerr 1985, Jackson and Sweet 1972, Owens and Blake 1985, Ross and Pharis 1985, Puritch 1972, and Matthews 1963) examined many of the reports discussing mineral nutrition and flower production in conifers. They agreed that the results of studies are erratic because time of application, site quality, and precipitation can all affect results. To date, we still do not understand the basic reason why nitrogen may stimulate flowering. Some evidence suggests that natural flowering is greater on fertile sites for several species and that enhanced nutrient levels, especially N, are necessary for the growth of reproductive structures.

Puritch (1972) reviewed several papers presenting varied effects of mineral nutrition on flowering. He noted that Douglas-fir cone crops have been increased by applying nitrate nitrogen, but warns that a range of environmental factors and timing of applications may produce varying results. He stated, however, that fertilizer applications are the most common treatment to stimulate flowering.

Investigation of the effect of mineral nutrition on flowering in Douglas-fir have been concerned primarily with nitrogen, although Ebell has reported that neither phosphorous nor potassium stimulated flowering. He also noted that application if nitrate nitrogen (but not ammoniacal nitrogen) at bud break greatly increased production of flowers the following year on 20-year-old Douglas-fir trees. Though the treatment did not stimulate bud initiation, it apparently permitted more buds to develop. The dependence upon treatment during the period of vegetative bud break in mid-May for positive results is in sharp contrast to the treatment results of Bonnet-Masimbert and Lanares (1978) discussed earlier. Ebell speculates that coning may result from a sharp change in nitrogenous compounds rather than from increased vigor after nitrogen uptake, but he does not present data to substantiate his hypothesis. Owens and Blake (1985) agreed with Puritch when they noted that results of fertilizer trials in stimulating initiation of reproductive structures have been erratic, in part because careful attention had not been applied to the timing of the fertilizer, soils have not been analyzed to determine possible nutrient deficiencies, and other environmental factors, particularly soil moisture, have varied during and after fertilizer applications. And Silen and Copes (1972) noted that "regular applications of fertilizer have little influence on the cyclic pattern of good and bad cone years." Smith et al. (1968) presented data that show N fertilization increased cone production of Douglas-fir by 26% in a good year for cone crops, but none in a poor year. In an earlier report, however, Ebell and McMullan (1970) showed that levels of the amino acids arginine, lysine, and ornithine, and of soluble nitrogenous compounds, especially other guanidine substances, were higher in trees treated with nitrate nitrogen than in those treated with ammoniacal nitrogen. In contrast, the saplings treated with ammoniacal nitrogen incorporated a higher percentage of absorbed nitrogen in protein than did the nitrate-treated plants. Ebell and McMullan (1970) suggested that specific amino acids participate in development rather than initiation of flower buds. Their hypothesis that arginine levels may regulate flowering in Douglas-fir is not upheld, however, at least for seedling plants, by the data of Ching et al. (1973), which showed that fertilization increased free amino acids 10-fold and arginine 40-fold. In later observations, however, no flowers were noted on either treated or control populations. Further studies are needed to clarify the role of mineral nutrients.

Steinbrenner et al. (1960) reported that applications of nitrogen (primarily) and phosphorus stimulated male and female buds in a thinned stand of 20-year-old Douglas-fir and they reviewed papers that reported increased cone production of several conifers. Owens (1991, p. 256) noted that "all things being equal, trees growing on fertile soils produce more seed than those growing on less fertile sites." Masters (1982) reported that fertilizing 12-year-old Douglas-fir seed orchards with 224 kg nitrate per hectare as $CaNO_3$ resulted in 2.5 × the control number of cones. Smith et al. (1968) found that applying 224 kg/ha of nitrate N stimulated increased flowering on mature Douglas-fir trees. No such effects were noted in a year with no natural cone crop. Even though Daoudi et al. (1994) reported that $CaNO_3$ was more efficient in stimulating flowers on 6-year-old Douglas-fir cuttings than was $GA_{4/7}$, the general trend appears to suggest that $GA_{4/7}$ is more effective than $CaNO_3$ for flower initiation.

Temperature

Shoots

Relatively few references discuss the effects of temperature on flowering in conifers: several that do, report temperature as a component of climate. According to Matthews (1963, p. iii), "a certain minimum degree of heat is apparently necessary for flower bud formation, probably higher than that required for the formation of vegetative buds." He noted that the importance of higher-than-average temperatures in June and July for flower initiation has been demonstrated for several species, however, but whether the reproductive bud initiation occurred during those months was not clear. Owens and Blake (1985, p. 20) reviewed papers that also reported on effects of higher temperatures during periods of flower initiation, but noted that separating the effects of temperature from those of light intensity was difficult. Owens (1987) reviewed much of the same literature. Ross and Pharis (1987, p. 50) noted that warm thermoperiods may stimulate female flowering, but cool thermoperiods may be associated with increased male flowering. Owens (1991) reviewed several papers reporting that high summer temperatures were implicated in increased flowers in diverse conifer species, including Douglas-fir: "High temperatures during floral initiation may affect metabolic processes, but we know little about these processes in reproductively mature trees" (p. 254).

Although data are lacking for Douglas-fir, researchers assume that Douglas-fir flower buds have a cold requirement. Nor does that suggest that the chilling requirements for initiation of potential flower-bud primordia in the quiescent vegetative bud in early spring, nor does their subsequent differentiation during extension of the vegetative shoot, in late spring and early summer, differ from that of a vegetative bud containing only vegetative primordia. One can infer, however, that the reason for the cold requirement of vegetative Douglas-fir buds: protection against activity during an unseasonable midwinter warm spell, obtains equally well for reproductive buds. Studies by Lowry (1967), Van Vredenburch and LaBastide (1969) and Eis (1973a) suggest that the meteorological sequence two years before cone maturity influences the size of cone crops, but the sequence does not indicate a chilling requirement for reproductive buds. Further, such meteorological data do not necessarily reflect conditions required for flower bud initiation or differentiation because abortion of buds or flowers could result in a poor cone crop. Bonnet-Masimbert (1970) and Lanares (1978) noted that reproductive buds can develop on lammas shoots that have had no chilling. Douglas-fir flower buds require mild temperatures during the spring to continue development.

Root temperature

Only one report examining the efficacy of low root temperatures in stimulating flowering yielded negative data. Zaerr and Bonnet-Masimbert (1987) found that temperatures of 5°C did not stimulate flowering of Douglas-fir. Lavender and Ching, working with two-year-old Douglas-fir seedlings grafted with scions from mature trees, recorded the data found in Tables 6.1 to 6.4.[1]

Seedlings were placed in water baths in December 1974. In early March 1975, half of the seedlings were maintained with an ambient soil temperature and the second half with soil temperatures from 2° to 4°. All containers were watered at intervals. The shoot environment was a function of weather patterns in that the cold root treatment was terminated in late October, and all seedlings were overwintered under natural conditions; however, containers were insulated to prevent freeze damage to the roots. In early March 1976, each seedling population was halved again, with one-half of each installed in the environments described above.

During the study, records were maintained of seedling phenology, incidence of strobili, and the elongation of the shoots on the scion wood. Table 6.1 summarizes the pattern of response to the treatment. All strobili were borne on scion tissue that developed on either the parent tree (1974) or on the non-grafted control seedlings (1975). Two data are of particular interest:

- The staminate strobili production was confined to plants maintained with cold roots, and;
- The great majority of the ovulate strobili production in both 1975 and 1976 was associated with the cold root treatment the spring of strobilus development.

Low temperatures are well known to restrict moisture movement, and therefore, such treatment may be analogous to drought. Other workers (Ching et al. 1973, Ebell 1967, Silen 1973) have reported substantial reduction of vegetative growth as one response to increased moisture stress. The data in Table 6.2 indicate no such reduction for the pres-

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[1] DP Lavender and KK Ching, unpublished data, 1976, 1984.

Table 6.1 Effect of seedling root temperatures on developing reproductive structures in Douglas-fir.

	Control (10°C to 15°C)	Cold roots (2°C to 4°C)
Number of ovulate strobili that developed on 1974 tissue of scions*	4/36	11/53
Number of staminate strobili that developed on 1975 tissue of scions	0/33	135/45
Number of ovulate strobili that developed on 1975 tissue of scions (all but one strobilus on seedlings with cold roots in 1976)	2/33	9/45
Proportion of living grafts with strobili, 1976	1/29	21/35

Note: All staminate strobili in 1976 - percentage on plants with cold roots: 4 strobili on 36 grafts; 11 strobili on 53 grafts.
Source: DP Lavender and KK Ching, unpublished data, 1976, 1984.

Table 6.2 Effect of seedling root temperatures on the growth of vegetative shoots in Douglas-fir.

	Mean length of shoot (mm)	
Shoot	Control (10°C to 15°C)	Cold roots (2°C to 4°C)
Terminal	102	97
Lateral	70	72

Source: DP Lavender and KK Ching, unpublished data, 1976, 1984.

Table 6.3 Effect of seedling root temperature upon the mineral content of scion and seedling tissue in Douglas-fir.

	Mineral content (%)					
	Control (10°C to 15°C)			Cold roots (2°C to 4°C)		
Tissue	N	P	K	N	P	K
Seedling	0.94	0.133	0.67	1.23	0.081	0.41
Scion	1.21	0.204	1.13	0.91	0.147	0.89

Source: DP Lavender and KK Ching, unpublished data, 1976, 1984.

Table 6.4 Effect of seedling root temperature upon plant moisture stress in Douglas-fir.

			Plant moisture stress* (atms)	
Date (1976)	Weather	Control soil temperature (°C)	Waterbath seedlings (Roots @ 2°C to 4°C)	Control seedlings
9 April	Partly sunny, 15°C	10	13.0	12.7
6 May	Warm, N.E. wind	12	13.2	11.5
10 May	Cool, moist	16	11.5	6.2
19 May	Partly cloudy, cool	11	13.0	6.3

* At noon measured with pressure bomb.
Source: DP Lavender and KK Ching, unpublished data, 1976, 1984.

ent populations. Further, a comparison of the 1976 growth of plants maintained as control both years with that of plants grown with cold roots in 1975 and as controls in 1976, demonstrates no significant reduction in growth of the latter (which might be expected if these plants did, in fact, undergo drought stress in 1975).

The nutrient contents of foliage collected from both seedling and scion tissue in the fall of 1975 is summarized in Table 6.3. The erratic nature of the nitrogen content does not support a hypothesis relating this element to flowering response.

The data describing the plant moisture stress of seedlings in the spring of 1976 is shown in Table 6.4. Surprisingly, in spite of references to "drought-induced" flowering in conifers, we could find no comparable published data. Although Owens (1987) suggested that apical meristems may be more sensitive to small increases in moisture stress than previously thought, during the summer months, Douglas-fir frequently experiences moisture tensions in excess of 25 atmospheres. So it is difficult to assess the importance of the differences shown in this table.

The above data appear to add just one more to the list of treatments known to induce a "flowering response" in Douglas-fir. And, if the mechanism of the present response is drought-mediated, the above results are not unique. Most of the treatments cited in this book can be interpreted as affecting root metabolism, however. Unpublished observations of significant precocious strobilus production in young plantations in the Willamette Valley, which are sufficiently moist to permit double flushing of many seedlings, but which support stands of grasses known to produce materials toxic to tree roots, provide yet further evidence for this concept. Finally, the tremendous "distress crops" found in seed orchards when the scion and understock are incompatible, may reflect export of regulatory compounds from roots. If root-exported regulatory compounds are involved in floral initiation in Douglas-fir, however, the lack of a flowering response in the juvenile tissues of the present population indicates that such compounds can be no more than one factor and that a strong response to a treatment such as low root temperatures can be expected only when this factor is limiting.

The incidence of ovulate strobili production is of interest because the development of such structures is believed to be determined no later than mid-summer of the previous year (Silen 1973). If the present data are reliable, however, the transition from vegetative bud to ovulate bud apparently may happen until bud break.

The difference in the above results and the negative data of Zaerr and Bonnet-Masimbert (1987) may be because these latter workers used a minimum temperature of 5°C. Lavender and Wareing (1972) showed that Douglas-fir seedlings maintained at 4°C responded with good root growth. And Lavender et al. (1973) demonstrated that applications of GA_3 to Douglas-fir seedlings maintained with cold roots stimulated bud break, data that suggest root-synthesized plant-growth regulators may be involved in floral initiation.

Douglas-fir seedlings can produce roots at temperatures at least as low as 4°C (Lavender and Wareing 1972). Such root growth follows the pattern described by Hellmers (1963), however, with morphology distinctly different from that of roots grown under higher temperatures. Given the foregoing, and the results of growth substance content of xylem exudate of *Zea mays* (Atkin et al. 1973), assaying Douglas-fir roots cultured at a range of low temperatures for plant growth regulatory activity might be of interest. If little or no root activity is, in fact, a strong stimulant to flowering, this cold root treatment may be ideal for seed orchards in greenhouses because seedlings may be exposed to this treatment for an entire growth season.

Although several workers have found that cone crops correlate with weather sequences occurring as long as 27 months before cone maturity, but none have elucidated possible causative effects of weather on flower production. Ross and Pharis (1985) summarized that, "studies correlating seed crops in conifers with weather data indicate that the proper sequence of optimal environmental conditions (such as dry or even droughty, with high solar insulation during the late spring or summer before initiation and differentiation of cone buds) for flowering may occur, but infrequently, in nature" (p. 18).

Puritch (1972), Owens (1991), and Jackson and Sweet (1972) reviewed reports that indicated that warm, dry climates favor cone production by conifers, and Ross (1976) noted that the warm dry climate of Sequim, Washington, and Saanich Peninsula, Vancouver Island, have been correlated with precocious flowering of Douglas-fir. Several studies, Eis (1973a), Van Vredenburch and LaBastide (1969), and Lowry (1966) have shown correlations between weather patterns in years immediately before heavy Douglas-fir cone crops and the number of cones produced. Lowry suggested that a cool July two years before the cone crop, a moist March-April 18 months before cone harvest, and a warm January and mild June the year of the crop are associated with heavy cone crops. But Ching and Lavender (1973, unpublished data) were unable to demonstrate that modifications of the environment around Douglas-fir seedlings and seedlings grafted with tissue from mature trees, (according to Lowry's recommendations) stimulated cone production on the test populations. They used both ordinary seedlings and seedlings with scion material from mature trees grafted into their crowns to test the 2-year weather sequence that Lowry suggested stimulates flower production.

Four seedling populations were subjected to the prescribed sequence of weather modifications, one population initiating the sequence in each of four successive years. Flowers appeared only occasionally and were not related to the treatments. In addition, Lowry (1967, p. 3) noted that the foregoing "has produced not a definitive explanation, but only a portion of an inferred generalization." He reviewed the problems of analyzing the data set discussed in 1966. Giertych (1987) noted a trend to move seed orchards to warm, dry sites, and Sweet and Bollman (1972) report that there was variation in Douglas-fir seed production across New Zealand, but they do not suggest a reason for these differences.

Rowe (1964) reviewed the strong effect that factors of the environment have on flower initiation of a range of trees. Silen (1967) demonstrated that Douglas-fir male bud abortion increased with increased elevation during the summer. Similarly, the number of female buds fell with increased elevation, reflecting the fact that climatic differences associated with elevation had a negative effect on productive buds. Enescu (1987, p. 260) noted that, "among all the climatic factors, humidity and temperature are the most important ones affecting flowering and wood production." He cited a range of examples in which high and low moisture and temperature favored flowering, noting that "oak formation of female buds is determined by low temperatures," and that "the transfer towards warmer geographic regions can favor seed maturation, early flowering and, undoubtedly, the physical isolation against undesirable foreign pollen . . . if the difference between the sum of annual temperatures in the natural habitat and the place where seed orchards are to be established is 200-300 degree days then flower production can increase by 160%" (p. 263).

And Ross and Pharis (1985) noted that warm, dry sites are associated with both earlier and more prolific flowering of Douglas-fir than the cooler, moister sites in this species range. Roeser (1942) presented a detailed description of the mega- and micro-sporangiate flowers of Douglas-fir with elevation over a period of 12 years at elevations between 2042 and 2865 m in Colorado. He noted a general correspondence between levels of "staminate" and "pistillate" flowers, a strong relation between elevation and delay in flowering, and the fact that the flowers are most susceptible to frost damage at the time of bud break.

Sweet and Bollman (1972) noted distinct differences in the number of seed per Douglas-fir cones in varying collection areas in the North and South Islands of New Zealand, but the data do not permit conjecture on possible climatic effects.

Greenwood and Hutchinson (1996) noted that flowering is greater in the southern part of a species range. They reviewed several reports indicating that potted indoor seed orchards frequently are profuse flowerers, but also warned of aftereffects in seedlings grown from indoor seed.

Eis (1972, 1973a) noted that weather over successive summers—a cool, moist summer, followed by a warm, relatively dry summer the following year—was associated with cone production in both Douglas-fir and grand fir. These results are roughly similar to Lowry's (1966) and Van Vredenburch and LaBastide (1969), discussed previously. Interestingly the foregoing was true for both early- and late-flushing trees. Sweet (1975) emphasized that the choice of site is the most important decision for seed orchards and that sites with warm, dry summers favor seed production and not necessarily vegetative growth.

Cultural treatments

The following section summarizes the effects of a range of cultural treatments on flower initiation.

Girdling

Numerous reports substantiate the hypothesis that perennial woody plants may be induced to flower by girdling individual branches or the main stem. Presumably, this treatment checks the basipetal movement of substrate, making more carbohydrate available to support development of reproductive buds. The low soil temperature that stimulates flowers on Douglas-fir may in fact be a girdling mechanism that reduces transport of carbohydrate into the roots, leaving more carbohydrate available to support reproductive development. Girdles, whether applied directly or indirectly, as in the instance of graft incompatibility, may kill the affected part. Flowers produced immediately before death are often seen as "distress crops," and they may not be a result of normal stimulation and development.

Several trials (Ebell 1971; Skadsen 1975; Wheeler et al. 1985; Bonnet-Masimbert 1982, 1987; Philipson 1990; Ross 1990; Woods 1989) all demonstrated that girdling Douglas-fir could result in enhanced flowering. Ebell's trials showed that the optimum time for treatment was about a month before bud break. His work was particularly impressive in that he treated one stem of trees with dual trunks and only the treated stem responded with increased flower production. Wood's trials included one poor cone-crop year when the general promotive effect of girdling was absent. The mechanism by which girdling affects flowering is not known, although it is a general phenomenon in both gymnosperms and angiosperms. One suggestion is that the girdle prevents translocation of photosynthate which resulted in an elevated C/N ratio in the foliage. The evidence of Ebell (1971) is inconclusive on the role of carbohydrates in flowering and an elevated C/N ratio contradicts the data resulting from nitrogen fertilization, that lowers the C/N ratio. The data resulting from Ebell's paired stem trials are particularly interesting in that they appear to rule out an influence of the root system unless each stem is served by its unique portion of the roots.

Further, according to Ebell (1971, p. 465), "Girdling will be most promotive when applied in years of cone crop failures, rather than years when abundant flowering exists." This result is the opposite of results reported for effects of hormones, however. Webber and Stoehr (1998) noted that for girdling which is more promotive than GA in inducing flowering. Jackson and Sweet (1972, p. 15) reviewed several successful girdling trials and they noted that while girdling does tend to increase levels of carbohydrates above the treatment, "there is no unequivocal evidence carbohydrates play a direct role in flower initiation." Rather, "the important factor may be a particular biochemical situation which is frequently associated with high carbohydrate levels." Sweet (1975) reviewed several flower induction treatments and noted that, though girdling may be harmful, it can also be very effective. Ebel (1971) girdled Douglas-fir at different times and concluded that girdling at the time of vegetative bud break was most effective. Wheeler et al. (1985) reported that girdling Douglas-fir definitely increased the number of cones and that the cumulative effect of annual girdling was greater than that of biennial girdling. They also found that girdling did not affect seed parameters or long term health of trees. Woods (1989, p. 12) tested various timing and types of girdling and made the following recommendations:

Based on the results from this and other studies, and experience beyond these data, the following recommendations are made for girdling to increase seed production:

1. Girdle from 1 to 3 weeks before vegetative bud flush.
2. Perform a single cut into the xylem (hard wood) with a sharp knife.
3. Proceed cautiously in local areas, with incomplete (90% to 98%) girdles at first, and complete bands if experience indicates this is necessary.
4. Girdle above at least one whorl of live branches. This will not usually affect cone production, and will aid tree vigor by leaving some crown to supply photosynthates to the roots.
5. Treat the girdle wounds with an insecticide at the time of girdling, or wrap the wound with several layers of breathable cloth.
6. Fertilize girdled trees at the time of treatment with ammonium nitrate (Ebell and McMullan 1970) at the rate of about 300-400 kg N/ha. (Base on locale experience.)
7. Girdle trees every second year or less. Annual girdling may cause excessive stress on existing cone crops and on the trees' ability to produce future crops.
8. Girdling should be preceded by a survey for reproductive buds to avoid possible damage to the current year's seed crop.

Woods also found that effects of girdling were found the year after treatment and that girdling did not stimulate flowering in a generally poor seed year.

Wheeler et al. (1985) reported that girdling alone or with fertilizer increased flowering over the 12 years of the study, had significant effects on seed parameters and only a minor effect on tree vigor. Masters (1982) reported that girdling increased flowering and that culturing trees for long internodes was beneficial. Owens and Blake (1985, p. 39) noted that girdling may increase cone production, but that "results vary depending on the time of application, the method of girdling or strangulation used (the latter is generally not as effective as girdling) and the use of adjunct treatments." Ross and Bower (1989) showed that girdling and $GA_{4/7}$ both alone were about equivalent in stimulating flowering on Douglas-fir, and together they were additive. Bower and Ross (1985), however, showed that girdling greatly stimulated staminate buds on Douglas-fir.

Bonnet-Masimbert and Zaerr (1987), Owens and Blake (1985), and Puritch (1972) reviewed a substantial number of girdling studies that vary in technique and timing; one conclusion of this work is that girdling should be timed to have a major effect at the time of flower bud initiation in the spring. Faulkner (1966) described several experiments, including Douglas-fir and a range of girdles. Melcher (1960) discussed effects of timing of girdling on floral initiation—prior to May 30—increased the number of flowers especially female, the following year. Girdling between end of June to July increased flowering two years later. And Sedgely and Griffen (1989) noted that "while girdling is probably the most widely successful of the treatments designed to stimulate flower initiation, it is no panacea. Use is limited by unpredictable responses relating to time, season, and cultivar, and by the long-term deleterious effects on tree vigor" (p. 248).

Noel (1970) presents an extensive review of girdling, in which he discusses several trials of both perennial angiosperms and conifers that have demonstrated that girdling frequently resulted in increased flowering. Although he devotes a section to physiology, he does not offer a unique reason for such results. Pharis et al. (1980) noted that girdling branches did not stimulate flowering on six-year-old Douglas-fir seedlings, and Ross et al. (1980) reported that girdling may reduce the number of seeds per cone and, hence, may be detrimental. And Masters (1982) reports that girdling 12-year-old Douglas-fir trees resulted in a doubling of cone production in a seed orchard.

Top pruning and branch thinning

Ross and Currell (1989) reviewed reports indicating that top pruning both enhanced and reduced cone production and report the same responses for Douglas-fir. They suggested the effect may vary with the vigor of the branches with the less vigorous trees sustaining the greatest relative reduction in number of cones. In contrast, the branch thinning reduced the cone crop.

Root pruning and grafting

Owens and Blake reviewed several reports that indicate that these treatments may increase flowering in conifers and speculate that flowering of grafts may be caused by incompatibility, which, in effect, was an incomplete girdle. We have seen examples of such behavior in a Douglas-fir seed orchard near Corvallis, Oregon.

We noted earlier that root pruning or cold soil temperatures could stimulate flowering. Several reports have implied an influence of roots on flower initiation, most of which suggest a reduction in root metabolism as the causative factor. Zaerr and Bonnet-Masimbert (1987) noted that flooding the root system of potted Douglas-fir seedlings was associated with flowering. Several other workers have shown that root pruning may stimulate flowering; Masters (1982), for example, reported that root pruning increased flowering 5.2 x the control in a 12-year-old Douglas-fir seed orchard, the greatest increase of any treatment. Bonnet-Masimbert and Zaerr (1987) reviewed trials in which reduction or absence of root growth was correlated with flowering in several species, including Douglas-fir. Interestingly, they showed that treatment with $GA_{4/7}$ blocks Douglas-fir root growth. We noted earlier that girdling was very effective in stimulating flowering and that such treatment is detrimental to roots. Similarly, Douglas-fir trees in the final states of *Phelinus weirii*, a virulent root pathogen, frequently produce heavy cone crops. Owens (1987) noted that root pruning delayed development of auxiliary apices until mid-July, when they developed into vegetative, reproductive or latent buds. He speculated that midsummer environment may have favored reproductive development. Silen (1973) reported that about 65% of sapling Douglas-fir trees (1.2-3.1 m tall) flowered in July after moving on June 30-July 1 (13-14 weeks) after spring flush, while only 1 of 91 control trees bore cones (1972 was a poor cone year, after a heavy crop in 1971); and that the transplanting treatment resulted in drought symptoms and pruned roots.

Finally, Ross et al. (1985) noted that root pruning of Douglas-fir, which resulted in a 0.3 mp moisture stress at mid-day, was more effective in stimulating female flowering of Douglas-fir than was applying of $GA_{4/7}$. Root pruning did not result in increased male flowering, however. Finally, Bonnet-Masimbert (1987) and Philipson (1990) found that root pruning stimulated flowering in Douglas-fir, but Bonnet-Masimbert and Doumas (1992) suggested that any effects of root pruning to roots may well be indirect.

Gravimorphism, shading

Longman et al. (1965) found that training larch branches downwards resulted in increased flowering. The same treatment has been used successfully with horticultural species, but in larch, which bears cones on downward oriented branchlets, the treatment may have reinforced the natural tendency. Lavender and Ching (unpublished data, 1968) were unable to report this effect with Douglas-fir, where bent branches resumed a nearly horizontal orientation. Silen (1973) observed that shade (13%-23% of full sunlight) increased the numbers of female flowers the year of application and decreased female flowering the following year. Furthermore, the treatment had greatest effect when applied during shoot elongation; nonetheless, the experiment left open the earliest time of flowering enhancement.

Much of this research occurred years or decades ago and, though it may have been carefully done, the design of this work generally suffers as Romberger (1967) and Giertych (1987) noted in their papers.

A second major effort to induce flowering uses plant growth regulators. The compounds apparently most successful are gibberellic acid and analogous $GA_{4/7}$. Because more than one hundred papers describe the effects of applying gibberellins to trees, we will consider only those that review the literature or discuss the interaction of gibberellins and other methods that have successfully stimulated flowering and report dealing with Douglas-fir.

Plant growth regulators

Gibberellins

These compounds were first recognized in Japan late in the 19th century, when the compound found to cause the “bakanae” or “foolish seedling” disease of rice was shown to be produced by the fungus *Fusarium moniliform* Sheld., “the asexual or imperfect stage of the ascomycete *Gibberella fujikuroi* (Saw.) Wr. . . . T. Yabuta, at University of Tokyo, assigned the name ‘gibberellin’ to the active factor in *G. fujikuroi* culture filtrates in 1935, and in 1938 Yabuta and Y. Sumiki announced the isolation of two crystaline, biologically active substances, which they named ‘gibberellins A and B’” (Moore 1979, p. 90). Studies of GAs in western countries, however, did not begin until after World War II. At least 86 gibberellins were identified (Pharis et al. 1992, p. 13). “However, a large proportion of the GAs exhibit little or no biological activity, probably because they lack the capacity to fit a receptor molecule“ (Pallardy 2007, p. 369). Pharis et al. (1992, p. 13) noted that “The structural characteristics of highly florigenic GAs depend very much upon the plant species/family in question.” “In the Coniferae, GAs of a wide variety of structures are highly florigenic for *Cupressaceae* and *Taxodiaceae* families, but only the less polar monohydroxolated native GAs; GA_4 and GA_7 can routinely and effectively promote flowering with the *Pinaceae* family. According to Pharis et al. (1992, p. 14), GA_3 has been shown to play a role in dormancy physiology of Douglas-fir (Lavender et al. 1973). Perhaps species that do not require physiology that withstands extremely low temperatures can use GA_3 in flower induction because it would not interfere with control of cold hardiness or, as Dunberg and Oden (1983, p. 275) noted: “Conclusions regarding the hormonal physiology of conifers must be based on data from experiments with conifers. There is also evidence that fundamental differences exist between the Pinaceae on one hand and the Cupressaceae and Taxodiaceae on the other. It is therefore recommended that these two groups should be treated separately when generalizations are to be made.”

These authors also pointed out that the conflicting results noted in reviews and reports of gibberellin’s effects on flowering before 1983 are the result of the extreme difficulty in working with GAs and poor experimental design. In like manner, Bonnet-Masimbert (1982, p. 1183) reviewed research with GAs and made these observations:

- A positive flowering response to specific exogenous GAs does not mean that they naturally affect the flowering. More convincing evidence is the endogenous increase of less polar GAs ($GA_{4/7}$), as opposed to stability or decrease of GAs observed after a root pruning, which dramatically increased flowering of 10-year-old Douglas-fir seedlings."

- Data showing relations of GA_1, GA_3, GA_4, and GA_9 to flowering are contradictory; such results demonstrate the need for metabolic studies to determine the conversion rate between GAs, as well as quantitative analyses.

McMullan (1980) reported on an intensive survey of the relations of growth regulators applied to cut twigs at the projected time of floral initiation, and noted that neither bud extracts from trees with a good cone production record nor those from trees that seldom produced cones stimulated flowering in 10-year-old Douglas-fir seedlings. She noted no difference in growth regulator content of cone producing or non-cone producing trees. $GA_{4/7}$ stimulated flowering on all trees, both cone producing and non-cone-producing. But the large quantities used caused some tissue damage, so she questioned whether the effect was normal and, cited (p. 411) Reeve and Crozier (1975) to the effect that applying super physiological doses of GAs could destroy their subcellular compartmentalization, which made difficult knowing whether a response observed was due to the natural effect of the applied hormone or whether it is a non-specific effect resulting from abnormal chemical modification. Similarly, Durley et al. (1975) raised the possibility that injecting large doses of GA_{20} into leaves may have given rise to abnormal metabolites. McMullan (1980) also presents the results of successive time separated samples of Douglas-fir foliage and found no correlation with GA content and cone production.

Puritch et al. (1979) reported that $GA_{4/7}$ treatment resulted in a significant increase in cones from 8-year-old Dougals-fir seedlings and 8-to-11-year-old grafts in seed orchards over a range of sites on Vancouver Island. The seed orchard with the highest endogenous production showed the greatest increase. Pollen cones were not significantly increased by treatment. The IAA increased seed germination rate and total. The GA may have changed the balance of latent vs. reproductive, vegetative buds. Pharis and Ross (1976) reported that 400 μgm $GA_{4/7}$ per branch applied at fortnightly intervals between March and late June increased ovulate flower production 5x over the control of 4-year-old grafts and staminate flowers, 3x. They suggested that rapid conversion of GA_4 (p. 185) to more polar forms of GA is why relatively high amounts were needed. The treatments were effective only on the clones, which flowered naturally.

Wample et al. (1975) found that seedling Douglas-fir rapidly metabolized GA_4 to GA_{34}, GA_2, and unknown products at each of three stages of shoot development—that is, bud break, shoot elongation, and budset. This finding demonstrated that Douglas-fir can metabolize active forms of GA to more polar forms inactive for vegetative growth, but the GA_4 was active in promoting flowering in Douglas-fir. Accordingly, they suggested (p. 277), "therefore, Douglas-fir's unresponsiveness (at least in terms of shoot elongation to exogonenous GAs may reflect either a surplus of GAs or a highly effective system for 'inactivating' biologically active GAs by (a) oxidation to more polar acidic products and b) conjugation)."

Ross (1976), working with equi-sized 2-year-old Douglas-fir grafts and 4-year-old seedlings showed that non-polar GAs ($GA_{4/7}$) and, to a lesser extent, GA_5 and GA_9, stimulated male and female flowering on both grafts and seedlings, but that GA_3 did not unless applied with 1AA. The trials were conducted out of doors near the droughty Sequim area on the Olympic Peninsula. Although none of the control seedlings flowered either in this population did, and the author hypothesizes that the seedlings were therefore no longer "juvenile."

The report of Pharis et al. (1976) is in substantial agreement with the ones above in that endogenous amounts of non-polar GAs were high in mature, flowering trees and GA_3 was high in non-flowering, similarly mature Douglas-fir. They also noted that applying $GA_{4/7}$ at the appropriate time was successful in stimulating flowering on four- and six-year-old Douglas-fir seedlings. Ross (1983) hypothesized that $GA_{4/7}$ in Douglas-fir is first used for vegetative growth and only when this use is satisfied does the chemical stimulate flowering. He further noted (p. 98) that, when $GA_{4/7}$ was applied early in the spring, it resulted in minimal flowering response and maximum vegetative growth; the reverse was true if it was applied within 4.5 weeks of bud break.

In a series of four papers, Ross et al. (1985), Webber et al. (1985), and Owens et al. (1985, 1986) the authors discussed the effects of $GA_{4/7}$ and root pruning on the flowering and vegetative growth of nine-year-old Douglas-fir seedlings.

In the 1985 paper, Ross et al. concluded that root pruning stimulated female flowers in all families, both those with good and those with poor flowering, but, GA was effective only on good-flowering seedlings. Root pruning was more effective than GA. Root pruning between 6 weeks before bud break until early July and GA and root pruning were the most effective methods to stimulate flowering.

Owens et al. (1985) reported that the apices from GA-treated and control trees were similar and followed a normal growth sequence. In contrast, root pruning delayed development until mid-July, after that date, normal development of vegetative, reproductive, and latent buds proceeded, with the greatest delay being associated with the greatest subsequent cone production. They agreed with Pharis and Ross (1976, p. 220) on the following: "Another hypothesis is that conifers utilize endogenous GAs preferentially for vegetative growth and it is only when environmental or other factors restrict this growth that GAs are available for cone initiation." Owens (1987) largely agreed:

> McMullan (1980) and Dunberg and Oden (1983) proposed that cone induction treatments using exogenous GAs enhance cone bud differentiation because GAs are applied, and taken up in amounts far exceeding those required for cone-bud differentiation, and induction is not a direct morphogenic effect but a stress effect. In the present study, GA alone had no effect on apical size, MF, or anatomy and did not enhance cone-bud differentiation in the trees used for anatomical study and only slightly enhanced cones in the general study trees (Ross et al. 1985). This indicates the GA effect was more subtle than a stress effect. However, until techniques are developed which allow analysis of GAs within small apices as opposed to whole shoots, the actual effect of GAs on apical morphogenesis will remain unsettled. . . .
>
> Histo-chemical tests used in this study show that GA, RP and RP + GA treatments did not increase total insoluble carbohydrates in potential cone-bud apices. Unfortunately, soluble carbohydrates could not be studied histochemically because they were extracted during fixation and embedding. (Owens 1987, p. 95)

Ross and Pharis (1987) reviewed many of the papers discussed above and concluded that GAs are the only growth regulators to effect elongation in conifers.

Ross and Bower (1991, p. 23) discussed girdling and injections of $GA_{4/7}$ and noted the following:

> Girdling in combination with a single stem injection of the growth regulator gibberellin A 4/7 can be a highly cost-effective treatment for enhancing seed yield in Douglas-fir seed orchards. Diminished tree vigor and flowering response to biennial retreatment can result, however, unless tress are properly managed to minimize the physiological stresses associated with treatment and the heavy cone bearing which follows. Alleviation of compounding water and nutrient stresses through irrigation and possibly fertilization following treatment and during the off-treatment year will speed the recovery and should enable trees to be safely retreated on a biennial basis. (Ross and Bower, p. 23)

They also definitely established GA and girdling treatment as stresses. Clearly the combination of $GA_{4/7}$ and root pruning applied at the correct time is the best treatment for increasing flowering in Douglas-fir seed orchards currently used.

Other treatments with $GA_{4/7}$ that have been investigated include top pruning and branch thinning (Ross and Currell 1989). The former reduced cone and pollen cone production at a rate at least in proportion with its severity, and the latter caused a response that reflected the change in vigor of the residual branches. Treatment with $GA_{4/7}$ increased production of both male and female flowers.

Several reviews (Pharis and Ross 1986a,b; Bonnet-Masimbert 1987; Bonnet-Masimbert and Zaerr 1987; Pharis et al. 1987; Bonnet-Masimbert and Doumas 1992, Black 1998) examine the role of exogenous gibberellins in flowering of conifers and make the following points:

- Reasons for failure of GAs to promote flowering in Pinaceae include use of GA_3, timing of treatments, lack of adjunct treatments.
- GA is more than a "stress" treatment.
- Ratio of values of exogenous GA to endogenous GA reaching bud 250-500:1.
- Cupressaceae species, which are strongly stimulated to flower, utilize slowly metabolized GA_3. Pinaceae species, which are less efficiently stimulated, utilize rapidly metabolized, less polar GAs.

- Of all treatments designed to stimulate flowering, only root pruning in Douglas-fir is as consistent as the application of $GA_{4/7}$.

In another trial, Bonnet-Masimbert (1982) demonstrated that flowering of Douglas-fir with or without growth regulators occurred only when the roots were inactive. While Black (1998) reviewed a number of papers reporting either no relationship of endogenous $GA_{4/7}$ levels after flower inducing treatments or a concurrent increase in $GA_{4/7}$ and flowering.

Sex expression

According to Ross and Pharis (1987),

> relatively little is known about the endogenous control of sex expression (in forest trees) or its practical manipulation to aid pollen and crop management in seed orchards. Well defined patterns of sexual zonation exist within the tree crown and shoot, and these appear to be associated with hormonal and possibly nutritional gradients. No firm conclusions, however, are possible regarding the specific roles of different plant growth regulators in sex expression. This being as much as a problem of lack of critical study as the complexity of the process itself. (Ross and Pharis 1987, p. 37)

In spite of the foregoing, they noted for Douglas-fir (p. 39) “that strobili of both sexes differentiate from previously undetermined auxiliary primordia—female strobili from distal primordia that would normally become vegetative branch buds, and male strobili from primordia that would otherwise abort or remain latent.” And that both sexes apparently differentiate at the same stage of shoot development. They reviewed considerable evidence both for and against the theory that the sex of a strobilius is correlated with the vigor of the bud from which is differentiated or the shoot where it is found. They listed several studies which demonstrated that $GA_{4/7}$ stimulated female over male strobilii on Douglas-fir, but also noted that such results are not universal.

In a later paper, Ross (1990) reported that $GA_{4/7}$ stimulated female but not male flowering on *Picea engelmannii*. In contrast, Tompsett and Fletcher (1979) noted that gibberellin stimulated male, but not female flowerings on scions of mature *Picea sitchensis* maintained in a warm polyhouse. While Puritch et al. (1979) and Fogel et al. (1996) reported $GA_{4/7}$ stimulated female but not male flowering on Douglas-fir and jack pine, respectively.

Auxins

This group of chemicals was the first plant growth regulator studied. Indole acetic acid (1AA) was first isolated from fungi in 1934. These substances are primarily associated with cell elongation and were shown to be involved in the bending of stems and petioles as a result of differential destruction by light. 1AA has been shown to increase the flowering response of Douglas-fir when applied with gibberellin (Bonnet-Masimbert and Zaerr 1987). Ross and Pharis (1987) reviewed papers which relate auxin and ethylene to femaleness in forest trees. While Puritch et al. (1979) report 1AA did not stimulate flowering on Douglas-fir trees.

Cytokinins

Kozlowski and Pallardy (1997, pp. 311–313) reported that a substance, kinetin ($C_{10}H_9N_5O$), was active in promoting cell division. Since the report from Skoog’s laboratory, cytokinin has been isolated from a number of higher plants and is apparently synthesized in the roots and exported to plant shoots in xylem sap. Meilan (1997) summarized a number of reports which presented evidence that cytokinins are involved in the flowering process in angiospermous plants.

A number of trials at Oregon State University, INRA (Zaerr and Lavender 1984; Doumas et al. 1986; Zaerr and Bonnet-Masimbert 1987; Doumas and Zaerr 1988; Imbault et al. 1988; and Morris et al. 1990) reported the following in Douglas-fir: (1) quantities and species of cytokinin varied between male, female and vegetative buds; (2) levels of cytokinins varied with season but were highest in mid-spring; (3) female flowers were generally associated with low levels of cytokinin, but low levels of cytokinin did not guarantee flowering; and (4) high levels (5 microgram per shoot) of exogenously applied isopentenyl adenine significantly stimulated female bud formation. There are no later reports expanding on the foregoing. Pharis and Ross (1986a,b) report ed that cytokinins slightly enhanced $GA_{4/7}$ stimulated flowering in Douglas-fir, but not in other species.

Abscisic acid

The compound now termed abscisic acid, or ABA (Kozlowski and Pallardy 1997, pp. 312–313), was originally termed "dormin" (Phillips and Wareing 1958) and was found to be associated with dormancy in trees (although Zaerr and Lavender 1968 found it only weakly associated with dormancy in Douglas-fir seedlings). Addicott found that it was related to abscission and that when it was purified, it was identical to dormin. McMullan (1980) found that ABA did not stimulate flowering in Douglas-fir, while Meilan (1997) reviewed a number of papers that suggest that ABA promotes flowering in angiosperms by antagonizing GA, but no reference is made to conifers.

Carbohydrates

Pharis and Ross (1985) reviewed a number of papers dealing with flower-bud formation and noted that the environments and treatments reviewed here may well have an effect on the carbohydrate balance of trees. But they also noted that papers concerning actual carbohydrates failed to establish a relationship between carbohydrate content and flowering. Ebell (1971) and Ebell and McMullen (1970) reported that increased starch levels resulting from girdling Douglas-fir were associated with increased flowering. Ross and Pharis (1987), concluded: "Thus as with floral initiation/differentiation in general, a direct morphogenic role for carbohydrates in sex expression of conifers remains unproven" (p. 42).

Arginine

Ebell and McMullen (1970) related increased levels of arginine and basic amino acids with flowering in Douglas-fir and suggested that accumulation of arginine may lead to cell division favoring a continued development of sexual primordia. In a latter paper, however, McMullan (1980) reported that applied arginine did not affect level of flowering in Douglas-fir. Pharis and Ross (1986a,b) cited references which report negative results in flowering with applications of arginine to *P. menziesii*. Ching, KK, et al. (1973), reported that treatments which greatly increased the endogenous levels of arginine did not cause flowering in Douglas-fir, while Stewart and Durzan (1965) found that increased levels of arginine were associated with flowering in conifers. However, Ching et al. (1973) found no such relationship in Douglas-fir possibly because their populations were juvenile. Daoudi et al. (1994) reports arginine levels as much as 15-fold greater in trees treated with N+GA than control trees. The treated trees flowered but not the control. Daoudi et al. (1994) reports that arginine proline and total free amino acids are much greater in male buds than in vegetative or female buds.

Polyamines

Scientists at Orléans, France reported on the relationship between polyamines in buds and flowering in Douglas-fir (Daoudi et al. 1991 and 1994; Daoudi and Bonnet-Masimbert 1998). Daoudi et al. 1994) reported that "the accumulation of polyamines in the shoots accompanied bud sexualization, which suggests that polyamines may constitute potential markers, probably rather early ones (4–6 weeks after bud burst), of floral initiation in Douglas-fir" (p. 1854). They do not, however, present evidence that polyamines are causal to flowering. Further, conjugated polyamines are abundant in the shoots and buds of flowering plants.

Summary

This section has discussed many factors known to influence the evocation of flowering in Douglas-fir. Romberger and Gregory (1974) emphasize the usefulness of analytical morphogenesis as a tool to understand that developmental process leading to flowering and suggest that without such knowledge we will never understand fully the factors controlling flowering in trees. Giertych (1988) argues that research to the date of his paper had really not produced efficient, reliable scenarios for production of flowers in conifers and agreed with Romberger and Gregory that studies of development of floral anatomy were greatly needed. McDaniel reviewed flowering research in angiosperms (which is more advanced than that for gymnosperms), noting (p. 51) scientists should "adopt a more developmentally oriented view of floral initiation." O'Neill (1989) reviewed the range of studies which tried to identify "florigen" and concluded that "the multitude of biochemical changes associated with flowering are too complex to be controlled by a single factor and suggests that the riddle of flowering might best be elucidated through a study of gene expression."

The preceding comments reflect the fact that flower evocation has rarely been the subject of basic physiological research. One major exception to this pattern has been the increasingly detailed study of the role of $GA_{4/7}$ in the physiology of floral evocation by Odén et al. (1995) and Pharis et al. (1989). The former noted (p. 456) that, for Norway spruce, "the availability of active GAs is deliberately regulated in the specific organ departments of the shoot, and that their metabolism is directly influenced by various factors including root activity, stomatal turgor (e.g., tissue Y) and temperature," while the latter reported:

> The flowering response to exogenous application of GAs may imply that endogenous GAs play a part in the flowering process, but does not prove it. Support for a causal role for endogenous less-polar GAs in cone bud differentiation is provided by data where root pruning was used to promote flowering of Douglas-fir (*Pseudotsuga menziesii*) over 20 fold in the absence of exogenous hormone application. Extracts of the shoots (minus needles) on which cone bud primordia are forming showed that the root pruning treatment had increased the concentration and/or amount of less polar GAs by 2-4 fold while leaving the more polar GA_3 either unaffected (on a concentration basis, or diminished on a per shoot basis). (Pharis et al. 1989, p. 29)

They discussed further data suggesting that GA levels are influenced by plant moisture content and that environmental treatments associated with flowering generally result in plant moisture stress. McMullan (1980) found no relationship between endogenous $GA_{4/7}$ and flowering in Douglas-fir. Pharis et al. (1987, p. 72) noted that GAs of a less-polar nature appear to play a direct morphogenic role in the promotion of flowering in conifers, although the nature of this role remains obscure (see also Bernier 1988, p. 209). Additionally, Pharis et al. (1987) concluded that "both endogenous GAs and exogenous applied GAs of a less polar nature are 'conserved' in the presence of a variety of cultural treatments which are known to promote flowering. Such conservation would be expected to increase their effectiveness whether flowering was promoted by endogenous GAs, exogenously applied GAs, or both" (p. 77).

The research summarized here suggests that (1) for Douglas-fir (and many other conifers) the plant growth regulator, $GA_{4/7}$ is associated with the development of both male and female strobili, although the mode of action remains obscure, and (2) while there are many adjunct treatments which may favor "flowering", the most efficacious are those that reduce root growth. Again, the mechanisms for this possible reaction are unknown. It would be interesting to repeat the low temperature exposure of roots with the addition of examination of apices (Owens 1987) together with analyses of GA content. The juvenile-mature phase change remains a "black box," although Mellerowicz et al. 1995 (p. 443) suggest that there is circumstantial evidence of changes in chromatin organization or both, during maturation.

Embryogeny

Embryogeny and pollen are the subjects of a vast botanical literature, particularly for angiosperms. So, my discussion will be limited generally to Douglas-fir. Much of the material published before 1972 is reviewed in greater detail in Allen and Owens (1972).

Lawson's paper (1909) is the earliest thorough discussion of the embryogeny of Douglas-fir. He describes the male and female gametophytes in detail, noting that the pollen is globular in form with a distinct well-developed exine, but no wings to provide the buoyancy. Within the microspore there are two prothalial cells, two large free nuclei, one centrally located and termed the generative nucleus, the second, the tub nucleus. The research was started too late (30 March) to permit early description of the megaspore, which contained large quantities of sap and little cytoplasm, and three or four nucleii. Just prior to fertilization a ventral canal cell and an egg form. The nucleus of the egg becomes greatly enlarged and descends to the center of the archegonium. The pollen grains lodge in the upper chamber of the micropyle, where they are caught on the extended surface of the micropyle prior to the folding of this structure, which is typical of Douglas-fir. The pollen grains do not move to the nucellus, but germinate in place, extending a long pollen tube (another characteristic of Douglas-fir) through the nucellus to the archegonium. Just prior to the extension of the pollen tube, the generative nucleus divides, which results in the organization of two distinct cells, the larger one is the body cell, the smaller, the stalk cell, during fertilization the entire contents of the pollen tube are emptied into the archigonium. He concluded, "The account here given of the gametophytes of *Pseudotsuga* makes it clear that this genus is not closely related to the genus *Tsuga*. And considering the state of development of the various vestigal and semi-vestigal structures present, the view that the Abietineae are the most ancient group of the Coniferales is very much strengthened" (Lawson 1909, pp. 177-178).

Lawson's (1909) work was limited by the instruments available at that time and by the fact that his observations of the microspore commenced after the initiation of development of these structures in early spring. His observations and conclusions are reproduced here.

> The microspore at the time of pollination is globular in form and differs in appearance from that of the majority of other Abietineae in the entire absence of bladder-like appendages.
>
> The mature microspore contains four cells. Two of these are represented by the fragmented remains of two vestigial prothallial cells, and the other two represent the tube and generative cells respectively.
>
> Owing to the peculiar form of the micropyle, which has a stigmatic surface at the mouth, the pollen grains fail to reach the apex of the nucellus, but are caught at the mouth of the micropyle and here germinate.
>
> This pollen-receiving device and the formation of pollen-tubes so far removed from the nucellus is unlike anything yet reported for the Abietineae, and is evidently a novelty as far as the Gymnosperms are concerned.
>
> With the first appearance of the pollen-tube the generative nucleus divides, and as a result of this division two distinct cells are organized, one of which is considerably larger than the other. These are the body- and stalk-cells respectively.
>
> The pollen-tubes grow down the micropylar canal and attain a considerable length before the nucellus is reached.
>
> The tissue of the apex of the nucellus disintegrates in advance of the approaching pollen-tubes, so that the latter structures find little or no obstruction in their path towards the archegonial chambers.
>
> The division of the body-cell results in the formation of two male nuclei of unequal size.
>
> The entire nuclear contents of a pollen-tube are discharged into one archegonium.
>
> There are probably three megaspores resulting from a single mother-cell. Two of these are abortive and one functional.
>
> Upon the enlargement of the functional megaspore free nuclear division takes place, and this is followed by the formation of a large central vacuole.
>
> Completely enveloping the growing megaspore there is a single layer of large sporogenous-like cells which are closely packed together. This layer of cells, although single at first, soon becomes several layers thick, and eventually becomes quite loose and sponge-like—with numerous inter-cellular spaces—as the young prothallium increases in size. This tissue is regarded as sporogenous in origin and tapetal in function.
>
> The megaspore membrane makes its appearance at a very early period, and although quite thin at first it increases in thickness with the growth of the prothallium, and eventually becomes very conspicuous. In the mature stages it surrounds the prothallium except in the region of the archegoria. In this region is it entirely absent, in this regard differs quite markedly from *Tsuga*.
>
> With the increase in the size of the central vacuole, and the consequent formation of the parietal layer of cytoplasm, free nuclear division continues for some time.
>
> The parietal layer now increases in thickness, and the primary prothallial cells are formed in the ordinary way.
>
> These latter structures elongate in an inward direction, and gradually close the central vacuole. Free nuclear division now takes place within the primary prothallial cells, before cross-walls are formed to organize permanent prothallial tissue.
>
> The archegonia originate as superficial cells at the apex of the prothallium.
>
> They are generally four in number, and each is enveloped by a single layer of nourishing jacket-cells. There are generally two tiers, but frequently a single tier of neck-cells.
>
> The archegonia are separated from one another—especially in the region of the necks—by several layers of sterile prothallial cells, and each is provided with a separate archegonial chamber.
>
> A distinct ventral canal-cell is formed as a result of the division of the central cell.
>
> The membrane of the ventral canal-cell persists up to the time of fertilization.
>
> The fusion of the sex nuclei takes place in the middle of the archegonium.
>
> The female is many times the size of the male.
>
> The first segmentation-spindle is formed within the area bounded by the membrane of the fusion-nucleus. It is, however, of cytoplasmic origin. One or more dense masses of cytoplasm are carried into the egg-nucleus by the sperm-nucleus.
>
> The first division is very soon followed by a second, and the four free nuclei thus formed pass to the base of the archegonium.
>
> After the division that follows, cell-walls are formed separating the nuclei.
>
> Eventually the pro-embryo consists of three tiers of cells and one tier of free nuclei. The lowermost of these becomes the embryo proper. The middle one becomes the suspensor, and the next one the rosette. (Lawson 1909, pp. 176-177)

Buchholz (1920, 1926) discussed the question of simple polyembryony versus cleavage polyembryony in conifers. He presented evidence that simple polyembryony, wherein a single embryo develops in each archegonium, indicates that this type of embryo development is evolutionarily advanced over cleavage polyembryony, wherein more than one embryo is present initially in each archegonium. He further argued that simple polyembryony is associated with siphonogamy, or the development of pollen tubes and the lack of functional "rosette" cells. On this basis, Douglas-fir is the most advanced of the *Abietineae*, *Pinus*, the most primitive. He noted that, while Douglas-fir has simple polyembryony, there can be as many as eight archegonia in each ovule, and hence there is the possibility for significant competition at the embryo stage, and that the successful embryo is a product of superior egg and pollen tubes. It is interesting that, in his discussion of the possibility of pollen tubes and motile spermatozoa some four decades later, Christiansen made no mention of Buchholz's work. Gravatt et al. (1940) noted that one lot of Douglas-fir seeds had 5 of 1,214 multiple seedlings, a second lot, 47 of 1,174.

In a series of papers, Professor J. Doyle (Doyle 1926, 1945; Doyle and O'Leary 1935) discussed the ovule of Douglas-fir and its pollination in detail. He agreed with Lawson (1909) that the top of the micropilar tube is a stigmatic surface, which when it invaginates, brings the pollen near to the micropilar tube on the numerous hairs on its surface (Doyle 1926). However, he disagreed with Lawson, who thought that this method of pollen capture was unique to Douglas-fir, and he noted that *Larix leptolepsis* has a similar structure—the difference between the species being that Douglas-fir pollen germinates while attached to the hairs, whereas in larch, the pollen germinates after falling from the stigmatic surface to the nucellus, where it develops. He described how, after pollen has landed on the stigmatic surface, this structure invaginates, holding the pollen grains in a depression near the nucellus. By so doing, the stigmatic surface effectively closes the micropilar canal. Doyle (1926) observed the following:

> The micropilar differentiation is more elaborate than in *Larix*. Just above the nucellus the micropilar canal contracts to a very narrow slit. Above this, it is continued as two lips. On the side of the ovule, toward the centre of the scale, these lips are joined at their base, like the fused petals, of say, a *Veronica*; on the side towards the scale edge, they are completely separate. Both lips are differentiated, but the outer one much less so than the inner, which, slightly wider than the outer, is much larger, completely overtopping it. The two lips, at pollination are closely pressed together and project from the narrow ovular top as white turgid mass. (Doyle (1926, p. 177)

In a later paper (Doyle and O'Leary 1935), the pollination of Douglas-fir is described in detail as follows:

> In Douglas-fir, it is well known that the pollen remains at the top of the micropyle, more or less entangled by the hair-like outgrowths to be seen on the inside of the inturned rim and which have resulted from the collapse of the stigmatic expansion. Some of the grains, however, are to be found later a short distance down the micropyle, but none get at all near the nucellus. Lawson (1908) seems to suggest that they are prevented from reaching the nucellus by the contraction and kink, which appear some distance down the micropyle neck, and which reduce the canal to a slit-like passage. This, however, can hardly be the case. In the first place, the narrowing of the micropyle is not as marked as suggested by Lawson, a space quite wide enough for the passage of several pollen-grains being left. In the second place, the ovules in many of the cones are actually inverted spatially at pollination, so that only during the subsequent inversion of the cone could the grains fall down the micropyle. Even if the cones all lay horizontally the grains in some of the ovules could only fall a short distance down the micropyle as a result of the oblique lie of the upper part of it; and the subsequent complete inversion of the whole cone, which brings the actual ovules into an erect position, is so slow, and the grains so small, that, moist as they are, it is clearly unlikely that they can slip any distance during the process. During the closure, however, some doe become detached from the inturning rim and slip a little along the micropylar canal. The inverted position of so many ovules combined with the angle, but not the narrowness of the micropylar canal, puts a limit to their further passage. The grains, as is also well-known, ultimately germinate in situ sending their pollen-tubes through the lumen of the micropyle fairly directly to the nucellus. As the pollen-grains of the Douglas-fir are among the largest in the Coniferae, tubes, dissected out at this stage, form excellent material for the examination and demonstration of early growth of the Abietinean pollen-tube, the body-cell being very massive and distinct.
>
> There is, however, a considerable delay in the germination of the grain. The young cones, erect or sub-erect during pollen reception, remain so for perhaps a week, and then slowly begin to bend downwards, becoming markedly inverted, the process being completed in about three weeks from the original pollination. As far as can be ascertained no tube growth begins until a few days after inversion is complete. By this time, the whole micropyle tube has increased considerably, especially in thickness, the kink referred to has become largely obliterated, and, except in the case of grains tucked very completely under the remnants of the inturned rim, the tubes can grow directly downwards, as the ovules now, owing to cone inversion, stand spatially erect. It is tempting, of course, to suggest that some gravity stimulus is here effective, but as no experimental work has yet been carried out any suggestion is out of place. It is common also to find grains which have lodged on the scale, usually those resting in the groove between the ovule and the scale, germinating as they lie; and others which had been lodged so far back on the stigmatic expansion that they were not enclosed by its subsequent incurling, may frequently be found in early growth stages. These grains also seem to show no tube growth until cone inversion is complete; but they

> never develop for any length of time and die in about seven to ten days. During the growth of the functioning tubes within the micropylar canal the cells of the tissue are very succulent and turgid, and there is possibly an exudation of fluid within the micropyle, but the whole question of the growth of the grains, both in the ovule and in vitro, has still to be investigated. (Doyle and O'Leary 1935, pp. 199-200)

In a later paper, Doyle (1945, p. 47) observed that "an inverted ovule, an exudation of fluid from the micropyle, and a two winged (pollen) grain or some variant of it, are taken to be basal in the Pinaceae family." As he also noted, however, there are at least four variations occurring in the family of this basic pollination pattern:

> The *Larix*—*Pseudotsuga* type. This type shows, then, an extreme advance on the *Picea orientalis* type. The stigmatic function of the micropylar area has here become dominant, a large swollen stigma developing, which covers the opening. There is no fluid secretion at the time of pollination, and it is clearly of interest in relation to this that the large pollen grains caught externally on the stigma have completely lost their air-sacs, and with them the capacity to float. These grains have become so specialized from the primitive type that they show no real vestige of the germinal furrow the wall being uniform over practically the entire surface. Inversion and invagination of the stigma brings the grains within the ovular cavity.
>
> *Pseudotsuga* probably shows a slightly more advanced stage than *Larix*. The cones show no geotropic reaction at pollination but stand at any angle between erect and horizontal depending on the directional lie of the actual bud and branch that bears it. The characteristic drooping position of the older cones is one which is gradually assumed long after pollination. (Doyle 1945, p. 49)

Many of Doyle's observations have been confirmed by those of Allen (1943; 1946a,b; 1947a,b).

Microsporangiate strobilus

Gifford and Foster (1988) observed the following:

> The microsporangiate strobili of most conifers are relatively small, commonly measuring only a few centimeters or less in length. . . . [I]n all coniferous species, the microsporangia develop on the lower surface of the sporophylls … in the *Pinaceae* the number is constantly two. The initial cells of the microsporangia of conifers are asserted to lie below the surface or epidermal layer of the microsporophyll. (Gifford and Foster 1988, p. 422)

They noted, however, that in two membranes of the *Pinaceae,* the sporangial initials are superficial, as reported by Allen and Owens (1972), and that, "at maturity, the wall of the microsporangium consists of one layer of cell" (Gifford and Foster 1988, p. 423).

Singh (1978), who described the development of the gymnosperm microsporangium in detail, concurred with Allen (1946b) that the sporogenous cells are differentiated deep within the two sporangia (Singh 1978, p. 9). General observations on microspores (pollen grains) were made by Blackmore and Knox (1990):

> Sporogenesis, whether leading to the formation of isospores, microspores or megaspores, begins with the meiotic division of sporocytes (spore mother cells) in specialized organs termed sporangia and culminates with the germination of mature spores. The ontogenetic programme of the haploid generation following meiosis varies enormously between the major groups of land plants. (Blackmore and Knox 1990, p. 2)

Pennell (1988) noted that a major difference in the development of microspores (pollen in gymnosperms and angiosperms) is that in the former meiosis lasts much longer (almost 2 months in *Pseudotsuga*), whereas in angiosperms two or three days is more common. Further, almost all the extended period in conifers extends in the prophase. Pollen grains, the multicellular microspores of seed plants are equivalent to highly reduced gametophytes consisting ultimately of a single vegetative cell or two sperm cells.

Owens and Molder (1971) gave a detailed discussion of the development of Douglas-fir pollen. They noted (p. 1260) that meiosis begins in October and proceeds through to the early prophase stages of the pachytone. It is arrested until late February when meiosis is generally completed and the microspore region has several hundreds of haploid, thin walled microspores each containing a haploid nucleous and starch. The microspores then develop, until early in April, each pollen grain consists of a wall enclosing five cells, two small lens-shaped prothallial cells, a stalk cell and a large tube cell.

In their detailed discussion of the development of the grain, Owens and Molder (1971) found that, contrary to Christensen (1969a,b), there is definitely a generative cell, as in other conifers; they argued that the normal sequence of pollen grain development in Douglas-fir is the same as in *Pinus.* They found that at pollination, about 50% of the grains are at the five-cell stage, mature pollen grains normally have five cells, and that, when shed, the pollen "is no doubt quite variable in stage of development, being somewhere between the three and five celled stage" (pp. 1263, 1265). The paper confirms previous suggestions by Lawson (1909) and Allen (1943) regarding the development of Douglas-fir pollen grains to the five-cell stage. The structure of the pollen grain wall or sporoderm is similar to that of other conifers (Chamberlain 1935).

Allen and Owens (1972) found that when pollen grains are shed, they consist of five haploid cells and are actually an immature male gametophyte. Two processes are involved in pollen production: microsporogenesis "and the development of the mature multicellular pollen grain or male gametophyte from the one-celled microspore" (Allen and Owens 1972, p. 45). They described Douglas-fir pollen production in detail:

> Meiosis is usually completed in Douglas-fir by the end of February and each microsporangium is filled with several hundred tetrads of haploid microspores borne in a watery fluid. Each single-celled, haploid microspore develops into a pollen grain during March, within a few weeks following meiosis. Each microspore of the tetrad is angular and the four fit compactly together to form a sphere within the microspore mother cell wall. Each microspore contains a single, haploid nucleus and little starch. For the first three weeks following meiosis no cell divisions occur within the microspores. The cell wall of the microspore rapidly thickens equally on all surfaces. Microspores enlarge slightly but remain together within the microspore mother cell wall. Rapid accumulation of starch occurs until the cytoplasm of each microspore is densely packed with large starch grains. . . .
>
> The mature pollen grain of Douglas-fir at the time of pollination usually consists of five cells: two small lens-shaped prothallial cells; a stalk cell; a body cell, and a large tube cell. Mature pollen is 90-100 m in diameter, approximately spheroid, and is usually indented on one side. Unlike some other conifers (Chamberlain 1957), it lacks bladders (wings) and conspicuous pores or furrows (Barner and Christiansen 1962). The thin microspore cell wall thickens during microspore enlargement and pollen grain development. The exine or outer wall layer is thick and its surface is very smooth except for a very faint triradiate ridge indicative of the mutual contact among members of the spore tetrad. The intine, or inner wall layer, is about equal in thickness (approximately 2 m) to the exine. (Allen and Owens 1972, pp. 54-55)

In their conclusion, Allen and Owens (1972) compared Douglas-fir pollen to that of other gymnosperms:

> Pollen grain development and structure are variable within the conifers (Chamberlain 1957; Bierhorst 1971). All conifers are wind pollinated and two-thirds of the genera, including *Pseudotsuga*, have pollen with no wings or bladders. When wings are present, there are usually two, as in *Pinus*, but pollen grains of several genera in the Podocarpaceae have two to six wings. The wall of the pollen grain has two distinct layers – the exine and intine. Usually the exine is thicker, but in Douglas-fir they are equal. Like *Pinus*, Douglas-fir is an example of the prevalent course of pollen grain development in conifers. Prothallial cells are a constant feature of the Pinaceae, while in all the Taxaceae, most of the Taxodiaceae and many of the Cupressaceae, they are lacking. Wherever there are no prothallial cells, pollen development occurs as in the angiosperms and is interpreted as being more advanced. In most of the Podocarpaceae and all of the Araucariaceae, many prothallial cells develop. This results from division of two or three prothallial cells formed from the microspore nucleus. The male gametophyte of different genera can be found at various stages of development when the pollen is shed but, for a given species, this will vary little, if at all. Douglas-fir pollen may be shed at the four-celled stage but is more commonly shed at the five-celled stage. In some species of *Cupressus* and *Juniperus*, the uninucleate microspore is shed and subsequent development occurs within the seed cone before pollen-tube formation. . . .
>
> The pollen cone enlarges during the month, usually March, of pollen-grain development. . . . Elongation of the pollen cone within its bud scales begins at the end of February, at about the same time as pollen development. Bud scales do not enlarge but the pollen cone does, forcing the bud scales apart. Pollen-cone growth results from elongation of the entire cone axis, which causes separation of the microsporophylls and considerable elongation of the stalk at the base of the cone. No apical growth occurs and no new microsporophylls or microsporangia are initiated during this period of pollen-cone growth. Bud burst, resulting in shedding of the pollen, generally occurs early in April. (Allen and Owens 1972, p. 58)

According to Adams (1982), while there are differences between clones of Douglas-fir in pollen production, these differences are not great. He found that the range of weight in pollen grains was from 2323 to 3112 grains per milligram and that the number of microsporophylls varied from 52 to 89 per pollen cone with a mean of 74. Kurman (1990) noted that the great majority of the papers describing the ultrastructure of pollen development are concerned with angiospermous pollen and, in the reports which do report coniferous pollen, there is a wide range in the timing of development of pollen grains with species. She observed that "the earliest stages of pollen wall development occur as soon as the micro spores were separated from one another in the tetrad. During the tetrad period, a microspore surface coat is deposited and the two exine layers (the outer exine and inner intine) are initiated" (Kurman 1990, p. 157). Two decades after the work of Owens and Molder (1971) for Douglas-fir, Blackmore and

Knox (1990) summarized these processes for plants in general as follows:

> Not only are the processes of microsporogenesis generally continuous, but a number of processes usually occur concurrently (Blackmore et al. 1988). Thus as microspore wall deposition proceeds, programs of cytoplasmic and nuclear activity take place within the microspores and sporangial development progresses around them. This complex situation makes it impossible to recognize a single series of discrete developmental stages that will serve as the basis for comparison between all plants. This problem is not confined to the study of microsporogenesis but is confronted by every systematic and evolutionary comparison of ontogeny. A series of major developmental landmarks can be established for the discussion of microsporogenesis but it must be recognized that differences in timing are less significant than differences in the developmental processes involved. Blackmore and Knox (1990, p. 3)

In their lengthy monograph on pollen, Stanley and Linskens (1974) detailed pollen cell-wall formation and composition (primarily for angiosperms), finding that accumulated temperatures are an important determinate for time of pollen dehiscence (in gymnosperms), following the simple parting of the microstrobili sporephylls, and that, generally, pollen size is related to chromosome number and temperature. They noted that Douglas-fir pollen is among the largest of conifers (p. 27). Further, they reported that 27°C temperature accelerated dehiscence of Douglas-fir pollen by 4 weeks over natural conditions (p. 54). In reviewing the role of growth regulators in pollen physiology, they found that growth substances diffusing from pollen may stimulate maturation or receptivity of the egg cell" and that "growth substances can control tube extension in many ways, one of which is facilitating wall growth" (p. 258)

The pollen cone

In their excellent review, Allen and Owens (1972) noted the following, with respect to the microsporangiate strobili of Douglas-fir:

> All conifers bear pollen cones in the form of simple strobili. The pollen cone, a simple strobilus, consists of a single axis bearing a series of usually spirally arranged pollen-forming appendages, the microsporophylls. No structures form in the axils of the microsporophylls so it is not a compound structure. . . . The pollen cone has been referred to as microsporangiate strobilus, staminate strobilus, male strobilus, male flower or male cone. Microsporangiate strobilus is morphologically the most accurate but seldom-used term, and male flower has for years been in common usage. The use of male and female when referring to sporophytic (spore-producing) structures such as cones is incorrect. It is only the gametophytic (gamete-producing) structures, pollen grains and female gametophytes, that can correctly have a particular sex attributed to them. They are the only structures that ultimately produce male and female gametes. The misuse of male and female in this manner, however, seems too well-established to be easily overcome.
>
> Pollen cones vary in shape from globose in many Cupressaceae to the more familiar cylindrical shape in most other conifers. Their appearance is largely determined by the nature of the microsporophylls. Some appear very leaf-like, as in certain species of *Araucaria* and *Picea,* while in most other conifers, including Douglas-fir, they are very reduced, blunt, sac-like structures. In Douglas-fir, the leafy blade of the microsporophyll is much reduced and only the tip is apparent beyond the swollen microsporangia. . . . The microsporangia are commonly borne on the abaxial (lower) surface of the sporophyll. The dominant number of microsporangia is two, being considered throughout the Pinaceae, but many other coniferous species have more. . . . (Allen and Owens 1972, p. 39)

They described the phenology of the Douglas-fir pollen cone as follows:

> Unlike seed cones, the life cycle of the pollen cone is only slightly more than one year in duration. During this time they become conspicuous for a few weeks during pollination in the spring. Pollen-cone buds are initiated by the first of April as undetermined axillary bud primordia — the same as vegetative and seed-cone buds. Generally, by early June, pollen-cone apices can be distinguished from other apices only by histochemical means, but by early July, a distinction can be made by carefully removing the bud scales and observing the apex. . . . At that time microsporophylls begin to be initiated and the apex continues to enlarge. . . . Microsporangia develop on the microsporophylls throughout the summer and all microsporophylls and microsporangia are formed by early fall. . . . Pollen-cone buds can usually be distinguished externally from seed-cone buds by the end of July. Buds appear dormant by early December. Although the earliest stages of meiosis begin early in the fall, mature pollen does not form until spring. Cones enlarge during March and burst through the bud scales about the first of April. . . . Pollination may continue on a tree for about 2 weeks. The pollen cones become completely dry and usually fall from the tree within a few weeks. This cycle is similar to that in most other conifers in that pollen cones are initiated approximately 1 year before pollination. The precise time of pollen-cone initiation and pollination, however, may vary considerably among species. (Allen and Owens 1972, pp. 40)

Pollen-cone development is detailed as follows:

> Early development of the pollen-cone bud involves frequent cell divisions in all planes, which causes a small, dome-like apex to become visible in the leaf axil. . . . Bud scales begin to be initiated within a few days after lateral bud initiation, when the bud primordia are only a few

> cells in height. . . . The apex enlarges more slowly than potential vegetative and seed-cone apices. As a result, the zonation pattern described for pollen-cone apices . . . does not become apparent as early as in the other types of apices. The apex gradually assumes a more conical appearance, while bud scales continue to be initiated along the flanks of the apex, elongate, overarch and enclose the apex. . . . Toward the end of the period of bud-scale initiation, about mid-July, the pollen-cone apex shows a zonation pattern similar to but less distinct than that described for vegetative apices. . . . Bud scales enclosing the pollen cone are fewer in number than in vegetative buds. Whether this has any influence over pollen-cone development or is simply another manifestation of development has not been determined.
>
> The base of the developing bud, where it attaches to the branch from which it originated, broadens during apical enlargement. This results from both the broadening of the pith and the formation of a meristematic region, a receptacular meristem, in the cortex of the developing bud. Similar growth occurs in all lateral buds, but to a lesser extent in pollen-cone buds. as a result, pollen-cone buds attach less firmly to the branch. It is this region of the cone axis that breaks so readily after pollination and this partially explains why Douglas-fir pollen cones seldom remain long on the tree following pollination.
>
> Microsporophyll initiation begins after all bud scales have been initiated, about mid-July, and is complete by early fall. The pollen-cone apex at the onset of microsporophyll initiation is slightly smaller, about 200 μ high and 200 μ wide, than seed-cone or vegetative apices at the same stage of development. . . . The entire bud enlarges during microsporophyll initiation but because microsporophylls are initiated in rapid succession up the flanks of the apex, the apical dome is continually "used up" and gradually diminishes in size. . . . When microsporophyll initiation is complete, the apex is reduced to a flattened dome — 60 μ high and 200 μ wide.
>
> The method of initiation and early stages of development are very similar in microsporophylls and leaves. . . . Microsporophylls are first evident as a group of surface cells that elongate radially, divide periclinally and produce a symmetrical, hemispheric protuberance — the primordium. Continued divisions become organized in a predictable manner and, as in leaves and bracts, an apical form of growth occurs. Microsporophylls, however, do not elongate nor grow upward as much as leaves or bracts but form blunt foliar appendages. This is a result of equal growth on both surfaces and especially abaxial cells dividing in all planes, resulting in increased volume rather than causing elongation. The microsporophyll thus remains short, more massive, and stands more perpendicular to the cone axis than bract or leaf primorida. . . . Due to continued rapid growth, the abaxial side swells and gives rise to two microsporangia, one on either side of the midrib, completely joined along their inner surfaces. . . . The midrib extends beyond the adjacent microsporangial regions and forms a pointed, upturned tip that contains a large air space. . . . The mature microsporophyll then consists of a reduced foliar structure with a single vascular bundle anatomically similar to that in leaves and bracts. On the abaxial surface are two large, medianly fused micrsporangia that give the structure a blunt, pouched appearance. . . .
>
> Microsporangial initiation occurs when the newly formed microsporphyll is only about 75 μ long. Microsporangia originate by the division of several superficial (protodermal) cells on the abaxial surface of the microsporophyll. . . . (Allen and Owens 1972, pp. 40-41)

Christiansen discussed the development of Douglas-fir pollen and the fertilization mechanism in a series of reports (Barner and Christiansen 1962; Christiansen 1969, 1972). He made the following observations in the first report:

> (1) When the pollen is placed in water, it throws off the exine and elongates until it is 550 m. However, this response appears to be a purely mechanical process as the grain does not release male gametes at this time that and may not be viable. Barner and Christensen (1962) note that they have never been able to achieve true germination in vitro and speculate that the pollen requires some special stimulus produced by the nucellus when the egg cells are receptive. (2) They agree with Lawson's observations of the development pollen grains but note that their material limited their ability to thoroughly describe the ontology of pollen. (3) Three to four weeks after pollination, the grains swell, cast off the exine, and elongate. Seven or eight weeks after pollination, pollen grains are transferred to the nucellus top from the stigmatic flap (they do not know how this is achieved, but speculate that a pollination drop exuded from the nucellus may be the mechanism – later work by Allen and Owens 1972, refutes this hypothesis). (4) Non-motile gametes are discharged through a pollen tube into the nucellus. (5) The beginning of the receptive period of the megagametophyte is characterized by the rupture of the bud scales covering the inflorescence. (6) All stigmatic flaps on a megagametophyte do not open simultaneously, but 5-6 days after the receptive period begins, most are open. (7) The basal portion of the bracts is largely rectangular and the ovuliferous scales are about seven times their size at the beginning of the receptive period/at the end of this period, about 12–14 days after the opening of the megagametophyte bud. The end of the receptive period is characterized by the collapse of the stigmatic flaps. (Christiansen 1962)

In a subsequent report, Christiansen (1969) described the development of the pollen grain in detail, confirming his earlier work to the effect that meiosis takes place in March (in Denmark), meiosis during the following 2–3 weeks, and pollination in May. The pollen grains are globular at pollination time and elongate during the next 3-4 weeks. During this period, the embryonal cell moves toward the middle of the pollen grain. At germination time (mid-June), the body cell dissolves and two male cells appear. Christiansen (1969) noted, however, that the structure of the cell and the mitotic divisions of the pollen grain are extremely difficult to analyze:

> The spermatozoid of *P. menziesii* evidently is a unicellular, multiciliated organism with a powerful locomotor apparatus, a neuromotor system and organs for orientation, etc. (Christiansen 1969, p. 98).
>
> The elongated part of the pollen grain is sometimes termed "pollen tube", but in view of the fact, that it does not grow into a style or apex of nucellus, but sprouts a special tube, through which male cells are discharged, it seems doubtful if this term is justified. It may also be questionable whether the special short tube is a pollen tube in the usual sense of the word; it is not clear if it is always a grown tube, or a tube made by chemical means. (Christiansen 1969, p. 101).
>
> It is suggested that at germination the spermatozoids, remaining inside the membrane surrounding the body cell complex, are propelling themselves and the contents of the membrane through a short (pollen) tube into the apex of the nucellus and on to the vicinity of the egg cell. (Christiansen 1969, p. 103).

In the final report, Christiansen (1972) continued his description of the pollen grain and pollination mechanism, primarily of *Larix*, but also of *Pseudotsuga*. He argued that, as far as pollination and pollen grains are concerned, the two species are closer to the *Ginkgoales* than to the *Coniferales*. Christiansen confirmed earlier work to the effect that *Pseudotsuga* does not produce a true pollen tube and that the pollen grain is moved from the stigmatic flap to the nucellus by a drop of liquid. The intine is said to be rather homologous differentiated into an outer layer, which swells readily and an inner very thin layer.

In his discussion of the structure of the male gametophyte in gymnosperms, Sterling (1963) noted that the archegonia of gymnosperms are very similar to those of bryophytes, but that the same cannot be said for the male gametophyte. He also noted that "the development of the male gametophyte of *Pinus* can serve as the type for the family" (p. 188). Sterling proposed a new nomenclature, following which in *Pinus,* the embryonic cell gives rise to the antheridial initial, which in turn gives rise to the generative and tube cells, the former, to the spermatogenous and the sterile cells. Finally, the spermatogenous cell produces the two male gametes.

Ho and Owens (1974) observed the following:

> (1) The size of the microstrobili increase acropetally along the shoot. (2) The average microsporophyll contains 64.5 (33–106) micro sporophylls. While Sziklai reports from 61 to 96 with an average of 77, demonstrating considerable variation. (3) While microsporangia commonly bear two microsporophylls, some were found with one. (4) Average number of pollen grains per microsporangium was 462 (258–724). The number was greatest at the base of the microsrobilis. Each microstrobilus produces approximately 59,600 pollen grains. There are about 3 million pollen grains per gram. (Ho and Owens 1974, p. 561)

Dr. George Allen authored a series of reports (Allen 1946, 1947) discussing in great detail the anatomy and ontology of the mega- and microsporangium and embryology of Douglas-fir and their relationship to published data for other species. The detail is, perhaps, not appropriate for this volume, so we will limit the reference to quoting his summaries and noting his major points. After a lengthy discussion of the origin (upon the shoot) of the microsporangium, he concluded,

> The microsporangium of *Pseudotsuga* is a superficial structure and the generally accepted concept of a hypodermal origin for the sporangium in conifers is open to question. The sporangium cannot be traced to a single cell or group of cells. It has an ontogeny similar to that of the lower tracheophytes, and, unlike the angiosperm microsporangium, is at no time invested by a protoderm or epidermis genetically continuous with that of the shoot. Bower's (1896) concept that a relationship exists between stratification of the shoot apex and stratification of the young sporangium is borne out by this study. (Allen 1946a, p. 555–556)

Allen had argued that "the mature pollen grain is intermediate between *Pinus* and *Abies* with respect to division of the antheridial cell" (1943, p. 660), and he largely agreed with Lawson (1909) regarding the development of the female gametophyte. In a later paper, Allen (1946b) described the ontology of the microsporangium of *Pseudotsuga* in detail, noting that for this species, "the sporangium is not invested by a true sporophyll epidermis as in the case of angiosperms" and that on this basis "the microsporangium of *Pseudotsuga* is closely homologous with the sporangia of the lower eusporangiate tracheophytes. Furthermore, there is a close similarity between the non-stratified structure of the vegetative shoot apex and the non-stratified structure of the microsporangium" (p. 551).

Another paper by Allen (1946a) summarized the proembryology of Douglas-fir:

> An intensive study of several hundred archegonia of *Pseudotsuga* has provided evidence that proembryo formation is essentially similar to that in *Pinus* with the

> exception that the completed proembryo of the former consists of only three tiers.
>
> All four pollen-tube nuclei are discharged into the egg; three of these, the "supernumerary nuclei," may behave in various ways. They may disorganize, they may fragment "amitotically," mitoses may take place often accompanied by cytokinesis, they may "fuse" with one another and finally degenerate. Apparently there is no normal behavior and more than three nuclei are commonly present near the neck region of the egg. . . .
>
> Although no evidence for a pairing of maternal and paternal chromosomes at syngamy was obtained, in the two preparations showing critical stages of the first metaphase, there was an indication of loose pairing of chromosomes of similar size. The suggestion is made that some of the peculiarities of later embryology in certain conifers may be the result of pairing of chromosomes at syngamy.
>
> Simple polyembryony occurs in *Pseudotsuga* and there is no evidence of cleavage. All four embryo lineages from the one zygote may contribute equally to the late embryo, or two lineages may overtop the others and give rise to the apical initials. The latter appears to be the more common program. There is some evidence that occasionally one lineage may overtop the other three and that its terminal cell may become the apical cell of the entire embryo. Certain facts support the concept that simple polyembryony is less specialized than cleavage although the reverse viewpoint seems to be generally accepted. It is concluded that the relation between simple and cleavage polyembryony is as yet obscure.
>
> Embrogeny has been divided into *early* and *late* stages, the artificial separation being suggested by the appearance of root generative initials which set apart the two highly meristematic regions—the stele promeristem, and the massive rib meristem which is continuous with the suspensor system. (Allen 1946a, p. 676)

In yet another paper in this series, Allen (1947b) discussed the development of the apical meristems of Douglas-fir:

> Arber (1941) has speculated upon the nature of the angiosperm root and suggested that the shoot may be likened to a periclinal chimera the inner component of which is of root nature. She pointed out that the root has no power of producing either leaves or sporogenous tissue which usually arise from the more superficial layers of the shoot; that the root may represent a partial shoot with external imcompleteness. Arber suggested that the tendency of the root to divest itself of layers corresponding to the external shoot layers may be significant. Thus, especially in the dicotyledons, the original cortex is cast off more or less completely by cork formation.
>
> In view of the fact that the present investigation has dealt with the origin and development of the root and shoot apices, and that the behavior of the root apex is consistent throughout the various stages examined, it would seem both permissible and desirable to examine Arber's hypothesis in the light of the available evidence. The writer cannot agree with Arber's hypothesis because the limited evidence suggests an entirely different relationship between the root and the shoot in *Pseudotsuga* and perhaps in many other seed plants. The important points considered are listed in order to present clearly a new viewpoint. . . .
>
> (1) The shoot initials are superficial from the beginning; the root initials are always internal. The former-add cells in one direction only; the root initials add cells both inwardly to the stele and outwardly to the mantle. The derivatives of the shoot apical initials may be homologous with the inner derivatives of the root initials, the peripheral mantle of the root apex may have no homologue in the shoot, and the stele of the primary root may be homologous with the entire primary shoot.
>
> (2) The embryonic cortex of the embryo is set off from the embryonic stele by the appearance of the root initials and the development which follows; it is a mantle which completely surrounds the stele of the hypocotyl and radicle and, in the dormant embryo, has no connection with the embryonic shoot apex. Outward derivatives of the initials add to the cortex of the root and the fundamental pattern laid down in embryogeny is maintained indefinitely. The cortex arises in the root in close proximity to the initials. On the other hand, inward derivatives of the shoot apical initials give rise to the shoot cortex; development of the latter is retarded and is possibly related to foliar differentiation or at least to the provascular differentiation of the leaf traces (Louis 1935, Kaplan 1937, Barthelmess 1937, Wetmore 1943). There is no region of the primary root which can be considered homologous with the cortex of the shoot unless the root pericycle is cortical in nature. Cortex and rootcap of the root apices of *Pseudotsuga* appear to be two regions of one and the same mantle, the rootcap being set off from the remainder by the addition of new cell lineages from the initials, which displace a part of the mantle tissue and result in its eventual sloughing.
>
> (3) Lateral appendages originate from the peripheral tissue of the root stele and not from the superficial layers of the root itself; the pericycle is analogous and may be homologous with the generative layers of the shoot apex.
>
> (4) The first formed phellogen often arises in the outer cortex of the shoot (Foster 1942, p. 107) but takes origin in the pericycle region of the root (loc. cit., p. 134). As Arber has pointed out, there is a general tendency in woody plants for the superficial layers of the root to be cast off very early in development. Once secondary growth occurs, the structure of root and shoot is remarkably similar.
>
> (5) Lateral roots originate from the pericycle and a considerable mass of tissue is formed before there is any differentiation of apical initials. Then the latter appear deep within the massive primordium (Reinke 1872, Guttenberg 1941). The apical meristem of the lateral root has an origin almost identical with that of the embryo radicle. It seems likely, therefore, that similar factors operate which destine the endogenous primordium to become a root and not a leaf, and to develop initials which lie deep within the tissue (Bloch 1943, pp. 290-293).
>
> (6) Some similarity exists between the zonal pattern of the stelar apex of the root and the zonal pattern of the entire shoot apex. The peripheral tissue zone and the central

> tissue zone of the shoot apex have their counterparts in the stele of the root. . . . The peripheral tissue zone of the root stelar apex produces procambium, pericycle, and branch roots.
>
> (7) There is no "true epidermis" in the root according to Strasburger (1872, 1887), Kroemer (1903), Rumpf (1904), Plaut (1910), and Guttenberg (1941). The homologue of the shoot epidermis may be represented by the endodermis, or by the outer cells of the root stele which, in *Pseudotsuga*, do not form a definite "layer" because of plastic adjustments and gliding growth.
>
> (8) The suggestion has been made that the complex tissue pattern of the root apex is a result partly of active elongation of the stele and passive expansion of the peripheral mantle (Lundegardh 1914). If the root stele is indeed homologous with the whole shoot, it might be expected that the primary forces of polarity, whatever their nature, would take effect largely in the central core of the root.
>
> (9) According to Goebel (1905, pp. 226-227), in the Pteridophyta and Spermatophyta "there are a number of cases in which, sometimes regularly, sometimes occasionally, roots become transformed into shoots at the apex by throwing off their rootcaps and forming leaves." On page 228, he added, "The transformation of roots into shoots is, in my opinion, only an individual case of the general phenomenon that shoots arise upon roots." Finally, Goebel stated (p. 233) "An actual transformation of a shoot into a root has, as yet, not been shown." Bower (1908, p. 219) observed: "It may be found that roots grow on directly into normal leafy shoots, as in certain Ferns, Aroids, and Orchids, etc.; the converse, however, has not yet been shown to occur." Such data are in accord with the hypothesis here outlined but are hardly explainable on the basis of Arber's hypothesis.
>
> The hypothesis is advanced and may be tested experimentally that *the primary root of Pseudotsuga is homologous with the whole primary shoot, having in addition an outer mantle of tissue which has no counterpart in the shoot*, that the primary root has the same tendencies and capacities as the primary shoot but that these are expressed in different ways, partly because of the outer mantle and the internal position of the root initials, and partly because of the unknown factors which influence the root and which are different from those which affect the shoot. A study of the transition zone of seedlings might provide further clues as to the homologies between the root and the shoot.
>
> Finally, it should be emphasized that toti-potentiality of embryonic surface cells (Schüepp 1926) is exhibited by *Pseudotsuga* in their actual contribution to many and varied tissues of the plant body, including the sporangia (Allen 1946b). This is not surprising in view of the fact that all cells of the primary shoot may be traced ultimately to the divisions of superficial cells at the shoot apex. (Allen 1947b, pp. 209-210)

Allen (1947b) then summarized as follows:

> The apical zonation of the root as laid down during embryogeny changes very little as the plant grows older and is fundamentally the same in embryo, seedling, and older sporophyte. With increasing age there is a tendency for more rapid differential and maturation of rootcap tissues and for a more complete contribution by the column to the peripheral tissue of the rootcap.
>
> The embryo shoot apex is simple and undifferentiated but that of the growing seedling shows a gradual increase in complexity and specialization. The shoot apex of a seedling 3 months old resembles quite closely that of an adult plant. The latter has a zonal pattern very like that of *Ginkgo* or *Sequoia*.
>
> A major theme characteristic of *Pseudotsuga* and probably of other gymnosperms is the toti-potentiality of surface cells. The various appendages of the shoot and of the reproductive strobili originate from the activity of surface cells and all tissues of the shoot and strobilus are traceable back to surface initials. This contrasts with the behavior in many angiosperms which exhibit distinctly stratified structures and organs.
>
> A recent theory as to the nature of the root is discussed and certain evidence presented in favor of an alternative hypothesis. The stele of the primary root is considered homologous with the whole primary shoot; the peripheral tissues of the root, that is, the "cortex" and the rhizodermis, have no counterparts in the shoot. (Allen 1947b, p. 210)

In the penultimate paper of the series Allen (1947a) summarized as follows:

> The *stele promeristem* of the embryo at the beginning of the late stage is delimited at its ends by the free embryo apex and by the root initials, and is surrounded by the poorly defined *cortex promeristem.* The stele and cortex promeristems enlarge mainly by intercalary growth to form the *embryonic stele* and the *embryonic cortex* of the dormant embryo. The rib meristem, lying between the root initials and the suspensor system, adds to the embryonic cortex and to the suspensor but contributes mainly to the rootcap region of the mature embryo. The shoot apex of the embryo arises from the free apex as a result of the activity of surface cells and precedes the cotyleden in appearance. The latter, usually six or seven in number, are initiated by the activity of surface cells in the shoulder of tissue which surrounds the shoot apex. During embryogeny there is at no time a discrete "dermatogen" or protoderm.
>
> The "histogen" concept cannot logically be applied to the root apical meristem. The latter has been divided into three mother-cell zones for descriptive purposes but predetermination is not implied. From each zone is derived in large part respectively the embryonic stele, the embryonic cortex, and the column, the latter giving rise to the bulk of the rootcap. The differentiated dermal system of the primary root is termed the "rhizodermis" because of certain fundamental differences between it and the epidermis of the shoot, hypocotyl, and cotyledons, differences which were recognized by the botanists of the nineteenth century. (Allen 1947a, p. 79)

The development of the ovule in Douglas-fir is detailed in these excerpts from Allen (1963, numbering added):

> 1. Morphological differentiation of ovulate buds can usually be recognized in July ... but ovules do not appear until the following March. Megaspore mother cells, however, are evident in the late fall—usually by October and as early in one instance as August [in Vancouver, British Columbia]. (Allen 1947a, p. 387)
>
> 2. The theoretical implications of the timing of megaspore mother-cell appearance and the development of the ovule are interesting: the site of the mother cell foreshadows ovule differentiation—whether or not it predetermines it. Meiosis occurs soon after the integument has begun to form from the enlarging nucellus. (Allen 1947a, p. 387)
>
> 3. Growth of the developing ovule and its scale produce a shift in the orientation of the mother cell which begins to elongate prior to meiosis. . . . Mother cell and integument begin to face the outer edge and base of the scale, the position assumed at pollination. The adaxial portion of the integument grows much more than the abaxial . . . to produce the completely one-sided ovule tip described by Doyle (1926) and by Doyle and O'Leary (1935). This stigmatic tip is nearly spherical, its surface is well supplied with unicellular hairs, and the crack between the two unequal lips is oriented away from the cone axis and upward in the erect and receptive conelet. (Allen 1947a, p. 391)
>
> 4. By the time pollination takes place, the integument tip consists of two unequal "lips" appressed together to form a closed crack facing upward in the erect strobilus and toward the interscale cavity. The slit between the two lobes is, in effect, the closed mouth of the micropyle. The near spherical tip is well covered with unicellular hairs, presumably sticky since pollen grains adhere to them. When receptive, most of the stigmatus protrudes beyond the edge of the subtending scale. . . . The tips, in total, occupy a substantial part of the space between the scales and form an effective pollen-catching screen. (Allen 1947a, p. 391)
>
> 5. Within a week or so after pollination, the pollen grains have been effectively trapped and largely covered as a result of growth of the integument tip. When pollen is abundant, some or many pollen grains may be excluded and germinate futilely on the surface of the neck along with those that adhered to scales or bracts. . . . The effective pollen grains are contained within a chamber which is in direct connection with the relatively narrow micropylar channel leading to the nucellar chamber. . . . The pollen grains remain attached to the stigmatic hairs and become free only when the young male gametophyte escapes from its exine. (Allen 1947a, p. 392)
>
> 6. In *Pinus* the pollen is picked up by a pollination droplet and floats or is drawn into the micropyle to rest on the surface of the nucellus. In *Pseudotsuga*, the pollen remains in the micropylar chamber, held there initially by the stigmatic hairs; only the pollen tubes eventually reach the nucellus. In contrast, pollen of *Larix* is transferred by fluid to the nucellus after it has been contained temporarily within the integument tip. In this respect, *Larix* represents a genus midway between *Pseudotsuga* and *Pinus* insofar as the pollination mechanism is concerned. (Allen 1947a, p. 393)

Ovulate strobilus

The research papers discussing the female strobilus and the enclosed ovules and female gametophyte are not nearly as voluminous as that concerning pollen. Nonetheless, as Florin (1954) observed, the ovulate strobilus of conifers has been the subject of a number of papers during the past two centuries (see previous discussion on flowering). Much of this work has been concerned with morphological questions. Chamberlain (1935) argued as follows:

> There can be no doubt that in the evolution of the archegonium there has been a gradual reduction in the length of the neck and in the number of neck canal cells, which, phylogenetically, are probably eggs. In the lower Filicales there are two neck canal cells; in the higher homosporous forms, only one neck canal cell with two nuclei; and in the heterosporous genera, even the mitosis has failed to take place, so that there is only one neck canal cell with one nucleus. In the gymnosperms the mitosis which, in the pteridophytes, gives rise to the neck canal and ventral series, is suppressed, so that the ventral canal mitosis takes place in the cell which, in *Pteris,* gives rise to a primary neck canal cell and a central cell. (Chamberlain 1935, p. 330)

While Bierhorst (1971) wrote, "Both mega and micro sporangiate fructifications are clearly strobiloid in the *Pinaceae* unlike members of certain other conifer families in which the cone like nature of the fructification may be obscured by reduction and modification" (p. 433).

According to Maheshwari and Singh (1967), "the female gametophyte of gymnosperms is a large and multicellular structure, and serves the double function of bearing the gametes as well as the nourishment of the developing embryo. This is in contrast to the situation in angiosperms whose female gametophyte is microscopic and generally eight-nucleate with a single functional gamete. Archegonia, although almost invariably borne by the female gametophyte of gymnosperms . . . are unknown in angiosperms" (p. 88). *Welwitschia* and *Gnetum* are the only exceptions (Maheshwari and Singh (1967). As they explained,

> The female gametophytes of the pteridophytes and the gymnosperms are comparable in the following respects: (1) both are multicellular; (2) both serve the dual function of bearing the archegonia and of nourishing the young embryo; and (3) the structure of the archegonium is essentially similar in the two groups; in both cases they have a venter, an egg cell, a ventral canal cell (not of universal occurrence in gymnosperms) and a variable

> number of neck cells. However, in the pteridophytes the gametophyte is usually free-living and green, whereas in the gymnosperms it is parasitic on the sporophyte. Further, there are no neck canal cells in the gymnosperms. These differences appear to be related to the direction of evolution, which has resulted in a diminishing capacity of the gametophyte for independent existence. The similarities, on the other hand, speak strongly for the homologies in the structure of the female gametophyte of the two groups. (Maheshwari and Singh 1967, p. 1967)

More recent investigations have discussed the physiology of the development of the strobilus and its enclosed ovules, archegonia, and female gametophyte. There are a number of reviews in this area, including Konar and Oberoi (1969), Maheshwari and Singh (1966), Allen and Owens (1972; this excellent paper discusses the research of the female cone of Douglas-fir until 1972), Owens and Blake (1986), Pennell (1988), and Sedgeley and Griffen (1989). Much of the material discussed in these papers is, perhaps, too detailed for this book, or is not specific to Douglas-fir. Accordingly, we will attempt to synthesize the major points these papers discuss.

Maheshwari and Singh (1967) found that "the female gametophyte of gymnosperms is a large multicellular structure, and serves the double function of bearing gametes as well as the nourishment of the developing embryo" (p. 88). Konar and Oberoi (1969) noted that the ovuleaf *Pseudotsuga* in unitegmic and crassinucellate and that the number of archegonia vary from 1 to 7 in the micropylar end of the gametophyte. Allen and Owens (1972) made the following observations (numbering added):

> 1. The seed cone is a compound strobilus, in that it consists of an axis or stem bearing a series of usually spinally arranged bracts. (Allen and Owens 1972, p. 61)
>
> 2. Bracts are initiated over a period of 2½ months, from mid-July until the end of September, but the rate of bract initiation is not constant during this time. Half the final number of bracts are initiated during the first month . . . (Allen and Owens 1972, p. 65)
>
> 3. Ovuliferous-scale initiation begins about the first of September, 5 months after the seed cone is initiated and after over half the final number of bracts have been initiated . . . (Allen and Owens 1972, p. 65)
>
> 4. Although, morphologically, ovuliferous scales are modified lateral shoots (Doak 1935), their initiation and early development are different from other types of lateral shoots. The ovuliferous scale is more truly axillary in origin instead of arising from cortical cells above the axillary region as do vegetative lateral shoots. (Allen and Owens 1972, p. 65)
>
> 5. In the latter part of September, megaspore mother cells begin to differentiate and most have differentiated by mid-October. (Allen and Owens 1972, p. 66)
>
> 6. Unlike pollen-cone buds, no evidence of early stages of meiosis in the fall or the diffuse diplotene stage has been observed in the megaspore mother cells. (Allen and Owens 1972, p. 66)
>
> 7. The seed-cone bud shows mitotic activity in both ovuliferous scales and bracts until early November at lower elevations, when they become dormant. (Allen and Owens 1972, p. 66)
>
> 8. Development of the ovule resumes about mid-February and coincides with meiosis of both pollen mother cells and megaspore mother cells. (Allen and Owens 1972, p. 66)
>
> 9. The female gametophyte of Douglas-fir is not fully developed until late in May, just before fertilization and almost two months after pollination. (Allen and Owens 1972, p. 76)
>
> 10. In Douglas-fir, four megaspores appear to result from meiosis of the megaspore mother cell. . . . development of more than one megaspore has not been observed. (Allen and Owens 1972, p. 77)
>
> 11. Most, if not all, of the superficial cells at the apex of the archegonium are potentially archegonial initials even though the number that fully develops is usually four to six. The most common number in Douglas-fir is four . . . (Allen and Owens 1972, pp. 77-80)

According to Owens and Blake (1985, p. 68), "the archegonial jacket, neck cells, ventral canal cell, and egg constitute an archegonium." Owens and Blake (1985) and Allen and Owens (1972) noted that Douglas fir is monoecious and that the reproductive buds and vegetative buds are initiated at the onset of vegetative bud growth in the spring. The buds are found primarily on lateral and lower surfaces of the shoot. The megasporangiate buds are primarily on the distal end of the shoot, the microsporangiate buds, proximal. A given bud initial may follow one of the five pathways, abort, become latent, be vegetative, or either male or female.

The bud differentiation as shown by histochemical tests occurs in early June while the buds may be identified anatomically in July, when shoot growth ceases. The numbers of cones produced in a given year is a function of the differentiation, not initiation of the buds.

Pennell (1988) argued that, "in comparison with the development of the microsporangium the events which take place within the ovules of conifers are poorly explored by modern technique. (Why does only one of the four megaspores resulting from the meiosis of the spore mother cell develop?) And little is known about differentiation within the ovule in conifers" (p. 190).

By contrast, Florin (1954) observed that the ovulate strobilus of conifers has been the subject of research for centuries. Much of this work, however, has been concerned with the anatomy, not the physiology of cones.

In their review of the research concerning the development of female reproductive structures, Sedgley and Griffen (1989) noted the following:

> The area where the nucellus and integument join and are attached to the ovuliferous scale is called the chalaza. A cell within the nucellus enlarges to form the megaspore mother cell. In most gymnosperms the ovule does not develop any further than this prior to pollination.
>
> Meiosis occurs in the megaspore mother cell around the time of pollination (Owens and Blake 1985). Three of the four products of meiosis degenerate, and the remaining megaspore is generally the cell at the chalazal end of the tetrad. This megaspore undergoes numerous nuclear divisions without cell-wall formation resulting in hundreds of free nuclei in a common cytoplasm. (Sedgley and Griffen 1989, p. 31)

Owens (1987) studied the effects of cone inducing treatments, i.e., root pruning and gibberellin 4/7, upon the apices of Douglas fir. He found the following: (1) root pruning did not affect the initiation of apices but retarded their development until early July. At this time, the apices of shoots differentiated into vegetative or cone buds or became latent. It is hypothesized that the slight moisture stress occasioned by root pruning may have been a result of reduced, but statistically, none significant reduction in water. (2) The $GA_{4/7}$ treatment did not affect cone bud initiation or differentiation.

Pollen physiology

Much of the investigations dealing with various aspects of coniferous pollen physiology have been generally reviewed in several publications (Webber and Painter 1996, Sedgley and Griffen 1989, Owens and Blake 1985, Binder et al. 1974, Stanley and Linskens 1974). The following is largely based on discussion in these papers; however, no attempt will be made to reference the papers they discuss, save those dealing specifically with Douglas-fir.

Storage

Generally, pollen stores better at low temperatures and low moisture content. A number of papers have investigated factors affecting pollen vitality after storage because the use of stored pollen is an integral part of supplemental pollination programs. Livingston (1964) reported on pollen viability after 1, 2, and 3 years of storage at several temperatures and moisture contents, and of the effects of freeze drying upon subsequent pollen viability. The results demonstrated that pollen moisture was the more limiting factor affecting pollen viability, with optimum levels below 10%. Freeze drying aided pollen survival if it followed air drying, but proved detrimental to pollen that was not dried. The author hypothesized that the damage at low temperatures or freeze-drying was caused by the formation of ice crystals in pollen with moisture contents greater than 30% (Ching and Slabaugh 1966). In other trials with freeze-drying, Livingston and Ching (1967) found that if freeze-drying were preceded by air drying and cold, a high level of viability might be maintained. In contrast, pollen stored under room temperature and ambient humidity degenerated within a year. Other reports (Charpentier and Bonnet-Masimbert 1983, Webber and Bonnet-Masimbert 1993) demonstrated that rehydrating Douglas-fir pollen stored for a year at about 4% moisture content improved germination, while Mellerowicz and Bonnet-Masimbert (1986) found that storing pollen at 4% moisture content damaged the pollen unless it was rehydrated prior to germination. Dumont-BéBoux et al. (1999) suggested that this response is caused by "imbibition shock when [the stored pollen is] put directly onto culture media" (p. 11). Webber (1995) argued that pollen should be stored at moisture contents between 4% and 8%. Copes (1985, 1987) found that mature pollen at 4% to 7% moisture content stored successfully for 1 and 3 years in liquid nitrogen (-196°C), whereas fertility of pollen stored at 0°C decreased after 2 or 3 years. These results demonstrate that the pollen may be considerably more cold hardy than sporophytic Douglas-fir.

Viability of pollen

The vigor of a pollen lot has been estimated in several ways:

Germination in vitro. This method involves placing pollen on a growth medium under controlled physical conditions and recording the percent of grains that "germinate." Barner and Christiansen (1962), Christiansen (1969), and Ho and Sziklai (1972) argued that Douglas-fir pollen cannot be germinated in vitro. However, Douglas-fir does not form a pollen tube in vitro (Webber 1987), so it is difficult to determine what constitutes "germination." Traditionally, pollen that elongated to two or three times its original diameter was considered to have "germinated" (Ching and Ching 1976, Shirazi and Muir 1998). However, this method is most sensitive to assay conditions (Webber 1995).

Conductance. A technique developed by Ching and Ching (1976) used measurements of the conductance of a solution containing pollen; it was basically a measure of the integrity of pollen membranes. But this method is very sensitive to the hydration state of the pollen (Webber 1995).

Respiration. Binder and Ballantyne (1975) and Webber and Bonnet-Masimbert (1993) found that the respiration of pollen is correlated with other measures of vitality. According to Webber (1995), "respiration is the least sensitive test to assay conditions and consistently gives the best indication of pollen fertility potential in Douglas-fir" (p. 512).

The above tests estimate *in vitro* germination; the results generally are correlated with estimates of sound seed resulting from the use of a pollen lot in standard pollination applications (Binder and Ballantyne 1975, Ching and Ching 1975, Webber 1986, Webber and Bonnet-Masimbert 1993). The latter noted, however, that media effects and pollen hydration effects must be considered before regressions of *in vitro* viability tests against seed set can be made.

Pollen biochemistry. There are few studies of the biochemistry of Douglas-fir pollen. Binder et al. (1974, p. 16) observed that studies of the physiology of pollen date to 1829 and that 8,000 papers were published on the subject in the 50 years prior to 1963; however, neither they nor Stanley and Linskens (1974) referenced Douglas-fir in their reviews. Ching and Ching (1976) presented data detailing the presence of 21 essential amino acids and of sucrose and glucose in Douglas-fir pollen. They further noted that these compounds leached much more readily from dead as opposed to vigorous pollen. Ching and Ching (1976) also found that "the total enzyme activity of ribonuclease, amytase, acid phosphatase and protease per 10 mg pollen was reduced with reducing germinability." The "specific activity of these enzymes, however, increased with decreasing pollen viability, indicating a preferential retention and perhaps activation of these hydrolases over other enzymes" (p. 520).

But the relationship of these changes to reduced viability during storage remains obscure. In an earlier paper, Ching and Ching (1962) reported that 0.76% to 0.89% of the dry weight of Douglas-fir pollen is fatty acids, most of it oleic, palmitoleic and linoleic acids. In another report, Ching and Ching (1959) found that pollen "germinated" best under moderate conditions and that such "germination" is stimulated by gibberellic acid. There was, however, no evidence of pollen tubes presented. In other trials (Ching et al. 1975), the content of adenosine triphosphate (ATP) in dry pollen was found to be correlated with germination rate. Finally, Muren et al. (1979) conducted a metabolic study of Douglas-fir pollen germination and found that starch is the sole food reserve; that it was adequate for four days of growth without exogenous sugars; that the energy charge increased during the first 24 hours of germination; that GA did not affect germination; and that respiratory rates remained constant during the first 48 hours, and then increased fourfold during the last half of the 4-day period.

As noted previously, in all the foregoing papers, pollen was considered to have "germinated" when it elongated to 2-3 times its original diameter, and it was generally believed that it was impossible to stimulate growth of a true pollen tube. Growth of a pollen tube is essential to the germination *in vitro*. However, Dumont-BéBoux and von Aderkas (1997) demonstrated that, if the phase procedures were followed, a tree pollen tube would grow *in vitro*. Their procedure consisted of incubating pollen grains for 7 days on a modified Brewbaker and Kwack (1963) medium until the pollen grains elongated. The pollen was then transferred to fresh media supplemented with flavanols (Kaempferol, quercetin and myricetin). This procedure resulted in pollen tubes analogous to those found *in vitro*. Although Dumont-BéBoux and von Aderkas (1997) found the two-phase technique to be essential to pollen tube formation, an earlier paper from the same laboratory by Fernando et al. (1997) reported successful tube growth without flavanols; and, in a later report, Dumont-BéBoux et al. (1999), agreed. Aft (1961) had shown that dehydroquercetin is endogenous to Douglas-fir. The survey of papers concerned with Douglas-fir pollen has found no references that discussed how the results of the above procedure might be affected by environmental or procedural factors; however, since the first step involved the elongation of pollen grains, it is assumed that the procedure by Dumont-BéBoux and vonArderkas (1997) would have been affected in a manner similar to that discussed for earlier *in vitro* trials.

Other studies discussing the effects of various procedures upon pollen viability (as measured by elongation or staining, rather than pollen tube formation) include (1) Livingston and Stetller (1973), who found that gamma radiation speeded pollen elongations (possibly causing increased metabolism); and (2) Shirazi and Muir (1998, p. 341), who reported that "formaldehyde at target concentrations of 300, 600, 900 and 1200mmol m^{-3} reduced germination of Douglas fir [*Pseudotsuga menziesii* (Mirbel) Franco.] pollen *in vitro*," as measured by pollen grain elongation. Shirazi and Muir (1998, p. 341) also presented evidence that live Douglas-fir pollen, as shown by 2–3-5-triphenyltetrazolium chloride (TTC) staining, had the capacity to significantly reduce levels of formaldehyde in the germination media, "potentially attributable to uptake by pollen or a detoxification mechanism."

Dumont-BéBoux et al. (1999) reviewed studies demonstrating that moisture content may have a significant affect on pollen growth, particularly in the case of dry stored pollen; rapid rehydration may damage membranes. They also noted that the major effect of PGE (prostaglandin E) is as an osmoticum. The mechanism is complex, but this material apparently acts to stabilize membranes. Other materials shown to be important to pollen growth include $Ca(NO_3)_2$ and H_3BO_3 (Brewbaker and Kwack 1963, Fernando et al. 1997). Finally, Copes and Vance (2000) showed that suspension in cool water reduced pollen viability by about 3% per day, and that frost damage to pollen in the spring was not uncommon.

Fertilization

Pollination and fertilization in Douglas-fir represent a series of events that terminate in the fertilization of the egg cell by male gametes released from the pollen tube. Owens and Blake (1985, p. 71) state that "discussions of fertilization may include all stages from pollen structure through gamete fusion (syngamy)." We will limit our discussion to the events including the arrival of pollen on the stigma until the fusion of male and female gametes.

Fertilization in conifers has been the subject of research for about a century. However, as Allen and Owens (1972, p. 101) noted, "most of the information available (refertilization in conifers) is based on very early work, which, though carefully done, did not have the benefit of our modern, refined equipment and techniques."

In an excellent, detailed discussion, Allen and Owens (1972) gave the results of their research and reviewed the previous papers concerned with pollination and fertilization of Douglas-fir. Their presentation is too technical and detailed for this book, but we strongly recommend that readers concerned with all the numerous events inherent in the reproductive physiology of this plant consult this excellent monograph. We will confine our coverage to what appear to be their major points.

1. Bracts are first initiated in mid-summer, and this initiation continues until dormancy in mid-September. Growth resumes in early spring so that the mature bract functions as a funnel to guide pollen grains to the stigmatic tips.
2. The stigmatic tips are unequal and are part of the integument of the ovule; the adaxial part of the integument forms a time covered with fine, sticky hairs. After the pollen grains are trapped on the stigmatic surface, the two stigmatic tips grow together, sealing the pollen grains at the mouth of the micropyle.
3. Development of the female gametophyte is slow at first; archegonia start to form in early May, (there are commonly archegonia in Douglas-fir) and are mature in late May, just before fertilization when the female gametophte is mature.

4. Pollen germination:

> Pollen need not be in the micropyle to germinate but full normal development would probably not occur on the surface of the bract or ovuliferous scale. Pollen germinates within the micropyle about three weeks after it is engulfed by the stigmatic tip of the integument. Pollen grains are not in contact with the nucellus when they germinate; rather, germination occurs when pollen is still adhering to the stigmatic tip just inside the micropylar canal and a considerable distance (several hundred microns) from the nucellus. . . . (Allen and Owens 1972, p. 91)

5. There is no pollination drop in Douglas-fir:

> The absence of a pollination drop means that the pollen grain has to grow (elongate) inward to the tip of the nucellus. . . .
>
> At germination, the pollen grain swells and the exine of the spore wall splits open. There is no apparent pore or line along which the exine splits. The intine remains intact and forms the very plastic wall as the pollen grain elongates. Normally, the distal end of the pollen grain (opposite the prothallial cells) forms the advancing tip of the elongating pollen grain. The proximal end usually remains within the broken exine, or the exine is shed entirely. In either case, no distinct pollen tube forms at this time but the entire pollen grain forms a long tubular structure. . . . The intine is very plastic and capable of considerable extension. This could be attributed to the nature of the intine which, in Douglas-fir, consists of cellulose and pectin . . . and possibly callose, as in other plants. . . . although tests for the latter were not made in Douglas-fir. . . . The thick intine becomes very thin during pollen elongation . . . which continued for several weeks. (Allen and Owens 1972, p. 91)

6. Fertilization:

> The term fertilization as applied to plants may involve more than the fusion of a male gamete with an egg. In gymnosperms, fertilization may involve several other and often unusual events from the time the pollen tube reaches the neck of the archegonium until the first division of the zygote. The fate of all nuclei and cells passing through the pollen tube of Douglas-fir must be considered, since they do not all disappear after fusion of the male gamete and the egg. The misinterpretation of these structures once they are within the egg has led to erroneous conclusions regarding the normal pattern of fertilization and early embryo development. . . .
>
> Fertilization in Douglas-fir normally occurs between June 1 and June 20 at lower elevations in the Pacific Northwest and British Columbia. In any one year there is a variation of several days between ovules on an individual tree. Certain trees tend to be much earlier or later than the average and exhibit this behavior year after year. . . .
>
> The female gametophyte is fully developed at the time of fertilization. . . . (Allen and Owens 1972, p. 97)

Additionally, they noted the following:

> The pollen tube penetrates the nucellar tissue and the neck cells of the archegonium and then releases, through its tip, its entire contents into the egg cell; the tube nucleus, the two male gametes and the stalk cell. . . . Details of this process are difficult to observe because of the disruption of tissues during pollen-tube penetration. The larger male gamete moves rapidly toward the egg nucleus where nuclear fusion occurs. . . . The remaining supernumerary nuclei are often left close to the neck or somewhere between the neck and the fusion nucleus . . . Several fates are possible for the supernumerary nuclei: (1) they may disorganize during a period of several days; (2) they may fragment and thus increase the number of apparent free nuclei in the neck region; (3) one or more of them may divide mitotically and cell walls may form in the next region, . . . or (4) the nuclei may fuse to form larger nuclei which gradually degenerate.
>
> The ventral canal nucleus may fuse with supernumerary nuclei or undergo independent division within its own cell wall. . . . This may appear similar to triple fusion in angiosperms, where the endosperm tissue results. The significance of fusion, division or fragmentation of supernumerary and ventral canal nuclei is not known but their presence can result in the misinterpretation of the normal course of fertilization and early embryo development. . . . It should be recognized that these do not represent either the endosperm of angiosperms or a second embryo.
>
> Fusion of male and female nuclei in Douglas-fir is similar to that described for other members of the Pinaceae. . . . The egg nucleus flattens somewhat on the side nearest the approaching male gamete, as in *Pinus*. The male gamete meets and gradually sinks into the egg nucleus but retains its identity for some time. . . . The membranes around both the male and female nuclei soon disappear, the two groups of chromosomes become evident . . . and spindle fibers become visibly associated with each group of chromosomes. . . . The two spindle figures come together laterally to form a common, multi-polar spindle with its main axis usually perpendicular to the long axis of the egg. The multi-polar spindle figure appears to contract and become bipolar by metaphase of the first division of the zygote. . . . (Allen and Owens 1972, p. 100)

A significant amount of research concerning various aspects of fertilization in Douglas-fir has benefited from improved technology, much of it by scientists working in Professor Owen's laboratory in Victoria, British Columbia.

Owens et al. (1981) reported that seed cones remained most receptive to pollen for at least 4 days, but that 6 days after the conelets became receptive, the stigmatic tips showed less receptivity, and that by 10 days, the entrance to the micropyle was closed. They recommended that the best time for pollination to occur was 4 days after the seed cones were half out of the scales; that the optimum number of pollen grains per stigmatic tip was 11; and that the optimum number of pollen grains within each mycropylar canal was 3. In a later report (Owens and Simpson 1982), it was noted that pollen applied to female cones 3 to 5 days after they became receptive was taken into the micropyle more than pollen applied at later dates. They further noted that the seeds produced after an average of 1.2 pollen grains per micropyle were as viable as those resulting from 3.4 or more grains per mycropyle. Webber and Painter (1996) reviewed substantial data demontrating that first arriving pollen has a distinct advantage in subsequent fertilization. Knox and Singh (1987) observed that for angiosperms, studies of the significance of pollen load on subsequent fertilization have just begun.

Owens and Morris (1988) presented the results of an ultrastructural study designed to investigate the mode of inheritance of mitochondria in Douglas-fir; some of their observations follow:

> Pollination occurred in April and was followed by 6 weeks when pollen elongated within the micropylar canal. A pollen tube then formed, penetrated the nucellus and fertilization occurred by mid-June . . . . Embryos developed over the next 2 months.
>
> The engulfed pollen swelled, ruptured the exine and elongated. The nucellus tip formed a minute secretion stimulating pollen-tube formation. A narrow pollen tube penetrated between the loose outer nucellar cells. Deeper in the nucellus, cells which came in contact with the tip collapsed. Two to four pollen tubes commonly penetrated each nucellus. During pollen-tube growth the tube nucleus remained near the tip of the pollen tube followed by the large body cell and small stalk cell. . . .
>
> Pollen tubes grew to the distal end of the megagametophyte, penetrated the megaspore wall then grew into one of the archegonial chambers found above each group of neck cells. . . . The body cell settled into this pocket and divided to form the two male gametes. (Owens and Morris 1988, pp. 339-340)

They concluded,

> In Douglas-fir and perhaps other conifers, the mechanism by which cpDNA, thus plastid-associated characters, are paternally inherited, is by compartmentalisation of plastids in the body cell and exclusion and destruction of maternal plastids during egg development. Our ultrastructural observations of Douglas-fir and earlier reports for *Pinus* (Camefort 1962), *Larix* (Camefort 1967), Douglas-fir and *Chamaecyparis* (Chesnoy 1973) agree with the pattern of strictly paternal cpDNA inheritance reported by Neale et al. (1986) using restriction fragment length polymorphism (RFLP) techniques on Douglas-fir and other members of the Pinaceae, Cupressaceae and Taxodiaceae. Preliminary studies using RFLP techniques in conifers . . . . indicate that mtDNA inheritance is maternal. The mechanism by which mtDNA, thus mitochondrial characters, are maternally inherited is by the aggregation of mitochondria in the perinuclear zone of the egg. However, there is some paternal contribution resulting from the compartmentalization of paternal organelles which migrate as a cluster with the neocytoplasm. Ours and earlier ultrastructural studies suggest that mitochondria are primarily of maternal origin with some contribution from the cluster of paternal organelles. These observations suggest further studies of mitochondrial inheritance are needed using RFLP techniques. (Owens and Morris 1988, p. 342)

In a subsequent report, Owens and Morris (1990) verified the above. In yet another paper concerned with mechanisms of fertilization, Owens and Morris (1991) made the following observations:

1. The body-cell (of the pollen) did not divide until the pollen tube reached either megaspore membrane or entered the archegonium. At this point it formed the male gametes (p. 1514).
2. No pollen entered more than one archegonium, and only one tube was found on an archegonium (p. 1517).
3. The male nucleus enters the egg cell (p. 1518).
4. The male cluster of organelles does not mingle with maternal cytoplasm (p. 1519).
5. Male gametes are non-mobile (p. 1923).
6. “Future and more complete RFLP and ultrastructural studies will reveal the true variation that exists in the mode of cytoplasmic inheritance in all conifer families” (p. 1926).

Crook and Friedman (1992) suggested that increased embryo competition (as evidenced by simple polyembryony) results in better adapted germinates than supplemental pollination (which results in more pollen tubes per ovule) and the use of clones with higher levels of archegonia per ovule—both of which increase embryo competition—should result in more vigorous germinates.

The detailed study by Takaso and Owens (1995) on the movement of pollen within the cone of Douglas-fir largely confirms earlier work by Owens (1973, 1981). They noted that the curved bract base effectively guides pollen to the ovular apex, but that the pollen does not rest on the surface of either the bract or the ovuliferous scales (1995, p. 437).

In a series of reports, Takaso and Owens (1994, 1996), Takaso et al. (1996), and vonArderkas and Leary (1999) discussed ovular secretions and their effects on pollen tubes. Takaso and Owens (1994, p.

504), reported that the morphology of the outer in line and of the plasma membrane of the pollen appeared to be affected by secretions from the ovule. They noted further that pollen tube formation may be stimulated by material from the ovule. The apical degeneration of the occurred before pollen tube formation (Takaso and Owens 1994, p. 512).

Takaso and Owens (1996) presented detailed evidence for the presence of three major secretions in the mycropyle during the fertilization period. They also noted that archegonia formed 4 weeks prior to fertilization, and that cells in the proximal portion of the nucellus started to degenerate 5 weeks before fertilization and ceased 1 week prior to fertilization (p. 151). The three secretions were

1. an aqueous secretion from the ovular integument, which appears to result from cellular breakdown in the apical part of the nucellus
2. a secretion originating in the female gametophyte, which either directly or indirectly stimulates pollen growth
3. secretion from egg and prothallial cells, which "is liberated to begin and reach to the micropylar canal when egg cells are ready to accept male gametes and induces the formation of pollen tubes" (p. 157).

Takaso et al. (1996, p. 1214) confirmed much of the above. Homogenates of megagametophyte, but not the nucellus or integument, stimulated pollen activity.

Von Aderkas and Leary (1998, p. 356) found that drops of secretion occur in the micropylar canal during the 2 weeks of late central cell and egg cell development, and that the total volume of material produced was 1-4 times the micropylar volume. They speculated that such material (which is post-pollination phenomenom) may play a role in prefertilization events including male secretion (p. 356).

The material thus far discussed concerns in vitro fertilization. Fernando et al. (1997, 1998) reported repeated trials of in vitro fertilization, resulting in the first known in vitro fertilization of a conifer. Finally, Dumont-BéBoux et al. (1998), utilizing the methodology developed in the above studies, showed in vitro fertilization between genera, coculturing *Larix occidentalis*, *Picea sitchensis*, and *Pinus monticola* with megagametophytes dissected from cones of other genera—*Pseudotsuga menziesii, Larix* × *eurolepis* (now *Larix* × *marschlinsii* Coaz) and *Pinus monticola*—and demonstrated no signals between pollen and megagametophytes.

Pollen distribution

According to Stanley and Kirby (1973),

> Determining quantity, shedding time, and dispersal patterns of pollen is important for ecologists, plant breeders, fruit orchard growers, allergists, palynologists, and farmers. Ecologists are interested in the range of viable pollen flight as a contributing factor to interspecific variation; plant breeders are concerned with the distance necessary to isolate seed production plots from contaminating pollens. Orchard managers must consider factors such as probable pollen mix and the number of male trees or pollinator varieties required to pollinate dioecious female trees of compatible varieties. Allergists evaluate air-borne pollens capable of inducing allergies in humans; palynologists analyze the distributions and selective survival patterns of pollens in ground and water sources. (Stanley and Kirby 1973, p. 303)

There have been many papers in which the movement of pollen and the weather factors—such as temperature, wind movement, and rain—that have been shown to affect the movement of anemophilous pollen have been discussed. Generally, it is recognized that the sedimentation factor, which is determined by the shape, density, and volume, strongly affects the distance pollen may move. Schwendemann et al. (2007) developed a computational model based on structural characters of pollen grains to investigate pollen flight in different conifers, quantitatively demonstrating the adaptive significance of sacci for the aerodynamics of wind pollination.

Topography also plays a role: Silen and Copes (1972) reported that contaminating Douglas-fir pollen may move several miles in level areas, but that this effect was greatly enhanced in narrow valleys. In another study, Silen (1962a) found that the greatest amounts of Douglas-fir pollen fell within 17 m of the tree, but then 40% as much pollen was found 610 m from the source, and that a significant amount of pollen moved 2.4 km. Wright (1952) found that nearly all of the Douglas-fir pollen was found within 61 m of the source tree, but noted that the sample size was small and that the tree was short; he estimates that the error could be 2 or 3 times the result.

In a second paper (1953), he estimated the standard deviation of pollen dispersion distance as 18 m; whereas Prat (1995) found the effective distance of pollen dispersion in a Douglas-fir seed orchard to be 20–30 m and depended on the wind. Potter and Rowley (1960) reviewed a large number of studies reporting pollen distances of 160–100 km, and Douglas-fir pollen at 320 km. Similarly, Wodehouse (1935) and Erdtman (1943) noted reports of pollen movement in the hundreds of kilometers. Ebell and Schmidt (1964) reported that pollen in bulk moved over 1.6 km (but noted that the experimental site was particularly windy) and that it could move upslope from 305 m to 1,219 m. Webber and Painter (1996) noted that the "dispersal of pollen from a source tree depends on several factors including pollen size, morphology, sedimentation velocity, wind properties (i.e., turbulent flow and convection currents), and meteorologic conditions (especially temperature and humidity)" (p. 52).

Lanner (1966) argued, however, that reports involving measurements of the lateral movement of pollen by wind do not consider the great movement of pollen by air "shells" and hence do not provide a true measure of pollen movement. He reviewed a number of papers that reported pollen movement in miles, not feet. Unfortunately, there have been no well-designed studies to evaluate his hypothesis since its publication.

Sorensen (1972) presented an approach whereby pollen from female flowers with an albino strain could be used to estimate effective pollen movement in a seed orchard, utilizing a female tree as a receptor. He demonstrated how such a scheme could measure local pollen movement and estimate the bulk-distant movement discussed by Lanner (1966). Adams et al. (1992) expanded Sorensen's approach utilizing genetic characteristics of pollen grains and female trees to estimate effective pollination distances. Although they found that pollen may move 0.5–2.0 km, most of the effective pollen originated from trees within two ranks of the female tree, and that no pattern of pollen movement could be detected at distances of less than 30 m from the mother tree. In contrast to the foregoing, Lowe and Wheeler (1993), working primarily with southern pines, showed that 122-m isolation zones were not sufficient to prevent significant contamination and suggested that "whenever it is possible, orchards should be established outside the species range, in areas where the species is scarce, or areas where the phenological overlap of orchard and surrounding populations is nil" (p. 51).

Both Bramlett (1981) and Squillace and Long (1981) reviewed a number of papers confirming that local pollen distribution patterns are characterized by a rapid diminution of pollen grain numbers with distance from a source tree. Boyer (1966) suggested that reduction in pollen from a source tree occurred primarily through dilution for longleaf pine.

Pollination

Earlier we discussed the development of the microsporangiate strobilis prior to the formation and release of pollen. Pennell (1988) noted that for conifers generally, "once meiosis has been completed a complex series of events occurs within the cytoplasm of the spores, and these are ultimately responsible for the patterning of the sporoderm" (p. 185). Southwork (1988) noted that when pollen grains hydrate, the exine, which is largely sporopollen, separates from the intine, the inner wall of the pollen grain. Fechner (1978) stated that increasing temperatures and reducing humidity generally stimulate the development of coniferous "flowers" and that, in wind-pollinated species, the flowers open and shed pollen during warm, dry periods. Conversely, low temperatures and rainy weather retard these events; Owens (1982) agrees for Douglas-fir.

Douglas-fir is a wind-pollinated species. We discussed the vagaries of pollen movement in another section. Whitehead (1983) discussed the various factors affecting the success of wind pollination as follows:

> Wind pollination is most likely to be successful if certain idealized conditions are met. These include (1) the production of large numbers of pollen grains; (2) pollen grains with appropriate aerodynamic characteristics; (3) flower and inflorescence structure and location on the plant designed to maximize the probability of pollen's entrainment in moving air; (4) stigmatic surfaces structured and positioned to maximize collection efficiency; (5) pollen release timed within both the season and the day to maximize the possibility of pollen capture by receptive conspecifics downwind; (6) relatively close spacing of compatible plants; (7) vegetational structure

> that is relatively open to minimize filtration of pollen by nonstigmatic surfaces; (8) wind velocity within an acceptable range to ensure transport and minimize downwind dispersion; (9) relatively low humidity and a low probability of rainfall; and (10) unambiguous environmental cues to coordinate flowering. (Whitehead 1983, p. 98)

Many of these factors have not been evaluated specifically for Douglas-fir. However, given data such as those reported by Silen (1962a), Whitehead further noted that relatively large pollen grains, like those of Douglas-fir, have a better chance of being captured by stigmatic surfaces than do lighter grains. Whitehead also found that "the frequency of wind pollination increases with elevation in mountainous regions, both in temperate and tropical latitudes" (p. 103). He noted that "anemophily is much more common in temperate and boreal zones, than it is in tropical climates," and that "anemophily is rare in extremely arid environments" (p. 106).

Regal (1982) suggested that the preponderance of animal pollination may be correlated with aridity, possibly because of short climatic uncertainty. Dowding (1987, pp. 421–22) compiled the following advantages and disadvantages of anemophily:

> The advantages of wind pollination are:
>
> 1. Lack of dependence on an animal agent for pollination and seed set. This is of particular advantage in higher latitudes where peak insect populations are reached in late summer, more than halfway through the growing season. Wind-pollinated flowers often open before the growing season starts.
>
> 2. Male gametes by consumption of pollen as food by the vector.
>
> 3. Much lower capital and maintenance expenditure on showy non-photosynthetic petals and on nectaries.
>
> 4. The possibility of very long distance dispersal (Erdtmann 1938, Potter and Rowley 1960), though . . . the probability of successful pollination at distances greater than 10 km from the source is very small indeed.
>
> The disadvantages of wind pollination are:
>
> 1. Dependence on particular weather patterns for successful dispersal and deposition . . . (Andersen 1980).
>
> 2. Wastage by sedimentation and by impaction onto nonreceptive surfaces, through washout by rain, and by premature death caused by UV irradiation and possibly drying.
>
> 3. A very small chance of multiple cross-fertilization by many pollen grains on each stigma, hence ovaries usually have single ovules (Corner 1964).

Dowding also stated that wind pollination is both a "primitive" in gymnosperms and an "advanced" characteristic in angiosperms (p. 421). He justified the latter by noting that wind-pollinated angiosperms have evolved from insect pollinated plants.

Regal (1982) argued that "pollen rain at one point can result from many individuals even hundreds of miles away. But because the pollen rain from a single amenophilous tree delutes rapidly (probably as the inverse of the square of the distance). The individual's probability of fertilization is much reduced by distances of 6-30 m" (p. 505).

In discussing a relatively rare researched phenomenon, Stephenson and Borsin (1983) reported that "plants may compete in terms of male reproductive output either before or after pollination. Prepollination competition seems probable in many plant populations, but an unequivocal demonstration of competition which would involve monitoring male success before and after removal of certain donors, has not been made" (p. 124).

Working with pollen from trees with low and high self fertility, Nakamura and Wheeler (1992) found that male reproductive success is not related to degree of self-fertility; whereas Apsit et al. (1989) demonstrated that differential male success is apparently genetically determined and that there is male-female complementarity in Douglas-fir. Willson and Burley (1983) argued that male reproductive success is a function of the quantity of pollen produced and the number of matings (p. 45).

Webber and Painter (1996) surveyed a number of reports indicating that for Douglas-fir, the major factor affecting pollen success in fertilizing the ovule, without regard to pollen quality, is the order in which the pollen grains arrive at the stigmatic tip; the first arriving grains apparently occupy the most favorable sites and, hence, are most successful (pp. 43–44).

A series of unique reports by Niklas (1984, 1985ab, 1987) and Niklas and Paw U (1982, 1983) discussed the aerodynamics of the pollen grains of a range of conifers and the air flow patterns around ovulate cones of the same species, concluding that the joint effect of these two factors is to ensure that the pollen of a given species will arrive preferentially at the stigmatic type of the same species. The species studied did not include Douglas-fir, but the results were the same for all species observed, so it may be that the same relationship holds for Douglas-fir.

7. Seeds

Denis P. Lavender

A true seed has been described as "A fertilized mature ovule that possesses an embryonic plant, stored food and a protective coat or coats. The embryo is made up of one or more cotyledons, a plumule (embryonic bud), hypocotyl (stem portion), and a radicle (rudimentary root)" (Kozlowski and Gunn 1972, p. 5). The major differences between seeds of angiosperms and that of gymnosperms such as Douglas-fir are that the former are the product of double fertilization within an ovary, whereas gymnosperm seeds result from a single fertilization and are "naked"—not enclosed in an ovary. The vast volume of seed research has focused primarily on the 250,000 species of angiosperms, which are tremendously important to the human food supply. At less than 1,000 species, gymnosperms have received far less research attention.

Research on Douglas-fir seed has often been concerned with either seeds that are dormant or are actively germinating. The classic definition of dormancy is "any case in which a tissue predisposed to elongate does not do so" (Doorenbos 1953, p. 1). Kozlowksi and Gunn (1972, p. 16) noted that seed dormancy is the resting stage of seed embryos between development and germination. The other major physiological state of seeds, germination, also as defined by Koller (1972, p. 14) is "a process which starts with the supply of liquid water to the dry seed and ends when the growth of the seedling starts, most commonly by protrusion of the embryonic radicle through the seed coat." As Bewley and Black (1994) and Bewley (1997) noted, however, these definitions do not provide a physiological basis for dormancy or germination, the mechanisms of which are not fully understood.

Seed Dormancy

An increasing number of research efforts have dealt with dormancy in seeds (the seed is an entire organism, well adapted to experimental manipulation and, as such, a favored subject for a range of experimental botanists, including physiologists, biochemists, geneticists, and ecologists). As a result, the number and complexity of reports dealing with seed dormancy has expanded greatly during the past half century. Vegis (1964, p. 197) suggested that seed dormancy has phases, including true dormancy and conditional dormancy. These ideas were expanded upon, particularly for seeds, and discussed in a comprehensive review by Baskin and Baskin (1998). Although much of the vast volume of references they discussed are concerned with angiospermous seeds, there is information relevant to Douglas-fir or other conifers in pages 27–39. They discussed the six broad classes of seed dormancy suggested by Nikolaeva (1969): physical, morphological, morphophysiological, chemical, mechanical, and physical plus physiological dormancy, and later noted that Douglas-fir has physiological dormancy, which is a function of the embryo (p. 354).

Although the basic physiology of the dormancy of seeds is not known, its several manifestations have resulted in the following terms:

- embryo dormancy—dormancy is seated in the embryo itself
- seed-coat dormancy—dormancy is caused by some feature of covering tissues that limit the access of the embryo to environmental factors essential to germination
- para dormancy—imposed dormancy, caused by an environment unfavorable to growth

- ecto dormancy—innate dormancy, dormancy seated in the seed
- induced secondary dormancy, seeds not originally dormant but forced into dormancy by the environment
- relative, conditional dormancy—growth possible only in a narrow range of environments
- primary dormancy—dispersed from plant in a dormant state
- summer predormancy

Baskin and Baskin (1998, p. 29) noted that "physiological dormancy is caused by a physiological inhibiting mechanism of the embryo that prevents radicle emergence. Nikolaeva (1977) distinguished three levels of physiological dormancy:

Non-deep physiological dormancy is frequent in weeds, vegetables, flowers and is broken by exposure to high, not low temperature.

Intermediate physiological dormancy is found in angiospermous tree seeds and may be broken by extended stratification.[1] GA may substitute for cold.

Deep physiological dormancy, the only treatment which breaks this dormancy is an extended chilling period.

The authors do not specify the type of physiological dormancy Douglas-fir has, but other works suggest that it is intermediate. Bewley and Black (1994 p. 201), Bradbeer (1988 p. 39), and Villiers (1972, p. 224) all agreed that there are at least two general types of seed dormancy: (1) dormancy seated in the embryo (physiological) and (2) dormancy caused in such a manner by the seed coat. However, they were all concerned with angiosperms, so it is difficult to assign a definite dormancy to Douglas-fir on the basis of their classifications. Seeley (1994), also working with angiosperms, noted that "in most cases, we have not adequately determined whether a treatment really breaks endodormancy (embryo dormancy). (The controlling mechanism of which we do not know) or does the treatment promote growth by some other mechanism also unknown" (p. 615).

Ching and Ching (1973), working primarily with gymnosperms, suggested four mechanisms by which the seed coat may cause dormancy: impermeability to water, mechanical resistance and inhibitors in seed coat, and low permeability of seed coats to gases. They also suggested that seed dormancy may result from immaturity of the embryo or endogenous dormancy of the embryo. Villiers (1972) largely agreed with Ching and Ching (1973) that many species have this last type of dormancy, probably including Douglas-fir. These species can be divided into two groups: the positively photoblastic and those whose dormancy is broken by extended exposure to low temperatures, with Douglas-fir and the pines falling into this last group. Although this requirement is true for all Douglas-fir, it apparently varies with ecotypes. For example, Allen (1960a) reported that coastal Douglas-fir required longer periods of stratification than did the interior variety. A rationale for this difference is that the requirement for stratification reflected the fact that dormancy protected the germinates against winter frost damage and that the erratic nature of spring frosts in coastal areas necessitated a longer period of protection. Fowler and Dwight (1964) and Mergen (1963) reported similar findings for eastern white pine (*Pinus strobos*) seed, but Olson and Nienstadt (1959) did not find this to be true for eastern hemlock (*Tsuga canadensis*). Powell (1987a) hypothesized that stratification is the equivalent of a "chilling requirement" for buds and that plants with long chilling requirements have long stratification periods. The length of the chilling period required to stimulate germination has been used as a measure of the depth of seed dormancy. Seely (1997) was critical of this interpretation, arguing that "germination is a measure of growth, not dormancy" (p. 615). Bewley and Black (1994) presented a long, detailed discussion of seed dormancy, and concluded that dormancy represents a block to processes essential to germination, that it may be affected by environmental factors such as light and temperature, and that a genetic component is definitely in its control. But, despite very detailed analyses, they failed to define the physiology basic to seed dormancy. Bewley (1997) noted that, "it's worthwhile pondering why so little progress has been made toward understanding dormancy.

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[1] The term "stratification" originally derives from the historic farming practice of digging a pit in the fall and filling it with alternating layers of sand and seeds. The seeds would then be retrieved after exposure to low temperatures during winter. Stratification will be discussed more fully in a subsequent section.

Undoubtedly, one contributing factor is that we do not know the defining events in germination" (p. 1056).

Wareing (1965) defined dormancy "as the state in which germination of the seed is in some way prevented, even though external conditions are apparently favorable" (p. 103). Bradbeer (1988) noted that dormancy mechanisms may occur in two generalities, embryo coverings and the embryo. In their encyclopedic review of seed germination and dormancy, Baskin and Baskin (1998, p. 27) noted that two general causes of dormancy exist: the environment and the seed itself, and that Douglas-fir has physiological dormancy: "physiological dormancy is caused by a physiologically inhibiting mechanism of the embryo that prevents radicle emergence. Structures that cover the embryo, including endosperm, seed coats, and inhibitors in walls may play a role in preventing germination" (p. 29). They noted that about half of the tree species in moist, warm temperature woodlands have a non-dormant seed (p. 352), and that "in the temperate/arctic vegetation types in which trees occur, the proportion of trees with non-dormant seeds decreases with decreases in precipitation" (p. 562). Corbineau et al. (2002, p. 315) stated that Douglas-fir has an embryo dormancy, but Bianco et al. (1997, p. 117) reported that the dormancy is a function of the seed coat. Bewley and Black (1994) noted "that dormancy confers the advantage that because seeds of a given seed crop are differentially dormant, their germination is temporally diverse, which means that seeds are faced with environments that are differentially favorable to growth and survival of germinants" (pp. 199–200). Although they discussed a wide range of factors associated with seed dormancy, however, their examples are overwhelmingly angiosperms.

Biochemistry and Seed Dormancy Breaking

Seed scientists often believe that the breaking of seed dormancy and germination are separate events. For example, according to Leadem (1987):

> The breaking of dormancy and the initiation of germination are two separate and distinct processes, yet it is apparent from reading the literature that this somewhat obvious fact is often overlooked. Researchers must concentrate on the very earliest stages of germination, i.e., during dormancy release, if they are to learn how PGRs regulate tree seed dormancy. Little attention has been given as well to seed maturation, but in many tree seeds the induction of dormancy takes place during the final stages of seed development and thus the investigation of PGRs levels during this period should be revealing. . . . The relatively few tree seeds in which PGR research has been reported indicate the necessity for increasing the number of species which are selected for study. The lack of comparative work between gymnosperm genera is especially noted. However, this does not eliminate the need for intensive, in-depth studies of individual species. The detailed studies of Acer, Coryllus, and Fraxinus provide examples of the desirability of cooperative work on the same genera. (Leadem 1987, p. 85)

Kermode (1995, p. 274) asked, "What are the important factors or regulatory "cues" that maintain embryos in a developmental state and prevent them from undergoing a premature transition to germinative events?" Kermode then gave a lengthy discussion of the role of abscisic acid (ABA): "Following the termination of dormancy, seed germination is completed, usually under conditions different from those that (originally) triggered the release from dormancy." According to Bewley (1997),

> Much more needs to be learned about the key processes involved in germination and dormancy. Both germinating and dormant seeds must undergo many cellular and metabolic changes in common after imbibition, and yet only the embryos of the former emerge from their surrounding structures. The real block to germination in dormant seeds may occur at the very last stage: radicle cell wall extension. Even so, there may still be many steps that must be completed between the perception of the signal for dormancy breaking and the final emergence of the radicle. In the past decade, most research on the cellular aspects of dormancy has focused on the secondary events, the metabolism of seeds during and after release from dormancy, but to little avail. New approaches that can be or are being tried to an attempt to identify germination- and dormancy-associated genes include T-DNA mutagenesis, differential display, subtractive cDNA hybridization, and the use of nondestructive reporter gene technology. Perhaps it is time to focus also on the primary events: perception and transduction of the dormancy-breaking signal. Finally, we need to determine how radicle extension occurs, the ultimate manifestation of germination. (Bewley 1997, p. 1063)

Taylor et al. (1993, p. 120) determined that cold treatment affected gene expression, but they did not identify the genes. Jarvis et al. (1997) reported that "late embryogenesis abundant protein encoding genes increased in Douglas-fir seed after one week of stratification at 4°C," and that "seeds exhibit an improved dormancy and embryos excised from dormant seeds are capable of germination" (pp. 255, 256). They also found that the proteins encoded by the genes are hydrolytic and may have a role in cold-induced dormancy breakage. Forward et al. (2001) found that metalloproteinase and serine proteinase activity increased during early stratification and that "degradation of major soluble proteins probably occurs through the action of multiple proteinases acting in a specific development cascade" (pp. 626, 628). They noted that during conifer seed development, large amounts of lipids, carbohydrates and storage proteins accumulate (p. 625). Misra (1994) found that lipids made up about 50% and 30% of Douglas-fir megagametophyte and embryo dry weight, respectively, and that proteins made up about 12% and 10% of Douglas-fir megagametophyte and embryo dry weight, respectively (p. 360).

Ching and Ching (1973) suggested that "germination specific MRIVA is essential in breaking dormancy" (p. 3). They also showed that stratification resulted in an increased energy change and adenosine triphosphate (ATP) content of Douglas-fir seed, while Malavasi et al. (1986, p. 35) showed that stratification raised ATP 13x in the embryo and 6x in the gametophyte. Sorensen (1971, pp. 10, 12) noted that seeds with "white mutant" embryos did not require stratification and germinated more rapidly than normal seeds.

Jarvis et al. (1996) reported that late embryogenesis abundant (LEA) protein genes are expressed during dormancy breakage of Douglas-fir seeds and suggested that the proteins may be involved in moisture relations. They stated that their report was the first paper presenting evidence for these genes in gymnosperms and that the level of genes is enhanced with stratification and correlated with depth of dormancy (p. 565). They also noted that Douglas-fir seed dormancy is seated in the structures surrounding the embryo, which does not have endogenous dormancy. In a second paper, Jarvis et al. (1997a) suggested the above and noted that "while de novo synthesis of ABA was important for the expression of dormancy, four weeks of chilling only led to a 36% reduction in endogenous ABA" (p. 457). They also noted that methyl jasmonate stimulated dormant seeds to germinate. In another paper, Jarvis et al. (1997b) again supported the above.

Chatthai and Misra (1998) discussed seed storage protein genes that occur in the late embryo genesis of Douglas-fir seed. Although they diverge from similar proteins in angiosperms, the translational products share a structured homology and indicate a common ancestor for angiosperm and gymnosperm 2S storage protein genes. Misra and coworkers discussed the biochemistry of proteins in the zygotic embryo of Douglas-fir (Owens et al. 1993) during the early germination of Douglas-fir seed (Misra 1993) and during embryo genesis dormancy release and germination (Misra 1994).

Owens et al. (1993) reported the following:

> The ultrastructural, histochemical, and biochemical development of the post-fertilization megagametophyte and the zygotic embryo of Douglas-fir megagametophyte and embryo development were studied from fertilization until seed maturity, a period of about 71 days. The most important morphogenetic events occurred during the first 43 days. During this time lipid bodies and protein bodies increased rapidly in the megagametophyte. Lipids, proteins, and starch became evident in the embryo toward the end of the morphogenetic phase. The subsequent embryo maturation phase showed slight increases in size and number of megagametophyte lipid bodies and protein bodies, as well as an increase in protein body complexity. Later, in the mature seed, lipids and proteins were distributed uniformly in the megagametophyte. Starch was abundant in some regions of the embryo but not abundant in the megagametophyte. In mature seeds soluble sugars made up 2 and 3%, proteins 16 and 11%, and lipids 60 and 45% of the megagametophyte and embryo dry weight. They continue (p. 823) from 14 to 43 days after fertilization "dry weight and soluble sugars did not increase but lipid and especially protein increased in the combined megagametophyte and embryo." Owens et al. (1993, p. 816)

Misra (1993) found that "mobilization of storage proteins is rapid between 4 and 6 days of germination" (p. 77). The preceding has discussed a number of aspects of "dormancy." However, the most appropriate summary is a statement from Taylor et al. (1993): "Despite many years of research on tree seeds the mechanisms underpinning dormancy break at low temperatures are virtually unknown" (p. 120).

In an excellent, detailed review, Misra (1994) discussed several aspects of seed biochemistry, but much of the material is about angiosperms. Some references to Douglas-fir seeds are included, however, especially regarding their seed proteins. She noted the three broad classes of seed proteins: "structural proteins, associated with membranes and ribosomes,

(2) enzymes e.g., those required for mobilization of storage reserves, and (3) storage proteins which are utilized during seed germination and seedling growth, thus supplying the necessary free amino acids and amino nitrogen" (p. 362). With reference to conifers, she included the following:

> In the conifers examined so far (including Douglas-fir) the protein bodies consist of globoid and crystalloid inclusions embedded in a buffer-soluble, amorphous proteinaceous matrix. In mature seeds of Douglas-fir (*Pseudotsuga menziesii*) crystalloid aggregates of highly insoluble polypeptides make up 70-80% of the total storage proteins and are located in protein bodies. Douglas-fir also contains a 55-kDa complex as major storage protein. (Misra 1993, p. 364)

In discussing the LEA proteins, which we previously noted, Misra observed,

> Generally the LEA proteins are hydrophilic and contain a large number of uncharged as well as hydroxylated amino acids arranged in conserved protein domains. They are believed to stabilize other proteins and possibly membranes, thus protecting seed tissue during desication and dormancy or cellular disruption upon subsequent rehydration. Most of the LEA genes can also be induced in other plant parts by exogenous ABA application (rab genes—ABA responsive genes) in the absence of water stress. Other stress treatments, such as wounding, salt, and cold, can elicit expression of these genes. Therefore, the function of these proteins may reflect a common protective role in plant cells when stressed. (Misra 1993, p. 366)

The gene expression studies in conifers have focused mainly on storage proteins and recently on LEA proteins. Misra (1993) noted that "maximum expression of crystalloid protein genes in conifer megagametophytes was achieved during the embryonal mass stage before the formation of the meristogentic regions of the embryo" (p. 368).

Growth regulators

Bradbeer (1988) discussed seed dormancy and germination in some detail, but the material is confined to examples of angiosperms. He suggested that the chilling that causes the breaking of dormancy in hazel is associated with gibberellin synthesis. Taylorson and Hendricks (1977, p. 337) noted that "gibberellins are active stimulants of seed germination." While Taylor and Wareing (1979a) showed that, at first, stratification increased gibberellins in Douglas-fir, but as the dormancy was reduced, gibberellin levels fell; stratification had little effect on cytokinins. Applications of either GA_4 or GA_7 did not stimulate germination of unstratified seeds, possibly because it did not penetrate the seed coats. In addition to the gibberellins, growth regulators commonly include the auxins, cytokinins, and abscisic acid (the latter is frequently classed as a growth inhibitor).

Gibberellins

In her review of the role of plant growth regulation in seeds, Leadem (1987, p. 2) noted the following:

> Gibberellins actively stimulate seed germination of many species of angiosperms and gymnosperms. Over 60 different GAs have been identified, but those most frequently used exogenously in forest tree seeds are GA_3, GA_4, and GA_7. Dormancies with chilling and light requirements are often overcome by GAs, and synergistic interactions between phytochrome and applied GA have been cited. Increases in endogenous GA are usually, although not always, coincident with the termination of dormancy in seeds undergoing dormancy-releasing treatments such as stratification and light. Although germination of seeds is frequently associated with increased GA levels, it is unclear at what stage of the germination process this increase occurs. It can only be stated that exogenous GA relieves dormancy and is an endogenous component of many tree seeds—*a priori* evidence for a significant role for GA at some point in the termination of dormancy, or the initiation of germination. (Leadem 1987, p. 2)

Only two of the references she cited mention Douglas-fir: the preceding paper by Taylor and Wareing (1979a) and Richardson's (1959) contribution, which reported that 5 ppm GA accelerated germination of non-stratified Douglas-fir seed incubated in light at 20°C. Although the review (1987) cited no papers that related any of the remaining growth regulators to Douglas-fir seed dormancy, Leadem (1987) commented that "in depth studies of plant growth regulators (PGR's) in conifer seeds have not been reported and it is not legitimate to extrapolate results with angiospermous seeds to those of gymnosperms" (p. 83), concluding,

> The germination of tree seeds appears to be controlled by a variety of external and internal factors. PGRs figure prominently among these factors, but the range of mechanisms by which PGRs control is mediated may vary considerably—from physical to metabolic. Although significant support exists for PGR involvement in the regulation of angiosperm seed dormancy, the evidence for gymnosperms is still inconclusive. This is because our present understanding of the control of germination is unsatisfactory. Our knowledge of dormancy regulation—by PGRs or other means—in tree seeds is superficial and fragmented. Seed dormancy studies tend to be scattered among a limited number of species, and only rarely is

> any one species investigated extensively. Coordination between various studies is difficult because in some case investigations have been confined to entire seeds, while in others, only to parts of seeds. Adding to the confusion is the extrapolation from studies of exogenous PGRs to experiments in which endogenous PGR levels are correlated with dormancy-breaking events. Because of the uncertainty of PGR permeability, or the extent of their metabolism, it is impossible to deduce from exogenous PGR experiments the effective concentrations of PGRs at their site of action." (Leadem 1987, p. 84)

Abscisic acid (ABA)

Bianco et al. (1997) showed that seed dormancy was correlated with ABA levels; levels of this compound fell as dormancy increased, and seed covering tissues allowed denovo-synthesized ABA to accumulate in the embryo and maintain its dormancy. Corbineau et al. (2002) noted that the content of ABA in the embryo or megagametaphyte tissue fell with dormancy release, further catabolism of ABA by the seed increased, and synthesis decreased with dormancy release. Additionally, "the inhibitor effect of ABA on seed germination was more effective at 15°C, a suboptimal temperature than at 25°C thermal option" (Corbineau et al. 2002, p. 318). According to Bewley and Black (1994), "maturation drying is the normal terminal event in the development of many seeds, after which they pass into a metabolically quiescent state" (p. 122). They suggested that such desiccation results in a decline of ABA content, possibly lowering the embryo's sensitivity to ABA, and that ABA may contribute to desiccation tolerance at the end of the maturation phase. These data are from experiments with angiosperms; we are aware of no similar work that has been done with Douglas-fir.

Corbineau et al. (2002) cited several reports that supported the involvement of ABA in seed dormancy and others that disputed such a relationship. They argued that the "involvement of ABA in the germination of gymnosperms is poorly documented" (p. 314). Corbineau et al. stated that "dormancy in Douglas-fir is seated mainly in the embryo; however, the seed coat and megagametophyte may also play a role" (p. 316). They showed that chilling greatly lowered the level of ABA and increased the ability of the seed to germinate, concluding that the longer the chilling treatment the lower the capacity of ABA biosynthesis and/or the higher is the catabolism of ABA in seed transferred to 15°C (p. 317). They also found that breaking dormancy was associated with decreased sensitivity to ABA.

Germination

Bewley and Black (1994) defined germination as beginning "with water uptake by the seed (imbibition) and end[ing] with the start of elongation by the embryonic axis, usually the radicle" (p. 1). As defined by Leadem (1996), germination is the "resumption of active growth in the embryo, which results in the protrusion of the embryo from the seed and the development of the embryo into an independent plant" (p. 18). Kolotelo (1997) wrote that "seed germination is recognized by the emergence of the radicle from the seed … when the cotyledons emerge, germination is termed episeal and this is characteristic of the conifers. Much of the research concerned with Douglas-fir seeds has investigated internal and external changes associated with germination" (p. 25). Koller (1972) wrote that the germinating seed has few requirements that must be satisfied by the environment:

> This leaves the immediate post-germinative growth activity with virtually few and simple requirements from the environment. One of these is an adequate moisture supply, yet which would not interfere with the gaseous exchange which is essential for aerobic respiration and adequate supply of metabolic energy. Another such requirement is for "normal" temperature, i.e., within the range which is suitable for normal growth of the more mature seedling. (Koller 1972, p. 3)

In contrast, studies of the germination of coniferous seeds have been dominated by an as yet unsuccessful attempt to generate a parameter that will estimate the capacity of a given seed lot to produce numbers of vigorous seedlings. Examples of these efforts include the work of Campbell and Sorensen (1979), and Thomson and El-Kassaby (1993).

Ching (1973a, p. 76) discussed seeds in general (her work has included angiosperm seeds and seeds of Northwest conifers, including Douglas-fir):

> The germination process in turn can be divided into three distinct, yet overlaping and interacting, phases: (A) reactivation of preexisting systems, (B) synthesis of enzymes and organelles for catabolism of reserves, and (C) synthesis of new cellular components.
>
> Reactivation of conserved systems from the maturation period in cells of both storage tissue and embryo
>
> At maturity, dry seeds have many conserved but inactivated systems. Some of the systems, such as sol-

> uble enzymes, transfer ribonucleic acids (tRNAs), and mitochondria area, easily reactivated by water at optimum temperature and proper atmospheric conditions. Ribosomes, however, need to be dissociated to subunits or reactivated to become functional in protein synthesis. Long-lived messenger ribonucleic acids (mRNAs) are generally not available as templates in dry seeds until they are freed from protein or exposed during imbibition. The in vivo sequence of activation of these systems can be illustrated in the wheat embryo. The reactivation process often requires an energy supply from the biological fuel, adenosine triphosphate (ATP) which is usually low in dry seeds as shown by lettuce seeds. The ATP content is soon built up during imbibition through glycolysis, fatty acid oxidation, respiration, and synthesis of adenosine diphosphate (ADP). This reactivation phase appears to be accomplished during imbibition or soon after. The major events of this phase probably are:
>
> - First, reactivating conserved systems to start basal cellular metabolism, such as turn-over type maintenance, protein synthesis, glycolysis, fatty acid oxidation, solute and ion transport, cytoplasmic streaming, respiration, and so on;
> - Second, building up ATP content for various synthetic activities after imbibition; and
> - Third, providing enough substrates for respiration and protein synthesis. Sugars and fatty acids are common substrates for respiration. The sugars are conserved and easily produced from starch by the action of pre-existing phosphorylase and b-amylase. The fatty acids, usually pre-existing, are the hydrolytic product of triglyceride by conserved lipases.
>
> This reactivation phase sets the metabolic wheel in motion. The faster the initial speed and the more functional the conserved systems, the greater the germination force.
>
> Synthesis and sustenance of enzymes and organelles for catabolic degradation of reserves
>
> This phase occurs mostly in the storage organs of the seed, usually in response to an instruction (for example, hormone or long-lived mRNA) either pre-existing or coming from the embryo or embryonic axis. The activity or quantity of the protein-synthesizing machinery (ribosomes, mRNA's and tRNA's – polysomes), mitochondria, glyoxysomes, enzymes, coenzymes, cofactors, substrates, and other factors increase during and after imbibition, reach a peak at about 50% exhaustion of reserves, and then decline to complete exhaustion of reserve. (Ching 1973, p. 76)
>
> Synthesis for anabolism in embryonic or embryo axis
>
> The pre-existing substrates and biochemical systems and the rapidly increased respiration during imbibition provide ATP for protein synthesis, which in turn supplies enzymatic, structural, and soluble proteins required for the myriad processes of growth. The radicle then emerges through the seed coverings, using substrates transported from the storage organs. Again, this phase is conditioned by early reactivation processes and catabolic activities in the storage organs and is controlled by environmental conditions. (TM Ching 1973, p. 80)

Imbibition of mature dormant seeds initiates several metabolic processes that result in a transformation of storage products into energy and anabolic substrates for germination and seedling growth. In a series of papers, Te May Ching and colleagues described some of these reactions that occur in Douglas-fir (TM Ching 1959, 1961, 1963a, 1963b, 1965, 1966, 1968; TM Ching and Fang 1963; TM Ching and Schoolcraft 1968). TM Ching (1959) reported that the normal course of germination has four stages:

> The 1st, imbibition, is accomplished in 12 hours with almost a linear increase of respiration and water uptake. The 2nd stage, to 36 hours, is characterized by a constant respiratory rate and R.Q., and a temporary cessation for further water uptake. The 3rd stage prior to emergence consists of a gradual increase of water uptake and respiratory rate, and a rapid rise of R.Q. to approximately 1.15 at the time of radicle emergence (seedling stage A). The 4th stage consists of a further increase of respiratory and water uptake but with a decline of R.Q. in the seedling and the attached partially digested endosperm.
>
> The 1st stage is common to most seeds studied; the uptake of water probably creates the proper intracellular environment or a degree of hydration which is essential for enzyme systems to function, and in the meantime the raised respiration probably supplies the energy requirement for the onset of the germination process.
>
> The 2nd stage has been observed by other workers at the stage prior to seed coat rupture (24). The low diffusion coefficient of an O_2 (15) for a uniform rate of oxidation throughout the tissue, the low concentration of essential substrates and cofactors for enzymatic reactions in catabolic as well as anabolic work, and/or the slow rate of enzymatic activities might be the limiting factors. It may be considered as an antephase of mobilization.
>
> The 3rd stage is the active mobilization of energy source and cellular components preparatory to the later stages of germination that are accompanied by true growth in terms of cell number, cell size, and tissue differentiation.
>
> The 4th stage after radicle emergence symbolizes a remobilization for cotyledon emergence, as evidenced by a lowering of R.Q. and increased respiration and water uptake.
>
> During the above, fatty subtances are oxidized with the production of ATP. (TM Ching 1959, p. 560)

During germination of Douglas-fir seeds, TM Ching (1963a) found that “a marked reduction of saponifiable lipids observed in germinating seed after stratification was accompanied by an increase in sugars and starch. With germination, nitrogen content per individual seed remained constant, while fresh weight increased 3 to 4 fold and dry weight decreased 5% to 15%. Some decrease in oligosaccharides and free fatty acids, and a slight increase in reducing sugars and total extractable lipids was found in stratified seed."

TM Ching (1963b) also reported the following:

> In contrast to angiosperm seeds, little is known regarding the metabolic pattern of formation, quiescence, and germination in gymnosperm seed. . . . The major food reserve in Douglas-fir seed was found to be fats . . . and an increase of carbohydrates accompanying a rapid decrease of glycerides was observed during germination of the seed. (TM Ching 1963b, p. 722)
>
> Total fats decreased rapidly with germination from 36% to 12% of the dry weight, which also decreased from 13.1 mg to 12.1 mg per individual seed. Glycerides were utilized during germination and a diminution of 86% to 59% of the total fats was found. Acetone-insoluble phospholipids increased gradually in the early stages, then rapidly at later stages of germination. They increased from 5% to 25% of total fats, of which fatty acids comprised approximately 30% at any stage of germination. A small reduction from 2.5% to 1.5% of total fats, then an increase of 5% was observed in the fraction of free fatty acids during germination. (TM Ching 1963b, p. 727)

Earlier, Ching (1961) had found that Douglas-fir seeds contain 40% to 45% fatty substances, of these 70% glycerides, 7% acetone precipitable phospholipids, 3% free fatty acids, and 1% nonsaponifiable material. In two papers, she discussed the compositional changes in Douglas-fir seed during germination (TM Ching 1965, 1966), reporting that "lipids, proteins and reserve phosphorus compounds in these gametophyte were utilized for the synthesis of carbohydrates, structural components, and soluble compounds in the seedling"(1966, p. 1313).

In the final paper of the series, Ching noted that the highest activity of lipases "was found to be with the heavy fat bodies." She also found that Douglas-fir seed contained "35% lipids, 32% protein, 29% fibers (seed coat), 1.8% minerals, 1.7% starch and sugars, 0.2% RNA, 0.04% nucleotides and 0.03% DNA.… Acid lipase activity increased sevenfold and neutral lipase, fourfold during germination" (TM Ching1968, p. 482).

Table 7.1 shows the changes found in Douglas-fir cone scales and seed during their development (TM Ching and Fang 1963, p. 551). Cones were collected during the summer from a single tree near Corvallis, Oregon (Table 7.1). They found that at maturity—156 days after pollination—the seed had "12 mg in dry weight, 40% fatty substances, 30% nitrogenous compound, 20% fiber, 4% other carbohydrates including a trace of starch and 4% minerals" (p. 553). Other data demonstrated that "seed absorbed 4 times as much glucose as the scale in early developmental stages, then declined to twofold at the last stage of the experiment. Synthesis of fat and cellular components from labeled glucose was demonstrated, and the rate of fat synthesis in the seed increased with maturity. A preferential utilization of carbon-1 for respiration and carbon-6 for synthesis was indicated by the differential radioactivity in various fractions" (p. 554). We have noted that the germinating seed has few requirements that must be satisfied by the environment; nonetheless, several environmental factors do influence germination, including light, moisture, and temperature.

Light

In the section discussing flowering, many plant responses are governed by "phytochrome," a chemical whose form is affected by the duration and quality of light. The germination of seeds affected by phytochrome (and light) is termed "positively photo blastic." The following reports present evidence for this condition in Douglas-fir seeds.

Johnson and Irgens-Møller (1964) found that "the rate of germination of unstratified seed of *Pseudotsuga menziesii* (Mirb.) Franco was increased

Table 7.1 Change of weight, moisture, and nitrogen content of developing Douglas-fir cone scale and seed.

Days after pollination	Fresh weight (mg)		Dry weight (mg)		H_2O content (%)		N content (% of dry weight)	
	Scale	Seed	Scale	Seed	Scale	Seed	Scale	Seed
75	710.5	25.4	137.6	3.9	80.8	84.6	1.38	3.01
85	662.9	26.8	173.0	5.7	73.9	78.2	0.98	2.99
95	578.4	22.4	174.0	6.6	69.7	70.8	0.86	3.28
105	711.1	25.1	236.8	11.9	66.7	59.4	0.91	4.53

Figures listed are the average of two determinations which deviated less than 10% of the average (Ching and Fang 1963).

significantly by interruption of the dark period with two hours of white light compared with the rate obtained without interruption of the dark period but with the same total amount of light per 24-hour cycle" (p. 200). These results were limited to trials in which the temperature was below 25°C and confirmed earlier studies by Richardson (1959). Johnson and Irgens-Møller also tested the effects of red and far-red light on the germination of Douglas-fir seeds. The data showed that red light stimulated, whereas far-red light inhibited germination at 23°C, but that raising the temperature to 30°C did not eliminate the retarding effect of far-red. These data agree with the findings of Pons (1983), and suggest that where plant competition creates shade and shifts the red/far red in the light to far red, seeds respond to this signal by failing to germinate. The foregoing agrees with early work by Allen (1941c), which indicated that light treatment just before germination was stimulating to unstratified Douglas-fir seed. The stimulating effect of light was greater at higher temperatures, but because neither temperature nor light were controlled, drawing definitive conclusions is difficult. Similarly, workers at the California Forest Experiment Station found that photoperiods (even with intensities less than 100 foot-candles) greatly stimulated the germination rate of unstratified seed, but not of stratified seed (1957, p. 19). Recognizing these effects, the standard germination protocol for seed germination tests include 9 hours daily of fluorescent (red-light rich) light.

Interestingly, an experiment designed to determine whether seed orientation affected germination showed that the greater light transmission of one side of the seed was not responsible for more rapid germination (Sorensen and Campbell 1981). Other reports examined light stimulation of pine and spruce seed (Ackerman and Ferrer 1965, Taylor and Wareing 1979b). Devlin et al. (1995) discussed a range of phytochrome species, describing red-far reversibility as "the classical hallmark of phytochrome action; . . . responses of this type are considered to reflect the so-called low fluence response (LFR) mode of phytochrome action" They continue, "phytochromes are reversibly photochromatic, red/far-red light absorbing lipoproteins" (p. 160). Bewley and Black (1994) noted that "almost all light-requiring seeds have coat-imposed dormancy" (p. 236). Although the Service Testing Manual (Stein 1966) recommended a daily exposure of 8 hours to cool, white fluorescent light (possibly to inhibit moulds), Baskin and Baskin (1998, p. 412-414) noted that Douglas-fir seed germinate equally well in light or dark. Bewley and Black (1994) gave a lengthy discussion of possible phytochrome activity in seeds but, unfortunately, no conifers were mentioned. Li et al. (1994) noted that daily photo periods increased both total germination and germination speed of nonstratified Douglas-fir seed, while only the rate of germination increased for stratified seed. Alosi et al. (1990, 1992) found that, unlike for angiosperms, light is not necessary to promote chlorophyll and other pigments in Douglas-fir seed.

Moisture

Leadem (1988) noted that an adequate moisture supply is necessary for germination; Bewley (1997) argued that "by definition, germination incorporates those events that commence with the uptake of water by the quiescent dry seed and terminate with the elongation of the embryonic axis" (p. 1055). According to Koller and Hadas (1982),

> The first requirement for germination is water for hydrolysis, as a medium for translocation by diffusion, for hydration of enzymes, cell membranes and organelles to their conformation, and finally to provide the driving force for cell expansion that is initiated by germination. . . . Consequently, the amount of water required for germination itself is that which suffices to bring the relevant tissues of the seed to the adequate level of hydration. These are minute amounts of water. (Koller and Hadas 1982, pp. 402-403)

Most research on the role of water in the germination of Douglas-fir seed has been devoted to the moisture level of seeds during the stratification or pregermination phase. Early on, moistening the seed to an optimum level was considered sufficient, but this procedure may allow radicle emergence before the release of dormancy of many seeds in a given seed lot. Such actively elongating seeds cannot be used in projects to produce seedlings. Allen (1967, p. 63) noted that "after extended stratification many of the seeds will germinate near the freezing point and the radicles continue to grow at that temperature (0–2°C)." Allen (1962a) found that moisture at 60% to 70% on a dry-weight basis was adequate for the stratification of Douglas-fir seeds, and that seed stratified with a moisture content (MC) of 70% retained the effects of stratification after a period of drying. Seed stratified at 40% moisture germinated less well after drying. Most complete germination at 15°C occurred after 70% moisture during stratification. The more recent papers are primarily concerned with the moisture level of the seeds and with drying either during or after stratification. Copeland (1976, p. 160) noted that presoaking, followed by drying, has been shown to benefit many agricultural seeds.

Danielson and Tanaka (1978) stratified Douglas-fir seed and then dried it to three moisture levels (no drying, air drying, and oven drying) before storing at different temperatures for 3, 6, and 9 months. Seeds at highest moisture content did not store as well as those at the lowest. The stratification effect was not lost after the 2°C storage. They found that "air drying immediately following stratification (to 37%) is a method which may be used to safely store seeds germinating during extended stratification periods" (Danielson and Tanaka 1978, p. 16). Edwards (1986) reviewed several studies over a range of species (including Douglas-fir) where drying after stratification, followed by cold storage of the dried seed, increased seed germination parameters, particularly germination speed. Edwards believed this latter effect was a result of more synchronous germination in seed lots because the drying step "does not prevent those processes that accompany dormancy removal from occurring" (p. 164), so that the more dormant seed have time to catch up during the storage phase of the procedure, and, when moisture stress is relieved by a free water supply in a favorable germination environment, all seeds that can germinate do so synchronously.

In two papers, Malavasi et al. (1985, 1986) discussed the effects of stratifying Douglas-fir seed for 28 days (fully saturated, 3°C) followed by storage at 3°C at a moisture content of 25%, 35%, or 45% for 1 or 3 months. Stratified seeds were dissected after storage and the effects of moisture treatments measured for the seed coat, embryo, and gametophyte tissue. These latter data showed that drying seeds to 35% moisture content did not affect the moisture content of the embryo (5% of whole seed weight) or of the gametophyte; drying the seeds to MC of 25% reduced the embryo MC from 50% to 32%. They reported the following:

> Three months of storage did not alter moisture distribution within seeds. Stratification reduced the germination percentage of interior-source seeds but hastened germination speed for seeds from both coastal and interior sources. Redrying stratified seeds to 35 and 25 percent moisture content increased seed vigor and seedling length and dry weight remarkably, a response similar to the <<invigorating effect>> reported to improve seed performance for other types of plants. Storing stratified seeds, without redrying them, for 1 or 3 months generally reduced seed vigor, as reflected by germination speed and seedling length and dry weight, yet redried seeds stored no better than nondried. Levels of biochemical compounds studied were strongly correlated with germination speed. Results suggest that it would be advantageous to redry seeds to a range of 25 to 35% moisture content directly before sowing to produce vigorous seedlings or allow expression of stratification benefits. (Malavasi et al. 1985, p. 371)

Malavasi et al. (1986) reported the following:

> Certain biochemical attributes (adenosine phosphates, nucleic acids and total nucleotides) were analyzed in Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] seeds and seedlings from a coastal and an interior seed source in Oregon to explore how seed stratification, redrying and storage interact to produce vigorous seedlings. Seeds were stratified at 45% moisture content (MC) and then redried (to 35 or 25% moisture content) and/or stored (for 1 or 3 months) in a range of treatment combinations. Stratification increased ATP 13-fold in the embryo and 6-fold in the gametophyte; energy charge rose from 0.4 to 0.8, and RNA increased 60 to 80% in the embryo and 150 to 300% in the gametophyte. Redrying stratified seeds to 35 or 25% moisture content increased RNA and DNA greatly in the embryo but not in the gametophyte. Storing redried seeds generally reduced all biochemical attributes. Stratified, redried seeds produced the most vigorous seedlings, though their biochemical attributes showed no constant advantage, possibly due to their rapid metabolism. However, the benefit of stratification and redrying was not preserved in stored seeds of either source. (Malavasi et al. 1986, p. 35)

Responses of the seeds were similar, whether or not the embryos were dried. This similarity suggests that control of seed metabolism is not seated in the embryo.

Jones and Gosling found that stratifying seed at a target MC of about 2% below saturation resulted in the same response as the regular stratified procedure, but that the seeds remained surface dry and did not germinate during the treatment. Paulsen (1996) found that extending the stratification of Douglas-fir seed at MCs of about 30% (fully imbibed MC is about 40%) yielded good germination data. Her data also demonstrated that maintaining moisture at predetermined levels was critical. In his review, Jensen (1996) noted that the critical moisture content for controlled moisture stratification was commonly between 3% and 8% below full hydration (p. 297) and for Douglas-fir, 32% to 36% (p. 302). He also noted that if MC was kept in this range, stratification may be prolonged significantly (p. 299).

Moller et al. (1999) found that prechilling Douglas-fir at 32% MC for 34 weeks at 3°C enhanced germinability and germination speed; subsequent storage at 6.7% MC and 3°C for 6 months did not have a detrimental effect on germination, but raising MC to 8.1% did. These data are interesting, particularly when compared to those of Malavasi et al. (1985), who found that differences in seed moisture were not necessarily reflected by differences in embryo moisture: "comparisons between seeds prechilled at controlled MC before storage and those stratified with the traditional method resulted in better performance of the first ones, both in the laboratory and the nursery."

Data from Gosling et al. (2003) showing differences in individual seed moisture content at target moisture are also interesting in this respect. In their study, Douglas-fir seeds were moist-prechilled at target MC of 10%, 15%, 20%, 25%, 30%, 35%, and 40% for 2, 4, 8, 16, 32, 48, 64, or 120 weeks and then incubated at 15°C (the temperature that most strongly reflected dormancy release). The procedure yielded several relationships: (1) optimal dormancy breakage occurred in Douglas-fir seeds at moisture contents on a fresh-weight basis of between 30% and 35% and, after prechills of durations between 25 and 48 weeks, the MC of most of the combinations tested were between 15% and 30%. (2) The authors made the interesting observation that dormancy breakage of Douglas-fir seed under dry, warm storage occurred only at MC below 20%, but that the maximum effects of stratification occurred at MC >25%. (3) Finally, they noted that prolonged stratification at higher MC (30%-40%) resulted in seed death, possibly because of respiratory diminution of carbohydrate reserves. This diminution may be the reason Douglas-fir seed is viable under natural conditions for only 1 year after seed fall.

A summary of the above studies suggests that, for Douglas-fir seed, a moist prechill where the moisture content of seed is held near to, but below saturation, is most effective in releasing dormancy without premature germination. These and other studies, however, fail to describe the basic mechanisms of dormancy.

Temperature

Laboratory manuals containing protocol for Douglas-fir seed germination recommend temperatures between 20°C and 30°C and a pretreatment (stratification) at 4°C. As noted previously, there is an interaction between light and temperature, which produces varying germination. Danielson and Tanaka (1978) reported that stratified Douglas-fir seed germinated more rapidly at 5°C than at 2°C. Allen (1960a, 1962a,b) reported that the length of the stratification period had a strong effect on seed germination in the subsequent incubation period—the longer stratification permitted germination at a lower incubation temperature. He also noted a strong difference in the temperature requirements for coastal and interior Douglas-fir seed (Allen 1960a, 1962a,b). The coastal seed required higher temperature. Sorensen (1991) reported similar results: seed germinated at an incubation temperature of 15°C required 84 days of stratification for full germination, whereas seed incubated at 25°C required only 21 days of prechill.

According to Gosling (1988), "the effect of temperature on the germination of seeds of many species has been frequently examined. However, a statement by Lang (1965) that 'precise and unequivocal information on the complete germination temperature range of different species is surprisingly rare' is almost as true today as it was 20 years ago" (Gosling 1988, p. 90). His data showed that non-stratified seeds did not germinate at 10°C or 35°C and that the maximum germination increased with temperature between those points. Stratification increased germination between 15°C and 30°C; no stratified seed germinated at 35°C. Koller and Hadas (1982) argued as follows:

> The temperature range within which germinability is maximal is considerably wider than that which is conducive to maximal rates. The optimal temperature is the range within which both parameters are maxi-

> mal. Above this optimum, the progressive decline in germination rate, and eventually also in germinability, probably involve a time-dependent thermal denaturation of proteins and a phase change of the cell membranes. (Koller and Hadas 1982, p. 404)

The effect of low temperatures was reported by Hawkins et al. (2003). They found that freezing dry Douglas-fir seed to −19°C had little effect on seedling germination (p. 1237). Freezing tolerance was much lower for imbibed seed, however, and reached a minimum at the stage of germination when hypocotyls were rapidly elongating. Cold hardiness of seed lots and germination rate were negatively correlated.

Studies have been conducted to define three major effects of temperature upon Douglas-fir seed: (1) effect of temperature; (2) effect of high temperature upon viability of seed; and (3) effect of a range of lower temperatures during storage upon the subsequent viability of the seed. This last effect of temperature will be discussed in the section on seed storage.

Early field observations (British Columbia Forest Service 1940) indicated that the effect of soil temperature on seed germination was far greater than the effect of light. Similarly, Lavender (1958) noted that seed placed on a south-facing slope germinated more rapidly than seed on nearby easterly, westerly, or northerly slopes.

The first published account of a study designed to quantify the temperature necessary for optimum germination is that of Allen (1941c), who suggested 20°C as a standard for germination tests, but presented no data demonstrating the effect of higher or low temperatures upon germination rate in total. Slightly later work by the same author (Allen 1947) demonstrated a greater germination rate and total for seed lots held under a 38°C to 15°C thermoperiod than obtained under thermoperiods of either 27°C to 15°C or 21°C to 12°C. However, the experimental control of the temperatures was rather crude and no mention was made of the duration of any of the temperatures employed, so it is difficult to compare these data with other data in the literature. Later workers (Allen and Bientjes 1954, Holmes and Buszewicz 1958, Johnson and Irgens-Møller 1964, Jensen and Noll 1959) agreed that either about 25°C constant or a daily cycle of 8 hours at 30°C and 16 hours at 20°C produced the most rapid and greatest total germination.

Besides the absolute effect of temperature upon seed germination noted above, several workers have reported an interaction of temperature with other environmental factors or with previous seed history; Allen (1941c), Richardson (1959), and Johnson and Irgens-Møller (1964) all noted a light-temperature interaction at temperatures below 25°C. We further speculate that seeds falling from the cones in the spring may require high temperature to germination, since they were not exposed to natural cold moist conditions on the soil surface.

While Finnis (1950) reported that stratified seed germinated at lower temperatures than did similar unstratified seeds, Allen and Bientjes (1954) noted that the optimum germination temperature of seed stratified for 1 week was higher than that of seed stratified for 6 weeks. The latter is probably an example of Vegis's (1964) theory that as an organ is released from dormancy it is able to resume growth under an increasingly wide range of temperatures. Although the limited data describing the direct effect of environmental factors such as light, moisture, and temperature does permit defining an optimum range for each for seed germination, much more work is required if we are to understand the interaction of environmental factors in stimulating or inhibiting seed growth.

Only three references were found (Willis 1917, Hofmann 1917, Morris 1936) which dealt with the effects of extreme heat upon Douglas-fir seed viability. Willis (1917) discussed a study conducted with relatively crude equipment, but which yielded data generally confirmed by later work. He concluded that the possible damaging effect of temperatures employed in drying cones was a function of the cone moisture. Thus, 49°C for 10 hours greatly reduced the viability of seeds from cones that were green when the drying started, but had little ill effect on similar seeds extracted from cones that were partially dry before the heat was applied. Hofmann's (1917) concern was with the effects of forest fires upon the subsequent germinative capacity of seed in the duff. His laboratory trials demonstrated that at 71°C in dry heat, the seedcoat began to darken and pitch began to exude from the seed. Seed in moist heat did not show the shriveling of endosperm or the marked darkening that seed might if exposed to temperatures as high as 82°C for 10 hours in a dry atmosphere without losing viability; temperatures above 60°C for 10 hours severely reduced the germinative capacity of the seed which was exposed in a very moist atmosphere. Field tests with seeds placed about 2.5 cm under forest floor materials showed that a hot slash fire did not damage the seed; nor were the temperatures of the seeds raised above 49°C.

In contrast to the above, Morris (1936) utilizing more elaborate experimental apparatus, which may have measured the actual seed temperature more accurately, found that temperature as low as 55°C for 3 hours would reduce the viability of seeds with an initial MC of 77% (dry seed) while temperatures of 45°C were damaging to seed with an initial MC of 60% (wet seed). Morris's tests were conducted with seed in closed glass tubes, while Hofmann apparently employed open lots.

Allen (1958a) employed several kiln temperatures, from 40°C to 60°C, to dry preconed cones. He found that kiln temperatures between 40°C and 52°C produced seeds with significantly higher (>90% vs. about 70%) germination capacities, but that the cones dried at 55°C or 60°C yielded seeds that germinated more rapidly than did those from cones dried at the lower temperatures (50% germination = 12 to 25 days for stratified seed). Finnis (1955) employed laboratory conditions to test the effects of 37 days of 10°C, 16°C, and 24°C temperatures upon total germination after a subsequent 24°C for 32 days; his data demonstrated that 10°C limited and 16°C partially limited germination.

The above confirms the hypothesis that one cause of low germination of spring-sown seed during one year was due at least partially to temperatures in June. With projected global warming, soil temperatures may not be low enough to satisfy stratification requirements and would hence impact field germination (Lavender, unpublished data).

Seed Tests

Germination tests

The viability of seeds (frequently noted in this work) is based on the results of one or more germination tests, cutting, or biochemical ("quick") vigor. In 1816, the first standard germination test was developed in Europe. Today, the testing of Douglas-fir and other seeds follows the specifications in publications of regional (Stein 1966) and international seed testing bodies, such as the Association of Official Seed Analysts and the International Seed Testing Association (1985). Reported germination trials with Douglas-fir seed (Toumey and Stevens 1928) were in soil on greenhouse benches. They noted that "blue" Douglas-fir seeds germinated quickly and completely, but that "green" Douglas-fir seeds from California were much slower. Holmes (1951, p. 10) discussed a variety of tests in Europe, many of which were abandoned, and reported a close correlation between germination tests and tetra-zollium tests via biochemical trials for several slowly germinating species. Jensen and Noll (1959) discussed early testing of Douglas-fir at the Oregon Cooperative Seed Laboratory, noting the following examples (see (Tables 7.2, 7.3, 7.4):

> Testing Before 1950
>
> In the search for a method for testing Douglas-fir seed, several factors were considered. The temperature of germination chambers; the need for and the length of prechilling, and the use of presoaking as a treatment before germination. Before 1950, fewer samples of Douglas-fir seed were received for testing than in later years [Table 7.3].
>
> Temperature was checked by using three alternations (20 and 30°C, 10 and 30°C, and 15 and 30°C) and one constant temperature (20°C). In the alternations, the lower temperature was held for 16 hours daily and the higher for 8 hours daily. Fluorescent light of 75 to 100 foot-candles was supplied at the higher temperature. A mechanical counter planted the seeds in closed transparent containers (plastic or glass) on a moist substratum (usually sand, otherwise paper toweling). Two to four replicates were tested under each condition. Average germination results for the 13 lots tested at these temperatures were 68, 70, 56, and 47%, respectively. The constant temperature (20°C) was not satisfactory; all lots except three gave incomplete germination at this temperature. At the alternating temperatures, tests of only three samples had ungerminated seeds remaining which appeared to be sound when dissected at the end of the test period of about 42 days. The first two sets of alternating temperatures gave better results than did the 15-30°C alternating and the 20°C constant temperatures. The Woody-Plants Seed Manual (5)2/ recommends 60-95°F (15.5-35°C) as the most favorable temperature for Douglas-fir seed. (Jensen and Noll 1959, p. 107)

Jensen and Noll (1959) also reported erratic responses to prechilling and a negative effect from presoaking.

They recorded the effects of prechilling by years, for a total of 840 samples (Tables 7.2, 7.3, and 7.4).

> A somewhat similar pattern was shown by the 114 samples of Douglas-fir seed received in 1951-52. Although the biological history of individual samples varied, the trend toward periodic dormancy is interesting. The survey by months showed that response to treatment fell into several classes. The first comprised samples that showed slight response to prechilling. Samples tested in July, November, January, April, and May showed little difference between methods. No sound seeds remained at the end of the tests. The difference between methods did not exceed 8% for any lot. Slightly higher results were obtained by prechilling. For example, in January the average germination was 63.7% with no prechill and 66.9% with prechill.
>
> The second class was characterized by a simple dormancy, as evidenced by a definite response to prechilling and the sound seeds in replicates not prechilled. Most samples received in August, September, October, and March followed this pattern. . . . Prechilling increased germination by 4 to 80%, with an average gain of 38.9%.
>
> The third class was characterized by complex dormancy, as shown by the sound seeds at the end of the test period under both testing methods. This dormancy

Table 7.2 Average percentage of germination without prechilling and with various periods (from Jensen and Noll 1959).

			Prechilling time in weeks at 5°C			
		No prechill	2	3	4	5
Year	Number of samples	Germination (%)				
1941	9	52.6	60.6	—	64.1	61.3
1944	6	65.3	—	67.7	—	—
1945	10	59.8	67.9	—	70.7	—

Table 7.3 Average germination by years using no chilling or prechilling of Douglas-fir seed (from Jensen and Noll 1959).

Year	Number of samples	No chilling (%)	Prechilling	% gain from prechilling
1941-42	10	52.6	60.6	8.0
1943-44	8	65.3	67.7	2.4
1945-46	31	59.8	67.9	8.1
1947-48	6	61.5	57.8	-3.5
1948-49	14	61.5	57.0	-4.5
1949-50	45	67.8	74.1	6.3
1950-51	161	64.7	70.6	5.9
1951-52	114	58.2	70.7	12.5
1952-53	22	74.5	76.6	2.1
1953-54	69	69.9	72.5	2.6
1954-55	237	74.9	77.6	2.7
1955-56	192	76.1	78.5	2.4

Table 7.4 Comparison of germination results by range and difference between no treatment and for 2 weeks of prechill.

		Number of samples						
		Higher, with no prechill (%)			Same	Higher, with prechill (%)		
Year	Total samples	1–7	8–15	16+		1–7	8–15	16+
1949–50	45	6	3	3	—	20	5	8
1950–51	161	33	2	3	3	60	46	14
1951–52	114	21	5	—	2	40	21	25
1952–53	22	6	—	—	1	13	2	—
1953–54	69	9	4	—	—	38	17	1
1954–55	237	46	17	2	16	108	42	6
1955–56	192	36	5	—	14	100	36	1
Totals	840	157	36	8	36	415	169	55

> probably was different from those encountered in other months because neither method gave complete germination. Such samples were received during February and early March. No difference in germination was found between the two methods, but all tests contained sound ungerminated seeds at the end of the testing period. . . . Further study may develop a method that gives the optimum germination of the exceptional sample that shared a type of dormancy that does not respond completely to present methods.
>
> Results of tests during September and October illustrated another problem in testing coniferous tree seed. The total of percent germination plus percent sound seed obtained under unfavorable test conditions generally does not equal the percent germination obtained under more favorable conditions. . . . Without prechilling, the average germination plus sound seed was 57.6% and with prechill was 72.4% for these 16 samples. (Jensen and Noll 1959, p. 108)

Evidently, some seeds decayed that would have germinated under favorable conditions, which argues for testing in the most favorable environment. The results so obtained did not necessarily correspond to the percentage of plants found after field sowings, however; Jensen and Noll (1959) reported that a 2-week prechill period was adequate for dormant seed germination and that no one treatment gave good results for all seed lots. They also recommended that tests should include two, 100-seed samples with no pretreatment and two similar samples given a 2-week prechill.

There have been a number of studies for evaluating the potential of seed to produce viable seedlings, given a favorable environment (Anon 1954; Jensen and Noll 1959; Campbell and Sorensen 1979; Stein 1966, 1967; Ching and Jensen 1959; Thomson and El-Kassaby 1993). Ching and Jensen (1959, p. 52) examined the variation in seed weight, purity, moisture content, and viability of a Douglas-fir seed lot. Their results showed that these seed parameters varied among storage containers and by how many seeds were in a container. They recommended sampling each container for each lot. Gosling and Peace (1990, p. 796) noted that laboratory germination and probably field germination of Douglas-fir seed benefited from a pretreatment of 2 weeks of stratification, and that this condition is sufficiently common to warrant that laboratory germination tests should be limited to seed that has received this pretreatment. They urged revision of ISTA standards.

Thomson and El-Kassaby (1993, p. 125) noted that, for Douglas-fir seed, the probability of a seed germinating on a given day is a better measure of the speed of germination than either the time to 50% germination or the main daily germination of the most vigorous component of a seed lot. This conclusion, however, was based on the performance of a seed given a relatively short (2 wk) stratification period and leaves open the question as to whether it would be the same after longer stratification. The authors did show that a fast-germinating seed lot with low viability could have the same peak value (P.V.), a parameter suggested previously as a similar value combining germination speed and total viability, as a seed lot with slow germination and high viability (p. 130), and hence would be of questionable value for container nurseries. The thinning in containers in nurseries is generally guided by the speed of germination and therefore may result in seedlings with different genetic makeup.

Working with loblolly pine seed (which, like Douglas-fir, can be dormant), Barnett and McLemore (1984, p. 161) found that total laboratory germination was a better estimate of nursery performance than was peak value for all but slowly germinating seed lots. In contrast, Czabator (1962) argued that, "as a rule, nursery germination generally closely approximates the laboratory figure only in the case of rapidly germinating seeds of high quality" (p. 387). He cited data from several workers—as well as his own—showing that germination speed and total germination were superior estimates of nursery performance than was total viability alone (p. 388).

Standard germination test

Stein (1965, p. 22) reviewed the value of the standard viability test, which includes a germination trial and the determination of the percentage of pure seed and seed weight. Laboratory and field germination results correlated well: the points were on or close to the 45° line. Obviously, total germination of Douglas-fir seed in the germination chamber provides only a weak approximation of nursery performance, however. One interesting variant of the standard germination test, and one that may increase the variations in the germination rate, was reported by Sorensen and Campbell (1981). They found that the speed of germination was affected by the side of the seed that was in contact with the germination medium. They reported the following:

> The physical basis for the polymorphism resides in the shape and development of a Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seed. A wingless, mature seed is flattened and ovate, approximately 8 mm x 3 mm x 2mm. The seed coat is differentiated into three layers, of which the outer is continuous with the adaxial surface of the ovuliferous scale. Separation of the seed wing from the scale results from dissolution of the middle lamella beneath the ovule and seed wing. When the seed is separated from the scale, the side previously adhering to the scale is lighter in colour and somewhat flatter than the upper side. Because the seed is somewhat flattened, it tends to rest on a more or less even surface with the scale side up or down. . . . (p. 467)
>
> The evidence for an adaptive basis for the variation pattern comes from the observation that both mean germination rate (day^{-1}) for a provenance and the difference between germination rate scale-side-up and scale-side-down increased with distances from the ocean. In addition, the differences between germination rates scale-side-up and-down were very closely related to mean germination rate for provenance. In other words, provenances whose seeds had the most rapid germination rates also showed the greatest response to orientation, and both germination rate and response to orientation increased with increasing distance from the ocean. Length of frost-free season and mean annual precipitation decreased regularly with increasing distance from the ocean in the area sampled. (Sorensen and Campbell 1981, p. 470)

Cutting test

Perhaps the simplest seed-evaluation procedure is the cutting test: the seed is dissected lengthwise and the contents examined. This technique can determine if the embryo is fully formed; the technique is particularly useful before cone harvest in determining the seed maturity. The embryos should be at least 90% of the length of the embryo cavity and should be examined for the degree of insect damage and to determine whether the megagametophyte tissue is mature (it should be firm and white; Eremko et al. 1989, pp. 25–26). Finally, the seeds are examined several hours after cutting. No shrinkage of the megagametophyte tissue should be present, indicating tissue maturity (which may occur after embryo maturity). This tissue condition is important to maximize seed storability and germinative vigor.

Biochemical quick tests

Because the standard germination test for Douglas-fir requires several weeks to complete, a significant effort has been made to develop "quick tests" or a more rapid scheme of evaluating seed viability.

Hydrogen peroxide

Ching and Parker (1958) reviewed previous trials, and presented their test results of Douglas-fir seed viability with this chemical. In their trials, seeds with the radicle end excised were soaked for 5 days in a 1% solution of hydrogen peroxide (H_2O_2) maintained at daily alternating temperature of 20°C for 16 hours and 30°C for 8 hours. At the end of this time, seeds with radicle elongated 1–8 mm were tallied as viable. The average viability determined by this method was 3.3% higher than that shown by the standard germination test, tetrazolium chloride (2,3,5-triphenyltetrazolium chloride).

Flemion and Poole (1948) and Copeland and McDonald (2001) reviewed work with this chemical. Viable seeds were identified by the reduction of tetrazolium chloride, a colorless chemical, to bright red formazan by the action of dehydrogenase enzymes. Healthy, viable seeds were identified by red staining. This test requires only a few hours, but the technician must be skilled at interpreting the results. Flemion and Poole (1948, p. 252) noted that although there was general agreement between seed viability, as measured by tetrazolium, and that determined by the excised embryo test, the differences that existed were enough to question the accuracy of any single tetrazolium test.

Buszewicz and Holmes (1952) reviewed the literature, particularly the German trials, and their laboratory results, which showed a correlation of 0.931 between 119 trials of tetrazolium chloride and parallel germination tests of Douglas-fir seeds. They found the tetrazolium procedure to be superior to a test, using several different chemicals (p. 142), and concluded that “the regression equations will assist in obtaining a more reliable estimate of seed quality than has been possibly hitherto” (p. 150), providing the tests are conducted by a trained and skilled analyst.

Excised embryo

Flemion (1948) presented data for 21 families and 87 species (but not Douglas-fir) showing a correlation of 0.949 between viability, as measured by excised embryos, and parallel germination tests (p. 235). Flemion (1938, 1941) reported a fair correlation between the results of excised embryo tests and germination tests for Douglas-fir seed. According to Copeland and McDonald (2001, pp. 136–137), this test is particularly useful for woody shrubs or trees whose dormant seeds may require germination tests extending for months. They further noted that although many seed laboratories routinely conduct these trials, one disadvantage is that these tests require very skilled analysts.

Seed-vigor tests

McDonald (1993, p. 93) observed that seed vigor testing began with developing the standard germination tests and reflected seed performance under ideal conditions. Although such testing may not estimate seed performance under adverse field conditions, it has become a routine method for testing field performance capability. No references were made to vigor testing of Douglas-fir seed in Copeland and McDonald (2001), which includes an extensive review of this subject.

In an unpublished manuscript on the collection and handling of Pacific Northwest forest tree seeds, Edwards et al. discussed germination and seed vigor as follows:

> Germination refers to the reactivation of physiological processes that result in the growth of the embryo to form an independent seedling. “Reactivation” is the operative word for almost all PNW species because a majority of the seeds entered the state of greatly-reduced metabolism known as dormancy as they matured, and more so when they were stored. When mature seeds naturally detach from the mother tree in the fall, or are collected by foresters, their moisture level is quite low, an evolutionary step designed to limit immediate germination with winter approaching. Whereas a small proportion of the naturally-falling seeds may germinate if temperatures are favorable, most seeds lie dormant in the forest floor over winter. . . . (p. 53)
>
> All forest tree seeds vary widely in their ability to produce vigorous, healthy seedlings. Whereas germination tests determine seed lot quality as the potential of a sample of individual seeds to develop into independent seedlings under ideal germination conditions, some lots may not do well under sub- or supra-optimal conditions. Seedlots that germinate well, and produce seedlings under a wide range of conditions, are said to be of high vigor. Thus, vigor tests try to predict seed performance under a variety of conditions. No single tests has been developed to quantify the vigor attribute, especially for tree seeds, but the tests that are used are based on other attributes that distinguish more-vigorous and less-vigorous seeds. Vigorous seeds germinate rapidly and compete better for water, light and nutrients over a wide range of environmental conditions, especially temperature. While respiration varies according to the internal moisture level, and the stage of germination, higher respiration may signal impaired physiological activity, i.e. lower vigor. In some vigor tests, seeds are incubated at low temperature (the cold test), or high temperature combined with high humidity (accelerated aging technique), to compare vigor levels. Not only do vigorous seeds germinate better, but they are more resistant to disease organisms. Vigor tests are often used to predict field germination, since field conditions are less certain and controllable than in the laboratory. Comparisons between laboratory tests and field results for the same seedlot continue to bedevil seed users. (Edwards et al., unpublished manuscript, pp. 56-57)

Ching (1973a) discussed seed vigor for all seeds:

> Seed vigor may be defined as a potential for rapid and uniform germination and fast seedling growth under general field conditions. Germination processes can be divided into three distinct, yet overlapping and interacting stages: reactivation of conserved systems from maturation period; synthesis for catabolic activities, mainly in storage organs; and, synthesis for anabolic activities in the embryo. Growth involves three sequential components, namely increase in cell size, cell number and degree of differentiation. While the basic pattern of germination and growth is programmed by the genetic makeup of the species in question, the eventual expression of the pattern, however, often is modified by environmental conditions under which seeds are grown, harvested, processed, stored, treated and planted. Therefore, the status of vigor in a seed lot stems from the interaction of all parameters involved. Some factors assert more stress on seed vigor than others, depending mostly upon the degree and the timing of stresses.
>
> Not all the sequential biochemical events of seed germination and embryo growth are precisely identified yet. We may, however, summarize some experimental data in the literature and from our own laboratory indicative of some specific factors affecting seed vigor.
>
> Of the conserved biochemical systems in seeds, enzymes, proteins, mitochondria, ribosomes and membranes appear to be major sites of aging caused by poor storage conditions. High humidity and temperature in seed storage also reduce substrates for early enzyme activities. Seed maturity seems to affect the functional status of long-lived messenger ribonucleic acids (mRNA) which encode germination events. Over-drying of seeds denatures proteins and inactivates enzymes. Low germination temperature fails to reactivate the pre-existing

> ribosomes and mRNA, thus eliminating polysome formation and protein synthesis. Any reduction, lesion or defect mentioned above will lower seed vigor as any physiological process results from a cooperative effort of component biochemical systems. The weakest link or the lowest substrate, effector, coenzyme or co-factor concentration often limits enzyme activities, germination and growth. (Ching 1973a, p. 73)

Ching (1973a) argued that it "is difficult to define seed vigor to suit everyone. But to a practical agriculturist or a seed technologist, vigorous seeds have the potential to germinate rapidly and uniformly after planting, and the emerging seedlings have the ability to grow vigorously under general, sometimes relatively adverse, field conditions" (p. 76). She concluded, "the common correlation of seed respiration and seed vigor indicates that poor growth must be related to some impairment in mitochondrial activity" (p. 84). In another report, Ching (1973b) noted that "ATP content in imbibed seeds is significantly correlated with seedling size in fatty, starchy and proteinaceous seeds, and it indicates viability in seed lots. ATP content thus appears to be a useful biochemical index of seed vigor" (p. 400). She argued that "the level of ATP in plant tissue appears to be a very sensitive index to environmental and developmental changes" (p. 402). Data describing ATP levels may possibly predict seedling vigor.

Stratification

Stratification treatment, whether in the laboratory or under field conditions, involves exposing moist seeds to temperatures of about 2°C. The net effect of such treatment is to relieve the state of dormancy and prepare the seed for uniform, vigorous germination. A study by Lavender (1958a) demonstrated that field stratification had a significant effect on subsequent seed germination, and it served as a guide to aerial seeding of the Tillamook Burn. A large fire in the Oregon Coast range was seeded after February 1. No germinates were found the following year and the area was subsequently planted. These results were confirmed by Carmichael (1957). Warming trends predicted for the coming decades may result in soil temperatures, particularly at low elevations, that are too warm to properly chill Douglas-fir seed and, hence, result in lower natural regeneration.

Stratification is used in lab tests because it results in more rapid germination than occurs with the use of non-stratified seed; thus, it is normally used in tests of Douglas-fir seed (Lavender 1978a). Although agriculturists have recognized the positive effects of stratification on seed germination since the middle of the 17th century (Evelyn 1664), the last 50 years have seen several papers adding to various aspects of stratification to the pattern of germination in Douglas-fir seeds. Allen and Bientjes (1954) found that the details of the stratification that yielded the highest seed germination varied with seed lot. They recommended 6 weeks at 0° to 2°C, with MC of about 60%. In a series of reports, Allen (1960a, 1962a,b) examined the effects of the variation of factors involved in stratification on the germination parameters of treated seed. In his 1960 report, Allen noted that the rate of germination increased with the length of the stratification period and that incubation temperatures showed less difference in germination with longer stratification. Allen (1962a) reported the following:

> An initial moisture content of 60-70% was confirmed as an effective one for stratifying more and less dormant seed of Douglas fir. Furthermore, the moist seed can be dried, after stratification, at room temperature for 24 hours and stored at 0-2°C in closed containers for extended periods without loss of germinative capacity or decrease in rate of germination. The initially drier seed is sensitive to much further drying particularly the more dormant lots.
>
> For these reasons an initial moisture content of about 70% is recommended. Previous unpublished data have indicated that seed so treated can be partially dried after stratification for 20–150 days and then stored for as long as one year without loss. (Allen 1962a, p. 307)

According to Allen (1962b),

> The results suggest that good quality seed can be dried after stratification, if not needed, and stored at 0-2°C for at least one year with little loss. It can be stratified for 120 days or longer without loss of viability in most cases and then either used, continued in cold storage with gradual drying, or dried down to 10% quickly and re-stored at 0-2°C. Even limited room-temperature storage at 10% moisture is satisfactory for period of a few months. (Allen 1962b, p. 490)

Edwards (1986) reported four main prerequisites for successful chilling:

> First a source of moisture is required to rehydrate seed tissues, which in conifer seeds have usually been dried to moisture contents below 10% for preservation in cold storage. Uptake of water allows essential biochemical changes to begin. Second, temperatures between 1°C and 5°C are required to favor certain biochemical changes and morphological developments, while delaying embryo

> elongation (and sprouting) in individual seeds which have lost their dormancy. Low temperatures also reduce decay caused by microorganisms and prevent damage by respiratory overheating. Third, good aeration is necessary to prevent carbon dioxide accumulation and minimize heat accumulation. Fourth, treatment must be of the correct duration. (Edwards 1986, p. 152)

He reviewed work demonstrating that the germination performance of the seeds of a number of conifers including Douglas-fir may be improved by subjecting them to a period of cold storage with reduced moisture after a "standard stratification period."

A study by El-Kassaby et al. (1992) using seed collected from several trees demonstrated that a stratification period as short as 3 weeks resulted in dramatic differences in the germination parameters of the different seed lots. In a series of studies, Sorensen (1980, 1991, 1996) found that longer stratification periods produced higher germination values, particularly when the incubation temperature after stratification was low. Sorensen noted that seeds stratified for 128 days produced higher germination when the incubation temperature was 15°C, but not 25°C (1980); and that seeds stratified for 84 days germinated better at 15°C than those stratified for 21 or 42 days (1991). Finally, he reported that seed germinated on cool, but not warm, nursery soils (temperatures not given) germinated better after than seed stratified for 14 or 33 days (1996). Sorensen also reviewed data describing stratification trials with a range of conifers, including Douglas-fir, that reported the same results (p. 197).

The previous discussion has focused on the effect of low temperature storage on the physiology of presumably fully inbibed seeds, although Edwards (1986) noted that "little attention has been given to controlling seed moisture levels before, during, or after prechilling" (p. 155). About three decades ago, however, a series of trials were reported that discussed the effects of drying seeds after a period of prechilling or stratification before returning the seeds to storage. The drying was implemented to reduce the undesired sprouting of seeds after lengthy moist prechilling and to provide the time necessary to break the dormancy of all the seeds in a given seed lot and thus result in more uniform post-storage germination. In a lengthy review, Hagery (1978) discussed a range results from hydration/dehydration treatment on subsequent seed germination, and noted that such treatment may allow embryo development, while preventing germination. According to Edwards (1986),

> The traditional view of breaking seed dormancy at full inhibition has been challenged in both conifer and broadleafed species and, while the new procedures (drying back seed after a period of prechill but before storage) present difficulties in application on a practical scale. They offer increased flexibility to the plant producer in terms of timing the initiation of prechilling and in its prolongation to negotiate operational problems caused by climatic conditions, equipment failure, changes in planting schedules, and so on. Some evidence shows that through seed moisture regulation, dormancy can be more thoroughly overcome and higher germination capacities are possible. But the most significant advantage related to increases in germination speed brought about by synchronous germination. . . .
>
> Moisture management in tree seeds may not be a universal solution in all species, but it appears to have a broadly based relevance that has been largely overlooked until the last decade. (Edwards 1986, p. 168)

Gosling (1988) demonstrated that prechilling increased Douglas-fir seed germination at all incubation temperatures between 10°C and 30°C, concluding, that "relative dormancy can be suspected whenever (1) seeds germinate over a narrow range of conditions, and (2) seeds germinate slowly under any onset of conditions," and that "relative dormancy can be confirmed if pretreatment either; (1) widens the range of temperatures over which seeds can germinate; (2) improves the maximum percentage at some, but not all temperatures; and (3) increases the rate of germination" (p. 95).

A later report by Jones and Gosling (1994) showed that maximum germination and germination speed occurred after pre-chilling Douglas-fir seed for 36 weeks at 10°C and MC of 38% (2% below full imbibition). None of the seed extended their radicles, but all seed were apparently primed. Jenson (1996) discussed the theory of prechilling at a controlled moisture content in detail, noting that the procedure allows dormancy release to occur, but eliminates the ability of nondormant seed to germinate. Paulson (1996) found that 2 weeks fully imbibed, followed by 12 weeks of stratification at a controlled MC of about 8% below that of fully imbibed seed, allowed high and rapid germination of seed, particularly at an incubation temperature of 15°C. She also showed that the seed could be dried back to 8% MC and stored without losing germination capacity. According to Muller et al. (1999),

> Two main conclusions can be drawn from seedling emergence tests. First, the benefits of long pretreatment on germination at suboptimal temperature in the laboratory were also found in the nursery when similar, nonoptimal temperatures are likely to prevail. Secondly, prechilled seeds stored at the lowest MC performed better than all the others also in the seedbeds, especially when rehydration before sowing was applied. For the poor performance of traditionally stratified seeds, one can assume that dormancy removal was incomplete because of the shorter chilling duration. On the other hand, in common nursery practice, stratification periods range from 6 to 12 weeks to avoid the risk of premature germination (Jones and Gosling 1994).
>
> The combination of prolonged chilling treatments at controlled moisture content with dry storage of nondormant seeds represents an improvement in Douglas-fir seed technology as it offers several advantages. Extended prechilling allows germination at the low spring soil temperatures in tree nurseries and reduces the risk of failure in the field as germination is rapid and more synchronous, because the variability of dormancy degree within a seedlot is completely overcome. Drying and storage of nondormant seeds offers the possibility to delay the sowing date in case of bad weather; at any time seeds can be withdrawn from storage and sown immediately, since they are ready to germinate. Moreover, stored seeds are surface dry so they flow properly through sowing machines. Results obtained with these Douglas-fir seedlots are encouraging, but further experiments are needed as differences among seedlots might be considerable. (Muller et al. 1999, pp. 176–177)

Sorensen (1998) sought to determine whether "various lengths of dry storage could be confounded with genetic or other treatment effects in comparisons of germination response" (p. 97). The study findings were as follows:

> Storage main effects and interaction with family were significant for storage periods up to 3 to 4 months, and for storage longer than one year if storage temperature was above freezing. With storage at –12°C, the storage effect was small and the maximum effect was a delay in mean germination time at 15°C of 3.6 hours compared to the germination time of fresh seeds. Family main effects were much larger. In general, it appears that any confounding effect of storage on germination rate of Douglas-fir seeds will be small compared to genetic differences and to many treatment effects. Where small storage effects could be important, it is probably best to use either fresh seeds or seeds stored more than 6 months. Long-term storage should be at subfreezing temperatures, probably −10°C to −20°C. (Sorensen 1998, p. 97)

In all of the foregoing reports, seed moisture was reported on a whole-seed basis; no attempt was made to determine the effects of moisture control on individual seed components, such as seed coat, embryo, and megagametophyte. Further, no measurements were made of the effects of seed manipulations upon compounds known to be involved in Douglas-fir seed germination, physiology, or on the vigor of resultant germinates. In a pair of reports, Malavasi et al. (1985, 1986) addressed these deficiencies. The data clearly demonstrated that drying seed to 45% MC did not affect the moisture content of the embryo or gametophyte, whereas drying to 25% did result in lowering the moisture content of all seed parts. But the post-drying behavior of all seeds was very similar, which leaves open the question as to the mode of action of the moisture content of the embryo.

Downie et al. (1993) reported that polyethylene glycol (PEG) priming did not improve the speed of germination of seed of a range of conifers, but an interesting variant on stratification showed that membrane tube invigoration at 30% MC was equivalent to stratification. Again, the mean moisture content of the seeds was critical, but no measurements were made of the MC percentage of seed components. Accordingly, research has shown that seed moisture content is critical to germination, but it does not explain why. To date, the authors have found no work with coniferous seed similar to that reported by Vertucci and Leopold (1987) for angiosperm seeds. Perhaps this approach would clarify moisture effects.

Gosling et al. (2003) reported that both stratification duration and seed moisture content affected the breaking of dormancy of Douglas-fir seeds. Their results showed that stratification periods of 48 weeks at 4°C stimulated germination at all subsequent incubation temperatures from 10°C to 35°C. The optimum MC was 25% to 35%. Interestingly, fully inbibed Douglas-fir seed at 40% MC did not germinate as well as seed at 35%. The exceptionally long stratification period, together with the long chilling requirement (14 weeks) of Douglas-fir buds (McCreary et al. 1990) is in accord with the hypothesis suggested by Sorensen to the effect that the stratification requirements and the chilling requirements of species are correlated.

The foregoing has discussed several aspects of stratification. Although this technique has been used and studied for many years, the nature of the responses it stimulates is not known. As Taylor et al. (1993) summarized,

> Despite many years of research on tree seeds the mechanisms underpinning dormancy-break at low termperatures are virtually unknown. A favored hypothesis has been that growth regulators . . . play a role, either individually or in concert. However other significant physiological changes occur during stratification including increased gluconeogenesis (e.g., LaCroix and Jaswal 1967, Davies and Pinfield 1980) and modifications to respiratory pathways (Pitel et al. 1989, and references therein). Responses to stratification are therefore numerous and complex. Many may be the result of dormancy break rather than causal events. (p. 120).

Cone and Seed Production

In the section discussing the incidence of flowering in Douglas-fir, we noted that there were many factors associated with the differentiation and development of micro- and megasporophylls. Naturally, there can be no cones that were not preceded by female "flowers." However, the reverse is not true: a good crop of flowers does not necessarily result in abundant cones; accordingly, there are still more variables that affect cone production.

Issac and Dimock (1958) summarized the incidence of cone crops as follows:

> Cone crops in natural Douglas-fir stands are neither uniform in character nor regular in occurrence—either among stands or among trees within a stand. Not all trees produce cones, and even during years of good cone production a rather low percentage of individual trees may be heavy cone producers. Similarly, a crop considered good throughout the region may show extensive local variation ranging from bumper crops to failures. Moreover, cone production of both stands and individual trees is affected by a complex of biological factors, the combined effect of which is only partially understood. Therefore, anything but the broadest application of generalized observations may be seriously misleading. . . .
>
> The quantity of Douglas-fir cone crops is quite unpredictable—even at short range. The current flower crop can be used as a rough indication of prospective cone production for the end of the growing season. Likewise, the ratio of pistillate to vegetative buds may be useful to predict cone crops a full year in advance (Allen 1941a). Finnis (1953) found this method somewhat impractical, however, due to the difficulty of obtaining a representative bud count sample—particularly in older stands. If flowers (or reproductive buds) are scarce, then the cone crop must necessarily be light. An abundance of flowers on the other hand is no positive assurance that the crop will be heavy. Many things that may decrease or even destroy the crop can happen between bud setting and cone maturity. (Issac and Dimock 1958, p. 11)

The first report exploring factors affecting cone and seed production of Douglas-fir is that of Willis and Hofmann (1915). These workers discussed the results of a study designed to survey the relationship of the following variables to the production of cones and seeds (p. 142):

1. Altitude, high or low
2. Locality, northern or southern
3. Soil, good or poor
4. Age, young, medium, or old trees
5. Size, small, medium, or large trees
6. Health, good or poor because of conkiness trees
7. Stand, open or dense

They concluded that the "yield of cones per tree is highest with medium aged, rather large trees, which grow in open stands, in warm localities" (p. 146). It should be noted, however, that Willis and Hofmann (1915) recognized that there may be exceptions to the foregoing. Furthermore, although they presented some data, there is no evidence that the experimental design permitted the examination of any factor independent of possible interaction or that any of the differences would be considered "significant" by modern statistical analysis.

Seed size and anatomy

Douglas-fir seed is a medium-sized coniferous seed; the seeds of pines and firs are significantly larger than those of hemlocks and spruces. According to the Forest Service *Woody-Plant Seed Manual*, the average number of Douglas-fir (var. *menziesii*) seeds per pound ranges from 30,000 to 35,000 for California seed sources to 49,000 from British Columbia seed sources (USDA Forest Service 1948). In general, seeds from southerly locations and exposures are heavier than those from northerly sites and slopes. Sziklai (1969) presents data describing cone and seed collections from 1,335 trees between 42° and 53° in British Columbia. There was a distinct clinal trend whereby seed length increased from north to south. Robinson (1963) showed that both seed length and width and wing length and width differed significantly over an area of three degrees of latitude by six degrees of longitude. Allen (1961) found that seeds from coastal British Columbia had a longer, more pointed and pinched-in seed tip than those from the interior; interior seeds were more triangular, with greater sheen. White et al. (1981) found that individual seed in southwestern Oregon averaged 0.015 g (30,000/lb). According to Edwards and El-Kassaby (1996), “seed size varies within and among parents. These variations are caused by both environmental (i.e. position within seed cone, height and aspect of cone in the crown) and genetic factors” (p. 482).

The anatomical structure of conifer seeds, as shown below, has a dominant maternal contribution. Loopstra and Adams (1989) reported extensive genetic variation in Douglas-fir in southern Oregon: “seedlings from drier southern units had heavier seeds and were smaller (shorter, fewer branches), earlier bud set, more subject to second flushing and less damaged by frost than were those from northern units” (p. 240), and “families from higher elevations having lighter seeds and producing seedlings with earlier bud set and less frost damage, on average, than families from lower elevations” (p. 241).

Tables 7.5 and 7.6 demonstrate the great yearly variation in Douglas-fir cone crops in both the Pacific Northwest and Europe. Gashwiler (1969, p. 390) found that the annual seed fall for one clearcut varied from 400 to 168,800 over a 12-year period. He noted that the percentage of good seed was positively correlated with the size of the seed crop. Reukema (1982, p. 249) found that the seed fall in a young Douglas-fir stand varied from none to 3 million per year over a 29-year period, and that heavy seed crops occurred at 1- to 4-year intervals. (Perhaps the only general statement that can be made is that heavy cone crops do not occur on successive years.) Neustein (1940) noted that 4 of 18 seed years were heavy in Great Britain. Interestingly, even during heavy cone-crop years, not all trees produce. As Isaac (1943) points out:

> Even in years of heavy cone crops not all the trees produce. When there are cones on trees in virgin stands, there are usually cones on open-grown trees, but the reverse is not always true. Even open-grown trees fail to flower some years, and individual forest-grown trees probably produce seed less than half the time, i.e., some trees may rest even during good seed years. A record of the variation in seed-producing habits of individual trees is furnished by the record of a Douglas-fir seed-tree plot during 1927, when there was a good seed crop. In this instance 24% of the trees bore a heavy crop, 41% medium, 23% light, and 12% none. A variation always exists regardless of crop abundance. (Isaac 1943, p. 15)

Further, all species in a stand do not produce seed in a synchronous manner. Isaac found that the cone crop was "usually heavier on poor sites, such as gravel soils or wind swept ridges, than on good sites” (p. 15). This is in agreement with Garman (1951): “Analysis shows all the production factors (of seeds, cones) were higher per unit area of the poorer site” (p. 5), referring to site index 110 and 140. But these observations contradict the data of Willis and Hofmann (1915, p. 150), who found heavier seed crops on good sites. They reported 9,500 sound seeds per bushel of cones from trees on shallow, gravelly soil, as opposed to 14,700 seeds from a bushel of cones from trees grown on a good soil.

Earlier, we noted references that described increased flower production as a result of nitrate fertilization. Smith et al. (1968) reported that the effect of fertilizer was erratic, but that successive applications of nitropills over a period of 4 years increased cone production by 26%. They noted, however, that their data "shows conclusively that seasonal variations resulting from largely unknown causes and individual tree differences, probably under strong genetic control are most important” (p. 8). In contrast, Orr-Ewing (1965, p. 281) reported a strong flowering response to nitrogen fertilization on 8-year-old Douglas-fir seedlings.

Several workers have reported that seed production varies with tree age. Eis and Craigdallie (1981) suggested that cone production begins at 20 to 25 years; Lavender and Zaerr (1985, p. 8) observed that female strobili on trees 5 to 8 years old are not rare in Christmas tree plantations. Isaac (1943, p. 18) reported cones on trees 12 to 16 years old; Willis and Hofmann 1915, p. 158) found seed cones on 14-year-old trees; Winjum and Johnson (1968, p. 4) did not cite a minimum age, but found cones on 13-year-old trees; likewise Finnis (1950, p. 122) found female buds on 20-year-old trees.

Isaac and Dimock (1958), Hofmann (1924), and Garman (1951) all argued that mid-aged Douglas-fir produces the greatest quantity of seed, and noted that even trees over 600 years old are seed producers. Garman (1951) found that “in stands 40, 100, and 275 years old, dominant firs observed for three crops averaged for each crop 95, 135, and 1,340 cones per tree respectively” (p. 31). Hofmann (1924) stated

Table 7.5 General rating of Douglas-fir (*Pseudotsuga menziesii*) cone crops in Washington and Oregon from 1909 to 1954.

Date	Failure	Light	Medium	Heavy
1909	—	—	X	—
1910	X	—	—	—
1911	—	—	—	X
1912	—	X	—	—
1913	X	—	—	—
1914	—	—	—	X
1915	—	X	—	—
1916	X	—	—	—
1917	—	X	—	—
1918	—	—	—	X
1919	X	—	—	—
1920	—	X	—	—
1921	—	X	—	—
1922	X	—	—	—
1923	—	—	—	X
1924	X	—	—	—
1925	—	X	—	—
1926	—	X	—	—
1927	—	X	—	—
1928	—	X	—	—
1929	—	X	—	—
1930	—	—	X	—
1931	—	X	—	—
1932	—	—	X	—
1933	—	—	X	—
1934	—	—	—	X
1935	—	X	—	—
1936	—	—	—	X
1937	—	X	—	—
1938	—	—	X	—
1939	—	—	X	—
1940	X	—	—	—
1941	—	—	—	X
1942	—	X	—	—
1943	—	X	—	—
1944	—	—	X	—
1945	—	—	X	—
1946	—	—	X	—
1947	—	X	—	—
1948	X	—	—	—
1949	—	—	X	—
1950	—	X	—	—
1951	—	—	X	—
1952	—	—	X	—
1953	—	X	—	—
1954	—	X	—	—

Source: Isaac and Dimock (1958, p. 13).

Table 7.6 The following sequence of seed years noted in The Netherlands 1931–67.

Year	Crop
31	Bad
32	Bad
33	Moderate
34	Bad
35	Fairly good
36	Very bad
37	Very bad
38	Very bad
39	Very bad
40	Poor
41	Very bad
42	Fairly good
43	Very bad
44	Very bad
45	Very bad
46	Moderate
47	Very bad
48	Good
49	Very bad
50	Poor
51	Very bad
52	Very bad
53	Very bad
54	Very bad
55	Failure
56	Average
57	Very bad
58	Fairly good
59	Very bad
60	Average
61	Very bad
62	Very bad
63	Very bad
64	Moderate
65	Very bad
66/7	Failure/poor

After vanVredenburch (1969) and LaBastida (1969).

that 15-year-old trees may be expected to produce 4,000 seeds; 100- to 200-year-old trees, 40,000 seeds; and 600-year-old trees, 7,000 seeds.

Shearer (1985), Garman (1951), and Isaac (1943) all noted that trees with large crowns produced more cones than those with relatively narrow crowns. Isaac (1943) observed "that open grown trees with large crowns have yielded as high as 648 liters of cones in one picking, but the average forest-grown tree, which has a narrow crown, yields about 54 liters during a good cone year" (p. 16). Garman (1951, pp. 12–13) found that dominant trees produced 5 to 10 times the number of cones of intermediate trees. And Kozak et al. (1963) noted that large trees produce more cones.

The report of the Research Branch of the British Columbia Forest Service for 1939 (British Columbia Forest Service 1940) stated the following: "Cone crops may fail because of (1) rainy weather at time of pollination" [in the section on flowering, we noted that Silen and Copes (1972) contradicted this contention]; and "(2) Preceding large crops, and (3) effects of weather on bud differentiation" (p. 16). According to Reukema (1961), "thinned stands produce much more seed than unthinned stands in good but not poor seed years," and "sound seed percent varies with size of seed crop by year, but is not affected by thinning" (p. 3). In a 10-year period there was one good, one moderate, and one light cone crop. Cone production in other years was negligible. In contrast to other reports, Roy (1960) found that the highest percentage of sound seed (50%) occurred during a poor seed year. Working with young, open-grown Douglas-fir, Winjum and Johnson (1962) found the largest cones in the most vigorous portion of the crown, which probably had the highest photosynthesis. Tappeiner (1969, p. 174) found that cones were strong sinks and that reduction in foliage length and diameter growth were correlated with their presence.

As we noted in the beginning of this section, seed and cone production is affected by a multitude of poorly understood factors; hence it is both extremely variable and unpredictable.

Seed flight

Natural movement (generally by wind) of pollen and seed is the principal mechanism whereby the genes of Douglas-fir are distributed over its range. Studies of the genetics of this species have demonstrated that this spread of genes is quite limited, and the following observations of seed flight certainly confirm this conclusion. Perhaps the first observation of Douglas-fir seed flight was recorded by Hofmann (1924). He found that wind seldom carried seed farther than the tree height and concluded that rodent activity was a more effective means of distributing seed widely. His hypothesis has not been supported by other workers, however; for example, Isaac (1943) noted that "animal movement of seed is not important"(p. 22). Sissons (1933) also wrote about wind distribution of coniferous seeds, but did not cite Hofmann's (1924) work:

> Where reliance is placed upon natural regeneration, the seeding habits of the species involved are matters of fundamental importance. For species, which depend on the wind for transportation of their seed from the parent tree to the place where the young tree is to grow, an understanding of the factors governing wind distribution of seeds would appear to be essential. The majority of the most important coniferous timber tree species of the world bear seeds adapted to wind distribution, but a search of forestry literature dating to 1925 fails to bring to light any material of definite value on this subject. Most of the observations which have been made seem to have been based on studies of existing regeneration, accompanied by estimates (or guesses) as to the probable source of seed supply. . . (Sissons 1933, p. 119)
>
> (1) Seeds with marginal wings, such as redwood or birch, fall very rapidly for their weight. In these seeds the center of gravity corresponds closely to the center of surface area. (2) Seeds with short broad terminal wings, such as the firs, have a less rapid rate of fall for their weight. In these seeds the center of surface area is somewhat removed from the center of gravity, though not far from the wingward end of the long seed. (3) Seeds with terminal wings much longer than their width, such as the pines and spruces, fall least rapidly for their weight. In these seeds the center of surface area is considerably removed from the center of gravity. (Sissons 1933, p. 121)

According to Isaac and Dimock (1958), "Douglas-fir seed, like that of most conifers and many broadleaf trees, has a wing that whirls the seed as it drops from the cone and thus retards its fall. Whirling seed falls at the rate of 46 to 76 m per minute" (p. 3). A number of researchers have investigated seed flight of Douglas-fir and the various factors affecting it (Boe 1953; Dick 1955; Frothingham 1909; Garman 1951; Gashwiler 1969; Haig et al. 1941; Dick 1955; Isaac 1927, 1929, 1930, 1943, 1949; Isaac and Dimock 1960; Lavender et al. 1956; Pickford 1929; Roy 1957, 1960;

Sissons 1928, 1933). These studies used a variety of techniques to evaluate the various factors involved in seed fall. The following conclusions are a summary of their results.

1. Most of the sound seed falls under the stand or within 91 m of the stand edge.
2. Most of the seed falls between September and March.
3. Variations in the terrain and in wind speed make it impossible to predict the distance seed will travel.
4. Down drafts and updrafts, particularly those often associated with a fire, have strong effects on seed movement. Some seeds are blown tens of kilometers by winds associated with fires.
5. Sufficient seed for regeneration falls within 125 m of timber edge.
6. The distance of seed fall is correlated with the height of the release point.
7. The incidence of seedlings, but not total number, is related to the distance from seed source.

Seed size and germination

In an earlier paper, El-Kassaby et al. (1992) stated that "Douglas-fir seed germination, especially germination speed, is under strong maternal control; however, no relationship between seed size, expressed by 1000-seed weight on either germination capacity or speed was observed" (p. 49). Finally, working with seed collected from 40 widely spaced trees, Lavender (1958, p. 8) showed no relation between seed size and germination speed. El-Kassaby et al. (1992) noted that, "germination of conifer seeds is the result of much complex metabolic activity involving three distinct genomes: the diploid embryo, the haploid, maternally-derived, nutritional megagametophyte; and the diploid, maternal seed coat" (p. 51) as below.

Clearly, although the genetic inheritance of the embryo derives from both the male and female parents, seed size is a function of the female parent only. It should not be surprising, then, that the correlation between seed size and seed physiology is not strong.[2] Sweet (1965) and Ching and Beyer (1960) noted that Douglas-fir seed weight increased with elevation in both California seed sources (Sweet 1965) and those in the Pacific Northwest. Rafn (1915) summarized 25 years of seed testing, finding the average weight of Douglas-fir *var. menziesii* samples to be 13.3 mg and *var. glauca* to be 11.3 mg. Bialobok and Mejnartowicz (1970), working with more than 100 collections in the Pacific Northwest, reported that germination increased with increased seed size.

In two papers (1958 a,b), Lavender reported that although the heavier Douglas-fir seeds generally produced heavier seedlings, this effect lasted for only one year. This finding may have reflected that the larger megagametophyte represented a better environment for the embryo. Sziklai (1969), working with collections from 1,335 Douglas-fir trees between 42° N and 53° N, reported that seed length—but not width or wing size—increased clinally from north to south. With the exception of wing width, the dimensions of coastal seeds were greater than those of interior seeds. Working with seeds collected from 15 open-pollinated trees in three separate years, Silen and Osterhaus (1979) demonstrated significant differences in seed weight by year from individual trees and showed that, although seed size and weight were strongly correlated, neither was related to seedling growth after 10 years. They also showed that grading seeds by weight in a given seed lot would reduce its genetic base. Sorensen and Miles (1978) reported that the seed weight of Douglas-fir increased with distance of the seed source from the Pacific Ocean, presumably in response to demands of an increasingly arid environment.

In a similar paper, Sorensen (1983) presented data for the Coast Range in southwestern Oregon showing that seeds collected on dry slopes were larger and germinated more rapidly than did those from more moist microsites. Baker (1972) reviewed seed-size statistics for thousands of plants in California, from herbs through trees, and concluded that increasing seed weight of tree seeds is primarily correlated with increasing drought, the major limiting environmental factor.

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[2] Winn (1998) reviewed studies indicating that seed size can affect germination percent, rate, and seedling size for angiosperms, concluding that, despite "strong selection favoring large seeds, no evolutionary response is possible because genetic variation is lacking or ismasked by environmental variation" (p. 1543). Schupp (1995) speculated that seed size may not be a determinant of successful colonization, and that "the conflict, then, is between benefits of small seed size, which promotes dispersal, and thus seed survival, and large seed size, which promotes seedling vigor, and thus seedling survival" (p. 407). We know of no data that examines these alternatives for Douglas-fir.

Sorensen and Campbell (1985) reported a sophisticated study in which Douglas-fir seed weight was artificially altered on each of several seed trees by differentially bagging cones during seed and cone development. The procedure resulted in increasing average seed weight from 10.70 mg to 11.85 mg, an increase of 10.7%. The treatment did not, however, increase the resultant seedling height from 29.9 cm to 31.1 cm. They reviewed literature reporting inconsistent relations between seed weight and resultant seedling size, and offered the following possible reasons (p. 1111):

- maternal genetic factors that affect seed size differently than they do growth
- interactions between seed weight and genetic differences in seedling growth habit
- influence of test environment on effects of seed weight on plant size
- competitive effects among seedlings

Sorensen and Campbell (1985) also noted that a 3- to 4-year difference in 2-year-old seedling height was associated with 10% differences in seed weight, and suggested that "increasing seed size compares favorably with other nursery treatments for enhancing growth" (p. 1113). They did not appear to have made further progress in this area, however.

In a later paper, Sorensen and Campbell (1993) suggested that the relation between seed size and subsequent seedling vigor has two components: environmental seed weight, an effect that diminishes over time, and genetics, which reflects the fact that the same genes that cause greater seed growth are also reflected by greater vegetative growth in the parent and in the seedling, and that these effects do not necessarily diminish with time.

According to St. Clair and Adams (1991),

> In conifers, variation in the average weight of seed collected from different female parents is a consequence of three factors: the mean diploid genotype of the embryo, the mean haploid genotype of the megagametophyte, and the environmental effects common to the mother tree. The latter two factors are maternal effects. Evidence suggests that family differences in seed weight and other seed traits largely result from maternal effects. (St. Clair and Adams 1991, p. 987)

Based upon 35 families, the percentage of filled seed was shown not to be correlated with seed size. St. Clair and Adams (1991) also noted that "seed size was only weakly correlated positively with seedling weight" (p. 993) and that this correlation may be expected to diminish with time. They reviewed several papers indicating that, for Douglas-fir and coniferous species generally, any correlation between seed size and seedling size was either weak or transitory, and they suggest that this finding may be influenced by environmental factors, stratification, and maturity on seed characters (p. 993).

Seed development

From the moment that fertilization results in a zygote, a complex series of biochemical events occurs in the various tissues of the coniferous megagametophyte, the end result of which is the mature seed. In a lengthy and detailed description, Bowley and Black (1994, pp. 35–140) discussed this sequence for angiospermous plants. As Edwards (1980) noted, "according to Nitsch (1965) there are four phases of growth and development in seeds, which may be described briefly as (i) cell initiation and multiplication within the flower bud, (ii) pollination, pollen growth and fertilization. (iii) cell enlargement in the fruit and cell multiplication in the seed and (iv) maturation and finally senescence" (p. 627). That work was based on research with gymnospermous plants; much less information is available for gymnospermous species: "For conifers, opening of the cones on the tree and seed shedding usually signifies that the seeds are mature." (Edwards, p. 627).

Perhaps the first study of Douglas-fir seed maturity was that of Finnis (1950). Cones were collected weekly between July 19 and September 28. The data showed that cone specific gravity and seed weight were not related to seed maturity, and that germination for both stratified and non-stratified seed rose sharply for collections of the week of August 16–23. The increase in embryo length, but not changes in cone color, appeared to be correlated with seed maturity, as measured by germination. Allen (1958b) worked with seed collected at 2-week intervals between August 15 and October 10. Every precaution was taken to ensure that the seed response reflected any possible effect of collection date and not of processing procedures. Considerable variation was found among trees, but the highest germination and most rapid germination occurred with seed from the last collection. Ching and Ching (1962) collected cones from April 6 until September 9. The data showed these trends: respiration, moisture content, and specific gravity of cones decreased with increasing maturity; weight of cone and seed, length of embryo, seed production per cone, and seedling vigor (from germinated seeds) increased with increasing maturity: however, none of the foregoing defined the point of maximum maturity. Ching and Ching (1962) also noted the following for cones:

> From the chronological changes, five distinct developmental stages were indicated; receptive—in the middle portion of April; enlarging—from late April to June; filling and seed developing—from June 1 to August; maturing—from early to late August; and drying—from late August to early September.
>
> Browning of the cone bracts and length of embryo more than 90% of the embryo cavity in seed will be good practical indices for maturity of Douglas-fir cones. (Ching 1962, p. 29)

(Note that cone bracts should be brown, the embryo 90% of embryo cavity.)

Rediske (1961) studied changes in the biochemistry of Douglas-fir seed as it matured. He found that reduced sugar levels of immature and mature seed (22 mg/gm and 13 mg/gm, respectively) were a good measure of seed maturity. He also found small differences in starch, soluble protein, and nitrogen with maturity state, as well as differences in crude fat associated with decreasing seed moisture of the cone. He agreed with Ching and Ching that seedlings from immature seed were less vigorous than those from mature seeds.

Generally, maximum seed maturity and germinability occur when seed is shed, but maturity varies between trees, stands, and between cones on the same tree (Kolotelo 1997). The megagametophyte tissue of mature seed does not shrink when seed are bisected (Eremko et al. 1989, p. 26). This finding is in agreement with that of Harrington (1972, p. 148), who noted that mature seeds can generally withstand damage from drying. In a review of previous studies, Tanaka (1984, p. 28) noted that color and firmness of embryo and megagametophyte, seed wing and cone scale color, and loss of cone and seed moisture may all be used to estimate seed maturity. The studies discussed thus far have been concerned with physiological maturity of seed. Although establishing the exact time of maturity is difficult, it is important because—as Harrington (1972, p. 148) pointed out—immature seeds are not resistant to stresses such as drying, and do not store well. Also, according to Harrington (1972), "physiological maturity, even if not a precise point in the life of a seed or not precisely determinable, is still of extreme importance since it marks the moment when the seed begins to age. At this point, the seed has its highest vigor, there after declining to senescence and eventually no longer able to germinate" (p. 152).

Several studies of the effect of cone harvest at various dates, in effect at different stages of seed maturity, on subsequent seed germination show clearly the importance of seed maturity on subsequent seed vigor. Rediske (1969) studied seeds collected on four dates. Seeds from the earliest date (July 23) were clearly immature, and only 1% germinated. Seeds collected later were more mature, had a higher germination rate, were heavier, and produced larger seedlings. Sorensen (1980) worked with seed collected 6 and 2 weeks before natural seed fall. The seeds collected later had higher germination, were 19% heavier, and produced larger seedlings than the early-collected seeds. All stratification benefited late-collected seeds, but immature seeds were adversely affected by stratification periods greater than 30 days.

Olson and Silen (1975) collected cones between August 12 and September 14, with the following results: "Cones, seeds, and seedlings from 70 of 309 parent trees were collected too early, resulting in poor cone yields, reduced seed weight, poor germination, bacterial susceptibility, reduced seedbed density, and greater expenditure of time"(p. 11); and "seed weight and nursery germination continued to improve steadily for collections made even during the last two weeks before seed fall" (p. 10).

Theisen (1980, p. 8) reviewed a range of reports for conifers (including Douglas-fir), which indicate that properly stored cones collected before seed fall can yield fully mature seeds. Silen (1958) reported that Douglas-fir cones stored in damp peat moss can yield mature seed from cones collected a month before seed fall; however, Tanaka (1984, p. 29) noted that the method is not widely used in the Pacific Northwest, probably because of a higher risk of poor germination and reduced seed yield. Silen (1958,

p. 413) observed that fully mature seed weighed more than 8 mg, and suggested that seed weight be a measure of seed maturity. Harrington (1972) noted that “the most generally accepted measure of maturity is the time when the seed has reduced its maximum dry weight” (p. 151). Edwards (1980) found that "hormonal levels appear mostly to be associated with meristematic activity and the highest levels are found in immature seeds" (p. 627). No references were found relating plant growth regulators to maturity in conifer seeds, however.

The presence of starch in cone or seeds did not provide a definitive measure of seed maturity (Ching and Ching 1962). In an early study of Douglas-fir seed metabolism before and during germination, TM Ching (1959, p. 554) noted that the first sign of germination of a seed is the rapid increase of respiration that often starts within 1 hour after the commencement of water imbibition, and that “seeds soaked in H_2O_2 had a higher respiratory rate than those soaked in water” (p. 560). Other studies (Ching 1963a,b) noted that mature Douglas-fir seed had a high fat content (in common with 90% of seeds studied by Bradbeer 1988, p. 24), which was used during germination (Ching and Fung 1963, p. 551). To investigate this further they initiated a study of labeled glucose. They found that the dry weight of seeds and cone scales increased, while their moisture content percentage fell with increasing seed maturity. With increasing maturity, the uptake of glucose and the respiratory rate declined markedly, but the seed respiratory quotient (RQ) remained above 1 for the entire study.

The rate of fat synthesis from the labeled glucose increased with increasing seed maturity, so that increasingly mature seeds contained (p. 553) 40% fatty substances, 30% nitrogenous components, 20% fiber, 4% other carbohydrates, and 4% minerals. Seeds increased in dry weight from 3.9 mg to over 12 mg during the study, and decreased in MC from 84.6% to 59.4%. These changes did not define the point of maximum maturity, however. Working with mature seeds, TM Ching (1968, p. 482) noted that lipids made up 35% of seeds. Her data showed a significant decrease in protein body-nitrogen during the first 14 days of germination, and that the reaction products of lipases increased. In an earlier paper TM Ching (1963a) noted that lipids are the true reserve of Douglas-fir seed, used during germination. She also noted that “the glycerides are probably the major component which provides energy through oxidative degradation and carbon fragments for synthesis of cellular material in future growth” (p. 231). She also found that “there was no apparent change in total nitrogen content of various stages of germination” (p. 231). In a second report, TM Ching (1963b) found that “total fats decreased rapidly with germination from 36 to 12%” (p. 724), and that “a preferential utilization of linoleic acid in glycerides and a preferential increase of linoleic and palmitic acids in phospholipids were clearly demonstrated” (p. 728). In a later paper, TM Ching (1966) noted that “lipids, proteins and reserve phosphorous compounds in the gametophyte were utilized for the synthesis of carbohydrates, structural components and soluble compounds in the seedling . . . data presented in this paper indicate that the metabolic events of germination in gymnosperms are similar to those characteristic for angiosperm seeds” (p. 313).

The findings of Ross (1969) largely supported those of Ching (1963). He showed that seeds were completely ripened after 10 days of stratification, lipid reserves largely disappeared during stratification, and seeds’ respiratory activity increased after ripening from the low level of dormant seeds. Unfortunately, neither Ross nor Ching presented a quantitative measure of “after ripening.” Ross found that stratification facilitated a faster mobilization of storage reserves and suggested that there “was a block preventing lipid breakdown in dormant seeds” (p. 272).

Sorensen (1999) showed that drying storage of Douglas-fir seed at 3°C or −12°C for up to 32 weeks slightly reduced seed dormancy, whereas longer storage of up to 2 years at 12°C did not affect germination rate or total germination. Gosling et al. (2003, p. 244) compared dormancy release during drying after ripening and during prechill, and noted that after-ripening in dry storage generally took place most rapidly at low moisture content (in the range of 5% to 20% MC fresh weight). The moisture content fresh weight of the seeds Sorensen used was 8.46%, so a greater effect of storage on seed after ripening than he reported.

Seed processing (damage)

Although Douglas-fir seed frequently falls from the top of trees that are 60+ m in height, the wing, which acts as a miniature helicopter, reduces the impact of landing. About five decades ago, frequent erratic data of germination tests inspired some scientists to research the ability of the supposed "tough" seed coat to withstand the stresses common to the cone and seed processing scenario used by commercial seed processing facilities. In two publications (Allen 1957b, 1958a), seeds were sampled at stages of their journey through the several operations necessary to remove seeds from the cone and to separate seeds from extraneous material released from the cones with the seed. These trials demonstrated that, though the actual reduction in seed viability resulting from processing, particularly dewinging, was frequently a function of seed moisture content and maturity, the overall pattern was that seed processing equipment generally reduced seed viability.

Allen (1958) supplemented his samples from seed processing with trials in which measured blows were administered to individual seeds. The results from these trials demonstrated that relatively minor impacts could crack seed coats, and that where a single impact resulted in no measurable damage, repeated mild blows could destroy seed viability. Further, this work showed that any crack in the seed coat resulted in reduced viability, discolored radicle, and generally poor germination, and for even slightly damaged seed stored poorly, dewinging was identified as a major cause of seed damage. More modern equipment, however, largely reduced the destructive impact of dewinging (Edwards 1985, p. 90). Leadem et al. (1990, p. 202) advised caution in order to avoid damage from excessive abrasion that may result in poor germination. Barnes (1985) warned that worn rubber paddles on dewinging machines can cause seed damage. Edgren (1968) noted that helicopter seeding devices may damage seed. Stoleson and Hallman (1972) reported data that supported Edgren's conclusions.

Copeland and McDonald (2001, pp. 112–113) noted that mechanical damage can affect agricultural seeds, resulting in cracked and broken seeds, baldheads, and other germination abnormalities. Although mechanically damaged seeds may appear normal, there may be subtle, detrimental effects on seedling vigor. The physiological basis for this loss of vigor is poorly understood; causes may be physiological deterioration triggered by impaction or physical damage resulting from cryptic, microscopic breaks at crucial spots in the seed. Other researchers have examined the role of thigmomorphogenesis in reduced plant growth (Telewski 1990, Telewski and Jaffe 1986). In conclusion, Douglas-fir seeds are fragile and must be handled carefully to avoid damage.

Seed storage

Harrington (1972) defined the initiation of seed storage as "the moment when the seed is physically mature" (p. 152). He also noted that physical maturity may not be precisely determinable, but that the timing is extremely important because it marks the moment when the seed begins to age. The external changes in Douglas-fir cones during seed maturation are summarized in Table 7.7 (Ching and Ching 1962). The seed was mature by about August 12, although changes in cone appearance were too gradual to afford a precise guide to seed maturity.

One guide to determining seed maturity is squirrel activity. In late July or early August, squirrels frequently cut a few cones and then tear them to pieces, leaving a pile of cone scales. This sampling continues until the seeds are mature, when the squirrels harvest many cones without cutting them apart. Thus, when squirrels are actively harvesting cones, the seeds are mature.

Table 7.7 External changes in Douglas-fir cones during the period of seed maturation as indicators of maturity

Collection date	Cone appearance
July 23	Seed wing browning
July 30	Seed wing all brown
August 5	Bracts yellowing
August 12	Bracts yellowish
August 19	Bracts yellow to brown
August 26	Cone greenish-yellow, yellow, or brown
September 2	Cone yellowish to brown, 0%–100% open on different trees
September 9	Cone brown, 0%–100% open on different trees

From Ching and Ching 1962.

A second and perhaps more frequent practical guide to seed maturity is the relation between embryo length and the length of the embryo cavity. When the length is at least 90% of the cavity, the seed is mature. Immature seed are generally further characterized by a *milky* megagametophyte, whereas the megagametophyte of mature seed is firm. A discussion of seed storage may logically be divided between factors affecting artificial storage and storage under field conditions.

Storage under controlled conditions

Storage begins when the seed is mature, but seed is often collected before cone and seed maturity. Under these conditions, storage begins with the seed in the cones—a procedure that has led to conflicting data on the viability of seed after a ripening period in the cone. Shea (1960) suggested that fungi caused the loss of germination of seed stored in cones. Rediske and Shea (1965) demonstrated that, if cones were stored with more than 40% MC or above 20°C, a great loss of seed occurred after 16 weeks. Bloomberg (1969) noted that "in general germinabilty losses after up to 120 days cone storage appear to be minor," (p. 181) although he did find some diseased seeds in the germination dishes. Lavender (1958), working with seeds collected from 40 widely spaced trees in the Willamette Valley, found that "storing cones (up to 4 months at temperatures near 50°F) does not affect the germinative capacity of Douglas-fir seeds" (p. 8). Unfortunately, the moisture content of these cones was not determined. Ching and Ching (1962) suggest, however, that for cones at the stage of maturity described in the Lavender (1958) study, the moisture content was about 15%.

A second form of storage under controlled conditions is initiated after the cones have been dried and the seed extracted, dewinged, and cleaned. As Harrington (1972, p. 145) pointed out, learning how to best store seed from the harvest was essential in the shift from hunting and gathering to the cultivation of crops. Early farmers had to learn how to guard against high temperature and high humidity in the stored seeds; the same problems faced foresters. That the problems stimulated a large volume of research dealing with the storage of tree seeds was particularly important because many forest trees, including Douglas-fir, are characterized by widely varying seed crops from one year to the next, so the only way to assure sufficient seed for reforestation in a given year is to successfully store them. Holmes and Buszewicz (1958, p. 25) reviewed the literature on storage environments for temperate tree species and noted that, for Douglas-fir, low moisture content (around 6%–9%) and low temperature (−18°C) provided the best storage conditions. Belcher (1982) reported that "stratified Douglas-fir seed can be dried to between 21% and 26% MC and held at 3°C and stored for 10 months without a significant decrease in germinability" (p. 24). In their review of forest tree seed, Edwards et al. (unpublished note) stated that "optimum conditions vary with species, but moisture levels between 6 and 9% (of fresh weight) and temperatures around −18°C are widely used to maximize seed longevity." The general relation between storage temperature and moisture content is that, at any given moisture content, seed viability deteriorates faster as temperature rises (within limits), and the lower the storage temperature, the greater the tolerance to high moisture content. Thus, storage temperature is more important when moisture content is high. Refrigeration equipment is expensive to install and maintain, so paying close attention to moisture content, which can be controlled more economically, makes sense.

In the Pacific Northwest, seeds are commonly stored at −18°C, but the British have found 0°C to be equally effective (personal communication, AG Gordon, 1978). In two reports, Barton (1954 a,b) found that, after 3 years, seed stored at −18°C retained higher viability than seed stored at −4°C or −11°C, but that the seed also had the lowest MC, 10%. Seeds stored at higher temperatures had higher MC (15% and 16%), so the MC likely interacted with storage and temperature. Subsequent trials showed that seed at 5.8% MC retained greater viability at both −18°C and 5°C than did seed with 13.6% MC at the same temperature. Allen (1957) reported that Douglas-fir seed stored better at −17.8°C than at 0°C or at room temperature for 7 years. Seed moisture was about 6%. Rediske (1967), reviewing the literature, noted that high quality Douglas-fir seed could be stored for at least 8 years at 6% to 10% moisture content and −17.8°C temperature without loss. Schubert (1954) reported that Douglas-fir seed stored at 5°C (no mention of moisture) showed 66% viability after 6 years and 31% after 16 years. The germination tests were conducted in greenhouses without environmental control. Work reported by MacMorran (1946) demonstrated that seed stored at 2°C to 4°C for 3 years retained its viability better than did seed stored at room temperature, regardless of whether seeds were maintained in sealed or open bottles. A later paper by Rudolph (1952) showed that seed maintained its full viability for 4 years when stored at 5°C in sealed containers. He emphasized that, if seeds were to be stored for prolonged periods, they should have no more than 7% MC when placed in storage. Sorensen (1999, p. 96) working with Douglas-fir seed at 8.49% MC, found that seed stored at 3°C deteriorated, and concluded that long-term storage should be at subfreezing temperatures (−10°C to −20°C).

One interesting variation on seed storage trials was reported by Allen (1962a,b,c). He presented data describing the effects of canning Douglas-fir seed with and without vacuum (20 inches) and storing it at room temperature and 70% and 7.1% MC. Germination tests demonstrated that vacuum storage could not substitute for low-temperature storage. This variation is, perhaps, occasioned by difference in seed maturity and processing, both of which can influence the effects of storage (Schubert and Adams 1972). But for mature, undamaged seed, low moisture content (6%–9%) and low temperatures (below freezing) are apparently most effective in maintaining seed viability.

In contrast to the long-term storage described above, a short-term storage experiment by Lavender (1954) demonstrated that exposing seed to 30°C temperature and 93% relative humidity at 10°C for 11 weeks did not reduce seed germination. A second study (Lavender 1958a) showed no superiority for storage at −17°C over that at 0°C or at the uncontrolled temperatures in an unheated warehouse during 6 months of the fall, winter, and early spring, when seed moisture was about 7%. Further, no difference was shown between the viability of seed overwintered under field conditions and any of the above storage regimes.

A third study (Lavender 1958b) was designed to determine whether seed viability was reduced when cones were not extracted shortly after picking. Populations of cones collected from 40 widely separated trees in the Willamette Valley were stored in an unheated warehouse for 0, 2, and 4 months before drying and extraction. No reduction was found in seed vitality, as measured by germination of seeds in greenhouse flats. All the data discussed above are compatible with the concept that moisture is essential for the hydrolysis of seed substrate necessary for germination and growth (Koller and Hadas 1982) and that respiration that uses seed energy reserves increases with temperature. Accordingly, long-term preservation of seed substrates is best achieved under cold, desiccating conditions. Schubert and Adams (1971 pp. 50, 52) recommended below freezing temperatures and 4%–8% MC.

Although substantial research has been concerned with the storage of Douglas-fir seed, data describing the effects of moisture, temperature, seed maturity, and processing—and their interactions over a period of at least 10 years—are lacking.

Storage under natural conditions

Obviously, nearly all of the above work dealt with storage under controlled conditions. But substantial effort has dealt with a second type of storage: that is, storage under natural conditions.

Early in the 20th century, Douglas-fir seed storage in the duff was controversial. In three papers, Hofmann (1917, 1920, 1924) argued that the pattern of natural regeneration after harvest or burning of Douglas-fir stands could best be explained by hypothesizing that it originated from seeds stored in the duff. But he presented no data to demonstrate that was possible. But Isaac (1935), using seed stored for various periods under various natural conditions, demonstrated that Douglas-fir seed had a maximum life of 1 year in forest duff. Later work by Haig et al. (1941) demonstrated that interior Douglas-fir seed did not retain its germinative capacity for more than a year under natural conditions in the western white pine region of Idaho. Finally, Isaac (1943) reviewed the results of 9 years of trials with Douglas-fir seed stored in the duff under a variety of conditions, finding conclusive "that Douglas-fir seed does not commonly retain its viability for more than a year after it ripens. There may be conditions in nature under which Douglas-fir seed is germinable for more than a year, but the evidence is now very strong that the amount is too small to be a factor in reforestation, and forest managers should not count upon seed surviving on the forest floor more than a year (Isaac (1943, p. 26).

Garman (1955) noted early Canadian research demonstrating that Douglas-fir seed either germinated or died under natural conditions during the first year after it was produced. Garman and Orr-Ewing (1949, p. 15) found, however, that only 12% of the total germination of stratified Douglas-fir seed sown in May occurred during the first summer.

8. Seedlings

Denis P. Lavender

Shoot growth in Douglas-fir and many other conifers (e.g., spruce, fir, pine) is indeterminate in the first year, but determinate thereafter. In many species, buds contain primordia for all the leaves that will develop the following season. Species that produce buds that contain, in miniature form, all the growth that they will accomplish in the subsequent year are called *determinate* (restricted in growth). Species that do not produce buds, or have buds that contain apical meristems capable of initiating further leaf primordia and internodes (e.g., hemlocks), are termed *indeterminate.*

Seedling Dormancy

Dormancy (from the French verb, *dormir*, to sleep) is a term that refers to the vegetative buds and tissues of a perennial plant. The remainder of the plant does not have dormancy, but is strongly influenced by this stage of bud physiology. Dormany differs from *cold hardiness,* which frequently develops at a similar time for Douglas-firs and is systemic for all plant tissues. In general, dormancy develops before the onset of weather unfavorable for growth and represents a survival mechanism, wherein growth is suppressed for *stress resistance*.

The classic definition of dormancy (Doorenbos 1953, p.1) is "a tissue predisposed to elongate does not do so." A woody plant is generally said to be "dormant," by common usage, when buds have formed on the terminals of shoots. With many temperate plants, the dormant period may extend from mid-summer until sometime in the following spring, a period that can be more than 75% of the annual growth cycle. Although the external morphology of the plant shows little change during this time, the growth physiology undergoes significant changes during this period, which govern the response of the plant to the environment.

The dormancy phase of seedling physiology is difficult to discuss because researchers have investigated it with dramatically different approaches, because the subject has engendered a bewildering array of terminology (Lang et al. 1985), and because methodology involved has resulted in data that are frequently not comparable (Lavender 1991). The two major approaches to the study of dormancy in Douglas-fir are (1) a study of the morphology of the terminal shoot from bud break until and including bud set and the growth responses to defined environments; and (2) a study (largely performed by Prof J.N. Owens and associates) of the anatomy of apical meristems and adjacent tissues, including cellular activity and its biochemistry.

The first approach defines the annual growth cycle of Douglas-fir as consisting of two contrasting states: (1) a period of active shoot elongation, generally from late March until mid-August, wherein bud break and subsequent stem growth are accomplished by the elongation of pre-formed initials; and (2) dormancy, a period, including bud set, of apparently no growth from mid-August until March. This pattern is typical of determinate gymnosperms, as discussed below. As noted in the introduction, there are a number of reviews that discuss the subject of dormancy, so this section will refer primarily to these sources and to individual reports that present data particularly germane to Douglas-fir.

Sarvas (1974) proposed at least two stages of dormancy: (I) the "chilling" period, (II) separated by definite cytological events. He considered the Dormancy I period to function as a mechanism to set the physiology of a plant to the zero point of

Dormancy II, i.e., bring all plants to an equal state of readiness to utilize heat to initiate spring growth. Sarvas suggested that there is a distinct difference in Dormancy I and II, albeit the dividing line is difficult to define. In contrast, Campbell (1978) argued that for Douglas-fir, at least, dormancy is a period of transition "with potential developmental rates changing continuously in response to cool-season environmental stimuli" (p. 20).

Most of the research dealing with dormancy has been discussed earlier in this paper, i.e., the effects of environmental factors in slowing shoot elongation and initiating bud germination and the environmental requirements for bud break. These studies have introduced the concepts of summer dormancy or quiescence, rest or winter dormancy (Romberger 1963), and post-dormancy or quiescence, all based upon the response (usually short-term) of a plant to favorable environmental, i.e., warm temperatures and long photoperiods. This work has left a somewhat amorphous period between bud set and bud burst for which there are few published data concerning either the physiology of the plant or the environment most favorable for the development postulated by Campbell (1978), other than, of course, low temperatures. The remainder of this contribution will be concerned with these references.

Several unpublished and published (Lavender and Wareing 1972) studies with Douglas-fir seedlings suggest strongly that photoperiod response, in this species at least, may be more subtle in nature than bud break. Two-year-old seedlings grown in pots under natural conditions during spring and summer until resting buds were well developed in late August were then exposed to either 3 or 6 weeks of mild days with 9-hour photoperiods, followed by 4, 8, or 12 weeks of 9-hour days at 5°C, or were placed directly into 9-hour days at 5°C from the natural conditions obtained in August. After chilling, the seedlings were maintained with 12-hour photoperiods at 20°C to evaluate bud break. The results showed clearly that the short-day (SD) treatment prior to chilling was essential for vigorous growth after chilling. Similar trials (Lavender and Wareing 1972) demonstrated that the sequence of long days-chilling resulted in 13% mortality, as opposed to no mortality for SD-treated seedlings. Similarly, Jacobs et al. (2008) showed increased cold hardiness and root growth for Douglas-fir seedlings hardened under SD regimes. MacDonald and Owens (2010) recommended a 3-week SD period for coastal Douglas-fir (var. *menziesii*) seedlings after comparing the effects of different SD treatments on bud development, bud endodormancy, and morphology of first-year containerized coastal Douglas-fir (var. *menziesii*) seedlings in the nursery, together with seedling survival and growth after one growing season in a common garden. On the other hand, Taylor et al. (2011) found no differences in field performance between Douglas-fir seedlings treated with short-day dormancy induction and those for which dormancy was induced with conventional moisture and nutrient stress.

As earlier noted, "dormancy" is defined by a number of terms, none of which are truly definitive. The following two tables (Table 8.1 and 8.2) list some of the variety of terms used historically. Table 8.2 presents the nomenclature suggested by Lang et al. (1985) in an attempt to present more consistent, definitive terminology. The above terms are not

Table 8.1 Historical nomenclature of dormancy phenomena.

Reference	Approximate definitions and equivalence of terms for physiological dormancy		
	Dormancy imposed by the environment—no internal control	Dormancy imposed by agents or conditions within the plant, but outside the dormant organ	Dormancy maintained by agents or conditions within the organ itself
Johannsen (1913)	Forced idleness (*Erzwungene Untätigkeit*)	Pro-rest middle rest after rest (Vorruhe, Mittelruhe. Nachruhe)	
Doorenbos (1953)	Imposed dormancy	Summer dormancy	Winter dormancy
Samish (1954)	Quiescence	Correlated inhibition	Rest
Romberger (1963)	Quiescence	Correlated inhibition	Rest

Table 8.2 Ecodormany, paradormancy, and endodormancy.

	Ecodormancy	Paradormancy (later ectodormancy)	Endodormancy
	Regulated by environmental factors	Regulated by physiological factors outside the affected structure	Regulated by physiological factors inside the affected structure
Examples	Temperature extremes Nutrient deficiency Water stress	Apical dominance Photoperiodic responses	Chilling responses Photoperiodic responses

After Lang et al. (1985).

without some criticism (Salisbury 1986 and Junttila 1988) and certainly do not correct the deficiencies pointed out by Lavender (1991), but they have been in use by The American Horticulture Society for 20 years, so we will follow the above.

Webber et al. (1979) defined dormancy in Douglas-fir as follows: "the period between formation of a terminal bud (mid-July) to the flushing of buds and beginning of spring growth. In this period, Samish (1954) has described four distinctly different physiological states: quiescence, preliminary rest, midrest, and after rest (each defined by growth response in a favorable environment)" (p. 536). In Douglas-fir, these states have been established from physiological trials largely concerned with response to photo period (Lavender et al. 1970).

Environment and dormancy initiation

By definition in Table 8.2, "ecodormancy"— which in Douglas-fir, extends from mid-August until late September—is imposed by the environment. Vegis (1964) suggested that the environment stimulating dormancy is that which occurs prior to potentially damaging weather. Accordingly, Douglas-fir generally initiates dormancy in response to the environment in August, i.e., shortening photoperiods and dry soils. Several reports have suggested that dry soils are a major cause of dormancy (Blake et al. 1979; MacDonald 1996; MacDonald and Owens 1993a,b; MacDonald and Owens 2006), while others have found shortening photoperiods to be generally associated with dormancy initiation (Lavender 1962, Lavender et al. 1968). Some reports have indicated that low temperatures may delay dormancy (Lavender and Overton 1972).

Owens and Molder (1973) presented a microscopic description of buds throughout dormancy. They offered evidence that the vegetative apices pass through five stages each year: dormancy (November-March), early bud-scale initiation (April-May), late bud-scale initiation (May-June), early leaf initiation (July-August), and late leaf initiation (August-October). These stages are based on anatomical and biochemical measurements which differ strongly during the annual cycle and which are more definitive than the morphological descriptions more commonly used to define dormancy and active shoot growth.

Dormancy and physiological response

In the detailed discussion of the apical meristem described on the previous page (Owens and Molder 1973) there is little correlation between the stages of dormancy and the dormancy phases described by Lang et al. (1985). The concept of dormancy, as described by lack of mitotic indices by Owens and Molder, is much shorter than that of Lang et al. In as much as the mitotic index (MI) defines cell division, Owens and Molder's concept may be more distinct. Grob and Owens (1994), who define MI as "a measure of the percentage of cells undergoing mitosis at the time of fixation," note the following, however:

> Interpretation of MI data requires an understanding of the factors responsible for changes in MI, and the realization that MI does not indicate changes in all cell parameters under all conditions. More rapid physiological tests are required to predict seedling performance. Cytological methods such as MI and the ability to resume mitosis under promotive conditions (Grob 1990) may be more accurate and rapid than tests such as days to bud burst. This is because they measure one process, mitosis, which is more closely related to biochemical and molecular processes [during dormancy] than the more complex process resulting in bud burst. (Grob and Owens 1994, p. 480)

Plant growth regulators and dormancy

For probably as long as dormancy has been studied, scientists have had the unsubstantiated belief that plant growth regulators (PGRs) have regulated this phenomenon. However, the following summaries of PGRs and dormancy generally agree that much of the evidence is erratic and contradictory and has been generated by insufficient methodology. Wareing and Saunders (1971), Deyoe and Zaerr (1976), Doumas and Zaerr (1987), and Webber et al. (1979) all noted correlations between dormancy and levels of PGRs, but Zaerr and Lavender (1980) and Lavender and Silim (1987) agreed that varying methodology made it impossible to establish unequivocally the role of PGRs in dormancy. While much of the foregoing research was concerned with abscisic acid (ABA), the same conclusions are true for indoleacetic acid and other PGR compounds (Lavender and Silim 1987, Saunders 1978). Perhaps the best conclusion is the following, from Borchert (1991):

> The hypothesis that bud dormancy in trees might be caused by inhibitory plant hormones, such as abscisic acid (ABA), was introduced 40 years ago, since the level of growth inhibitors in extracts from dormant *Fraxinus* buds declined during winter in parallel with bud dormancy. Later, it was proposed that short photoperiods cause an increase in the ABA content of buds, while chilling reduces ABA levels and thus enables bud break in spring. None of these hypotheses withstood experimental testing [Lavender and Silim 1987, p. 171; Powell 1987b, p. 539], and the following assessment of hormonal control of bud dormancy, written 25 years ago, remains valid [Romberger 1963]: "Our knowledge of endogenous growth regulators (including morphogenetic receptor pigments), and their interactions under various conditions, is so inadequate that intelligent discussion of the subject is not yet possible." Indeed, neither shoot growth periodicity nor any other aspect of plant development involving correlations between organs (e.g., apical dominance, flower induction, or tuber formation) has been satisfactorily explained in terms of hormone interactions [Davies 1987]. The genetic and physiological control of morphogenesis is so complex even in a relatively simple system such as the isolated shoot meristem of tobacco [Meeks-Wagner et al. 1989] that any attempt to deduce hormonal control of shoot growth periodicity in woody plants from crude correlations between extracted hormones and shoot development appears overly simplistic. There can be little doubt that plant hormones are involved in the regulation of growth periodicity. However, the complex interrelations between environmental (photoperiod, drought, and cold), nutritional, and hormonal factors remain to be unraveled. (p. 240)

Erez (2000) offered an elegant discussion relating dormancy and cold hardiness in woody plants, suggesting that the duration of dormancy is controlled by changes in lipids in bud cell membranes, i.e., the saturation and desaturation of the linoleate and linolenate. Arora et al. (2003), who emphasized "the multiple and complex nature of the dormancy phenomenon," explored bud dormancy in woody plants:

> The path to endormancy induction is a continuum, which in some plants begins as early as budbreak in the spring. While it has been tempting to explain bud dormancy on the basis of hormonal regulation alone, dormancy is controlled by numerous integrated plant structures and functions (Crabbé 1994, Simpson 1990). Initial studies (e.g., Dennis and Edgerton 1961, Nitch 1957, Phillips and Wareing 1958, Samish 1954, Wareing 1956) were followed in the next 3 decades by a series of studies that monitored endogenous levels of hormones within whole buds, leaves, stems, cambium, and root tissues under natural fall and dormancy-inducing controlled-environment conditions. While relatively easy to apply and measure responses, many other problems are associated with traditional exogenous application of hormones in addition to degradation and differential responses between the widely available commercial (±) −ABA and the natural (+) −ABA (Wilen et al. 1996). (Arora et al. 2003, p. 912)

Certainly, the role of hormones in Douglas-fir dormancy is not yet fully understood. The PGR most commonly associated with dormancy is abscisic acid (ABA), previously referred to by Phillips and Wareing (1958) as "dormin." In unpublished data, Lavender and Wareing (1969) noted that ABA reduced apical dominance of 2-year-old Douglas-fir seedlings, but did not cause dormancy. A report by Webber et al. (1979) noted that the concentration of ABA was highest in buds and needles in the autumn and lowest in the same tissues just before bud break. However, the authors do not assign a causative role of ABA in initiating dormancy in Douglas-fir.

Dormancy Breaking

The breaking of dormancy is at least a two-stage phenomenon. The first occurs over a period of time (probably 3-4 months for Douglas-fir) wherein the factors responsible for paradormancy are gradually dissipated, generally by temperatures between 0°C and 10°C and the bud enters endodormancy. The second phase, the elongation of the shoot and concurrent bud break, occurs as a result of mild spring temperatures (5°C to 20°C).

The mechanism of the first phase is not understood, but is generally referred to as the "chilling" requirement of the bud, whereby the bud must be exposed to temperatures of 5°C or lower for up to

17 weeks before it will resume normal elongation (McCreary et al. 1990, Van den Driessche 1975, Wells 1979). It is difficult to assign a definite time period under natural conditions because interruption of the "chilling" by warm temperatures (15°C to 25°C) may undo some of the previous chilling, depending on the timing and duration of the warm periods. This "chilling" requirement, which is almost universal for woody determinate perennials native to areas with frost events in fall-winter, is not fully understood.

More recent reports, conducted with Douglas-fir seedlings in exposed environments (Guak et al. 1998, Bailey and Harrington 2006), demonstrated that Douglas-fir needs chilling; however, the studies differ in that they employ air temperatures rather than bud temperature and, as Chandler (1957) stated, this can make a substantial difference.

In a biochemically oriented review, Arora et al. (2003) concluded,

> Finally, while most work to date has focused on hormonal control of dormancy release, which, when, how, and to what degree hormones are involved is still uncertain, and evidence both supporting and refuting various growth regulators can be found in recent literature. What is clear is that, aside from more useful hormonal localization studies and use of mutants and transgenics, continued gross-analysis of hormone presence or absence during dormancy release will not enable definitive mechanisms to be tested. (Arora et al. 2003, p. 913).

Climate Change and Chilling

As part of its cold hardiness, Douglas-fir has evolved the requirement for a period of cool temperature to break paradormancy. This requirement has undoubtedly saved the species considerable frost damage. McCreary et al. (1990) demonstrated that Douglas-fir seedlings grown from either seed collected in an area with a relatively warm winter or from seed collected from trees growing in an area with a cold winter break their buds more rapidly and produce more vigorous shoot growth when chilled at a temperature of 5°C than when chilled at temperatures of 7°C or 9°C.

The significance of these data is that, while the present climate of coastal North America has winters sufficiently cold to satisfy the chilling requirements of endogenous Douglas-fir, a relatively small mean temperature rise in the warmer portions of the Douglas-fir range during October to February could well be sufficient to prevent this species from receiving its necessary chilling. Therefore, the trees will die, either as a direct effect of lack of chilling and failures of bud break or by damage from bark beetles (Lavender 1989). For example, Copes (1983) reported that a Douglas-fir seed orchard established near the Monterrey Coast in California demonstrated very weak shoot growth as a result of average winter temperatures between 9.3°C to 12.2°C from November to March.

Long-term weather records from stations located in the Oregon Coast and Cascade Mountains contain data from stations whose mean temperatures in December, January, and February are between 5°C and 8°C (Simonson 1963). Many papers cite data that predict a mean global warming of 3-4°C within this century. Furthermore, the majority of this warming is predicted to occur during winters. If, then, the mean winter temperatures of forested areas below 300 m elevation in the Oregon Coast Range and in parts of the Oregon Cascades are raised by even those few degrees, the average winter climate in those areas would be too warm to satisfy the chilling requirements of Douglas-fir and a situation similar to that reported by Copes (1983) would result. The findings of McCreary et al. (1990) suggested that the chilling requirement of Douglas-fir is not influenced by the winter climate of the seed source. If this is generally true for the species, it may prove difficult to reduce the chilling requirement through forest tree breeding techniques.

Perhaps of more immediate concern to foresters is the effect of a trend toward increasing winter temperatures upon the success of reforestation. The majority of the present nurseries that grow Douglas-fir seedlings in Oregon, Washington, and even British Columbia are in areas that currently receive only slightly more chilling hours each year than are required by Douglas-fir seedlings. Further, the methodology of harvest, shipping, and planting forest tree seedlings definitely impacts their ability to respond to chilling temperatures. Seidel and Keyes (1983) predicted that winters with a mean temperature as much as 5°C above the present average would be within the expected range of climatic variation after the year 2000. Accordingly, we may expect that poorly conditioned nursery stock will be increasingly at risk in the coming years (Lavender and Stafford 1985).

Dormancy and Growth Potential

Lavender and Hermann (1970) and Lavender et al. (1970) demonstrated different degrees of growth during para-, endo-, and ectodormancy. They reported that no lateral or terminal buds were stimulated during paradormancy, and that maximum growth was stimulated during the change from paradormancy to endodormancy. Root growth declined from October to February. Lateral cambia did not respond to stimulus until December and made maximum growth in January and February.

Owens (1967) presented a detailed description of the growth and maturation of tissues after the buds break dormancy. Although these development details are beyond the scope of this book, the major points Owens made are as follows:

- The first indication of increased activity within the buds after dormancy occurs during mid-March. Positive staining for succinate dehydrogenase appears at this time, first in the apical meristematic region of the bud.
- The dormant buds usually begin to expand and initiate axillary shoots during the last week of March (in the Victoria area).
- The shoot and its leaves elongate rapidly and push the bud scales apart, which results in bud burst during the second week of April.
- The shoot area grows rapidly during bud scale initiation, completed by mid-June and into July.
- Leaves are initiated rapidly during July and August, and then more slowly until nearly mid-November (during this period the developing bud is considered to be in endodormancy).
- Maturation of the foliage over the growing season (after dormancy), although a truly mature leaf is not formed until the tree becomes dormant.

Stress resistance and cold storage

Although for many years cold, dark storage was thought to be neutral, later studies found that it is stressful (Camm et al. 1994). After summarizing a number of reports, Lavender (1985) concluded that stress resistance in Douglas-fir was minimal in October through early December, while Van den Driessche and Cheung (1979) found that seedlings lifted in early fall or May were more sensitive to conditions in cold storage than were those lifted during the winter. Hermann (1967) found that cold storage of seedlings in November and March was associated with lower survival than when seedlings were lifted and stored in January. Mckay (1992) and Mckay and Mason (1991) found greater electrolyte leakage in seedlings lifted in the fall than in the winter; Folk et al. (1999) reported similar results. Common operational practice in the Pacific Northwest is to begin lifting and storage in mid-December. The date of lift and the duration of storage depend on whether the seedlings will be cold- or freezer-stored, and where or when they will be outplanted.

Camm et al. (1994) reviewed some of the research on the methods of cold storage and the physiological effects on seedlings, summarizing as follows:

> Stress resistance is generally lowest in conifer seedlings in a natural field habitat at times when the seedlings are actively growing. Conversely, plants are most resistant to a number of stresses (frost, mechanical, darkness, etc.) during those periods when growth is minimal or zero. In seedling nurseries, the cycle is interrupted by fall or winter lifting and subsequent cold storage where the plants receive none of the clues of the natural environment.
>
> Cold storage of conifer seedlings is widely practiced in the temperate and boreal regions of North America, as well as in Scandinavia. Successful management of this technique involves an understanding of the ways in which plants respond to changes in temperature and photoperiod in yearly cycles of growth and dormancy. Operationally in nurseries, moisture stress or lengthening nights in midsummer stimulate the formation of resting buds (Lavender 1990). Early fall conditions (mild temperature and long nights) promote rest, or true dormancy, in the apical meristem and initiate cold hardiness in the entire plant. Late fall condition (low temperatures and very long nights) terminate rest and maximize cold hardiness. In principle, seedlings put into cold storage at this stage and protected from naturally occurring environmental variations over the course of winter should remain cold hardy and able to break bud upon receipt of the appropriate heat sum after planting the following spring. In practice, cold storage is used primarily to facilitate nursery and planting schedules, and growers sometimes work against, rather than with, the biology of the tree. (Camm et al. 1994, p. 311)

In reponse to these and other reports and others, additional studies have been conducted on cold storage of Douglas-fir with and without a daily photo period (see Table 8.3; Lavender et al. 1970, Hermann et al. 1972).

Cold storage with light

There are few references to this storage regime, as it is limited primarily to Douglas-fir. Camm et al. (1994) reviewed several publications and unpublished work that demonstrated the increased seedling vigor and survival potential for seedlings stored with a short photoperiod. They emphasized that the work was done with photoperiod intensity too low to permit photosynthesis, and that the greatest positive effect occurred when seedlings were stored in September-November, although seedlings reacted positively in later winter. They suggested that the results may be due to the photoperiod on training circadian rhythms (Lavender 1988). Douglas-fir seedlings lifted in October were stored at 20°C with root temperatures either 5°C or 20°C and with light or in the dark for 1 month, with survival as shown in Table 8.4. When the study was repeated with seedlings lifted in January, survival was 100%.

Cold storage without light

It has been generally felt that cold storage was a safe, neutral way to maintain seedlings between lifting and planting. But this procedure does not take into account the endogenous rhythm of seedlings; continuous darkness at a constant temperature produces an environment that does not entrain these rhythms. As a result, seedling vigor is consistently reduced in cold, dark storage, which subsequently results in reduced seedling vigor after planting. Ritchie (1987) noted that cold storage slows release from dormancy, and that significant quantities of food reserves are lost through respiration during storage. McKay recommended storing Douglas-fir between mid-January and mid-March, and found that survival was better after storage at +2°C than after –2°C. McKay (1992) found that Douglas-fir lifted and stored in early fall had lower survival than did later-lifted stock, and that electrolyte leakage from fine roots was a good measure of seedling vitality. Mason and Sharpe (1992) reported that Douglas-fir lifted and stored in mid-December survived and grew well. McKay and Mason (1991) found that post-storage survival of Douglas-fir that was lifted and stored in the fall was relatively low. They also found that the correlation between survival and root electrolyte leakage was strong, and suggested that weather in Britain did not allow Douglas-fir to proceed normally through a dormancy cycle. O'Reilly et al. (1999) found that the mitotic index of Douglas-fir seedling shoots was at a minimum in November-February, while that of roots was erratic for this period, but generally high. Cold hardiness was affected by weather, but was maximal in November-February; seedlings lifted and directly planted survived well during late winter and spring. They emphasized that the dormancy cycle in northern Britain and Ireland differed from that in northwestern North America.

Table 8.3 Effects of a daily photoperiod during cold storage upon the growth responses of coniferous seedlings.

Previous trials			
Douglas-fir seedlings stored from mid-October to mid-November and then placed in a growth-promoting environment.			
Seedling mortality	5%		
Photoperiod	8 h		
Dark	55 h		
Douglas-fir seedlings stored from mid-January until mid-April were then outplanted and mean date of seedling bud break tallied.			
		Date of bud break*	
Mean	Dark	8-h daily photoperiod	16-h daily photoperiod
50%	June 4	June 2	May 26
	May 31	May 27	May 19
Douglas-fir seedlings maintained from mid-January until September in a constant 4°C environment			
		Date of bud break*	
	Dark	8-h daily photoperiod	16-h daily photoperiod
	September	August 2	July 15

*Only seedlings with 16-hour daily photoperiod had a normal budbreak.
All the above seedlings were stored at a constant 2°C. Light intensity was 500 Lux.

Table 8.4 Storage condition and survival for seedlings lifted in October.

Storage Condition		Survival (%)
Light (1 mo)	Warm roots (20°C)	100
	Cold roots (5°C)	95
Dark (1 mo)	Warm roots (20°C)	90
	Cold roots (5°C)	45

Van den Driessche (1977) showed that Douglas-fir of any provenance stored poorly at −5°C to −9°C. He found that "cold storage at 2°C in a sealed plastic-lined paper bag, satisfied the chilling requirement for bud flushing in two coastal provenances of Douglas-fir to the same extent as open nursery conditions" (p. 130). A comparison of European and North American results demonstrated that the dormancy cycle in Douglas-fir in the northwestern United States is strongly influenced by summer drought and cold in the winter, and is definitely different from that in Britain. Carlson et al. (1980) presented a figure that relates the various concepts of dormancy. They noted that "the expansion of preformed stem and leaf primordia occurs during the bud scale initiation phase. Free growth can occur during the rapid leaf initiation followed by a return to bud scale initiation. Vegetative bud set occurs at the end of scale initiation" (p. 371).

Hawkins and Binder (1990) summarized research on the concept of mitotic index to that date:

> The wide operational use is probably due to its apparent complexity and lack of applied operational publications. However this should not detract from the test. There are sufficient data to suggest that M.I. could play an important role in optimization of stock quality during the bridging phase (lifting to planting hole) in conjunction with testing of seedling stress resistance. For example in Douglas-fir, M.I. should remain at or near zero for seven days prior to lifting and storage. (Hawkins and Binder 1990, p. 104)

One of the weaknesses of studies of the gross morphology of the apical shoot, however, is that they do not identify the stage of dormancy at a given time. Techniques such as the OSU vigor test (McCreary and Duryea 1965) are acceptable, but require several weeks. Interest in more rapid evaluation of dormancy status has stimulated research in the areas that follow.

Chlorophyll fluorescence

Hawkins and Lister (1985) discussed chlorophyll fluorescence and the measure of the state of the photosynthetic complex in seedling foliage (chlorophyll a and b carotenoid contents), concluding that such data may well be correlated with phases of dormancy. The advantage is that fluorescence measurements may be made non-destructively and rapidly. Binder and Fielder (1996) suggested that fluorescence curves may be used to estimate dormancy, but their data reflected more correspondence between fluorescence characteristics and frost resistance than dormancy. Binder et al. (1997) noted that "chlorophyll fluorescence is a non-destructive and rapid assessment of in vivo photosynthetic activity." It follows, then, that for chlorophyll fluorescence to identify discrete stages in seedling dormancy, such stages must differ abruptly and sharply in photosynthesis. We know of no data to support this hypothesis. As Binder et al. (1997) noted, however, "before chlorophyll fluorescence can be widely used for forestry applications, standardization of techniques and fluorometer parameters are required" (p. 64). They summarized a wide range of trials, all involving physical damage to seedlings, in which chlorophyll fluorescence could successfully estimate seedling performance.

Perks et al. (2001) presented a detailed summary of chlorophyll fluorescence characteristics and relationships:

> Measurements of root growth potential (RGP) can be preempted by using assessments of shoot photosynthetic processes, under ideal conditions. . . . The positive relationship found suggests that photosynthetic reactivation is rapid after removal from cold storage to conditions "ideal" for growth, and this result may be of particular relevance in post-planting assessments, that are used for prediction of survival. The findings also suggest that RGP may not necessarily predict future performance and field survival, as poor root growth was evident for plants which established successfully. . . . This reinforces the notion that R.G.P. provides unreliable estimates of the quality of cold stored stock . . . and should not be used as a stand-alone test. (Perks et al. 2001, p. 233)
>
> The relationship between measures of RGP and PSII photochemistry offers the potential for a significant reduction in the time required to predict the ability of the plant to produce new roots, under favorable conditions . . . but the utility of such measurements in predicting seedling survival appears limited. . . . Thus, modulated fluorescence measurements have the potential to provide an "instantaneous" measure that, with further parameterisation to take into account seasonal variability, could be used to identify and predict the vitality of stock, particularly that previously subjected to cold storage. (Perks et al. 2001, pp. 233-234)

Dormancy and the Concentration of Inorganic and Organic Constituents

We found little material with reference to dormancy and the concentration of inorganic and organic constituents in the literature. Tables 8.5 and 8.6 are from Ketchie and Lopushinsky (1981, pp. 4-5) and represent values of root pressure exudate. Aspartic acid, glutamic acid, and glutamine were the main amino acids in the exudates from all species. This finding is similar to the results reported by Barnes (1963) and is to be expected, since these compounds are the main amino acids involved in xylem transport of N and in the transamination process. Exudates from Douglas-fir also contained large amounts of leucine and alanine. Grannel et al. (1990) found a constant level of 10% to 15% dry weight of non-structural carbohydrates, which rose sharply with growth initiation in April. (Krueger and Trappe 1967) presented a detailed description of food reserves in Douglas-fir seedlings and associated growth:

> Increased root activity was strongly correlated with lowered reducing sugar concentrations in seedling roots of the faster growing source. Sucrose and raffinose increased markedly during early winter and were apparently converted to starch in spring prior to growth. Concentrations of reducing sugars, crude fat, and protein nitrogen changed little with seasons. . . . (Krueger and Trappe 1967, p. 192)
>
> Starch in tops remained low in autumn and early winter, but increased rapidly beginning in March. . . . A peak was reached by mid April, followed closely by a rapid decline. Subsequently, concentrations increased moderately during June and July. (Krueger and Trappe 1967, p. 198)

Lopushinsky (1980) and Ketchie and Lopushinky (1981) examined the root exudates of 2-0 Douglas-fir seedlings. Lopushinsky (1980) noted the following: “The fact that exudation occurred from the bare-root

Table 8.5 Concentration of constituents in root pressure exudates from individual Douglas-fir seedlings.

Seedling number	Concentration (%)							
	Sugars	Amino acids	Organic acids	N	K	Ca	Mg	pH
1	0.20	0.01	0.01	0.011	0.016	0.007	0.001	5.4
2	0.12	0.01	0.01	“	“	“	“	5.4
3	0.23	0.01	0.02	“	“	“	“	5.4
4	0.21	0.01	0.03	“	“	“	“	5.4
5	0.13	0.02	0.01	0.014	0.018	0.004	0.001	5.4
6	0.25	0.03	0.01	“	“	“	“	5.4
7	0.29	0.03	0.01	“	“	“	“	5.4
8	0.34	0.04	0.01	“	“	“	“	5.4
S.E.[a]	± 0.08	± 0.01	± 0.01	± 0.001	± 0.001	± 0.001	-	-
Composite[b]	0.18	0.02	0.01	0.011	0.019	0.005	0.001	5.4

[a] S.E. = standard error

[b] Combined sap samples from eight other seedlings.

From Ketchie and Lopushinsky (1981).

Table 8.6 Sugars and amino acids in root pressure exudates of conifer seedlings.

Species	Sugars	Amino acids
Engelmann spruce	[a]	Aspartic acid, leucine, glutamine, glutamic acid, glycine, serine
Grand fir	Glucose, fructose, sucrose, unknown 1[b], unknown 2[c]	Aspartic acid, asparagines, glutamine, glutamic acid, glycine, serine, arginine, leucine
Noble fir	Glucose, fructose	
Lodgepole pine	Glucose, unknown 1[b]	
Ponderosa pine	Glucose, unknown 1[b]	
Pacific silver fir	Glucose	Aspartic acid, glutamine, glutamic acid, leucine
Douglas-fir	Glucose, unknown 1[b,d], unknown 2[c]	Aspartic acid, arginine, asparagine, alanine, leucine, glycine, serine, glutamine, glutamic acid

[a] Sugar concentration was too low for identification.

[b] Unknown 1 had the same rf value on chromatograms as rhamnose.

[c] Unknown 2 had the same rf value on chromatograms as ribose.

[d] Unknown 1 was found in the exudates of only one of eight seedlings tested.

From Ketchie and Lopushinsky (1981).

Douglas-fir seedlings with completely subarized root systems lacking any root growth clearly demonstrates that exudation was not dependent on active root extension" (p. 278). He concluded,

> The reasons for the abundant and persistent exudation observed in the previous experiments are not entirely clear. Apparently the combination of healthy seedlings, minimum moisture stress as a result of enclosing the seedlings in plastic bags, and cold storage created conditions conducive to exudation. Exudation immediately after detopping normally occurs only in well-watered, turgid plants so moisture equilibration probably was a factor in the present experiments. However, prolonged cold storage of the seedlings probably was the key factor enhancing exudate production. It is well known that low temperatures favor starch-to-sugar transformations in plants (Meyer and Anderson 1952, p. 385-386; Siminovitch and others 1953). An increase in soluble sugars could influence exudation both through stimulation of respiration-dependent ion transport into the root xylem, and a lowering of the osmotic potential of the xylem sap because of increased sugar content.
>
> The present results not only demonstrate the ability of these particular species to exhibit root pressure exudation but also emphasize that the failure of some conifers to show exudation under certain conditions is not conclusive evidence that it never occurs in those species. The results of the present experiments suggest that the best opportunity to observe exudation in field-grown conifers probably is during early spring following snowmelt because of a combination of desirable factors including ample moisture supply, low evaporative potential, and high plant sugar content. (Lopushinsky 1980, p. 279)

Roberts et al. (1991, p. 439) noted that a 30-kDa protein began to accumulate in the (terminal) bud tissue in early November and that by late November, this protein had reached its maximum level; it remained at this level throughout the winter. The apical bud began to swell in early April, and by the middle of the month, needles were protruding from the bud scales. The levels of the 30-kDa protein had declined to indetectable levels in seedlings by early April. Concentrations of reducing sugars, crude fat and protein nitrogen changed little with seasons. Starch intake remained low in autumn and early winter but increased rapidly beginning in March. Peaks were reached by mid-April followed closely by a rapid decline.

9. Cone and Seed Insects and Diseases

Denis P. Lavender

Although, strictly speaking, cone and seed insects are not part of the biology/physiology of trees, their impact on the production of viable Douglas-fir seed can be considerable, as Mattson (1978) noted: "Large fruit and cone crops preferentially mobilize and utilize an abundance of nutrients and photosynthates. In doing so they reduce cambial, shoot, root and leaf growth (Matthews 1963, Tappeiner 1969, Kozlowski and Keller 1966, Kozlowski 1971, Puritch 1972). Cone insects can drastically reduce the amount of nutrients and photosynthates that are allocated to reproductive structures because they kill the flowers, conelets, and cones early in their development before such structures have utilized large stores of energy and nutrients" (p. 339).[1]

Cone and Seed Insects

The first published reports that discussed insects associated with Douglas-fir cones and seed originated in Europe in the late nineteenth and early twentieth centuries. Early work in Europe (Wachtl 1893, MacDougall 1906a,b) focused on the genus *Megastigmus,* while investigations in North America were concerned with both this genus (Crosby 1909, 1913; Rohwer 1913; Miller 1916) and the genus *Barbara* (Cooley 1908, Miller and Patterson 1916). Dr. Fritz A. Wachtl first described *Megastigmus spermotrophus*[2] from insects that emerged from seed he received in Vienna in 1893. MacDougall (1906a,b), Crosby (1909), and Rohwer (1913) all presented data describing this same insect.

Early reports concerning cone and seed insects in the Pacific Northwest included those of Miller (1914 and 1916), Willis and Hofmann (1915), and Hofmann (1924). Miller (1914) noted significant damage to conifer seed by a number of unnamed insects in southern Oregon. Publications by silviculturists (Willis and Hofmann 1915, Hofmann 1924, Isaac 1943) detailing insect damage to Douglas-fir seeds were primarily taxonomic until about 1950, when interest in cone and seed insects increased markedly. This paralleled increases in both reforestation and in the development of seed orchards, which produced expensive seed in the western United States. The great majority of papers discussing cone and seed insects of Douglas-fir appeared during this 40-year period from about 1950 to 1990.

Keen (1958) listed more than 60 species of insects that have been reared from Douglas-fir cones and seeds. However, only 18 species were described as phytophagous, and only a scant half dozen of this group are sufficiently wide spread and numerous enough to have engendered appreciable research. Accordingly, this discussion will be limited to the following insects, which most authorities (Keen 1958, Koerber 1960, Schowalter et al. 1985, de Groot et al. 1994, Meso 1979, Miller 1986a, Miller and Ruth 1989) consider to have the most important impacts on Douglas-fir cones and seeds. *Megastigmus spermotrophus* (Hymenoptera: Torymidae), *Barbara colfaxiana* (Kearfott) (Lepidoptera: Olethreutidae), *Contarinia oregonensis* (Diptera: Cecidomyiidae), *Dioryctria abietella* (Denis & Schiffermüller 1775)(*Lepidoptera, Phyoitidae*), *Leptoglossus occidentalis* (Heidemann) (Hemiptera: Coreidae) and three insects, whose damage is generally minor, but which maybe important in some areas: *Lepesoma lecontei* (Coleoptera:

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[1] Obviously this does not apply to *Megastigmus*.

[2] The name "*Megastigmus spermatotrophus,*" which appears in some references, has been retained in quotations only.

Curculionidae), *Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae) and *Contarinia washingtonensis* Johnson (Diptera: Cecidomyiidae).

Keen (1958) reported that,

> the cones of Douglas-fir are infested with a great number of species of insects, the most destructive being a seed chalcid and two species of moths [Bedard 1938]. In general about 10 percent of the seed crop is destroyed by these insects, although in different localities, and in different years the damage may vary from practically nothing to 50 percent or more of the seed destroyed. The insect damage is usually heaviest in years when the seed crop is light [Hofmann 1920]; and in any one year the damage is usually worse in the warmer places [Hofmann and Willis 1915]. (Keen 1958, pp. 26-27)

The following species have been cited as of economic importance (Keen 1958, p. 27): *Barbara colfaxiana* vars., *Dioryctria abietella, Eupithecia albicapitata* Packard, *Eupithecia spermaphaga* Dyar, and *Megastigmus spermotrophus* Wachtl. Johnson and Winjum (1960) concurred in the importance of the first two insects and the seed chalcid, but suggested the following species as more destructive in the Pacific Northwest than the two *Eupithecia: Henricus fuscodorsana, Contarinia oregonensis*, and *Contarinia* n. sp. The following sections will summarize some of the key research relevant to Douglas-fir seed and cone damage for several of the above insects.

Kozak (1963) conducted a lengthy, detailed analysis in British Columbia on the distribution of and interactions among three major species of insects that damage Douglas-fir seed: *Contarinia oregonensis* Foote, *Megastigmus spermotrophus* Wachtl, and *Dioryctria abietella* D. & S. The study was based on more than 7,500 cones total (taken from 93 trees in 1961 and 97 trees in 1962). Kozak (1963, p. ii) found high variation in damage among trees for each insect species: "In *C. oregonensis* this variation was significantly related to the height of the trees and dates when cones became pendent"; i.e., taller trees had greater attack. For *M. spermotrophus,* "the percentage of filled seeds and average cone size of the trees were important": greater attack was associated with a higher percentage of filled seed; smaller cones (with perhaps thinner cones scales) had greater attack. Finally, "average cone size of the trees and duration of vegetative bud flushing were significantly associated with For *D. abietella*": larger cones and short duration of flushing were associated with higher damage (Kozak 1963, p. ii). Data presented demonstrated that *C. oregonensis* was the most destructive and *D. abietella* was the least destructive to cones and seeds of the insects studied. Insect-caused seed loss varied widely with location and year, from less than 5% to more than 90% of Douglas-fir seeds. The findings showed that *D. abietella* damaged 18.2% and 5.7% of cones in 1961 and 1962, respectively (Kozak 1963).

Meso (1979) found that the greatest percentage of losses occurred in years of light to medium seed crops following years of heavy crops; Kozak (1964) noted that the greater the number of cones, the less insect damage per cone. In 1983, *C. oregonensis* and *M. spermotrophus* together destroyed 70% of Douglas-fir seed in 17 seed orchards in California, Oregon, and Washington (Schowalter et al. 1985). Hall (1955) noted that 97.8% of the seed was destroyed on the Klamath National Forest; 91.6% on the Six Rivers Forest, 53.2% on the Lassen; overall, during the light cone year of 1954, 82.2% of Douglas-fir seed was destroyed by insects.

Barbara colfaxiana

Barbara colfaxiana (Kearfott) insect was apparently discovered in 1900 by R.A. Cooley. Cooley prepared a bulletin, "The Douglas spruce cone moth," in which he identified it as *Cydia pseudotsugana* Kearf. Keen (1953) corrected the nomenclature to the present *Barbara colfaxiana.*

The adult insects emerge from overwintering pupae about the time the pollen matures on Douglas-fir trees. The female moth oviposits primarily in the late afternoon and evening. No preference is shown for levels in the crown, but exposed cones are attacked more frequently than are those shaded by foliage. The female deposits her egg on the outer surface of the bract (in areas of heavy infestation, several eggs may be deposited on a single bract). The pearl-colored egg is glued to the bract, where it remains for a 2- to 3-week incubation period. When the larva hatches, it must find the angle between the bract and the cone scale where it can force itself through the heavily pubescent surface of the scale to begin feeding. If the larva does not locate this point, it will perish. Mortality at this stage is generally high; as Hedlin (1960) noted, only 55% of the larvae were able to establish themselves in cone scales. And, even if the larvae are successful in penetrating the cone scales, many more are killed by high levels of pitch in the feeding tunnel. The initial tunnel is very small, but becomes gradually larger as the larva burrows towards the cone axis, feeding primarily on cone scale material. When the first seeds are destroyed, the larva is small enough to burrow into the seed; later it will consume the entire seed.

The insect passes through four instars by mid-July, and more than one larva may inhabit the feeding tunnels in the cone without cannibalistic behavior. The mature larva constructs a tough cocoon, which becomes covered with pitch adjacent to the cone axis, and pupates. The insect remains dormant in the cone until the following April or May, when most of the adults emerge. However, Hedlin et al. (1982) found that a significant proportion of the insects may enter a diapause of 1 year or longer, and hence avoid extreme competition for limited resources in years of light cone crops. The findings of Hedlin et al. (1982) are interesting in that they showed that factors such as daily maximum and mean temperatures during the period of larval development were strongly correlated with degree of diapause the following year and with the level of cone crops. When the year following larval development had no cones on Douglas-fir trees, as many as 80% of the *Barbara* pupae were in diapause.

Although by the time the insect has reached the fourth instar, one to three larvae may have consumed much of the interior of the cone, there may well be little external evidence of such activity in cones of coastal Douglas-fir. If, however, as many as five or six larvae are present, the cones wither prematurely. In contrast, the cones of var. *glauca*, which are somewhat smaller than those of var. *menziesii*, commonly have external signs of the presence of even a single larva.

Keen (1958) lists 12 hymenopterous species as parasites of *B. colfaxiana* and suggested that such parasitism, which can be as high as 83% of the cone moth larvae, is a major control of this insect. Hedlin (1960) noted that *Glypta evetriae* Cush. females lay eggs in early instar larvae of *B. colfaxiana*. The parasitized cone moth larva develops normally with the parasite feeding internally until the cone moth larvae spins a cocoon, at which point the parasite kills the host. Hedlin noted that only 2% of the cone moth eggs tallied on one tree produced larvae which lived to pupate, and that 92% of the pupae were parasitized by *Glypta*.

As in the case of *Megastigmus spermotrophus*, reports of damage caused by *Barbara colfaxiana* vary greatly, although the consensus of workers in the field is that this is a major predator of Douglas-fir seeds. Kozak (1963) was unable to find evidence of the cone moth in coastal British Columbia, but Radcliffe (1952) found that this insect destroyed about 60% of the seed on Vancouver Island, and that one larva per cone would consume about 45% of the seed, three would consume 75%, and more than three insects per cone, about 100%. Hedlin (1974) noted that *B. colfaxiana* was more damaging in the interior of British Columbia than in the wetter coastal regions. Schowalter et al. (1985) found that the cone moth was responsible for very little seed predation in Oregon and Washington, but other workers have identified significant seed loss due to this insect.

Volney (1984) and Koerber (1960) presented data demonstrating that although wild populations of *Barbara colfaxiana* may be limited by cone crop size, this insect can compete more effectively for the food resource than its competitors. Miller et al. (1984) found that the degree of damage to Douglas-fir seeds by *B. colfaxiana* in the interior of British Columbia, but not on the coast, was significantly related to the size of the seed crop the previous year. However, differences in cone crop size during the year of damage and seed predation were not correlated. Light crops following heavy crops during the 33-year study were generally heavily damaged. The authors suggested that the fluctuating cone crop size limits populations of *B. colfaxiana* in the interior of British Columbia (see Roy 1960).

Leptoglossus occidentalis

An insect first described by Heidemann (1910) is the western conifer seed bug, *Leptoglossus occidentalis* (Heidemann). It is widely distributed in the timber regions of western North America, where it feeds on a range of coniferous seed. Koerber (1963) presented a detailed life history of this insect. The larvae have five instars and feed on seeds during the summer months. The adults feed on the ripening seed in the fall, until cold weather when they find shelter; they reappear in mid-May to feed on year-old cones and seeds. The insect feeds by forcing its stylets into the seed, dissolving the contents with its saliva, and imbibing same. A slight wound is the only evidence of the insect attack, but the seeds are largely hollow because the endosperm has been destroyed.

Zhang and Schowalter (1997) reviewed the literature, noting that, "feeding by the seed bugs . . . causes an undetermined amount of seeds to abort or not fill out" (p. 29) Given this, the "conifer seed bug occurs sporadically and generally destroys fewer seeds" than does *Contarinia* or *Megastigmus*. However "at densities of 0.5 insects per cone, seed bugs significantly increased seed abortion—from 45 seeds in protected cones to 75 seeds in cones caged with seed bugs during seed development in June." The seed bugs "also significantly increased the number of partially filled seeds from 0.5 seed in control cones to 32 seeds in cones caged with bugs during July. Seed yields were reduced 20 to 30% by seed bugs feeding." Zhang and Schowalter (1997) noted that although the studies "indicate potential losses to seed bugs, methods for measuring seed bug populations in orchards are necessary to predict impacts on seed yields" (p. 29).

Bates et al. (2000a) reported the following:

1. The major storage reserves of Douglas-fir seeds are proteins and lipids, with the latter making up the greatest proportion of the dry weight of the seed. They further note that the feeding procedure of *L. occidentalis* is unknown and that it is difficult to determine whether blank seed are the results of the *L. occidentalis* feeding or some other cause, so that absolute damage by seed bugs remains unknown.

2. Seed lightly damaged by *L. occidentalis* had >55% reduction in both lipid and crystalloid protein resources and such seed showed a >80% reduction in germination.

3. Feeding by nymphs, adult males, and adult females was similar and resulted in a reduction of full seeds in cones of »70% in a 2-week feeding period, compared with coastal cones. Earlier feeding by nymphs resulted in a threefold increase in the number of unextractable seed.

Blatt and Borden (1996) found that *L. occidentalis* occurred in patches and showed a clonal preference; interestingly, seed losses from this species were less than 5%. In a subsequent study, Blatt and Borden (1998) found that seed bugs did not feed on seed infested with *Megastigmus*, although they could feed on *Megastigmus* larvae. The authors concluded that "the impacts of *L. occidentalis* and *M. spermatotrophus* are segregated and additive" (p. 775). Lait et al. (2001) reported the development of a polyclonal antibody that can identify salivary gland extracts of *Leptoglossus occidentalis* and which is useful in identifying light to severe damage of Douglas-fir seed.

Schowalter and Sexton (1990) examined the possible effects of the timing of seed bug feeding on Douglas-fir in seed:

> Results of this study supported the hypothesis that seed bug feeding on Douglas-fir seed has different effects at different stages of seed development. Seed bugs caused substantial seed abortion, >50% greater than control levels . . . during the early and mid-stages of seed development. Significant increases in partially filled seed resulted from seed bug feeding during mid- and late stages of seed development.
>
> While partially filled seed is detectable by X ray and has been a recognized effect of seed bug feeding on Douglas-fir seed (Koerber I963), seed abortion has been attributed to other, largely unknown factors (Dombrosky & Schowalter I988, Schowalter et al. 1985). Unexplained abortion typically ranges from 30-80% of potential seed among Douglas-fir seed orchards (Dombrosky and Schowalter I988, Schowalter et al. 1985). A 50% increase in aborted seed resulting from seed bug feeding, at densities comparable with those observed in seed orchards, suggests that effects of *L. occidentalis* on Douglas-fir seed production has been greatly underestimated. (Schowalter and Sexton 1990, p. 1486)

Theisen (1976, p. 2) noted that damage at an Oregon seed orchard had been severe, with damage to full-size seed as high as 80%. It is interesting that the only post-1990 reports concerning insects and Douglas-fir seed known to the present authors discuss the seed destruction by *Leptoglossus occidentalis*.

Megastigmus spermotrophus

The genus *Megastigmus* in the family Torymidae (superfamily Chalcidoidea, order Hymenoptera) contains about 40 species, of which one-third are known to feed upon coniferous seeds (Milliron 1949, Hanson 1952, Keen 1958). The Douglas-fir seed chalcid (*Megastigmus spermotrophus* Wachtl) probably has been the subject of more research than any of the other insects known to damage Douglas-fir seed. Undoubtedly, its life cycle, which favors distribution of the insect with the seed, is the major reason for the relatively wide-spread interest in this wasp.

The geographical distribution of this species follows well the distribution of its host. Infestation is reported on Douglas-fir from California, Idaho, Colorado, Washington, British Columbia, Oregon, and New Mexico (Keen 1958). It was introduced in infested seeds to Great Britain, western Europe, and New Zealand. Jarry et al. (1997) discussed the movement of *Megastigmus* in France, and its invasion in seed orchards. This insect almost certainly feeds on seeds of Douglas-fir only.

The life history of *Megastigmus* is well studied, but little is known about the ecological factors affecting the distribution and intensity of attack. Hussey (1955, 1956) published a detailed study on the life history and habits of this species. Mating takes place on the Douglas-fir needles soon after the adults emerge from the pupal stage. The female can lay fertile eggs without fertilization, but all the adults from such parthenogenetic eggs are males. The act of oviposition was described by Miller (1916). He reported that the female rests on a cone scale with her head pointed toward the base of cone, drives her ovipostor through the cone scales and deposits an egg in a young seed. Two to five minutes are required for oviposition. According to Hussey (1954), normally only one egg is laid in a seed, but where there is considerable competition between the egg-laying females for seed, as many as seven eggs are found in one seed. Only one larva develops to the adult stage when several eggs are laid within the same seed. No specific information is available on whether or not the female would lay an egg into an unfertile or empty seed, although it is known that a potentially sound seed is necessary for the development of a *Megastigmus* larva. It is conceivable that the female selects by some means the fertilized seeds for oviposition, which is indicated by the fact that she spends a considerable time “choosing” the scale into which her ovipostor is inserted.

The earliest reports describing *Megastigmus spermotrophus* Wachtl appeared in European journals. As previously noted, the insect was first described and classified by Wachtl in Vienna in 1893. Contrary to the general belief of entomologists of the time concerning *Megastigmus* spp., Wachtl noted that this wasp is phytophagous. His conclusion was supported by a number of papers published in the early part of the twentieth century (MacDougall 1906 a,b; Crosby 1909, 1913; Rohwer 1913; Miller 1914, 1916). These reports outlined briefly the life history of this insect as follows. The adults emerge in the spring about the time that the young Douglas-fir cones are turning down and are still relatively unlignified. The female inserts her ovipostor directly into the developing seed to lay a single egg. The insect is apparently able to detect the presence of the seed, but not whether it contains an egg laid by another *Megastigmus*. If more than one egg is laid in a seed, only one larva will survive. The larva develops during the summer, feeding on the contents of the seed until, in the fall, it occupies the entire seed cavity. The larva overwinters in the seed. If the seed remains in the cone, the larva is subject to parasitism by the larvae of *Amblymerus apicalis*. Or, if the seed is released from the cone, the larva is subject to predation by seed eating mammals (Hussey 1955). If the larva survives the winter, it may pupate and the adult emerge in a rather restricted period of 2 weeks (between mid-May and mid-June in Britain), depending upon the latitude (Hussey 1955, 1956).

Hussey noted further that the development of *Megastigmus* is much more closely controlled by temperature than is the development of Douglas-fir cones. For example, the time of earliest *Megastigmus* emergence varied from May 20 to June 4 in three consecutive years. But, during the same years, the time of maximum susceptibility to attack of the cones varied only 5 days (June 8–13). It was found that pupal development had a threshold temperature of 5.8°C and that about 390 degree-days (in excess of 5.8°C) were required to complete pupation. Therefore, since the period when the cones are subject to attack is relatively short, either an unusually warm or cold spring may result in the peak of insect emergence and activity before or after, respectively, the optimum time for oviposition. Such years obviously provide a check on *Megastigmus* populations. However, low temperatures during the spring months frequently increase the number of larvae that remain in diapause for a second or third year, a strategy which appears to be the insect's *modus operandi* for dealing with the widely fluctuating production of cones by Douglas-fir from one year to the next. And, not only does cold weather delay the development of the adult insect, it inhibits the ability of the female to oviposit, according to Miller (1964), who found that the females were active primarily during sunny days in southern Oregon.

Hussey (1955, 1961) observed that the optimum time for oviposition differed between the cones of variety *menziesii* and variety *glauca* trees in Britain. The former were successfully attacked after they were pendant, 4 to 8 cm in length, and until all but the apical fringe of the scales was brownish. This period commonly extends from 2 to 3 weeks. The cones of the variety *glauca* trees are most susceptible to attack when the cones are nearly full grown, 4 to 6 cm in length, and the ovuliferous scales are a deep mauve pink.

The larvae hatch a few days after the eggs are laid. Larval development proceeds through five instars until, at the end of 6 to 7 weeks, the mature larva has eaten the contents of the seed and occupies the entire megagametophyte cavity. The seed coat and testa develop normally, and the infested seed cannot be separated from sound seed by external examination. Larvae then enter a resting stage, which most commonly lasts until the following spring; in cooler climates such as northern Britain, however, as many as half of the larvae may not pupate for an additional year or two. The delayed pupation means that the level of infestation for any one year is related to the levels of infestation and the size of the cone crop for the previous two years. Roux et al. (1997) noted that low temperatures described as "chilling" are required for diapause to be complete (p. 176).

Graham and Prebble (1940, 1941) noted that crown position, cone size, tree age, and tree position all can affect the level of insect infestation. Findings in subsequent studies varied greatly, both within a given species and between species, in level of insect predation upon Douglas-fir seed. Kozak (1963) reported a significant level of damage by *M. spermotrophus* in cones collected in coastal British Columbia and no evidence of damage by *B. colfaxiana*. In contrast, Hedlin (1964a) working in the same area, reported substantial damage by *B. colfaxiana* and only light predation by *M. spermotrophus*. Schowalter et al. (1985) noted increasing damage by all insects from north to south between British Columbia and northern California. And Baron (1971, p. 491), noted heavy insect damage of Douglas-fir in California. Finally, both Hedlin and Ruth (1978) and Schowalter and Haverty (1989) reported clonal differences in Douglas-fir in resistance to *M. spermotrophus* attack. However, the former authors noted that such differences probably have no practical significance.

Hofmann (1924) observed that "when the seed crop is light the seeds are generally attacked by an insect (*Megastigmus spermatotrophus* Wachtl), which destroys before maturity a large percent of the few seeds which would otherwise be produced" (p. 49). Overall the degree of seed damage by *M. spermotrophus* reported varies from less than 10% of sound seeds to more than 50% in western North America to almost 100% in Europe (Jarry et al. 1997, Krístek 1967, Lessman 1974). The much higher figure in Europe may reflect the fact that *M. spermotrophus* has no competitors in Europe, whereas it does not compete well in North America against *B. colfaxiana* (Volney 1984) or *C. oregonensis* (Rappaport and Volney 1989).

Later reports (Niwa and Overhulser 1992, Rappaport et al. 1993, Skrzypczynska 1994), however, suggested that the earlier reports, which based measures of damage by *M. spermotrophus* on the hypothesis that the insect attacked only those seeds whose female gamete had been fertilized, were incorrect. They found that when an egg of *M. spermotrophus* is laid in a seed that contains an unfertilized gamete, the seed will continue to develop. Normally, the contents of seeds of Douglas-fir that are not fertilized will be resorbed by the plant (Allen and Owens 1972) and such seeds will then be tallied as empty. This suggests, then, that the level of damage occasioned by *M. spermotrophus* is a function not only of the frequency of such attacks, but also of the degree of fertilization of the seeds. Accordingly, previous estimates of insect damage have been either slightly high, when there was a high level of successful fertilization, to as much as 50% too high, when there were low levels of pollen.

Contarinia oregonensis

Hedlin (1974) and Miller and Ruth (1989) reported that the Douglas-fir gall midge, *Contarinia oregonensis,* is one of the most serious pests of Douglas-fir cones, particularly in the wetter portions of its range in British Columbia. Owston and Stein (1974) agreed that it is a serious pest of Douglas-fir seed. Schowalter et al. (1985) noted an increasing incidence in western Oregon and Washington, however, and reported that *C. oregonensis* and *M. spermotrophus* together had destroyed 70% of the filled seed in seed orchards (1985, p. 1228). As many as 30 *C. oregonensis* larvae may form a single gall, which will destroy both seeds on the scale. More commonly, the major damage is caused by the galls, which make extraction of the seeds from the cone impossible.

The adult insects emerge from cocoons in the litter in early spring and are the first insects to lay eggs, frequently before the abortion of conelets is complete. Volney (1984) reported that conelet abortion was 50% in 1980 and 30% in 1981 in California. The midge lays eggs near the ovules. The eggs hatch in 2 to 3 weeks, when the larvae invade the seed tissue and cause a gall to form around the seed. This gall may either fuse the seed and cone scale, which either effectively prevents the extraction of the seed or inhibits further seed development. Johnson (1963a) noted that the cone midge is capable of attacking the cones only while they are receptive to pollination, a period of 7 to 10 days. As a consequence, a major portion of the mortality of the larvae may be caused by death of the cone before the development of the insects.

Although the cone moth, *B. colfaxiana* is capable of destroying the gall midge galls and larvae, the two species apparently can co-exist in the same cone. However, Stein et al. (1988) reported data suggesting *Lepidoptera* predation of *Contarinia*, and Miller (1984a) noted that numbers of midge larvae were reduced from 193 to 8.3 per cone in cones with 2 *Lepidopterous* larvae per cone. This may occur only when there are light cone crops. In a 6-year study Hedlin (1964a) found that the gall midge larvae were always more numerous than those of other insects. One possible reason is that *Contarinia* is capable of colonizing the sterile cone scales at the base and tip of the cone, which are not attractive to its competitors (Volney 1984). Even so, however, several studies (Rappaport and Volney 1986, Miller 1986a, Schowalter and Sexton 1990) reported a high propotion of *C. oregonensis* larvae in the mid-cone area.

Once the gall is formed, the larvae remain in a V-shaped configuration, where they obtain most of their food by absorption (Hedlin 1961a) until the fall, when they complete their development and it drops to the ground. There are three larvae instars (Hedlin 1961a). The larvae will not leave the cone until fall rains moisten it and low temperatures favor the exit of the larvae (Hedlin 1959). Often, larvae will select an old male cone in which to make a cocoon and overwinter; however, *C. oregonensis* may have a diapause as long as 4 years (Miller and Hedlin 1984, Danks 1987). Both Miller (1986a) and Schowalter et al. (1986) reported clonal differences in the infestation of Douglas-fir cones by the cone gall midge. But, while the former noted that such differences were not significant, Schowalter et al. (1986) reported statistical significance in their data and suggested that the two-fold difference between families with high infestation and those with low is heritable.

About half of the pupae enter diapause each year (Johnson and Winjum 1960, Hedlin 1961a, Hedlin et al. 1980, Schowalter 1984). This trait, together with the fact that the insect is well adapted to its environment, assures continuing populations, as Hedlin (1961a) observed: “adults are active over a wide range of temperatures and so are able to deposit eggs even under relatively unfavorable weather conditions. In the autumn, larvae are able to survive for long periods in dry cones, and after leaving the cones, in winter. Larvae concentrate in litter below the tree. This concentration of population probably facilitates mating when males and females emerge in the spring” (p. 965). Given the foregoing, the lack of consistent effect of cold misting upon midge infestations (levels of insect attack were significantly reduced only when the cold mist caused a greater than 10-day delay in bud activity) may have been due to the fact that the midge was able to oviposit during the application of mist (Miller 1983).

Two parasites of *Contarinia oregonensis, Torymus* sp. and *Platygaste* sp., have been observed, but neither caused a high level of mortality (Hedlin 1961). These data were confirmed by Miller (1984b), who noted that numbers of eggs deposited accounted for 73% to 100% of the variation in midge populations, and that the incidence of parasitoids was small. However, Johnson and Heikkenen (1958) noted that an unidentified species (Chalcidoidea) parasitized 40% of *C. oregonensis* in some cones. Miller also suggested that predation by the larvae of cone moths or worms may have accounted for some midge mortality, but that neither are commonly present in high numbers on the British Columbia coast.

Contarinia washingtonensis

The presence of a second species of Itonididae in Douglas-fir cones was first reported by Johnson and Heikkenen in 1958, but the insect was not identified. The following year, Hedlin (1959) described the Douglas-fir cone scale midge, *Contarinia washingtonensis* Johnson (Diptera: Cecidomyiidae), as follows: "Although this midge lives in close proximity to *Contarinia oregonensis* in Douglas-fir cone scales, it can be readily separated on the basis of appearance and habits" (p. 10). He noted that larvae of this insect were very plentiful and that mature larvae were deep orange in color, compared with the quite pale color of *C. oregonensis*. When feeding, the larvae lies along the cone scale fibers and does not form a gall. "Damage was observed readily in July when the larvae were reaching maturity. The areas where damage occurred turned brown, and expanded as feeding increased. By the time the larvae are fully grown, they may be lying almost fully exposed on the inner surface of the scale, and at this time leave the cone readily"; and that there were as many as 36 larvae found per scale. "Examinations were not carried out to determine the extent of damage caused by these insects but there is no doubt that they contribute to seed loss" (Hedlin 1959, p. 11). However, Miller and Ruth (1989, p. 30) found that *C. washingtonensis* rarely consumes seed.

Subsequently, Johnson (1963a) published a description of this insect, which he named *Contarinia washingtonensis*. He noted that *C. washingtonensis* is generally smaller than *C. oregonensis*, that the adults lay eggs beneath the long bracts after the cones are pendant and closed (about 3 to 5 weeks later than *C. oregonensis)*, and that the larvae leave the cones early in the fall, in contrast to those of *C. oregonensis,* which remain in the cones until onset of fall rains. A further difference between the species is that *C. washingtonensis* larvae feed on the cone scales at some distance from the seeds and do not form galls. Hedlin and Johnson (1963) confirmed the foregoing, noted that the orange colored larvae of *C. washingtonensis* seed fully extended rather than in a curved position, and reported damage by this species in western Washington of up to 47% of the seed. They suggested that this insect has a more flexible life cycle than that of *C. oregonensis* and may pose a significant threat to seed orchards.

Hedlin and Johnson (1963) contended that "the midge, *Contarinia washingtonensis* is capable of causing serious seed loss in Douglas-fir" (p. 1168). Johnson and Winjum (1960) described the Douglas-fir scale midge as "an undescribed species found attacking the cones of Douglas-fir. It has been abundant the last two years in Washington and also in British Columbia. The adults emerge from the soil where larvae have over wintered in cocoons and deposit their eggs under the bract of the pendant cone in early June. The larvae upon hatching from the egg bores into the cone scale where they feed" (p. 10). Johnson (1963a) presented a detailed anatomical study of this insect, described the species, and reported the morphological characteristics of the different stages (see also Hedlin and Johnson 1963). The females lay eggs when the cones are closed and pendent. The eggs are laid beneath the bracts of cones. The newly hatched larvae mine in the cone scales and do not cause galls, like *Contarinia oregonensis* larvae, when the cones are still greenish. The authors could find no information on either the ecology of the insect, or on the factors affecting the insect in the different stages of development.

According to Johnson and Hedlin (1967), "adults emerge during late May and early June to lay their eggs in young cones about the time foliage buds are bursting. The eggs are laid in small clusters in the angle between the cone bract and scale. Young larvae tunnel into the cone scale tissue where they feed in the central part of the scale, usually in small groups. Infested scales turn brown before the cones are mature, but galls are not formed" (p. 5). Theisen (1976) reported, however, that the "*Contarinia* midge adult lays eggs near ovules when flowers are open for pollination. Damage to seed slight, usually no external evidence of damage" (p. 4).

Dioryctria abietella

Yates (1984) gave the following overview of *Dioryctria abietella* Denis & Schiffermüller (Lepidoptera: Pyralidae, Phycitinae):

> If there is one genus universally identified as a conifer cone and seed destroyer, it is *Dioryctria*—the cone worm. Best known is the cone pyralid, *D. abietella* (Denis and Schiffermüller), which is one of the most widespread cone and seed insects in the world. The distribution of *D. abietella* includes Europe westward through Asia to Japan and southward into Pakistan and India. Hosts include nearly all conifers growing within this region. Because of this species' wide distribution and varied host preferences, the biology varies considerably. (Yates 1984, p. 33)

Dioryctria abietella has not been intensively studied on Douglas-fir. The work that has been done indicates the wide range of distribution and habits of the insect. The wide distribution of the species is shown by the fact that specimens in the United National Museum are from *Abies* spp., Douglas-fir, and all *Pinus* spp. in North and Central America, from the Canadian provinces of British Columbia and Newfoundland and Labrador south to Guatemala.

Lyons (1957) noted that *D. abietella* "infests the cones, shoots, and bark of many conifers, and is apparently Holarctic in distribution" (p. 71). It may produce "two generations per year in the western United States" (p. 76), and has been reported overwintering in several different stages, partly grown larvae, prepupae and pupae. According to Johnson and Hedlin (1967),

> This insect occurs sporadically but is capable of causing considerable destruction. The moth usually emerges in spring but may emerge in the fall. The egg laying habits are not fully known, but eggs laid in the spring hatch in early summer. The larva feeds in a manner similar to that of the Douglas-fir cone moth, except that it feeds throughout the cone and one larva may destroy a cone completely. Large quantities of frass are common on the surface of infested cones (Figure 2). The larva is larger and darker in color than that of the Douglas-fir cone moth. In the fall, the mature larva leaves the cone to spin a soft round cocoon in which to overwinter. The immature larva remains dormant over winter to resume feeding in the spring and complete its metamorphosis in late summer. (Johnson and Hedlin 1967, p. 2)

The life history of *Dioryctria* is not yet clear. Keen (1958) also noted that there may be two generations per year. With global warming there will probably be two generations in the range of Douglas-fir. Lyons (1957) found only one generation per year in Ontario. As Keen (1958) described, some eggs are deposited by moths reaching the adult stage in October. More eggs are deposited by another group of moths that emerge in May or early June. After hatching, the larvae bore through the scales and feed indiscriminately on scales, bracts, and seeds. As the cones ripen, the larvae leave them and form their cocoons on the ground. Some of them pupate immediately and emerge in October; the rest of the population (probably most of them) spends the winter as prepupal larvae, and pupates and emerges the following spring. No information is available on diapause in this species.

The eggs are 1 mm long, white, oval, and flattened with finely roughened surface. Larvae have five instars with respective headwidths of 0.45, 0.71, 1.10, 1.35, and 1.70 mm (Lyons 1957). They are red or purple in color, sometimes with a greenish tinge. The absence of anal comb helps to distinguish *Dioryctria abietella* from the Douglas-fir cone phaloniid (*Henricus fuscodorsana* (Kearf.). The pupa is 10 to 12 mm long, with straight, slender caudal hooks. The forewing of adults is predominantly grey, with white transverse zig-zag lines. The wing spread of adults was described as 23 to 28 mm by Lyons (1957).

Koerber (1960) stated that "the larvae of *Dioryctria abietella* usually do not bore as deeply into the cones as do the larvae of *Barbara colfaxiana*. As a result less seed is destroyed by *Dioryctria abietella*" (p. 11). But Johnson and Hedlin (1967) noted that the larvae feed throughout the cone and that one may destroy all of the seed.

According to Koerber (1960),

> There is almost no information on ecological factors which might affect this species. Only six species of parasites and predators are known to attack it in western North America. Its wide distribution might be taken to indicate a tolerance for a wide range of climatic conditions. Because of its variable feeding habits, population levels of *Dioryctria abietella* are probably relatively independent of the supply of cones and thus are not likely to suffer from competition for food supplies.

Kozak (1963) noted that the level of damage to Douglas-fir cones by *D. abietella* was highly variable (5.7% to 18.2% cones damaged) and that this species was less important in coastal British Columbia than were *Contarina* spp. or *Megastigmus spermotrophus*. Hedlin (1958) did not include it in his survey of insect damage in British Columbia; Schowalter et al. (1985) noted that *D. abietella* was not a major pest of Douglas-fir seed and cones in western Washington and Oregon, but that the damage from this insect increased from north to south. Ruth (1980) found that while rarely present in large numbers, larvae of *D. abietella* may destroy all the seeds in a cone by indiscriminate feeding on cone scales and seeds. The damage is characterized by large holes, coarse frass on the exterior of the cone, and, in the case of Douglas-fir, almost complete destruction of the cone (Hedlin 1974).

Fatzinger and Asher (1971) reported that *D. abietella* males were attracted to females by a sex pheromone; Coulson and Franklin (1970) presented a review of a closely related species, *D. amatella,* and emphasized the complexity of the life cycle and the great variety of structures colonized. Although Rappaport and Volney (1989, p. 146) suggested that damage by *C. oregonensis* may be reduced by *D. abietella*, their data showed that any such differences were not significant.

Lepesoma lecontei

Schowalter (1986) and Dombrosky and Schowalter (1988) suggested that a flightless weevil, *Lepesoma lecontei* (Coleoptera: Curculionidae), may have been responsible for seed losses (5.8%) equivalent to those caused by *Megastigmus* or *Contarinia* in seed orchards of the Pacific Northwest in 1984 and 1985. Surveys of arthropods emerging from Douglas-fir litter in a 50-year-old Douglas-fir stand in seed orchards (Schowalter 1984a) demonstrated that populations of *Lepesoma* were greater in seed orchards, so it is not clear (1) whether the seed orchard data reflected conditions in "wild" forests and (2) whether the management of the seed orchards in some way favored the life cycle of *Lepesoma*. It is interesting that the damage to the early stages of ovulate strobili strongly resembled frost damage; this may have been the reason that the extent of damage caused by this insect was not recognized earlier. Schowalter (1986) demonstrated that the damage caused by *L. lecontei* was the result of conelet destruction rather than feeding on a seed.

Choristoneura occidentalis

The western spruce budworm, *Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae), is commonly considered to be a defoliator rather than a predator of cones and seeds. But studies from the Rocky Mountains have reported that this insect can be responsible for significant destruction of developing cones. The first report of budworm damage to Douglas-fir cones (Dewey 1970) indicated that this insect destroyed an average of 36% of the seeds in Montana and in Yellowstone National Park and that it was by far the most numerous of 13 seed and cone insects collected. He noted that several second-instar larvae might be found in one cone with other insects. But a single fifth- or sixth-instar larvae could destroy all the seeds in a cone and might consume the larvae of *Megastigmus* or *Contarinia*. Larval development was generally complete by mid-July, when the larvae formed a pupae, sometimes in the hollowed-out remainder of the cone. Shearer (1984) confirmed Dewey's (1970) data for western Montana, although the proportion of Douglas-fir seed reported destroyed by budworm was lower. Finally, Frank and Jenkins (1987) found that the western spruce budworm caused significant damage to all reproductive structures on Douglas-fir in west-central Idaho, and that the number of seeds destroyed was exponentially related to the degree of defoliation this insect caused. According to Reardon et al. (1985),

> In the northern Rockies, the most serious pest affecting Douglas-fir cones is the western spruce budworm, *Choristoneura occidentalis.* Early instars of the western spruce budworm can destroy conelets before and after pollination, whereas later instars feed on the many developed cones. . . . Larvae often feed on more than one cone during their development, and most seeds in infested cones are either destroyed directly or retained within cones because of growth distortions and excess rosin exudation induced by insect feeding. (Reardon et al. 1985, p. 961)

Diapause

Dormancy in insects or "diapause" has been described as a "'physiologically' controlled ... programmed rest of growth, development, or reproduction resulting in a reduction of active physiological functions" (Danks 1987, p. 8). It is discussed in detail in Danks (1987); however, the following points drawn from that reference are helpful for this discussion (numbering added):

> 1. Insect life cycles are timed so that active stages coincide with favorable conditions so that periods that do not provide requirements for development can be passed safely. (Danks 1987, p. 4)
>
> 2. Diapause affects food storage, largely fat and general biochemistry. (Danks 1987, p. 19)
>
> 3. Insect structure is more resistant to drought in diapause. (Danks 1987, p. 23)
>
> 4. [D]iapause has coincided times with cold hardiness but is not interdependent. (Danks 1987, p. 41)
>
> 5. Diapause is primarily cued by photoperiod although there may be interactions with temperatures, moisture and other environmental parameters, light intensity required generally less than 1 lumen, affected by light quality. (Danks 1987, p. 230)

Danks (1987) emphasized the great varieties of terms associated with diapause and the difficulties engendered in research efforts designed to establish parameters. Stadnitskii (1986) concluded,

> Hence, we may consider the conobiont diapause as an adaptation to cone crop dynamics, appointed by natural selection. Carpobionts of leaf-bearing tree and shrub species, as a rule, have no diapause, excluding *C. glandium* and some other strictly adapted species.
>
> Cone insect diapause and tree reproduction dynamics are induced by similar natural factors. We may consider them to be a total result of a long-term coevolution of coniferous species and their phytophagous insects. (Stadnitskii 1986, p. 244)

Perhaps the first mention of dormancy[3] in western cone and seed insects was that of Miller (1914), who noted that as much as half of an insect brood may be dormant for 2 or more years. In a study focused on *Megastigmus strobilobius* and the cone moth, *Cydia strobilella,* in Finland, Annila (1984) observed that "a high proportion of cone and seed insects do not emerge after one hibernation but remain in diapause for several years," and that the "duration of diapause is an important factor having an effect on population fluctuations of cone and seed insects. . . . Prolonged diapause has been considered to be a means of adapting to the varying cone crop of the host tree" (p. 57). Annila concluded that "it seems possible that seed insects have not only adapted to fluctuations in the annual cone yield but also the fluctuations in the cone destroyer population as well" (p. 63). Hedlin (1964a), working with cones infested with insects on Vancouver Island, noted that "apart from availability of cones, the phenomenon of diapause was probably the most important single factor influencing insect population fluctuation" (p. 124). In examining diapause in *Barbara colfaxiana*, Sahota et al. (1982) reported the following:

> Pharate adult (adult within the pupal cuticle) diapause was discovered in *Barbara colfaxiana*. This phenomenon is uncommon in insect development. It was also shown that both the termination of diapause and the subsequent advancement of pharate adult development can occur at 0°C. . . . In many insects, the normal progression of the life history is interrupted by a state of dormancy resulting in a discontinuation of growth development. The most advanced of these dormancies, induced well before the onset of adverse conditions and maintained for sometime irrespective of environmental conditions, is commonly known as diapause. (Sahota et al. 1982, p. 1179)

According to Hedlin et al. (1982),

> Studies were carried out in the field and in the laboratory to determine if prolonged diapause of the Douglas-fir cone moth, *Barbara colfaxiana* (Kearfott), was correlated with the sizes of the cone crops maturing in the year of larval feeding (N) and in the year following larval feeding (N+1), and to determine if weather during the period of larval feeding (year N) influenced the size of the maturing cone crop or the incidence of prolonged diapause the following year (N+1). Field studies showed that prolonged diapause induction in *B. colfaxiana* was not rank correlated (but approached significance) with the size of the cone crop maturing in year N, but was negatively rank correlated with that in year N+1. Two of seven weather parameters, mean maximum temperature and mean daily temperature, measured during the larval feeding period were positively rank correlated with cone crop size. No parameter was correlated with the incidence of prolonged diapause. In the laboratory, the incidence of prolonged diapause was negatively correlated with temperature. Photoperiod and parental diapause habit had no direct effect. (Hedlin et al. 1982, p. 465)
>
> The relationship between prolonged diapause and cone crop size the year following larval seeding suggests that factors which affect cone development the summer prior to year of maturation also affect inversely the induction of prolonged diapause. This relation may be necessary for the survival of *B. colfaxiana* populations, in that prolonged diapause prevents excessive intraspecific competition for food resources in years of low food abundance. (Hedlin et al. 1982, p. 468)

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[3] The term "diapause" was not in use at that time.

They noted that both *Barbara* and *Contarinia* larvae also frequently go into diapause.

In other reports concerning diapause on *Barbara colfaxiana*, Sahota et al. (1983) noted that the pharate phase of insect development starts within 24 hours after pupation in both 1-year and 2-year diapause individuals. Sahota et al. (1985) found that year-1 and year-2 diapause of *B. colfaxiana* can be identified by the color of individuals and anatomical features. Sahota and Ibaraki (1991) showed that diapause was not related to insect dry weight, but that 2-year diapause insects had a slightly higher dry-weight to fresh-weight ratio.

Radcliffe (1952) reported that in the Cowichan Lake area, from 3% to 11% of the pupa of *B. colfaxiana* were in diapause. Miller and Hedlin (1984) noted that "induction of prolonged diapause in the cone moth in a dry interior area was correlated inversely with cone crop size the year following larval feeding and directly with cone crop size the years of larval feeding" (p. 91). Miller and Ruth (1986) noted that "high temperatures during May to August terminate prolonged diapause" of *B. colfaxiana* (p. 1073), and that "the termination of prolonged diapause by summer temperatures would allow for greater moth emergence when larger cone crops are produced as production of cones by Douglas-fir is also positively correlated with summer temperature the year prior to cone maturation" (p. 1074).

Roux et al. (1997) reviewed the literature concerning diapause, particularly in spermatophases, discussed the relation of temperature and photoperiod to simple and prolonged diapause in *Megastigmus spermotrophus*. They concluded that "in the Douglas-fir seed chalcid, chilling is a prerequisite for the completion of the development of the two kinds of diapause, low temperatures in autumn and winter activating the development of both simple and prolonged diapause. This finding indicates that environmental information can influence the nature of larval diapause (simple or prolonged), but we cannot eliminate other factors, such as genetic factor (genetic polymorphism) or 'bet-hedging' strategies" (p. 176). The "chilling" in this work refers to natural temperatures in autumn and winter, but these temperatures are not given, nor is their duration. Miller et al. (1984, p. 49) found no apparent correlation between prolonged diapause and cone crop size for Douglas-fir cone gall midge at Lake Cowichen. In an early report of diapause in cone and seed insects, Hussey (1956, p. 193) noted that 68% and 76% of *Megastigmus* larvae in England extended diapause in 1952 and 1954, respectively, but only 6% did so in 1951.

Control

For many years, when seeds were collected from wild stands, control of seed and cone insects was not a problem. Although it was generally recognized that insects could destroy significant quantities of Douglas-fir seed, efforts to control such damage began only in the 1950s, with the advent of costly seed orchards in the northwestern United States (Hedlin 1961b, Schowalter et al. 1985).

Surveys

With tree breeding programs came increasing emphasis on protecting valuable seed crops, as well as more detailed evaluation of potential damage to aid in determining whether preventive treatment was justified. A number of papers proposed evaluation techniques utilizing the principals of sequential surveys to estimate parameters such as cone and seed efficiency. Such studies identified seed losses caused by insects previously not implicated as seed predators, established the relative importance of known and unknown environmental factors and insects in reducing potential seed crops, submitted cost analyses of seed production, and provided a measure of the effectiveness of chemical treatments (Miller 1983, Dombroski and Schowalter 1988, Schowalter and Sexton 1989). Research in this area has included the development of a sequential sampling system of seeds to estimate predation by *Contarinia oregonensis* Foote (Miller 1986b) and *Megastigmus spermotrophus* (Kozak 1964), the distribution of the eggs of *Contarinia oregonensis* and *Barbara colfaxiana* (Miller 1986c, Sweeney and Miller 1989), and the development of a partial life table for *Barbara colfaxiana* (Nebeker 1977 and Miller 1989).

Artificial control

Systemic and chemical

The first attempt to control insects that feed on Douglas-fir seeds was that of Rudinsky, who applied

DDT in a water emulsion with ground-based spray equipment in 1955 (Koerber 1960). The results were inconclusive, but there appeared to be a reduction in the damage caused by *Barbara* and *Megastigmus,* but not by *Contarinia*. In the years that followed, a number of reports (Johnson 1963b,c; Koerber 1963; Hedlin 1964b; Johnson 1964; Johnson and Rediske 1964, 1965; Buffam and Johnson 1966; Hedlin 1966; Johnson and Meso 1966; Johnson and Hedlin 1967; Johnson and Zingg 1967) were published that detailed efforts to employ either ground-based spray apparatus or aerial systems to treat Douglas-fir trees with a range of insecticides. Chemicals used included contact insecticides such as lindane and dieldrin and systemics such as Meta-Systox R, Bidrin, and Dimethoate. While investigators reported that in most of the trials, the chemicals appeared to be effective in reducing seed loss, as Miller (1980) noted, the results were erratic, affected by weather, varied with chemical used and insect targeted, weakened by the fact that they rarely presented statistical analyses, and suffered from the lack of efficient sampling designs to estimate insect populations.

The past 30 years have seen the emphasis in research to control insect seed predators shift from aerial or ground applications of insecticides to the development of (a) techniques to inject systemic insecticides into tree boles; (b) sampling methodology to provide accurate measures of the need for insect control prior to implementing control measures; and (c) alternative systems to manage insect populations.

The shift toward the injection of insecticides was occasioned by the fact that such an approach was not subject to a specific time to be effective and, because the chemicals were enclosed in capsules, the danger to the applicator was reduced over that associated with sprays. Several papers reported the effect of injected systemic insecticides upon target insect populations (Schenk et al. 1967, Johnson et al. 1984, Koerber and Markin 1984, Reardon and Barrett 1984, Reardon et al. 1985, Stein and Markin 1986, Stein et al. 1988, Stein and Koerber 1989, Stein et al. 1993, de Groot et al. 1994). These trials were superior to the earlier work in that they all had competent statistical designs. Nonetheless, the results were erratic and varied with chemical and insect: dimethoate was not effective in any study; acephate demonstrated positive control of only *Dioryctria;* and oxydemeton-methyl (Metasystox-R) was generally effective against *Barbara, Dioryctria* and *Contarinia,* but not *Megastigmus*. It is possible that the negative results with *Megastigmus* reflected the fact that this insect competes poorly with other seed predators (Rappaport and Volney 1986, 1989; Volney 1984). Miller (1986a) noted that chemicals were the only practical method for controlling insects in Douglas-fir seed orchards at that time. Schowalter (1984b, p. 1437) reported that both *C. oregonensis* and *M. spermotrophus* were capable of dispersing over at least 85 m, and that destruction of debris within seed orchards would not protect them against these insects. Summers and Ruth (1987) found that sprays of permethrin and dimethoate, but not diatomaceous earth, were effective against *L. occidentalis*.

Chemical attractants

Although chemical attractants (pheromones) have been used in the management of mountain bark beetle (British Columbia Ministry of Forests 1995a) and defoliators and nursery pests (Lavender et al. 1991), there is little evidence of their use in management of pests of Douglas-fir cones. Hedlin and Ruth (1968) demonstrated that male *Barbara colfaxiana* moths were attracted by females, and Hedlin et al. (1983) showed that mixtures of (Z)-9-dodecyl acetate and dodecanol were effective in attracting male *Barbara* moths. There were no published reports on the use of these materials in the management of seed orchards, however.

Phenology

Cold water spray

Trials by Silen and Keane (1969) demonstrated that spraying Douglas-fir seed orchards with cold water during the period of reproductive bud development could delay such growth by as much as 12 days compared with that of unsprayed trees. These results stimulated later tests in British Columbia designed to determine whether such asynchrony might reduce the incidence of predatory insects in cones of treated trees. Miller (1983) noted that when the delay in reproductive bud break was at least 10 days and when early bud break trees were the primary targets of *Contarinia oregonensis* Foote, damage by this insect could be reduced as effectively as by applications of the insecticide dimethoate. However, the delay occasioned by the spray treatment was affected by weather patterns during the spray period—low temperatures reduced the effect of the cooling treatment—and, hence the effects of spraying upon levels of insect damage could not be predicted. The author suggested that accurate determinations of the heat sum requirements of the insect and of the seed orchard were needed. El-Kassaby et al. (1990) reported significant reductions in the incidence of *Megastigmus spermotrophus* Wachtl larva when a Douglas-fir seed orchard received the cold water spray.

Barriers

Zhang and Schowalter (1997) noted that physical barriers such as sticky material (tanglefoot), which reduced weevil damage to from 25% to 5%, may be effective in some locations. We know of no other reports describing such control, however.

Seed treatment

Hussey (1954) noted that the larva of *Megastigmus spermotrophus* Wachtl could be killed by the temperatures employed to dry cones prior to seed extraction, but did not quantify the treatment. Later trials by Ruth and Hedlin (1974) examined the efficacy of a range of temperatures and treatment times to kill *Megastigmus* larva and determined that exposure of infested seeds to a temperature of 45 C for 40 hours resulted in 100% mortality of the larva without significantly affecting seed germinative vigor. They cautioned, however, that seed moisture content (MC) should not exceed 9% at time of treatment initiation.

Richardson and Roth (1968) demonstrated that exposure of *Megastigmus* infested *Picea abies* (L) Karst seed to hydrocyanic acid for 2 hours was sufficient to kill the larvae, but that this insect demonstrated significant resistance to methyl bromide. Further trials (Roth and Strasser 1971) confirmed the resistance to methyl bromide and showed that a mixture of carbon disulfide and carbon tetrachloride was effective against larvae of both *Megastigmus* spp. and Cecidomyiidae in seeds of Douglas-fir and Port Orford cedar, respectively. Neither report discussed the effects, if any, on seed viability, although the later paper noted that another researcher had found no ill effects of carbon disulphide on Douglas-fir seed germination. Finally, Sweeney et al. (1991) reported that the incubation drying separation method was effective in separating most of the infested seeds from sound seeds, in that the infested seeds floated after treatment whereas the sound seed sank.

Natural control

Schowalter (1984a) noted that the destruction of the litter where many insects overwinter will not protect seed orchards, most of which are within the range of insects bred in wild stands. Schowalter et al. (1985) noted that the insects discussed here, "frequently destroy over half of the Douglas-fir seed crop" (p. 1223).

Competition

Because Douglas-fir cones are commonly attacked by several insects, the question of the extent to which the various species limit or impact the damage each causes is of both theoretical and practical interest. The success of chemical control methods, for example, depends on whether the elimination of a target insect, such as *Contarinia* spp., which attacks the conelets early in the growing season, may affect the damage caused by *Megastigmus spermotrophus*, which may deposit eggs after the insecticide has been metabolized by the tree or otherwise rendered innocuous. Also of interest is the relative level of damage caused by *Megastigmus spermotrophus* in western North America, where it must compete with other insects, and in Europe, where it has no competition for Douglas-fir seeds.

For the following reasons, Rappaport and Volney (1989) suggested that competition between insect species indigenous to Douglas-fir cones may affect the level of damage of any one insect:

> 1. Competition occurs most often when the food resource is limiting and the erratic occurrence of Douglas-fir cone crops, together with the extended diapause habit of all save *Dioryctria abietella,* suggest that quantity of seed available frequently limits insect populations.
>
> 2. Both *Contarinia* spp., and *Megastigmus spermatotrophus* have no defense against predation by *Dioryctria* or *Barbara*, and *Megastigmus* is generally not found in cones heavily parasitized by *Contarinia* spp.
>
> 3. Levels of *Megastigmus* are significantly higher in Europe despite the fact that parasities by autochtho-

> nus insects in Europe is higher than that occasioned by the depauperate North American parasite complex and there are no known pathogens of *Megastigmus* on either continent.
>
> 4. The tentative evidence from chemical control projects suggest that when one insect is controlled, levels of competing insects rise to occupy the niche created. (Rappaport and Volney 1989)

Given the foregoing, research in northern California has shown that potential competition between *Barbara* and *Contarinia* spp., was reduced because the former feeds primarily in the center of the cone, whereas the latter favors the ends (Volney 1984)—although Rappaport and Volney (1986), Schowalter and Sexton (1989), and Miller (1986a) all reported a majority of *Contarinia* larvae in the center of cones; however, *Barbara* and *Megastigmus* larva may coexist in the central portion of the cone (center between the ends). Subsequent trials (Rappaport and Volney 1986) confirmed the hypothesis that intraspecies competition was minimized by the spatial pattern of insect feeding within the cones; Rappaport and Volney (1989) found, however, that *Contarinia* spp. infestations reduced the level of *Megastigmus,* but that the reverse did not occur. The authors suggested that in North America *Megastigmus* may be eliminated from the portions of cones occupied by competing dipteran and lepidopteran species, and that the increase in levels of *Megastigmus* occasioned after some insecticide treatments may be the reason that such trials failed to result in increases in numbers of sound seeds.

Biological control

There have been investigations of insects that attack seed and cone insects (Koerber 1960; Hedlin 1960, 1961a; Bringuel 1968; Miller 1983). Hedlin (1960) reported that that *Torymus* sp. parasitizes the larvae of *Contarinia oregonensis* and *Glypta evetriae* that of *Barbara colfaxiana*. He also reported that many *B. colfaxiana* larvae perish while attempting to be established in the cone, with only about half of the original number of larvae surviving lived beyond the first instar. Other parasites of *B. colfaxiana* include *Tetrastigmus strobilus* and *Platymesopus* sp.; these chalcids were observed to kill 48% of *B. colfaxiana* larvae. In one collection, 78% were parasitized by *Glypta evetriae*. Miller and Ruth (1986) reported a mortality rate for *B. colfaxiana* of 35%, virtually all caused by parasitoids and predators (p. 1074). However, Roques (1991) noted that there are relatively few parasites and predators of cone and seed insects (p. 303): “Parasite colonization thus apparently requires adaption to both phytophagous host and cone host” (p. 307).

One of the basic tenets of integrated pest management is that natural predators or parasites of insects predacious upon crop plants may be effective controls of the pest populations. There has been little evidence that this concept has been employed successfully against seed and cone pests of conifers (Yates 1989), and thus there has been little discussion of the biological control of cone and seed insects in the literature reviewed. Exceptions insofar as Douglas-fir seed pests are concerned include the following two organisms, which have been shown to have potential for controlling *Barbara colfaxiana: Pyemotes*, n. sp. (Acari: Pyemotidae) and *Trichogramma minutum* Riley. Moser et al. (1987) reported on new species of *Pyemotes* that was parasitic upon *Barbara colfaxiana* as a possible natural control of this seed pest. Hulme and Miller (1988) conducted initial trials of *Trichogramma minutum* in which it was demonstrated that this parasitoid could successfully attack eggs of *Barbara colfaxiana* under field conditions; however, factors possibly unique to this trial prevented the intensity of parasitism necessary to control *Barbara* populations. We found no additional references to these two organisms relative to cone and seed insects after these initial reports, however. Keen (1958) noted that parasites of the insect complex predatory on Douglas-fir cones have been reared under laboratory conditions. However, the cryptic nature of the larvae of seed pests, as well as the fact that much seed damage occurs prior to parasitism, greatly limits the effectiveness of such insects as control agents.

Other cases of mortality include micromammals, the joint action of birds, rodents, and entomopathogenic fungi. Janzen (1971) reported that “the insects preying on large temperate-zone seed crops characteristically support large parasite populations” (p. 481). Several papers by Schowalter (1986, 1988, 1995) discussed the interaction of forest management techniques and the causes on possible control of "pest" insect populations. Schowalter (1986) noted that "silvicultural treatments can promote or prevent insect population growth depending on the ecological strategies represented in the forest arthropod community. Forest management or pest control strategies that fail to address underlying causes of insect population outbreaks or that fail to anticipate responses of non-target insect species will be ineffective in protecting forest resources in the long term" (p. 64). According to Schowalter (1995), "reduced [insect] predator diversity increases the probability that herbivores with rapid response to environmental change will escape population regulation by surviving predators" (p. 124). Although he recommended natural forests as the best overall approach, the foregoing references do not detail the practical employment of such an approach.

Diseases

Nelson et al. (1986) observed that "seed and cone insects have long been known to reduce Douglas-fir seed production. Loss in productivity from fungi or other pathogens, however, has not been measured, nor is it generally accepted that significant losses from diseases occur in developing cones" (p. 1). Shea (1960) noted that "little attention has been given to fungi on forest tree seed prior to sowing. Few seedborne diseases of trees are known" (p. 2). Cooley (1983) observed that "cone and seeds of conifers can become diseased on the tree, during storage, or when processed. Molds, a large diverse group of fungi, and bacteria cause the majority of seed and cone damage in the Pacific Northwest" (p. 1). According to Bloomberg (1966), Salsbury (1955) "found that a high mold content did not necessarily cause a reduction in the viability of Douglas-fir seed (*Pseudotsuga menziesii* (Mirb.) Franco) and it can be inferred that fungi exist endophytically in seed without affecting the ability to germinate" (p. 413). Theisen and Goheen (1980) reviewed the literature and observed that "not much information is available on the amount of damage caused by cone and seed disease of northwest conifers" (p. 1). Finally, according to Sutherland et al. (1987, p. vi),

> Although North American foresters and forest pathologists have always been aware of certain cone and seed diseases, particularly cone rusts, it is only with the recent advent of seed orchards, tree improvement programs, and intensively managed forest nurseries that the importance of already-known and newly discovered diseases has been recognized. A major technological change that has sparked interest in cone and seed disease has been the change from collecting cones from wild stands to the production of cone crops in seed orchards. There, the high value of the crop has increased the importance of diseases. Sutherland et al. (1987, p. vi),

Fungi

Perhaps the earliest report describing the possible role of fungi with Douglas-fir seed is that of Isaac (1935). This worker placed a large number of seed in a rodent-proof enclosure in the dense shade of a virgin forest. Seed germination was recorded for both the year of placement and the following growing season. The seeds that failed to germinate were recovered and examined. Many were found to be decayed, but the fungus species involved were not identified. In contrast, later studies designed to evaluate the effects of field stratification and seeding date upon seed germination utilized several thousand seeds placed in rodent-proof enclosures (Lavender 1958a). Subsequent tallies of field germination and of laboratory evaluation of non-germinated seed after the growing season demonstrated little evidence of the destruction of viable seed by fungi. However, again in contrast, Lawrence and Rediske (1962), utilizing seed treated with scandium 46, found that fungi destroyed about 20% of the seed before germination, another 9% during the germination period, and, finally, that damping-off organisms killed yet another 9% of the seed placed after germination. The difference between these results and those of Lavender (1958, a-e) may have been due to the much less vigorous field germination of the seed employed in the former study. Such response could reflect either lack of stratification or weak seed. Laboratory data has demonstrated that the incidence of moldy seed in laboratory dishes is inversely correlated with the vigor of the seeds. Alternatively, as Lawrence and Rediske (1962) suggested, "fungi accounted for the greater part of seed loss during the pregermination period. The early spring of 1958 was cool and wet, favorable to growth and development of seed mould. As environmental conditions vary from year to year, so undoubtedly does the relative importance of the biotic agents responsible for seed loss" (p. 217). Laboratory evaluations of the fungi associated with Douglas-fir seeds (Salisbury 1953, Holmes and Buszewicz 1955, Shea 1960, Bloomberg 1969) have shown that *Penicillium* spp., *Aspergillus* spp., *Aureobasidium* spp. (*Pullularia), Gliocladium* spp, *Spicaria* spp., *Trichoderma* spp., and *Mucor* spp. are among the more common of the over two score fungi species isolated from Douglas-fir cones and seeds.

In his review, Shea (1960) noted that the first two genera frequently are much more common on seeds and cones in storage. Additionally, fungal infection of the cones, especially those cones gathered before the seeds were fully mature, resulted in reduced viability of the seeds. In extreme cases, when cones were stored under particularly unfavorable conditions, fruiting bodies of *Aureobasidium pullulans* (formerly *Pullularia pullulans)* were found on decayed embryonic tissue. Shea suggested that part of the loss in viability reported for seed stored above freezing may be due to fungal attack. He further noted that most seed was stored below freezing and was free from active fungal attack during storage. However, fungi have been shown to retain viability "for at least 12 months when seeds are stored at −12°C and approximately 8% moisture content. During this time no reduction in germination was noted. However, seed carried ample evidence of fungi which needed only favorable conditions for continued mold growth development on and in the seed" (p. 6).

Given the foregoing, much of the early work investigating effects of molds on Douglas-fir seed was concerned with cones stored prior to processing. Lavender (1958) stored lots of cones collected from 40 trees in the Willamette Valley. Germination tests conducted with seed stored for up to 4 months showed no effects of storage time upon seed vigor. Unfortunately, no record was made of cone moisture; however, the cones were placed in small groups and probably dried during the storage period in a manner similar to that noted during other tests of cone storage. No observations of mold growth on cones were made. A more controlled experiment that demonstrated the effects of fungi upon seeds stored under conditions favorable to fungus growth was reported by Rediske and Shea (1965). Cones maintained by these workers for 16 weeks at 20°C and 60% MC were covered with white mycelial mats of *Schizophyllum commune* Fr. and yielded badly decayed seeds. However, cones held at 0°C and 60% MC for the same period showed only slight fungal attack. The authors also reported that cones stored 40% MC or less had little loss due to fungi after 16 weeks, so apparently, unless the environment is favorable to fungal growth, these organisms do not infest Douglas-fir seed.

Bloomberg's (1969) report was similar to the above in that 125 days of storage in cones, under conditions generally not very favorable to fungal growth, resulted in little loss of seed vitality, even though fungi that could attack the seeds were present. But, when the seeds were placed in germination dishes in an environment apparently favorable to fungi, significant numbers of seeds were diseased. Bloomberg suggested that "the low percentage of healthy non-germinable seeds strongly indicates that the responsible fungi and bacteria were facultative pathogens of low viability seeds" (p. 180). According to Bloomberg, the following genera were common on Douglas-fir cones: *Gliocladium, Spicaria, Penicillium,* and *Trichoderma*; *Rhizopus* and *Aspergillus* were less frequent. A basidiomycete, *Corticium pini-canadensis* was often observed. The practical implication of this research finding is that if mature seed lots can be identified, they can be left for extraction later than immature lots. The latter may fall into two categories: those that continually decrease in germinability, and those that decrease and then regain some of their original germinability. Other research concerned with Douglas-fir seed disease has studied *Caloscypha fulgens* and *Fusarium* spp.

Sutherland (1979) reported *Caloscypha fulgens* on 3% of Douglas-fir seed lots examined, but, since it is a soil-borne pathogen, it was found only in seeds from cones collected on the ground, particularly in squirrel cashes. Sutherland et al. (1987) described *C. fulgens* as "an operculate discomycote with bright orange (exterior often stained blue-green) cups shaped fruiting bodies (1–5 cm in diameter). It grows under conifers and fruits in the spring, especially soon after snow melt" (p. 28). They found that the degree of infection in seeds was a function of the length of exposure to cool, damp soil; the disease can spread from infected to healthy seed during stratification; it mummifies rather than rots the seed contents; and it can survive for several years on the dead seed (p. 31). Sutherland and van Eerden (1980) found that the problem with *C. fulgens* may "intensify further if moist, stratified seeds are cold stored prior to sowing. Additional spreading and killing can occur following seed sowing, particularly during prolonged periods of cool, wet weather" (p. 14).

There has been considerable interest in the role of seeds as carriers of a complex of fungi that are among the most virulent of plant diseases, *Fusarium* spp. However, of the early reviews of Douglas-fir seed disease examined (Harvey and Carpenter 1945; Shea 1960; Rediske and Shea 1965; Bloomberg 1966, 1969, 1970, 1973; Lock et al. 1975; Theisen and Goheen 1980; Cooley 1982) only Bloomberg (1966) mentioned *Fusarium*. James (1986) and Graham and Linderman (1983) reported low levels of *Fusarium* on Douglas-fir seed, although the latter suggested that the significant mortality of Douglas-fir seedlings caused by *Fusarium* may have come from seedborne propagules.

Sutherland et al. (1987, pp. 44–49, 52) discussed pilch canker, *Fusarium moniliforme* var. *subglutinans,* a major disease of southern pine, and *Fusarium oxysporum,* a lesser problem of Douglas-fir cones and seeds. Sutherland and vanEerden (1980) noted that *Fusarium oxysporum* causes root disease and top blight of Douglas-fir seedlings but made no mention of it on seeds. Nelson et al. (1986) reported a single seedborne incidence of *Fusarium* on Douglas-fir, but noted the following:

> We consider recovery of only a single isolate notable, however, because we sampled a broad range of families on a broad range of sites over an entire growing season. Finding only one isolate does not mean that spores of the fungus could not have been on tissue surfaces. If *Fusarium* spp. gain access to nursery beds through infested seed, our results would suggest that invasion of seed tissues occurs after cone harvest and not while cones are developing on the tree. (Nelson et al. 1986, p. 3)
>
> We believe that seed and cone pathogens do not cause significant losses in Pacific Northwest seed orchards, but additional study of the pathology of cones in early stages of development is needed. (Nelson et al. 1986, p. 5)

In an interesting variation on *Fusarium* research Hoefnagels and Linderman (1999) reported that bacteria (*Pseudomonas chlororaphis*) could reduce the incidence of *Fusarium* spores found on stratified Douglas-fir seed. James (1986) noted that the "extent of *Fusarium* contamination on seed varies greatly among conifer species and seed lots" (p. 268). Lori and Salerno (2002) summarized literature concerning *Fusarium* spp. and coniferous seed (including Douglas-fir):

> Seed-borne *Fusarium* may cause losses during seed development, storage or germination and damage may then result from loss of seed viability or from seedling infection following germination. *Fusarium* may be found on and in the seedcoat and in the gametophyte and embryo. They may enter during seed and cone development or through cracks in the seedcoat, especially after the seed has been extracted from the cone. External fungi on the other hand could develop on the seed at any time after the seedcoat is formed. (Lori and Salerno 2002, p. 560)

Bloomberg (1966, p. 419) found endophytic fungi in the seed, but not in the embryo or megagametophyte. Axelrood et al. (1995) noted that "less than 2% of 67 Douglas-fir seed lots from coastal British Columbia had *Fusarium* and the incidence of individual seeds varied from 0.3% to 95.4%. Running water during imbibition reduced fungal incidence over that found after standing water" (p. 35). Allen (1947c, p. 51) noted that disease-free germination of Douglas-fir seed may be achieved in the laboratory through the use of 30% hydroxy mercuric chlorophenol.

From the foregoing discussions, we may conclude that much of the fungal growth associated with seed is non-pathogenic—with exceptions of but not limited to *Caloscypha, Fusarium, Gliocladium*, *Trichoderma Trichothecium, Cephalosporium,* and *Aureobasidium;* fungi generally are not a major cause of seed mortality in seed orchards; and mature seed is more resistant to mold than is immature seed (this is similar to the response of spruce seedlings, wherein those that were exposed to natural photoperiods prior to fall lifting molded in storage, whereas those given short photoperiods did not), and is further evidence of the importance of annual physiological rhythms to seed. And, if as appears likely, global warming is affecting the dormancy of Douglas-fir saplings, the current virulence of Swiss needle cast (*Phaeocryptopus gaeumannii*) may reflect reduced resistance of trees occasioned by insufficient chilling, or in trees whose dormancy is interrupted, intact seeds are more resistant than damaged seed. This calls for extreme care in all phases of seed handling.

10. Roots

Denis P. Lavender

Although tree roots have been studied for over a century, progress in understanding their physiology has been slow, partly because until about 50 years ago, studies were confined to the anatomy and morphology of roots; partly because roots grow in an opaque medium (soil), making it difficult to conduct the necessary observations to permit relating root growth to endogenous factors and to components of the environment without creating artifacts; and partly because root growth is much more variable than shoot growth, and therefore much larger populations are needed if the data are to be significant statistically. In spite of these qualifications, there are numerous reviews of tree growth and function (see, e.g., Hermann 1977, 2005; Sutton 1991; Fayle 1968, 1980; Reynolds 1975; Van Erden and Kinghorn 1978; Coutts 1987; Lyr and Hoffmann 1967; Sutton 1980, 1990, 1999; Loescher et al. 1990; and Comerford et al. 1990). Accordingly, sufficient study of tree roots has been accomplished to permit the following generalizations, many of which apply specifically to Douglas-fir, but which are probably equally true in general, if not in detail, for the roots of all coniferous trees.

Characteristics

1. Root growth is dependent upon carbohydrates exported from shoots and other as yet unidentified substances, also exported from the shoots.
2. Douglas-fir root systems do not develop dormancy, although there remains much to learn about this subject for Douglas-fir and other trees. Hermann (1977) noted, "equally disputed and unresolved is the question of whether or not roots of trees in the temperate climates become truly dormant" (p. 10). Some workers have suggested that tree roots may have dormancy (Lathrop and Mecklenberg 1971; Coutts 1987, p. 763). If being dormant requires chilling to initiate active growth, however, then Douglas-fir roots do not have true dormancy (Lavender et al. 1970). According to Hermann (1977), "observations of different cycles of root activity between different species under similar environmental conditions would seem to strengthen the notion that at least some degree of endogenous control exists, however" (p. 11).

   Krueger and Trappe (1967, p. 193) cited two references noting that Douglas-fir roots may elongate throughout the year. Reynolds (1975, pp. 172–173), however, equated root dormancy with metacutization of root apices, and, on this basis, noted that the roots of Douglas-fir growth in the mild oceanic climate of England become dormant as a strategy to reduce respiration. Fielder and Owens (1989, p. 543) found that some root activity occurred in coastal but not interior Douglas-fir all year, and that maximum growth occurred in fall and early spring. Individual roots may become dormant and are generally unaffected by the dormancy of the shoot, except that, when shoots are actively elongating, they attract most of the carbohydrate resources (are a stronger sink) of the plant and, as a consequence, root growth is diminished.
3. While root growth may occur during the entire year, except when soils are frozen or below about 2 MP moisture tension, there are normally two periods of strong root growth each year. The first, when most of the annual root growth occurs, is just before and during the period of bud break. The second, somewhat smaller peak, occurs in

the fall after rains have remoistened the soil (Lyr and Hoffmann 1967, pp. 192–206).

4. Root growth is affected by the environment of the roots much more strongly than it is by shoot environment.
5. The principal environmental factor which determines whether a root or stem will develop is pressure (Fayle 1968).
6. Roots will grow in a temperature range of from 0°C to about 35°C, but maximum growth normally occurs at soil temperatures between 18°C and 25°C.
7. Coniferous seedlings generally have a limited root elongation rate, rarely more than a very few centimeters per day. In contrast, a single rye plant is capable of growing more than a kilometer of roots in a day.
8. Most conifers are capable of forming a symbiotic relationship with one or more species of mycorrhizal fungi. Because the fungal portion of the symbiosis has many times the absorbing area of the root and can access soil particles and minerals that are not available to roots, mycorrhizae are essential to the uptake of nutrients and water by the higher plant.
9. Data describing the annual turnover of root biomass are limited, but it appears that a similar or even greater biomass of plant material is lost every year by root mortality than occurs in litterfall. We describe the root turnover in Douglas-fir stands later in this section.

Function

Tree roots have four major functions:

1. Uptake of nutrients and water
2. Synthesis of organic compounds
3. Storage and transport of carbohydrates
4. Anchorage of the tree and support of the aerial portion of the tree

The first to the third functions are definitely compatible with each other and can be conducted in relatively fine root systems. Such roots demand relatively little photosynthate for growth and maintenance and are capable of exploring small soil pores. In contrast, the great weight and stresses that tree roots must support require a platform of heavy suberized roots (McMinn 1963). As Coutts (1987) noted,

> Although successful soil exploitation for the absorption of water and nutrients requires a finely divided root system, in trees the physical laws governing the strength of beams under bending stress limit the degree of subdivision at the stem root juncture commensurate with the firm platform required for effective anchorage. In beams circular in cross section, stiffness is proportional to the fourth power of the diameter; thus, for effective support the tree requires few but thickened roots at the base. These develop by secondary growth of a limited number of primary roots (i.e., roots of primary structure) present on the seedling. (Coutts 1987, p. 761)

Such a design is obviously not efficient for water or nutrient uptake. To compensate for this deficiency, trees have evolved a symbiotic relationship with fungi, whereby the fungi (mycorrhizae), with their very fine hyphae and external enzymes, serve the function of fine roots, while the roots of the tree offer the necessary support (Read 1991). Hunt and Fogel (1983, p. 644) noted that the mean diameter of fungal hyphae at about 3.0 to 4.5 μm in a Douglas-fir forest in western Oregon; accordingly, these structures are well suited to penetrate the finest soil pores. As Finlay (2008) noted, "by virtue of their small diameter the hyphae are also able to penetrate soil microsites which are inaccessible to plant roots" (p. 1117). By comparison, fine tree roots have been characterized at 1 mm and small roots at 1 mm to 5 mm in diameter (Santantonio and Hermann 1985, p. 113).

The following presents a comparison between the architecture of the very fine roots of a grass (winter rye) plant (Dittmer 1937) and the relatively coarse, fine roots of trees (Table 10.1). These data are not strictly comparable, as the rye plant figures show

Table 10.1 Root growth comparison between rye and Douglas-fir.

Species	Root length	Root growth per day	Reference
Winter rye	620 km	5 km	Dittmer (1937)
Douglas-fir		15 cm*	Lopushinky and Max (1990)
Trees in general	3-	56 mm	Hermann (1977)
2 – 0 Douglas-fir			
Total root/growth/ seedling/day		15 cm	Blake and Linderman (1992)

* Per seedling

growth for the entire plant, whereas the tree data are for individual roots. However, a seedling with more than 100 elongating roots is rare. All data are for seedlings less than 3 years old. In addition to the above the following tables provide additional parameters of rye root growth system produced in 4 months by a single seedling. A comparison of these data with similar data from conifers, where daily root growth is measured in centimeters, shows the great superiority of grass root growth. This same relationship is evidenced by data describing density of roots in the soil, i.e., 30–50 cm of grass root per cm^3 of the upper 15 cm of soil, as opposed to 2 cm in the upper 8 cm of soil under a Monterey pine stand (Barber 1977). Dittmer (1938) found that a 16 cm^3 soil sample from under Kentucky bluegrass would have approximately 2,000 roots, 1.2 million root hairs, with a combined length of over 372 m and a surface area of about 419 cm^2 (Dittmer 1938, p. 482).

Given the foregoing, it is clear that the mycorrhizae, whose extra-matrical hyphae may have a surface area that dwarfs that of roots, is the major uptake organ of tree roots and that the roots function primarily as support organs, translocate materials absorbed, and serve as a site for carbohydrate storage and compound synthesis. In a comparison of the cultivated rye plants grown in competition with a non-competing greenhouse rye plant previously surveyed, it was found that the field rye had approximately 5 times the number of root hairs per unit of root length as the non-competing greenhouse plant. However, the indoor plant had far more and longer roots, and consequently a greater total number of root hairs.

Relevance of Root Systems for Seedling Survival and Growth

Ever since Wakely (1949), stimulated by erratic survival of planted seedlings, introduced the concept of varying physiological grades in seedlings, researchers have looked for measurable seedling parameters that might define seedling vigor and, hence, predict the survival potential of a given seedling lot.

Root regeneration potential

The interest in root generation as a possible predictor of seedling vigor and survival spread from the South to the West, where researchers at the University of California (Berkeley) conducted a number of trials (Stone and Schubert 1958, 1959a,c) on root regeneration potential (RRP)[1] with Douglas-fir and ponderosa pine, and to Washington (Ritchie and Dunlap 1980) and British Columbia (Burdett 1979). Workers at Oregon State tallied the incidence of new roots, but they believed that those were a symptom of seedling physiology and that seedling survival was correlated with seedling dormancy (as previously discussed). Root generation was the choice of a majority of investigators because root systems apparently do not have a dormancy cycle that could affect results and because it was intuitively believed that rapid root growth after planting was essential to seedling survival. Accordingly, with the exception of container-grown lodgepole pine, which were subject to "toppling" (Burdett 1979), the inferred emphasis was on the role of roots as absorbing organs. Wakely (1949) hypothesized that (a) initial survival and height growth of planted southern pines depended on an excess of water intake over water loss; and (b) the excess of water intake, in turn, often depended on the formation of new root tissue promptly after planting (Sutton 1990, p. 260). We note here that the many papers detailing root regeneration potential generally do not mention mycorrhizae, although there are numerous papers detailing mycorrhizae formation on coniferous seedlings (as will be discussed in a later section).

Ritchie (1985) and Ritchie and Tanaka (1990) suggested that root growth capacity (RGP) reflected the stress resistance of Douglas-fir seedlings:

> I am suggesting, therefore, that when we measure RGP we are obtaining an estimate of relative cold and stress resistance in the seedling and it is these properties—not the ability to grow roots per se—that influence how the seedlings will perform on the site. A test of this hypothesis would be to measure RGP, cold hardiness and stress resistance over the course of a winter and following different durations of cold storage. If the relationship held up in the storage trials it would seem to be valid.

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[1] Slightly different terms have been used to refer to these measures; in an effort to "overcome current confusion in the literature," Day (1982, p. 83) reviewed the use of "root regenerating potential" (RRP) and "root growth capacity" (abbreviated "RGP"); Burdett (1987, p. 768) abbreviated "root growth capacity"as "RGC"; and Ritchie (1985, p. 93) used the abbreviation "RGP" for "root growth potential."

> . . . RGP is a robust, relatively inexpensive and very flexible method for assessing seedling physiological quality. (Ritchie 1985, p. 102)

We agree—but it is difficult to understand why the root growth should be maximal during winter months, when roots generally do not grow, and minimal in the early fall and spring when Lyr and Hoffmann (1967) have found root growth maximal just prior to bud break.

In contrast, Burdett (1987), working in root growth capacity (RGC) tests, made the following points (numbering added):

> 1. Published evidence on the relationship between lab-RGC and field-RGC is virtually nonexistent. (Burdett 1987, p. 769)
>
> 2. Thus the evidence seems convincing that root growth capacity plays a major role in determining the ability of newly planted trees to avoid moisture stress [by assuring good contact of roots with soil]. (Burdett 1987, p. 769)
>
> 3. It is probable, therefore, that moisture stress is normally a factor limiting establishment of planted seedlings. (Burdett 1987, p. 770)
>
> 4. Thus early survival after planting in cold [limiting to root growth] soil is not necessarily unrelated to root growth. (Burdett 1987, p. 770)
>
> 5. Thus RGC tests may provide evidence of many types of plant injury" (Burdett 1987, p. 771)
>
> 6. Thus RGC does not predict survival but survival potential. In general, the higher a seedling's RGC the greater its chance of surviving. (Burdett 1987, p. 773)
>
> 7. The RGC of forest tree seedlings measured under standardized conditions in the laboratory often predicts relative field performance. Evidence to show whether this relationship can be explained by a correlation between lab-RGC and field-RGC does not exist. (Burdett 1987, p. 773)
>
> 8. RGC tests provide a simple method of evaluating the performance potential of forest planting stock, which is probably cheaper than alternative methods of similar predictive value. (Burdett 1987, p. 774)

But, as was noted for previous reports, the above suffer by ignoring the probable effects of mycorrhizae.

Binder et al. (1990) presented data demonstrating that RGC can vary greatly with test conditions, and summarized other publications that agreed. They concluded that while RGC may have great value in carefully controlled research trials, it has definite weaknesses for project plantings. Krasowski and Owens (2000, p. 1670) reviewed a number of reports concerning root volume and growth and suggested that such factors are not necessarily related to survival and growth. They noted in the discussion of their excellent study, that "the initial size and early post-planting expansion of root systems is not predictive of long term seedling (white spruce) performance" (p. 1679). And Folk and Grossnickle (1997, p. 121) noted that the predictive power of Douglas-fir seedling tests may be improved by conducting them under unfavorable environments.

In essence, RRP is the lifting of seedlings at varying times during the fall and winter, planting them in containers, maintaining the containers with favorable light, temperature, and water for 2 weeks, and then examining the seedlings for the number of new roots greater than a centimeter in length and, possibly, for the total number of new roots. Large numbers are interpreted to predict high survival. During the 1960s, when the pattern commonly reported was low survival of seedlings and poor root growth in the fall (Stone and Schubert 1959, a-c), this was true given fall vs. winter planting. More recent planting practice has been to avoid late spring and early fall planting, when both the survival and root growth were low, so that root growth capacity is no longer well-correlated with survival—because survival then becomes more a matter of seedling environment and not physiology. In 2000, Gourley and Lavender (unpublished data) noted, however, that Douglas-fir seedlings that had received long-night treatments in later summer survived well after fall planting (see Chapter 8 for more detailed discussion of seedlings).

Because of the great number of papers on this subject, we will limit our discussion to the following references, which either favor or criticize RRP as a measure of seedling viability, and cite several major reviews (i.e., Jenkinson et al. 1993, Sutton 1990, Richie and Dunlop 1980). According to Krasowski and Owens (2000), "it is obvious from the results that the initial size of the root systems did not predict post planting performance of white spruce seedlings and our study also concluded that the initial growth of the roots in the first post-planting weeks did not predict seedling growth performance"(p. 1678). (Seedlings in this trial did not encounter drought stress.) In contrast, Nambiar (1981), working with *Pinus radiata* seedlings, reported that "the configuration and physiological state of the seedling roots developed in the nursery strongly influence the survival and speed of growth when outplanted" on relatively dry sites in Australia (p. 118). These two reports emphasized the role of the environment in root function.

Root regeneration potential has gained considerable credence with regeneration workers because it may measure a trait considered vital to seedling survival. However, no report known to us describing root regeneration mentions the role of mycorrhizal association in the phase of root growth most important to nutrient and water uptake, i.e., mycorrhizae. Accordingly, root regeneration is possibly an indirect measure of seedling viability, but it is strongly influenced by a number of factors (also including seedling dormancy), and, until we understand this thoroughly, a true evaluation of root regeneration will not be clear.

In essence, root regeneration potential represents seedling vigor after a stress, i.e., lifting and any possible storage, and not the endogenous root growth cycle. While many of published trials show a correlation between the root growth potential and field performance, as noted above, this is truly primarily for the high-low extremes; and, as Ritchie (1994, 1985) noted, the data supported only a correlation and not a cause-and-effect relationship. It is not clear whether seedlings do not produce roots and then fail to survive because they lack new roots or that they fail to survive because they are not vigorous. Generally, the correlation between dormancy and survival is stronger than this correlation.

Root electrolyte leakage

McKay and co-workers discussed the rationale for the root electrolyte leakage (REL) technique and its usefulness in determining seedling quality in a number of publications (McKay 1992, 1993, 1994, 1998; McKay and Howes 1996; McKay and Mason 1991; McKay et al. 1993). McKay (1992) described the theory of this test as follows:

> The movement of cell contents to and from cells is controlled mainly by the structural proteins present at points along the lipid bilayer of the cell membrane [i.e., the transmembrane pumps]. When healthy tissue is put in water almost free of ions, there is a slight leakage of cell contents, including ions, into the surrounding water which can be detected using a conductivity meter. If the cell membrane is ruptured or the transmembrane protein pumps impaired, the cell contents leak at a greater rate. Electrolyte leakage rate is therefore a measure of damage to the cell membranes. (McKay 1992, p. 1372)

The methodology of REL involves measuring the quantity of electrolytes that leak from some sections of root prior to and after the sections are killed with heat; the higher values reflect increasing membrane damage. In general, a plot of these values over date of lifting had a strong correlation with seedling survival for the same dates and with root regeneration data, although McKay and White (1997) noted that the strongest correlations were for seedlings out-planted on dry sites. They found considerable variation between REL and Douglas-fir seedling growth and survival over a range of sites: "A linear negative relationship described the 3 significant relationships between REL and Douglas-fir survival but there was no clear pattern in the form of the relationship between REL and Douglas-fir growth" McKay and White (1997, p. 149).

Electrolyte leakage from fine roots is a robust and easily measured parameter that has a rapid turn-around time and can be used to evaluate the viability of seedling root systems. REL measures the ability of membranes within the root system to contain ions. Damaged membranes tend to leak ions so, if ion leakage is quantified, it can provide an indicator of root viability. Ritchie and Landis (2006) noted the following:

> REL has been used successfully to evaluate the effects of cold damage, rough handling, desiccation, cold and warm storage, and other stresses on root viability and seedling vigor.
>
> REL is sometimes closely correlated with seedling survival, but in other cases these correlations are weak. This is because factors other than root damage can affect REL. Some of these factors are species, seedlot, seedling age, season, and bud dormancy intensity. When REL is calibrated for these effects it can offer a simple, easy test of seedling root system viability. (Ritchie and Landis 2006, p. 9)

It should be recognized that like root regeneration, REL is strongly affected by seedling dormancy, and, until we thoroughly understand the role of dormancy, we shall probably not know the basis for either test. Ritchie and Landis (2006) discussed this in detail, noting that REL varied with species "and even seed source with species" (p. 9). They cited the finding of Folk et al. (1999) that REL "must first be calibrated to bud dormancy status before it can be effectively used to assess root damage in Douglas-fir" (p. 9). This is additional evidence that stress resistance in Douglas-fir is seated in the dormancy state. They summarized the effectiveness of REL as a predictor of outplanting performance as follows:

> The ultimate objective of any seedling quality test is to predict how well nursery stock will survive and grow after outplanting, and many studies have used REL for this purpose. Unfortunately, results have been mixed. With Sitka spruce and Japanese larch seedlings, for example, REL was closely related to both survival and height growth. . . . In Sitka spruce and Douglas-fir seedlings, REL was correlated with survival on some sites but not others (McKay and White 1997). REL predicted establishment of Japanese larch (*Larix leptolepis*) seedlings to some extent, but Root Growth Potential (RGP) was a better predictor (McKay and Morgan 2001). Similar results were found with black pine (*Pinus nigra*) (Chiatante and others 2002), while Harper and O'Reilly (2000) reported that REL was a poor predictor of survival potential in warm-stored Douglas-fir seedlings. (Ritchie and Landis 2006, p. 8)

They noted further that REL is used in Europe but rarely in North America.

We have discussed the two tests used most commonly to estimate seedling survival and growth in Douglas-fir plantations. Other trials have included seedling vigor tests, wherein both control seedlings and stressed seedlings were grown under favorable conditions and speed of bud break determined (McCreary and Duryea 1987), variable chlorophyll fluorescence, tetrachlomide, and mitotic indices and stress induced volatile emissions. Perks et al. (2001) presented an interesting, useful discussion of the possible role of chlorophyll fluorescence in predicting Douglas-fir seedling vigor, particularly after cold storage. All the tests depended to some extent on determinations of seedling dormancy. Perhaps the subject was best summarized by Dunsworth (1997) and Van Eerden (1994). As Dunsworth (1997) observed, "for organizations that are currently using operational tests, adding new tests are likely to result in diminishing returns since survival may already be near optimum (90%) and large growth gains from physiological testing are unlikely" (p. 439). According to Van Eerden (1994),

> Not withstanding significant expenditures during many years of research and development effort, meaningful and readily measurable description of seedling quality still elude nursery men and reforestation personnel. As a result, seedling quality is largely described only in terms of crude characteristics, principally morphological parameters, unless sound and practical seedling characteristics that can be readily and inexpensively applied and developed soon, of further research and development efforts to characterize seedling quality may become redundant and met with expression of "So what?" (Van Eerden 1994, p. 67)

None of the tests consider the vigor and nature of mycorrhizal component of the root system. Obviously mycorrhizae are extremely difficult to test meaningfully, but, given the importance of the mycobiont portion of the root system, it is perhaps not surprising that investigations that ignore it have not been more successful in estimating seedling vigor.

Temperature (heat)

Nielsen and Humphries (1966) reviewed the effects of soil temperature on root growth and metabolism and noted "knowledge of how root temperature affects plant growth is woefully incomplete" (p. 5). Over the next few decades, more studies began to appear that provided more information in this area. In one of the few reports describing trials wherein soil and air temperatures were each independently controlled, Lavender and Overton (1972) investigated the effects of thermo periods and soil temperatures on the growth and dormancy of Douglas-fir seedlings. They found that the best growth of Douglas-fir seedlings grown from eight provenances occurred at the highest of three soil temperatures (10°C, 15°C, 20°C), and that the soil temperatures had a greater effect on root growth than did air temperature. Some of their results are presented in Table 10.2, where each weight represents the mean of 112 seedlings, 14 from each of 8 seed sources. The mean length of roots from "dry" seed sources was 38 cm and the moist was 33 cm. They reported that "a change of 1°C in soil temperature had a greater effect upon both shoot and root dry weights of the entire seedling population than did a change of 1°C in day air temperature over the entire range of air and soil temperatures studied"; however, "changes in day air temperature between 12°C and 18°C were equivalent to similar changes in soil temperature in their effect upon seedling dry weight" (p. 10). The

Table 10.2 Relation between ovendry weight of seedling shoots, roots, and entire plants to thermoperiods and soil temperatures.

	Weight (mg) by soil temperature (°C)*								
	Shoot			Root			Seedling		
Night temperature	20°C	15°C	10°C	20°C	15°C	10°C	20°C	15°C	10°C
Day temperature 30°C									
24	475	389	261	255	232	186	730	621	447
18	499	374	279	265	197	153	765	571	433
12	471	351	304	285	270	195	756	621	499
6	518	355	251	260	187	204	774	542	455
Day temperature 24°C									
24	602	327	250	301	182	161	903	509	412
18	390	368	278	251	187	189	644	554	467
12	430	347	227	233	215	166	663	562	394
6	446	311	262	238	207	168	685	51/8	431
Day temperature 18°C									
24	497	332	216	218	192	196	714	524	412
18	465	300	224	227	210	173	692	510	397
12	397	300	215	234	189	211	631	489	426
6	406	263	221	181	161	229	588	425	450
Day temperature 12°C									
24	308	248	195	229	213	166	537	461	361
18	260	212	190	209	187	181	470	399	371
12	201	175	127	181	174	143	383	349	270
6	194	177	138	203	183	171	397	360	310

* Each weight represents the mean of 112 seedlings, 14 from each of 8 seed sources.
After Lavender and Overton (1972, p. 10).

strong effect of soil temperature upon seedling dry weight found in Lavender and Overton (1972) agreed with the observations of Irgens-Møller (personal communication), "who noted that reduction of soil temperature from 20°C to 10°C reduced both shoot and root growth of seedlings grown from Douglas-fir seed collected in Arizona and British Columbia when the plants were grown under a constant 20°C thermoperiod and 16-hour photoperiod" (p. 10). The results sharply disagreed with the earlier data of Steinbrenner and Rediske (1964), however. As Lavender and Overton (1972) noted, Steinbrenner and Rediske reported "a strong negative effect upon both shoot and root weights with decreased air temperatures, but a slight increase in shoot weight and a small decrease in root weight with lower soil temperature (Lavender and Overton 1972, p. 10).

Heninger and White (1974) found that soil temperatures between 15°C and 27°C were optimum for root growth for a range of species. Parke et al. (1983d, p. 660) reported maximum root growth of Douglas-fir seedlings between 18.5°C to 24°C. Landis et al. (1993) found that soil temperatures may affect container-grown seedlings more than air temperatures. Lopushinsky and Max (1990) tested the effects of root temperatures between 0.5°C and 30°C on the root growth of (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco). They found that root growth began at 5°C, was at a maximum at 20°C, declined at 25°C, and ceased at 30°C. Plants of high-elevation (1,372 m) seed source were lifted in mid-March and grown in a greenhouse with a 22°C to 15°C and a 16-hour photoperiod for 5.5 weeks. (A very small amount of root growth occurred below 5°C and at 30°C.) Minore (1988, p. 217) found that Douglas-fir roots were heavier in 16°C soil than in 8°C soil when light intensity was about 420 Em^{-2} (20% full sun), but not when light intensity was 1% of full sunlight.

Krueger and Trappe (1967, p. 197–98) noted that Douglas-fir seedlings from Wenatchee, WA had some active roots at soil temperature of 1°C, but many more at 4°C to 5°C in the nursery. Peak root growth occurred in July and March. Lopushinsky and Kaufman (1984) noted that there was no root growth of Douglas-fir seedlings during a 21-day period at 0.2°C. Surprisingly, these temperatures are well below those (5°C to 8°C) for boreal species *Pinus sylvestris* and *Picea abies.* Vapaavuori et al. (1992) and Hawkins et al. (1999, p. 61) found that fast-growing Douglas-fir seedlings had a lower shoot/root ratio, but not significantly so, than slow-growing seedlings. Reviews such as Lyr and Hoffmann (1967) and Sutton (1991) emphasized that, in general, root growth was more affected by soil conditions than by temperatures and by moisture in the air. Hermann and Lavender (unpublished data) found that this was certainly true for Douglas-fir.

Ambient soil temperature

In their review, Lyr and Hoffmann (1967) noted that tree root growth can occur under natural conditions between 2°C and 35°C. However, they also stated that "it is difficult to give useful values for minimum, optimum, and maximum temperatures for root growth of trees. Most authors have not distinguished between a physiological and an ecological optimum and have neglected the influence of other factors on these cardinal values. The method of measuring growth is very important in determining the temperature values. Therefore most data are not strictly comparable" (202).

Nightingale (1935) found that for apple and peach trees, the optimum temperature for root growth was 19°C: "at 19° C and lower the newly developed roots of both genera were typically white, of relatively large diameter extremely succulent, lacking in mechanical strength and they characteristically exhibited few fine laterals and that at 24° C in both genera and the cortex turned brown and gradually sloughed off. The remainder of the root, the central cylinder, was typically very woody, of considerable strength and lacking in succulence" (p. 633).

Douglas-fir roots grown when the entire seedling was held at 4°C were also larger in diameter and succulent (Lavender and Waring 1972). Parke et al. (1983d, p. 658) found that Douglas-fir root growth occurred at temperatures from 7.5°C to 31.0°C. According to McMichael and Burke (1998), "in general, root growth tends to increase with increasing temperature until an optimum is reached above which root growth is reduced" (p. 947). In their review, Kaspar and Bland (1992) stated that "root system expansion is a function of two temperature-dependent processes, growth and development. Growth processes, like cell elongation, increase root length and diameter. Development controls duration of growth processes and initiation of new roots and reproductive organs" (p. 291). Much of the work on tree roots has emphasized growth; however, as they note, "further studies are needed to resolve uncertainties concerning the effects of temperature on root diameter, root hairs, root turnover and root orientation" (p. 297). In discussing the outplanting of seedlings, Sutton (1994) observed, "soil conditions that are particularly important are soil temperature and soil moisture, but any of a number of factors can be dominant in any given situation."

Soil moisture

Under natural conditions, it is difficult to separate the effects of high moisture from low temperature because wet soils are often cold. Lieffers and Rothwell (1986) showed that under controlled conditions, the roots of black spruce and eastern larch were more limited by anaerobic conditions with high water tables under high—rather than low—temperatures. Von der Gonna and Lavender (1988) reported similar results from field experiments with white spruce in British Columbia; and Heineman and Lavender (unpublished data) had similar results.

Minore and Smith (1971) demonstrated significant differences among Northwest tree species in their ability to grow roots over shallow water tables: lodgepole pine, red alder, Sitka spruce, and western redcedar all tolerated shallow water tables, while Douglas-fir did not. In a lengthy review of root growth, Hermann (1977) noted that "both lack and over-abundance of water profoundly effects root growth" (p. 13), citing references to trees, including Douglas-fir. According to Sutton (1991), "the interrelated effects of soil moisture, soil drainage, soil aeration, soil fertility, soil temperature, and soil mechanical impedance, individually and collectively are the prime determinant of root system architecture"

(p. 11). McCaughey and Weaver (1991) demonstrated that Douglas-fir did not tolerate submergence for more than 14 days at temperatures between 13°C and 24°C. Lyr and Hoffmann (1967) noted that studies on the influence of low soil moisture on root growth have been very infrequent. They also observed, however, that "generally root growth decreased at low moisture content," and they quoted Ladefoged (1939) to the effect that root growth stops in most species when soil moisture is reduced to 12% to 14% on an oven-dry basis (Lyr and Hoffmann 1967, p. 207). Additional considerations (and complications) are that soil moisture is not uniform and that roots in moist areas may absorb sufficient moisture to allow roots in dry soil to continue growing. Lyr and Hoffmann (1967) noted that root suberization increased in dry soils, reducing the absorbing portion of the root system.

Ritchie and Dunlap (1980) reviewed data for a number of species, finding that root growth generally fell with soil drying and that little growth occurred at soil moisture tensions of –1300kPa. Working with Douglas-fir, they found that root growth decreased to soil moisture tensions of –1500 kPa, and that stock listed in the winter always made some root growth, even in dry soils. They cited Stone (1967), speculating that "if new growth is just getting under way and is potentially high when the seedling is planted, the roots may continue to elongate when planted in dry soil" (Ritchie and Dunlap 1980, p. 238). Lyr and Hoffmann (1967, pp. 207-9) made the following points relevant to this discussion:

- Root/shoot ratios were higher in dry soils.
- Lack of water inhibited root growth before shoot growth.
- Root suberization increased in dry soils, hence water absorption was less.
- Reduction of water, salt intake reduced photosynthesis and hence root growth.

Light

Obviously, photosynthesis, which may vary with level of light is essential to growth of all parts of the plant, but, as Lyr and Hoffmann (1967, p. 218) found, shading primarily influenced root growth and shoot-to-root ratios were increased. Thompson and Timmis (1978) reported that a number of new roots of Douglas-fir seedlings increased with an increase in photoperiod from 8 to 12 to 16 hours. Van den Driessche (1970) noted that seedlings of Douglas-fir and Sitka spruce were independent on current photosynthesis for root growth and that the root growth was proportional to light intensity. Van den Driessche (1987) utilized radioactive carbon to demonstrate that root growth of seedlings after planting in the spring was dependent on current photosynthesis. Other work showed that new root growth was proportional to photosynthesis under a range of light intensity, although a small amount of root grew in complete darkness. Philipson (1988) argued that "new root growth in Douglas-fir plants is dependent on a living connection, the phloem, with the shoot. This is consistent with the view that in this species root growth requires current photosynthate and possibly other compounds translocated from the shoot" (p. 106).

Zaerr and Lavender (1974) utilized girdling to test the effects of materials exported from the shoot on root growth of Douglas-fir seedlings. They found that root growth was absolutely dependent upon shoot exports, and that food stored in the roots did not substitute for current photosynthate, in accord with Philipson's later (1988) results. In other trials, Zaerr and Lavender found that photosynthesis levels in Douglas-fir seedlings were not correlated with root growth. Gilmore (1965) found that a material from the shoot other than carbohydrates stimulated root growth of Loblolly pine seedlings. Minore (1988, p. 219) found little root growth at 1% of sunlight at either 8° or 16°C soil temperature. Van den Driessche (1991) found that light played no role in root initiation, other than permitting photosynthesis, and that current photosynthesis was not required. A small amount of root growth was possible, probably utilizing carbohydrates stored in the roots (p. 294). One-year-old seedlings could grow limited roots in the absence of photosynthate, but 2-0 seedlings could not. This may be related to the rapid loss of adventitious rooting ability in Douglas-fir.

Organic residues

As we mentioned earlier, ecosystems with ectotrophic mycorrhizae are characterized by a layer of

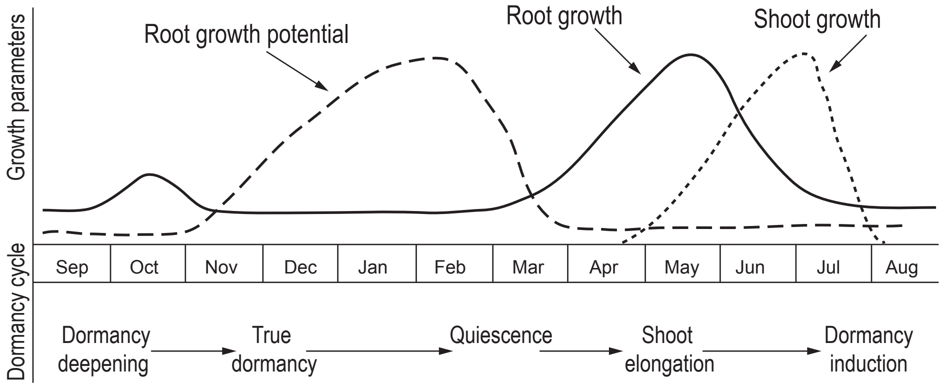

Figure 10.1 Root growth periodicity in Douglas-fir, with maximum and secondary cycles (after Ritchie and Dunlap 1980, p. 224).

organic material (litter and humus) over the mineral soil, where most of the tree roots are found. This is the major source of nitrogen and has the highest concentration of nutrients. It is where the majority of the microflora and microfauna organisms that collectively maintain soil production are found. Harvey et al. (1987) presented a detailed discussion of organic matter in the forest soils of the inland Pacific Northwest and noted that 75% of the mycorrhizae and 96% of the roots in the Douglas-fir (*Pseudotsuga menziesii* var. *caesia*) zone are found there. Harvey et al. (1987) recommended an organic matter content of 31% to 45% in soils of the Douglas-fir type. Such content is characterized by the highest mycorrhizal populations and should be composed of litter, humus and woody materials, all of which are necessary to maintain soil biological material and productivity. Parke et al. (1983c) found that litter enhanced the growth of Douglas-fir seedlings, apparently through some biological effect other than that of mycorrhizae.

Root growth periodicity

Lyr and Hoffmann (1967) argued that data to support a general pattern of root growth of trees does not exist, but noted that a period of maximum root growth occurs in early summer, with a secondary peak in the fall. We have observed a similar pattern in Douglas-fir (Figure 10.1), which was illustrated by Ritchie and Dunlap (1980, p. 224).

11. Mycorrhizae

Denis P. Lavender

The famous line from English poet John Donne's 1624 "Meditation XVII" says that "no man is an island, entire of itself." In the introduction to *Les Symbiotes* nearly two centuries later, the French scientist Paul Jules Portier wrote, "All living beings, all animals from Amoeba to man, all plants from Cryptograms to Dicotyledons are constituted by an association, the "emboîtement" of two different beings" (Portier 1918, p. vii, as quoted in Lane 2005, p. 14). This book is obviously concerned primarily with Douglas-fir, but we digress here to discuss the fungal components of the Douglas-fir mycorrhizae. The term "mycorrhiza" is itself descriptive, as it is derived from the Greek and means literally "fungus root." Hacskaylo (1972) described mycorrhizae as the ultimate in reciprocal parasites (see also McDougall 1918, and Allen 1991). This symbiosis is of a class that may be one of the major associations in botany, one that is only slightly less significant than mitochondria or chloroplasts. Indeed, the partnership is so close that Wilhelm (1966) argued, "under agricultural field conditions, crops do not, strictly speaking, have roots; they have mycorrhizae" (p. 65). There are three major types of mycorrhizae, which differ primarily by the nature of the seed plants: (a) the ericoid mycorrhizae, which occur primarily on the dwarf shrubs of the heaths covering the fringe areas of the world; (b) vesicular-arbuscular mycorrhizae (VAM) on herbaceous plants, particularly in the lower latitudes; and (c) ectomycorrhizae on trees of the Pinaceae (pine), Betulaceae (birch), Fagaceae (beech), and Salicaceae (willow) families in forests of Europe, Asia, and North America. Douglas-fir has ectomycorrhizae, so we shall be concerned with this form.

Ectomycorrhizae

Over time, land plants evolved into more complex and organized forms. The earliest convincing evidence of VAM (vesicular-arboscular mycorrhizae) is of a cycad dating from about 220 million years before present, during the Triassic period, although older records (350 million years BP) of lycopod-like plants harboring vesicle-like structures have been considered. Ectomycorrhizae would have appeared later, likely prior to 70 million years BP, or perhaps in time to witness the great cataclysm and the dinosaur decline, some 65 million years ago. The principal nutrient-absorbing organ of these symbioses are the mycorrhizae, which are found primarily in the litter layer that characterizes these forests. This material, which has a C:N ratio lower than that found under ericaceous plants is, nevertheless, slow to decompose and hence form an acidic layer enriched with organic material (Read 1991). The litter layer varies from acidic more to mull, which forms over base-rich soils. Research has shown that some of the fungi have the ability to mobilize nutrients from complex organic molecules. Mycorrhizal roots have long been known to take up phosphorus, but nitrogen is frequently the limiting nutrient in these ecosystems; fungi, such as the important *Amanita, Suillus, Boletus,* and *Thelephora* have the ability to produce an acid carboxypeptidase and hence have the capacity to mobilize nitrogen from protein (Read 1991). The pH range for these fungi is 4.0–5.0, about the same as that which favors litter layer accumulation. It is interesting and important ecologically that the higher plant has access to organic nitrogen only when it forms mycorrhizae with an appropriate fungus.

Douglas-fir forms ectotrophic mycorrhizae with about 2,000 non-species-specific mycobiants (Trappe 1988). According to Pirozynski (1981), "three events involving mycotrophic symbioses appear to have been landmark events in the progression of plant life on Earth: (1) the evolution of endotrophic symbiosis, (2) the evolution of ectotrophic symbiosis, and (3) the evolution of independence from mycotrophic symbiosis" (p. 1824). Pirozynski (1981) discussed ectotrophic symbiosis in detail as follows:

> The evolution of ectotrophic symbiosis predictably had very different consequences because the peculiarities of ectomycobionts contrast sharply with those of endomycobionts. First, there are at least 5000 morphologically and physiologically distinct species of ectomycorrhizal fungi (Eumycota, mostly basidiomycetes and a few ascomycetes), suggesting that the selective pressure has been on the ectosymbiont which, in this case, is the mycobiont forming a sheath on the outside of roots. Secondly, ectotrophism has evolved only in some 2000 species of plants, chiefly in Pinaceae, Fagaceae, Betulaceae, Salicaceae, and within Dipterocarpaceae, Caesalpiniaceae, and Myrtaceae. Thirdly, the evolution of ectomycorrhizal symbiosis may be a relatively recent event: the ectotrophs are selective in more extreme environments; the mycobionts involved belong to more recently evolved "higher" fungi; the fossil record of ectotrophs extends back to the second half of the Mesozoic; and the geographical disjunctions of ectotrophic communities reflect tectonic events of the same interval. The distribution patterns imposed by these events are maintained by relative immobility of ectotrophic systems, which probably stems from the necessity for concomitant dispersal of both components.
>
> The evolution of ectotrophism did not result in an major taxonomic discontinuity: in anatomy and morphology the ectotrophs have not diverged significantly from their endomycorrhizal progenitors and relatives. But another glance at the ectomycorrhizal groups of plants from the point of view of their habits and habitats will reveal shared characteristics: they are woody, arborescent plants which tend to form species-poor, "pure stand" forests. In ectotrophic forests the diversity at the root-soil interface appears to be provided by the mycobionts. The dominant trees can select as many as 2000 different species of mycobionts according to topography, soil type, or growth phase. Individual trees behave as physiologically different organisms; they do not seem to compete directly with each other and this may allow them to grow in close proximity. Closely linked with gregariousness is a frequent occurrence of anemophily and of dry, unpalatable fruits.
>
> To recapitulate, forest communities can be viewed as mosaics of species with diversity deriving from plants in one and from fungi in the other, being above the ground in one and below in the other. Furthermore, if differences in the composition of forests have a mycotrophic basis, the pecularities of each community may have evolved in consequence. (Pirozynski 1981, p. 1826–1827)

Pirozynski noted that the mycorrhizal habit is necessary for uptake of phosphorus and boron in particular. These two elements were found to be low in hemlock. In one fertilizer trial, hemlock saplings were fertilized with elephant-grade urea, which raised the pH around the mycorrhiza in surface litter layers from about 4.0 to about 7.0 and killed the mycorrhizae. As a result, the phosphorus and boron content was lowered and tree growth reduced (Gill 1981). Gill and Lavender (1983a,b) argued that boron is necessary for lignification and hence, the mycorrhizal habit permitted the evolution of woody stems. Malloch et al. (1980) observed the following:

> Those plants having endomycorrhizae usually occur in forests of high species richness, whereas those with ectomycorrhizae usually occur in forests of low species richness. The roots of ectomycorrhizal trees, however, support a large species richness of fungal symbionts, probably amounting to more than 5000 species worldwide, whereas those of endomycorrhizal trees have low fungal richness with only about 30 species of fungi known to be involved worldwide. Ectomycorrhizal forests are generally temperate or occur on infertile soils in the tropics. The soils are characterized with an acid humus layer. They have apparently expanded in a series of ecologically important events through the course of time from the Middle Cretaceous onward at the expense of endomycorrhizal forests. (Malloch et al. 1980, p. 2113)

According to Amaranthus (as quoted in Wells 2000), "several miles of fungal filaments can be present in a thimbleful of temperate-forest soil. . . . When they connect with the roots of plants, they can increase the plant's ability to take in water and food by 10 to 1,000 times" (p. 22). Certainly, the evolution of this relationship has provided trees with absorbing capacities comparable to that of grasses, and allowed development of roots as primarily supporting or anchoring organs. Interestingly, none of the root regeneration papers discussed in the section on roots has considered the role of the presence or absence of mycorrhizae on seedling survival and growth.

Anatomy

Massicotte (1994) noted that "there are two main components to a mycorrhiza: the fungus and the root," and described the anatomy as follows:

> The Ectomycorrhizal Fungus
>
> Hyphae or mycelium: fine thread-like cells which comprise the body of fungal structures. These can be a single hypha or they can be packed together to form a mantle surrounding the root or clustered together in a coherent structure like a fruit-body, or hyphal strand.
>
> Mantle: the layer of fungal hyphae covering the root surface. It can range from a single, loose layer to a multiple-layered compact covering. It can have a variety of colors.
>
> Extraradical hyphae: loose, free-ranging hyphae extending outwards from the fungal mantle.
>
> Clamp connection: a small, semi-circular connection between two cells of a hypha which allows the transfer

> of a nucleus to a new apical cell in growing mycelium. It is a characteristic of Basidiomycete fungi which form ectomycorrhizae.
>
> Septa: cross walls which divide fungal cells.
>
> Hartig net: labyrinthine branching of fungal cells found between root epidermal and cortical cells in an ectomycorrhiza. The multiple branches derive from fungal cells in contact with the root cells.
>
> The Root
>
> Apex: the growing tip of a root.
>
> Lateral root: a root branch which has derived laterally from another root.
>
> Root hair: a hair-like cell extension radiating outwards from a epidermal cell on the root surface.
>
> Root cap: a collection of root cells covering the root apex.
>
> Apical meristem: the zone of dividing cells at the root apex which give rise to new cells in a growing root.
>
> Epidermis: the outer most layer of cells of the root and the ones indirect contact with the soil micro environment (or covered by fungal portion of mycorrhizae).
>
> Hypodermis: the layer of cells underlying the epidermis (fungal hyphae extend between cells).
>
> Exodermis: the layer immediately beneath the epidermis, but only called exodermis when the cell walls contain a Casparian band. Some deposit suberin lamellae as well.
>
> Cortex: the cells between the epidermis and endodermis (fungal hypha are not present).
>
> Endodermis: the cell layer surrounding the vascular cylinder in the middle of the root. (Fungal hyphae do not invade this tissue.)
>
> Vascular cylinder or stele: the zone internal to the endodermis which contains root vascular tissue (xylem and Phloem).
>
> Pericycle: the cells immediately interior to the endodermis which give rise to lateral roots and part of the vascular cambium.
>
> Apoplast: the zone outside of the plasmalemma of cells within the root.
>
> Symplast: the continuous zone inside the plasmalemma of living root cells of the entire root.
>
> Middle lamella: the zone of pectic substances connecting root cells together.
>
> Plasmodesmata: the microscopic connections between the symplast of adjacent root cells.
>
> Intercellular space: spaces outside the root cells usually in the cortex at the junction of cells. (Massicotte 1994, p. 12)

Dexheimer and Pargney (1991) described the interface of vesicular arboscular mycorrhizae in two passages as folllows:

> The fungus produces a network of intercellular hyphae within the root cortex. From the hyphae of this network, branches penetrate the cell wall and form ramified intracellular structures, the arbuscules. . . . Often the hyphae dilate to produce ampoules with thickened walls, the vesicles. . . . In most VA mycorrhizas, the hyphae of the intercellular network are located in the spaces between the cortical cells where they are in close contact with the outer surface of the walls of the cells and sometimes penetrate between two cells by separating the middle lamella. This network presents an organization similar to the one of the ectomycorrhizal Hartig net . . . (Dexheimer and Pargney 1991, p. 312)
>
> Ectomycorrhizas comprise a mantle of hyphae around the root . . . and a network of intercellular hyphae, the Hartig net, . . . in which the symplastic continuity between the cortical host cells is maintained. . . . The Hartig net constitutes an important area of contact between the fungus and the root cortical cells. ATPpase activities, demonstrating active transport, have been localized on the plasmalemma of both partners, . . . and most exchanges are considered to take place in this part of the mycorrhiza. (Dexheimer and Pargney 1991, p. 317)

Dexheimer and Pargney (1991) noted that, although there are different kinds of mycorrhiza,

> The interfaces between the symbiotic fungi and the cells of the host plant are always bordered on the one side by the fungal plasmalemma, and on the other by the plasmalemma of the host plant or the persisymbiont membrane derived from it. The cytoplasms of the two partners never come into direct contact and are separated by a mixed apoplast comprising a fungal wall and a part originating from the host plant (wall or isolation layer). . . . However, the interfaces of the endomycorrhizas and ectomycorrhizas are not exactly identical.
>
> In ectomycorrhizas, the part derived from the host plant is the cell wall . . . (Dexheimer and Pargney 1991, p. 318)

Mycorrhizae

Parke et al. (1983b) noted that ectomycorrhizae are often assumed to increase water uptake of coniferous hosts. They presented a detailed study of the effects of mycorrhizae during drought periods and concluded that at least one fungus (*Rhizopogon vinicolor*) reduced transpiration of Douglas-fir seedlings and increased water uptake, and that these seedlings recovered faster from drought than did non-mycorrhizal plants and seedlings with different fungi. Castellano and Trappe (1985, p. 616) succeeded in inoculating Douglas-fir seedlings with *Rhizopogon vinicolor*. After 2 years in the field, survival of those seedlings was 11% higher than survival of non-inoculated plants, and the inoculated seedlings were 245% larger. Bledsoe et al. (1982) found that incubating Douglas-fir seedlings with *Hebeloma crustuliniforme* or *Laccaria laccata* did not increase survival on a dry site east of the Cascades. The mycorrhizal fungi did not compete well, reduced seedling biomass, and, since they were from western Cascades isolates, were probably not well adapted to the planting site.

Parke et al. (1983b) reported that *Rhizopogon* greatly increased the drought tolerance of Douglas-fir seedlings, noting that the "net photosynthetic rate of *Rhizopogon* inoculated seedlings 24 hours after rewatering was seven times that of non-mycorrhizal seedlings. The transpiration rate of *Rhizopogon* inoculated seedlings was low before dessication, declined rapidly during the drought period, and, after rewatering, quickly resumed a rate higher than for other treatments" (p. 83). Molina et al. (1999) noted in a review paper that "*Rhizopogon* is the largest genus of hypogenus *Basidiomycota* with worldwide distribution among *Pinaceae.* They occur in young and old forest stands alike and in diverse habitats" (p. 129). They also noted that this fungus produces prolific rhizomorphs that play an important role in water uptake by seedlings (p. 153). Dosskey et al. (1990) demonstrated greater tolerance to drought when Douglas-fir seedlings were infected with *R. vinicolor*. Molina et al. (1997) found that *Rhizopogon* can colonize both Douglas-fir and manzanita (*Arctostaphylos)* and that this may facilitate the survival of Douglas-fir under droughty conditions.

Dosskey et al. (1991) reviewed a number of papers indicating that mycorrhizae can increase seedlings' tolerance to drought and presenting data that demonstrated that *Rhizopogon*-infected (but not *Hebeloma crustuliniforme* or *Laccaria laccata)* mycorrhizal Douglas-fir seedlings had increased photosynthetic rates under drought stress. *Rhizopogon* had no effect on water uptake, reduced the length of roots, and enhanced the stomatal conductance, but reduced leaf-water potentials (p. 332). Duddridge et al. (1980) discussed the rhizomorph function in the uptake and transport of water and demonstrated that mycorrhizal pine seedlings survived for several weeks under drought conditions that killed the non-mycorrhizal control seedlings.

Molina (1981) reported that seedlings inoculated with *Pisolithus tinctorius* survived better on hot, dry sites in southwest Oregon and that "early plantation mortality in Southwest Oregon is not attributable to root disease but is related to deficiency in mycorrhizae formation and function. Unfortunately, many trials have been unable to successfully inoculate seedlings with fungi in S.W. Oregon" (pp. 89–90). Owston et al. (1992) concluded,

> *Rhizopogon vinicolor* is the best candidate for inoculation of nursery seedlings. It is easily inoculated, aggressively colonizes roots and competes well against other mycorrhizal fungi, and produces abundant quantities of hyphal strands that extend long distances into the soil to help seedlings take in water and nutrients. Furthermore, *R. vinicolor* persists and spreads on root systems of seedlings after outplanting so that seedlings can continue to benefit for several years" (Owston et al. 1992, p. 322).

Coleman et al. (1990) found that infection of Douglas-fir roots with any one of several fungi did not affect root hydraulic conductivity. Further, this result was not affected by phosphate levels. There was no relationship between seedling levels of either zeatin riboside and abscisic acid and root conductivity. Johnson and Ferrell (1982) studied abscisic acid and its metabolites through two drought cycles with Douglas-fir seedlings:

> Three year-old intact seedlings were water-stressed, watered, and restressed over a period of 30 days. . . . Needle content of absicsic acid and 2-*trans*-absciscic acid and their saponifiable conjugates were quantified with gas-liquid chromatography. The typical water potential threshold in branch conductance, decreasing abruptly at −2.0 Mpa corresponded to an increase in absciscic acid content of 240 ng g^{-1}. The relationship between abscisic acid and water potential was not definitive, though the general trend was an increase in the hormone with intensifying stress until water potential was −5.0 Mpa, when concentration sharply declined. (Johnson and Ferrell 1982, p. 431)

We have made a number of references to mycorrhizae and stress in the material covered thus far. The importance of the mycorrhizal habit in establishment and survival of forest trees is not in doubt. Which fungi stimulate particular tree species under specific abiotic and biotic conditions is still an open question. Most biotic and abiotic parameters are not studied rigorously enough to allow coherent predictions across a wide range of conditions.

Considerable research on effects of ectomycorrhizal inoculation on outplanting performance of forest seedlings continues. Unfortunately, most of the current work is similar to previous work using species of Pinaceae as the hosts and Pisolithus species as the inoculated mycorrhizal fungus. Additional attention needs to be focused on native plants and host-specific mycorrhizal fungi. Although the applicability of the results are not as wide ranging, the potential for outplanting improvement may well be higher.

Summary

The reports cited demonstrate that some mycorrhizal fungi may increase the survival of Douglas-fir seedlings under drought stress; however, the species and ecotype must be chosen as carefully as the seedling source.

Ecology

Parke et al. (1983c) reviewed the literature concerning the role of forest litter in the growth forest trees and noted that its effects on soil chemistry and physical state increased site productivity: "Litter amendment usually enhanced growth of host seedlings but growth enhancement could not be fully attributed to addition of mycorrhizal inoculum or nutrients provided by litter. These findings suggest that other biological factors stimulated growth of conifer seedlings and (or) activity of mycorrhizal fungi" (p. 666). Parke et al. (1983d) found that the soil temperature range of 18°C–24°C was optimal for the growth of mycorrhizal fungi in southwestern Oregon. They also noted that disturbed soils from clearcuts and soils from old growth stands had equivalent mycorrhizal inoculum. Parke et al. (1983a) found that there was less mycorrhizal inoculum in clearcuts, whether burned or not, than in undisturbed forest soil. However, there was sufficient mycorrhizal inoculum in burned soils; thus, common plantation failures in southwestern Oregon were probably not due to lack of mycorrhizae on the seedlings. Wright and Tarrant (1958) found that, in the Wind River area of southern Washington, the occurrence of mycorrhizal roots of Douglas-fir was inversely correlated with degree of burning; however, this was not true on the H.J. Andrews Experimental Forest in the Oregon Cascades. Mycorrhizae were not found on roots in decayed wood or in rocky or compacted soil. There was no relation between soil pH and incidence of mycorrhizae. As a group, mycorrhizal fungi are found over a wide range of soil environments, but individual fungi are strongly influenced by soil moisture, temperature, pH, fertility, and organic matter. As noted previously, ectomycorrhizal forests on a worldwide basis are characterized by acid litter layers that decompose slowly.

Pankow et al. (1991) briefly reviewed the ecology of mycorrhizae and suggested that the principal ecological role of these symbionts is "in protecting ecosystems in the final stages of succession, where they keep nutrient cycles closed and prevent loss of resources from the entire system" (p. 312). Simmard et al. (1997) found that, while mycorrhizae did not increase the growth of Douglas-fir seedlings, "the influence of overstory trees and pattern of ectomycorrhizal formation are important to *P. menziesii* seedling performance in deeply shaded forest environments" (p. 327). Trappe (1988) argued that the classification of mycorrhizal fungi ignored the physiology and ecology of fungi and recommended instead a classification of mycorrhizae, "by mycorrhizal dependence of hosts as it interacts with dispersal strategy of the [fungi]" (p. 347).

Mexal and Reid (1973) found that both flooding and drought were limiting factors in ectomycorrhizal formation. They reported that *Cenococcum graniforme* made maximum growth at –15 bars moisture, whereas *Thelephora terrestris* failed to grow and *Suillus luteus* grew poorly: "While some species may grow or even thrive at ψ approaching −40 bars, the species studied here were severely limited by ψ below −15 bars" (p. 1584). Cordell and Marx (1994) noted that coarse, well-drained soils promoted mycorrhizal growth and that the pH range favored by the host plant also favored the fungi; high soil organic content also favored the fungi, while excessively high nutrient content of fertilized soils inhibited the development of mycorrhizal fungi.

Parke (1985) observed that "mycorrhizal fungi occur in a large diversity of plant communities and their adaption to extremes of environment is widely acknowledged" (p. 107). According to Trappe (1977), "temperature profoundly influences growth, metabolism and colonization of roots by mycorrhizal fungi" (p. 211). Husted (1991) and Husted and Lavender (1989) found that soil temperatures of 15°C–17°C were more advantageous to mycorrhizal fungi endogenous to northern British Columbia than were temperatures of 6°C or 26°C. Trappe (1977) noted that *Pisolithus tintorios* grew well at 40°C and that "temperature is an important parameter of mycorrhizal growth" (p. 211). Dighton (1991) citing Read (1984), noted the following:

> Changes in vegetation, soil organic matter accumulation and mycorrhizas [occur] on both an altitudinal

> and latitudinal gradient. [Reid's] scheme shows that as one ascends in altitude or progresses toward the poles from the equator, in general one moves from soils which are mainly inorganic (due to rapid decomposition and nutrient cycling) through soils of increasing organic matter content (due to lower decomposition) to very poor, shallow and mainly inorganic soils (due to limited plant productivity in climatically adverse conditions at extreme altitude or close to the poles). . . . Consequent changes in mycorrhizal flora are from vesicular-arbuscular mycorrhizas through the ectomycorrhizas to the ericaceous mycorrhizas. Thus, it is expected that the ability of mycorrhizas to degrade organic matter and become involved in direct cycling of nutrients is of major significance in the ectomycorrhyzal and ericaceous mycorrhizal dominated communities. (Dighton 1991, p. 363)

Parke et al. (1983c) found that forest litter, particularly from undisturbed forest stands, stimulated seedling and mycorrhizae growth. They suggested possible saprobism for mycorrhizae.

Disease

Linderman and Hoefnagels (1993) noted that "while mechanism to reduce root diseases (by mycorrhyzal seedlings) is not clearly understood, it appears to involve some morphological or physiological changes that occur when the mycorrhizal association is well established." The authors emphasized the importance of mycorrhizal-caused changes in root membranes in the formulation of bacteria colonies adjacent to roots in controlling *Fusarium* spp., and described the development of studies designed to identify soil microorganisms antagonistic to *Fusarium* and other seedling root diseases.

In a series of papers, Sinclair and coworkers investigated several methods of reducing the pathology of *Fusarium oxysporum* on Douglas-fir seedlings. Stack and Sinclair (1975) investigated the ability of two common mycorrhizal fungi in Pacific Northwest nurseries, *Laccaria laccata* and *Inocybe lacera*, to reduce *Fusarium oxysporum* infection. They found that *L. laccata*, but not *I. lacera*, offered some protection. In a further trial, *L. laccata* provided protection before mycorrhizae were formed. It was shown that when *L. laccata* was placed between the *Fusarium* and the seedling, infection was reduced, but the reason was not clear. Sylvia (1983) and Sylvia and Sinclair (1983a) investigated the inhibition of *Fusarium* by extracts of *L. laccata* over a range of conditions and found *L. laccata* was effective, thus antibiosis under laboratory conditions was demonstrated. These workers examined the roots of Douglas-fir seedlings (Sylvia and Sinclair 1983b) and found that phenolics induced in the cortical tissue by *L. laccata,* and not antibiosis, was the mechanism for the reduction of *Fusarium* pathogenicity. Additionally, Sinclair et al. (1982) showed that *L. laccata* stimulated greater seedling and shoot/root growth. In a later publication, Strobel and Sinclair (1991a) showed that *L. bicolor* stimulated flavonolic infusions in the cortical cell walls that restricted fusarium to intercellular spaces. In a later report, Strobel and Sinclair (1991b) noted that, in previous trials, "a high degree of root protection [prevention of lesion formation] was obtained against a relatively non-aggressive isolate of *F. oxysporum* at a temperature below optimum for disease development" (p. 420). They concluded: "The timing and intensity of wall infusion with phenolics may be crucial determinants of resistance of Douglas-fir to *F. oxysporum*. . . . Unfortunately, the highly specific nature of the requirement for this induced resistance and variable expression of induced resistance mechanisms appear to preclude its practical exploitation" (p. 424).

Marx (1973) reviewed a large number of papers, some of which presented evidence that mycorrhizal fungi may protect roots against pathogens. The effects varied with mycorrhizal fungi and pathogens and may have been the result of the physical barrier posed by the fungus, the production of biocides by either the fungus or the host plant, or the development of a bacterial population in the mycorrhizal rhizosphere. Finally, he cited Zak (1964), who suggested that the mycorrhizal fungus may utilize the carbohydrates that would otherwise attract and feed pathogens.

Sinclair et al. (1982) demonstrated that *Laccaria laccata* protected Douglas-fir seedlings against *Fusarium oxyparum* even in the absence of mycorrhiza. Marx (1973) concluded: "In all probability most of the proposed mechanisms of root protection by mycorrhizae are functional at any given time since several appear to be inseparable (i.e., mantle barriers, host origin inhibitors, differences in chemical exudations, etc.). This broad spectrum of defense mechanisms acting in concern assures greater opportunities for biological control of feeder root pathogens by mycorrhizae" (p. 877). Unestam and Damm (1994, p. 175) largely agreed with Marx's hypothesis, noting that long roots on mycorrhizal seedlings, which are non-mycorrhizal, suffered less disease than those of non-mycorrhizal seedlings, suggesting that the acid environment strongly inhibited nursery pathogens. They also stated, however, that "the work on mycorrhizae as a control agent has been conducted entirely on a basic level with tree seedlings, no apparent applications have yet been developed for use in the nursery and doing outplanting in the field. The reason for this is the lack of knowledge on fungal behavior in different soils, since the methods work elegantly in some environments but root protection is often difficult to predict and not ubiquitous" (p. 173).

Mycorrhizosphere

Linderman (2000) noted that the "rhizosphere" phenomenon was first discussed in 1904. In a number of papers, Linderman (e.g., 1985, 1988, 2008) extended the concept to include mycorrhizae, terming the phenomenon "the mycorrhizosphere." He presented data supporting the concept of a community of soil microorganisms "wherein roots attract mycorrhizal fungi and the latter attract bacterial associates." Chanway (1997), Chanway and Holl (1992, 1994) and Chanway et al. (1991a) discussed soil bacteria in the Douglas-fir rhizosphere that stimulated seedling growth. One major effect of this group of soil microoranisms is to suppress root pathogens. Linderman (2000) described this concept in detail, crediting it with the general lack of root disease in natural soils. Linderman and co-workers published a series of reports that implicated the soil microbial populations formed as a result of mycorrhizal infection with the concurrent change in exudates from the mycorrhizae with a definite role in enhancing the host plant's health and vigor (Linderman and Hoefnagels 1993). Linderman (2000) presented several hypotheses as a cause of this effect:

> (a) enhanced nutrition, (b) competition for nutrients and infection sites, (c) morphological changes, (d) changes in the chemical constituents implant tissues, (e) alleviations of abiotic stress, and (f) microbial changes in the mycorrhizosphere. Depending on the disease and environmental situation, any or all mechanisms could be involved, but changes in the microbial populations in the miccorhyizosphere seems to be the best explanation, yet least studied. . . .
>
> The mycorrhizal association with roots of land plants has existed for hundreds of millions of years and logically includes associations with other functional groups of soil microbes. . . . Currently, we observe that plants have little or no disease, or at least no strong impact of disease on their growth and survival, in natural ecosystems where microbial balance (including mycorrhizas) has not been disturbed. (Linderman 2000, p. 345-346)

Of course, Linderman was concerned with soil diseases. Unfortunately, although there have been numerous attempts to draw conclusions about mycorrhiza-disease interaction, the lack of data has limited such approaches. Linderman (2000, p. 359) concluded that "the primary mechanism of mycorrhiza-disease interactions is through the induction of changes in the microbial community" (caused by altered root and hyphal exudations).

Nutrient and water uptake

In addition to exploring great volumes of soils, the small diameter of fungal hyphae allow wider penetration of soil. Mycorrhizae have external enzymes that enable dissolving phosphorus from rock and produce chelators that prevent the phosphorus from binding with other elements. Accordingly, they are much more efficient at taking up phosphorus than are higher plants. Nutrients, particularly phosphorus and boron (Gill 1981), are transferred to the host plant, while the fungus derives carbohydrates from its host. Trappe and Strand (1969) reported the stunting of non-mycorrhizal Douglas-fir seedlings in an Oregon nursery. They found that severe phosphorus deficiency in Douglas-fir seedlings was associated with a lack of mycorrhizae. Rygiewicz and Bledsoe (1984) reported that mycorrhizae appeared "to enhance K uptake and storage in roots by increasing the vacular pool sizes, increasing influx rates and decreasing efflux rates" (p. 123). Perry et al. (1987, p. 929) stated that "mycorrhizae improve seedling survival and growth by enhancing uptake of nutrients (particularly phosophorus)."

Duddridge et al. (1980) demonstrated that water flow in fungi rhizomorphs was sufficient to enable *Pinus sylvestris* seedlings in a dry soil to remain viable for several weeks after control seedlings died. They noted that rhizomorphs are necessary to provide increased seedling survival. Parke et al. (1983a) reviewed a number of studies demonstrating that mycorrhizal coniferous seedlings tolerated drought better than control seedlings did; furthermore, they recovered more rapidly after drought stress. Parke et al. (1983b) compared mycorrhizal and non-mycorrhizal Douglas-fir seedlings during and after drought stress. The performance of seedlings inoculated with *Rhizopogon vinicolor* was superior to that of control seedlings or those inocculated with other fungi. A second fungus that has been reported to tolerate low soil moisture is *Cenococcum geophilum.* In general, however, mycorrhizae develop poorly under moisture stress. Further, most mycorrhizal hyphae are in the upper soil layers and do not contact the moisture that may be in the deeper portion of soil horizons. According to Trappe (1977), "Of all the ectomycorrhizal fungi, *Conococcum geophilum* is best recognized as drought resistant" (p. 212). Trappe also noted that *Hymenogaster alnicola* and lacternius *obscorutus* tolerate very wet soils.

Physiology

Scagel and Linderman (1998) noted that mycorrhizae formed in Douglas-fir by the fungi, *Laccaria laccota* and *Rhizopogon vinicolor* increased the root concentration of Indole-3-acetic acid (IAA). The mycorrhizal seedling height, diameter, and shoot/root ratio were all increased and correlated with the IAA concentration in the roots: "In several cases, the extent of colonization was correlated with in vitro IAA or ethylene production capacity of the fungus and the IAA concentration of the roots, indicating a possible relationship between relative capacity for IAA or ethylene production and mycorrhizal formation" (Scagel and Linderman 1998, p. 746). These results support the hypothesis that mycorrhizal fungi can stimulate increases in root IAA that can affect the growth of roots and shoots after transplanting.

Dosskey et al. (1990) found that *Rhizopogon vinicolor,* but not *Hebeloma crustuliniforme* or *Laccaria laccata,* caused a significant increase in photosynthesis of Douglas-fir seedlings, and that the probable cause was the increased photosynthetic sink of extensive fungal growth. In a second paper (1991), they noted the same effect of *R. vinicolor* under conditions of drying soil.

Simmard et al. (1997) elegantly demonstrated that the hyphae of mycorrhizas could translocate photosynthale from one host species (*Betula papyrifer)* to Douglas-fir under field conditions. Noting that the results were similar to those of a number of studies in laboratory conditions, they suggested the following: "Consequently, the theory that plant community dynamics operate mainly within the constraints of resource supply should be reformulated to consider mutualism between plants and their mycorrhizal fungi, as well as microbial resource sharing" (p. 520).

Hacskaylo (1973a) reviewed the carbohydrate metabolism of a range of sugars by a range of fungi and warned against generalizations, since the data were erratic. As he wrote, "In nature, ectomycorrhizal fungi depend primarily upon the roots of their hosts for carbohydrates, usually sucrose, glucose, and fructose. Certain species of fungi may, however, possess enzymes to hydrolyze cellulose and other carbohydrates, but this characteristic does not appear to be widespread" (p. 227). Some ectomycorrhizae fungi have the capacity to covert the foregoing sugars to mannose, trehalose, and glycogen, which are not utilized by the host phytobiont.

Soil

In greenhouse trials, Borchers and Perry (1989) demonstrated that soil collected under hardwoods favored mycorrhizal and seedling growth. Amaranthus and Perry (1987) found that soil from established plantations greatly increased mycorrhizal development in sites with repeated plantation failure. In contrast, Rose et al. (1983) found that litter could inhibit mycorrhizal formation. MacFall (1994) summarized literature indicating that "ectomycorrhizae have the capability of altering the rhizosphere biogeochemistry, and of creating mineralization patterns which differ from those of bulk soil" (p. 217).

In his review of mycorrhizae in ecosystems worldwide, Read (1991, p. 379) noted that ectomycorrhizae are found on soils with a leaf litter accumulation with a relatively low carbon:nitrogen ratio, which forms a layer of acidic, organically enriched material on the soil surface characterized by such low rates of N mineralization that this element is frequently growth limiting. The layer may be a mor, a medium mull, or a mull when over base-rich substrates. Read (1991) noted that many mycorrchizal fungi have the potential to mobilize organic nitrogen and, hence, are more important ecologically than previously thought. Read (1991) observed the proliferation of absorptive hyphae in areas of local nutrient concentration and described examples, such "fungal wefts associated with the mycorrhizal roots proliferating in the decomposition horizons of coniferous forest soils and in the mycelial mats formed by Hysterangium and related species underneath the organic horizons of Douglas-fir forests" (p. 382). Read (1991, p. 382) reported that "it has been estimated that the mycelium of *H. crassa* can occupy 9.6% of the A horizon of a forest soil to a depth of 10 cm. . . . These mats are known to be sites of elevated enzyme and respiratory activity."

According to MacFall (1994), "fungal mats formed by *Hysterangium setchellii* (Fisher) in association with Douglas-fir may colonize up to 27% of the forest floor and account for 45-55% of total soil biomass" (p. 227). Read (1991) suggested that "late" stage fungi are likely to colonize seedlings and, hence, to integrate them into a network of absorptive mycorrhizal fungi. Such integration can compensate for poorly formed root systems and result in greater seedling growth.

Fire

The numerous references on the effect of fire on mycorrhizae are erratic and probably reflect the intensity of a given fire, with fewer mycorrhizal fungi in severly burned sites.

Cost-Benefits of Mycorrhizae

We have previously noted that mycorrhizae are generally essential to the survival of the host plants (including Douglas-fir). However, it may be of interest to examine the cost, in terms of plant resources, of this relationship. Fitter (1991, p. 350) noted that about 10% of the carbon translocated to the root goes to mycorrhizae. However, this may not be a drain on plant resources if it stimulates a higher rate of photosynthesis. Further, photosynthesis rates are frequently limited by phosphorus, an element largely taken up by the fungi. Fitter suggested that the rate of P uptake may very well be correlated with productivity, although noting that such a relationship had been found only in carefully controlled laboratory trials. Studies that attempted to relate mycorrhizae and yield resulted in erratic data. Fitter concluded that more data describing uptake by roots and mycorrhizae under field conditions are needed. St. John and Coleman (1983, p. 1011) cited numerous papers suggesting that a mean of about 50% of the photosynthate is translocated to fungi.

Conclusion

We have cited a number of papers that discussed the relation between mycorrhizal fungi and Douglas-fir, although this is not an extensive review. Much is summarized in the following from MacFall (1994):

> It can be concluded that ectomycorrhizae play a significant role in soil biogeochemistry and soil structure. Greater selective nutrient uptake from the increased absorptive surface area provided by the mycelial network has been shown with *H. arenosa* and other ectomycorrhizal associates. Although not clearly demonstrated, efficiency of uptake is likely to also be increased with mycorrhizae. Mechanisms for accelerated, biologically-mediated weathering of minerals and organic materials through the production of enzymes, organic acids, and siderophores are present in many ectomycorrhizae. Higher rates of carbon and nutrient mineralization have been observed within fungal mats compared to non-mat soils, suggesting the potential for a similar role in more diffuse hyphal structures. Significant water uptake and transport may also be accomplished through mycorrhizae, but is likely to differ between mycorrhizal types. Clearly these symbiotic associations have the potential to alter the soil chemistry of the mycorrhizosphere, and as our understanding of their physiological processes emerges, we can better develop a model for their role in nutrient mobilization and cycling at the ecosystem level. (MacFall 1994, p. 232)

As Amaranthus (1994) and later Steinfeld et al. (2003) observed, more information is needed "on the ability of specific mycorrhizal fungi to establish at the nursery and improve seedling performance in the outplanted environment," particularly given that "fertilizing and irrigating practices in seedling production nurseries are very different than field conditions at harsh outplanting sites" (Steinfeld et al. 2003, p. 197). The importance of the mycorrhizal habit in the establishment and survival of forest trees is not in doubt. Which fungi stimulate which particular tree species under which specific abiotic and biotic conditions remains an open question, however. Most biotic and abiotic parameters are not studied rigorously enough to allow coherent predictions across a wide range of conditions. Considerable research on the effects of ectomycorrhizal inoculation on the outplanting performance of forest seedlings continues. Unfortunately, most of the work is similar to previous work using species of the family Pinaceae as the hosts and the genus *Pisolithus* as the inoculated mycorrizal fungus. Additional attention needs to be focused on native plants and host-specific mycorrhizal fungi. Although the applicability of the results is not as wide ranging, the potential for outplanting improvement may well be higher.

12. Adverse Abiotic Factors

Richard K. Hermann

Both abiotic and biotic factors can have an adverse effect on the growth and survival of Douglas-fir.

Frost

Observations on frost damage and research on frost hardiness of Douglas-fir have focused primarily on the coastal variety. That focus reflects the fact that coastal Douglas-fir is considerably less frost resistant than the interior variety (Sakai and Weiser 1973), and the predominant role of coastal Douglas-fir in the areas of introduction outside its natural distribution. The susceptibility of the coastal variety to frost injury became a matter of concern as early as the last quarter of the 19th century in German trials of Douglas-fir (Danckelmann 1884).

Frost leads perhaps more often than any other abiotic factor to injury of Douglas-fir. Damage can become particularly severe with the influx of abnormally cold air masses. Such climatic events, with their ensuing damages, have been recorded for the Pacific Northwest in November 1955 (Duffield 1956) and December 1972-January 1973 (Hermann 1977).

Douglas-fir grown outside its natural range has also experienced particularly injurious cold spells. Extremely low temperatures in October 1908 (Abele 1909); the winter of 1928/1929, when temperatures dropped to a low of −45°C (Kahl 1930); October 1955 and February 1956 (Jahnel and Watzlawick 1957); and in the fall and winter of 1978/1979 (Jestaedt 1980), resulted in widespread injury to coastal Douglas-fir in German nurseries and plantations. The winters of 1923/1924, 1928/1929, and 1946/1947 caused much damage to saplings and pole-sized stands of coastal Douglas-fir in Denmark (Thulin 1949). A report from New Zealand (Director of Forestry 1943) mentions the destruction of experimental plantings of Douglas-fir by an unusually severe early frost on the plateau of central North Island.

Identification of frost injury

The damage inflicted on tree nurseries by the cold spell of December 1972 provided a drastic example of the consequences of such a climatic event (Hermann 1974). Although exact figures are not available, losses for all the nurseries in Oregon and Washington probably amounted to several million seedlings. That event emphasized the need for the correct identification of frost injury to avoid compounding losses in the nursery by preventing outplanting or injured stock, with its risk of lost planting investments and future wood production. Although frost injury is generally not as serious in older trees as it is in seedlings, identifying the type of injury may help in deciding on the need for salvage measures.

Needles

Injury to needles is probably the most common and usually the most easily recognizable kind of frost injury. Injured foliage tends to lose its normal green color from 24 to 72 hours after a return to above-freezing temperatures; its color changes to a reddish-brown, sometimes preceded by a purplish or dull gray hue (Hermann and Zaerr 1973). Color change however, may not occur for several days if temperatures remain below freezing. Nevertheless, the possibility exists to identify damage immediately. The freezing of plant cells ruptures their membranes and alters electric properties of membranes. Changes in electric impedance can be determined with special equipment; thus, damaged needle tissue can be detected minutes after it has thawed out (Zaerr 1972).

Buds

Frost injury to buds is not immediately apparent from their external appearance. Injured buds begin to look dried out or start to shrivel 4 to 6 weeks after frost injury. If buds are injured, however, damage can be determined by slicing them open shortly after temperatures are again above freezing. Damaged tissue inside the bud, most commonly the leaf primordium, develops a light-to-dark brown discoloration (Hermann and Zaerr 1973).

Trunk

Frost injury to trunks of seedlings, saplings, and pole-sized trees may show external signs, such as lesions or shriveled bark. Depending on the severity of injury, various degrees of browning by cambium and phloem can appear after some bark is removed. Another indication of damage to the trunk is progressive defoliation. Needles may be shed even if they themselves have not been killed by frost. That phenomenon appears to be associated with injury to the needle traces and cortical tissues of the trunk. Injury to the boles of mature trees is rare and usually is not visible.

Roots

Injured roots show brown or almost black discoloration when bark is stripped away. Injured bark becomes mushy and can easily be pulled off. At this stage, however, freezing injury can easily be mistaken for symptoms of fungal diseases (Hermann 1990).

Consequences of frost injury

Frost injury is seldom severe enough to kill the entire tree immediately, but it may weaken the tree enough for it to die if it is stressed.

Needles

If seedlings lose most or all of their frost-damaged foliage without injury to buds and stems, the loss is seldom lethal. But it can still have serious consequences. Artificial defoliation of 2-year-old seedlings in August, November, and February to investigate the importance of needles in the dormancy cycle of Douglas-fir indicated their role in initiating acclimation (Hermann 1974). If needles are removed or killed in early fall, buds appear to be incapable of responding to chilling, because the message for that response appears to be routed through the foliage. The consequences are increased susceptibility to frost injury, delayed bud burst, and shoot growth in spring. If needles are lost after hardiness has been acquired, bud burst and shoot development will be normal.

Needle loss by saplings, even when severe is not necessarily lethal. The development of 6-year-old trees in Christmas-tree plantations injured by the cold spells in December 1972 and January 1973 was followed for 3 years. Large losses of needles without severe injury to the trunk had not resulted in either immediate or delayed death of trees. Of a sample of 2,000 trees, less than 5% had suffered a needle loss exceeding 80%. Severity of injury to needles did not always indicate injury to other tissues, although extensive damage to trunk tissues was most frequently found in trees with severe foliar injury. The trees were an economic loss, however, because they had become unmarketable (Hermann 1977). Zieger et al. (1958) reported that the survey of frost damage to coastal Douglas-fir in eastern Germany by the February 1956 freeze showed that only 6% of the frost-injured trees never recovered. They were mostly saplings and suppressed pole-sized and mature trees that had lost between 70% and 80% of their foliage.

Buds

The main effect of frost injury to the terminal bud of 1- and 2-year-old seedlings appears to be a temporary growth reduction lasting through two or three growing seasons, unless combined with severe damage to the trunk and foliage. In a study by Edgren (1970), who followed the development of 2-0 Douglas-fir seedlings injured by an early frost in September 1965 at the Wind River Nursery near Carson, Washington, through three growing seasons, 95% of 500 seedlings outplanted in the field failed to burst terminal buds in spring 1966. A shoot from a lateral bud took over as the new leader in these trees. The height growth of damaged trees lagged for two growing seasons behind that of trees whose terminal bud had not been damaged. But by the end of the third growing season, the height increment of seedlings whose initial terminal bud had been killed had caught up with and even surpassed the height increment of trees whose terminal bud had escaped damage. A similar phenomenon, illustrating the remarkable regenerative ability of Douglas-fir to replace a damaged terminal bud or shoot, was reported from Germany (Mörmann 1956a). A late frost in May 1953 had killed the terminal shoots of 4- to 6-year-old trees in plantations of coastal Douglas-fir. Not only did these trees quickly form new leaders from a lateral bud, but many of them displayed unusually large increments in the next growing season.

Buds are especially prone to injury by late frosts because deacclimation has usually ended by that time. Seedlings and saplings growing in valleys and depressions frequently suffer from repeated frost damage in the spring. The frost damage delays or even prevents the growth of trees beyond the height of the layer of air subject to freezing temperatures. The trees tend to acquire a shrub-like appearance that is sometimes mistakenly attributed to wildlife browsing. Damage inflicted on buds by a late frost is clearly illustrated by an event in May 1967 in the Soltau forest district in northern Germany (Rack 1974). The injured trees were coastal Douglas-firs, mostly 2- to 5-year-old. A first inspection of the east-west aligned rows of trees after the freeze hinted they had suffered more damage on their south- than north-facing side. A count of killed buds on 15 trees confirmed that damage was indeed greater on their south than on the north side. The tally showed an average of 42 dead buds (range, 1–100) on the south and 31 dead buds (range 0–83) on the north side. Rack (1974) attributed the difference in damage to an earlier bud break on the south side and, therefore, buds on that side were more damaged by a late frost. Rack came to the conclusion because the developmental stages of buds on the two sides showed corresponding differences.

The temperature gradient in the air layer near the ground also contributed to differences in the amount of damage (Rack 1974). A count of dead buds on 18 trees at five 50 cm-intervals from ground level to a height of 200 cm showed a decrease of killed buds with increasing height on the tree. Branches up to a height of 50 cm height had 65% of dead buds compared to 29% on branches at heights of 151 to 200 cm.

In one of the Christmas tree plantations in Oregon's Willamette Valley, the December 1972 freeze killed the terminal buds in 69 trees out of 1,000 sampled (Hermann 1977). Of the 1,000 trees, 530 had sustained injury to lateral buds on the trunk. The number of injured buds on the trunk was generally five to six of those checked on each tree. Fortunately, injury to the terminal bud does not pose a problem to Christmas tree growers because the leader is usually pruned away. Massive injury to lateral buds would be more serious because of the gaps in the crown. But as this survey suggested, massive injury to lateral buds is probably uncommon even during a severe freeze in mid-winter. Frost damage to lateral buds in spring, especially in consecutive years, is more likely to render trees unmarketable. Some of the trees sampled in spring 1973 apparently had suffered bud injuries in previous years and, in these trees, the additional injuries from the freeze of December 1972 were sufficient to make them unmarketable. Plantations and young natural stands of interior Douglas-fir in the central interior of British Columbia showed widespread injury or death of buds in parts of trees above the winter snow line in spring of 1989 (Van der Kamp and Worrall 1990). That damage was apparently the result of a rapid drop of temperatures from above freezing to −30°C, when a mass of arctic air moved into the region on January 30, 1989. That event was preceded by four unusually warm months, with temperatures of 1.0°C to 4.7°C above normal. Damage became visible in mid-June, when most buds above 1 m (the putative mid-winter snow line) had failed to flush. Buds below that line had flushed normally. Inspections in severely affected 10- to 15-year-old plantations east of Williams Lake, British Columbia (52°20′N, 121°30′W) indicated that, of the buds above the snow line, fewer than 5% had been killed, but between 50% and 90% were severely injured. In most of the damaged buds, the central meristematic dome had been killed, but injury was rare to the basal stem segments bearing the bud scales. These injuries resulted in the replacement of the terminal bud by a whorl of nearly equal buds or by a whorl of short shoots, each bearing a complete set of buds. Van der Kamp and Worrall (1990) concluded that the major long-term damage from this type of bud injury probably increased the frequency of multiple leaders, affecting adversely the form of the main bole.

Reproductive buds

Observations in the field and freezing tests have shown that reproductive buds appear to be the least cold-hardy organs. Frosts during flowering periods have caused heavy seed losses in Douglas-fir stands and seed orchards in the native range of this species and in areas of introduction. The magnitude of such losses was illustrated by the damage done by frosts in winter 1972/73, which killed 77% of all female buds in a Weyerhaeuser seed orchard in Oregon (Timmis 1977). The research prompted by this event indicated that the hardiness of female buds increased to a maximum by mid-December. A 50% kill (LT_{50}) of female buds in freezing tests ranged from −19°C and −23°C from mid-December to early March. Hardiness then decreased at 1.6°C per week to a LT_{50} of −6.5°C; by the time the first external morphological changes in buds were visible, hardiness had nearly reached its minimum. After bud swelling, significant differences in hardiness were not found between female flowers at different stages of their development. LT_{50} averaged −4.5°C throughout flowering for the five clones used in this investigation (Timmis 1977).

Temperatures leading to frost kill of female buds on older trees during flowering apparently are in the same range as those for female buds on younger trees. A frost with temperatures between −2°C and -3°C in spring of 1953 completely destroyed flowers in 60- to 70-year-old coastal Douglas-firs in eastern Germany (Krauss 1955). Male and vegetative buds are apparently slightly hardier than female buds. Timmis (1977) found male buds to be 1°C or 2°C and vegetative buds 2°C or 3°C hardier than female buds, especially from March to May. The January 1989 freeze in central interior British Columbia had only minor effect on vegetative buds of mature interior Douglas-fir, but apparently killed all of their reproductive buds, both male and female. The 1989 Douglas-fir cone crop was a complete failure in that region (Van der Kamp and Worrall 1990).

Frost damage to immature cones is probably rare. A severe frost in the night of May 26–27, 1966, over most of Vancouver Island injured cones 35 to 45 mm in length at the Gordon River clone bank. Ovuliferous scales were discolored and the central axis of the cones showed complete necrosis. Bract scales, however, were still green (Orr-Ewing 1966a). Another such event was recorded in southwestern Germany where a late frost on May 23, 1953, destroyed immature cones on 60-year-old coastal Douglas-firs (Mörmann 1956a).

Stem tissue

Injury to stem tissues, especially the phloem and cambium, are generally more critical than injury to either buds or needles. A seedling usually will die if the injury extends over more than half the circumference of the stem. Such injury has essentially the same effect as girdling the stem. Seedlings injured in this manner often do not develop external signs of injury and may even commence to grow new shoots before dying (Hermann 1974).

The long-term consequences of frost damage to the trunk of older trees have been shown particularly well in the aftermath of the November 1955 cold wave in the Pacific Northwest. Severe frost damage sustained by an 11-year-old Douglas fir plantation near Elma, Washington, resulted in top kill throughout the stand. The stand's average height of 4.3 m before the freeze dropped to 2.4 m immediately after that event. Five years later, the height of injured trees that had developed new leaders averaged 5.5 m versus 6.4 m for leaders of uninjured trees. Injured trees that had failed to form a definite new leader averaged only 4.0 m in height (Wiley 1960).

A follow-up study (Shea 1962) of injured trees in the Elma plantation at age 17 indicated invasion by several species of wood-destroying fungi, as well as other forms of damage. Frequently, damage to the cambium had resulted in the formation of a partial or complete frost ring. Shake had developed in some trees and had separated wood formed before the freeze from that formed afterwards in portions of the trunk. Partial separation of the 1955/1956 growth rings had occurred in other trees. Shea concluded that the presence of wood destroying fungi and the prevalence of shake in outwardly sound-looking trees would result, at best, in poor quality wood from the butt log and that pulp would be the most likely end product.

A case in which serious frost injury to trunks by the November 1955 freeze that had not become immediately evident was described by Childs (1961). In 1957, hundreds of small groups of trees, apparently scattered randomly, showed red crown in an extensive well-stocked stand of Douglas-fir in northwestern Oregon. Trees ranged in age from 25 to 30 years, averaging 20 cm in dbh. In 1958, many of these trees were dead. Examination revealed callus layers, as wide as an annual growth ring, completely encircling the boles between 2.45 and 3.56 m above their bases. Smaller banks of callus tissue, about one-half to two-thirds as wide as the preceding annual ring, were also found slightly higher on their trunks. Many of the still-living trees, immediately adjacent to the groups of killed ones, displayed cracked bark about 0.6 to 2.7 m above the base as a result of callus formation where small areas of cambium had been killed. Conspicuous frost rings were present between the 1955 and 1956 annual rings. In most of the trees with partially killed cambium in the basal part of the bole, the upper 1.2 to 1.5 m of the crown had died. Although information about further development is not available, most of this stand has probably become a total loss because of the severity of injuries sustained.

Johnson (1971) followed the development of trees injured by the November 1955 freeze in a 17-year-old plantation on Vancouver Island. He examined the frost lesions on severely injured trees at 3-year intervals. Three years after the initial injury, the frost lesions had exposed sapwood. Callus tissue had formed over 50% of the lesions within 6 years of the injury and over 70% after 11 years. Girdling by either a single large lesion or multiple lesions frequently resulted in the death of the leader. In all these cases, a lateral shoot had assumed dominance, and little evidence of damage was found after 11 years. Johnson's statement that "this study revealed that even with severe frost injury Douglas-fir of this age recovers rapidly with little lasting effect" is perhaps too much of a generalization in view of the findings of Childs (1962) and (Shea 1962).

A study by Reukema (1964) demonstrated the effects of frost injury on the radial growth of 50-year-old Douglas-fir that appeared to be only moderately damaged by the November 1955 freeze in the Pacific Northwest. He analyzed the radial growth of 14 codominant trees from a site III stand in western Washington for the years from 1950 to 1959. The trees, averaging 31.5 cm in dbh and 30.5 m in height, had been felled and dissected for growth analysis.

Fluctuations in the amounts of annual growth during the 10-year-period (1950–1959) were common and were apparently related to variations of temperature and precipitation. In none of the other 9 years, however, were growth reductions as great as in 1956. Ratios of 1956 growth to 1954–1955 average growth in internodes 20 to 40, roughly from base of live crown to breast height, ranged from 10% to 71%, averaging 57%. The range in growth reduction reflects the fact that trees that had the fastest growth before the freeze suffered the greatest reduction of growth. In general, growth was more curtailed in the lower part of the trunk than near the base of the crown, but even in the crown, stem growth was reduced substantially. Radial growth began to improve in 1957, but it had still not reached the growth rate of the years 1954 and 1955 by 1959.

Roots

Lethal injury to roots beyond the seedling stage is probably rare. Soils seldom reach temperatures low enough to kill the roots of older trees. Direct kill of roots of seedlings in nurseries or newly established plantations appears also to be rare, which may be inferred from a study in a Scottish nursery (Cannell et al. 1990). The study demonstrated that hardiness levels of roots of 2-year-old seedlings were already well above lethal soil temperatures in October. We are aware of only one report (Soljanic 1968) attributing the mortality of Douglas-fir seedlings in a plantation to frost kill of roots.

Cold acclimation and deacclimation

Douglas-fir, like other coniferous evergreens, undergoes seasonal changes in frost hardiness. The processes that lead to the development and loss of cold hardiness are governed by complex and varying interactions of environmental, genetic, and physiological factors. The first stage of cold acclimation usually begins in early fall with the onset of cool nights and shortening photoperiods (Irgens-Møller 1957, Van den Driessche 1969a). When night temperatures drop to near freezing, they trigger the beginning of the rapid (second) hardening stage that leads to the peak of hardiness in mid-winter (Lavender et al. 1968, Van den Driessche 1969a). During winter rest, Douglas-fir cannot be induced to grow until its chilling requirements are met (McCreary et al. 1989). Then, growth resumes under favorable conditions. Deacclimation is induced in late winter or early spring by rising temperatures (Van den Driessche 1969a, Schuch et al. 1989a). But experiments by Worrall and Timmis (1974, 1975), with 2-year-old seedlings of coastal and interior Douglas-fir, indicated that only the initial dehardening occurs in response to warming temperatures. Their findings suggested that final loss of hardiness depended on growth-promoting hormones from expanding shoots, indicative of a two-stage dehardening process, presumably preventing premature loss of hardiness.

Alden (1971) found that acclimation and deacclimation is not simultaneous in all tissues of Douglas-fir. Working with cut terminal twigs of 10-year-old Douglas-fir from a Willamette Valley seed source, he demonstrated, seasonal variation in cold hardiness among tissues of the stem, needles, and terminal and lateral buds. For instance, injury in early winter to the most susceptible tissues in hardened twigs, such as transfusion tissues and interfascicular parenchyma of the bud trace, began at −15.1°C with slow cooling rates, and all cells in these tissues were killed at −30°C. By contrast, the more resistant bud scales and cortex could be cooled to −30°C before injury became evident. Furthermore, the relative susceptibility of some tissues to freezing injury changed during the development and loss of hardiness. The pith, for example, was more susceptible to injury than were other tissues of the stem in fall, but more resistant in spring. Timmis (1976), Aitken and Adams (1996), and Rose and Haase (2002) also reported relative seasonal responses to freezing stress among tissues.

Assessment of cold hardiness

The assessment of cold hardiness after damaging frost events in the field is, in general, poorly suited for studying variations in cold hardiness between and within populations of Douglas-fir. As Larson (1978) and Anekonda et al. (2000) pointed out, "incidence of natural frost injury is typically sporadic across field test sites and over time, leading to uneven testing and poor statistical precision." To avoid these problems, investigators have turned to artificial freeze testing, where the temperature of freezing whole plants of their detached parts can be strictly controlled and uniformly applied. Frost injury can be assessed quantitatively by measuring freeze-induced electrolyte leakage (Burr et al. 1990) and chlorophyll fluorescence (Rose and Haase 2002) of freeze-tested tissue, or subjectively by visual scoring. Cold hardiness is usually expressed either as the temperature that inflicts lethal damage to 50% of tested tissues or simply as the percentage of damage at one or more temperatures.

A simple method for assessing cold hardiness using visual scoring of frost injury was developed at the Forest Research Laboratory of Oregon State University (Anekonda et al. 2000). Frozen tissue is allowed to develop damage symptoms for several hours after freezing and then is scored into damage classes. The method has the advantage that large numbers of samples can be efficiently processed at one time because the visual assessment of injury is quick and easy. Although injury is assessed less accurately than with electrolytic conductivity or chlorophyll fluorescence, visual damage scores have been found to be strongly correlated (r^2 0.90), with injury assessed quantitatively by freeze-induced electrolyte leakage (Shortt et al. 1996) and chlorophyll fluorescence (Rose and Haase 2002).

To what extent the results of artificial freeze-testing reflect cold hardiness under actual field conditions is not clear. Aitken and Adams (1997) and O'Neill (1999), however, in their studies of fall and spring cold hardiness of breeding populations of coastal Douglas-fir found moderate to strong estimated genetic correlations between visual injury scores after artificial freezing and natural frost events (mean = 0.82, range = 0.47–1.00). Their findings suggest that artificial freeze-testing can provide reliable predictions of the relative hardiness of families to both fall and spring frosts.

Time of bud set and bud burst has been used as an indirect assessment of cold hardiness. Genotypes having the earliest bud set can be expected to be the least susceptible to injury by a fall frost, and those late flushing to be the hardiest when exposed to a spring frost. Anekonda et al. (2000) stated, by citing several references, that these expectations are generally met in coastal Douglas-fir.

Age

Douglas-fir is most susceptible to frost injury as a seedling and becomes less likely to suffer damage with advancing age. Experiments by Timmis and Worrall (1975) demonstrated that seedlings of both coastal and interior Douglas-fir were unable to develop freezing tolerance in the initial weeks after germination and hence were extremely vulnerable to frost damage. But even as their ability to acclimate increases gradually with age, seedlings still remain very vulnerable, which is attributable to their small size, their tendency to continue growing into late summer or fall (Campbell and Sorensen 1973), and their proximity to frost layers near the ground. That vulnerability has been particularly well documented by reports of extensive frost damage to seedlings in forest nurseries. Examples in the Pacific Northwest are the losses caused at the Wind River Nursery of the USA Forest Service by a fall frost in 1916 (Munger and Morris 1936), in early September 1965 (Edgren 1970), and by a late spring frost on May 31, 1933 (Munger and Morris 1936).

Although trees become less vulnerable to frost injury as they mature, they may suffer damage in unusually severe freezes such as the one in November 1956 in the Pacific Northwest or the extremely cold winter of 1928/29 in Europe. An illustration of decreasing frost damage with increasing age is provided by a survey after the February 1956 freeze in eastern Germany (Zieger et al. 1958). Results of the survey listed by 20-year age classes indicated that most of the damage was in the youngest age class (Table 12.1). The frost, which lasted through all of February 1956 as a result of the influx of arctic air masses, was preceded by an unusually mild December and January. This particular sequence of climatic events may have led to early deacclimation of trees, and thus compounded the damage caused by the February freeze (Zieger et al. 1958).

Genetics of cold hardiness

Observations of frost injury in the field and in laboratory experiments have shown genetic variation in fall, winter, and spring cold hardiness of both the coastal and interior varieties of Douglas-fir. Moreover, significant variation has been found not only between but also within populations. But as Aitken and Adams (1996) wrote, "Genetic variation in cold hardiness of Douglas-fir appears to result mostly from variation in timing of acclimation and deacclimation rather than variation in absolute levels of cold hardiness achieved."

Fall cold hardiness

An unintentional mass selection made in 1883 by the forerunner of the Saxon Forest Experiment Station (Bellmann and Schönbach 1964) led, 65 years later, to the initiation of a study that provided, perhaps for the first time, proof of genetic variation in fall cold hardiness within a population of coastal Douglas-fir. Seed, probably of western Washington origin, provided by J. Booth was sown in a nursery in spring 1882. Many of the seedlings suffered frost damage in early winter of 1882.

Frost-damaged and uninjured seedlings were transplanted separately in spring 1883 and were later planted in the Tharandt Forest, with the damaged plants in compartment 29 and the uninjured in compartment 50 (Schönbach 1953). Cones were harvested in 1948 from 10 open-pollinated, then 65-year-old trees in each of the two compartments, 29 and 50. Seeds from each of the 20 trees were sown separately in spring 1949. A night frost in October 1949 caused injury to progeny from the mother trees in compartment 29, but little or none to progeny from mother trees in compartment 50.

Seedlings were outplanted as 3-year-old transplants in two different locations, one under shelter and the other without shelter. Eight-year survival

Table 12.1 Percentage of trees damaged by the February 1956 freeze in eastern Germany, listed by age class (from Zieger et al. 1958).

Age class	Injured trees %
1 – 20	37
21 – 40	20
41 – 60	14
61 – 80	13
81 – 100	10
101 – 120	6

of progeny from mother trees in compartment 29 and 50 in the plantation without shelter (Table 12.2) showed a striking difference between the two. The low survival of progeny from mother trees in compartment 29 was almost entirely the result of losses from fall and winter frost injury (Schönbach 1958). The difference in frost hardiness between the parent trees in compartments 29 and 50 was further demonstrated by Schönbach (1958, pp. 329, 355) with cuttings from these trees. Difference between vegetatively propagated progeny were less pronounced, however, than those between sexually propagated progeny.

Scheumann (1962), in a complementary study, used freezing tests of needles from 10-year-old progeny of two parent trees (No. 20 and 23) in compartment 50 and two parent trees (No. 3 and 4) in compartment 29 to investigate the seasonal course of their frost hardiness. Families 20 and 23 contained 96% and 76%, respectively, of the originally outplanted trees. In families 3 and 4, only 32% and 19% of the originally outplanted trees had not been killed by frost. An LT_{50} was used as a measure of the relative frost hardiness over the course of the seasons. Hardiness of the needles was nearly the same from May to September 1958 for all families with an LT_{50} of about −8°C. Hardening of family 20 saplings began already in September, ahead of the other families by nearly a month (Figure 12.1). Hardiness increased to a LT_{50} of −21°C by the end of January 1959 for families 20 and 23, with a LT_{50} of about −16°C for families 3 and 4 to begin decreasing again from February to May. Scheumann's findings that differences in cold hardiness among families continued to find expression with increasing age of trees corroborated Schönbach's (1959) results.

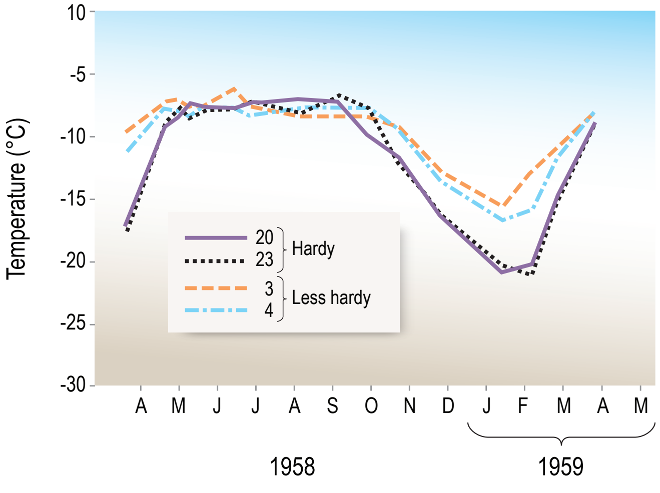

Figure 12.1 Course of relative frost hardiness in four single tree progenies from April 1958 to May 1959 (from Scheumann 1962).

Quantitative genetics

Coastal Douglas-fir

A comprehensive picture of the quantitative genetics of fall, winter, and spring cold hardiness in coastal Douglas-fir has emerged from a series of investigations supported by the Pacific Northwest Tree Improvement Cooperative. The materials used by the investigators represent 291 families in five breeding populations from British Columbia (1), Washington (2), and Oregon (2). Artificial freezing of cut terminal shoots from first-order lateral branches of 4- to 7-year-old saplings in the laboratory and subsequent visual scoring of damage to stem, needle, and bud tissues were used in these studies to assess cold hardiness.

Fall cold hardiness. Studies of cold hardiness in the fall were conducted with four breeding populations, two in western Washington (Aitken et al. 1996) and two in western Oregon (Aitken and Adams 1996). Investigations of cold hardiness in winter were added in the Oregon study.

The two studies demonstrated considerable within-population variation for fall cold hardiness in both the Washington and Oregon breeding populations. Considerable variation among families was apparent for cold injury of stems, needles, and buds in early

Table 12.2 Percent survival of progeny from mother trees in compartments 50 and 29 in the first 8 years after outplanting (from Schönbach 1959).

Fall	1952	1953	1955	1956	1957	1958	1959
Compartment 50	77.3	74.7	73.4	72.9	72.6	72.0	72.0
Compartment 29	40.1	36.2	25.0	20.2	16.8	16.3	16.2

fall to mid-fall, but differences were often small or insignificant in late fall and mid-winter. The genetic correlations for cold injury among these tissues were generally not strong, indicating that genes controlling hardening in the fall differ somewhat for different tissues. Genetic correlations between fall and winter cold hardiness suggested that hardiness at these two stages is apparently under separate genetic control. Moreover, mid-winter cold hardiness was shown to be weakly inherited. Therefore, selection for cold hardiness in fall will probably have little, if any, impact on hardiness to extreme winter temperature. Because cold injury to coastal Douglas-fir in mid-winter is unlikely to pose much of a problem in the Pacific Northwest, the region's breeding programs seem to have little need to consider midwinter hardiness as a separate trait (Aiken and Adams 1996).

Spring cold hardiness. Spring frosts are common in the natural range of Douglas-fir and in regions of its introduction, and often cause considerable damage to Douglas-fir in nurseries, young plantations, and recent natural regeneration. Injury caused by spring frost may occur before bud burst when tissues deacclimate or after bud burst as damage to newly flushed shoots. As stated by Aitken and Adams (1997), bud phenology was widely used to indicate spring cold hardiness while knowledge remained incomplete about the genetics of spring cold hardiness before bud break and the degree of variation in the rate of deacclimation among families. Aitken and Adams (1997) began a study in 1993 to close that knowledge gap. The material for the investigation were 7-year-old saplings from the same two breeding zones—one in the Cascades, the other in the Coast Ranger—and test sites for the study of fall cold hardiness in western Oregon (Aitken and Adams 1996). Samples consisted of shoots cut in March and April 1993 and in April 1994, subjected to artificial freezing, and visually scored for cold injury to stems, needles, and buds. Additionally, in April and May of 1993, bud burst was recorded bi-weekly on a single, marked branch of each tree from which shoot samples had been collected.

Results of the study indicated that cold hardiness in spring is under considerably stronger genetic control than is cold hardiness in the fall. Individual heritabilities for scores of spring cold injury averaged 0.76 in the coastal zone and 0.42 in the Cascade zone. Conversely, heritability estimates for scores of cold injury in mid-fall, with material from the same breeding zones and test sites, were all under 0.40 and averaged 0.27. The authors surmised that the high heritabilities for cold injury in spring suggest that fewer genes may control cold hardiness in spring than in fall. Although heritabilities for cold injury in fall were low, Anekonda et al. (2000) considered them to be still large enough to permit good progress in genetically improving cold hardiness by selection and breeding.

Another finding related to understanding the processes involved in the development and loss of cold hardiness is that cold hardiness of stems, needles, and buds is strongly correlated in the spring, contrary to weaker correlations in the fall (Aitken and Adams 1996). Thus, the authors proposed that different shoot tissues deacclimate apparently in synchrony in response to the cumulative effects of chilling and heat sum, whereas cold acclimation rates and timing vary among tissues. Genetic correlations between spring cold injury scores for all tissues and date of bud burst were strong and negative, with genotypes that break buds early having high cold injury scores for all tissues.

Seedlings versus saplings. The studies on the genetics of cold hardiness of coastal Douglas-fir by Aitken et al. (1996), Aitken and Adams (1996, 1997), and Anekonda (1998) used saplings (4-to 7-year-old trees) because of their widespread and immediate availability in established progeny tests. These investigations were followed by a study (O'Neill 1999) of the cold hardiness of seedlings in fall, winter, and spring after their second growing season. Seedlings were raised from seed of open-pollinated Douglas-fir. The seed stemmed from 40 parent trees within each of two breeding zones in western Oregon, one in the Cascades and the other in the Coast Range. They represented the same breeding populations used in the investigations by Aitken and Adams (1996, 1997). Seedlings were grown in raised nursery beds and subjected to two soil moisture regimes, one avoiding and the other creating moisture stress, to assess how drought during the growing season affected cold hardiness among families. Samples consisted of shoots detached in September, October, and November, and in March before the third growing season. They were subjected to artificial freezing and then were visually evaluated for cold injury to stems, needles, and buds.

The freezing tests demonstrated that, at the seedling stage, significant genetic differentiation exists between the Coast Range and Cascades populations for cold hardiness in the fall, but not in the spring. Despite its significance, genetic differentiation between the two breeding populations was for the most part exceeded by genetic variation among families within each of the two populations. Cold hardiness of seedlings in fall and spring varied widely among families in both breeding zones, indicating strong genetic control, with mean estimates of individual heritabilities for cold injury of 0.37 in fall and 0.57 in spring. Variation among families and estimates of heritability ($h^2 = 0.22$) were weak for cold hardiness in winter, however. Seedlings that experienced moisture stress during the growing season incurred significantly less cold injury in the fall than did those grown without moisture stress. Family rankings for cold hardiness in fall and spring were nevertheless fairly consistent across the two soil moisture regimes. O'Neill's study allowed the evaluation of cold hardiness in the fall and spring at both the seedling and sapling stage in the two Oregon breeding populations. High genetic correlations and thus consistent family rankings suggested that cold hardiness in seedlings and saplings appears to be controlled largely by the same set of genes.

Inbreeding. Lacking knowledge as to how inbreeding affected frost hardiness of conifers led Shortt et al. (1996) to design an experiment to investigate the effect of inbreeding on cold hardiness of coastal Douglas-fir in the spring. For their study, they selected 19 families representing four inbreeding levels within five common ancestor groups from an experimental plantation established in 1988 with one-year-old seedlings on Vancouver Island. Founder clones came from the low-elevation coastal breeding zone in British Columbia. Sections, 10-cm in length, of secondary lateral branches were collected for two kinds of artificial freezing tests from five randomly selected trees per family. Four branch tips from each sample were assessed for cold injury by the visual method and the remainder of the branch by the freeze-induced electrolyte leakage (FIEL) method.

The results indicated the lack of a strong consistent relationship between cold hardiness and inbreeding in Douglas-fir. Although different tissues were used in the two kinds of hardiness tests, overall, trends in damage were found to be similar. All the analyses of the tests demonstrated that trees within common ancestor by inbreeding groups accounted for significant amounts of variation. The authors surmised that the large family and within-family variability in hardiness may have reflected a limited sample size or be explained by the range of physiological factors that can influence cold hardiness. They concluded that "inbreeding does not appear to have a significant deleterious effect of the frost hardiness of Douglas-fir from the coastal breeding zone; and loss of productivity due to frost damage in related progeny should not be a major concern for tree breeders." Most likely, that conclusion may be valid for coastal Douglas-fir in general.

The investigations that focused on the genetic aspects of cold hardiness in coastal Douglas-fir have demonstrated considerable genetic variation in both fall and spring cold hardiness within populations. The relevance of that variation for practical applications was expressed by Anekonda et al. (2000) as follows: "This variation can be exploited in tree improvement programs in two ways: (1) in selection and breeding to maintain or enhance levels of cold hardiness of improved strains and/or (2) in choosing specific families for planting in frost-prone sites."

Interior Douglas-fir

Douglas-fir in the Inland Northwest occupies a range of extremely heterogeneous environments with frost-free period varying from 60 to 150 days (U.S. Department of Commerce 1968). The first indication of genetic differentiation of cold tolerance in populations of Douglas-fir in the northern Rocky Mountains came from a provenance study by Wright et al. (1971) and an investigation by Rehfeldt (1974a) of local differentiation of Douglas-fir populations in northern Idaho. Rehfeldt's subsequent investigations on the cold hardiness of populations of Douglas-fir from eastern Washington, northern central Idaho, and western Montana were aimed at gaining knowledge as to how "differentiation of populations in cold hardiness may reflect ecological adaptations that should be considered in limiting seed transfer for reforestation" (Rehfeldt 1979b). Rehfeldt (1978) studied growth and cold hardiness of 90 families, 5 each within 18 populations of open-pollinated trees from five warm and three cool habitat types in northeastern Washington, northern Idaho, and western Montana. Seedlings had been raised in two Idaho forest nurseries, one (Coeur d'Alene) representing a relatively warm environment and the other (Priest River Experimental Forest) a relatively cool environment. At the end of the fifth growing season, twigs cut from current growth in mid-September and in late November were subjected to freezing tests. Injury to leaves, buds, and stems, was scored visually by judging the degree of discoloration of tissues. The temperature at which injury to each tissue was first observed was used as a measure of cold hardiness.

Initial analysis of the results indicated that differences among populations in regard to growth, bud phenology, and cold hardiness could be related to habitat types. Much of the effect of habitat type appeared to be attributable to the differing performance of saplings from cool compared with warm environments. Further analysis suggested that populations from relatively warm environments could be divided into two physiographic groups: (1) western Montana and (2) eastern Washington and northern Idaho. Populations represented in the study apparently reflected adaptations to three different environments, which Rehfeldt termed "environmental provinces." Populations from relatively cool environments—regardless of geographic origin—represent an "ecological" province. Populations in this province are characterized by slow rates of growth, early bud set, and, as shown by the freezing tests, high levels of cold hardiness. The populations representing the other two provinces, eastern Washington and northern Idaho on one hand and Montana on the other, differed in these three traits, both from each other and also from the "ecological" province.

In his study on the genetic differentiation of Douglas-fir populations in the northern Rocky Mountains, Rehfeldt (1978) showed that cold tolerance was generally greater in Douglas-fir from western Montana than in Douglas-fir from Idaho and eastern Washington. In a subsequent study of variation of cold acclimation among populations of Douglas-fir, Rehfeldt (1979c) focused on northern Idaho and eastern Washington. Tolerance to low temperatures is necessary for the survival of seedlings and saplings because freezing temperatures can occur during any month of the year, and temperatures reaching −40°C are not rare in winter. The study was conducted with 47 populations from northern Idaho and eastern Washington, but included two populations each from the Okanogan Mountains in north-central Washington and the Blue Mountains in northeastern Oregon. Freezing tests to determine levels of cold hardiness were conducted on six dates between August and December in the second growing of seedlings raised for the study at Moscow, Idaho. Twigs cut from the current growth of seedlings representing each population were used for the freezing tests.

Rehfeldt assessed cold tolerance by regression analyses that were made for each population according to a mathematical model. He made separate analyses for each population on data obtained before and after the first frost on October 3, that is for phases one and two of cold acclimation. Tolerance of each population to freezing during both phases of cold acclimation was expressed as the injury predicted from the mathematical model when 50% of the twigs from all populations exhibited injury. Differentiation of populations in relation to latitude, longitude, and habitat type was assessed by multiple regression analysis. Rehfeldt demonstrated a close correlation of cold acclimation with daily minimum temperatures at Moscow by estimating the temperature associated with injury to 50% of the twigs for each sampling date (Figure 12.2). Low levels of hardiness developed after the first frost on October 3. After that date, hardiness increased moderately during a relatively warm period in late

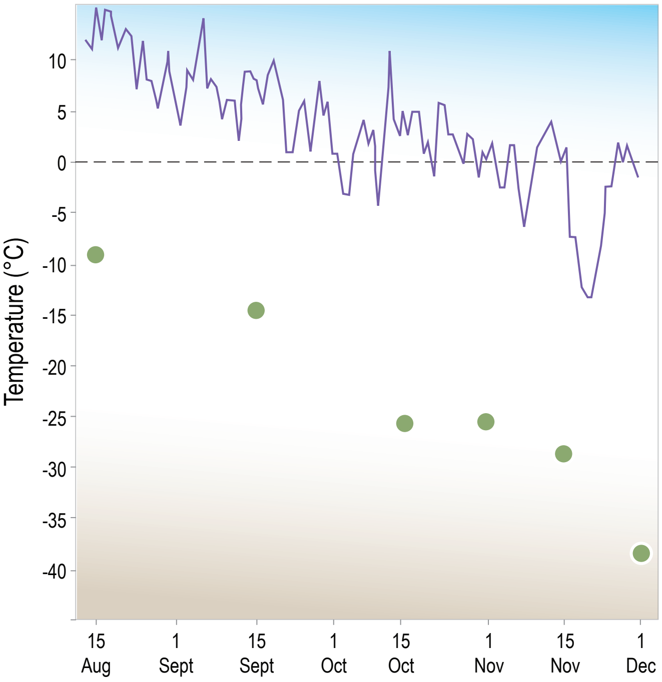

Figure 12.2 Frost hardiness and injury (from Rehfeldt).

October, but increased greatly after the first cold wave in mid-November.

Rehfeldt's models suggested that latitude and elevation of the seed source controlled differentiation of populations for hardiness, but only during phase one of acclimation. Longitude and habitat type had little effect. Of the four populations from areas peripheral to the central area of the study, the two from the Blue Mountains in eastern Oregon hardened similarly to populations from northern Idaho. The two populations from the Okanogan Mountains in north-central Washington showed a different pattern of hardening. They apparently approached maximal hardiness already in mid-November and, unlike populations from farther east, failed to become still hardier in response to late November's cold wave.

In the next study, Rehfeldt (1982) investigated patterns of genetic variation among Douglas-fir populations from Montana west of the Continental Divide. He excluded the extreme northwestern portion of Montana from the study, which presented patterns of environmental variation and genetic differentiation similar to those of northern Idaho. The 50 populations selected to represent the ecological amplitude in the region came from sites differing in elevation by as much as 1,300 m, and representing habitat types ranging from dry and warm to cool and moist. Additionally, eight populations from northern and central Idaho were included for the freezing tests.

The freezing tests were carried out on terminal shoots cut from 2-year-old seedlings in mid-September, when first autumnal frosts can be expected. Rehfeldt chose that single date because "northern Idaho populations expressed greatest differentiation in cold hardiness after bud set but prior to the first fall frost and because previous test indicated that the ranking of populations according to hardiness did not change at subsequent sampling dates." One set of shoots from each population was frozen at the rate of 5°C/h to one of five test temperatures between −14°C and −18°C. Injury to each shoot was scored by discoloration of needles. Differentiation of populations was assessed by an analysis of variance of random effects on the percentage of shoots of each population exhibiting injury at each test temperature. The freezing test revealed significant differences in cold tolerance among the 58 populations. Although test temperatures spanned only 5°C, percentage of injury to all twigs ranged from 19% at −14°C to 75% at −18°C. Across this range of temperatures, mean injury to populations from western Montana ranged from 16% to 69%.

In the third of the series of investigations of ecological adaptations in Douglas-fir populations, Rehfeldt (1983a) looked at adaptive differentiation of populations from central Idaho. For that study, he used 69 populations representing the geographic distribution and ecological amplitude of the species in central Idaho. Five-month-old container seedlings raised at Moscow, Idaho (46°05′N, 116°07′W) were transplanted into four test environments. Two of those were at Moscow, at an elevation of 700 m and with an average frost-free period of 130 days. The other two environments were at the Priest River Experimental Forest (48°05′N, 117°00′W). One was at 670 m elevation with an average frost-free period of 90 days; the second was at 1,500 m elevation where growing seasons are extremely short and snow commonly covers the site for 8 months, reaching a depth of about 300 cm. The test environments markedly influenced the phenology of seedlings. Those at the three lower elevations burst buds in the last week of April and nearly all had already set buds by mid-

August. Budburst at 1,500 m did not occur until the first week of June and only 77% of seedlings had set buds by mid-August. Thus, phenological differences resulted in injury from early but not late frost to seedlings at the lower elevation sites, and those at the high elevation site suffered injury from late frost only as well as from impacts of snow depth.

Results of the study covering central Idaho (Rehfeldt 1983a), as well as those of the two previous studies (Rehfeldt 1979c, 1982) demonstrated that populations from within northern Idaho, western Montana, and central Idaho displayed a different tolerance to early fall frosts when acclimating in a common environment. But the cold tolerance exhibited by a particular population in one study was not directly comparable to that of populations in other studies for several reasons listed by Rehfeldt (1986a). In the northern Idaho study, cold tolerance was assessed throughout the period of acclimation; in the other two studies, tolerance was observed on a single date. In the central Idaho study, conducted as a field test, injury from a single night's natural frost, representing a single treatment, resulted in a mean injury of 8%. In the northern Idaho and western Montana studies, injury resulted from artificial freezing of detached twigs at several test temperatures representing numerous treatments that produced a range in mean injury from nearly zero to almost 100%.

In an update of the models built from these three studies, Rehfeldt (1986a) developed a single model describing genetic variation in cold tolerance of Douglas-fir in the Inland Northwest. In Rehfeldt's words (1983a), results have shown "ecological adaptations that differentiate populations within these three regions based on a network of traits that reflect adaptations to the cold. Populations from severe environments display greater cold hardiness but lower growth potential than populations from mild environments. Genetic differentiation therefore, is strongly related to environmental gradients."

Frost hardiness prediction models

Models to predict frost hardiness of Douglas-fir have been built for both of its varieties. They represent attempts to identify areas with the potential for frost damage and to aid in the selection of genotypes suitable for establishing regeneration on frost-prone sites.

Interior Douglas-fir

The model made by Rehfeldt (1986a) to show genetic variation in cold tolerance during acclimation was based on studies of populations belonging to the northern subgroup of interior Douglas-fir within the Inland Northwest. The model described genetic variation in fall frost tolerance of Douglas-fir along relatively steep elevational and geographic clines. Rehfeldt noted, however, that elevations above 1,800 m are apparently of relative uniform severity, so that additional adaptive differentiation fails to happen. A frost in late September 1984 that injured 2-year-old seedlings in the Coeur d'Alene nursery of the USDA Forest Service provided an opportunity for Rehfeldt to verify his model. Differing injuries were inflicted on the 5 million 2-year-old seedlings in the nursery belonging to 179 seed lots, of which 159 were from the regions represented by the model. Injury was recorded as a proportion of injured trees for each seed lot, and the resulting data then were correlated with those predicted by the model. The statistical significant relationship between predicted and observed injury demonstrated the effectiveness of the model for predicting actual injury.

Coastal Douglas-fir

Timmis et al. (1994) built a heat-sum, fall-hardening and spring-dehardening model to assess the risk of frost kill to coastal Douglas-fir in Washington and Oregon west of the crest of the Cascades, allowing prediction of LT_{50}. The aim of the model was "to provide foresters with quantitative, operational guidelines to allocate families within or across current breeding zones based on frost damage risk" (Timmis et al. 1994). The model was based on the results of freezing tests of 2-year-old seedlings over four winters and on weather data of 80 stations on the west side of the Cascades in Washington and Oregon from 1948 through 1990.

According to the model, the risk of fall frost is highest at elevations above 500 m in the Cascades and the Olympic peninsula, but lower at comparable elevations in the Coast Ranges. The risk of spring frost, strongly associated with elevation, is higher in the western Oregon Cascades than at equivalent elevations in the Washington Cascades. Also, an apparently anomalous area for the risk of spring frost in the Coastal Ranges, between lat 45° N and 46° N, extends southeast into the Willamette Valley. The model indicated that the greatest risk of frost damage exists at the lower slopes of the western Oregon Cascades. The authors concluded that, "the results are in general agreement with observations that spring frost damage is more common than fall damage, that Oregon has more higher-risk sites and that some damaging frosts known to us are among those predicted."

Geographic Variation

Geographic variation of cold hardiness in Douglas-fir has been shown in both its coastal and interior variety. Geographic variation in frost hardiness appears to be an adaptive response to factors of the operational environment, especially photoperiod, temperature, and moisture. Campbell and Sorensen (1973) provided probably the first experimental proof of a north-south latitudinal gradient in frost hardiness of coastal Douglas-fir based on natural frost damage. They scored first-year seedlings growing in raised nursery beds (cold frames) at Corvallis, Oregon (lat 44°30′ N, long 123°40′ W; elevation 90 m), for damage sustained by a night frost in mid-October 1969. The plants stemmed from seed collections in five stands, each along two latitudinal transects from northern Washington to southern Oregon. The western transect followed the Pacific coast along the 124° meridian; the eastern transect was about 1° (about 80 km) farther inland, skirting the east side of the Pacific coast mountain ranges. Stands in which the collections had been made were separated by approximately one degree increments from lat 48° to 43° N.

The frost damage observed indicated distinctly lower frost hardiness in seedlings from the southern than the northern seed sources. The authors pointed out that their findings confirmed observations on frost damage of 1-year-old seedlings in nurseries at Corvallis (Ching and Bever 1960) and at Kornik, Poland (Bialobok and Mejnartowicz 1970). The study by Ching and Bever involved 14 provenances covering a latitudinal range from 49°19′N to 42°20′; Bialobok and Mejnartowicz's study included 104 provenances from the 1966/67 IUFRO seed collection covering about the same latitudinal range. The frost damage reported by Campbell and Sorensen was considerably more severe (with percent damage from least to most damaged provenances ranging from 9 to 77) than that reported by Ching and Bever (4 to 36) and Bialobok and Mejnartowicz (0 to 43). Considering plants at the same stage of bud development for each degree of latitude separating seed sources, the percentage of plants frosted differed by 4% in Campbell and Sorensen's study, and by 2% in their reanalysis of the Ching and Bever data.

Likewise, observations of frost damage in German provenance tests indicated a north-south cline in frost resistance of coastal Douglas-fir. Frost damage to 1- and 3-year-old seedlings, representing 72 provenances, occurred in the three nurseries where they were raised for the 1970 international Douglas-fir provenance trial in the Federal Republic of Germany (Kleinschmit et al. 1974). Although the extent of frost damage varied among nurseries located in the northwest, southwest, and southeast of the country, plants from northern seed sources sustained less damage than did those from southern seed sources in each of the nurseries. Compared with British Columbia provenances, those from California suffered nearly 100% more damage, provenances from Oregon about 20%, and those from Washington about 10%.

Damage by a late frost to 3-year-old seedlings in a provenance trial by the Federal Institute of Forest Genetics and Forest Tree Breeding at Schmalenbeck near Hamburg provided additional evidence for a north to south cline of frost resistance in coastal Douglas-fir (Reck 1978). The seedlings represented 85 provenances whose seed sources ranged from lat 51° N in British Columbia to lat 42° N in California. The gradient of damage with 33% at 51° N to 42% at 44° N was nearly linear. From lat 44° N, the percentage of damage increased abruptly to 58% at 43° N and to 63% at 42° N.

Tallies of new shoots killed by late frosts in 1968, 1969, and 1973 in three provenance plantations in Michigan provided another example of geographic variation in cold hardiness of Douglas-fir (Steiner and Wright 1975). These plantations were established in 1961 with 1-2 stock for testing provenances from

128 seed sources throughout the species' natural range (Wright et al. 1971). These authors divided Douglas-fir into nine groups, one coastal and eight interior, based on genetic similarities. Steiner and Wright (1975) found provenances belonging to the northern groups to be consistently less damaged than those from the southern groups (Table 12.3). Date of flushing recorded for trees at one of the plantations in 1973 was shown to be highly correlated with the amount of frost damage ($r = -79$). They concluded that this trait is the major determinant of susceptibility to late frost because provenances with the earliest bud break were the least susceptible to frost damage (Table 12.3).

Larsen and Ruetz (1980) used a transect nearly along lat 44°25′ N from long 121°45′ W on the Pacific Coast in the west to long 123°40′ W at the Ochoco Mountains in the east to study frost resistance of Douglas-fir along a longitudinal gradient. The 11 provenances represented by the study stemmed from a seed collection made in 1976 in Oregon by the Bayrische Landesanstalt für forstliche Saat und Pflanzenzucht at Teisendorf, Bavaria. One-year-old seedlings were subjected to freezing tests in the laboratory in fall, mid-winter, and spring using LT_{50} of buds as a measure of frost resistance. The tests indicated that resistance to fall and winter frost increased with increasing distance from the coast. The tests, however, did not demonstrate an increasing resistance to late frost with increasing distance from the coast.

Another indication of a west-east gradient in resistance to fall frost of coastal Douglas-fir came from a study by Loopstra and Adams (1989). They reported on damage by a late October frost to first-year seedlings planted in cold frames at Corvallis, Oregon. The seedlings stemmed from seed collected in six breeding units in southwestern Oregon. Seventy-two percent of seedlings from the coastal breeding unit suffered damage; damage to seedlings from each of the other units, 80 to 170 km further inland, averaged less than 15%.

Larsen (1978b) investigated frost hardiness of 4-year-old seedlings along two elevational transects, one in northern and the other in southern Washington, on the west slope of the Cascades. The sample from northern Washington comprised five seed sources and that from southern Washington four seed sources. Seedlings were tested for cold hardiness in fall, winter, and spring with artificial freezing in the laboratory. He used LT_{50} of needles and buds as a measure of hardiness. The results did not show a straight linear relation of increasing frost hardiness with increasing elevation along either transect. Plants from the low elevation seed sources (350–500 m) were very resistant to early and late frost. Seedlings of sources from elevations between 500 and 650 m were the least resistant to early, winter, and late frost. Seedlings from high elevation seed sources (800 m) were particularly resistant to fall and winter frost. Larsen sought to explain the relative high frost tolerance of the low elevation provenances as an adaptation to poor cold air drainage at their sites of origin.

Reck (1978) detailed the amount of damage to 3-year-old seedlings by a late frost according to elevation of their seed source. The trees belonged to 41 Washington and 23 Oregon provenances of coastal

Table 12.3 Performance of Douglas-fir provenances within 8 groups at the Kellogg plantation in 1973 at age 12 from seed. The COAST group is not included because most coastal Douglas-firs, unable to adapt to Michigan's climate, died (modified from JW Wright et al. 1971).

	Susceptibility to frost	Time of bud burst *
Northern Rocky Mountains – NOROC	Very low	8.4
Inland Empire – ILBNEMP	Very low	8.1
Central Montana – CMON	Low	6.2
Alberta – ALB	Medium	5.1
Central Washington – CWASH	Medium	4.1
Southern Colorado – SOCOL	High	3.3
Northern Colorado – NOCOL	Very high	3.0
Arizona and New Mexico – ARINEM	High	2.9

*1 = early, 10 = late

Douglas fir from the IUFRO seed collections used in the 1970 provenance trial of the Federal Institute of Forest Genetics at Schmalenbeck. He analyzed damage from sea level to 1,050 m by intervals of 150 m. Reck found an elevational pattern of damage similar to that reported by Larson (1978): low amounts of damage at low and high elevations and highest percentage of frost injury at medium elevations. Percentage of damage at all elevational intervals was, on the average, 20% higher for Oregon than for Washington provenances.

Aspect of site

Abele (1909) was perhaps the first to observe that different directions of aspect of a site can result in differing degrees of frost damage. He reported that damage to young plantations of Douglas-fir in Bavaria by a late frost in spring of 1908 was most severe on sites with exposure towards the south and southwest. In his survey of damage by the November 1955 freeze in the Pacific Northwest, Duffield (1956) found that damage was generally greatest on south and southeast slopes. A review of frost damage to coastal Douglas-fir in the extremely cold winters of 1928/29 and 1955/56 in central Europe (Jahnel 1959) showed that trees on sites with north aspect had suffered remarkably little damage compared to those on south-facing sites.

Frost-induced drought

A phenomenon referred to as frost dryness (Schönhar 1965) or winter desiccation (Sakai 1970) causes a particular kind of frost damage. It happens when soil is frozen and trees lose more water through transpiration on sunny days than they can compensate for because of impeded water uptake from the frozen soil. Such damage is common in central Europe and becomes usually apparent in early spring. The symptoms are a brown-red discoloration of the foliage that frequently tends to begin at the tip of the needles (Schönhar 1965). Young trees are often damaged so much that they die.

Nanson (1964) surveyed frost damage to Douglas-fir in Belgium after the winter 1962/63, the coldest in that country since keeping of climatic records in 1833. The soil remained frozen until the beginning of April 1963. February and March had periods of days with below-freezing air temperatures at night and above-freezing air temperatures during the day. The days had strong solar radiation and dry east winds. Nanson found that plantations with a south-facing aspect had suffered more damage than those facing north. Stands stocking on shallow soils had sustained more damage than those on deep ones. At the Groenendal tree-nursery, soil in the open was frozen to a depth of 80 cm, but only to 10 cm under shelter. That led him to conclude that a combination of three factors, depth of frozen soil, depth of root penetration, and dry east winds, was the cause of the observed damage. Because the combination of these factors leads to desiccation of plants, he felt justified in ascribing the damage to physiological drought rather than direct frost injury.

Damage to Douglas-fir by frost-induced drought has been reported from southern Germany by Schönhar (1965) and Oeschger (1973). Seedlings were found to be especially susceptible to winter desiccation, so much so that in some years, losses of more than 30% of Douglas-fir seedlings in nurseries have not been a rare occurrence. Likewise, considerable damage has been observed in plantations of young Douglas-fir.

Suffering from physiological drought is not unique to seedlings and saplings. Color change of the foliage of pole-sized and mature Douglas-fir to red-brown has been observed in the mountains of western North America (Scheffer and Hedgecock 1955) and the Harz Mountains of Germany (Puchert 1954) on south-facing slopes in early spring. This phenomenon has been confined to a lateral belt, generally at elevations between 1,000 and 1,500 m, and has therefore been referred to as "red belt." Sakai (1970) stated that "it is reasonable to assume that the so-called 'red belt' is probably caused by intensive dehydration which arises from a combination of exposure to sunshine and freezing of the soil on the southern slopes." He theorized that a warm, dry air wall remaining at a definite height on south-facing slopes for several hours to a few days in late winter, known as a subsidence inversion, may be the decisive factor acting as a trigger to cause the red belt.

Larsen (1981) studied the geographic variation in resistance to frost-induced drought of Douglas-fir using growth chamber experiments. He used 2-year-old seedlings of 40 provenances from the IUFRO seed collection to investigate two components: drought avoidance and drought tolerance, of frost-induced drought. He measured avoidance of desiccation as the rate of negative increase in bars of water potential per day, and drought tolerance as bar of water potential resulting in 50% of plant mortality. His findings indicated that the 40 provenances could be divided into three groups based on their degree of drought avoidance and drought tolerance:

1. Those with a very low degree of drought avoidance and very low drought tolerance. They were from the coastal regions and the Cascade Ranges of British Columbia, Washington and Oregon.
2. Those with a very high degree of drought avoidance and drought tolerance. They came from Colorado, Arizona, and New Mexico.
3. Those that were intermediate between group 1 and 2 regarding degree of drought avoidance and drought resistance. They were from interior British Columbia and Idaho.

Among the relatively drought-sensitive provenances of group 1, Larsen found an increase in resistance to frost-induced drought with increasing elevation of origin.

Rossa and Larsen (1980) investigated in a companion study the effect of cuticular transpiration on resistance to frost-induced drought in 35 of the 40 Douglas-fir provenances used in Larsen's 1981 study of geographic variation in resistance to frost-induced drought. They measured cuticular transpiration of detached twigs of 3-year-old seedlings in a growth chamber. Based on their cuticular drying rate, the 35 provenances could be divided into the following groups:

1. Provenances from coastal British Columbia including Vancouver Island, Washington and Oregon west of the crest of the Cascade Range, and northern California having high cuticular transpiration rates. A definite influence of elevation or distance from the coast of their seed source on cuticular transpiration was not apparent within this group of provenances.
2. Provenances from Idaho, Colorado, Arizona, and New Mexico having very low cuticular transpiration rates.
3. Provenances from interior British Columbia with cuticular transpiration rates intermediate between those of provenances in group 1 and 2.

In addition, Rossa and Larsen (1980) studied cuticular thickness and stomatal depth in relation to cuticular transpiration in seedlings of 10 of the 35 provenances in their study. They found the thickest cuticula in the provenances that were from the southern part of the range of interior Douglas-fir. These were the provenances that had the highest resistance to cuticular transpiration. Provenances belonging to the coastal variety of Douglas-fir that were the most susceptible to desiccation had the thinnest cuticula. Provenances from interior British Columbia had cuticula of medium thickness. Stomatal depth was found to be greater in the provenances of interior than coastal Douglas-fir. The findings demonstrated that rates of cuticular transpiration of Douglas-fir are closely correlated with the anatomical characteristics of its needles.

Nutrients

Nutrient levels are among the many factors that influence cold hardiness of Douglas-fir. Alden (1971) found that trees from a plantation deficient in potassium and nitrogen developed significantly lower hardiness in the acclimation stage than did trees from a plantation not deficient in these nutrients. Larsen (1976) investigated the effects of different levels of fertilization with nitrogen, phosphorus, potassium, and boron on the cold hardiness of 4-year-old Douglas-fir seedlings. He found that an extremely low (0.9%) and a very high (2.2%) level of N had a detrimental effect on resistance to fall and winter frost. He could not show any effect of K, P, and B on cold hardiness. Larsen (1978) hypothesized that the better survival in winter of Douglas-fir with sufficient levels of K in their tissues is not a consequence of higher resistance to frost but to frost dryness.

In an experiment by Timmis (1974) with first-year coastal Douglas-fir seedlings, those deprived of N but receiving P and K were unable to harden off to an extent that would have allowed them to survive a normal winter in their native habitat. That finding indicated that low N may impede cold hardening only with a relative overabundance of P and K. The results of the study suggest that normal development of cold hardiness is probably more closely related to a balance between nutrients than to the level of any single nutrient element.

Intraspecific hybridization

Despite a long history of differentiation that may extend as far back as the Miocene, the coastal and inland varieties readily cross, both under controlled pollination and in the wild (Critchfield 1984). Ecklundh's experiments (1943) in Sweden (Schönbach 1958, p. 366) were the first to explore the possibility of combining the growth potential of coastal Douglas-fir with the frost hardiness of interior Douglas-fir. These crosses, however, were not successful because they only yielded empty seeds.

Nearly 20 years later, Schönbach of the Institute for Forest Sciences at Eberswalde, Germany, made two sets of reciprocal crossings of coastal and interior Douglas-fir. As a result, 22 combinations were available for tests in 1960 (Schönbach and Bellmann 1967), and another 35 combinations in 1964 (Braun and Schmiedel 1985). The crossing partners of the 1960 set were four 80-year-old coastal Douglas-firs, two from compartment 50, two from compartment 29 of the Tharandt Forest, and two interior Douglas-firs from a stand in the Elbsandstein region of Saxony. The crossing partners of the 1964 set, five coastal Douglas-firs, were from the same stands as those of the 1960 set (Braun and Schmiedel 1985). Trees from compartments 50 and 29 had been chosen as crossing partners because an earlier study of heritablility of frost hardiness (Schönbach and Bellmann 1964) had shown progeny from trees in compartment 50 to be more frost hardy than progeny from trees in compartment 29. Hybrids of the 1960 set were planted as 1–1 seedlings in spring 1963 at the Plaue forest district in the Ore Mountains of eastern Germany (Schönbach and Bellmann 1967). Hybrids of the 1964 set were planted as 1–1 seedlings in spring 1967 in the Tharandt forest district near Dresden (Braun and Schmiedel 1985).

Tallies of frost damage and height growth measurements of 1-year-old and 2-year-old seedlings in the nursery, and of 6-year-old saplings in the Plaue plantation, showed that the var. *menziesii* x var. *glauca* (h1) and var. *glauca* x var. *menziesii* (h2) hybrids but had better height growth than the var. *menziesii* x va. *Menziesii* (m) hybrids. Survival of g, h1, and h2 hybrids ranged from 96% to 100% 4 years after outplanting, compared to 60% for the m hybrids (Schönbach and Bellmann 1967). Survival of trees in the Plaue plantation was 90% for the g hybrids and 65% for the h1 and h2 hybrids, but only 10% for the m hybrids at age 18 from seed. Measurements 6 years later showed the best trees of some h1 and h2 hybrid progenies had attained a height of 21m and a dbh of 24 cm (Braun 1988). Mean tree height at the Tharandt plantation at age 18 from seed ranged from 11.45 m for the hybrids from one of the h1 combinations to 5.45 m for hybrids from one of the m combinations. Twelve of the progenies, all of which were h1 and h2 hybrids, ranked above the plantation mean of 9 m. Both the h1 and h2 hybrids showed—in general—better growth than comparable m and g hybrids. The m hybrids whose parents were relatively frost hardy (Schönbach and Bellmann 1967) showed better height growth than m hybrids with less frost hardy parents. The g hybrids were the slowest-growing hybrids (Braun and Schmiedel 1985). The best hybrids in the Tharandt plantation had produced, at age 16, a volume of 140 m^3/ha. That was twice the volume for site class I in the Germany yield tables of Hengst and of Bergel (Braun 1988). Referring to the performance of these hybrid progenies, Braun suggested (1988) a rotation of 70 years for stands established with hybrid seedlings, assuming such a rotation length would yield 1,400m^3/ha. But he also pointed out the main problem of using hybrids in reforestation practice, namely the difficulty of mass producing hybrid seedlings.

Duffield (1950) was probably the first in North America to suggest hybridization as a means for improvement of Douglas-fir. Orr-Ewing (1973) started a Douglas-fir arboretum in 1958 on Vancouver Island, British Columbia to provide as wide a gene pool as possible for intraspecific crosses. In 1973, the arboretum already contained 216 provenances and 121 clones collected throughout the natural range of the species. Their sites of origin ranged from 30 m to 3,300 m elevation, from lat 19°40′ to 55°05′ N, and from long 98°07′ to 125°40′ W. That also solved the problem of having both seed and pollen parents at the right time of the year for crossing.

The first 44 intraspecific crosses made by Orr-Ewing (1966b) were limited to pollen parents from coastal Douglas-fir ranging from northern British Columbia to northern California. The subsequent 114 crosses included pollen parents from both the coastal and interior variety. Orr-Ewing et al. (1972) established 28 test sites on Vancouver Island and the lower mainland so that every cross could be planted under a wide range of climate conditions for the assessment of genotype/environment interactions. Orr-Ewing et al. (1972) concluded that the initial result indicated the absence of an incompatibility barrier preventing successful crosses between Douglas-fir separated by thousands of kilometers and growing in completely different environments. That was clearly demonstrated by the cross between a maternal parent from Madera, Chihuahua (29°10′N) and a paternal parent from Fort St. James, British Columbia (54°30′N). Although the distance between their geographic origins is nearly 26 degrees of latitude, viable seed was nevertheless obtained. Intraspecific crosses, however, have definite limits for obtaining increased growth (Orr-Ewing et al. 1972). Crosses with some of the Washington and Oregon paternal parents were very promising, but those with California paternal parents were not very successful. Crosses with paternal parents from the interior range of Douglas-fir gave no positive growth results in the maritime climate of southwestern British Columbia. Such hybrids, however may be of value in the interior of British Columbia (Orr-Ewing et al. 1972).

Rehfeldt (1977) began a study in 1971 to explore the potential of intervarietal hybridization for improving Douglas-fir in the northern Rocky Mountains. He produced 70 hybrid families by pollinating 20 interior Douglas-firs from 2 Idaho provenances with pollen from 25 coastal Douglas-firs representing 3 Oregon and 1 British Columbia provenance. Each parental tree was also represented in the study by seedlings derived from wind pollination in their native stands. The result was 33 half-sib families representing parental lines.

Seeds were sown in October 1971 at the Priest River Experimental Forest nursery and grown for 3 years. Performance of the hybrid families and their parental lines showed that the growth potential of hybrids was generally superior to that of the interior variety, but was similar to that of the coastal variety. The harsh winter of 1972, which brought temperatures as low as −26°C, led to high rates of mortality. The rate of survival was 44% for seedlings of hybrid and interior origin, but only 9% for those of coastal origin. Little additional mortality occurred during the next 3 years, suggesting that the capability of hybrid families to survive under the severe climate of the northern Rocky Mountains approaches that of the interior variety (Rehfeldt 1977). Surviving seedlings were planted in 1975 as 2–1 stock in row plots on a site at 1,036 m elevation near Grangeville (lat 46° N, long 116° W) in northern Idaho.

Caused by the losses of seedlings at the nursery, the Grangeville plantation of 3,025 trees contained an unequal number of crosses per parent, an unequal number of plots per cross, and an unequal number of seedlings per plot. Because these imbalances precluded statistical analyses, Rehfeldt compared survival and height of trees 10 years after planting without regard for statistical probabilities. Survival averaged 58% for hybrids, 63% for open-pollinated interior parent lines, but only 20% for open-pollinated coastal parental lines. Average height for hybrids was 222 cm, 128 cm for interior parental lines, and 104 cm for coastal parental lines. The performance of individual hybrid families varied considerably. Survival ranged from 34% to 80% and mean height from 140 cm to 335 cm. Thus after 10 years in the field, hybrids essentially equaled the survival of interior parental lines, but were almost twice as tall. The results of Rehfeldt's study demonstrated the high potential for intervarietal hybridization to increase the productivity of Douglas-fir on sites with a harsh climate, as had the earlier German studies initiated by Schönbach in 1960. Rehfeldt (1986b), however, pointed out a problem faced by using hybridization for improving productivity of interior Douglas-fir. He found that "the performance of a hybrid family could not be predicted from either the parental provenance of the specific parental tree. In addition, variance within families was high." He saw the solution for an expedient and safe means of using hybridization in breeding of interior Douglas-fir in the selection of superior hybrid trees without regard to parentage, and then backcrossing these selected trees to a large number of trees of the interior variety.

Interspecific hybridization

Duffield (1950) attempted unsuccessfully in 1947 to cross Douglas-fir with bigcone Douglas-fir as pollen parent. The 3 apparently sound seeds, out of a total of 438 seeds from the cross, failed to germinate. Ching (1959) made the first successful cross in 1956. The female parents were four trees in a 30-year-old stand in the Oregon Coast Range. The pollen parents were bigcone Douglas-firs on Baldy Mountain in Los Angeles County, California. Ching concluded that the crossability of the two species is rather low, although the cross yielded some fertile seeds. Orr-Ewing (1966b) made some crosses in 1962 on seven Douglas-firs growing on Vancouver Island, and again on seven other trees in 1964 with bigcone Douglas-fir as pollen parents. The 1962 cross yielded only empty seeds, and of the 14,199 seeds extracted from cones resulting from the 1964 crosses, only 8 seeds were viable. Orr-Ewing considered the difference in chromosome number—bigcone Douglas-fir has 2n = 24 chromosomes, Douglas-fir has 2n = 26 chromosomes—as the probable explanation for the evident incompatibility in this cross.

Pseudotsuga wilsoniana, the Formosan Douglas-fir, is the only known Asiatic species to have been crossed with Douglas-fir. According to Orr-Ewing (1966b), Roy Silen, a USDA Forest Service geneticist, attempted the first—but unsuccessful—cross with Formosan Douglas-fir as the pollen parent in 1962. An attempt in 1963 by Orr-Ewing (1966b) to cross the two species did not succeed, yielding only empty seeds. His conclusion, that the prospect of interspecific crossing with Douglas-fir is not particularly promising, has so far not been disproved.

Frost heaving

Repeated freezing and thawing of the soil causes frost heaving. The expansion and contraction of the soil slowly pulls plants out of the ground, leaving roots partially or completely exposed. First-year seedlings are most susceptible to frost heaving and will die usually after such exposure (Hermann 1990). Hermann has also noted 2–1 Douglas-fir seedlings lifted out of the ground by frost heaving in a newly established plantation, however.

Snow, Ice, and Hail

Snow, ice, and hail storms are climatic events that may cause serious damage to Douglas-fir. Heavy snowfalls in the late winter of 1963/64 and in early spring of 1964 on upper slopes of the Oregon Cascade Range inflicted much damage to young, mixed-conifer stands (Williams 1966). Leaning, bent, and fractured stems and broken branches were common for trees 1.2 and 6.0 m in height, but few trees below 1.2 m high suffered damage. Trees of saw timber size were not injured, except for a few broken branches. Douglas-fir suffered more damage than any of its associated species. The susceptibility of Douglas-fir to snow damage at high-elevation sites makes the establishment of Douglas-fir monocultures a questionable practice in cutover areas of upper slope forests in the Oregon Cascade Range.

Data collected from 32 permanent sample plots in forests of the Oregon Coast Range showed that young stands of Douglas-fir suffered severe snow damage at elevations above 300 m in the winters of 1964/65 and 1965/66, and above 760 m in the winter 1968/69 (Kangur 1973). His study demonstrated that trees that were widely spaced at seedling and sapling stages sustained less damage than did trees in densely stocked stands. The results also indicated that the degree and time of thinning can influence the amount of damage. Twenty-one-year-old stands, thinned 2 years before the snowfall suffered severe damage, but damage was very light in adjacent stands thinned 6 years before the snowfall. Both Williams (1966) and Kangur (1973) recommended early thinnings to make stands more resistant to snow breakage.

Puchert's (1954) account of snow damage in 21 stands of coastal Douglas-fir (established from 1880 to 1890 in the Harz Mountains of central Germany) described the effects of snow damage on long-term stand development at elevations between 260 m and 550 m. All trees planted with a spacing of 1.2 m^2 and 1.5 m^2 suffered greatly from snow breakage in the winter 1909/10; those planted at a spacing of 3.0 m^2 and 5.0 m^2 escaped damage. Losses of up to 40% of trees in 20- to 40-year-old stands did not adversely affect stand development. Snow break had the same effect as a heavy thinning. Puchert mentioned a stand at 360 m elevation, planted at 1.0 × 1.5 m spacing, that suffered thrice from much snow breakage until age 40. This stand had, at age 69, a volume of 551 m^3, which Puchert considered an indication that Douglas-fir can endure a considerable amount of snow damage in its youth without an adverse effect on volume production later in its life. He concluded that Douglas-fir is most susceptible to snow break, particularly in densely stocked stands, between ages 20 and 40.

Freezing rain forms layers of ice on trees that bends and breaks stems and branches. Three published records (McCulloch 1943, Anonymous 1971, Russell 1971) documented the extent of known damage from ice storms in Douglas-fir forest of the Pacific Northwest. McCulloch (1943) inventoried the damage from the January 1942 ice storm in three second-growth stands in western Oregon. Stand A, age about 90, average height 33 m, average dbh 34 cm, covered 4.05 ha. Half of the stand had remained uncut; the other half had been thinned twice, in 1933 and 1938. The two cuttings removed 371 mostly suppressed and intermediate trees and thus did not create large holes in the canopy. Yet this partially cut stand lost 267 trees by breakage and uprooting in the ice storm compared to a loss of 124 trees in the uncut half. Stand B, age about 80, average height 27 m, average dbh 26 cm, covered 3.24 ha. A 1941 thinning in half of stand B had removed 131 dominant and codominant trees, which resulted in a sizeable opening of the canopy. The thinned part lost 471 trees through breakage and uprooting by the ice storm, but the uncut part lost only 101 trees. Stand C, covering 2.025 ha, had been formed by the slow encroachment of Douglas-fir beneath an oak overstory. As the oak gradually died out, Douglas-fir filled the holes and created an unevenaged stand. An improvement cutting in half of the stand in 1935 removed 176 trees. An unusually heavy fall of wet snow in 1936 broke off 44 trees in the freshly cut half. Fifty-five of the remaining 73 trees in that half of the stand were broken or uprooted by the 1942 break in 1936, and 63 trees of the residual stand had ice damage in 1942. The volume lost by ice and snow damage in the three stands amounted to about one-fourth of the original volume (Table 12.4).

Freezing rain in January 1970 on both sides of the Columbia Gorge led to losses that ranged to 80% of trees in up to 40-year-old Douglas-fir stands on the Oregon side of the Gorge (Anonymous 1970). Damage was estimated to have occurred on 16,200 ha. Other factors sometimes contributed to the observed damage. A damage survey in a Douglas-fir stand in the Cascade Range of southern Washington after the January 1970 ice storm revealed large numbers of uprooted trees whose roots had already been weakened by infection with *Phellinus weirii* before the ice storm (Russell 1971).

Damage caused by hail is rare, but can be disastrous. A hail storm with hail stones of unusual size near Angers, France, in August 1944 mutilated trees in young Douglas-fir plantations to the extent that they had to be replanted (Vazeilles 1946).

Drought

Summer drought is common in many parts of the Douglas-fir region and has been responsible for some failures of natural and artificial regeneration of Douglas-fir. Outright kill of older trees, however,

Table 12.4 Volume lost in three Oregon Douglas-fir stands to ice damage in January 1942. Data from McCulloch (1943), converted to metric measurements.

	Stand A		Stand B		Stand C	
	m^3	%	m^3	%	m^3	%
Original volume	994	100.0	711	100.0	405	100.0
Volume cut	169	16.6	168	23.6	258	63.7
Lost in storm	236	23.7	145	23.1	117*	28.8
Residual volume	589	59.7	398	53.3	30	7.5

* Snow and ice storms.

appears to be rare. Childs (1960) reported on the effects of the unusually hot summer of 1958 and the unusually dry summer of 1959 on Douglas-fir. Death of young trees was common in a few localities in northwestern Washington at the end of the 1958 growing season. He observed drought damage in both years in Washington and Oregon manifested by partially dead crowns. Top kill was confined, however, almost entirely to Douglas-fir saplings and poles. Drought damage was especially conspicuous on clay soils along the east side of the Mt. Hood National Forest, where such damage had also occurred during the drought of the late 1920s and early 1930s. Childs (1960) stated that "on fair to good sites mortality in young stands is rarely extensive enough to impair stocking. Of the economic loss attributed to drought, by far the greater part has undoubtedly resulted from inconspicuous but general decrease in current increment throughout most of the region."

Child's observations of drought damage to Douglas-fir in the Pacific Northwest were followed by several greenhouse and laboratory studies of differences in drought resistance and drought avoidance between Douglas-fir of different geographic origins. Greenhouse studies by Ferrell and Woodard (1966) and Pharis and Ferrell (1966) showed seedlings from inland sources to be more drought resistant than those from Pacific Coast sources. They considered the higher survival of interior Douglas-fir in their tests to reflect true drought hardiness rather than drought avoidance. Their findings indicated that Douglas-fir from xeric habitats is more drought hardy than is Douglas-fir from mesic habitats. Zavitkovski and Ferrell (1970) theorized that "different kinds of natural selection operate in these 2 environments: drought in xeric habitats will favor drought-resistant individuals, but in mesic environments drought resistance is secondary to other ecological factors in natural selection. This circumstance suggests that seedlings from these 2 environments may differ in their physiological responses to drought."

That assumption was confirmed in studies by Zavitkovski and Ferrell (1968, 1970) on the effects of drought on photosynthesis, transpiration, and respiration of seedlings from moist and dry sites in Oregon and Washington. The 1968 investigation used 2- and 3-month-old seedlings; the 1970 study used 2-year-old seedlings. Although photosynthetic, respirational and transpirational rates showed similar declines in all seedlings with decreasing soil moisture, mesic source seedlings had significantly higher transpirational rates than did xeric-source plants. But mesic-source seedlings had considerably higher photosynthetic rates at soil moisture tensions between 1 and 15 atm. Zavitkovski and Ferrell (1970) considered that as a range of soil moisture stress existing probably under natural conditions most of the time during the growing season in the Douglas-fir region. They suggested that the high transpirational rates of mesic-source seedlings that resulted in more rapid exhaustion of available soil moisture would be detrimental to their establishment only on extremely dry sites. On moderately droughty sites, however, their ability to maintain high photosynthetic rates under low soil moisture stress may overcome the disadvantage of high transpirational rates.

Heiner and Lavender (1972) used a different approach to investigate the response of mesic- and xeric-provenance Douglas-fir to drought-caused stress. They collected seed from five trees on a site with annual rainfall of 508 mm in southern Oregon, and from many trees on a site with annual precipitation of 1,542 mm in the northern Oregon Coast range. Seedlings were raised in a nursery in the Willamette Valley. Seedlings from dry and wet seed sources were transplanted at age 2 into a lysimeter. The soil was wetted to field capacity at the time of transplanting and then allowed to dry naturally during the growing season. Depletion of soil moisture at depths of 10, 30, and 60 cm was measured fortnightly. A plastic canopy suspended above the lysimeter prevented rains from moistening the soil. Additionally, seedlings from each seed source were maintained in the nursery and kept well watered during the growing season. None of these seedlings died in their 3rd growing season. In the lysimeter, survival of progeny from each of the five trees from the dry site in southern Oregon ranged from 55% to 70%, compared with 16% for progeny from the wet site in northwestern Oregon. Weekly tallies of terminal and lateral but burst showed that the dry-source progeny had much earlier and more complete bud burst than the wet-source progeny. Measurements of root systems of live and dead seedlings excavated at the end of the growing season showed that the progeny of the five trees from the dry site in southern Oregon had mean root lengths ranging from 35 to 42 cm, compared with 31 cm for the progeny of trees from the wet site in northwestern Oregon. None of the dead trees from all seed source had roots longer than 23 cm. Seedling survival apparently was largely dependent upon the ability of roots to penetrate below a depth of 30 cm. The correlation found between early bud break and survival in turn reflected a correlation between early growth and survival. The principal survival mechanism identified by Heiner and Lavender (1972), vigorous early root growth, is actually drought avoidance rather than a drought-resistance mechanism.

White (1987) studied differences in drought tolerance between populations of Douglas-fir in southwestern Oregon, where summer drought in particular limits the success of natural and artificial regeneration on some sites. For his study, White used seed from 72 open-pollinated families from 2 parent trees each at 36 locations throughout southwestern Oregon. Sample locations were 61 km to 162 km from the Pacific Ocean and were between lat 42°00′ and 43°12′ N, and at 475 m to 1,630 m altitude. A drought regime was imposed in a growing room, a greenhouse, and an outdoor cold frame on some of the seedlings in their second growing season, and on others in their third. Seedling survival was measured under an extended soil drought designed to simulate that which often occurs in southwestern Oregon: adequate moisture early in spring, but little or no rain after budburst. Thus, watering was discontinued after budburst. The results were similar in the three test environments. They showed that drought-tolerant populations were from higher elevations, and to a lesser extent, from drier sites. The populations from higher elevations had an earlier budburst than those from lower elevations. Early budset was strongly correlated with increased drought tolerance in White's study. He considered the early budset, and hence early entry into dormancy, to be a possible explanation for the increased drought tolerance of populations from higher elevations.

Larsen (1983) studied the effect of nitrogen and potassium supply on drought hardiness of 2-year-old Douglas-fir from Snoqualmie, Washington, grown under 11 different levels in a growth room. He found that K had a large positive effect on drought hardiness. By contrast, an increasing supply of N caused a significant decrease in drought tolerance.

Development of the pressure bomb (Waring and Cleary 1967) made possible the measurement of plant moisture stress (PMS) in Douglas-fir and thus to assess directly the level of moisture stress, which was particularly helpful when working with seedlings and saplings. Waring and Cleary (1967) showed that with adequate soil moisture, PMS in Douglas-fir varies in the course of day, with its peak shortly before 10:00 a.m. and approaching a minimum by 8:00 p.m. They also demonstrated that stresses in plants are considerably higher than in the soils they grow on by showing that on a bright day trees growing on soils near field capacity can have stresses of 20 bars. The soil moisture at field capacity is 0.3 bar. The nature of soil on which Douglas-fir grows also has a bearing on the severity of PMS. Cleary (1969) followed PMS in Douglas-fir on different sites as the dry season in Oregon progressed. As early as the end of June, he found little night-time recovery of PMS on a very coarse granitic soil. By contrast, in a fine-textured soil, there was considerable recovery at night as late as August, although dawn minima in July and August exceeded 30 bars. The height of Douglas-fir also influences PMS. Waring and Cleary (1967) pointed out that when 1-m-tall trees had stresses nearing 40 bars, 25-m-tall trees had stresses of 20 bars, presumably because the larger trees could tap the deeper soil layers where more water was still available.

A study by Borer (1982) on the effect of drought on a mature Douglas-fir in a stand in Switzerland showed that drought may not result in visual damage, but nevertheless may cause damage through the reduction of growth. He investigated the water uptake and evapotranspiration of an 85-year-old Douglas-fir in 1975 and 1976. The tree was 43 m tall and had a dbh of 81 cm. Its root system extended to a depth of 2 m in the loess soil of the site. Evapotranspiration during the 1975 growing season (210 days) was on average 2.38 mm/day. Evapotranspiration in the growing season (202 days) of the much drier year, 1976, was only 1.46 mm/day. Moisture stress experienced by the tree during the drought period from June to mid-July did not result in visible damage. Borer attributed the lack of visible damage to a water reserve large enough in the 2-m layer of soil occupied by the tree's root system to enable the tree to come through the drought without lasting damage. He stated, however, that biomass production was reduced during the period of drought. Borer estimated wood production of the Douglas-fir tree to be about 0.3 m^3 in 1975, based on its consumption of water. For the production of that amount of wood, the tree had to take up 90,000 L of water during the growing season. More than 99% of this amount of water was lost by transpiration.

Fire

Wildfire has been a major natural disturbance in the Douglas-fir forests of western North America. The presence of charcoal layers below ash from the eruption of Mount Manzama 6,700 years BP indicate that wildfire has been a primary disturbance mechanism in the Cascade Range for at least 10,000 years (Morrison and Swanson 1990). Extensive fire activity occurred at least every decade or two in the Inland Northwest (eastern Washington and Oregon, western Montana and Idaho) between the 1500s and the early 1900s (Barrett et al. 1997). The annual area burned during these 350 years has been estimated at about 146,800 hectares of the nearly 7.7 million hectares covered by interior Douglas-fir and western larch.

Three different fire regimes, based on their severity, are recognized for describing fire events (Bradley et al. 1992). Low severity fires are surface fires that burn litter, duff, loose woody debris on the forest floor, and undergrowth vegetation. High severity fires cause high or complete mortality in an overstory stand of trees, and are often referred to as "stand-replacing" fires. Moderate severity fires define a broad range between those two extremes.

Methods used for the reconstruction of fire history include fire scars found on cat-faced trees and on cross sections of stumps, cores from live trees, post-fire regeneration age classes, and written records (Morrison and Swanson 1990). Cross-dating, the matching of tree-ring patterns to determine absolute dates for tree-ring series, permits establishing precisely the years of fire injury or tree origin. These can then be used to date wildfires (Weisberg and Swanson 2001).

Views have changed since the end of the 20th century on the frequency of fire regimes of different intensity in the montane forests dominated by coastal Douglas-fir in the area west of the crest of the Cascade Range and from northern California to Washington. According to Wetzel and Fonda (2000), for over half a century, Douglas-fir forests on the Pacific slope were depicted as supporting infrequent stand-replacing fires. Mean fire return intervals (FRI) of 200–400 years were commonly estimated for Douglas-fir forests in the Pacific Northwest, largely based on dates of stand establishment after high severity fires. (FRI is the mean time span between fires, specific for a given unit of land, vegetation type, or region).

But the fire regime associated with forests dominated by Douglas-fir is far more complex than originally reported. Studies of the fire history in Douglas-fir forests of the Pacific Northwest conducted since the late 1980s have shown that fire frequency is much shorter, and fire severity much less, than previously thought. Yamagushi's (1986) study of the fire history in old-growth Douglas-fir stands northeast of Mount St. Helens revealed a record of large stand-replacing fires and relatively frequent low severity fires following the eruption of the volcano in 1480. The frequency of these low severity fires was one fire per 40 to 50 years during the first 150 years of stand development and one fire per 125 to 150 years thereafter. That frequent moderate and low intensity fires were part of the fire regime in the Douglas-fir forests of the Cascade Range became even more apparently from the reconstruction of the fire history in two 1,940-ha areas in the central-western Cascade Range of Oregon by Morrison and Swanson (1990). From their study and several other studies, it has become clear that Douglas-fir forests from the northern Cascades in Washington (Agee et al. 1990) through the central Cascades (Wallin et al. 1996, Cissel et al. 1998), the Klamath Mountains (Taylor and Skinner 1998), and northern California (Brown et al. 1999) have experienced combinations of frequent low- and moderate-severity fires and infrequent stand-replacing fires. These studies also suggest a general pattern of increased frequency and decreased severity of natural fires from north to south.

The montane forests of the northeastern Olympic Mountains are dominated by Douglas-fir stands established after past burns (Fonda and Bliss 1969). A 600-year fire history of Douglas-fir forests developed by Wetzel and Fonda (2000) for a 2,500 ha drainage in the northeastern Olympics revealed that periods with many small-scale, and low- and moderate -severity fires were interrupted by two periods of stand-replacing fires in 1687–1720 and 1897–1904. That fire history shows that small patchy fires were much more common in the eastern Olympics than previously thought. The reconstruction of the fire record in the eastern Olympics indicated a low incidence of fires during the little Ice Age, a climatic period of low temperatures extending through the 17th and 18th centuries to the mid-19th century (Henderson and Brubaker 1986). The marked increase in the 1850/59 decade appears to signal the return of a drier and warmer climate at the close of the Little Ice Age (Wetzel and Fonda 2000).

Interior Douglas-fir in the forests east of the crest of the Cascades and in the Rocky Mountains grows as a climax of major seral species on a wide variety of sites, with climates ranging from warm semiarid to inland moist to high-elevation cold (Pfister et al. 1977). In the eastern mountains of Washington and Oregon, frequent low-severity fires for centuries maintained open forests with large, widely spaced, predominantly fire-tolerant trees: that is ponderosa pine (*Pinus ponderosa*), Douglas-fir, and western larch (*Larix occidentalis*) (Everett et al. 2000). Changes in forest management practices, notably fire suppression, led to a marked decline in fire events since about 1900. That enabled seedlings and saplings, particularly of fire-sensitive species such as grand fir (*Abies grandis*) to invade and persist beneath the overstory of the open forests; whereas the invaders would have previously been eliminated by frequent low-severity surface fires. The result was the development of ladder fuels and large fuel buildups, leading to moderate- and high-severity fires in forests that historically did not experience them (Agee 1994, Everett et al. 2000).

Pfister et al. (1977) distinguished forest zones defined by the potential climax species arranged into series and habitat types in the northern Rocky Mountains. The Douglas-fir series in the forests west of the Continental Divide forms an especially broad zone in Montana and central Idaho. The four principal tree species of the series are ponderosa pine, Douglas-fir, western larch, and lodgepole pine (*Pinus contorta*). Surface fires of low to moderate severity were very common in the Douglas-fir series. Suppression of fire after 1900 resulted in an accumulation of surface fuels and the development of a Douglas-fir understory on dry and moist sites (Arno 1988). In many dry Douglas-fir habitats, where ponderosa pine is seral, the establishment of an understory of Douglas-fir would lead in time to replacing the shade-intolerant ponderosa pine with a dense, disease- and insect-prone Douglas-fir climax (Arno et al. 1995). Consequently, stand-replacement fires became common (Harrington 1991, Bradley et al. 1992). Stand-replacement fires are sometimes followed within a few years by reburns. Perhaps the best known example is the 1953 Tillamook burn in Oregon that destroyed about 104,000 ha of old-growth Douglas-fir/western hemlock forest. The area experienced a 81,000 ha reburn in 1939, and a second reburn of nearly 73,000 ha in 1945 (Anonymous 1966). Reburn fires can be more intense because recently burned stands often have greater amounts of fuel than mature forests (Agee and Huff 1987).

The reestablishment of Douglas-fir after initial burns or reburns was often delayed by a limited seed source, invasion of brush, altered soil nutrient status, and damage caused by wildlife. Franklin and Hemstrom (1981), in a discussion of the impact of fire on succession in the coniferous forests of the Pacific Northwest, hypothesized that repeated wild fires were responsible for the slow establishment of many of the old-growth forests that originated about 500 years ago in the Cascade Range. Gray and Franklin (1967) studied the effects of multiple fires on the reestablishment of Douglas-fir in a 16,000 ha watershed in the Cascade Range of southwestern Washington. Most of the Douglas-fir in the watershed was probably older when a fire in September 1902 killed most of the trees in the drainage. The 1902 fire was followed by reburns in 1919, 1927, and 1932. Although of catastrophic intensity, they were much smaller than the initial 1902 burn. Their findings indicate that degree of intensity of burn and the site characteristics are among the factors determining the speed of regeneration. Reestablishment of Douglas-fir on single-burn sites took less time than on reburn sites. Reestablishment of Douglas-fir on single-burn sites took about 12 years on its wetter sites compared to 24 years or more on its drier sites.

The damage fire causes to Douglas-fir depends mainly on the intensity of fires and the tree's age. Morrison and Swanson (1990) attributed the ability of old-growth stands of Douglas-fir to withstand repeated low- to moderate-intensity fires to the stand's physical characteristics, namely height of trees and concentration of foliage in the upper 50% of the bole. That reduces the probability of crown fires because sufficient heat cannot easily reach the canopy to ignite the crowns. Thick bark and extensive root mass in mineral soil are other characteristics that make old-growth Douglas-fir fire-resistant. Saplings are vulnerable to damage by surface fires because of their thin bark, resin blisters, closely spaced flammable needles, thin twigs, and bud scales (Bradley et al. 1992).

Ryan et al. (1988) modeled long-term mortality of Douglas-fir associated with damage to cambium and crown. The authors used data from the study initiated by Norum (1975) and observations 8 years after the 1973 spring and fall burns for the construction of their model. Of the 166 trees in the sample, 83 were dead after 8 years. The majority (70 trees) died in 1974 and 1975. Another 13 trees died in the following 6 years. Their analysis showed that survival decreased with increasing scorch height, percent of crown scorch, and number of quadrandts with dead cambium at 1.4 m bole height, but increased with larger diameters. Ryan et al. (1988) found that percentage of crown scorched was a better predictor of tree mortality than scorch height, confirming findings by other workers (Peterson 1985, Wyant et al. 1986). The results of the study by Ryan et al. (1988) also confirmed observations by Bevins (1980) and Wyant et al. (1986) that tree size, expressed by dbh, is inversely related to mortality.

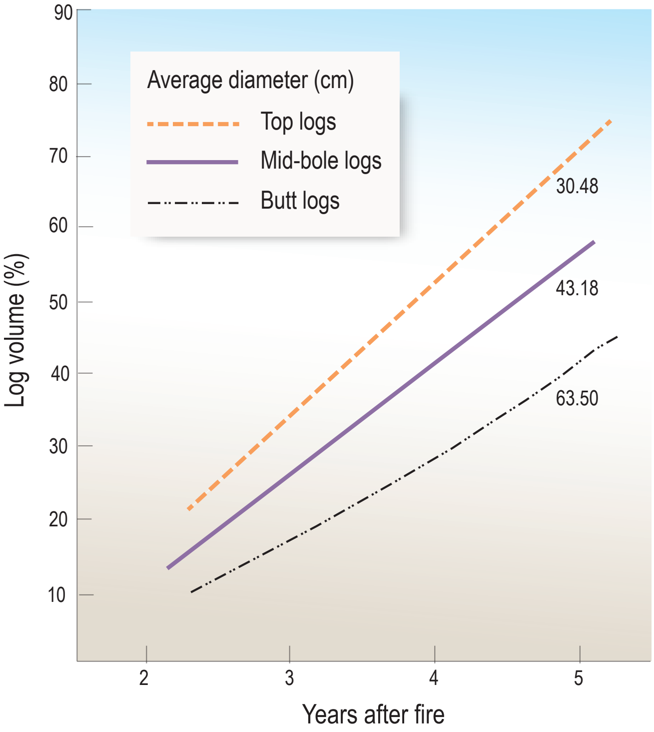

Figure 12.3 Percentage of total log volume of mature Douglas-fir decayed 2.5 to 5 years after fire-kill (from Wallis et al. 1974).

Peterson and Arbaugh (1989) evaluated factors related to the survival of coastal Douglas-fir 2 years after wildfires in the spring of 1982 at four sites in the western Cascades of Washington and Oregon. They used data collected on 294 trees with dbh >13 cm to develop a model for estimating post-fire survival. Their model showed that including both crown and bole damage greatly improved estimates of post-fire survival. The authors pointed out that "rapidly spreading surface fires cause relatively greater amounts of crown damage while ground fires with a long duration of burning have relatively greater potential for bole damage." Therefore, including variables that measure both crown and bole damage provides greater latitude in estimating damage for different types of fire. The authors emphasized that their study identified factors related to post-fire survival of coastal Douglas-fir, but did not address the physiological effects of fire-caused injury; as they stated, "carbohydrate production and allocation are clearly important to the survival of damaged trees but the relative impact of crown and bole injury on these processes is unknown."

Deterioration of fire-killed Douglas-fir

Wallis et al. (1974) determined the percentage of total log volume of mature Douglas-fir decayed 2.5 to 5 years after fire-kill (Figure 12.3).

Lowell et al. (1992) reviewed the literature on the rate of deterioration of fire-killed and fire-damaged

Douglas-fir. According to their review, factors that influence the rate of decay include local site conditions, aspect, elevation, slope, and soil, which influence deterioration by affecting the temperature and moisture of a site. Additionally, these factors, coupled with precipitation, can lead to different rates of deterioration:

- Diameter and age of tree. A large-diameter tree generally will deteriorate more slowly than a small-diameter tree, and a young tree will deteriorate more rapidly than an older tree.
- Severity of burn. Less severely burned trees on a moist site tend to deteriorate more slowly than those severely burned. The opposite is true on dry sites where severely burned trees take longer to deteriorate because of lack of moisture.

The thin sapwood of Douglas-fir has mostly deteriorated by the end of the third year post-fire; in the fourth year, the heartwood will begin to deteriorate. The heartwood of Douglas-fir is moderately durable: coastal Douglas-fir of 60 to 250 years old (diameter range: 53–76 cm) takes 3 to 4 years to reach 50% deterioration; trees 200 to 400 years old (diameter range: 51–60 cm) take 10 to 15 years to reach 50% deterioration; trees 400 years and older (diameter range: 130–152 cm) require 20 years to deteriorate by 50%.

Air Pollutants

Sulfur dioxide

Scheffer and Hedgecock (1955) wrote that SO_2 damage to Douglas-fir had been reported as early as 1912. The SO_2 emissions came from the Washoe smelter close to Anaconda, Montana. Douglas-firs were dying as far as 8–13 km in all directions from the smelter. Year-ring analyses showed a distinct decrease of radial growth from 1892 through 1910. Scheffer and Hedgecock (1955) investigated SO_2 injury to coniferous forests in the upper Columbia River Valley from smelters near Kettle Falls, Washington, and Trail, British Columbia. Douglas-fir was among the species damaged or killed. They stated that injuries caused by frost and drought resembled SO_2 injury in some respects, but were not responsible for the damage in the upper Columbia River valley.

Carlson (1980) documented damage to more than 2,000 ha of interior Douglas-fir by a sulfate pulp and paper mill in western Montana. Damage ranged from defoliation to various degrees of discoloration and necrosis of foliage. Histological study of needles showed that green-yellow color indicated initial breakdown of chloroplasts and plasmolysis of mesophyll cells. Yellow color reflected some collapse of mesophyll cells, hypertrophy of phloem elements and parenchyma, and partial collapse of albuminous cells and endodermis. Necrosis indicated collapse of mesophyll, endodermis, and albuminous cells. Carlson and Gilligan (1983) showed in laboratory and field studies that phytotoxic gases caused histological symptoms in Douglas-fir needles distinct from those induced by winter drying, normal drought, or salt. They emphasized that the "identification of injury and related forest damage near sources of phytotoxic air emissions may be confounded by insects, diseases, weather or other abiotic factors." Their study demonstrated that histological procedures can be very helpful for the correct identification of foliar chlorosis and necrosis. Leininger et al. (1991) ranked seedlings of Douglas-fir as the most sensitive of five coniferous species to simulated ambient SO_2 exposure. Their ranking was essentially the same as that by Scheffer and Hedgecock (1955) and by Carlson (1980) in field studies of older Douglas-fir.

Emissions of SO_2 caused annual increment losses of more than 50,000 m^3 in the forests of eastern Germany since the 1960s. To explore the possibility of breeding for SO_2 resistance, a program was begun in the former German Democratic Republic to investigate the heritability of SO_2 resistance in several conifers. Heritability was shown to be relatively high ($h^2 = 0.6$) in Douglas-fir (Tzschacksch 1981). Surprisingly, coastal Douglas-fir showed greater SO_2 resistance than did the more frost-hardy interior Douglas-fir (Tzschacksch 1982).

Fluorides

Fluorides are among the air pollutants known to damage conifers, including Douglas-fir. Estimates are that about half of fluoride emissions from industrial processes (Semrau 1957) are gaseous and half are particulate. Fluorides enter needles mainly through stomata. Once in the foliar tissue, they are in a soluble state and tend to accumulate at needle tips, causing necrosis. Treshow et al. (1967) documented growth decline and mortality of Douglas-fir near a phosphate reduction plant in Idaho. They found up to 100% reduced diameter growth when the foliar fluoride concentrations exceeded 50 ppm. Foliar fluoride levels in excess of 100–200 ppm caused mortality, but precise threshold levels could not be established. A study initiated by the USDA Forest Service in 1969 (Carlson and Dewey 1971) showed that fluoride emissions from an aluminum reduction plant in northwestern Montana caused varying degrees of visible fluoride injury to vegetation on 28,000 ha in parts of the Flathead National Forest and the southwestern portion of Glacier National Park. Elevated fluoride levels were found in vegetation on nearly 86,700 ha of forested lands of mixed ownerships.

Conifers that showed tissue necrosis and elevated fluoride levels were ponderosa pine, lodgepole pine, western white pine, and Douglas-fir. Trees differed in susceptibility to fluoride injury shown by visual burn symptoms. White pine was most susceptible, followed by ponderosa pine, lodgepole pine, and Douglas-fir. Carlson et al. (1979) conducted an intensive field study in an attempt to relate visible foliar degradation to foliar fluoride accumulation. They sampled 110,000 needles of Douglas-fir, western white pine, and lodgepole pine. Each sample consisted of needles that had formed in 1975, 1976, and 1977. Foliar injury generally appeared at foliar fluoride concentrations of less than 10 ppm. Mottling or chlorosis of foliage was evident at less than 6–8 ppm in Douglas-fir. Apparently, a threshold effect is absent; adverse effects began at slightly over baseline concentrations.

Wind

Wind can do serious damage to Douglas-fir by breakage of trunks and blowdown. That was spectacularly demonstrated by the Columbus Day windstorm on October 12, 1962, which caused more damage to the forests of the Pacific Northwest than any other windstorm in recorded history. The blowdown of timber, most of it Douglas-fir in western Oregon and western Washington, amounted to more than 26 million m^3, approximately equal to the annual cut in the two states at that time (Lynott and Cramer 1966). But less violent windstorms have also caused considerable damage to Douglas-fir stands within and outside its natural range. Among factors contributing to damage may have been cutting practices (Ruth and Yoder 1953, Munger 1954, Gratkowski 1956), topography (Steinbrenner and Gessel 1956), waterlogged soils (Prior 1959), root structure and penetration (Groth 1927, 1928; Soest 1954), crown size and shape (Brown and Jones 1989), stem and wood characteristics (Studholme 1995).

Douglas-fir ranks higher as a windfirm species than most commercially important conifers (Henkel 1960, Brünig 1974, DeChamps et al. 1982). This ranking is based mainly on observations made after storm events. An exception is a study by Moore and Gardiner (2001), who investigated the effect of silvicultural practices on the relative stability of Douglas-fir and *Pinus radiata* by calculating the critical wind speeds for damage at yearly intervals over the length of typical rotations of each species. They concluded that "a *Pinus radiata* stand grown on a 28-year rotation was three times more likely to suffer catastrophic wind damage than a Douglas-fir stand grown on a 45-year rotation. The most critical factor behind these differences was the lower drag coefficient of Douglas-fir foliage."

The genetic test site of the Pacific Forest Research Station of the USDA Forest Service in the Willamette Valley was in the main path of the wind storm of January 7, 1990, a storm of an intensity expected once in 20-25 years (Silen et al. 1993). The damage caused by that storm provided a rare opportunity for an investigation to estimate the genetic component in susceptibility to blow-down among F2 full-sib families of 6- and 7-year-old coastal Douglas-fir. The results indicated that susceptibility to windthrow differed by family and was significantly related to their height, but that height accounted for less than a third of the genetic component of variation. The authors concluded that their findings "suggested the possibility of successful breeding for resistance to windthrow in Douglas-fir," but they also cautioned that "breeding would probably be complex, expensive, and slow. In contrast to breeding, silvicultural techniques to minimize windthrow may be simpler and less expensive."

13. Ontogeny

Denis P. Lavender

According to Bond (2000), "woody perennials do not appear to go through a defined senescence phase but do have predictable developmental stages," i.e., juvenility, maturity, and old age. We agree and in this section, we will review the morphological, anatomical, and physiological changes that occur as Douglas-fir develops from a seedling to the tree we call "old growth." We will also discuss environmental and other factors such as insects and diseases that can affect Douglas-fir at different life stages.

Ontogeny – Growth

Foliage, anatomy, quantity, distribution

Perhaps the earliest report of leaf maturity changing with age is that of Goldfarb et al. (1991), who reported that the development of buds on cotyledons in response to applications of cytokinins decreased with cotyledon age. Ritchie and Keely (1984) found that needle weight declined with seedling age (from 1 to 9 years).

Working at the Wind River Canopy Crane site in Washington and in the Cascade Mountains of Oregon, Apple et al. (2002) found that the anatomy of Douglas-fir needles "differed significantly between old-growth trees and saplings at all sites, suggesting a developmental change in needle anatomy with increasing tree age," noting that "needles of saplings were longer and had proportionately smaller vascular cylinders, larger resin canals and few hypodermal cells" (p. 129). They also found that "needles of old-growth trees had an average of 11% less photosynthetic mesophyll area than needles of saplings. The percentage of non-photosynthetic area in needles increased significantly with increasing tree age from the chronosequence of 10-, 20-, 40- and 450-year-old trees at the Wind River site" (p. 129). Apple et al. (2002) speculated that the reduction in photosynthetic area in older trees may contribute to their decreased growth rates.

Meinzer et al. (2008) suggested that tension affected needle growth of tall trees. (Overton et al. 1973) found that the N content of old-growth foliage (0.96%), but not that of other elements, was lower than that commonly reported for young growth (1.42%).

Seedlings

Ritchie and Keeley (1994) studied Douglas-fir at ages 1 to 9 years and noted that needle weight appeared to decrease with age as did "Chlorophyll, chlorophylls and total chlorophyte concentrations which declined between 5 and 10% with aging between 1 and 9 years."

Mature trees

Meinzer et al. (2008) noted that foliage growth decreases with height. Silver (1962) found that 28% of the foliage of a 50-year-old tree was current and that 60% of the foliage in the upper third of the crown was current, as opposed to 50% of the lower third. Foliage of mature Douglas-fir trees is a transition type between juvenile and old growth foliage. Maguire and Bennett (1986) and Maguire and Batista (1996) reported that tree dimensions are a good estimate of foliage quantity.

Branches

Saplings

Ritchie and Keely (1994) found that as young Douglas-fir plants matured, the most consistent change was that nodal branches were shorter. Frothingham (1909) observed that "sapling Douglas-fir had long slender branches at relatively wide intervals on the trunk" (p. 9).

Old growth

Bond (2000, p. 349) noted that "the production of new primary branches generally stops when maximum height is achieved and branch extension also slows down. This is when the characteristics of old growth emerge. Leaf bearing stems tend to be thicker and the leaves themselves are often thicker and smaller on old growth compared with leaves on young mature trees."

Hummel (2009) reviewed several papers and cited previously unpublished material finding that branch size of trees in Douglas-fir forests of Oregon, Washington, and California varied with crown and tree parameters; for physically comparable trees, branches on old-growth had greater diameters, probably because lack of elongation focuses growth on diameter.

Ontogeny – Height

Seedlings

Douglas-fir in western Oregon, Washington, and British Columbia may be among the tallest trees in the world (Hermann and Lavender 1990), but early seedling height growth is slow for the first 5 years before it then begins to accelerate. Height growth of seedlings is very much a function of seedling age. Early height growth of seedlings is relatively slow (Williamson and Twobley 1983). Measurements in the nursery suggest that second-year seedlings may grow 270 cm (Krueger and Trappe 1967), whereas young trees on plantations commonly reach a mean of 135 cm in 5 years. After 5 years, the growth is much faster. Ten-year-old seedlings are commonly at least twice the height of 5 year-olds. And saplings grown in favorable environments have produced leaders 165 cm in length (Newton, personal communication). But perhaps the best measure of the effect of the environment on seedling growth is the 2-year-old seedling in a greenhouse under continuous long photoperiods, which measured 300 cm. Campbell (1972) and Overton and Ching (1948) both reported that the environment has a greater effect on seedling height growth than does genetics or age.

Saplings

The largest height increment occurs between 20 and 30 years, and the ability to maintain a fairly rapid height growth is maintained over a long period.

Mature trees

Hermann and Lavender (1990) noted that Douglas-fir in high elevation forests of the Oregon-Washington Cascade range can continue height growth at a substantial rate for more than 200 years. Frothingham (1909) recorded similar data for trees in the interior. Hermann and Lavender (1990) summarized height growth patterns for older Douglas-fir as follows:

> Height growth of Douglas-fir on dry sites at mid-side indices in the Cascade Range of western Oregon is similar to that of upper-slope Douglas-fir in the Washington and Oregon Cascade Range. At higher site indices, however, height growth on dry sites is initially faster but slower later in life; at lower site indices, it is initially slower but faster later in life.
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> On a medium site (III) at low elevations, height growth, which averages 61 cm (24 in) annually at age 30, continues at a rate of 15 cm (6 in) per year at age 100, and 9 cm (3.6 in) at age 120 (18,39). Trees 150 to 180 cm (60 to 72 in) in diameter and 76 m (250 ft) in height are common in old-growth forests (22). The tallest tree on record, found near Little Rock, WA, was 100.5 m (330 ft) tall and had a diameter of 182 cm (71.6 in). Coastal Douglas-fir is very long lived; ages in excess of 500 years are not uncommon and some have exceeded 1,000 years. The oldest Douglas-fir of which there is an authentic record stood about 48 km (30 mi) east of Mount Vernon, WA. It was slightly more than 1,400 years old when cut (39).
>
> The interior variety of Douglas-fir does not attain the growth rates, dimensions, or age of the coastal variety. Site class for Rocky Mountain Douglas-fir is usually IV or V (Site index 24 to 37 m or 80 to 120 ft at age 100) when compared with the growth of this species in the Pacific Northwest. On low sites, growth is sometimes so slow that trees do not reach saw-log size before old age and decadence overtake them. Interior Douglas-fir reaches an average height of 30 to 37 m (100 to 120 ft) with a d.b.h. between 38 and 102 cm (15 and 40 in) in 200 or 300 years. On the best sites, dominant trees may attain a height of 49 m (160 ft) and a d.b.h. of 152 cm (60 in). Diameter growth becomes extremely slow and height growth practically ceases after age 200. Interior Douglas-fir, however, appears capable of response to release by accelerated diameter growth at any size or age. The interior variety is not as long lived as the coastal variety and rarely lives more than 400 years, although more than 700 annual rings have been counted on stumps. (Hermann and Lavender 1990, p. 534)

Old growth

Bond et al. (2007, p. 441) presented a detailed study designed to separate size and age effects on tree height and growth. They found that,

> On high quality sites, maximum height growth of Douglas-fir can exceed 1.5 m year^{-1}, and trees may achieve heights greater than 75 m, whereas maximum height growth and total maximum height of trees with similar genetic potential on poor sites can be a small fraction of these values. . . . Clearly, height growth is strongly influenced by environmental conditions. However, new insights emerge when height growth is viewed as a function of height . . . .
>
> Under all site conditions, the maximum rate of height growth of trees occurs while they are relatively small; subsequently, growth declines as a linear function of height for more than a century. . . . [Douglas-fir] trees lose, on average, about 2 cm year^{-1} in height growth for each new meter of growth irrespective of site conditions after they reach their growth maximum. (Bond et al. 2007, pp. 441–442)

They examined the evidence for factors causing the above and concluded that "size, not age, drives developmental changes in height growth in Douglas-fir. Reduced carbon assimilation does not play an important role in height growth decline" (p. 441). They also noted: "We found that neither intrinsic aging nor photosynthetic reduction due to hydraulic constraints or other factors is a likely cause of DDHG" (p. 451) or "developmental decline in height growth."

Ryan and Yoder (1997) examined several hypotheses that attempt to explain why trees decline in height growth with age, after a maximum when relatively young: i.e., respiration, nutrient limitation, genetic changes in meristem tissue, and hydraulic limitation, concluding that the last is most likely. They supported this conclusion by noting factors that reduce the effects of each of the first three hypotheses, observing that "stomata and consequently, transpiration and photosynthesis is most responding to changes in hydraulic resistance. Hydraulic resistance must increase with tree height or tree age. Photosynthesis must be lower in the foliage of older trees" (p. 239). They present evidence supporting each of the above. Domec et al. (2006) concurred that hydraulic resistance increases with height.

Ryan et al. (1997) presented data for forest trees in general for height growth that agreed with observations of Hermann and Lavender: "Biomass accumulation and growth of even-aged forests follows a universal pattern as the trees increase in size, growth is slow initially, increases as leaf area develops, peaks as leaf area reaches its maximum, and then declines for the majority of the stands' lifespan" (p. 215). They discussed in detail the following possible reasons for growth decline: "(1) changes in photosynthesis, (2) change in nutrient supply, (3) change in respiration, (4) change in fine root production and longevity, (5) allocation to symbionts, (6) allocation to foliage and branches, (7) change in maturation" (p. 213). They concluded that only the first reason (changes in photosynthesis), as a result of reduced leaf area or photosynthetic capacity, is likely (p. 251). Ryan and Yoder (1997, p. 241) asked the same question with regard to maximum tree height and concluded that hydraulic limitation and not respiration, nutrient limitation, or genetic change is most likely (p. 241)

> A maximum height that varies with resource availability and slower height growth in older individuals appear to be universal for trees, old trees are different both physiologically and morphologically from younger trees. They have lower rates of photosynthesis, reduced height and diameter growth rates, and a distinctive architecture. Nutrition, Carbon allocation including respiration, meristematic activity, and trees' hydraulic architecture can all potentially change with tree growth and promote slower growth in older trees, in fact, these processes may interact. (Ryan and Yoder 1997, p. 244)

Bond (2000) presented a summary of the changes that occur with age in old woody plants, with particular emphasis on photosynthesis. She noted:

> Published studies from a variety of experimental situations generally indicate that both photosynthesis and stomatal conductance are reduced with the age of shrubs and trees. These degrees have been reported at all phases of development: seedlings versus older plants, seedlings versus juveniles versus mature plants, mature versus old growth. . . . Might immobilize Nitrogen in some aging forests, making it less available for new growth. Reduced photosynthesis is a likely consequence because Nitrogen content of leaves is closely correlated with photosynthetic capacity. (Bond 2000, p. 350)

Ontogeny – Phenology

A number of changes occur in seedlings between the germinant stage and 15 years. One major change is the development of reproductive capacity. Douglas-fir commonly initiates production of reproductive buds at approximately 10–15 years (Isaac and Dimock 1960) and the production of cones increases until the tree is 275 years old or older. Other indicators of changes in juvenility are "capacity of cuttings to root, seedling mainstem diameter, nodal branch length, diameter, all increased with increasing age" (Ritchie and Keely 1994). Robinson and Wareing (1969) concluded that phase change occurs after the meristems have undergone a number of divisions so that phase change is correlated, but not determined by attainment of a certain size. Interestingly, phase change in old growth is a function of size, not age per se.

Seedlings

Li and Adams (1993) found the following:

- Seedlings are indeterminate; bud set is in early fall.
- Late buds are susceptible to summer drought, positively correlated with height.
- Early bud break is weakly correlated with height.
- Bud burst phenology is under strong genetic control.
- Bud set is weakly inherited.

White et al. (1979) noted that seedlings from southerly or low-rain areas broke buds early. In France, Michaud and Najar (1980) found the following for populations of seedlings representing almost the entire natural range of Douglas-fir:

- Seedlings from east of the Cascades broke buds early.
- "Latitude has an important influence on flushing – late provenances are situated in a zone bounded by latitude 44° to the south and latitude 49° to the north. . . . Within this zone altitude has little influence on flushing" (p. 192).
- An important relationship between vigour and flushing date was observed, the most vigorous provenances are the least susceptible to late frosts.
- Sapling height, dbh, and bole volume are correlated with budburst.
- Bud burst phenology is under moderate to strong genetic control and is highly stable.
- Bud set is strongly inherited.
- Saplings are determinate.
- Bud set is in mid-June.

Emmingham (1997) noted that bud burst appeared to be triggered after soil temperatures reached 5ºC. Late wood formation generally began after 90% completion of leader growth. Under favorable conditions growth cessation was long; the cambial growth continued to late October. Walters and Soos (1963, p. 83) noted that lower branches had a shorter elongation period than the leader but that laterals had a greater growth rate than the leader. Annual growth is not correlated with bud burst date.

Saplings

Emmingham (1977) discussed in detail the phenology of several Douglas-firs seed sources shown at several different locations, and with all sources and locations from Oregon, generally midway between the Columbia River and California. His data showed that all seed sources initiated both root and height growth in April in the low elevation areas, but not until June at the plantation at 1,050 m in elevation. Cambial growth started a few days after bud swell for most seed sources. Growth appeared to be triggered after soil temperatures reached 5°C. He found that "leader growth was nearly completed by the end of August at low land sites and by mid-August at the Cascade Mountain plantation (1050 m). Drought was most severe in the Coast Range and Corvallis plantations, where shoot growth stopped first. Latewood formation generally began between 90% completion of leader growth and 90% completion of cambial growth (p. 154). Emmingham (1977) suggested that the "cessation of shoot growth while temperatures and moisture conditions were favorable, was keyed to shorter day length" (p. 161). Cambial growth continued to late October for all seed sources in all areas. Farther north, Walters and Soos (1963) examined the phenology of Douglas-fir saplings on two elevations, 100 m and 500 m, in southern British Columbia.

Ontogeny – Photosynthesis

It is very difficult to relate photosynthetic rates to the age of the tree because these rates are a function of both the needles and the environment. Bond (2000) noted in a detailed review "that published studies from a variety of experimental situations generally indicate that both the photosynthesis and stomal conductance are reduced with the age of trees and shrubs," and that "these decreases have been reported at all phases of development: seedlings vs. older plants; seedlings vs. juvenile versus juveniles vs mature plants; juveniles vs mature and or old growth" (p. 350). She noted reduced photosynthesis with reduced N, which is closely correlated with photosynthetic capacity.

Young trees

According to McArdle and Meyer (1930),

> The inability of Douglas-fir to live in its own dense shade insures, in well-stocked stands, the early and gradual shedding of the lower branches and the production of clean lumber thereafter. . . . Sensitivity to shade varies with age. Young trees being more shade-tolerant than old trees. Likewise, trees having favorable growth conditions are more tolerant of shade than those on poorer sites. Early in life, Douglas-fir is able to withstand some side shading, but after the 25th year the tree is unable to make satisfactory growth or live in either side or overhead shade. (p. 4)

Chen and Klinka (1997) found that shade grown Douglas-fir foliage had higher photosynthetic rates based on dry weight at all light intensities than did open grown foliage for *Pseudotsuga menziesii* var. *glauca* seedlings. Lewis et al. (2000, p. 454) suggested that "the high photosynthetic capacity of Douglas-fir is consistent with its dominance of early successional environments." As Bond (2000) noted, however, "shaded plants in the forest understory (presumably older than seedlings) generally have low photosynthetic capacity compared with sun-adapted plants." This probably explains changing tolerance to shade in Douglas-fir. A number of reports (Hodges 1967, Brix 1970, Del Rio and Berg 1979, Drew and Ferrell 1987, Chen et al. 1996, Emmingham 1997, Khan et al. 2000) have suggested that Douglas-fir seedlings tolerate some degree of shade, although Reed et al. (1983) reported that responses of tree species to varying light availability differed with availability of nutrients and water.

Mature trees

Overton et al. (1973) reported that 61% of the foliage of old growth trees was more than two years old. This is in strong contrast to the data reported by Silver (1962), Dice (1970), and M. Tohell (personal communication), all of whom noted that the majority of the foliage of young Douglas-fir is less than 2 years old. Woodman (1971) noted that the photosynthesis rates in foliage of young trees was maximal for current needles; while 1-year-old needles had photosynthetic rates 72% of maximum; 3-year-old needles, 50%. These differences complicate estimates of tree age effects.

Apple et al. (2002) noted that old growth needles are less efficient photosynthetically than those of young growth. Thomas and Winner (2007) conclude that "in general measure LMA (leaf mass/leaf area) ratio in old trees leads to a decreased photosynthetic capacity. A number of studies have discussed changing photosynthesis with tree age (Ryan et al. 1997, Ryan and Yoder 1997, Bond 2000, Thomas and Winner 2002, Ryan et al. 2006, Bond et al. 2007). Parker (1997) noted the difficulty of measuring light intensity in old growth stands and Thomas and Winner (2002) noted that LMA in mature trees leads to decrease in photosynthesis. Ryan et al. (1997) reported lower photosynthesis in older trees, suggesting the following reasons:

- increased hydraulic resistance
- reduced leaf area caused by crown abrasion
- reduced nutrient supply
- reproductive effort
- increased mortality of older trees
- genetic changes with meristem age

Several studies noted that photosynthesis may be limited by various factors of the environment (Helms 1964, 1965; Woodman 1971; Parker 1994). Helms (1965) noted that Douglas-fir may photosynthesize at low light intensities. None of these reports indicated differences with age.

Competition

Dawkins (2009) observes that competition results in trees 30 m tall instead of 3 m with no appreciable gain on the individual tree than possible increased light absorption, and Darwin (1860) noted that the most intense competition occurs between individuals of the same species. A number of reports (De Champs 1997; Timmis and Tanaka 1976; Van den

Driessche 1984,a-d; Smith and Reukema 1986; Curtis and Reukema 1970), and unpublished reports from Wind River, for ages from seedlings through young second growth all noted that tree diameter and height growth all increase with lesser competition. Perhaps, the most striking paper is that of Tappeiner et al. (1997), who found that the large trees' characteristics of old growth forests developed as seedlings and young mature stands of 100 trees per hectare, as opposed to young stands today of 600 trees per hectare and that growth of the former was significantly greater than that of current stands. Accordingly, large trees in the future will develop only if current stands are dramatically thinned. In addition, Latham and Tappeiner (2002), who reviewed a number of papers indicating that thinning Douglas-fir stands increases tree height and diameter, noted that old growth trees increase growth after reduction of competition.

In contrast to the above, Scott et al. (1998) found that growth of 7- to 9-year-old Douglas-fir seedlings increased growth with increased stocking. This may be a function of light reflected discussed earlier by Ritchie. A number of references (Chappell et al. 1992, Gessel et al. 1979) and the numerous references cited therein, noted that Douglas-fir is sensitive to nitrogen fertilization throughout its lifespan, but noted differences with age.

Ontogeny – Insects

Seedlings

Although are a number of insects that feed on Douglas-fir seedlings, we will discuss only those considered to have a major impact.

Conifer seedling weevil

The conifer seedling weevil (*Steremnius carinatus*) commonly feeds on bark near the groundline (Condrashoff 1968). It is particularly damaging to container seedlings, which typically have thin bark. Adult weevils overwinter in the soil and emerge in the spring; they are favored by warm, moist periods. Weevils may live 3 years and are favored by clearcutting, which produces many favorable breeding sites, and by logging slash. Burning, which destroys competing plants, may increase damage on Douglas-fir: 1-year-old seedlings were more damaged than 2-0 seedlings. Condrashoff (1969, p. 2) found as many as 17,500 weevils per hectare in cutover areas of British Columbia. Up to 10% of seedlings may be killed by this weevil and an equal number injured in the Pacific Northwest.

Black army cutworm

In their detailed report, Ross and Ilnytzky (1977) discussed the significant damage to agricultural crops and to newly planted conifers seedlings from the Black army cutworm (*Actebia fennica*). The cutworm can cause 40% to 80% mortality on replanted forest plantations that had previously been burned. It overwinters as a first or second instar or, possibly as eggs:

> Moths fly late in summer and oviposit in the soil, frequently on burned areas. Eggs hatch late in the fall and the young larvae overwinter in the soil. Feeding on sprouting vegetation begins shortly after the snows recede in spring. Most spring feeding in central B.C. in 1973-74-75 began after sunrise: night hours were frequently too cool for larval activity. Feeding was completed in the valley bottoms about the second week in June; it continued for a week or two longer at higher altitudes.
>
> There is some suggestion that a series of warm, dry years precedes a black army cutworm epidemic and that warm dry conditions during egg laying and hatching are necessary for development of infestations. Heaviest concentrations of cutworm larvae have appeared on clearings burned over the previous year or two. . . .
>
> Although few in number, the most severe or extensive epidemics in North America have, within a given region, occurred at about 20-year intervals, lasting for 2, 3 and, in one instance, 4 years. The epidemic in 1973 covered more than 1,400 ha (3,400 acres), in 1974 about 2,800 ha (7,000 acres) and in 1975 over 650 ha (1,600 acres). Logging and reforestation, including prescribed burning, as practised in recent years, may aggravate the duration and even the frequency of epidemics. (Ross and Ilnytzky 1977, p. 4)

Mortality of seedlings was highest on dry, burned sites (Shepherd et al. 1993).

Mature trees

Although defoliators are attack all ages of Douglas-fir, they are perhaps most significant in mature forests (primarily *Pseudotsuga menziesii* var. *glauca*). The *Defoliator Management Guidebook* (British Columbia Ministry of Forests 1995b) gave a detailed discussion of four insects that defoliate Douglas-fir: the western spruce budworm (Tortricidae: *Choristoneura fumifera-*

na) and the Douglas-fir tussock moth (Lymantriidae: *Orgyia pseudotsugata*), which are major defoliators, and the western hemlock looper (Geometridae: *Lambdina fiscellaria lugubrosa*) and the western black-headed budworm (Tortricidae: *Acleris gloverana*), which are lesser. The guidebook is a source for much of the following.

Western spruce budworm

The western spruce budworm is discussed in Chapter 9, so we do not cover it in detail here, other than a brief comment on research concerning potential factors involved in Douglas-fir resistance. Clancy (1992 a,b) related concentrations of mineral and organic compounds to the incidence of spruce budworm and found that susceptible trees had lower levels of sugars than resistant trees. "No detectable difference in foliar concentrations of terpenes, however, susceptible trees had a greater proportion of monoterpenes, whereas resistant trees had greater proportion of oxygenated monoterpenes. Resistant trees also had delayed budbreak and growth compared to susceptible trees" (see also Clancy et al. 2004, Brookes et al. 1985).

Douglas-fir tussock moth

"While there are thousands of insect species native to British Columbia, very few of them cause serious concern to foresters. One of these select few is a small caterpillar with a characteristic coat of rust coloured tufts and orange markings, known as the Douglas-fir Tussock moth, *Orgyia pseudotsugata*" (Anonymous 1990, p. 1). Beckwith (1978) discussed the physiology and ecology of this insect in detail, noting the following: "Number of instars and body color vary depending on factors such as genetic coding, sex, food quality and quantity, temperature, and population density. The females usually have one more instar than males" (p. 27). There are five to seven instars; "the final instar spins a grayish brown spindle-shaped silken cocoon, which incorporates some of the larval hairs, and is spun on foliage, branches, and boles of host trees" (p. 28). "If not disturbed, each female lays all her eggs in a single mass," which generally contains 150 to 200 eggs (p. 30). Egg hatch and tree bud break are generally synchronous and dependent upon heat accumulation (C° > −14.7). The only acceptable food is new foliage from buds. Larvae concentrate on the top of tree. Most dispersal is over short distances. Larval development is related to temperatures with alternating day and night lows. Mating and egg laying take place on the cocoon, generally the day the female emerges. The tussock moth may kill up to 40% of the trees in an infected stand. Further, "Douglas-fir trees that have been weakened by the tussock moth defoliation may also be susceptible to attack by other insect pests, such as the Douglas-fir beetle" (British Columbia Ministry of Forests, Lands, and Natural Resource Operations 2014). Thus, even light defoliation by the tussock moth may be responsible for the tree's untimely death.

Brookes et al. (1978) discussed the life history of the tussock moth as follows:

> The Douglas-fir tussock moth is a univoltine insect that overwinters in egg masses containing 150–250 eggs, usually on the underside of small branches. . . . Eggs hatch in the late spring . . . about the time that buds break and new shoots begin to expand. These events are closely synchronized, giving new larvae the food they need for growth and development. . . . Shoot elongation progresses rapidly in June and July, resulting in a supply of new foliage for the larvae to feed upon. Neonate larvae normally leave their egg masses at the time shoot elongation is about 50% completed; by the third instar, shoot growth has usually terminated. . . . Small larvae produce silk strands on which they can be dispersed by wind throughout the stand.

According to Gast et al. (1991), larvae on a host tree then "crawl to the top or to the ends of brances and feed on the new foliage. The first two instars of tussock moth feed exclusively on the underside of the succulent, new needles. This feeding damages the needles, causing them to dry and turn red-brown by midsummer. Faded foliage at the tops of trees is often the first sign of tussock moth infestation" (pp. 19–20). Brookes et al. (1978) detail the following:

> After the new foliage has been destroyed, later instars feed on old foliage; during an outbreak, large portions or even the entire crown may be defoliated. The five to six larval instars feed for about 60 days . . . and then spin cocoons in foliated portions of the crown, sometimes in crevices of the bark, or on dead branches and twigs in the lower crown. The moths emerge in late summer, and about 2 weeks after pupating. The wingless adult females . . . remain on the cocoon, where they mate with the winged male. . . . The cycle is complete when the female deposits a new egg mass on or near her cocoon. (Brookes et al. 1978, p. 191)

The tussock moth is found in the drier part of the Douglas-fir range, this it attacks only var. *glauca*.

Webb (1978) noted that defoliation of the upper crown by the tussock moth resulted in higher light intensity received by remaining needles and the photosynthetic efficiency of the tree is raised; soon, increases may not occur until the needles are accustomed to higher light levels. Hence, the long-term loss of photosynthesis by defoliation is not proportional to the quantity of foliage removed. This is accompanied by a significant drop in requirements by the remaining foliage. The tussock moth preferentially feeds on new foliage, which has, perhaps, the greatest photosynthetic capacity. In contrast, when the insect takes older foliage, that not only reduces photosynthetic capacity, but food.

Western hemlock looper

The western hemlock looper (*Lambdina fiscellaria lugubrosa*) "primarily attacks hemlock," but during outbreaks, "the looper feeds on almost any foliage, including broad leafed forest trees and shrubs" (British Columbia Ministry of Forests 1995b). It is "periodically destructive in coastal and interior forests, reaching outbreak proportions every 11 and 20-plus years, respectively. Outbreaks of the hemlock looper usually last about 3 years, after which they are generally brought under control by the action of parasites, predators, and diseases. Heavy rains during the moth flight period can reduce egg-laying and hasten the decline of an outbreak." From May through early July, feeding by early instars is slight. From mid-July until October, the larvae "feed voraciously on both new and old foliage." Feeding starts in crown tops, later, more of the crown is affected (British Columbia Ministry of Forests 1995b, p. 58). (McCloskey et al. 2009) noted that if global warming increases temperature and reduces moisture, it has the potential to increase hemlock moisture 100%.

Douglas-fir beetle

Zhong and Showalter (1989, p. 941) noted that each beetle species or functional group could be expected to inoculate and colonize boles with a distinct microflora and that patterns of wood utilization by various beetle functional groups may be instrumental in initiating decomposition and perhaps in determining long-term rates of decomposition in boles of different tree species.

The Douglas-fir beetle (*Dendroctonus pseudotsugae*) differs from the preceding insects in that it attacks the bole, not the foliage. Ross et al. (2006) reported the following:

> The Douglas-fir beetle is normally present in forests at low densities, breeding in Douglas-fir trees that are injured or have recently died. Tunneling by adults and larvae beneath the bark produces a characteristic pattern distinguishing the Douglas-fir beetle from other bark beetles. . . . Beetle larvae need fresh, moist phloem (inner bark) for food, so trees that have been dead for more than a year are not suitable habitat. Injured or recently killed trees have little or no defensive capability, making them ideal sites for beetle larvae to feed and develop. Periodically, natural or human-caused disturbances such as windstorms, fire, defoliator outbreaks, or logging, create an abundance of suitable breeding sites that allow the beetle populations, under favorable conditions, to rapidly increase to high densities. At high densities, beetles are forced to attack healthy, live trees because there are not enough stressed and dead ones to support the population By attacking a live tree in large numbers, the beetles are able to overcome the tree's natural defenses and successfully reproduce. (Ross et al. 2006, p. 5)

Global warming will create such conditions and result in massive beetle kill of previously healthy trees. Douglas-fir beetles preferentially attack large, old trees in dense stands with a high Douglas-fir component. As Ross and Daterman (1997) noted, the Douglas-fir beetle "usually breeds in portions of tree boles that are greater than about 20 cm in diameter. At low population densities, most infestations occur in trees that have recently died or live trees with limited defenses resulting from stress or injury. . . . When populations reach high densities, large numbers of healthy trees may be successfully attacked and killed" (Ross and Daterman 1997, p. 135). According to Ross and Daterman (1995), the beetle "is found throughout the range of Douglas-fir (*Pseudotsuga menziesii*) in western North America . . . [and] when suitable breeding material is abundant and weather conditions are favorable, beetle populations can reach high densities causing considerable tree mortality" (p. 805).

Douglas-fir beetles have only one generation per year. Adults fly from early spring through mid-August. It broods overwinter within phloem in the adult, pupal, or late larval stages. Stark (1965) noted that fertilization reduces bark beetles (p. 800). Ross and Daterman (1997) suggested that thinning may reduce bark beetle infection and that sanitation and salvage logging may reduce breeding sites.

Ontogeny – Disease

A distinct group of fungal pathogens attacks Douglas-fir at each stage, from seedlings through old growth. We shall confine our observations to those diseases deemed most damaging.

Seedlings

We have discussed nursery diseases previously. Natural reproduction is remarkably free of disease, primarily because forest soils frequently contain organisms that inhibit those causing disease, i.e., damping off, *Fusarium.* Peterson (2008), in a lengthy review of *Fusarium*, noted, however, that mishandled seedlings may develop *Fusarium* after planting (Linderman 2000).

An exception is *Phellinus*, which is spread by root contact and is not soilborne. *Phellinus weirii*, laminated root rot (Thies and Sturrock 1995), is one of several pathogens particularly destructive to Douglas-fir. Others are *Phaeocryptopus gaeumannii,* Swiss needle cast (Hansen et al. 2000), and *Armillaria solidipes,* formerly *Armillaria ostoyae* (Van der Kamp 1994, Filip and Ganio 2004).

Young trees

Phellinus weirii

Wallis (1976) stated that "*Phellinus weirii* (Murr.) Gylbertson is the most destructive disease in young growth Douglas-fir in British Columbia" (p. 3). Thies and Sturrock (1995) summarized research concerning *P. weirii*, noting that it is widespread in western Canada and the northwestern United States. There are two fairly distinct forms of the fungus. One is a common cause of root rot in western redcedar in the northern Rockies; the other commonly kills Douglas-fir and several other conifer species throughout northwestern North America. It forms red ring rot, and is the most destructive disease in the area. Trees weakened by this disease are often killed by bark beetles.

The pathogen is believed to have evolved with its host and is a natural, perhaps necessary part of many ecosystems. It does not destroy entire stands over large areas. The fungus does not spread from spores, but from root contact; this is why eliminating infected stumps is a method of control. Thies and Sturrock (1995) estimated that *P. weirii* occurred on 84% of commercial forestland in the northwestern United States and caused a loss in wood volume of 40% to 60% in areas affected. Nelson and Sturrock (1993) noted that grand fir and Douglas-fir are the most susceptible of Pacific Northwest conifers to *P. weirii*.

Van der Kamp (1993b) found that "young trees are killed quickly (1-3 years from first symptoms to death); older trees (40–60 years old when first infected) may survive for decades, but such trees produce little increment, instead the host spends much of the available energy producing new roots to replace those killed by the pathogen" (p. 5).

Bloomberg and Reynolds (1982) reported that transferred mycelium of *Phellinus weirii* was endotrophic rather than ectotrophic. They found that root diameter, rather than root depth, was positively correlated with infection.

Saplings, young growth

Armillaria root

Armillaria root disease is an important disease of both conifers and hardwoods throughout the world (Mallett 1992). There are currently 36 described species in the world (includng 10 in North America). Blenis (1995) observed that "Douglas-fir is very susceptible to *Armillaria ostoyae*. This fungus causes foliar discoloration, resinous and a light yellow stringy decay of the wood, but the most positive symptom is a mycelial fan." Blenis (1995) also noted, however, that *Armillaria* rarely kills trees over the age of 20; Van der Kamp (1994) agreed.

In a series of papers, Entry et al. (1990; 1991 a,b; 1992 a,b; 1993) related the density of the *Armillaria* attack to the level of carbohydrates and defensive phenols in seedling roots. Redfern (1978) reported that supressed trees were least resistant, but that Douglas-fir is relatively resistant in Britain. Filip and Ganio (2004) found that *Armillaria ostoyae* is the most common root disease in Douglas-fir plantations in Oregon.

Mature trees, old growth

Root and butt rots

Polyporus schweinitzii (Schweinitzii root and butt rot), *Fomes pini* (conk rot), *Fomitopsis officinalis* (brown trunk rot or quinine fungus), and *Fomitopsis cajanderi* (yellow brown top rot, formerly called *Fomes subroseus*) all attack old-growth Douglas-fir. Nelson et al. (1981) noted the "role of *P. weirii* as a perennial inhabitant of the site, substantially reducing productivity, surpassing importance as a killer of individual trees" (p. 1). Thomson et al. (1996) found that *P. weirii* reduced levels of chlorophyll *a* and nitrogen in foliage. Thies (1983) found that *P. weirii* reduced growth of Douglas-fir as much as 32%. Growth loss was not related to crown symptoms or number and size of infected roots.

Young stands

Phellinus weirii

Sturrock and Garbutt (1994) discussed the spread of *Phellinus weirii* and its characteristics in the two passages below:

> Infection by *P. weirii* starts when healthy roots of susceptible tree species contact infected roots of an adjacent tree or infected stumps and roots (residual inoculum sources) from the previous stand. Surface (ectotrophic) mycelium spreads from infected roots onto the surface of healthy roots. Ectotrophic mycelium eventually penetrates to the interior of host roots, likely gaining entry through both intact and injured bark. Once inside the root (as endotrophic mycelium), the fungus progressively destroys root tissue, depriving the tree of water and nutrients and weakening its structural support. (Sturrock and Garbutt 1994, p. 2)
>
> *Phellinus weirii* can be positively identified in living suspect trees by examining the root collar and lateral roots for grey-white to tawny to mauve colored ectotrophic mycelium. Brown crustlike mycelial mats commonly form over surface mycelium below the duff layer, particularly in the crotches of roots. Reddish brown hairlike structures called setal hyphae may be seen with the aid of a hand lens, scattered in surface mycelium or in pieces of wood with advanced decay. Setal hyphae, in conjunction with these other signs, are diagnostic of *P. weirii.* (Sturrock and Garbutt 1994, p. 5)

According to Thies and Sturrock (1995), "as yet no strong evidence exists that any individual site factor, or group of factors, is a reliable predictor of either the presence or intensity of laminated root rot in a particular stand" (p. 16). The distribution of *P. weirii* may be either diffuse or aggregated. Minor infections of both above diseases have been reported under laboratory conditions. *Tricoderma viride* was shown to be inhibitory to *P. weirii*, but we have found no reports of how significant such effects are under field conditions (Goldfarb et al. 1989 a,b).

Swiss needle cast

In a survey of the effects of Swiss needle cast (*Phaeocryptopus gaeumannii*), in western Oregon. Weiskittel et al. (2006) noted the following:

> The condition of young conifer plantations in Europe is often rated by foliage retention, alternatively defined as needle longevity or the average number of needle cohorts held by the trees (Innes 1993). Foliage retention is currently the primary index of Swiss needle cast (SNC) severity in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco; Hansen et al. 2000). Other foliage attributes such as crown color and crown density have been explored as indices of SNC severity, but foliage retention is less subjective and performs better than or as well as other alternatives for predicting tree and stand growth (Maguire et al. 2002). SNC is caused by an endemic fungal pathogen, *Phaeocryptopus gaeumannii,* whose hyphae grow into needles through stomates and interrupt gas exchange by occluding stomates with fruiting bodies, or pseudothecia (Hansen et al. 2000). The fungus causes premature loss of older foliage, reducing mean foliage retention to as little as 1 year and volume growth by as much as 50% (Maguire et al. 2002). The disease eventually changes several crown structural and morphological attributes such as live crown length, branch size, and specific leaf area (Weiskittel 2003). Currently, over 72 000 ha in the Oregon Coast Range are showing symptoms detectable by aerial survey, reflecting the dramatic increase in this disease since 1990 (Kanaskie et al. 2004). (Weiskittel et al. 2006, p. 1498)

They also noted that "with increasing SNC severity, the modes of the youngest three age-classes shifted upwards, while the modes for 4- and ≥5-year-old foliage were located lower in the crown relative to that of healthy trees" (p. 1506).

Swiss needle cast differs from most diseases of older Douglas-fir in that it is a foliage disease, not a rot of bole or roots, and that significant damage in western Oregon has been reported only during the last two decades. Losses as high as 25% in top height growth, 49% in volume, and 48% in basal area have been reported (Maguire et al. 2002).

Major losses to Swiss needle cast extend to a band within about 30 miles of the coast (the fog zone). Measurements of weather data and disease virulence show a strong correlation between maximum temperatures in the period from November to February (Manter et al. 2005) and incidence of disease severity. This suggests the possibility that the disease is favored by a lack of chilling of saplings and represents an early effect of global warming.

Weiskittel and Maguire (2007) noted: "Defoliation from the endemic SNC pathogen can drastically reduce LAI (leaf area index) and change both total and seasonal foliage litter fall patterns" (p. 121). Hansen et al. (2000) noted that many trees had high defoliation in the upper crown. They also reported that "fungicide applications reduced pseudothecial density and increased needle retention. Most infection occurs in newly emerged current season needles" Hansen et al. (2000, p. 775).

Mature stands, old growth

Swiss needle cast

Little research has concerned Swiss needle cast in stands of older trees, as Shaw et al. (2011) also noted. It has been found on old trees, however, and the symptoms follow the same pattern as found in young stands. Black et al. (2010), working in mature stands in the Oregon Coast Range, reported that Swiss needle cast is an increasing threat to old stands, and also noted effects from warmer temperatures: They found that "even mature forests of natural origin are susceptible to severe growth reductions by Swiss needle cast, that warmer spring and summer temperatures are associated with Swiss needle cast impacts, and that the disease appears to be increasing in severity" (p. 1673).

Fomes pini

Older stands of Douglas-fir are subject to the foliar and root diseases discussed earlier, but, as trees age the incidence of bole rotting fungi increases in occurrence and virulence, as discussed by Boyce and Wagg (1953). Much of the following is based on their report. They noted that "decay caused by *Fomes pini* has long been referred to as conk rot, because this fungus is unique in producing numerous conks, or fruiting bodies, which follow closely the progress of rot in living trees" (p. 5). The populations of old growth trees examined in their study had 80% to 90% decay by *F. pini*, making them effectively massive columns of decay surrounded by relatively thin layers of sapwood and bark. Such structures are subject to windthrow and bark beetle damage (Isaac 1956, Stathers et al. 1994). *Fomes pini*, which causes a red ring rot, is responsible for 81% of total board foot volume of decay in western Oregon and Washington, and can attack trees as young as 27 years (Boyce 1932, p. 33). Boyce and Wagg (1953) noted that "*Fomes pini* causes more decay on warmer sites" (p. 70); accordingly, global warming may well cause an increase in this fungus. According to Boyce and Wagg (1953),

> Several fungi are responsible for decay or rot in Douglas-fir. A previous investigation showed that 80.8 per cent of the total board foot volume of decay found in Douglas-fir on plots in western Oregon and Washington was red ring rot or conk rot caused by *Fomes pini* . . . Nearly all the remainder was divided among red-brown butt rot, caused by *Polyporus schweinitzii;* brown trunk rot, caused by *Fomes laricis;* and yellow-brown top rot, caused by *Fomes roseus*—all three being brown cubical rots. (Boyce and Wagg 1953, p. 7).

> Most of the other decay-causing fungi appear later in the life of a stand. As a stand approaches stagnation and then declines, brown cubical rots, particularly brown trunk rot caused by the quinine fungus, *Fomes laricis*, become increasingly important. *Fomes laricis* attacks not only sound trees but those already infected with *Fomes pini.* In the latter instance, brown trunk rot is able to overrun conk rot. . . . *Fomes laricis* commonly follows the major attack of *Fomes pini*, and is the most important fungus in the final break up of old-growth Douglas-fir stands.
>
> *Polyporus schweinitzii*, depending on wounds for entrance, may appear at any time during stand development. Its incidence is proportional to the amount of basal wounding. (Boyce and Wagg 1953, p. 10)

The incidence of *Fomes pini* was higher on good sites than poor, possibly because good sites have fewer trees with larger branches which offer infection sites of heartwood when the branches die. Pure stands of Douglas-fir had a higher percentage of Douglas-fir infected with *Fomes pini* than did mixed stands. Boyce and Wagg (1953, p. 89) observed that "*Fomes pini* is somewhat pathogenic, commonly encroaching on the sapwood, resulting either in the death of the tree directly or, as seems more likely, reducing its vigor so that it succumbs to competition. The most rapidly growing trees are infected first, their growth is reduced, and finally they drop out of the stand. Meanwhile, new infections are occurring in the remaining trees, and the process is repeated" (p. 89). Their conclusions were as follows:

> No relationship was found between the number of trees with conk rot in a stand and such factors as elevations ranging from 1,500 to 4,500 feet, curvature of slope, texture of the soil, and acidity of the soil. A greater amount of conk rot occurred in trees on steep slopes, on southerly aspects, on upper slopes or hogbacks, on soil with excessive drainage, and on shallow soil.
>
> In nearly all instances higher temperature is associated with the foregoing factors, so possibly temperature is the controlling factor. The incidence of conk rot was lower in stands that were on moderate slopes, on northerly aspects, on lower slopes and benches, on soils with good to restricted drainage, and on deep soils. Soils with a high percentage of total nitrogen produced more decayed trees than those with a low percentage. Where vine maple, vanillaleaf, oxalis, or rose predominated in the secondary vegetation, the incidence of conk rot was high, whereas salal, twinflower and rhododendron indicated a lower incidence of decay.
>
> Pure stands contained greater volumes of conk rot than did mixed stands; stands of poor quality were more defective than those of good quality; and stands that had been damaged by fire had more conk rot than those that had not been burned. (Boyce and Wagg 1953, p. 90)

Conclusion

Although this chapter has provided an overview, additional ontogenetic work is needed to continue to increase our understanding of the morphological, anatomical, and physiological changes that occur as Douglas-fir develops from a seedling to a mature tree. Finally, we must continue to expand our understanding of the environmental and other factors that can affect this important genus at its different life stages.

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Index

Note: this brief index is intended only as a supplement for the limited-edition print version and is not a complete index. Please see also the detailed table of contents, as well as the electronic version of the entire book, which is fully searchable and freely available online, in ScholarsArchive@OSU, at this address: **http://hdl.handle.net/1957/47168.**

Douglas-fir, the genus *Pseudotsuga*, has a wide distribution in North America, and includes some of the most widely distributed species outside of their natural ranges. Douglas-fir has been introduced to Europe, New Zealand, South America, and elsewhere around the world. It is an accepted and integral part of forest management in many countries because of its economic importance and its reputation as a tree that may be able to deal with climate change.

This book provides an overview of research activities and findings that highlight unique aspects of Douglas-fir physiology, genetics, and other related issues. The authors have pulled together a tremendous amount of information, beginning with the evolutionary history and distribution of Douglas-fir. They provide detailed descriptions of the introductions of Douglas-fir to other countries, including information about initial plantings, provenance trials, and genetic tree improvement activities. In sections about life history, the authors bring to bear their long-time research and teaching experiences, as well as detailed descriptions of flowering, seed, root, and seedling physiology, followed by sections on biotic factors, such as mycorrhizae, insects, and diseases, and abiotic factors, including frost, drought, and fire.

Douglas-fir: The Genus Pseudotsuga will stand the test of time as an invaluable collection and cornerstone of information that could have easily been lost as researchers, educators, and managers are inundated with new research results. It is intended as a resource for everyone interested in understanding the opportunities and challenges of managing Douglas-fir in a variety of regions and settings. It provides information for historians and social scientists investigating forestry trends; researchers, educators, and managers looking for detailed information in areas such as genetics and regeneration practices; and all others interested in the beautiful trees we call Douglas-fir.

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