AN ABSTRACT OF THE THESIS OF

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Title: Variation of Carbon Allocation and Competitive Ability of Different Tree Species as Related to Successional Position and Habitat

Abstract approved: ______________________________
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Early and late seral tree species were compared for inter- and intraspecific competitive ability; within-population genetic variability; and allocation patterns of soluble sugars and starch seasonally and in response to shade and nitrogen fertilization. Species were Douglas-fir (early seral) and western hemlock (late seral) from a low elevation habitat; and noble fir (early seral) and silver fir (late seral) from a high elevation habitat.

Mortality increased with density and peaked at 15% for western hemlock, 35% for Douglas-fir, 48% for noble fir, and 90% for silver fir. In general, early seral species grew faster and attained larger final size than late seral species, while species did not differ in response to competition. However, there were considerable differences among half-sibling families within each species.

Ranges in average top weights for families grown at low or medium (16 or 4 cm^2 of initial growing space) were: western hemlock, 50-300 mg; Douglas-fir, 100-900 mg; silver fir, 10-190 mg; noble fir, 90-250 mg. Root size was less variable resulting in highly significant density-correlated rank changes in shoot/root ratio (S/R ratio) for families of all species except noble fir. Western hemlock grown with Douglas-fir had shoots 24% smaller and roots 36% smaller than when grown with other western hemlock and Douglas-fir roots were 40% larger when grown with a mixture of Douglas-fir and western hemlock than when grown entirely with one species or the other. Families of both species differed in their S/R ratio response to varying neighbor composition. In contrast, neighbor composition had little effect on silver fir and noble fir.

Field-grown seedlings were 30% smaller and less responsive to treatments than pot-grown.

In all species, 66 to 70% of total dry weight was soluble sugars and starch prior to budbreak with roughly two-thirds of this as starch. Following budbreak, available carbohydrates decreased to 25 to 30% of total dry weight (maintained through the growing season). Late seral species had higher root sugars during the growing season than early seral species.

Shading either decreased or did not affect growth of early seral species and increased growth of late seral species. It had little effect on available carbohydrates. Nitrogen fertilization increased S/R ratio of western hemlock from 1.9 to 3.3 and of the other species from 1.2 to 2.2; and reduced sugar concentration in all species but had little effect on starch. Family variances in prebudbreak root sugars were 17 times greater in western hemlock than in Douglas-fir and noble fir. Family variance in growth traits was greater in the low elevation than in the high elevation species.

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CHAPTER I

INTRODUCTION

Genotypic Response to Competition

Over the life span of any organism, the internal and external environments change. In the former, costs of bulk and organization increase and allocation of energy between survival and reproduction becomes necessary; in the latter, an organism modifies its own environment as it grows and experiences changes in competition and environment.

Whenever a "limited" (or "unlimited" under some circumstances) supply of growth commodities is sought by more than one individual, there exists a problem of supply and demand. Competition (or interference) in plant communities has long been explicit in the writings of several plant ecologists (Tansley, 1920; Clements *et al*., 1929), who held that response to the physical environment is, to a considerable degree, conditioned by competitive interactions. These can be among related (intraspecific) as well as among unrelated (interspecific) individuals. The spatial distribution of individuals will influence the balance of intra- and interspecific competition. Due to species replacement in time the spatial arrangement is dynamic.

It is well known that density affects growth of plants (Harper, 1977). At high plant densities there may be (1) an increase in plant mortality (Harper and McNaughton, 1962), with little effect on the size of the surviving plants, (2) a reduction in growth of the individuals with little mortality (Harper and Gajic, 1961), or (3) a combination of both types of response (Raynal and Bazzaz, 1975). Intraspecific variation in density response has been widely investigated in agricultural (Bleasdale, 1973) and forage plants. Antonovics and Levin (1980) cite fifteen studies of genotypic differences in response to spacing and Cannell (1982) cites an additional four in which rank changes among genotypes with changes in density were demonstrated (grasses: van Dijk and Winkelhorst, 1978; wheat: Syme, 1972, Fisher and Kertesz, 1976; bean: Hamblin and Evans, 1976). In contrast, there are few studies of genotypic differences in response to spacing among natural plant communities (Antonovics and Levin, 1980). Genetic changes during self-thinning have been demonstrated in populations of Plantago lanceolata (Antonovics, 1978) and in Phlox drummondii (F. A. Bazzaz and D. A. Levin, unpublished, cited in Antonovics and Levin, 1980). Antonovics and Levin (1980) interpret these changes as evidence for genotypic difference in response to density.

Donald (1968) coined the term ideotype as a "biological model which is expected to perform or behave in a predictable manner within a defined environment." Donald and Hamblin (1976) identified two cereal ideotypes with respect to growth in stands, the "isolation/competition" ideotype, large and exploitive, and the "crop" ideotype, small and relatively efficient. Ford (1976) and Cannell (1978, 1982) have argued that, while tree breeders normally select for "isolation/competition" ideotypes, foresters might obtain better yields from stands of "crop" ideotypes. Despite the practical importance of the question, virtually no information exists on the amount of genetic variation with respect to density-response contained within natural populations of trees.

A question of equal importance relates to genotypic performance in mixtures. Relatively small differences in genotype of competing plants may affect competition. Adams *et al*. (1973) showed stronger competitive effects among unrelated than among related (1/2 sibling) families of loblolly pine (*Pinus taeda* L.). Several authors have investigated growth of mixtures of annual plants (reviewed by Simmonds, 1962; Baldy, 1963; Donald, 1963; Trenbath, 1974), with no firm evidence that a mixture can outproduce the higher yielding component monoculture, excluding legume and nonlegume mixtures (Donald, 1963; Trenbath, 1974). However, Parrish and Bazzaz (1982) found that species from a late successional community experienced less competitive growth loss in the presence of heterospecific neighbors than species from an early successional community. Thus, studies with agronomic plants (primarily early seral, "competition/isolation" ideotypes) may not be applicable to species interactions in natural communities, particularly those involving late seral species. Assmann (1970) summarized growth of a number of mixed tree species plantings in Germany. In quite a few cases yields are greater in mixed than in pure stands, depending on the species mixture and site, particularly the character of the soils; however, the German experience is largely anecdotal--plantings were not designed as experiments and are therefore impossible to rigorously interpret.

Environmental Effects on Carbohydrate Allocation

Carbohydrate accumulation and allocation varies with species. In annual grasses, proportionally more carbon goes into the stem than in perennial grasses (Ryle, 1970). Kramer and Kozlowski (1979) have separated forest tree species into those storing reserves as fats (primarily diffuse porous species), as starch (primarily ring porous species), and as a combination of those two forms. Deciduous and evergreen species differ in the timing and duration of energy production and consumption (Ziegler, 1964). In evergreen trees, proportionally greater amounts of carbon may remain in the mature leaf since they serve as important reserve centers for supply during shoot growth (Dickmann and Kozlowski, 1970). In Douglas-fir, Webb (1977) has shown that needles and roots, and particularly new needles, are consistently the major sinks of carbon in May, August, November, and January.

Shading is often a resultant of close spacing. Mutual shading in closely planted wheat was shown by Kravcova (1956), cited by Wardlaw (1968), to result in an increased proportion of assimilates moving to the ear from the lower leaves on the culm. In rice, Navasero and Tanaka (1966) noted that shading intensified the movement of assimilates to the ear from the upper exposed leaves. The overall effect of reduced light intensity seems to be an increase in the relative proportion of assimilates reaching the shoot (Wardlaw, 1968). However, it is well-established that shading affects early and late seral plants differently. Seeds of early successional plants are sensitive to light while those found in climax forests do not require light for germination (Holm and Miller, 1972; Sauer and Struik, 1964; Wesson and Wareing, 1969; USDA Forest Service, 1974). Rates of photosynthesis are often higher in sun- than in shade-adapted species (Boardman, 1977) and the rate of dark respiration decreases in late successional species (Bazzaz, 1979).

Water stress is likely to develop more quickly in high- than in low-density populations (Donald, 1951). Extension growth commonly shows an early response to water stress, whereas photosynthesis and the accumulation of assimilates continue for some time after stress is evident in extension (Iljin, 1957). As a direct result of reduced growth rate or of reduced photosynthetic rates there exist marked alterations in the pattern of distribution of photosynthetic assimilates (Gates, 1964).

Nitrogen is an important element in the plant photosynthetic apparatus as indicated by its high content in chloroplasts. According to Stocking and Ongum (1962) about 72% of the nitrogen content of green cells is located in chloroplasts, and correlation coefficients from 0.61 to 0.82 have been calculated between rates of photosynthesis and nitrogen content per unit leaf area in soybean (Ojima and Kawashima, 1968). Also, good correlation between nitrogen concentration and photosynthetic rate was found in leaves of black poplar (Keller, 1970), in spruce (Keller, 1971), in some Brassica species (Sasahara, 1971), all cited by Natr (1975), and in needles of black spruce (Roberge *et al*., 1968).

The number of quantitative studies on the dynamics of starch and sugar in tree species is limited (for a review before the 1960's, see Kozlowski and Keller, 1966). The array of species investigated includes Scots pine (Ericsson and Persson, 1980), *Eucalyptus* (Stewart *et al.*, 1973; Kile, 1981), Douglas-fir (Krueger and Trappe, 1967; Webb, 1977), larch and sycamore (Ledig and Botkin, 1974), white ash (Tepper, 1967), white pine (Shiroya *et al.*, 1966; Little, 1970), noble fir (Winjum, 1963) and white oak (McLaughlin and McConathy, 1979a,b). Even more limited is information on the effects of the environment upon carbohydrate dynamics. Ericsson (1979) investigated the effects of fertilization and irrigation on the seasonal changes in carbohydrate reserves in different age class needles of Scots pine (*Pinus sylvestris*). Linder and Axelsson (1982) concluded that irrigation and fertilization of Scots pine decreased the proportion of carbon exported to roots, however, they did not measure concentration of sugar and starch.

Study Background and Description

In the following chapters, I have attempted to characterize some differences in early and late successional pairs of tree species: one pair, Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] and western hemlock [*Tsuga heterophylla* (Raf.) Sarg.], from the relatively mesic environment of the Oregon Coast Range, and the other pair, noble fir [*Abies procera* Rehd.] and silver fir [*Abies amabilis* (Dougl.) Forbes], from higher elevation in the Oregon Cascades. Chapter II investigates performance of first-year seedlings as affected by density and genetic composition of neighbor seedlings. Chapter III compares development of and species variation in morphometric and physiological traits before, during, and after the second-year of growth.

In the work reported in Chapter II, I hypothesized that the different early environments of early and late seral tree species have produced differences in competitive ability and genetic structure of populations. Specifically:

1. Early seral tree species should be better competitors than late seral species, in that they preempt resources more effectively, but late seral species should be more tolerant, both in growth and survival, to competition than early seral species.
2. Genetic variability in both growth traits and competitive ability should be greater within populations of late than populations of early seral tree species.
3. The two species from the mesic environment should be more effective space-preemptors than those from the harsh environment, while the former should have a higher degree of within-population genetic variability (because of the more variable biological environment they face).

In effect, Hypothesis One states that early seral populations should contain a greater proportion of "isolation/competition" ideotypes than late seral populations, while late seral populations contain a greater proportion of "crop" ideotypes. This follows from the importance of capturing and holding space in the early stages of succession, and early seral trees have generally been shown to have higher rates of net photosynthesis in full light and faster earlier growth than associated late seral species (Krueger and Ruth, 1969; Bazzaz, 1979; Bazzaz and Pickett, 1980; Wierman and Oliver, 1979; Bicknell, 1982). Herein, I compare growth of associated early and late seral species as influenced by densities of conspecifics, and as influenced by species composition of neighbors. If indeed early seral species have a high proportion of "isolation/competition" ideotypes they should be significantly influenced by increasing density of conspecifics and by an increasing proportion of other "competition/isolation" ideotypes (in this experiment conspecifics) in the neighbor mix. If late seral species are more tolerant of competition, they should have relatively low sensitivity to density and neighbor mix.

Most tree populations which have been tested have high levels of genetic variability (Perry, 1978), however, there are differences according to life history characteristics and habitat. Early successional trees have been found to have less allozyme variability than late seral trees. Hamrick *et al*. (1979) attribute this difference to the relatively homogeneous, primarily physical, environmental conditions faced by pioneer tree species, compared to later successional stages in which the biotic component of the environment becomes more complex and heterogeneous. Tree populations from mesic habitats have greater allozyme variability than those from submesic and xeric habitats, perhaps for the same reason that early and late seral species differ (Hamrick *et al*., 1979).

Hypothesis Two follows evidence from allozyme studies, although the argument that biological diversity is greater in late than in early stages of succession is not necessarily correct (e.g., Swindel et al., 1983; Bormann and Likens, 1979). The seedling invading a disturbed area may face quite diverse levels of both intra- and interspecific competition.

Although the high elevation habitat of silver and noble fir is neither xeric nor submesic, biological diversity is likely to be less than in the mesic habitats of Douglas-fir and western hemlock. Therefore, I hypothesized, again consistent with allozyme data, that the low elevation species should have greater genetic variability in response to the biological environment (competition) than the high elevation species. This argument is clearly oversimplified. Different environments select for different sets of traits (Perry, 1978), but it is not always clear what selective factors may be most important. In high elevation sites, temperature is likely to be more unpredictable than in low elevation sites, and thus perhaps elicit greater amounts of adaptive variability within populations. Moisture supply, on the other hand, is likely to be more predictable in high- than in low-elevation habitats, and so requires less adaptive variability. Nutrient turnover is much slower at high than at low elevation, so the competition experienced by a high elevation seedling may be fairly high even though the aboveground competing biomass is less than on a mesic site, where competition is primarily for light. Thus, the complexity of factors influencing adaptive variability and the difficulty of identifying their relative importance make hypothesizing about differences in genetic variability an extremely tenuous exercise, at best.

To develop the rationale for the work reported in Chapter III, it is necessary to briefly discuss the influence of succession and habitat on nutrient cycling. Changes in nutrient cycling during the course of succession are likely to play a role in adaptation of tree species. Nutrient availability generally declines through the course of succession, primarily because decomposition rates slow and increasing amounts of nutrients become tied up in living and dead organic material (Vitousek and Reiners, 1975; Gorham _et al_., 1979; Sollins and McCorison, 1981). Similarly, slow decomposition rates in high-elevation habitats will lead to lower nutrient availability than in mesic habitats (Van Cleve and Alexander, 1981).

Plants respond to nutrient deficiency by increasing root production relative to tops, and by forming abundant mycorrhizae (Chapin, 1980). Results from the Scots pine experiments discussed earlier (Linder and Axelsson, 1982) clearly show that this type of response is, to a certain extent, plastic. But there may also be genetic differences between species which differ in life histories or habitats. For example, when grown under identical greenhouse conditions and in the same soils, western hemlock seedlings (late seral) form root systems which have a greater proportion of mycorrhizae than root systems of Douglas-fir seedlings (early seral) (Schoenberger and Perry, 1982). This suggests that late seral plants may be genetically adapted to form mycorrhizae more readily than early seral plants.

Although factors influencing mycorrhizal formation are not completely understood, there is good evidence that the level of carbohydrates, especially soluble sugars, in the root is important (Marx _et al_., 1977). Furthermore, the highest amounts of available carbohydrates should occur at the point of most active growth (Kozlowski and Keller, 1966). Therefore, Chapter III tests the hypothesis, suggested by R. H. Waring (personal communication), that the proportion of sugars and starches occurring in roots, relative to those in shoots, should be negatively correlated with the nutrient cycling characteristics of the species habitat and life history niche. Thus, early seral species and those from mesic habitats (nutrient-available niches) should have a smaller proportion of soluble sugars in roots than late seral and high-elevation species (nutrient- restricted niches).

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CHAPTER II

COMPARISONS OF COMPETITIVE ABILITY

INTRODUCTION

Early and late seral plant species differ in a number of respects. Photosynthesis of early seral species generally saturates at higher light levels than that of later seral species, and light compensation points are usually higher (Bazzaz, 1979; Bazzaz and Picket, 1980). Early seral species often have more rapid juvenile growth, at least aboveground, and commit fewer resources to secondary metabolites than late seral species (Bormann and Likens, 1979). The objectives of this study were to (a) compare competitive ability between population-pairs of early and late seral tree species from the same habitat, and (b) to compare within-population genetic variability, both in growth traits and in competitive ability, between the same population pairs.

Grime (1973) defined plant competition as the tendency of neighbors to utilize the same light, nutrient ions, water molecules, or spatial volume. In addition to direct preemption of resources, competition may occur indirectly as in allelopathic interactions (Harper, 1977). Early and later seral species encounter very different competitive environments. Lewontin (1965) suggested that competitive relations throughout a successional sequence shifted from interspecific to more intraspecific and back again. It is likely that during seedling establishment early seral species face, on the average, more variable physical environments than later seral species (Bazzaz, 1979). Fire, which has been the primary disturbance agent in most North American temperate and boreal forests, usually leaves a mosaic of soil environments ranging from relatively undisturbed duff to bare rock. The pioneer seedling may encounter competition from either conspecifics or individuals of other early seral species; or it may have to deal primarily with abiotic factors such as high radiant heat loss.

Pioneers which occupy relatively mesic environments will likely face high levels of light competition, while those occupying harsh environments will have evolved to deal with water and nutrient competition, and with extremes in the abiotic environment.

Late seral seedlings, in contrast, face a high level of pre-established competition and a relatively uniform abiotic environment. Establishment does not involve a race to preempt space and resources or an ability to deal with variable physical environments so much as the capability of tolerating uniformly low resources and the ability to persist in an environment which is characterized by a relatively high degree of biological interaction.

In this chapter, I have attempted to investigate some of the effects of density and neighbor composition on the competitive ability of first-year seedlings from four conifer species of the Pacific Northwest.

MATERIAL AND METHODS

In the early fall of 1980 cones from individual trees were collected from natural stands of Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco] near Hebo, in the Oregon Coast Range, and noble fir [Abies procera Rehd.] and silver fir [Abies amabilis (Dougl.) Forbes] near Zig Zag, in the western central Oregon Cascades of the 4000-foot level. Because it was a bad seed-year for coastal western hemlock [Tsuga heterophylla (Raf.) Sarg.], seeds collected in 1975 from near Hebo, Oregon were used. The half-sib identity of the seeds was kept throughout the experiment. Seed extraction, stratification and germination procedures followed those described elsewhere (U.S. Department of Agriculture, Forest Service, 1974). Preliminary germination tests with western hemlock showed values for most families around 100% while Douglas-fir families averaged values around 50%. Dissection revealed true fir seeds to average 72% and 56% empty for noble fir and silver fir, respectively.

Germinated seeds with radicles more than 2 mm long and germination dates a maximum of two days apart were sowed in a cold frame--at the Forest Research Laboratory, OSU, Corvallis--starting in March of 1981. The soil of the cold frame consisted of a 50:50 mixture of forest topsoil and river loam. The number of half-sib families representing each species varied from 6 to 19 depending on the germination obtained as well as on the closeness of germination dates. The sowing spatial arrangement resembled a "replacement series" (Harper, 1977) in which there was a five-level gradient of plant-to-plant specific contacts. The five levels of neighbor composition involved only species-pairs from the same habitat (i.e., Douglas-fir-western hemlock; noble fir-silver fir). The cold frame was divided roughly in three parts, each part having a different initial density--mean distances between neighbor seedlings of 1.4, 2.8 and 5.6 cm were used resulting in an average growing space per seedling of 1, 4, 16 cm^2. Experimental units were randomly assigned within each third with each experimental unit (one observation in each of the five-level neighbor composition per family) replicated two to four times depending on availability of seeds. The neighbor composition gradient was arranged either in a fashion similar to that described in Figure II.1, or its inverse, so that "non-test" seedling numbers could be kept at a minimum. The implication of such restriction in randomization is discussed in the statistical procedures.

Seedlings were watered every third day and kept weed free. By the end of the sixteenth week after planting, the seedlings occupying the central position within each level of the experimental unit ("test" seedlings, Figure II.1) were carefully harvested. Measurements included dry weight of tops and roots. Leaf area, determined by the average of four readings of detached needles through a portable area meter (Li-COR model LI-3000) of 2 to 5 randomly chosen families of each coastal species within each density level was also measured. Because families were chosen randomly within each density level those sampled at one density were not necessarily the same as those sampled at another.

STATISTICAL PROCEDURES

Differences in seed viability and germination resulted in a high degree of variability in the representation of each species. The number of half-sib families sowed at high, medium, and low densities were (1) 16, 16 and 12 for Douglas-fir, (2) 19, 19 and 14 for western hemlock, (3) 6, 11 and 4 for noble fir, and (4) 6, 9 and 6 for silver fir, respectively. Except for the combinations involving high density of the two coastal species, which were replicated four times, all other combinations were replicated twice. Preliminary calculations of Bartlett's test (Snedecor and Cochran, 1980) revealed heterogeneity among some of the population variances. As a result, the statistical procedures were performed on log transformed weights of shoots and roots.

Because of the small number of available germinants only four half-sibling families in each *Abies* species were represented across all three density levels whereas both Douglas-fir and western hemlock had eleven families represented in all density levels. Because of high mortality among high-density silver fir germinants, analyses comparing both true fir species were limited to the medium and low densities. The missing data due to mortality required the use of unbalanced designs in which the computational procedures for estimation of missing cells, or subcells, leads to a reduction in the error term degrees of freedom. Percent mortality figures within each combination of species-density, accrued by each level of neighbor composition were compared by a χ^2 test (Fleiss, 1981).

The effects of density on each species-pair were analyzed according to the variance table depicted in Table II.1A on data yielded by intraspecifically grown seedlings. An unbalanced design was used with crossed and nested factors (all fixed). Each density level was an unreplicated block and the families were used as replications of species within each block. The effects of density upon individual species were analyzed through an unbalanced block design (Table II.1B) with fixed factors.

The effects of neighbor composition on each combination of species and density were investigated through an unbalanced split-plot design with fixed factors (Table II.1C); main plots were the half-sib families and sub-plots were neighbor composition level. Ranking of mean responses was executed by the Student-Newman-Keuls test for multiple comparison among means based on unequal sample sizes.

RESULTS

I. Mortality

Reduced growing space led to increased mortality in all four tree species, however the pattern differed between individual species and between the low- and high-elevation pairs (Figures II.2, II.3, II.4, II.5). Mortality of Douglas-fir and western hemlock seedlings tended to peak at the intermediate and high density levels (declines in average mortality at the high density levels were non-significant), while no significant seedling deaths occurred in noble and silver fir except at the highest density. Mortality of western hemlock seedlings never exceeded 15%, while that of silver fir ranged from 60 to 90% at the highest density level. Mortality of Douglas-fir and noble fir was intermediate, with maximum values of 35% and 48%, respectively.

In general, neighbor composition had no significant ($P > .05$) effect on mortality, however there were two exceptions (Table II.2). At the highest density level Douglas-fir mortality was highest (29%) when competing with conspecifics, while western hemlock mortality was highest (13%) when competing with heterospecifics. In other words, seedlings of either species had poorer survival when grown with Douglas-fir than when grown with western hemlock.

II. Seedling Growth

A. Intraspecific Competition

Douglas-fir and western hemlock were affected similarly by intraspecific competition, however in both species there was a great deal of family-level variation in growth response to density, particularly in shoot weight and shoot/root ratio (Table II.3A). In both species top growth of some families was affected little or not at all by density, while in others it was closely correlated with growing space (Figures II.6, II.7). In some families top growth increased sharply between the highest and the intermediate density, but either decreased or remained constant between the intermediate and the lowest density.

Western hemlock families ranged from 50 to slightly over 300 mg average seedling top weight at the lowest density, while Douglas-fir families varied from 100 to 900 mg. At the highest density family ranges were 5 to 100 mg in western hemlock and 5 to 300 mg in Douglas-fir, although ten of the eleven Douglas-fir families were below 180 mg.

Families were more consistent in their root growth density-response than in their top growth response tending to increase root growth in proportion to increasing growing space (although there were still family differences, particularly in western hemlock) (Figures II.8, II.9). This resulted in highly significant differences among families of both species in shoot/root ratio at different densities (Figures II.10, II.11).

Average shoot/root ratio of western hemlock families varied from .5 to 5.0 at the highest density and .4 to 4.4 at the lowest density. Families with low shoot/root ratios at the high density tended to have high ratios at the low density and vice versa. In

Douglas-fir families shoot/root ratios varied from .3 to 4.0 at the high density and .5 to 2.1 at the low density. As in western hemlock, there was considerable change in family ranking with change in density.

Western hemlock families were more diverse in their shoot and root weight response to density than Douglas-fir families (Tables II.4A, II.4B). Lack of statistical significance in the density X family interaction for Douglas-fir top weight seems to belie the patterns shown in Figure II.7, and is largely due to the high error mean square, which reflected, at least in part, genetic variability within families (Rehfeldt, 1978; Perry and Lotan, 1978).

Leaf area index (average seedling leaf area per unit of ground area) of Douglas-fir seedlings remained relatively constant between the low- and moderate-density levels (average 6.4), however, at the lowest density it declined to 2.8, indicating that seedlings had not fully utilized the available growing space (Table II.5, neighbor composition 5). In contrast, leaf area index of western hemlock seedlings was highest (2.5) at the moderate-density level, and did not differ between the high and the low densities (average .95). Thus, density stress reduced the efficiency with which western hemlock seedlings packed leaves within the available space. Note that Douglas-fir seedlings displayed two to six times more leaf area per unit growing space than western hemlock seedlings.

With the exception of shoot/root ratio, growth of the true fir species was little affected by density (Tables II.3B, II.4C, II.4D; Figures II.12, II.13). However, comparison with western hemlock and Douglas-fir is misleading, at least for silver fir, which responded to the highest density with very high mortality. If dead seedlings were entered into the growth analysis as zero weight, the density response of silver fir would be at least as strong as that of the two low elevation species. Top growth of silver fir families varied with respect to density ($P < .10$), but root growth did not, resulting, as in western hemlock and Douglas-fir, in a highly significant density X family interaction for shoot/root ratio. Noble fir families showed no differential response to density, however the small number of families tested precludes generalization of these results.

In contrast to the two low-elevation species, greatest range in seedling size among high-elevation families occurred at the moderate, rather than the lowest, density level. At that density shoot weight of silver fir seedlings varied from 10 to 190 mg, depending on family, and that of noble fir seedlings ranged from 90 to 250 mg. Thus, as in the case of western hemlock and Douglas-fir, the early successional species produced the greatest maximum seedling size, but there was a large amount of overlap among families, precluding generalization about differences between the species. Maximum shoot/root ratios of the two high-elevation species did not exceed 2.5, about one-half the maximum of the two low-elevation species.

In all species except noble fir, family variance in top weight (expressed as a percentage of total variance) increased with increasing density (Table II.6); i.e., competition magnified expression of genetic differences between families. In noble fir the opposite was true, the greatest expression of between-family genetic difference being at the level of least competition.

B. Neighbor Composition

The effects of neighbor composition on growth were relatively small compared to those of density. Composition affected Douglas-fir root weight at both medium and high density levels (Table II.7; Figure II.15). In the high density treatment Douglas-fir roots averaged 40 mg when seedlings were grown with a mixture of western hemlock and Douglas-fir, and 56 mg when neighbors were all one species or the other (Table II.11A). The pattern was similar but less clear in the medium density treatment. Shoot and root weight of western hemlock was affected by neighbor composition only at the highest density, where both decreased with an increasing proportion of Douglas-fir on the neighbor-mix (Tables II.8, II.11B; Figure II.14). Average shoot weight of western hemlock seedlings grown entirely with Douglas-fir was 76% of that of seedlings grown entirely with other western hemlock (36.9 and 48.4 mg, respectively); and average root weight was 64% (12.5 and 19.4 mg, respectively). Neighbor composition did not affect leaf area or leaf area index on Douglas-fir and western hemlock seedlings (Table II.12). Shoot/Root ratio of noble fir was affected by neighbor composition at the highest density, although no clear pattern was present (Tables II.9, II.11C). There was a significant family X composition interaction in shoot weight of noble fir at the lowest density, and significant family X composition interactions for shoot/root ratio of both coastal species at the high density. Silver fir was unaffected by neighbor composition (Table II.10). However, as before, the absence of silver fir data for the high-density treatment precludes a valid contrast with the other species, for which neighbor composition effects generally emerged only at the highest density.

DISCUSSION AND CONCLUSIONS

Cannell (1978, 1982) distinguishes between "competition," "crop" and "isolation" ideotypes in trees. The competition ideotype preempts growing space rapidly and competes intensely with neighbors, while the crop ideotype grows less rapidly during early development and is more tolerant of competition. The isolation ideotype has rapid early growth when grown at low densities, but performs relatively poorly at high densities. In effect, we hypothesized that populations of early seral tree species have evolved both a greater proportion of competitive ideotypes, but less genetic variability in ideotypes than late seral tree species. We detected considerable differences both within and among species; however, our hypotheses of general differences between early and late species were not supported.

While western hemlock was indeed more tolerant of competition (in terms of its mortality) than its early seral associate, Douglas-fir, the opposite was true of the silver fir-noble fir pair. Both early seral species grew faster than their later seral counterparts, however members of a pair did not grow differently in response to density. Variability within species, particularly in response to density, precluded generalization about differences between species. We believe that this within species variability is genetic in origin; however, although our study seed was collected from trees with no obvious environmental gradient between them, the possibility exists that it is at least partially due to differential environmental effects on developing seed--for example, seed weight. Maternal effects can influence seedling growth (Perry, 1976), however this phenomenon varies considerably among tree species (W. T. Adams, personal communication). Adams and Joly (1977) found that estimates of heritability in Pinus strobus varied from one year to the next and were related to seed weight. In contrast, D. A. Perry (unpublished) and C. Loopstra (unpublished) found little or no effect of seed weight on seedling performance in lodgepole pine and Douglas-fir, respectively.

Higher plants react to density stresses plastically; that is, by varying birth, growth, and death rates of their parts (Harper, 1977). Plasticity allows plants to avoid mortality at high densities by reducing growth (Harper and Gajic, 1961), with mortality occurring when plastic responses are no longer possible. In general, plant populations respond to density stress both plastically and with mortality (Raynal and Bazzaz, 1975).

We may also think of plastic response to decreasing density, i.e., the ability of an individual to take advantage of increasing space, but without forcing the issue by dominating its neighbors. Behavior of this type might be called "opportunistic," and corresponds to Cannell's (1982) "isolation" ideotype. Classification of families into "competitive," "crop," and "opportunistic" or "isolation" ideotype oversimplifies the patterns of density response seen in our study; however, it provides a useful context for discussing genetic differences in density response.

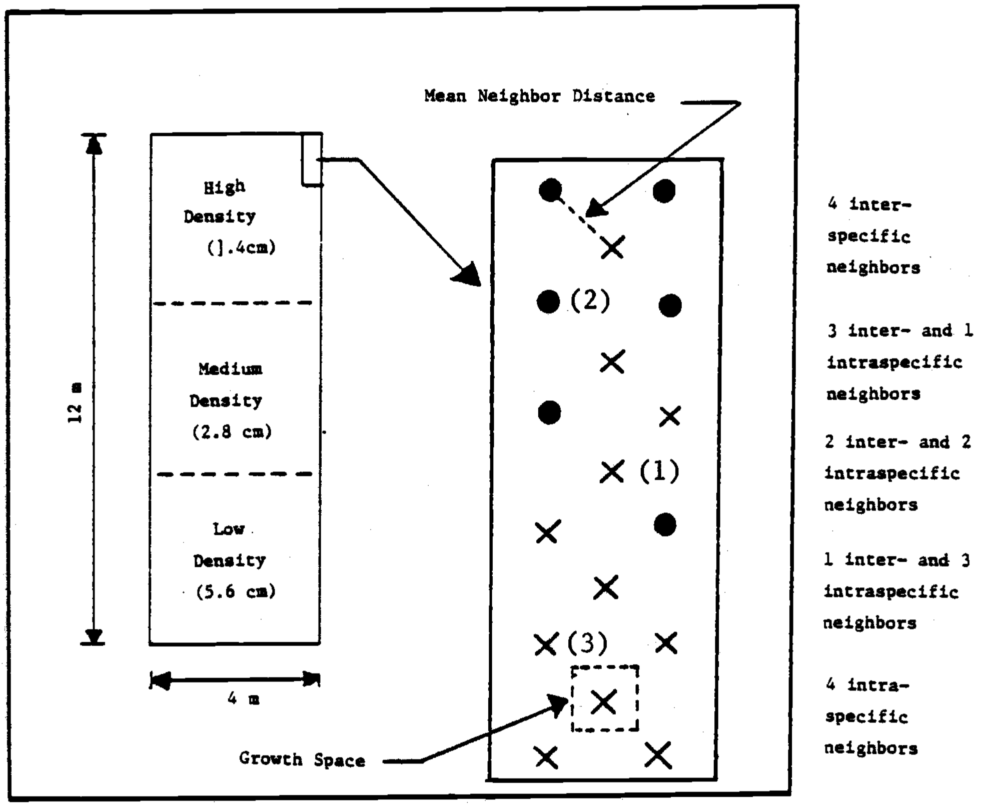
In western hemlock and noble fir, top growth differed among families in response to density. We assert that the same is true of Douglas-fir families, even though it was not statistically demonstrable, because of high genetic variation within families (the "error" component). Western hemlock family "Q" (Figure II.6) and Douglas-fir family "B" (Figure II.7) are examples of nonplastic-crop ideotypes, although at very high densities, because of non-plasticity, they may well behave like "competitive" ideotypes. In contrast, western hemlock family "V" and Douglas-fir families "F" and "D" are opportunistic ("isolation" ideotypes) producing relatively moderate or small-sized seedlings at the two higher densities, and larger seedlings at the lowest densities.

Only a few families (western hemlock "D" and "S", noble fir "3") produced relatively large individuals at both the low and the medium density levels (i.e., tending to a competitive ideotype). Interestingly, one to several families in each species grew better at moderate than at low densities, suggesting yet a fourth category of growth-density behavior, which might be termed "synergistic."

Root growth was quite different than shoot growth. There was no significant variation in root weight among families of either Douglas-fir, noble fir, or silver fir; nor did families within these species vary in their root growth response to density. In western hemlock, root growth variation among families and family x density interaction, though significant, was of lesser magnitude than variation in top growth. With a few exceptions, roots of all families were more plastic in response to density than shoots. This differential behavior between tops and roots resulted in significant family x density interactions for shoot/root ratio in all species except noble fir, where shoot/root ratios of families uniformly decreased with increased growing space. It cannot be concluded that noble fir differs from the other species in this respect, however, since four families are too few to allow generalization to the population level.

In Douglas-fir and western hemlock the greatest family variability in density response of shoot/root ratio was between the highest and the moderate density levels. With only two exceptions average shoot/root ratio of families of both species decreased between the moderate and the low density levels. Thus, for seedlings of these species, as for noble fir, root growth tends to be more "opportunistic"; i.e., better able to occupy increasing growing space than top growth. Change in the size ranking of genotypes with changes in density have been noted in a number of agricultural plants (reviewed by Cannell, 1982). This may be because of hormonal stimulation of top growth due to shading, although light effects upon physiological processes are numerous and often interrelated (Kramer and Kozlowski, 1979) at moderate density levels. Differential behavior of families at high densities could reflect genetic variation in sensitivity to this mechanism.

The relative insensitivity of all species to neighbor composition is surprising, especially in light of the size difference between members of a species-pair. Apparently for seedlings at this stage of development competition is determined more by neighbor density than by neighbor size.



(1) "Test" seedlings (species A)
(2) Competition seedlings (species B)
(3) Competition seedlings (species A)

Figure II.1. Density blocks within the cold frame with detail of an experimental unit depicting the 5-level gradient of neighbor composition.

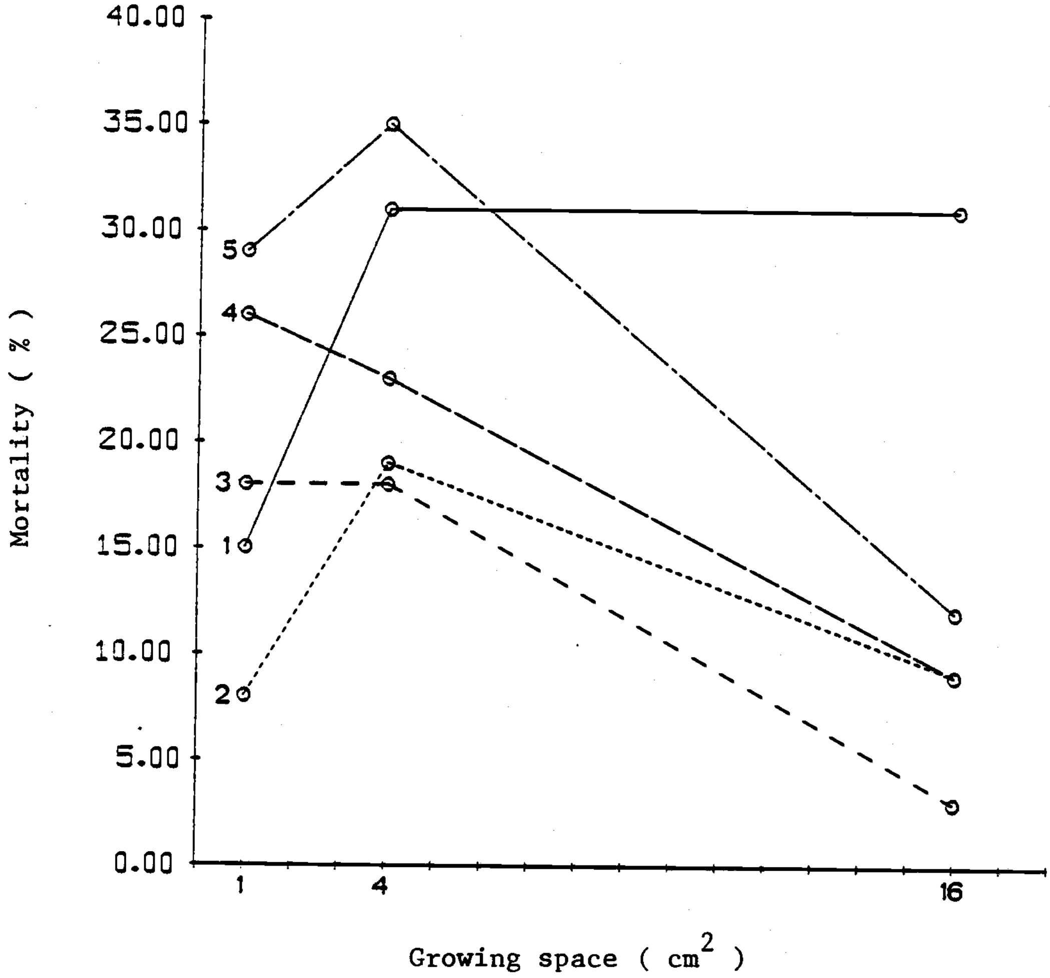


Figure II.2. Mortality of Douglas-fir seedlings as a function of growing space and level of neighbor composition.

Level 1 = 4 interspecific neighbors
Level 2 = 3 interspecific and 1 intraspecific neighbors
Level 3 = 2 interspecific and 2 intraspecific neighbors
Level 4 = 1 interspecific and 3 intraspecific neighbors
Level 5 = 4 intraspecific neighbors

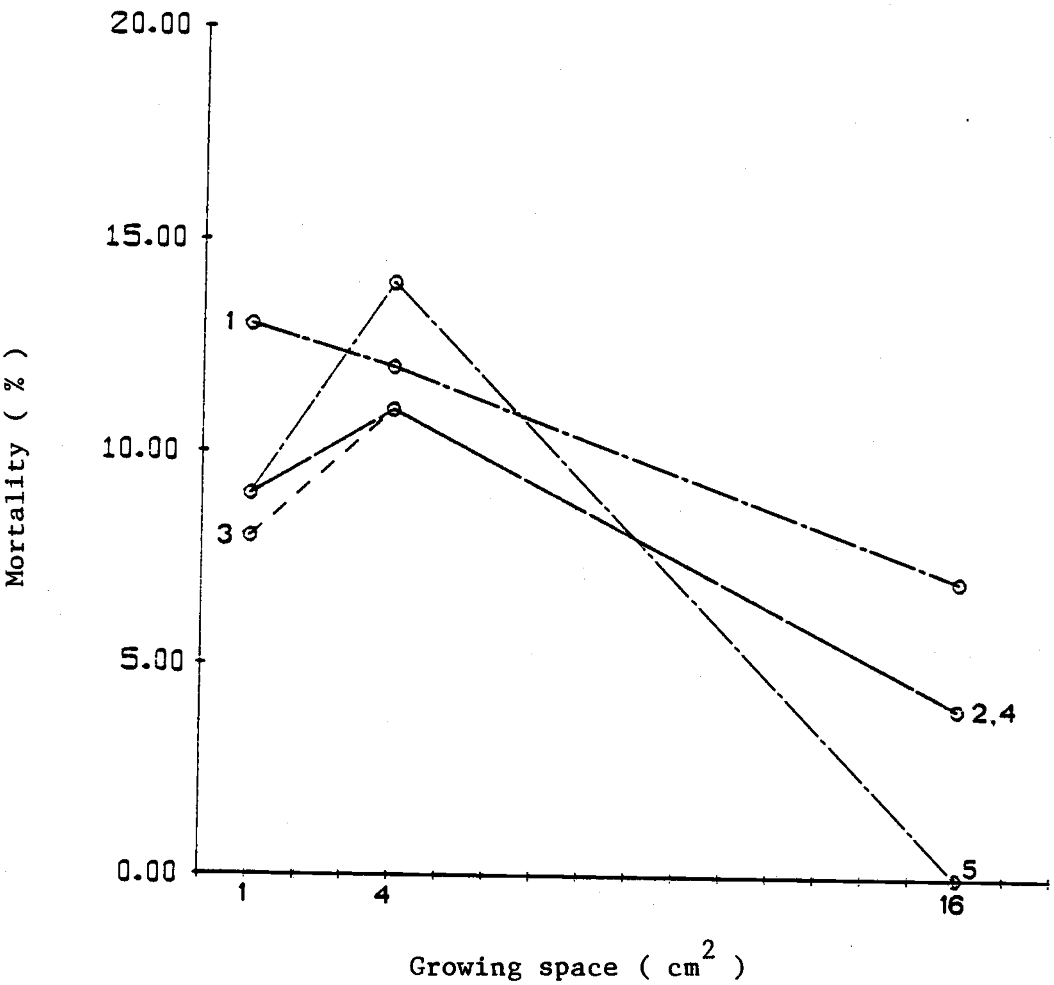


Figure II.3. Mortality of western hemlock seedlings as a function of growing space and level of neighbor composition.

Level 1 = 4 interspecific neighbors
Level 2 = 3 interspecific and 1 intraspecific neighbors
Level 3 = 2 interspecific and 2 intraspecific neighbors
Level 4 = 1 interspecific and 3 intraspecific neighbors
Level 5 = 4 intraspecific neighbors

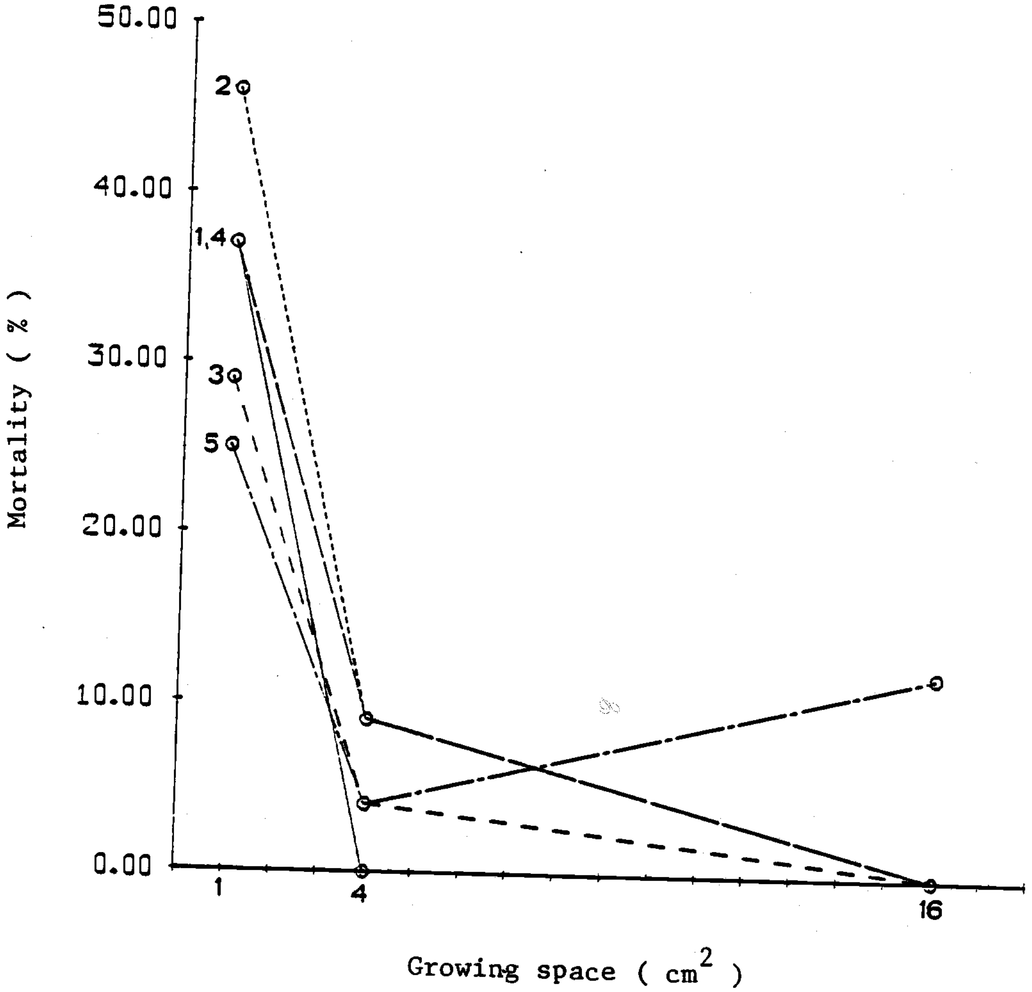


Figure II.4. Mortality of noble fir seedlings as a function of growing space and level of neighbor composition.

Level 1 = 4 interspecific neighbors
Level 2 = 3 interspecific and 1 intraspecific neighbors
Level 3 = 2 interspecific and 2 intraspecific neighbors
Level 4 = 1 interspecific and 3 intraspecific neighbors
Level 5 = 4 intraspecific neighbors

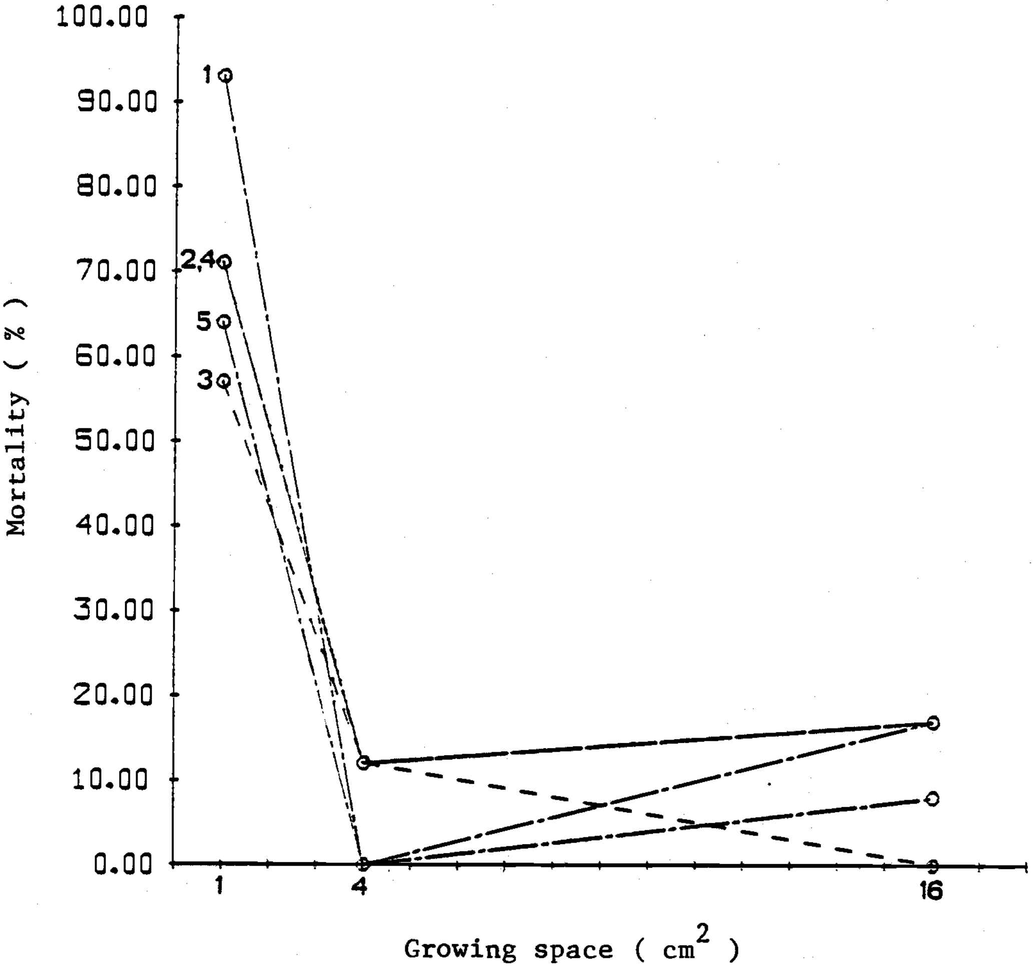


Figure II.5. Mortality of silver fir seedlings as a function of growing space and level of neighbor composition.

Level 1 = 4 interspecific neighbors
Level 2 = 3 interspecific and 1 intraspecific neighbors
Level 3 = 2 interspecific and 2 intraspecific neighbors
Level 4 = 1 interspecific and 3 intraspecific neighbors
Level 5 = 4 intraspecific neighbors

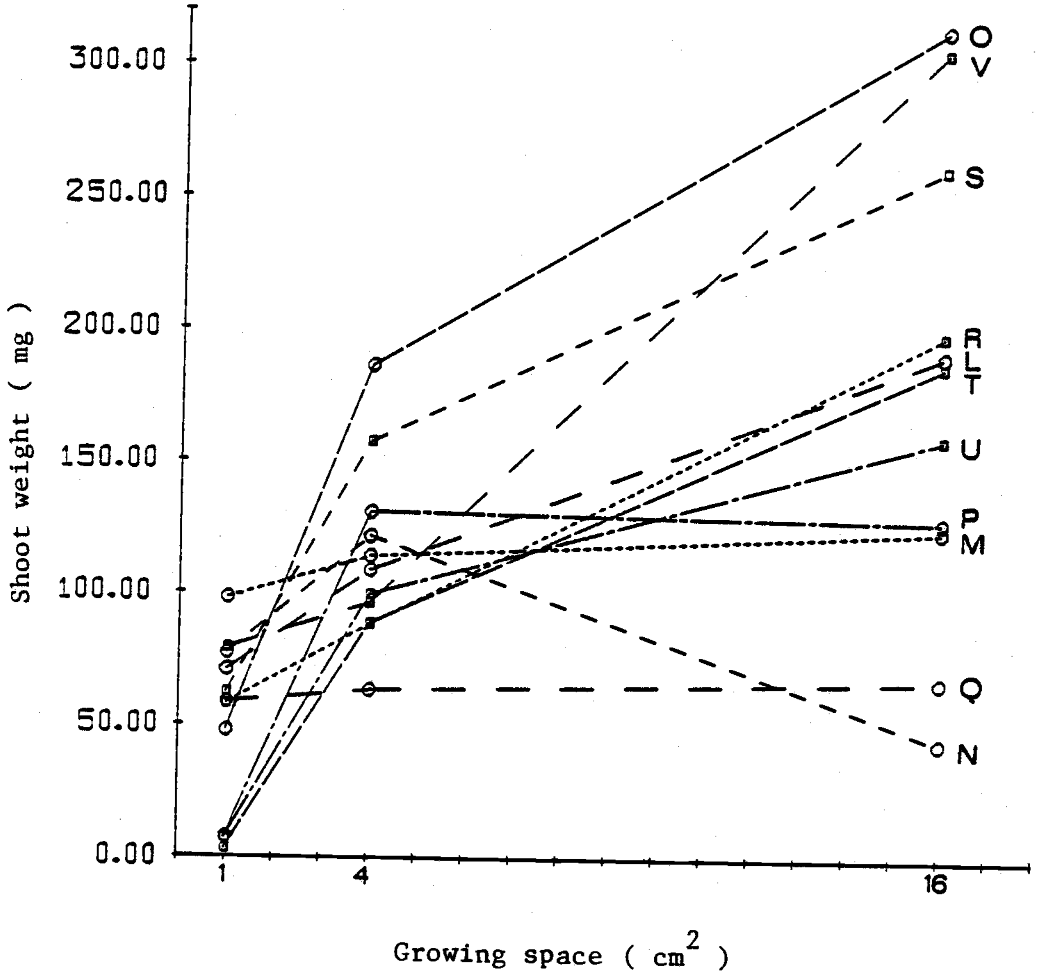


Figure II.6. Average shoot dry weights of intraspecifically grown western hemlock seedlings from eleven half-sib families under 3 densities. Letters identify individual families.

$S_{\overline{X}} = 0.43\ \overline{X}$ (for log transformed data)

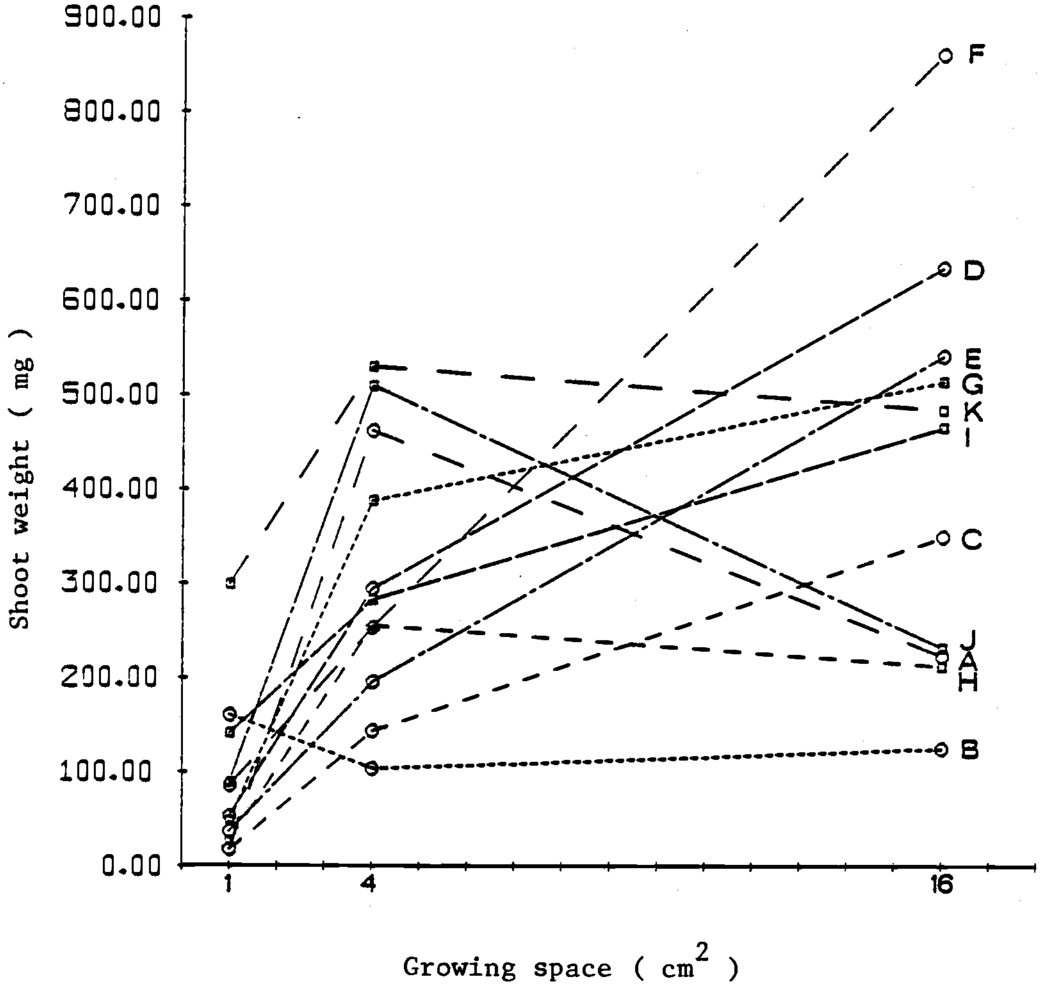


Figure II.7. Average shoot dry weights of intraspecifically grown Douglas-fir seedlings from eleven half-sib families under 3 densities. Letters identify individual families.

$S_{\overline{X}} = 0.71\ \overline{X}$ (for log transformed data)

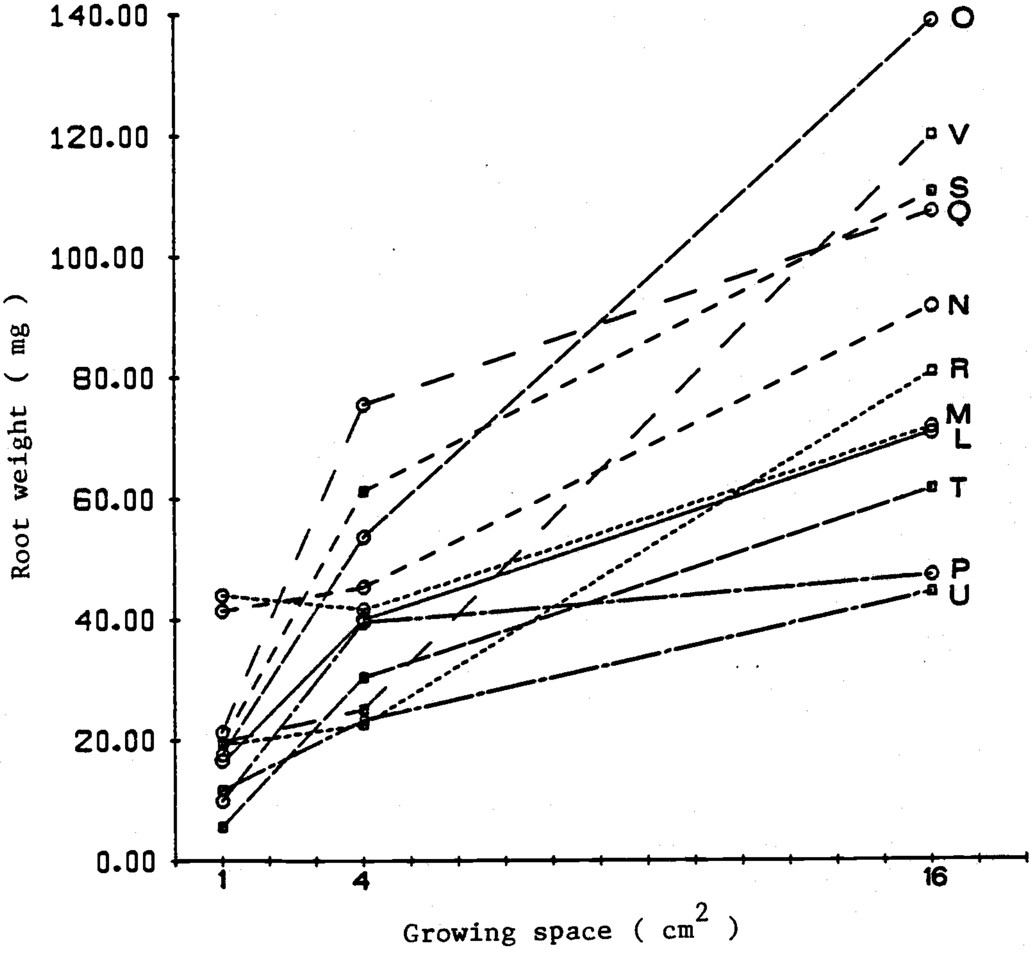


Figure II.8. Average root dry weights of intraspecifically grown western hemlock seedlings from eleven half-sib families under 3 densities. Letters identify individual families.

$S_{\overline{X}} = 0.46\ \overline{X}$ (for log transformed data)

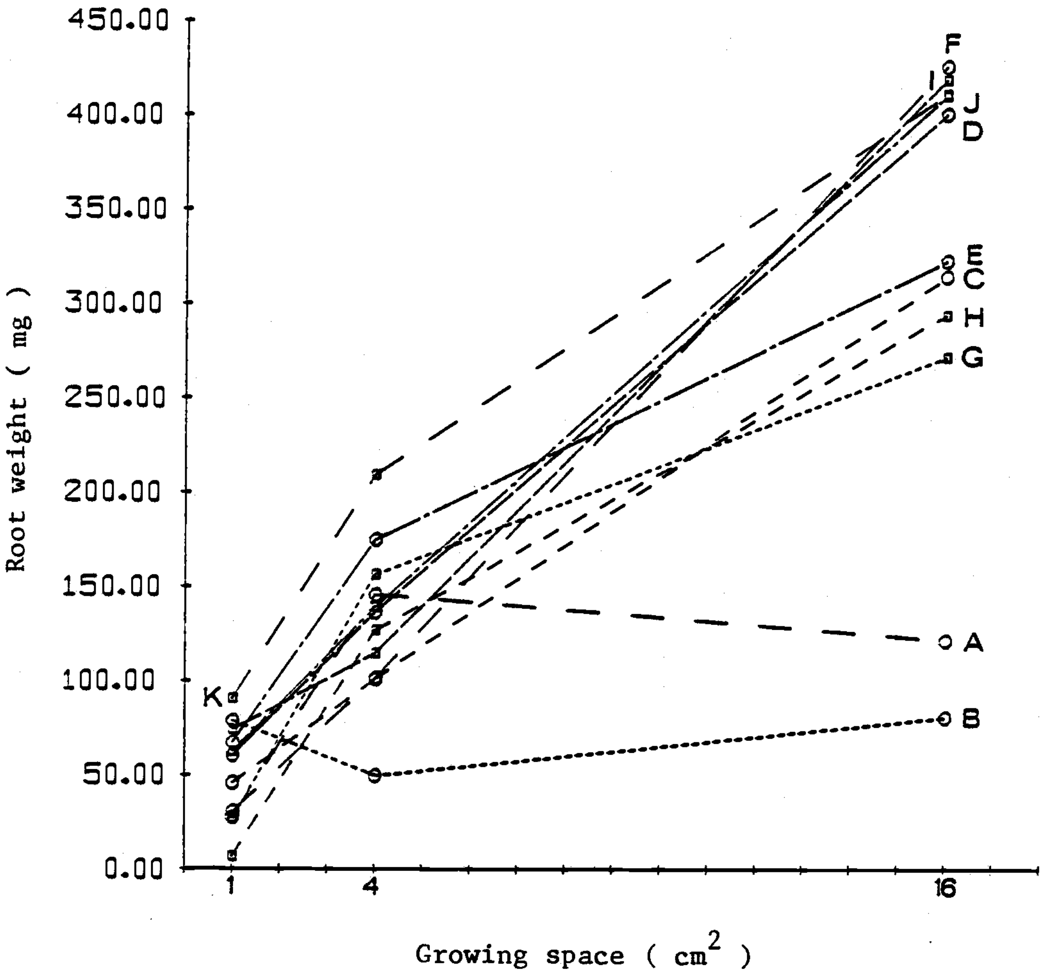


Figure II.9. Average root dry weights of intraspecifically grown Douglas-fir seedlings from eleven half-sib families under 3 densities. Letters identify individual families.

$S_{\overline{X}} = 0.54\ \overline{X}$ (for log transformed data)

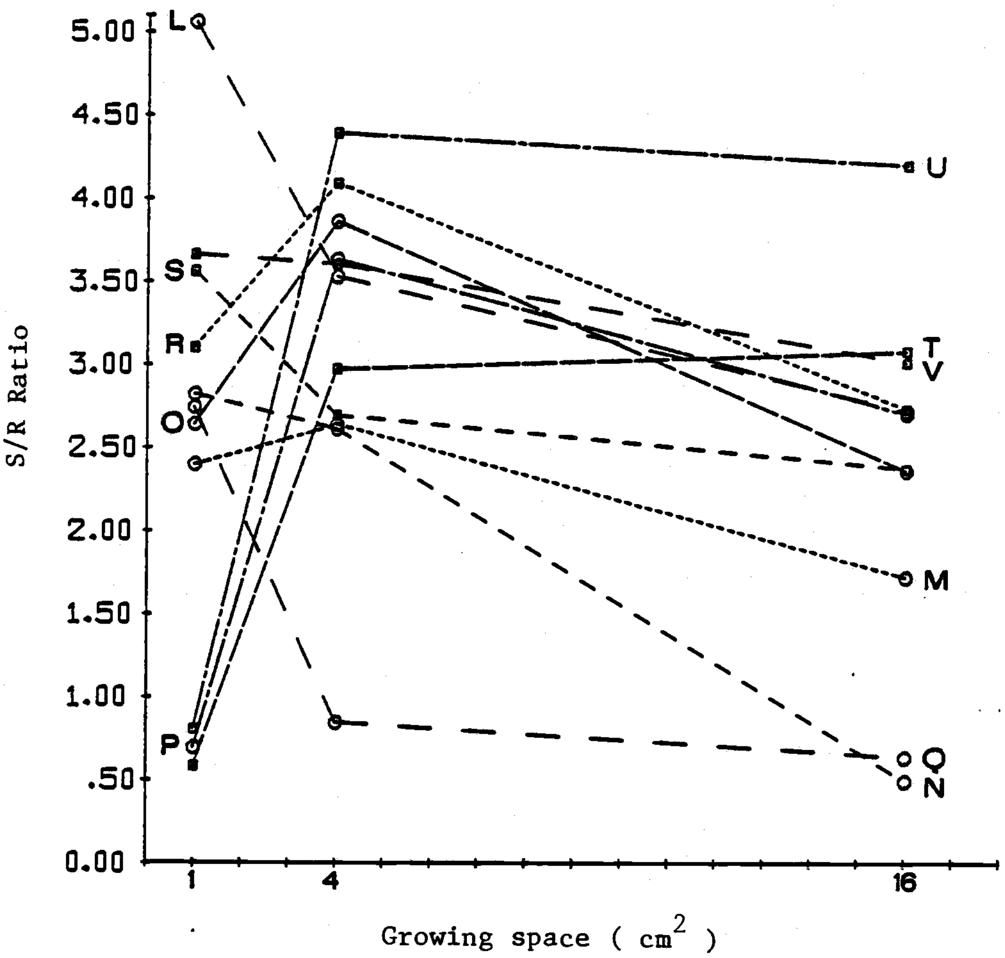


Figure II.10. Average shoot/root ratio (weight basis) of intraspecifically grown western hemlock seedlings from eleven half-sib families under 3 densities. Letters identify individual families.

$S_{\overline{X}} = 0.84\ \overline{X}$

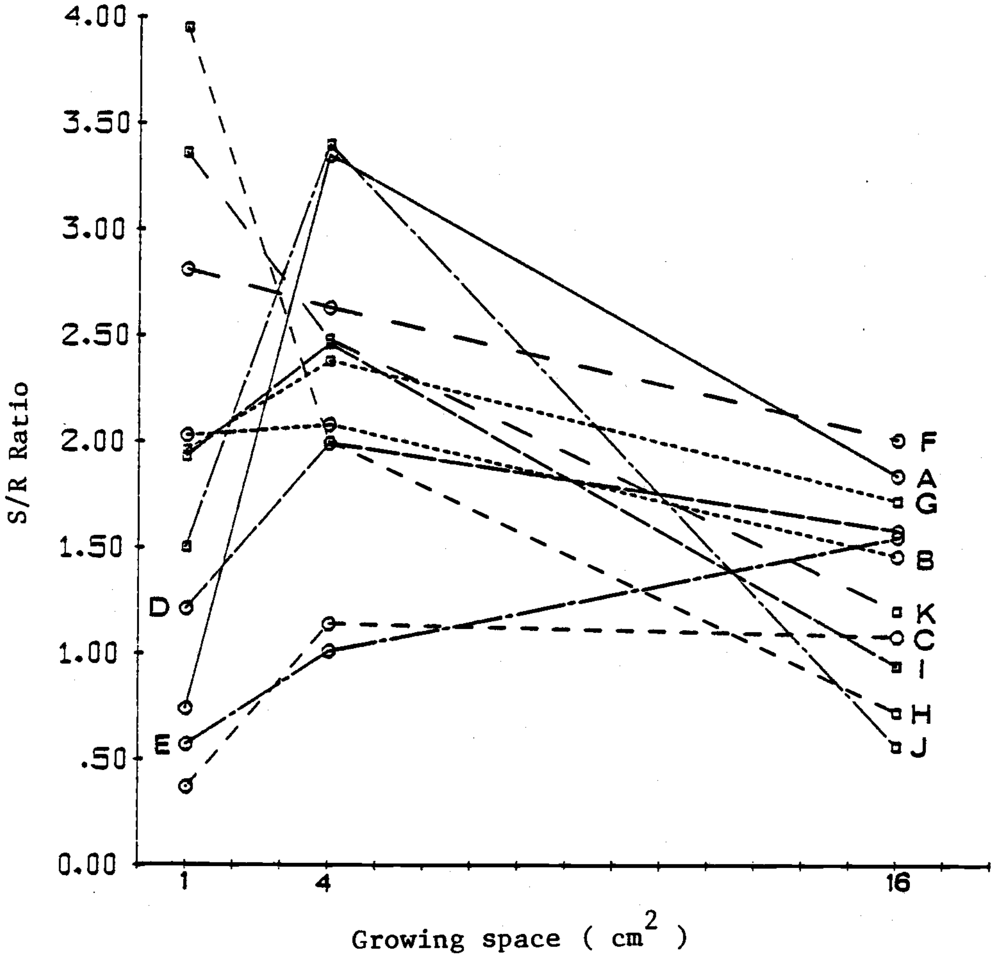


Figure II.11. Average shoot/root ratio (weight basis) of intraspecifically grown Douglas-fir seedlings from eleven half-sib families under 3 densities. Letters identify individual families.

$S_{\overline{X}} = 0.6\ \overline{X}$

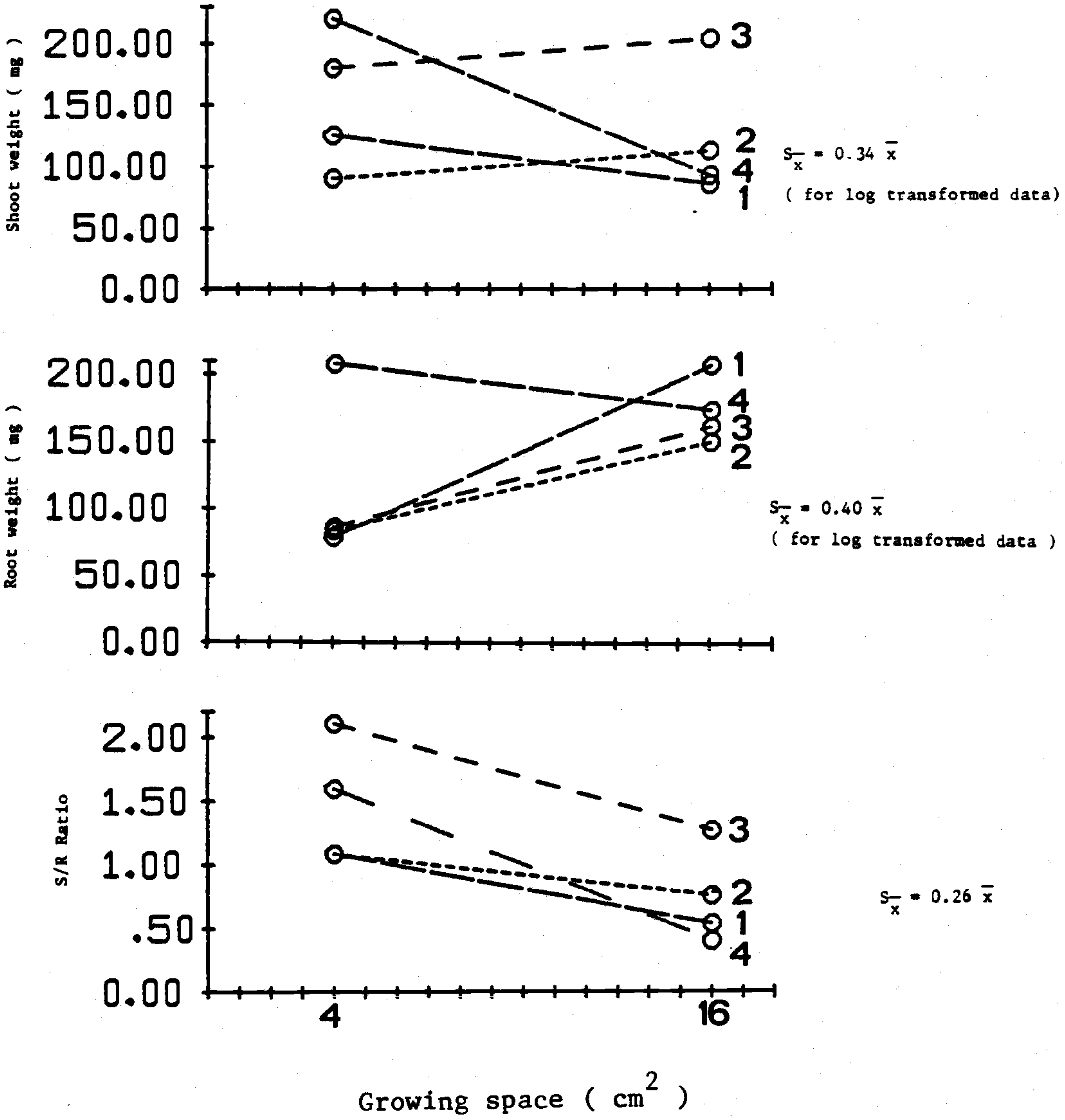


Figure II.12. Average shoot weight, root weight and shoot/root ratio of intraspecifically grown noble fir seedlings from four half-sib families under 3 densities. Numbers identify individual families.

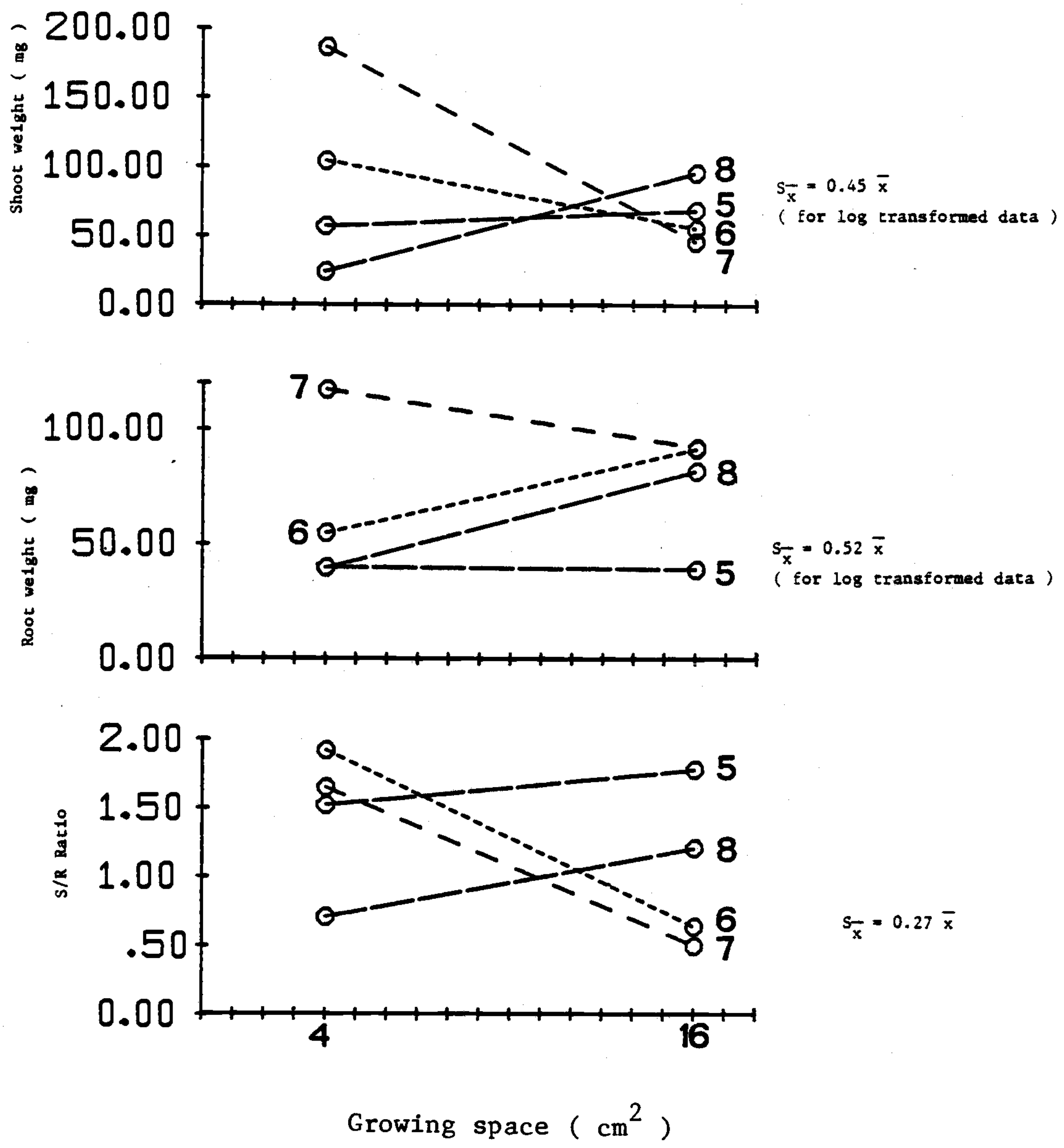


Figure II.13. Average shoot weight, root weight and shoot/root ratio of intraspecifically grown silver fir seedlings from four half-sib families under 3 densities. Numbers identify individual families.

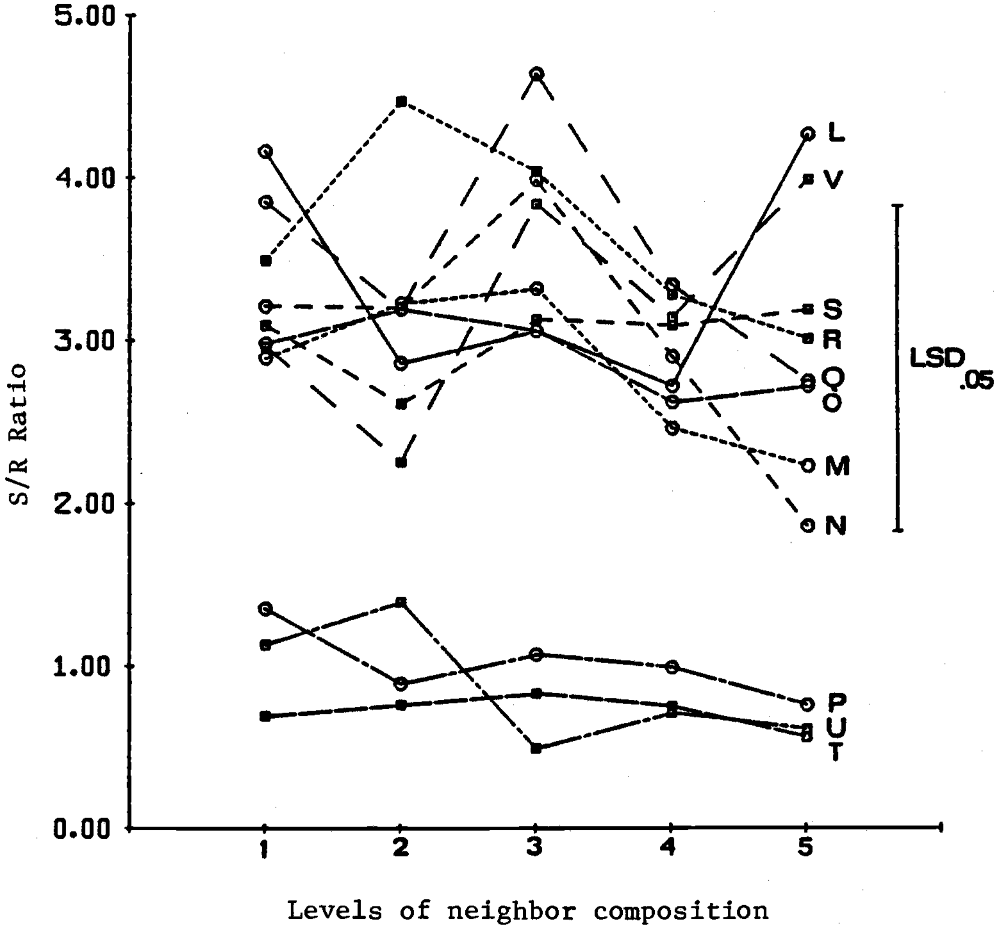


Figure II. 14. Average shoot/root ratio of western hemlock seedlings grown at high density under 5 levels of neighbor composition. Letters identify individual families. Vertical bar represents LSD $_{.05}$ for levels within a family.

Level 1 = 4 interspecific neighbors
Level 2 = 3 interspecific and 1 intraspecific neighbors
Level 3 = 2 interspecific and 2 intraspecific neighbors
Level 4 = 1 interspecific and 3 intraspecific neighbors
Level 5 = 4 intraspecific neighbors

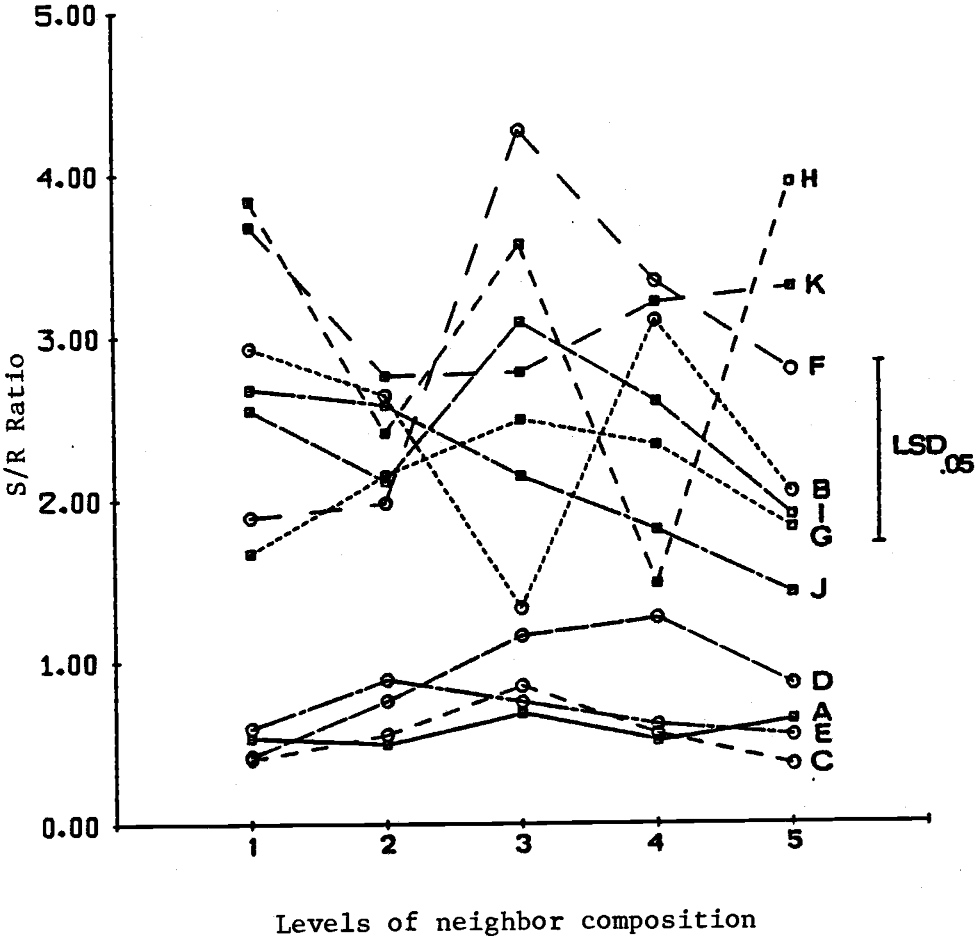


Figure II. 15 . Average shoot/root ratio of Douglas-fir seedlings grown at high density under 5 levels of neighbor composition. Letters identify individual families. Vertical bar represents LSD $_{.05}$ for levels within a family.

Level 1 = 4 interspecific neighbors
Level 2 = 3 interspecific and 1 intraspecific neighbors
Level 3 = 2 interspecific and 2 intraspecific neighbors
Level 4 = 1 interspecific and 3 intraspecific neighbors
Level 5 = 4 intraspecific neighbors

Table II.1. Analysis of variance tables with expected mean squares (EMS) used for analyses of density effects on each species pair (A), density effects on each species (B), and neighbor composition effects on each density-species composition (C).

Source of variation	EMS
(A)	
Density (Den)	sfRz σ^2 Den + σ^2
Species (Spp)	dfRz σ^2 Spp + dz σ^2 Rep x f/spp + σ^2
Families within species (f/spp)	dRz σ^2 f/spp + dz σ^2 Rep x f/spp + σ^2
Rep x f/spp	dz σ^2 Rep x f/spp + σ^2
Den x Spp	fRz σ^2 Den x Spp + σ^2
Den x f/spp	Rz σ^2 Den x f/spp + σ^2
Error	σ^2
(B)	
Density (Den)	fz σ^2 Den + σ^2
Families (Fam)	dz σ^2 Fam + σ^2
Den x Fam	z σ^2 Den x Fam + σ^2
Error	σ^2
(C)	
Rep	jklmg σ^2 Rep + lmg σ^2 Rep x Fam + σ^2
Families (Fam)	iklmg σ^2 Fam + lmg σ^2 Rep x Fam + σ^2
Rep x Fam	lmg σ^2 Rep x Fam + σ^2
Composition (Comp)	ijkmg σ^2 Comp + ijkg σ^2 Rep x Comp + σ^2
Rep x Comp	ijkg σ^2 Rep x Comp + σ^2
Fam x Comp	ikmg σ^2 Fam x Comp + σ^2
Error	σ^2

d = number of density levels
s = number of species
f = number of families
R = number of replications
z = random error within each family-density combination
i = number of replications
j = number of families
k = random error within levels of family.
l = composition levels
m = random error within levels of composition.
g = random error within levels of composition in each family.

Table II.2. Chi-square values for percent mortality among the 5 level gradient of neighbor composition.

Species	Growing Space (cm^2) 1	 4	 16
Douglas-fir	15.70**	6.50	3.20
Western hemlock	2257.00**	1.20	.60
Noble fir	2.80	.70	0
Silver fir	4.50	0	6.50

* $P < .05$
** $P < .01$

Table II.3. Mean squares for some growth parameters of seedlings from Douglas-fir - western hemlock (A) and noble fir-silver fir (B) species-pair grown intraspecifically under 3 and 2 densities.

A)

Source of Variation	Df	Shoot Weight	Root Weight	S/R Ratio
Density (Den)	2	23.382**	24.094**	5.779**
Species (Spp)	1	11.469**	33.009**	24.671**
Families within SPP (F/Spp)	20	1.199**	0.845*	1.958**
Rep x F/spp	22	0.353	0.348	0.480
Den x Spp	2	0.451	0.651	0.384
Den x F/spp	37	1.008*	0.355	1.809*
Error	31	0.424	0.437	0.767

B)

Source of Variation	Df	Shoot Weight	Root Weight	S/R Ratio
Density (Den)	1	0.094	1.393	2.521**
Species (Spp)	1	4.021**	5.412**	0.435*
Families within Spp (F/Spp)	6	0.254	0.287	0.522**
Rep x F/Spp	7	0.320	0.463	0.073
Den x Spp	1	0.133	0.017	0.214
Den x F/Spp	6	0.590	0.152	0.485*
Error	7	0.275	0.254	0.085

* $P < .05$
** $P < .01$

Table II.4. Mean squares for some growth parameters of Douglas-fir (A), western hemlock (B), noble fir (C) and silver fir (D) seedlings grown under different densities.

Source of Variation	DF	Shoot Weight	Root Weight	S/R Ratio	DF	Leaf Area	LAI
A)							
Density (D)	2	21.71***	26.62***	3.79***	2	2477**	4.0×10^{-3}**
Family (F)	16	2.08***	0.63	2.42***	8	198	3.0×10^{-3}
D x F	25	1.26	0.59	1.89***	2	25	6.0×10^{-4}
Error	74	0.76	0.44	0.54	25	282	1.6×10^{-3}
B)							
D	2	37.24***	31.23**	2.20	2	478**	1.0×10^{-3}***
F	19	2.11***	1.39**	5.03***	8	10**	1.2×10^{-4}*
D x F	30	2.16***	0.55*	4.79***	0		
Error	112	0.28	0.32	1.06	26	4	5.6×10^{-5}
C)							
D	2	0.15	0.48	1.47***			
F	12	0.52**	0.21	0.61***			
D x F	5	0.15	0.18	0.21			
Error	17	0.17	0.24	0.10			
D)							
D	1	0.17	1.15	0.54**			
F	8	0.20	0.48	0.40**			
D x F	4	0.84*	0.09	0.68***			
Error	13	0.31	0.40	0.11			

* $P < .10$
** $P < .05$
*** $P < .01$

LAI = Leaf Area Index

Table II.5. Mean leaf area index (standard error of the mean) for Douglas-fir and western hemlock seedlings as a function of growing space and neighbor composition. Leaf area index is defined, within each row (density comparisons), as total seedling leaf area per unit growing space. Means followed by the same letter are not different ($P > .05$). There are no significant differences among neighbor composition levels.

Species	Neighbor Composition Level	Growing Space (cm^2) 1	4	16
Douglas-fir	1	6.9^{a} (1.1)	7.9^{a} (1.4)	1.7^{a} (0.4)
	2	5.3^{a} (1.1)	7.0^{a} (1.4)	2.7^{a} (0.4)
	3	5.3^{a} (1.2)	5.8^{a} (0.6)	2.5^{a} (0.4)
	4	5.8^{a} (0.9)	$5.2^{a,b}$ (1.1)	2.7^{a} (0.4)
	5	7.3^{a} (1.1)	$5.4^{a,b}$ (1.2)	2.8^{b} (0.5)
Western hemlock	1	1.2^{a} (0.2)	2.4^{b} (0.2)	0.4^{a} (0.7)
	2	$1.2^{a,b}$ (0.2)	1.8^{a} (0.2)	0.4^{b} (0.09)
	3	0.9^{a} (0.1)	2.3^{b} (0.2)	0.7^{a} (0.1)
	4	1.8^{a} (0.3)	2.6^{a} (0.3)	0.8^{b} (0.08)
	5	1.1^{a} (0.2)	2.5^{b} (0.2)	0.8^{a} (0.1)

Level 1 = 4 interspecific neighbors
Level 2 = 3 interspecific and 1 intraspecific neighbors
Level 3 = 2 interspecific and 2 intraspecific neighbors
Level 4 = 1 interspecific and 3 intraspecific neighbors
Level 5 = 4 intraspecific neighbors

Table II.6. Within-species (between families) variance components as percentage of total variation (calculated from ANOVAs given in Tables II.7, II.8, II.9, II.10).

Species	G.S.	Shoot Weight	Root Weight
Douglas-fir	1	54.2	15.0
	4	19.6	4.0
	16	8.5	21.3
Western hemlock	1	75.0	36.9
	4	35.9	21.2
	16	47.5	22.3
Noble fir	1	14.7	0
	4	52.3	18.1
	16	63.7	9.2
Silver fir	4	53.7	23.9
	16	12.6	37.3

G.S. = growth space (cm^2)

Table II.7. Mean squares for some growth parameters due to neighbor composition effects for Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] seedlings grown at high (A), medium (B), and low (C) densities.

A)

Source of Variation	DF	Shoot Weight	Root Weight	S/R Ratio
Block (Rep)	3	1.626*	1.148	0.715
Family (Fam)	15	11.949**	2.059**	13.054**
Rep x Fam	45	0.414	0.406	0.647
Composition (Comp)	4	0.691	1.362*	0.983
Rep x Comp	12	0.529	0.342	0.551
Fam x Comp	60	0.581	0.505	1.185*
Error	141	0.423	0.422	0.758

B)

Source of Variation	DF	Shoot Weight	Root Weight	S/R Ratio
Block (Rep)	3	0.469	0.363	1.149
Family (Fam)	15	4.466**	0.808	7.596**
Rep x Fam	45	0.803	0.428	0.839
Composition (Comp)	4	1.286	1.484*	0.370
Rep x Comp	12	0.673	0.411	0.923
Fam x Comp	59	0.787	0.513	0.851
Error	114	0.702	0.406	0.619

C)

Source of Variation	DF	Shoot Weight	Root Weight	S/R Ratio
Block (Rep)	1	0.018	0.004	0.017
Family (Fam)	11	1.023	1.481*	2.685**
Rep x Fam	11	0.442	0.293	0.489
Composition (Comp)	4	0.624	0.550	0.183
Rep x Comp	4	0.763	0.479	0.453
Fam x Comp	44	0.700	0.506	0.393
Error	35	0.512	0.345	0.413

* $P < 0.05$
** $P < 0.01$

Table II.8. Mean squares for some growth parameters due to neighbor composition effects for western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] seedlings grown at high (A), medium (B), and low (C) densities.

A)

Source of Variation	DF	Shoot Weight	Root Weight	S/R Ratio
Block (Rep)	3	0.059	0.904	3.732
Family (Fam)	18	16.194**	4.494**	22.394**
Rep x Fam	54	0.307	0.375	1.289
Composition (Comp)	4	0.941**	1.928**	2.802
Rep x Comp	12	0.165	0.115	1.686
Fam x Comp	72	0.284	0.408	2.049*
Error	177	0.221	0.264	1.413

B)

Source of Variation	DF	Shoot Weight	Root Weight	S/R Ratio
Block (Rep)	3	0.431	0.187	1.074
Family (Fam)	18	4.043**	2.487**	25.802**
Rep x Fam	54	0.413	0.541	1.059
Composition (Comp)	4	0.644	0.383	1.476
Rep x Comp	12	0.234	0.298	0.599
Fam x Comp	72	0.271	0.314	1.138
Error	173	0.293	0.315	1.155

C)

Source of Variation	DF	Shoot Weight	Root Weight	S/R Ratio
Block (Rep)	1	0.695	0.202	0.131
Family (Fam)	13	2.452**	0.929**	7.686**
Rep x Fam	13	0.218	0.169	1.140
Composition (Comp)	4	0.676	0.775	0.175
Rep x Comp	4	0.305	0.246	0.265
Fam x Comp	52	0.238	0.189	0.514
Error	47	0.185	0.245	0.646

* $P < 0.05$
** $P < 0.01$

Table II.9. Mean squares for some growth parameters due to neighbor composition effects for noble fir (*Abies procera* Redh.) seedlings grown at high (A), medium (B), and low (C) densities.

A)

Source of Variation	DF	Shoot Weight	Root Weight	S/R Ratio
Block (Rep)	1	0.651	0.642	0.267
Family (Fam)	5	1.244	0.882	6.605
Rep x Fam	5	0.405	1.117	1.374
Composition (Comp)	4	0.098	0.346	2.139*
Rep x Comp	4	0.202	0.219	0.263
Fam x Comp	20	0.384	0.681	1.182
Error	14	0.479	0.555	0.876

B)

Source of Variation	DF	Shoot Weight	Root Weight	S/R Ratio
Block (Rep)	1	0.691**	0.131	0.649
Family (Fam)	10	1.695**	0.574**	1.569**
Rep x Fam	10	0.058	0.078	0.290
Composition (Comp)	4	0.159	0.344	0.280
Rep x Comp	4	0.087	0.192	0.585
Fam x Comp	40	0.232	0.232	0.224
Error	31	0.095	0.202	0.184

C)

Source of Variation	DF	Shoot Weight	Root Weight	S/R Ratio
Block (Rep)	1	0.163	0.397	0.018
Family (Fam)	3	2.730*	0.444	1.249*
Rep x Fam	3	0.208	0.222	0.059
Composition (Comp)	4	0.064	0.158	0.018
Rep x Comp	4	0.144	0.192	0.343
Fam x Comp	12	0.130**	0.180	0.038
Error	11	0.023	0.206	0.059

* $P < 0.05$

** $P < 0.01$

Table II.10. Mean squares for some growth parameters due to neighbor composition effects for silver fir [*Abies amabilis* (Dougl.) Forbes] seedlings grown at medium (A) and low (B) densities.

A)

Source of Variation	DF	Shoot Weight	Root Weight	S/R Ratio
Block (Rep)	1	0.065	0.384	0.099
Family (Fam)	8	3.175**	1.650*	2.545**
Rep x Fam	8	0.220	0.419	0.294
Composition (Comp)	4	0.176	0.119	0.228
Rep x Comp	4	0.388	0.345	0.313
Fam x Comp	32	0.223	0.337	0.357
Error	27	0.238	0.385	0.421

B)

Source of Variation	DF	Shoot Weight	Root Weight	S/R Ratio
Block (Rep)	1	0.041	0.001	0.041
Family (Fam)	5	0.287	1.166*	1.798*
Rep x Fam	5	0.109	0.152	0.049
Composition (Comp)	4	0.100	0.192	0.022
Rep x Comp	4	0.250	0.382	0.045
Fam x Comp	20	0.081	0.124	0.096
Error	13	0.090	0.107	0.053

* $P < 0.05$
** $P < 0.01$

Table II.11. Pairwise comparison of mean dry weights in Douglas-fir seedlings (A), in western hemlock seedlings (B), and in noble fir seedlings (C) according to ANOVA results (Tables II.7, II.8, II.9).

A)

Trait	Density	Neighbor Composition Level 1	2	3	4	5
Root Weight (mg)	High	58.77^{a}	$49.74^{a,c}$	$39.88^{b,c}$	38.87^{b}	53.17^{a}
Root Weight (mg)	Medium	$158.88^{a,b}$	160.51^{b}	$136.74^{a,b}$	117.31^{a}	$126.15^{a,b}$

B)

Trait	Density	Neighbor Composition Level 1	2	3	4	5
Root Weight (mg)	High	12.49^{a}	$15.47^{a,b}$	13.51^{a}	16.28^{b}	19.44^{b}
Shoot Weight (mg)	High	36.90^{a}	40.22^{a}	$40.92^{a,b}$	41.73^{b}	48.43^{b}

C)

Trait	Density	Neighbor Composition Level 1	2	3	4	5
S/R Ratio	High	$2.18^{a,b}$	2.59^{a}	$1.59^{a,b}$	$2.55^{a,b}$	1.56^{b}

Level 1 = 4 interspecific neighbors
Level 2 = 3 interspecific and 1 intraspecific neighbors
Level 3 = 2 interspecific and 2 intraspecific neighbors
Level 4 = 1 interspecific and 3 intraspecific neighbors
Level 5 = 4 intraspecific neighbors

Row means with similar superscripts do not differ ($P > .05$).

Table II.12. Mean squares for leaf area and leaf area index due to neighbor composition on Douglas-fir seedlings (A) and on western hemlock seedlings (B) grown at three densities. Initial growing space of 1(high), 4(medium), and 16(low) cm^2 per seedling.

A)

	Density								
	High			Medium			Low		
Source of Variation	Df	Leaf Area	LAI	Df	Leaf Area	LAI	Df	Leaf Area	LAI
Block (Rep)	3	7.24	$7.2\mathrm{x}10^{-4}$	3	580.38	$3.6\mathrm{x}10^{-3}$	1	230.41	$9.0\mathrm{x}10^{-5}$
Family (Fam)	4	98.56*	$9.7\mathrm{x}10^{-3}$*	4	288.64	$1.8\mathrm{x}10^{-3}$	2	2519.31*	$9.8\mathrm{x}10^{-4}$*
Rep x Fam	12	21.84	$2.2\mathrm{x}10^{-3}$	12	338.83	$2.3\mathrm{x}10^{-3}$	2	93.68	$3.7\mathrm{x}10^{-5}$
Composition (Comp)	4	17.60	$1.7\mathrm{x}10^{-3}$	4	369.25	$2.3\mathrm{x}10^{-3}$	4	66.03	$2.6\mathrm{x}10^{-5}$
Rep x Comp	12	21.57	$2.1\mathrm{x}10^{-3}$	12	295.04	$1.8\mathrm{x}10^{-3}$	4	685.44	$2.7\mathrm{x}10^{-4}$
Fam x Comp	13	12.18	$1.2\mathrm{x}10^{-3}$	15	411.77	$2.6\mathrm{x}10^{-3}$	8	224.05	$8.7\mathrm{x}10^{-5}$
Error	41	15.03	$1.5\mathrm{x}10^{-3}$	27	341.53	$2.0\mathrm{x}10^{-3}$	4	612.89	$1.9\mathrm{x}10^{-4}$

B)

	Density								
	High			Medium			Low		
Source of Variation	Df	Leaf Area	LAI	Df	Leaf Area	LAI	Df	Leaf Area	LAI
Block (Rep)	3	0.65	$6.5\mathrm{x}10^{-5}$	3	16.20	$1.0\mathrm{x}10^{-4}$	1	0.67	$2.6\mathrm{x}10^{-7}$
Family (Fam)	4	5.28**	$5.3\mathrm{x}10^{-4}$**	3	104.25*	$6.3\mathrm{x}10^{-4}$*	1	13.30	$5.2\mathrm{x}19^{-6}$
Rep x Fam	12	0.87	$8.7\mathrm{x}10^{-5}$	9	17.60	$1.1\mathrm{x}10^{-4}$	1	1.49	$5.8\mathrm{x}10^{-7}$
Composition (Comp)	4	1.07	$1.1\mathrm{x}10^{-4}$	4	35.22	$2.2\mathrm{x}10^{-4}$	4	45.36	$1.8\mathrm{x}10^{-3}$
Rep x Comp	12	0.48	$4.8\mathrm{x}10^{-5}$	12	18.43	$1.1\mathrm{x}10^{-4}$	4	16.42	$6.4\mathrm{x}10^{-6}$
Fam x Comp	14	0.71	$7.1\mathrm{x}10^{-5}$	12	16.53	$1.0\mathrm{x}10^{-4}$	4	17.14	$6.4\mathrm{x}10^{-6}$
Error	35	0.66	$6.4\mathrm{x}10^{-5}$	29	9.03	$5.4\mathrm{x}10^{-5}$	4	11.82	$4.6\mathrm{x}10^{-6}$

* $P < .05$ LAI = Leaf Area Index

** $P < .01$

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CHAPTER III

COMPARISONS OF CARBON ALLOCATION

INTRODUCTION

The way an organism allocates resources to growth, maintenance, reproduction and production of defensive structures and secondary substances will affect both its growth and its fitness. The timing, forms and amounts of these allocations represent the means by which plants react to their environment. Ledig (1969) has shown that an individual with higher allocation to aboveground structures (particularly leaf area) will outperform a second individual possessing a photosynthetic rate up to 40% higher. Decreased nutrient levels and plant competition reduced energy allocated to reproduction according to Snell and Burch (1975).

As pointed out by Larson (1969) the distribution of photosynthate within a tree should be viewed as a system of competing metabolic sinks (or areas of rapid growth) which draw and utilize photosynthate proportional to their degree of activity. The carbohydrate fraction of photosynthate makes up the largest contribution to the total and is often an important reserve component; carbohydrates provide the material for construction of cell wall and comprise 60% or more of the dry matter of higher plants. The products of photosynthesis, readily metabolizable carbohydrates are divided into soluble sugars and starch; the former is the translocated form, usually with a non-reducing end (i.e., sucrose, raffinose) while the latter occurs whenever a surplus of sugars builds up (Krammer and Kozlowski, 1979). During periods of growth, carbohydrates are usually depleted first rather close to the site of utilization. Hence, the pattern of depletion varies with growth of each plant part. Then, because each component grows not only at different times but also at different rates the utilization of carbohydrates is extremely variable throughout the tree (Kozlowski and Keller, 1966).

If carbohydrate movement is a function of meristematic activity, all factors influencing growth-related processes bear significantly on carbohydrate production, translocation and allocation. Wardlaw (1968) inferred that not only is the rate of photosynthesis reduced under low light but also is the proportion of assimilated carbon leaving the leaf. The accumulation of soluble carbohydrates in the stems of nitrogen-deficient plants indicates that photosynthesis and transfer of assimilates out of the leaf may be less affected by nitrogen deficiency than growth (Archbold and Mukerjee, 1942; Alberda, 1966).

The allocation of structural carbon to shoots and roots has been explained from a physiological or adaptive point of view. Brouwer (1966) explored the notion that there exists competition between the root and the shoot for limiting factors: the shoot produces its own carbohydrates but depends on the roots for water and mineral nutrients, whereas the root depends on carbohydrates from the shoot but has its own supply of water and nutrients. Troughton (1960) argued, on the other hand, that the flow of growth commodities between shoot and root is such that the overall performance of the plant is maintained at its highest level relative to the supplies of nutrients both organic (carbohydrates) and inorganic (minerals).

One additional aspect of carbohydate allocation may be significant for tree survival and vigor. Formation of mycorrhizae depends on numerous factors, some poorly understood; however, the level of carbohydrates in roots, particularly soluble sugars, seems important (Marx *et al.*, 1977). In situations in which nutrient cycling is relatively slow, such as cold habitats or late successional stages (Vitousek and Reiners, 1975; Van Cleve and Alexander, 1981), formation of mycorrhizae is especially important. Therefore, we might expect late successional and high elevation tree species to maintain a large proportion of starches and sugars in roots relative to early successional and mesic-site species (R. H. Waring, personal communication).

In this chapter, I have examined differences in the concentration of starch and sugar before, during, and after the second growing season of seedlings from four tree species. I have also examined allocation of starch and sugar to tops and roots, and how this is affected by shade and nitrogen fertilization.

MATERIAL AND METHODS

In the early fall of 1980, cones from individual trees were collected from natural stands of Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco] near Hebo, in the Oregon Coast Range, and noble fir [Abies procera Rehd.] and silver fir [Abies amabilis (Dougl.) Forbes] near Zig Zag, in the western central Oregon Cascades of the 4000 foot level. Because it was a bad seed-year for coastal western hemlock [Tsuga heterophylla (Raf.) Sarg.] seeds collected in 1975 from near Hebo, Oregon were used. The half-sib identity of the seeds was kept throughout the experiment. Seed extraction and stratification procedures followed those described elsewhere (U.S. Department of Agriculture, Forest Service, 1974). Preliminary germination tests with western hemlock showed values for most families around 100% while Douglas-fir families averaged values around 50%. Dissection showed true fir seeds to average 72% and 56% empty for noble and silver fir, respectively.

Stratified seeds were sowed in plastic plugs containing a peat-moss mixture early in 1981. During the first growing season the germinants were watered every third day and fertilized once a month (PETER'S 20-20-20 PLUS). In April of 1982, the seedlings were transplanted either to one gallon plastic pots kept on the grounds around the Forest Research Laboratory, OSU, in Corvallis, or to a field adjacent to the Peavy Arboretum Genetic Nursery, 20 miles north of Corvallis, Oregon. The plastic pots were filled with soil from the same lysimeter used in the study reported in Chapter II, consisting of a 50:50 mixture of forest topsoil and river loam.

Soil at the field location was classified as silty clay loam (PRICE) with a clay content of 30% to 50% depending on depth. At both locations each species was represented by the same number of half-sib families: 18 for Douglas-fir, 19 for western hemlock, 12 for noble fir and 12 for silver fir. Two seedlings from each half-sib family were randomly assigned within each replicate in the field (resulting in a total of 122 seedlings per replicate); seedlings of Douglas-fir were potted individually (because of size) whereas those of the other species were potted in pairs of the same family. A total of three replicates in each location was used per treatment and per sampling date, except for the first sampling date when 2 replicates were used.

The treatments, applied one week after transplanting, were (1) application of 200 lb/acre of nitrogen equivalent delivered as urea, (2) use of shade cloth rated to intercept 75% of the incoming solar radiation, and (3) control. Sampling dates were chosen to represent developmental stages before, during, and after the period of active shoot elongation. The first harvest (SD1) was before budbreak (which being done before the seedlings were transplanted has the same values for both locations); the second and third harvest (SD2 and SD3, respectively) were 30 and 60 days after budbreak. For each half-sib family budbreak date was defined as the point at which one-half the individuals had broken the terminal bud. The fourth, and last, collection (SD4) was done after one-half the individuals of a given family had set buds. Termination of shoot elongation was induced by withholding water beginning in July.

Immediately following each harvest shoot length and root length (to the nearest mm) of each seedling was measured (from tip to root collar); the specimen was sectioned and oven-dried at 70°C for four days before shoot and root dry weights (to the nearest 0.1 mg) were recorded. Within each replicate, the two seedlings of each family were pooled and run through a 40-mesh Wiley mill sieve. The material (roots or shoots) was then oven-dried for two hours and a sample (about 50 mg) was drawn and weighted.

Total available carbohydrates (TAC) of shoot and root structures, as given by the concentration of sugars and hydrolyzed starch fractions, were extracted by the procedures outlined in the Appendix (p. 127), and determined by a modified anthrone method (Yemm and Willis, 1954). The standard glucose curves yielded by the anthrone method are depicted in the Appendix (p. 126).

The coefficient of variation for laboratory determinations of sugar and starch varied from 5% to 10% when performed on replicates of tissue from the same Douglas-fir seedling.

STATISTICAL PROCEDURES

For statistical analyses the data were partitioned in two groups: one involving the four sampling dates (SD1 to SD4) and the other involving the two treatments plus data of the fourth harvest which was used as the control. The statistical design used for either group was a split-plot with fixed factors where the main plots were locations--with replications within each plot--and the split plots were species--represented by the half-sib families (Table III.1). Analyses on morphological traits (length and weight of shoot and root) were executed on log transformed data. The mean square error (for the family term) from one-way ANOVAs on each combination of location, species, treatment or sampling date and replication for each one of the recorded traits were pooled and used for assessment of within-species (between families) variation through a split-plot design similar to that already described; the analyses were performed on log transformed data according to Anderson and McLean (1974). Individual means were compared using the Student-Newman-Keuls test (multiple comparison of means with unequal sample sizes).

RESULTS

The results will be presented in two major headings: (1) differences among species and (2) within-species (between families) variation. In each, the trait responses will be presented according to the time sequence of harvests, with comparisons mainly within species, followed by the results yielded by nitrogen fertilization, shade, and the control.

I. Species Differences

A. Pattern of Growing Season Development

There was significant interaction of location x species x sampling date for all growth variables except shoot length and root weight (Table III.2). Pot-grown seedlings of all species increased in all size measures throughout the growing season except for silver fir which did not grow significantly in height after the second sampling date (Figures III.1, III.2, III.3, III.4). The same was generally true for field-grown seedlings, however there were some exceptions. Noble fir did not increase shoot weight after the third sampling date, and no species except noble fir, increased root length until the last sampling period. This resulted in field-grown seedlings having significantly shorter roots than seedlings grown in pots.

The two early seral species gained weight at a much faster rate than their late seral associates. Between the first sampling date in March and the final sampling date in August pot-grown Douglas-fir seedlings increased their average top weight over 800% (180 to 1700 mg) and average root weight more than 500% (210 to 1380 mg). In contrast, pot-grown western hemlock increased shoot weight 500% (100 to 600 mg) and root weight 300% (80 to 330 mg). In the same period, pot-grown noble fir seedlings increased top weight 490% (180 to 1060 mg) and root weight 450% (200 to 1090 mg), while silver fir seedlings gained 330% (60 to 260 mg) in top weight and 240% (80 to 265 mg) in root weight (Figures III.3, III.4). The same was not true for height. At the final sample Douglas-fir seedlings were taller than western hemlock (166 mm and 100 mm, respectively); however, they were also taller at the first measurement, and relative height growth over the growing season was slightly greater for western hemlock. Western hemlock commenced its most rapid height and weight growth later in the season than either Douglas-fir or noble fir. Noble fir was taller than silver fir at the final measurement (104 mm and 46 mm, respectively), and had a slightly faster relative height growth during the season (Figure III.1). For all species relative weight gain was much greater than relative height growth.

Comparative growth patterns were similar in field- and pot-grown seedlings. However, field-grown seedlings did not grow as rapidly, attaining only 60% to 80% of the final size of pot-grown seedlings.

Changes in shoot/root ratio (weight-weight) throughout the sampling period varied between pot-grown and field-grown seedlings. In both pots and in the field early seral species first increased then decreased shoot/root ratio (S/R). The magnitude of change was greater in field seedlings, which changed from S/R = 1.0 in March to a peak of about 2.0 in May, whereas pot-grown seedlings peaked at S/R = 1.3 (Figures III.5, III.6). Field-grown silver fir followed the same pattern as the early seral species, but with a higher peak (S/R = 2.1), while pot-grown silver fir maintained a constant shoot/root ratio (1.1) throughout the growing season. Shoot/root ratio of pot-grown western hemlock did not change until the last sampling date, when it increased dramatically from 1.1 to 1.8. In contrast, shoot/root ratio of field-grown western hemlock peaked at 2.0 in the June measurement, then declined to about 1.8.

There was a significant location x sampling date x species interaction for ethanol soluble sugars in both root and shoot (Table III.3). For all species except silver fir, shoot and root sugars were highest just before budbreak in both pot-grown and field-grown seedlings (Table III.4). Pot-grown silver fir followed the same trend, but differences were not statistically significant. In field-grown silver fir, shoot sugars increased following budbreak.

Pre-budbreak root sugars were highest in western hemlock (21.5%), intermediate in Douglas-fir (15.6%) and lowest in the two high-elevation species (average 14.2%). Root sugar concentrations dropped in all species following budburst, but the two late seral species had a higher average value (10.8%) than the two early seral species (8.0%) on the first sampling date following budburst (SD2); and silver fir maintained a higher value than the other species on the second sampling date following budburst (SD3). Performance of field- and pot-grown seedlings was similar.

Pre-budbreak shoot sugars were higher than root sugars and did not vary among species, averaging 21% (Table III.4). As in the case of roots, shoot sugars dropped in all species during the growing season (SD2 and SD3)--with the exception of field-grown silver fir. Douglas-fir and silver fir maintained higher shoot sugar concentrations during the growing season (average 16.1%) than western hemlock and noble fir (average 10.9%).

Starch concentrations did not vary with location. All species had highest starch concentrations in both shoot and root prior to budbreak (average 46.8% and 48.4%, respectively), declining to 18.2% in shoots and 18.7% in roots during the period of shoot elongation, and increasing slightly (to 22.8%) in shoots at budset (Table III.5). Western hemlock had a higher average root starch concentration (24.7%) than either Douglas-fir or noble fir (average 20.1%). Average root starch of silver fir was also higher than the two early seral species, but the difference was not significant at the .05 level. In contrast, shoot starch varied relatively little among species. Average shoot starch concentration of pot-grown seedlings was higher than field-grown seedlings.

All species followed the same general pattern with respect to total available carbohydrate and sugar/starch ratios. Prior to budbreak 66 to 70% of total shoot weight and 63 to 70% of total root weight were soluble sugars and starch, with roughly two-thirds of this starch. Following budbreak carbohydrates decreased to 25 to 30% of total weight in both shoots and roots, a level which was maintained fairly constant throughout the growing season. Post-budbreak reduction in total carbohydrates was accompanied by an increase in the proportion of sugars, particularly on the first sampling date following budbreak (Figures III.7,III.8).

B. Response to Shade and Nitrogen Fertilization

There were significant species x treatment x location interaction for shoot length and weight, and root weight (Table III.6). Among pot-grown seedlings shading reduced shoot and root weight (the latter not significant for Douglas-fir) but did not affect height of the early seral species, whereas it increased shoot and root weight and height of the late seral species (Table III.7). Shading did not affect root length in any species; however, it slightly decreased shoot/root ratio in Douglas-fir, from 1.25 to 1.15 (Figure III.7).

Shading had less pronounced effects on field-grown seedlings. With the exception of noble fir height, which was reduced, shading had no influence on the two high-elevation species when grown in the field. In contrast, the two low-elevation species behaved generally the same in the field and in pots, except that root weights of field-grown western hemlock were unaffected by shading. Western hemlock shoot/root ratio was increased (from 1.7 to over 2.0) by shading in the field (Figure III.10). Shade effects upon carbohydrate concentrations were very few (Tables III.8; III.9); it increased shoot sugar content of Douglas-fir seedlings from 14% to 16%, but did not affect other species.

In general, the low-elevation species were more affected by nitrogen fertilization than the high-elevation species. Shoot and root weight of Douglas-fir was reduced by fertilization in both pots and in the field. Western hemlock root weights were reduced at both locations by fertilization, while shoot weight was either increased (pots) or unaffected (field). Noble fir weights were unchanged by fertilization except in one instance, reduced root weight in pots. Silver fir root weights were unaffected by nitrogen, whereas top weights increased in pot-grown and decreased in field-grown seedlings (Table III.7).

Shoot/root ratios (S/R) of pot-grown seedlings of all species were sharply increased by nitrogen; however, in the field this occurred only for noble fir (Figures III.9, III.10). In pots, Douglas-fir, silver fir, and noble fir S/R averaged 1.16 in controls and 2.21 in the nitrogen treatment, while western hemlock seedlings averaged 1.91 and 3.33 in control and nitrogen treatment, respectively.

Nitrogen reduced shoot sugars from an average 14% to an average 9.6% for pot-grown seedlings; however, the reduction was not significant for noble fir (Tables II.8; III.9). Root sugars were reduced from an average 9.8% to 8.1% for all species, with no significant difference in location (Table III.9). Among pot-grown seedlings of all species, nitrogen lowered the ratio of sugar to starch from .57 to .38 (Table III.9; Figure III.11), but had no effect on sugar/starch ratios in field-grown seedlings.

II. Within-species Variation (among families)

A. Species Differences

There was greater variation among families of the two low-elevation species (western hemlock and Douglas-fir) than among families of the two high-elevation species (silver fir and noble fir) for shoot length, shoot weight, and root weight (Tables III.10, III.11). Family variance in root weight increased during the sampling period for all species, and variances at budset were significantly greater than at budbreak (with the exception of root weights of field-grown seedlings). Family variance in shoot weight increased in western hemlock and noble fir, but decreased in Douglas-fir seedlings with onset of shoot growth, while that of silver fir increased only after budset. Family variances in root length behaved somewhat the same, but increased sharply following budbreak and, except for silver fir, again at budset. Families of all species varied more in shoot weight and root length when pot-grown than when field-grown.

Patterns of family variation in shoot carbohydrate concentration were somewhat different. Pre-budbreak shoot sugars were more variable among families of high-elevation species than among families of low-elevation species, while family variances in pre-budbreak root sugars were greater in the late seral than in the early seral species (Table III.12). The latter effect was striking in the case of western hemlock, which had 17 times greater family variation than Douglas-fir and noble fir. There was a similar pattern in pre-budbreak shoot starch; variance among western hemlock and silver fir families was greater than Douglas-fir and noble fir, although differences with noble fir were not significant at $\alpha = .05$. Families of all species were highly variable in pre-budbreak root starch. Family variances in shoot sugars decreased in the first sampling period following budbreak for the two high-elevation species, probably because the level of total sugars dropped at the same time. Family variation in Douglas-fir more than doubled following budbreak, however the difference was not significant at the .05 level, while western hemlock did not change. Changes in variation of shoot starch were mainly confined to western hemlock and noble fir; there was a reduction after budbreak. Variation in root starch concentration was reduced after budbreak in seedlings of all four species.

B. Treatment Differences

Nitrogen fertilization and shading had relatively minor effects on variability among families within species (Table III.13). Family variance in shoot dry weight, almost twice as great in the low-elevation as in the high-elevation species, was not influenced by either treatment (Table III.14). Among pot-grown seedlings, nitrogen fertilization reduced root weight differences among families in the two late seral species. Nitrogen had the opposite effect in field-grown seedlings, however differences were not significant (Table III.14). Nitrogen reduced family variance in shoot starch in pot-grown western hemlock, and in field-grown silver fir (Table III.15).

DISCUSSION AND CONCLUSIONS

Perhaps the most significant outcome of this experiment is to show that seedlings may grow quite differently when in pots than when in the field. Pot-grown seedlings grew better and generally expressed more differences between species, between families within-species, and in reaction to treatments, than field-grown seedlings. Environments of the pot and the field likely differed in a number of respects (i.e., soil temperature, soil oxygen tension); however, we feel the main factor in this experiment was a dense clay soil in the field which restricted root development and therefore overall seedling growth. Minore *et al*. (1969) reported restriction of conifer root growth in artificially compacted soil columns. Because they had the greatest expression of potential differences among species and treatments, the following discussion will deal primarily with responses of pot-grown seedlings.

Species belonging to different successional stages generally differ in the following respects (for early and late stages, respectively): r versus K life history strategies, rapid versus slow development, and productivity versus efficiency (Pianka, 1970). In this experiment early successional species (i.e., Douglas-fir and noble fir) grew faster than the late successional species (i.e., western hemlock and silver fir). This trend agrees with Bicknell (1982) and Wiermann and Oliver (1979); and with unpublished data of John Aber (1976) (cited by Borman and Likens, 1979), which showed that early successional northern hardwood species grew faster than late successional species, especially at young ages. Unpublished data of Ledig (1981) showed the same trend for conifers. Several authors (Grime, 1965; Parsons, 1968; Borman and Likens, 1979) have proposed that selection for slow growth rates is a frequent adaptation to limiting levels of resource availability.

Growth differences between early and late successional species were greater for shoots than for roots. Priority for top growth fits Marks' (1975) hypothesis and Harper's (1977) statement that early successional species are resource preemptive competitors; their most limiting resource on many sites will be light. The lack of shoot elongation in silver fir seedlings may result from maladaptation to the experimental site. During their first growing season there was a considerable percentage of seedlings with needle browning (from the base to the tip) resulting in mortality. No conclusive cause could be determined but a lack of proper adaptation to growing conditions outside their ecological range could certainly have contributed to the problem.

There were few differences among root growth traits of low-elevation and high-elevation species. These observations do not agree with most of the autoecological rooting characteristics as reported by Minore (1979) perhaps because the latter dealt with field-grown, mature trees.

The carbohydrates extracted are assumed to be part of the "reserve pool" rather than products of the daily metabolized photosynthate. Several roles have been attributed to this reserve pool, among which the most important is to supply the plant with the necessary energy for growth (Kramer and Kozlowski, 1979). Significant reduction in the concentration of sugars and starch with the onset of shoot extension in seedlings of all species is coincidental with the seasonal fluctuations reported for various woody species--high sugar concentration in the winter and low in the summer (Krueger and Trappe, 1967; Little, 1970; Kozlowski and Keller, 1966). As might be expected, there is marked variation in the amount of carbohydrates in various parts of woody plants, perhaps because these parts not only grow at different rates but also at different times.

Accumulation of carbohydrate reserves in evergreen tree species can occur during the winter, reaching a maximum in early spring before decreasing with the onset of growth (Kramer and Kozlowski, 1979). Winjum (1963) reported that starch in Douglas-fir and noble fir seedling tops increased from a winter base level of about 150 mg/g (dry weight) to about 240 mg/g in the spring, while sugars tended to maintain concentrations around 50-60 mg/g during the same period. Root concentrations for sugars and starch in Douglas fir seedlings were reported to be 50 and 75 mg/g, respectively, before budbreak (Krueger and Trappe, 1967). Values obtained in this study were, on the average, twice as great as those above. Independent determinations performed by John Marshall (personal communication) of starch concentrations, using the perchloric acid method, gave values for the families used in this study that were about one-half those we derived. Thus, our starch values may have overestimated concentrations by 100%.

Opening of buds and expansion of shoots involves the utilization of large quantities of carbohydrates (Kozlowski and Keller, 1966). Seedlings from all four species significantly reduced sugar and starch concentration with the onset of shoot extension. In general, the sugar/starch ratios, on a whole seedling basis, increased with the start of shoot elongation; because both components of the ratio showed reduction at the same time there was probably a faster mobilization of starch than depletion of sugars (Priestley, 1962). After a mid-April peak, Krueger and Trappe (1967) reported that starch in Douglas-fir tops declined rapidly followed by a moderate increase during June and July; starch in Douglas-fir roots reached a broad peak from March to May after which it decreased to the former low level. In this study, the same pattern was observed in seedlings of all four species without large differences between early versus late or low versus high elevation species. Priestley (1962) has shown that one-year-old apple tree carbohydrate reserves were equally distributed above and below the ground.

Results given by the ratios of shoot TAC/root TAC (TAC = total available carbohydrates) indicate a predominant concentration in above-ground tissue, however it is significant that late seral species tended to have higher levels of available carbohydrate in roots during the growing season than early seral species. This supports the hypothesis of R. H. Waring (personal communication) that plants growing in nutrient-poor situations should devote a relatively high proportion of available carbohydrate to roots in order to stimulate mycorrhizal formation.

Light intensity and quality influence phenology (bud formation and expansion of inter-nodes and leaves) as well as physiology (chlorophyll synthesis, photosynthesis, hormone synthesis, stomatal opening and transpiration) of plant growth (Kramer and Kozlowski, 1979; Leopold and Kriedmann, 1975; Larcher, 1980). The overall effect of shade was to reduce shoot and root weights of early successional species with no effect on top length and to increase both top weight and length of late successional species. Shading did not (at least statistically) alter root length of any species. These results agree with the report of Brix (1971), except on the response of Douglas-fir roots, which he reported to increase in dry weight with shading, whereas in this study, there was a reduction in weight with shading.

Nitrogen fertilization resulted in an overall increase in the shoot/root ratio (on a weight basis) of pot-grown seedlings of all four species. The principal effect of nitrogen fertilization on crop plants seems to be an increase in the total area of photosynthetic surface (Watson, 1952, 1956), however in Douglas-fir nitrogen fertilization also increases photosynthetic rate (Brix, 1971). Shoot and root sugar concentration of all species except noble fir were reduced with nitrogen fertilization. Possibly, the daily photosynthate may have been used primarily for the production of new foliage leaving a small proportion for other uses and consequently drawing heavier on the pool of reserves. Also, with the application of nitrogenous fertilizer, there is an initial decrease in the non-structural carbohydrate fraction as they are incorporated into amino acids and proteins (Smith, 1973). Marx et al. (1977) also found that nitrogen fertilization decreased root sugars, which in turn led to a decrease in mycorrhizal formation. Comparing low and high levels of nitrogen fertilization, Meyer and Splittstoesser (1971) reported that high N plants grew more, produced more clorophyll and utilized more carbohydrates, with a subsequent smaller accumulation of carbohydrates within the plant in spring growth than the low N level treatment.

In general, within-species (between families) variation of growth traits in seedlings of low-elevation species were higher than those for the high-elevation species. Levins (1968) hypothesized that increasing environmental uncertainty would result in broader niches; one component of which could be genetic diversity. Perry (1978) suggested that selection acts on different sets of traits in different habitats; species from relatively benign environments evolving to cope with a predominance of biological factors and species from harsh environments evolving to cope with predominantly physical factors. Thus, diversity detected within any given population may depend on the traits studied. Reviewing the literature on isozyme analyses of 20 conifer species (in which Abies balsamea and Pseudotsuga menziesii were represented), Hamrick et al. (1979) stated that species of later successional stages, mesic habitat types, with open cones and a southern or western distribution have more genetic variation than species without those characteristics. Genetic variation may also be organized differently in different species (i.e., within or between families). Perry and Lotan (1978) found increased diversity of phenological traits between families of lodgepole pine with increasing elevation whereas the opposite trend was detected for within-family diversity. In a study of this type, genetic variation within-families appears as experimental error and therefore cannot be rigorously tested.

Differences between early and late seral species in the amount of family variation in root carbohydrates are consistent with results obtained from allozyme analyses of early and late seral tree species (Hamrick _et_ _al_., 1979). The biological significance, if any, of these differences is unclear; however, the importance of available carbohydrates for mycorrhizal formation, coupled with the variable biological environment faced by late seral species, may lead to diversifying selection for root-carbohydrate characteristics.

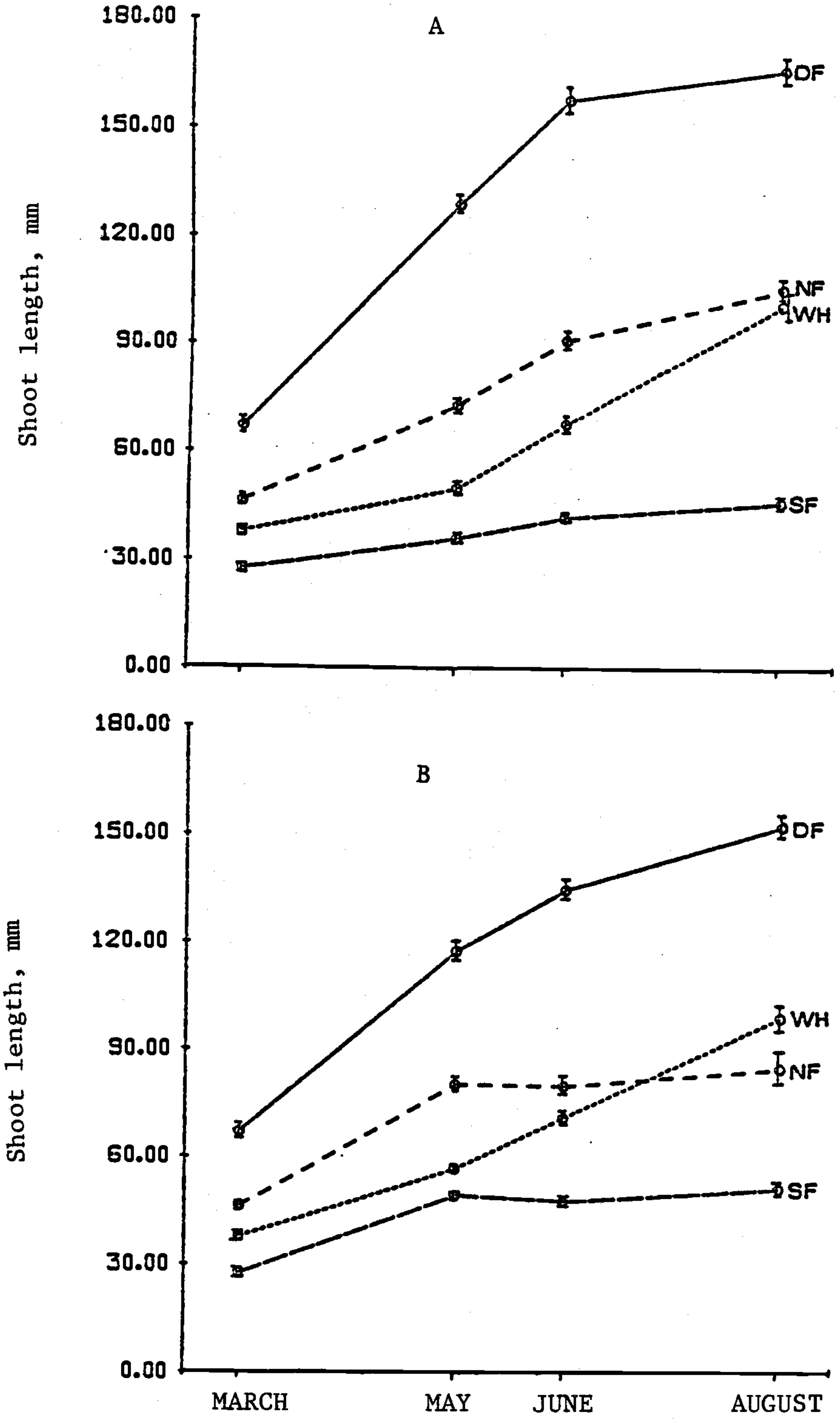

Figure III.1. Average shoot length of pot-grown (A) and field-grown (B) seedlings harvested before, during, and after shoot elongation phase. Vertical bars represent standard errors.

DF = Douglas-fir (n=54) NF = noble fir (n=36)

WH = western hemlock (n=57) SF = silver fir (n=36)

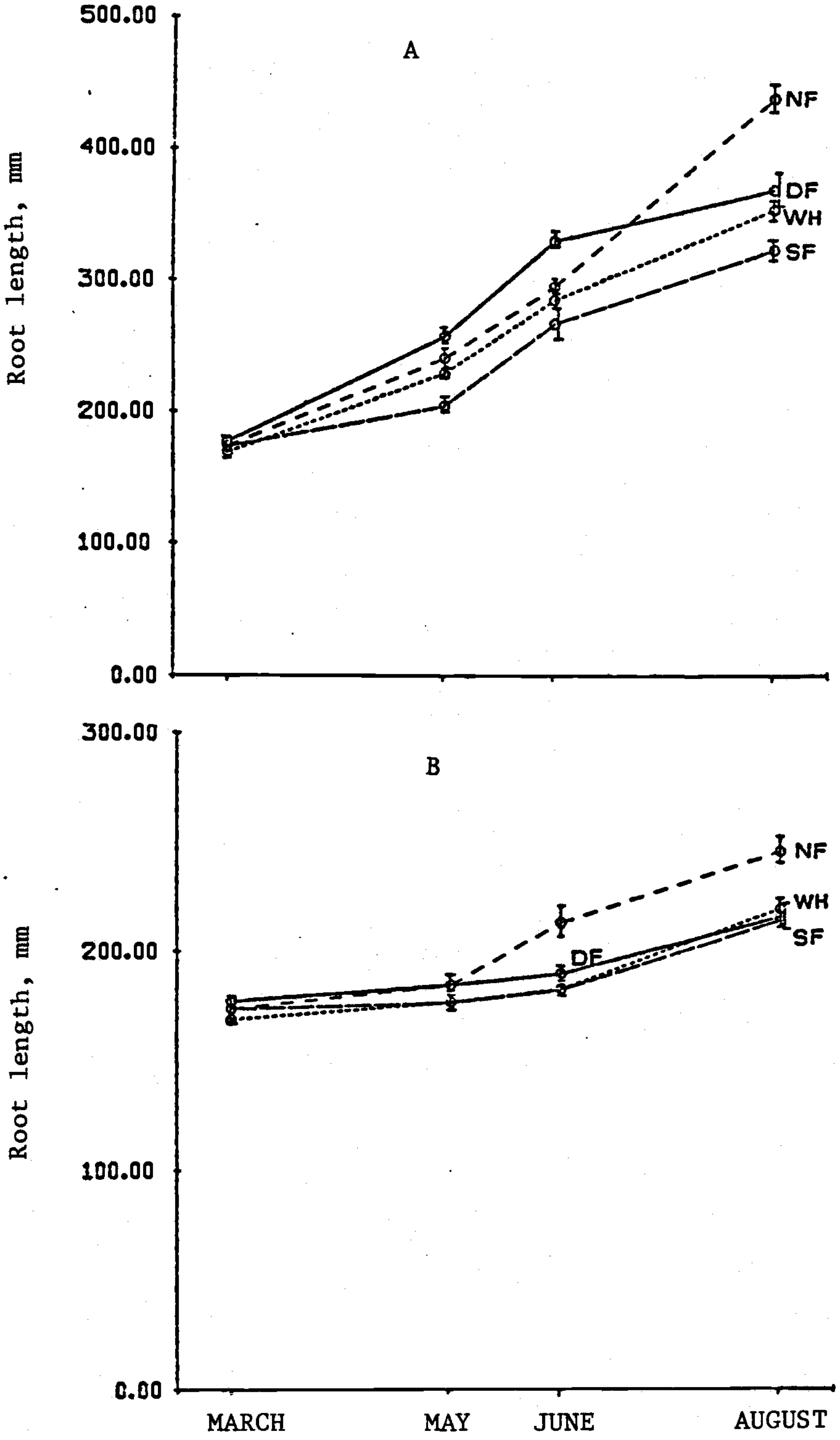

Figure III.2. Average root length of pot-grown (A) and field-grown (B) seedlings harvested before, during, and after shoot elongation phase. Vertical bars represent standard errors.

DF = Douglas-fir (n=54)
NF = noble fir (n=36)
WH = western hemlock (n=57)
SF = silver fir (n=36)

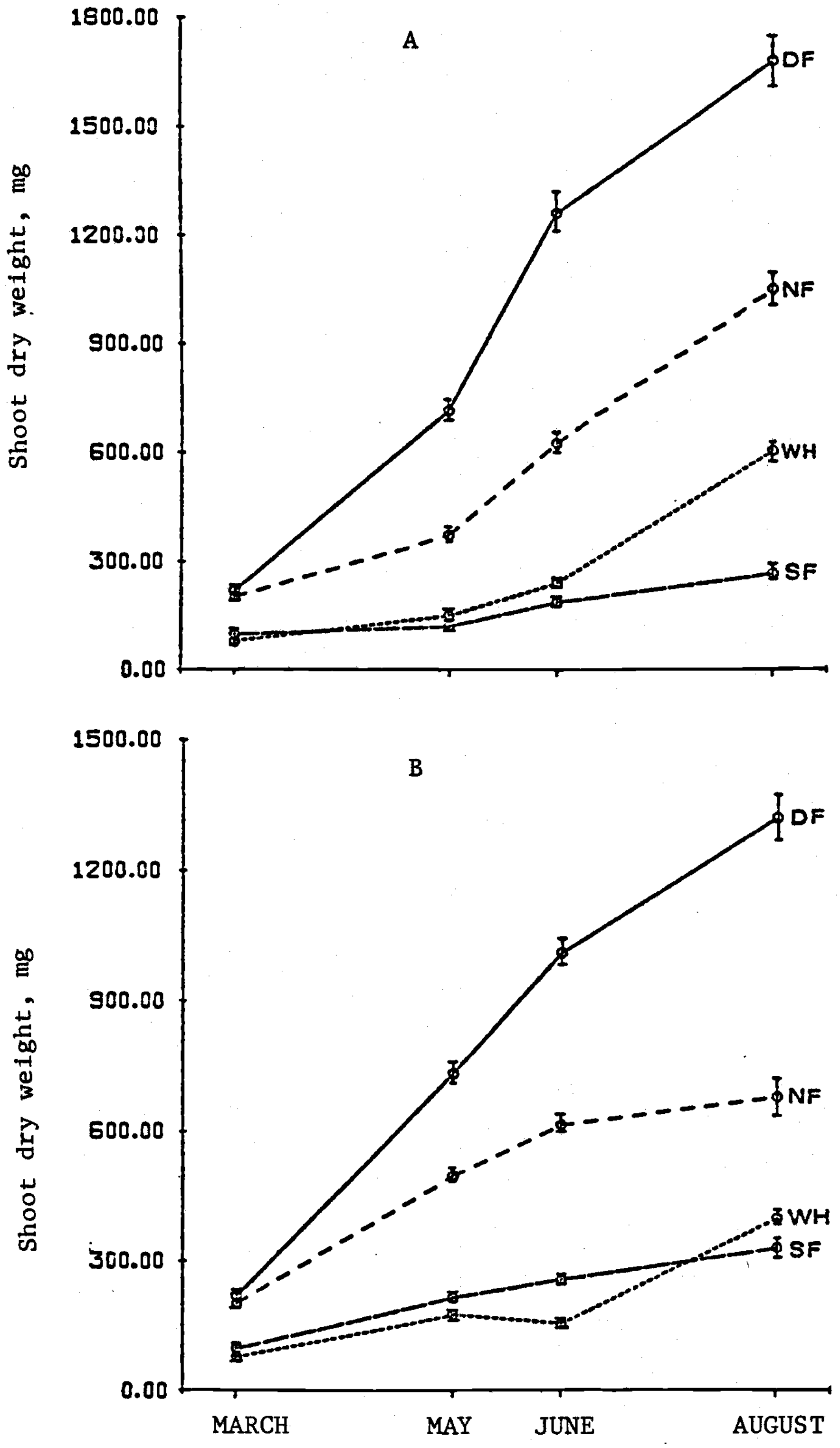

Figure III.3. Average shoot dry weight of pot-grown (A) and field-grown (B) seedlings harvested before, during, and after shoot elongation phase. Vertical bars represent standard errors.

DF = Douglas-fir (n=54) NF = noble fir (n=36)
WH = western hemlock (n=57) SF = silver fir (n=36)

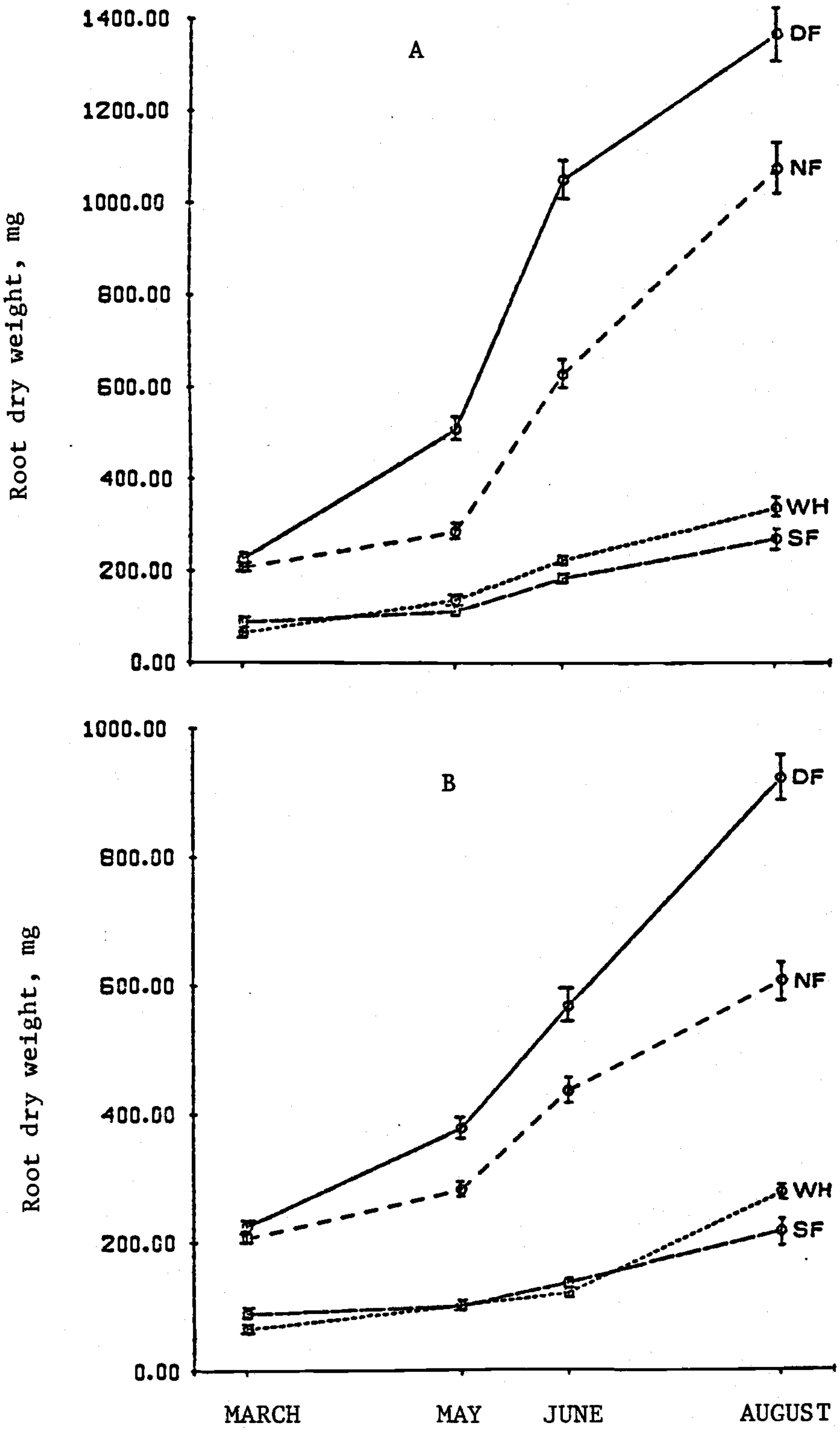

Figure III.4. Average root dry weight of pot-grown (A) and field-grown (B) seedlings harvested before, during, and after shoot elongation phase. Vertical bars represent standard errors.

DF = Douglas-fir (n=54) NF = noble fir (n=36)
WH = western hemlock (n=57) SF = silver fir (n=36)

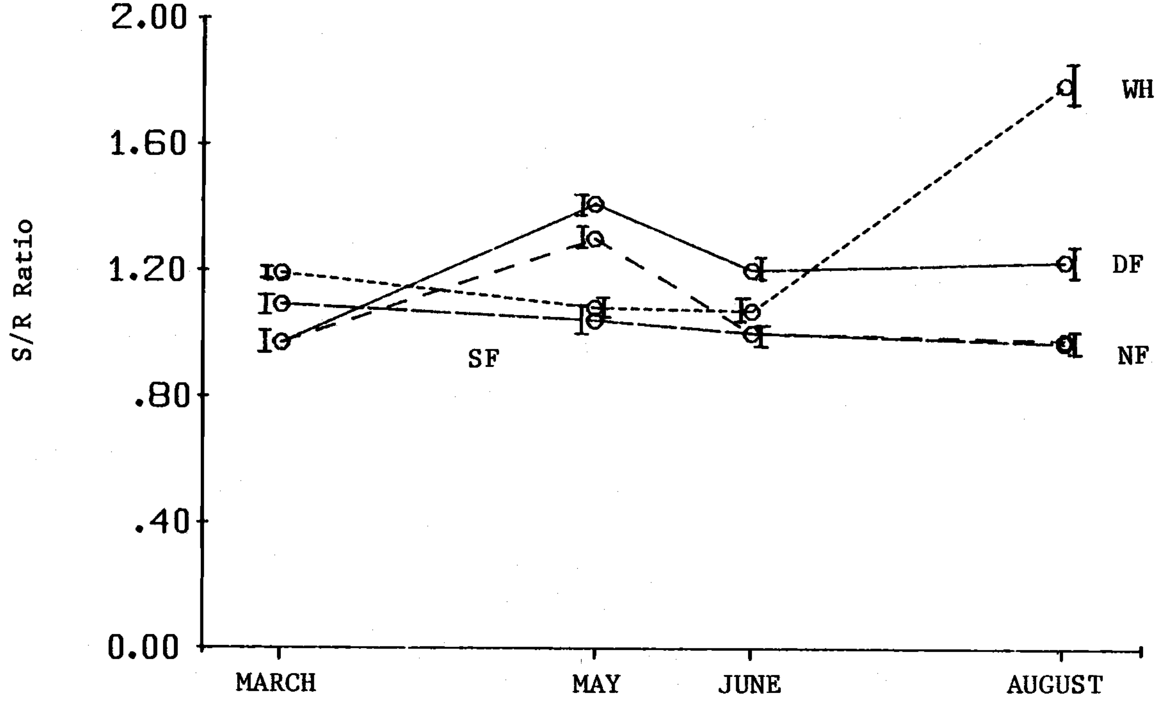

Figure III.5. Average shoot/root ratios, on a dry weight basis, of pot-grown seedlings harvested before, during, and after shoot elongation phase.
DF = Douglas-fir (n=54)
NF = noble fir (n=36)
WH = western hemlock (n=57)
SF = silver fir (n=36)
Vertical bars represent standard errors.

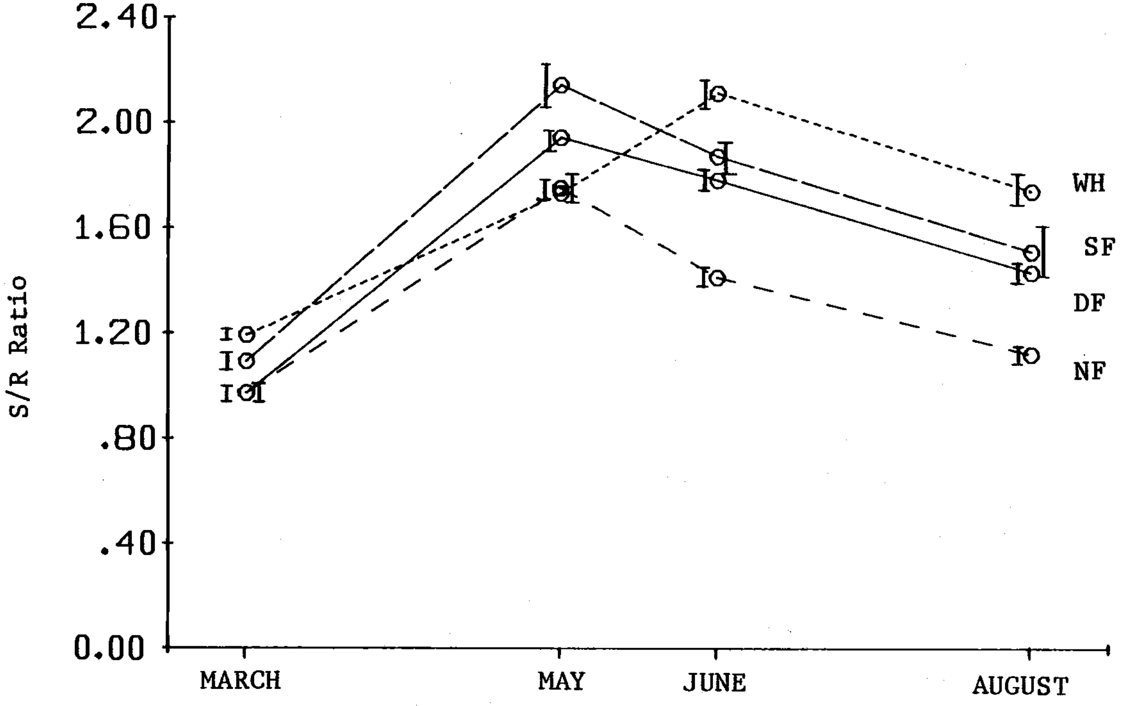

Figure III.6. Average shoot/root ratios, on a dry weight basis, of field-grown seedlings harvested before, during, and after shoot elongation phase.
DF = Douglas-fir (n=54)
NF = noble fir (n=36)
WH = western hemlock (n=57)
SF = silver fir (n=36)
Vertical bars represent standard errors.

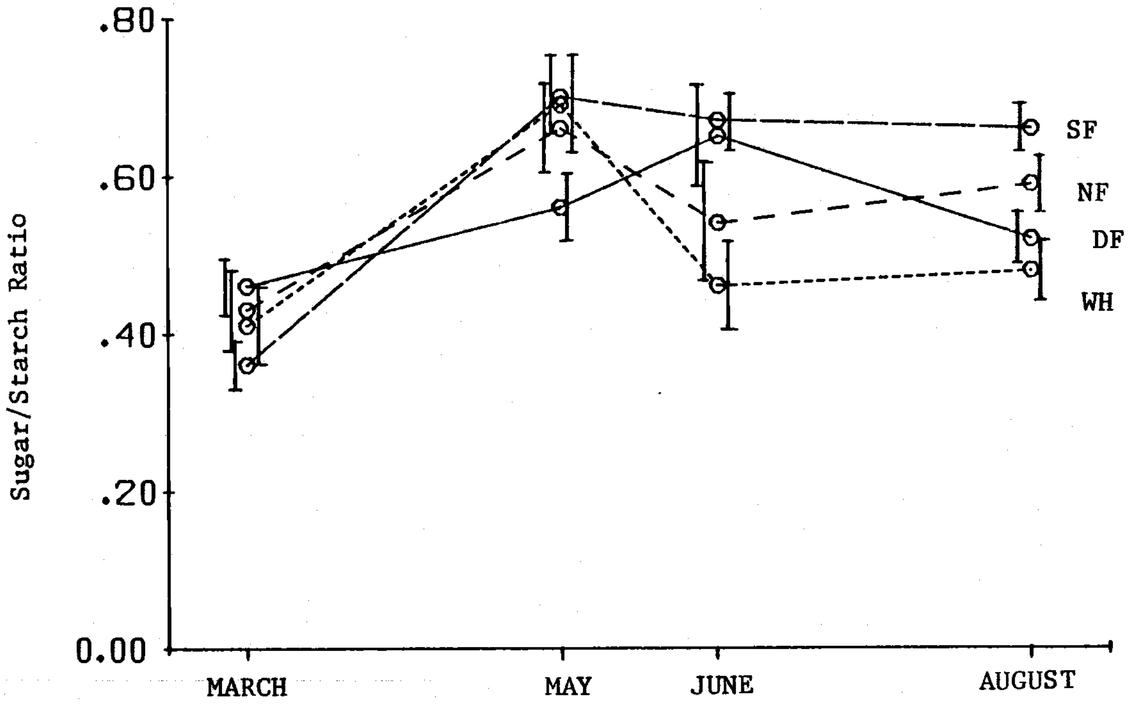

Figure III.7. Average ratios of sugar to starch concentrations, on a whole seedling basis, of pot-grown seedlings harvested before, during, and after shoot elongation phase.
DF = Douglas-fir (n=54)   NF = noble fir (n=36)
WH = western hemlock (n=57)   SF = silver fir (n=36)
Vertical bars represent standard errors.

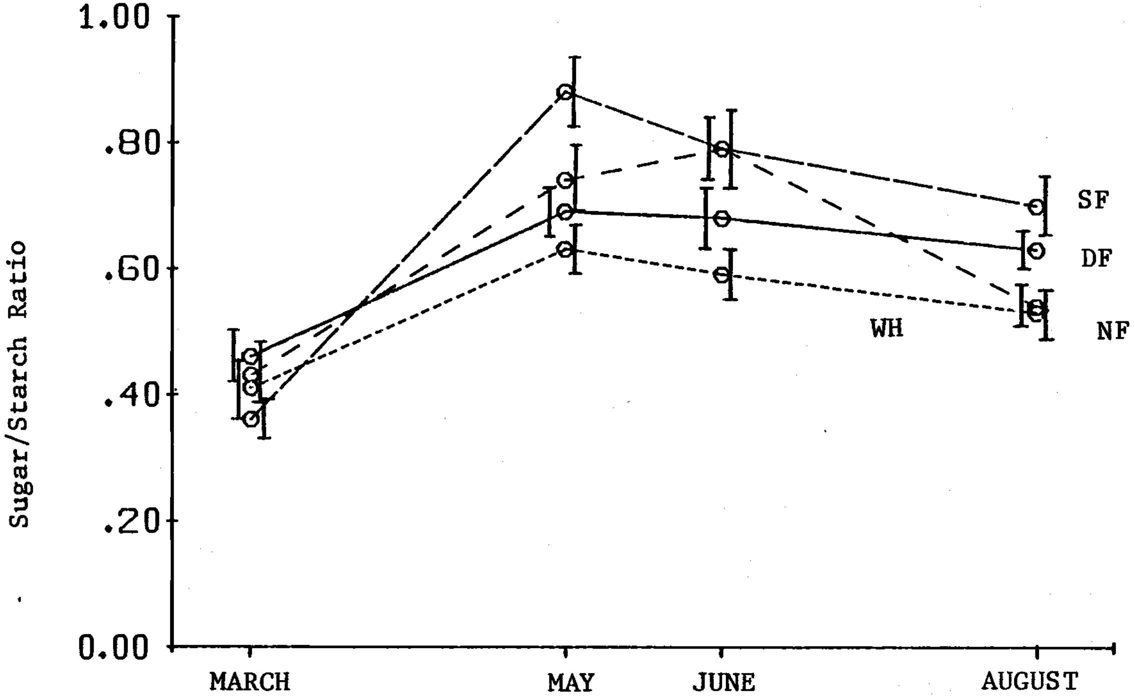

Figure III.8. Average ratios of sugar to starch concentrations, on a whole seedling basis, of field-grown seedlings harvested before, during, and after shoot elongation phase.
DF = Douglas-fir (n=54)
NF = noble fir (n=36)
WH = western hemlock (n=57)
SF = silver fir (n=36)
Vertical bars represent standard errors.

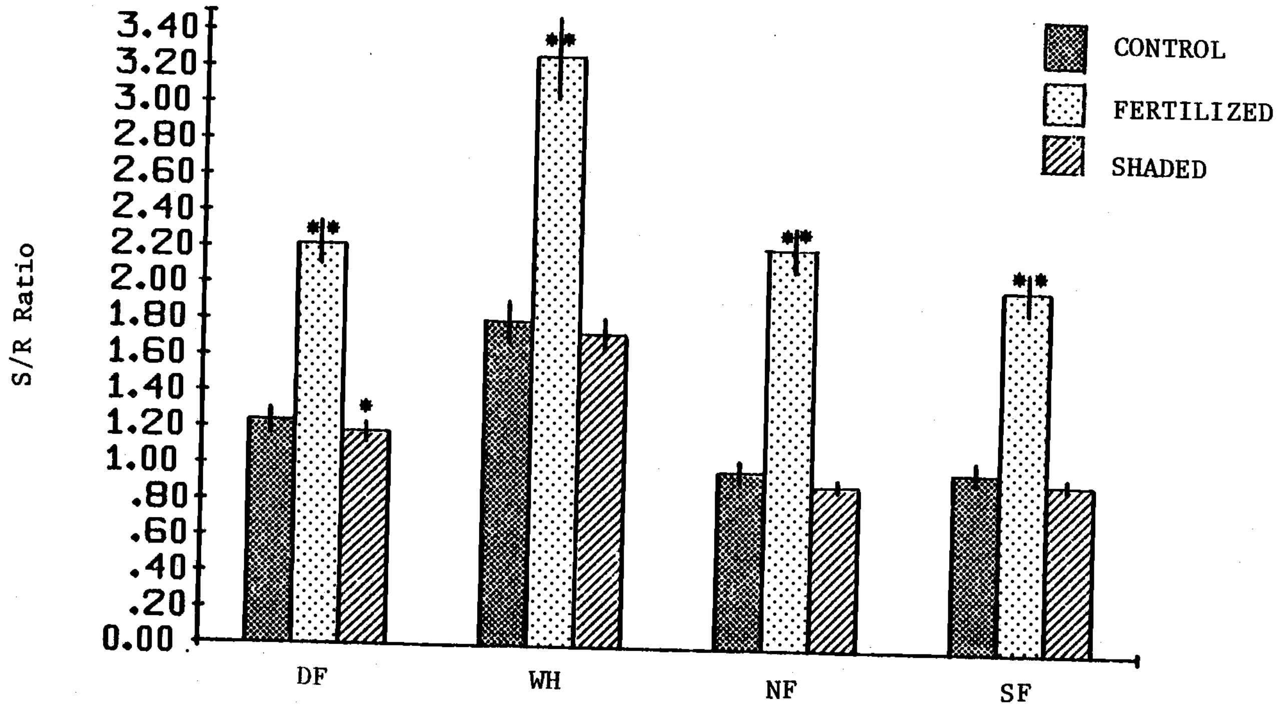

Figure III. 9. Average shoot/root ratios, on a weight basis, of pot-grown seedlings subjected to shade and nitrogen fertilization. Comparisons shown are within species: control x fertilized and control x shaded.

DF = Douglas-fir (n=54)
WH = western hemlock (n=57)
NF = noble fir (n=36)
SF = silver fir (n=36)
Vertical lines represent standard errors. * $P < .05$; ** $P < .01$.

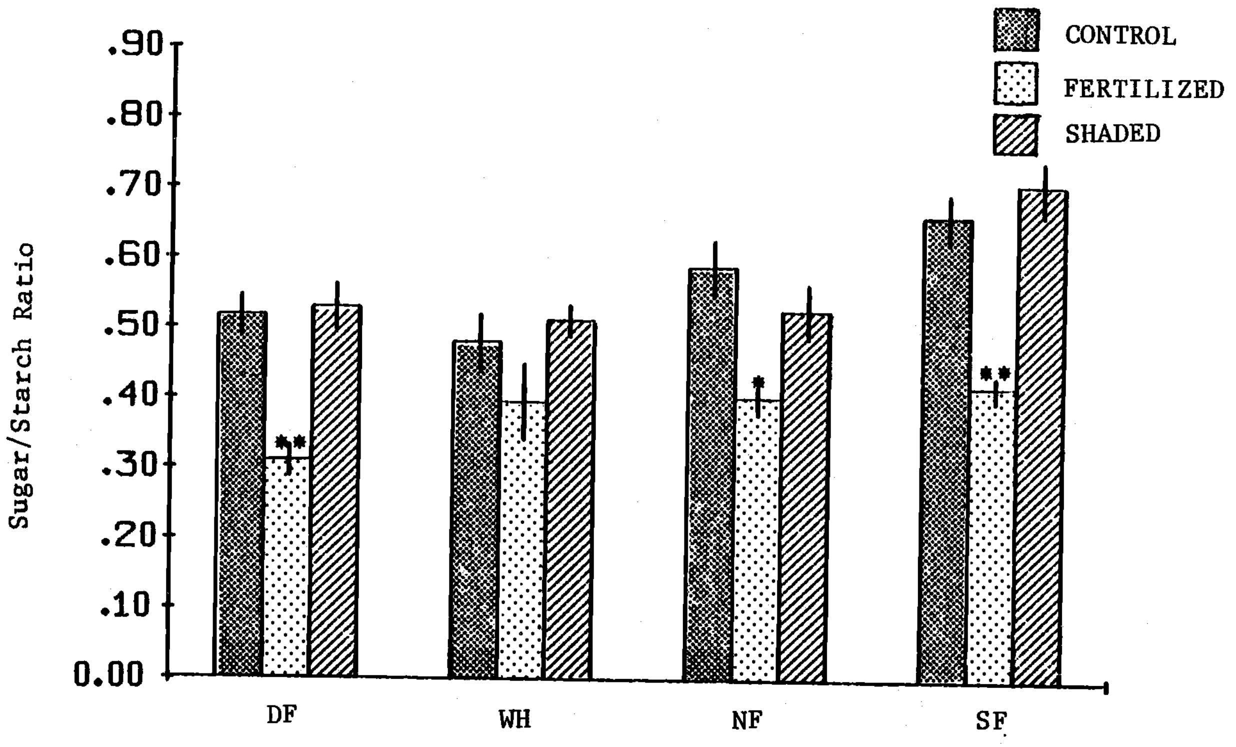

Figure III.11. Average ratios of sugar to starch, on a whole seedling basis, of pot-grown seedlings subjected to shade and nitrogen fertilization. Comparisons shown are within species: control x fertilized and control x shaded.
DF = Douglas-fir (n=54)
WH = western hemlock (n=57)
NF = noble fir (n=36)
SF = silver fir (n=36)
Vertical lines represent standard errors. * $P < .05$; ** $P < .01$.

Table III.1. Analysis of variance table and expected mean squares (EMS) used for treatments (TRT), as well as sampling dates (SD), effects upon seedlings of the four species grown in pots or in the field.

Source of Variation	Df	EMS
Location (LOC)	i-1	$jk\rho m\sigma^2_{LOC} + k\rho m\sigma^2_{R/LOC} + \sigma^2$
Rep. within LOC (R/LOC)	(j-1)i	$k\rho m\sigma^2_{R/LOC} + \sigma^2$
Treatments (TRT)	k-1	$ij\rho m\sigma^2_{TRT} + \rho m\sigma^2_{R/LOC \times TRT} + \sigma^2$
LOC x TRT	(i-1)(k-1)	$j\rho m\sigma^2_{LOC \times TRT} + \rho m\sigma^2_{R/LOC \times TRT} + \sigma^2$
R/LOC x TRT	(j-1)i(k-1)	$km\sigma^2_{R/LOC} + \sigma^2$
Species (SPP)	ρ-1	$ijkm\sigma^2_{SPP} + km\sigma^2_{R/LOC \times SPP} + \sigma^2$
LOC x SPP	(i-1)(ρ-1)	$jkm\sigma^2_{LOC \times SPP} + km\sigma^2_{R/LOC \times SPP} + \sigma^2$
R/LOC x SPP	(j-1)i(ρ-1)	$km\sigma^2_{R/LOC \times SPP} + \sigma^2$
TRT x SPP	(k-1)(ρ-1)	$ijm\sigma^2_{TRT \times SPP} + \sigma^2$
LOC x TRT x SPP	(i-1)(k-1)(ρ-1)	$jm\sigma^2_{LOC \times TRT \times SPP} + \sigma^2$
R/LOC x TRT x SPP	(j-1)i(k-1)(ρ-1)	σ^2

i = Number of locations.
j = Number of replications.
k = Number of treatments (or sampling dates).
ρ = Number of species.
m = Random error within each family and replicate.

Table III.2. Mean squares for some growth parameters of seedlings harvested before, during, and after shoot elongation phase.

Source of Variation	Df	Root Length	Shoot Length	Shoot Weight	Root Weight	S/R Ratio
Location (LOC)	1	52.158**	8.015	26.371	15.595	183.168**
Rep. within LOC (R/LOC)	4	0.696	1.827	8.051	5.403	0.709
Sampling dates (SD)	3	28.197**	39.304**	170.037**	175.888**	3.887*
LOC x SD	3	2.924**	0.547	5.193*	5.146*	21.247**
R/LOC x SD	12	0.058	0.351	1.160	0.775	0.593
Species (SPP)	3	1.884**	117.337**	298.011**	322.264**	9.746**
LOC x SPP	3	0.478**	1.465**	2.779**	0.594	4.097**
R/LOC x SPP	12	0.040	0.125	0.307	0.229	0.167
SD x SPP	9	0.273**	1.706**	4.735**	2.082**	5.118**
LOC x SD x SPP	9	0.100*	0.184	0.729**	0.685	1.545**
R/LOC x SD x SPP	36	0.029	0.105	0.174	0.174	0.154

*P < .05.

**P < .01.

Table III.3. Mean squares for some carbohydrate concentrations and ratios of seedlings harvested before, during and after shoot elongation phase.

Source of Variation	Df	Root Starch	Root Sugar	Shoot Starch	Shoot Sugar	Sugar/ Starch	Shoot TAC/ Root TAC
Location (LOC)	1	661,593	125,279	385,070**	5,364	29.857*	0.899
Rep. within LOC (R/LOC)	4	112,184	34,054	98,724	46,463	3.298	0.156
Sampling Date (SD)	3	114,987**	56,138**	983,143**	46,092**	17.835**	0.181
LOC x SD	3	2,905	9,491	2,711	14,589	1.379	0.287
R/LOC x SD	12	4,511	2,817	17,362	4,295	0.756	0.282
Species (SPP)	3	48,817**	13,744*	39,007*	86,591**	4.032*	3.265**
LOC x SPP	3	15,799	6,068	45,900	416,302**	0.059	1.531**
R/LOC x SPP	12	8,074	3,204	10,419	1,685	0.963	0.149
SD x SPP	9	8,665	6,051**	9,463	10,096**	1.719**	0.280
LOC x SD x SPP	9	6,256	5,444*	12,717	8,546**	0.979*	0.148
R/LOC x SD x SPP	36	4,226	1,761	7,364	2,370	0.305	0.144

*P < .05.

**P < .01.

TAC = Total available carbohydrates.

Table III.4. Pairwise comparison of means from pot-grown (A) and field-grown (B) seedlings according to ANOVA results of some carbohydrate concentrations (Table III.3.).

	Pot-grown				Field-grown			
	SD1	SD2	SD3	SD4	SD1	SD2	SD3	SD4
				Root Sugar (mg/g)				
Douglas-fir	$156^{b}_{1,2}$	$82^{a}_{2,3}$	71^{a}_{1}	84^{a}_{2}	$156^{b}_{1,2}$	82^{a}_{2}	104^{a}_{1}	$101^{a}_{1,2}$
Western hemlock	215^{b}_{1}	110^{a}_{1}	67^{a}_{1}	120^{a}_{1}	215^{b}_{1}	$102^{a}_{1,2}$	86^{a}_{1}	$84^{a}_{2,3}$
Noble fir	$144^{c}_{2,3}$	77^{a}_{3}	52^{a}_{1}	$111^{b}_{1,2}$	$144^{c}_{2,3}$	79^{b}_{2}	99^{b}_{1}	72^{a}_{3}
Silver fir	139^{b}_{3}	$106^{a}_{1,2}$	$107^{a,b}_{2}$	98^{a}_{2}	139^{b}_{3}	$111^{a,b}_{1}$	99^{a}_{1}	$114^{a,b}_{1}$
				Shoot Sugar (mg/g)				
Douglas-fir	228^{c}_{1}	$134^{a}_{1,2}$	195^{b}_{3}	$134^{a}_{2,3}$	228^{b}_{1}	$145^{a}_{2,3}$	132^{a}_{2}	148^{a}_{2}
Western hemlock	190^{c}_{1}	114^{a}_{2}	112^{a}_{1}	$141^{b}_{1,2}$	190^{b}_{1}	115^{a}_{3}	108^{a}_{2}	109^{a}_{3}
Noble fir	230^{b}_{1}	108^{a}_{2}	102^{a}_{1}	117^{a}_{3}	230^{c}_{1}	$159^{a,b}_{2}$	175^{a}_{1}	$123^{b}_{2,3}$
Silver fir	190^{a}_{1}	159^{a}_{1}	158^{a}_{2}	159^{a}_{1}	190^{b}_{1}	$237^{a,b}_{1}$	$199^{a,b}_{1}$	187^{b}_{1}
				Sugar/Starch				
Douglas-fir	$.46^{b}_{1}$	$.56^{a,b}_{1}$	$.65^{a}_{1}$	$.52^{b}_{2,3}$	$.46^{a}_{1}$	$.69^{b}_{2}$	$.68^{b}_{1,2}$	$.63^{b}_{1,2}$
Western hemlock	$.41^{a}_{1}$	$.69^{b}_{1}$	$.46^{a}_{2}$	$.48^{a}_{3}$	$.41^{b}_{1}$	$.63^{a}_{2}$	$.59^{a,b}_{2}$	$.53^{a,b}_{2}$
Noble fir	$.43^{a}_{1}$	$.66^{b}_{1}$	$.54^{a,b}_{1,2}$	$.59^{a,b}_{1,2}$	$.43^{a}_{1}$	$.74^{b}_{1,2}$	$.79^{b}_{1}$	$.54^{a}_{2}$
Silver fir	$.36^{b}_{1}$	$.70^{a}_{1}$	$.67^{a}_{1}$	$.66^{a}_{1}$	$.36^{a}_{1}$	$.88^{c}_{1}$	$.79^{b,c}_{1}$	$.70^{b}_{1}$

SD1 = Before budbreak harvest.

SD2 = 30 days after budbreak harvest.

SD3 = 60 days after budbreak harvest.

SD4 = After budset harvest.

Row means (sampling dates) within a location (pot or field), with similar superscripts (letters) do not differ ($P > .05$). Column means (species) with similar subscripts (numbers) do not differ ($P > .05$).

Table III.5. Pairwise comparison of means according to ANOVA results (Table III.3) of some carbohydrate concentrations as well as shoot to root ratio.

Shoot Starch (mg/g)

Douglas-fir	Western hemlock	Noble fir	Silver fir
245^{a}	$228^{a,b}$	207^{b}	243^{a}
SD1	SD2	SD3	SD4
468^{c}	188^{a}	195^{a}	228^{b}

Root Starch (mg/g)

Douglas-fir	Western hemlock	Noble fir	Silver fir
203^{a}	247^{b}	199^{a}	$224^{a,b}$
SD1	SD2	SD3	SD4
484^{c}	175^{a}	$185^{a,b}$	201^{a}

Shoot TAC/Root TAC

	Douglas-fir	Western hemlock	Noble fir	Silver fir
Container	1.52^{b}	1.10^{a}	$1.15^{a,b}$	$1.28^{a,b}$
Field	1.35^{a}	1.05^{c}	$1.44^{a,b}$	1.52^{b}

TAC = Total available carbohydrates (sugars + starch).

SD1 = Before budbreak harvest.

SD2 = 30 days after budbreak harvest.

SD3 = 60 days after budbreak harvest.

SD4 = After budset harvest.

Row means with similar superscripts do not differ ($P > .05$).

Table III.6. Mean squares for some growth parameters of seedlings harvested after budset and submitted to three treatments.

Source of Variation	Df	Root Length	Shoot Length	Shoot Weight	Root Weight	S/R Ratio
Location (LOC)	1	80.788**	8.308**	24.312**	25.815**	2.332
Rep. within LOC (R/LOC)	4	0.035	0.149	0.451	0.412	0.948
Treatments (TRT)	2	6.405**	0.006	2.011	18.997**	87.375**
LOC x TRT	2	5.294**	3.037*	1.650	13.774**	63.460**
R/LOC x TRT	8	0.149	0.388	0.499	0.251	2.285
Species (SPP)	3	2.596**	81.596**	165.921**	210.626**	67.541**
LOC x SPP	3	0.22	0.71*	2.628**	0.503	4.118**
R/LOC x SPP	12	0.086	0.142	0.331	0.145	0.645
TRT x SPP	6	0.239**	1.982**	3.024**	2.139**	0.256
LOC x TRT x SPP	6	0.136	0.758**	1.081*	0.954*	0.928*
R/LOC x TRT x SPP	24	0.064	0.115	0.299	0.282	0.339

*P < .05.

**P < .01.

Table III.7. Pairwise comparison of means from pot-grown seedlings (A), field-grown seedlings (B), and average between pot- and field-grown seedlings (C) according to ANOVA results of some growth parameters (Table III.6.).

	Co	N	Sh	Co	N	Sh
		(A)			(B)	
			Shoot Length (mm)			
Douglas-fir	165^{a}_{1}	144^{b}_{1}	177^{a}_{1}	152^{b}_{1}	145^{a}_{1}	$142^{a,b}_{1}$
Western hemlock	100^{a}_{2}	114^{b}_{2}	148^{c}_{2}	98^{b}_{2}	79^{a}_{3}	95^{b}_{2}
Noble fir	104^{b}_{2}	$105^{a,b}_{2}$	95^{a}_{3}	84^{b}_{3}	87^{b}_{2}	77^{a}_{3}
Silver fir	45^{c}_{3}	72^{a}_{3}	50^{b}_{4}	51^{a}_{4}	48^{a}_{4}	48^{a}_{4}
			Shoot Dry Weight (mg)			
Douglas-fir	1677^{b}_{1}	1436^{a}_{1}	1372^{a}_{1}	1321^{b}_{1}	1163^{a}_{1}	1158^{a}_{1}
Western hemlock	602^{b}_{3}	687^{a}_{3}	690^{a}_{3}	396^{a}_{3}	357^{a}_{3}	487^{b}_{3}
Noble fir	1047^{a}_{2}	1151^{a}_{2}	810^{b}_{2}	677^{a}_{2}	698^{a}_{2}	611^{a}_{2}
Silver fir	263^{a}_{4}	504^{c}_{4}	289^{b}_{4}	328^{b}_{3}	268^{a}_{4}	$302^{a,b}_{4}$
			Root Dry Weight (mg)			
Douglas-fir	1364^{a}_{1}	648^{b}_{1}	1169^{a}_{1}	921^{b}_{1}	789^{a}_{1}	737^{a}_{1}
Western hemlock	336^{b}_{3}	210^{a}_{3}	401^{c}_{3}	227^{b}_{3}	192^{a}_{3}	236^{b}_{3}
Noble fir	1073^{c}_{2}	521^{a}_{1}	899^{b}_{2}	606^{a}_{2}	$571^{a,b}_{2}$	502^{b}_{2}
Silver fir	270^{a}_{4}	252^{a}_{2}	311^{b}_{4}	217^{a}_{3}	192^{a}_{3}	223^{a}_{3}
			Shoot/Root Ratio			
Douglas-fir	1.38^{b}_{2}	2.31^{c}_{2}	1.17^{a}_{2}	1.44^{a}_{2}	$1.74^{a}_{1,2}$	1.59^{a}_{2}
Western hemlock	1.91^{a}_{3}	3.33^{b}_{1}	1.78^{a}_{3}	1.80^{a}_{3}	$1.92^{a,b}_{2}$	2.08^{b}_{1}
Noble fir	1.03^{a}_{1}	2.21^{b}_{2}	0.92^{a}_{1}	1.12^{a}_{1}	1.25^{b}_{1}	1.23^{b}_{4}
Silver fir	1.06^{a}_{1}	2.12^{b}_{2}	0.95^{a}_{1}	1.46^{a}_{2}	$1.40^{a}_{1,2}$	1.46^{a}_{3}

(C) Root Length (mm)

	Co	N	Sh
Douglas-fir	367^{b}_{2}	290^{a}_{1}	356^{b}_{2}
Western hemlock	352^{b}_{2}	226^{a}_{3}	354^{b}_{2}
Noble fir	437^{b}_{1}	$274^{a}_{1,2}$	428^{b}_{1}
Silver fir	322^{a}_{3}	262^{a}_{2}	327^{a}_{3}

Co = Control.

N = Nitrogen treatment.

Sh = Shade treatment.

Row means (treatments) within a location (pot or field), with similar superscripts (letters) do not differ ($P > .05$). Column means (species) with similar subscripts (numbers) do not differ ($P > .05$).

Table III.8. Mean squares for some carbohydrate concentrations and ratios of seedlings harvested after budset and submitted to three treatments.

Source of Variation	Df	Root Starch	Root Sugar	Shoot Starch	Shoot Sugar	Sugar/ Starch	Shoot TAC/ Root TAC
Location (LOC)	1	220,210**	9,511	75,074	202	17.207	1.358
Rep. within LOC (R/LOC)	4	5,827	49,548	62,162	10,733	3.723	0.363
Treatments (TRT)	2	15,599	14,098*	997	51,124**	19.935**	0.136
LOC x TRT	2	12,248	4,606	5,268	52,286**	15.032**	0.166
R/LOC x TRT	8	6,036	1,915	10,773	3,125	0.701	0.079
Species (SPP)	3	21,126*	4,756*	29,828	66,605**	5.157**	2.524**
LOC x SPP	3	26,012*	15,115**	96,172**	12,547**	2.578*	0.321
R/LOC x SPP	12	4,573	897	14,595	1,281	0.512	0.317
TRT x SPP	6	7,428	43	3,531	2,848**	1.085	0.093
LOC x TRT x SPP	6	7,884	951	10,133	1,991	0.679	0.250
R/LOC x TRT x SPP	24	4,033	1,245	6,987	159	0.785	0.118

*P < .05.

**P < .01.

TAC = Total available carbohydrates.

Table III.9. Pairwise comparison of means according to ANOVA results of some carbohydrate concentrations as well as shoot to root ratio (Table III.8.).

	Co	N	Sh
		Shoot Sugar (mg/g)	
Douglas-fir	140^{b}_{2}	$114^{a}_{1,2}$	160^{c}_{2}
Western hemlock	$126^{a}_{1,2}$	98^{b}_{1}	119^{a}_{1}
Noble fir	120^{a}_{1}	108^{a}_{1}	119^{a}_{1}
Silver fir	170^{a}_{3}	132^{b}_{2}	183^{a}_{3}
Pot-grown	140^{b}	96^{a}	167^{c}
Field-grown	141^{a}	137^{a}	132^{a}
		Root Sugar (mg/g)	
Overall mean	98^{a}	81^{b}	98^{a}

Shoot TAC/Root TAC

Douglas-fir	Western hemlock	Noble fir	Silver fir
$1.30^{a,b}$	1.06^{c}	1.22^{a}	1.40^{b}

Sugar/Starch

	Co	N	Sh
Pot-grown	$.57^{a}$	$.38^{b}$	$.58^{a}$
Field-grown	$.60^{a}$	$.60^{a}$	$.58^{a}$

TAC = Total available carbohydrate (sugar + starch).

Co = Control.

N = Nitrogen treatment.

Sh = Shade treatment.

Row means (treatments) with similar superscripts (letters) do not differ ($P > .05$). Column means (species) with similar subscripts (numbers) do not differ ($P > .05$).

Table III.10. Mean squares for within-species (between families) variation of some growth parameters and carbohydrate concentrations of seedlings harvested before, during, and after shoot elongation phase.

Source of Variation	Df	Shoot Length	Root Length	Shoot Weight	Root Weight	Root Starch	Shoot Starch	Root Sugar	Shoot Sugar
Location (LOC)	1	0.369	1.047**	0.373*	0.941*	0.269	0.002	0.579	0.078
Rep. within LOC (R/LOC)	4	0.079	0.026	0.039	0.043	0.543	0.697	1.341	1.128
Sampling date (SD)	3	0.029	4.381**	0.087*	0.014	6.526**	3.362**	2.331*	1.451*
LOC x SD	3	0.047	0.190	0.043	0.175**	0.025	0.058	0.323	0.107
R/LOC x SD	12	0.055	0.073	0.019	0.026	0.234	0.351	0.586	0.320
Species (SPP)	3	1.3644**	0.085	0.898**	0.249**	0.879	1.017**	0.763*	1.147**
LOC x SPP	3	0.0149	0.070	0.006	0.052	0.059	0.308	0.094	0.121
R/LOC x SPP	12	0.026	0.029	0.018	0.637	0.273	0.163	0.165	0.079
SD x SPP	9	0.103**	0.190**	0.108**	0.047	0.086	0.455**	0.401**	0.518**
LOC x SD x SPP	9	0.058	0.048	0.035	0.039	0.072	0.164	0.091	0.052
R/LOC x SD x SPP	36	0.033	0.037	0.023	0.030	0.128	0.142	0.104	0.068

*P < .05.

**P < .01.

Table III.11. Pairwise comparison of within-species (between families) variances in some growth parameters according to ANOVA results (Table III.10.).

	SD1	SD2	SD3	SD4
		Root Length		
Douglas-fir	$.0120^{c}_{2}$	$.0345^{a,b}_{1}$	$.0266^{a}_{2}$	$.0555^{b}_{1}$
Western hemlock	$.0026^{b}_{1}$	$.0339^{a}_{1}$	$.0500^{a}_{1}$	$.0894^{c}_{1}$
Noble fir	$.0088^{b}_{2}$	$.0352^{a}_{1}$	$.0390^{a}_{1}$	$.0701^{c}_{1}$
Silver fir	$.0046^{b}_{1}$	$.0336^{a}_{1}$	$.0412^{a}_{1}$	$.0513^{a}_{1}$
		Shoot Length		
Douglas-fir	$.1357^{a}_{1}$	$.1187^{a,b}_{1}$	$.0728^{b}_{2}$	$.0989^{b}_{1}$
Western hemlock	$.0520^{b}_{2}$	$.1191^{a}_{1}$	$.1350^{a}_{1}$	$.1020^{a,b}_{1,2}$
Noble fir	$.0389^{a}_{3}$	$.0445^{a}_{2}$	$.0432^{a}_{3}$	$.0596^{a}_{1,2}$
Silver fir	$.0274^{a}_{4}$	$.0333^{a}_{2}$	$.0380^{a}_{3}$	$.0444^{a}_{2}$
		Shoot Weight		
Douglas-fir	$.4645^{b}_{1}$	$.3779^{a}_{1}$	$.2688^{a}_{1}$	$.3064^{a}_{2}$
Western hemlock	$.1995^{b}_{2}$	$.2468^{a,b}_{1,2}$	$.3187^{a}_{1}$	$.2979^{a,b}_{2}$
Noble fir	$.0641^{b}_{4}$	$.1768^{a}_{2}$	$.1679^{a}_{2}$	$.1789^{a}_{1}$
Silver fir	$.1300^{b}_{3}$	$.1699^{a,b}_{2}$	$.1382^{a,b}_{2}$	$.2293^{a}_{1,2}$

SD1 = Before budbreak harvest.

SD2 = 30 days after budbreak harvest.

SD3 = 60 days after budbreak harvest.

SD4 = After budset harvest.

Row means (sampling dates) with similar superscripts (letters) do not differ ($P > .05$). Column means (species) with similar subscripts (numbers) do not differ ($P > .05$).

Table III.12. Pairwise comparison of within-species (between families) variances in some carbohydrate concentrations according to ANOVA results (Table III.10).

	SD1	SD2	SD3	SD4
		Shoot Sugar		
Douglas-fir	$1633^{a,b}_{1}$	3658^{a}_{1}	$1173^{b}_{1,2}$	1018^{b}_{2}
Western hemlock	2186^{b}_{1}	$1689^{a,b}_{1}$	916^{a}_{1}	2495^{b}_{3}
Noble fir	4257^{b}_{2}	2892^{a}_{1}	2038^{a}_{2}	413^{c}_{1}
Silver fir	14660^{b}_{3}	5205^{a}_{1}	3363^{a}_{2}	3058^{a}_{3}
		Root Sugar		
Douglas-fir	1517^{a}_{1}	1687^{a}_{1}	1503^{a}_{1}	500^{b}_{1}
Western hemlock	23546^{b}_{2}	1477^{a}_{1}	1624^{a}_{1}	$854^{a}_{1,2}$
Noble fir	1293^{a}_{1}	1548^{a}_{1}	1191^{a}_{1}	$1240^{a}_{1,2}$
Silver fir	6467^{b}_{2}	2284^{a}_{1}	1267^{a}_{1}	1796^{a}_{2}
		Shoot Starch		
Douglas-fir	6005^{a}_{1}	9959^{a}_{2}	5204^{a}_{2}	3919^{a}_{1}
Western hemlock	30698^{b}_{2}	$13311^{a}_{1,2}$	1439^{a}_{1}	3165^{a}_{1}
Noble fir	$12400^{b}_{1,2}$	3065^{a}_{1}	1390^{a}_{1}	2768^{a}_{1}
Silver fir	29578^{b}_{2}	$4368^{a}_{1,2}$	4239^{a}_{2}	26270^{b}_{2}
		Root Starch		
	29407^{b}	4223^{a}	4032^{a}	3686^{a}

SD1 = Before budbreak harvest.

SD2 = 30 days after budbreak harvest.

SD3 = 60 days after budbreak harvest.

SD4 = After budset harvest.

Row means (sampling dates) with similar superscripts (letters) do not differ ($P > .05$). Column means (species) with similar subscripts (numbers) do not differ ($P > .05$).

Table III.13. Mean squares for within-species (between families) variation of some growth parameters and carbohydrate concentrations of seedlings harvested after budset and submitted to three treatments.

Source of Variation	Df	Shoot Length	Root Length	Shoot Weight	Root Weight	Shoot Starch	Root Starch	Shoot Sugar	Root Sugar
Location (LOC)	1	.078	.756*	.073	.309	1×10^{-6}	.151	.082	3.318*
Rep. within LOC (R/LOC)	4	.092	.056	.055	.052	.422	.286	.325	.281
Treatments (TRT)	2	.01	.129	.018	.006	.328	.015	.141	.067
LOC x TRT	2	.117	.017	.040	.308*	.078	.056	.157	.272
R/LOC x TRT	8	.047	.055	.062	.059	.225	.309	.092	.207
Species (SPP)	3	.686**	.129	.541**	.379**	1.656**	.146	.755*	.329
LOC x SPP	3	.014	.023	.005	.002	.485	.234	.341	.543
R/LOC x SPP	12	.027	.053	.047	.035	.255	.148	.147	.176
TRT x SPP	6	.049	.085*	.099	.033	.144	.216	.373*	.146
LOC x TRT x SPP	6	.099	.075*	.066	.127*	.323*	.150	.154	.151
R/LOC x TRT x SPP	24	.042	.025	.057	.042	.118	.167	.136	.147

*P < .05.

**P < .01.

Table III.14. Pairwise comparison of within-species (between families) variances in some growth parameters according to ANOVA results (Table III.13.).

	Pot-grown			Field-grown		
	Co	N	Sh	Co	N	Sh
			Root Dry Weight			
Douglas-fir	$.3723^{a,b}_{1}$	$.4173^{a}_{1}$	$.2978^{b}_{1,2}$	$.2276^{a}_{1}$	$.3490^{a}_{1}$	$.2545^{a}_{1}$
Western hemlock	$.4103^{a}_{1}$	$.2214^{b}_{1,2}$	$.4996^{a}_{1}$	$.1934^{a}_{1,2}$	$.3141^{a}_{1}$	$.2663^{a}_{1}$
Noble fir	$.2669^{a}_{1}$	$.1967^{a}_{2}$	$.1884^{a}_{2}$	$.1251^{a}_{2,3}$	$.1941^{a}_{1}$	$.1442^{a}_{2}$
Silver fir	$.4461^{a}_{1}$	$.1967^{b}_{2}$	$.0803^{c}_{3}$	$.0962^{a}_{3}$	$.1967^{a}_{1}$	$.2387^{a}_{1}$
			Root Length			
Douglas-fir	$.0614^{a}_{1}$	$.0952^{a}_{1}$	$.0433^{a}_{2}$	$.0496^{a}_{1,2}$	$.0444^{a}_{1}$	$.0269^{b}_{1,2}$
Western hemlock	$.1037^{a,b}_{1}$	$.0412^{a}_{3}$	$.1403^{b}_{1}$	$.0751^{b}_{1}$	$.0415^{a}_{1}$	$.0335^{a}_{1,2}$
Noble fir	$.0937^{b}_{1}$	$.0422^{a}_{2,3}$	$.0640^{a,b}_{1,2}$	$.0466^{a}_{1,2}$	$.0507^{a}_{1}$	$.0466^{a}_{1}$
Silver fir	$.0690^{a}_{1}$	$.0649^{a,b}_{1,2}$	$.0358^{b}_{2}$	$.0336^{a}_{2}$	$.0257^{a}_{2}$	$.0278^{a}_{2}$

Shoot Length

Douglas-fir	Western hemlock	Noble fir	Silver fir
$.0904^{a,b}$	$.1096^{a}$	$.0666^{b}$	$.0390^{c}$

Shoot Dry Weight

$.3128^{a}$	$.3225^{a}$	$.1966^{b}$	$.1683^{b}$

Co = Control.

N = Nitrogen treatment.

Sh = Shade treatment.

Row means (treatments) within a location (pot or field), with similar superscripts (letters) do not differ ($P > .05$). Column means (species) with similar subscripts (numbers) do not differ ($P > .05$).

Table III.15. Pairwise comparison of within-species (between families) variances in some carbohydrate concentrations according to ANOVA results (Table III.13).

Shoot Starch

	Pot-grown			Field-grown		
	Co	N	Sh	Co	N	Sh
Douglas-fir	$4091^{a}_{1,2}$	3163^{a}_{1}	3312^{a}_{1}	$3748^{a}_{1,2}$	1859^{a}_{1}	3751^{a}_{2}
Western hemlock	$3813^{a}_{1,2}$	1054^{b}_{1}	3818^{a}_{1}	2516^{a}_{1}	3934^{a}_{1}	502^{a}_{1}
Noble fir	2894^{a}_{1}	4367^{a}_{1}	2329^{a}_{1}	$2642^{a}_{1,2}$	2235^{a}_{1}	3058^{a}_{2}
Silver fir	9148^{a}_{2}	6768^{a}_{1}	3812^{a}_{1}	43392^{b}_{2}	8744^{a}_{1}	$15387^{a,b}_{2}$

Shoot Sugar

	Co	N	Sh
Douglas-fir	1018^{a}_{2}	1276^{a}_{1}	1059^{a}_{1}
Western hemlock	2495^{a}_{3}	1321^{a}_{1}	1158^{a}_{1}
Noble fir	413^{a}_{1}	1159^{a}_{1}	854^{a}_{1}
Silver fir	3058^{a}_{3}	1122^{b}_{1}	3955^{a}_{2}

Root Sugar

Pot-grown	Field-grown
1529^{a}	637^{b}

Co = Control.

N = Nitrogen treatment.

Sh = Shade treatment.

Row means (treatments) within a location (pot or field), with similar superscripts (letters) do not differ ($P > .05$). Column means (species) with similar subscripts (numbers) do not differ ($P > .05$).

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APPENDIX

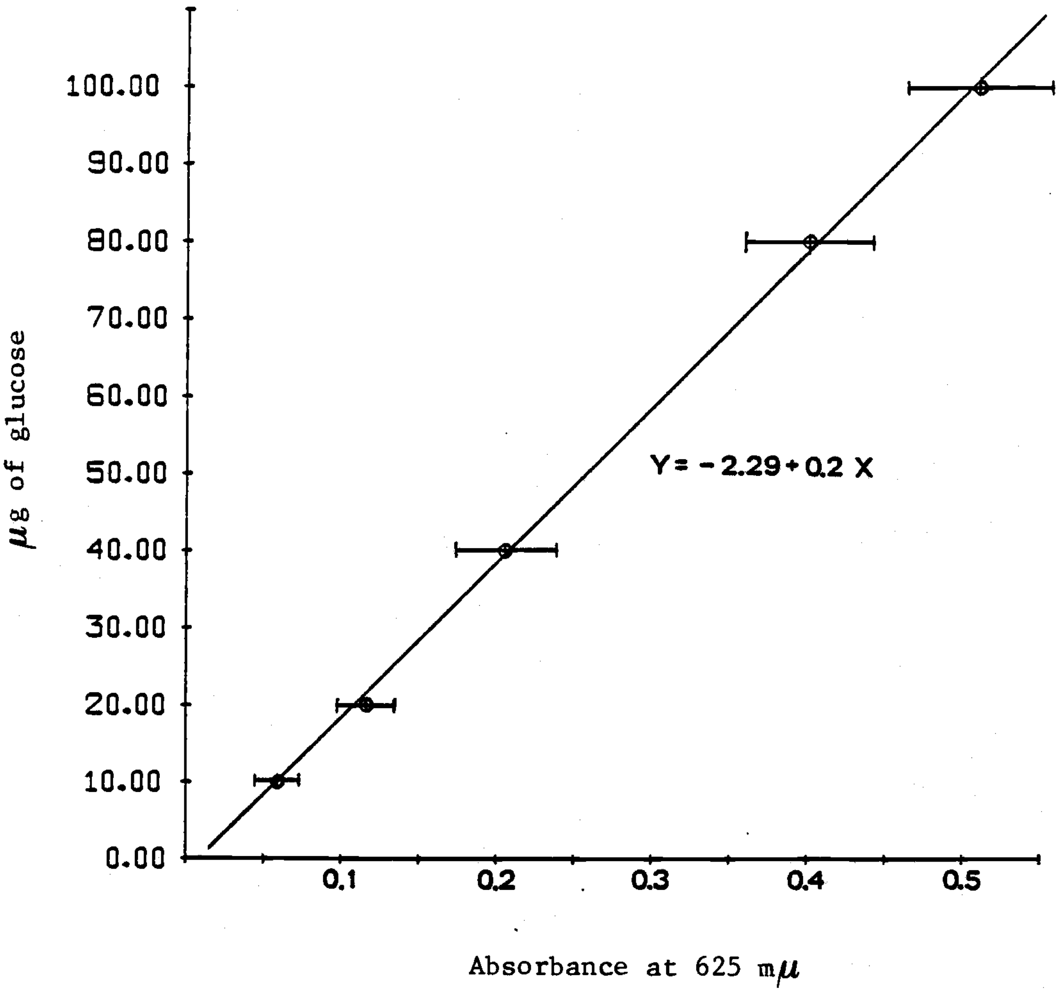

Figure A.1. Best standard curve for the anthrone method. Each point represents the mean of 110 readings. Horizontal bars represent standard errors. Values of R^2 varied from 0.93 to 0.99 .

Laboratory Procedures for Extraction of Sugar and Hydrolyzed Starch

A) Extraction of Soluble Sugars

Fifty milligrams of oven-dried and ground material was folded into a Whatman #1 filter paper (9 cm in diameter). The sample was placed in a test tube with 10 ml of 80% ethanol and kept in a warm water bath for 2.5 hours (warm enough to boil the ethanol slowly). The ethanol volume was replenished whenever its volume dropped to one-half of the initial volume. At the end of that period, the remaining ethanol was transferred to 100 ml volumetric flask. The test tube was rinsed several times with distilled water until final volume was reached.

B) Extraction of Hydrolyzed Starch

Into the same test tube (with the sample residue in the bottom), as mentioned in part (A), 10 ml of amyloglucosidase (0.25% solution) and 1 ml of acetate buffer (10.93% solution) of pH 4.2 was added. The test tube was kept in a warm water bath at 50°C for 3 hours. After that period, the test tube was cooled and the liquid fraction transferred to 100 ml volumetric flask. The test tube was rinsed several times with distilled water until final volume was reached. The soluble sugars (from (A) above) and the sugars (from (B) above) were then quantified by the anthrone method (Yemm and Willis, 1954).