AN ABSTRACT OF THE THESIS OF

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Title: Juvenile Development of Douglas-fir, Red Alder and Snowbrush Associations in Western Oregon

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The juvenile development of Douglas-fir, red alder and snowbrush associations was investigated in western Oregon. The relationship between Douglas-fir and red alder was studied and compared in the Coast, Willamette Valley and Cascade regions. Snowbrush-Douglas-fir stands were sampled in the western Cascades. Alder-Douglas-fir relationships were studied on clearcuts supporting at the same time mixtures of alder and Douglas-fir and open-grown Douglas-fir. Sites where snowbrush and Douglas-fir grew together were selected on the same basis. Total heights of alder and Douglas-fir were expressed as cumulative one-year growth measurements. Canopy height of snowbrush was measured at various ages to determine growth rate. Information pertaining to moisture, vegetation, slope, aspect, elevation and stand structure was recorded at each sample plot.

The data were analyzed with the aid of a multiple regression

program. Height and $(\text{height})^2$ were treated as independent variables, and annual height increment as the dependent variable.

Results indicate that early establishment of Douglas-fir is expected to aid its dominance-takeover and allow it to evade suppression by red alder. Douglas-fir trees growing on wet sites need to be established earlier than those on drier habitats for the same degree of suppression evasion. The rapid juvenile growth rate of red alder is a major threat for the successful establishment of Douglas-fir. Height growth curves of the two species intersected at an earlier age on non-wet as compared to wet sites. The two trees grow in direct competition up to about age 40 years on wet habitats, with alder able to suppress Douglas-fir during this period. Douglas-fir has virtually no chance of survival when it is established concurrently with red alder or after its appearance.

Snowbrush retards the growth of Douglas-fir trees during their first ten years of development. Trees that are delayed more than five years in establishment suffer a loss of more than 50% in total height as a result of the suppressive effect of the shrub. It is expected that the trees will compensate for some of this loss, but their growth may never equal that of comparable open-grown Douglas-fir developing under similar conditions.

Juvenile Development of Douglas-fir, Red Alder and Snowbrush Associations in Western Oregon

by

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INTRODUCTION

This thesis describes research towards an understanding of the influence of competitive shrubs and hardwoods in formative stages of Douglas-fir forests. Competition is generally regarded as a major ecological factor for the exclusion of some species and their replacement with other individuals. Moisture, light and nutrients are among the leading environmental factors for which plants compete. Sometimes none of these factors might be limiting; in such a case the genetic constitution and/or physiological mechanism of the individual plant plays a major role in growth pattern and successional status.

Red alder (Alnus rubra Bong.) and snowbrush (Ceanothus velutinus Doug.) are two broadleaved woody species frequently encountered in association with Douglas-fir (Pseudotsuga menziesii (Mirb) Franco var. menziesii), and both of which are capable of fixing nitrogen. The first of these is a tree which is characterized by rapid early growth, reaching an ultimate height of 20-40 m at the age of 70-100 years. Snowbrush is an evergreen shrub reaching a height of two to five m at maturity (Peck, 1961, p. 512). Both species occur as pioneers after logging, and dominate extensive areas of commercial forest land.

The dual role of alder and of snowbrush--as competitors and fixers of nitrogen--might be expected to influence forest management greatly. The possible benefits that accrue as a result of the nitrogen-fixing ability of these two species should be weighed against the expected loss in growth and survival rate of associated coniferous species. Estimates of loss of growth are needed as bases for management decisions. The practice of utilizing nitrogen-fixing species as a nurse crop for other more valuable trees is widely known in forestry, but the competitive influence of the nursing plants might sometimes be greater than the advantages gained from added nitrogen. It is essential, therefore, to study the compatibility of growth patterns of the species intended for nurse and crop, as well as to quantify the nitrogen fixed by these plants.

The primary intent of this study is to evaluate and compare the growth patterns of Douglas-fir, red alder and snowbrush. The age of assured dominance of Douglas-fir will be estimated for the red alder-Douglas-fir association. An attempt will also be made to determine the age-differential in favour of Douglas-fir that would enable it to evade all suppression by red alder. The impeding influence of snowbrush on Douglas-fir will be estimated through a comparison between growth of open-grown Douglas-fir and of that growing in mixture with snowbrush. Finally, an ecological evaluation of the role of red alder and snowbrush in secondary plant succession will be deduced from these interrelationships.

LITERATURE REVIEW

Red Alder

Red alder is an important hardwood species in the Pacific Northwest and Coastal Alaska. Among its common names are Pacific Coast alder, Oregon alder and Western alder. It ranges from Southeastern Alaska to Santa Barbara in southern California, extending inland to a maximum distance of 100 miles and at elevations not exceeding 2, 500 feet. This range is limited by extended periods of zero temperature or temperatures below zero (Fowells, 1965, p. 83). Similar altitudinal limits have been reported by Harmon (1963) and Tarrant (1961), but Randall (1962) claims that it ranges from sea level to 3, 500 feet in the Pacific Coast States, and Garmon (1953) gives an inland range of 200 miles east of the Coast Range.

Red alder is a tree with a fairly straight bole reaching a height of 50-120 feet at maturity. It is a prolific seeder with good seed years occurring at intervals of about four years. In the presence of seed source, it is the first tree that appears after clear cutting (Fowells, 1965; Tarrant, 1961). Red alder develops well on moist bottoms and moist mountain slopes where annual precipitation exceeds 40 inches (Bollen *et al.*, 1962). It is a fast growing species in its young stages of development and 3-4 feet per year is a common rate of height growth (Harmon, 1963; Worthington, Ruth and Matson, 1962). Newton (1964, p. 41) reports that its juvenile growth often exceeds that of coniferous seedlings by a factor of ten during the first five years. Its rapid early growth leads to quick overtopping of conifers (Tarrant, 1961).

Alder has been viewed as a weed plant that ought to be destroyed to release more valuable conifers, because of its fast growth rate. The elimination of alder competition is a major consideration for restocking conifers on fresh clearcuts. Two, 4-D, (2, 4-dichlorophenoxyacetic acid) and/or 2, 4, 5-T (2, 4, 5-trichlorophenoxyacetic acid) in diesel oil and other solvents are possible controlling agents (Ruth and Berntsen, 1956).

Red alder can also be considered as a nutrient supplier that contributes to soil fertility through symbiotic nitrogen fixation in its root nodules. This soil enrichment has resulted in increased growth for associated conifers, particularly Douglas-fir (Tarrant, 1961; Tarrant and Miller, 1963). As early as 1910 and 1917 observations were made on the fertility value of alder by Kellerman and Johnson respectively. Bollen et al. (1964) investigated the influence of red alder on soil microbial populations and the activities related to soil fertility. They found that microbial counts exhibited seasonal fluctuations and that nitrogen contribution to the soil was evident throughout the year.

The beneficial effect of red alder as a nutrient supplier should be weighed against the mortality and suppression effect on conifers growing with alder. The situation might be more intricate than this straightforward comparison. Red alder itself can be utilized as a commercial tree provided that a good market exists. Management for production can be considered seriously if there is a good market, when alder is approaching merchantable size (Harmon, 1963). On the other hand, if it is interfering with the development of more desirable conifers it may be given a high priority for control. Bollen et al. (1964, p. 36-38) maintain that alder should be encouraged for possible use as a nurse crop, a fire barrier, or as a source of wood pulp prior to establishment of more desirable coniferous species.

The growing commercial importance of alder in the Pacific Northwest has made further research on this species a necessity. Advances in technology of alder pulping, deterioration in the quality of eastern hardwoods, and flourishing of local markets are among the factors that created a growing demand for red alder (Worthington, Ruth and Matson, 1962, p. 1) and early research concentrated on growth and yield. Bishop et al. (1958) developed site curves through stem analysis of 43 felled and sectioned trees from varied ecological conditions in western Washington. Presently, Normal Yield Tables developed by Worthington et al. (1960) for naturally occurring, pure, and fully stocked alder stands are the accepted standard reference for yield estimation. Information on mixed and/or understocked stands is still needed (Berntsen, 1961).

Red alder generally occurs in pure stands, but can be found in association with Douglas-fir, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn), sitka spruce (*Picea sitchensis* (Bong.) Carr.), grand fir (*Abies grandis* (Dougl.) Lindl.), bigleaf maple (*Acer macrophyllum* Pursh), vine maple (*Acer circinatum* Pursh) and willows (*Salix species*) (Bollen *et al.*, 1964; Worthington, Ruth and Matson, 1962).

Alder enjoys an exceptional lack of susceptibility to diseases and damaging agents in the first 40 years of its life (Johnson, Hanzlik and Gibbons, 1926). Injured trees or overmature stands, however, are susceptible to attacks inflicted by certain fungi and insects (Fowells, 1965).

Douglas-fir

Douglas-fir is one of the world's most valuable timber trees. The variety *menziesii* extends along the Pacific Coast from Central British Columbia to Central California, a mild and humid region that is characterized by annual temperatures of about 45° to 55° F (Fowells, 1965, p. 547). Maximum altitudinal limit varies from sea level to 2, 700 feet in the northern range and 6, 000 feet in the south. On drier sites, in the middle of its range, Douglas-fir occurs in pure stands but southwards it is found in association with Ponderosa pine (Pinus ponderosa Laws.), sugar pine (Pinus lambertiana Dougl.), incense-cedar (Libocedrus decurrens Torr.) and various oaks (Quercus species). In western Oregon and Washington, Douglas-fir constitutes about 65% of all the timber volume (Fowells, 1965; Mc Ardle and Meyer, 1949). Douglas-fir growing on high quality site I reaches a height of about 210 feet at the age of 100 years and a breast height diameter (dbh) of more than 30 inches. At this age, a total volume of about 20,000 cubic feet/acre is not uncommon for good quality sites (Mc Ardle and Meyer, 1949).

Douglas-fir is a strong light demander and its growth is retarded under suboptimal light intensity. Performance is poor when it exists as an understory species (Hofman, 1924; Isaac and Hopkins, 1937). Moist, porous and well-drained sandy or loamy soils constitute a favourable edaphic factor.

Douglas-fir-Red Alder Association

Seedbed conditions favouring Douglas-fir and alder are similar, and mixtures of species at seedling stage is a general occurrence. Red alder is known to dominate completely certain sites excluding associated coniferous species.[1] Whether alder will eventually form

[1] Michael Newton, Assistant professor of Forest Management, Oregon State University, Corvallis. Personal communication.

a sub-climax species on a certain site may depend on its establishment prior to appearance of conifers and its complete adaptation to that site. Worthington, Ruth and Matson (1962, p. 5) have reported that red alder is usually succeeded by conifers except on soils of high organic matter and high moisture content, where it may end up as a climax type provided that it is of a suitable genetic strain. Presence of other competitive hardwoods and short life span of alder probably limit its status as a permanent dominant.

Douglas-fir and red alder are reported to grow on competitive bases until about the age of 40 years, beyond which the Douglas-fir usually predominates. Alder fades out of the competition scene at advance ages because of disease, age or other factors (Worthington, Ruth and Matson, 1962). Berntsen (1961) claims that the yield of a 20-year-old coniferous stand might on the average equal or exceed that of a comparable alder stand on the same site, and thereafter definitely outproduce it. On the other hand, Tarrant (1961) has studied the development of an atypical plantation of Douglas-fir and alder in southwestern Washington. He found that dominant trees between the ages of 25 and 27 years growing in mixture with "off-site" alder are of greater average diameter as well as of higher annual height increment than Douglas-fir in pure stands. He also found that in its juvenile phase, Douglas-fir was able to suppress red alder in this case as a result of the genetic unsuitability of the latter.

In summary, red alder is a vigorous competitor that quickly overtops associated conifers. On the other hand, some writers have furnished limited evidence that Douglas-fir can thrive well as a mixture with red alder and even benefit from its nitrogen-fixing ability that leads to improvement of soil nutrient status. Some of these apparent contradictions have been explained subjectively by genetic differences and site variations, but not in a predictable manner. A means of predicting the pattern of emergence of alder or conifers in terms of recognizable site factors is still needed.

Snowbrush

The genus *Ceanothus*, which is indigenous only to the continent of North America, belongs to the family *Rhamnaceae*. Snowbrush, *Ceanothus velutinus* Dougl., is an evergreen shrub ranging from California and Colorado north to the Mountains of British Columbia. Throughout its entire range, it is most frequently encountered at higher elevations (Peck, 1961, p. 512; U.S.D.A. Forest Service, 1954, p. 117-121).

Snowbrush has long-lived seed that remain dormant in the upper mineral soil. Fire or scarification is an aid to germination as evidenced by the great numbers of seedlings emerging after burning under natural conditions. Following this heat treatment the cold winter breaks dormancy, and germination takes place the following spring (Zavitkovski, 1966).

Snowbrush is among the non-leguminous plants that are capable of fixing nitrogen through their root-nodules. The nitrogen content in the litter and in the upper horizon of the mineral layer has been found to be higher beneath snowbrush than under other species (Dyrness, 1960). Zavitkovski (1966, p. 68) reports that a fully stocked stand of snowbrush may fix a maximum amount of 20 kg/ha-year of nitrogen. Higher values of up to 80 kg/ha-year have been reported by Wollum and Youngberg (1965). They grew nodulated seedlings of red alder and snowbrush on soils of low nitrogen content in a greenhouse for one year, and found that two snowbrush plants were able to fix about 35 ppm of nitrogen while red alder fixed about half of this amount (Wollum and Youngberg, 1964). Improvement of soil nutrient status and better development for conifers growing in association with <u>Ceanothus</u> species have also been claimed by Wahlenberg (1930) and by Wollum (1962). On the other hand, Zavitkovski (1966, p. 83) has found that during the first eight years of development no appreciable favourable effect can be expected for coniferous species established concurrently with snowbrush. Objective estimates of the beneficial or detrimental effects of snowbrush on conifers are still needed.

THE STUDY AREA AND SAMPLING TECHNIQUE

The Study Area

This study, conducted in the summer of 1966, covered an area that extended from the Oregon Pacific Coast through the Coast Range and Willamette Valley into the western Cascade Mountains (fig. 1). Coastal samples were observed near Tillamook, Hebo, Siletz and Alsea. The Valley plots were located in the vicinity of Hoskins, Blodgett and in the Oregon State University's Mc Donald Forest, near Corvallis. Samples near Fall Creek and in the headwaters of the South Santiam, Middle Fork Willamette and Mc Kenzie rivers (Lane and Linn counties), constituted the western Cascade plots. The Douglas-fir-Red alder relationship was investigated in each of these areas. The snowbrush--Douglas-fir stands were sampled near the junction of highways U.S. 20 and Oregon 22 at Lava Lake (eastern Linn County); and about 15 miles off highway U.S. 126 at Foley Ridge in the Mc Kenzie River watershed, in the type reported by Zavitkovski and Newton (1967).

Climate

The climate of the Coast Range is mild, with average maximum daily temperature of about 60 to 65° F and an average daily minimum

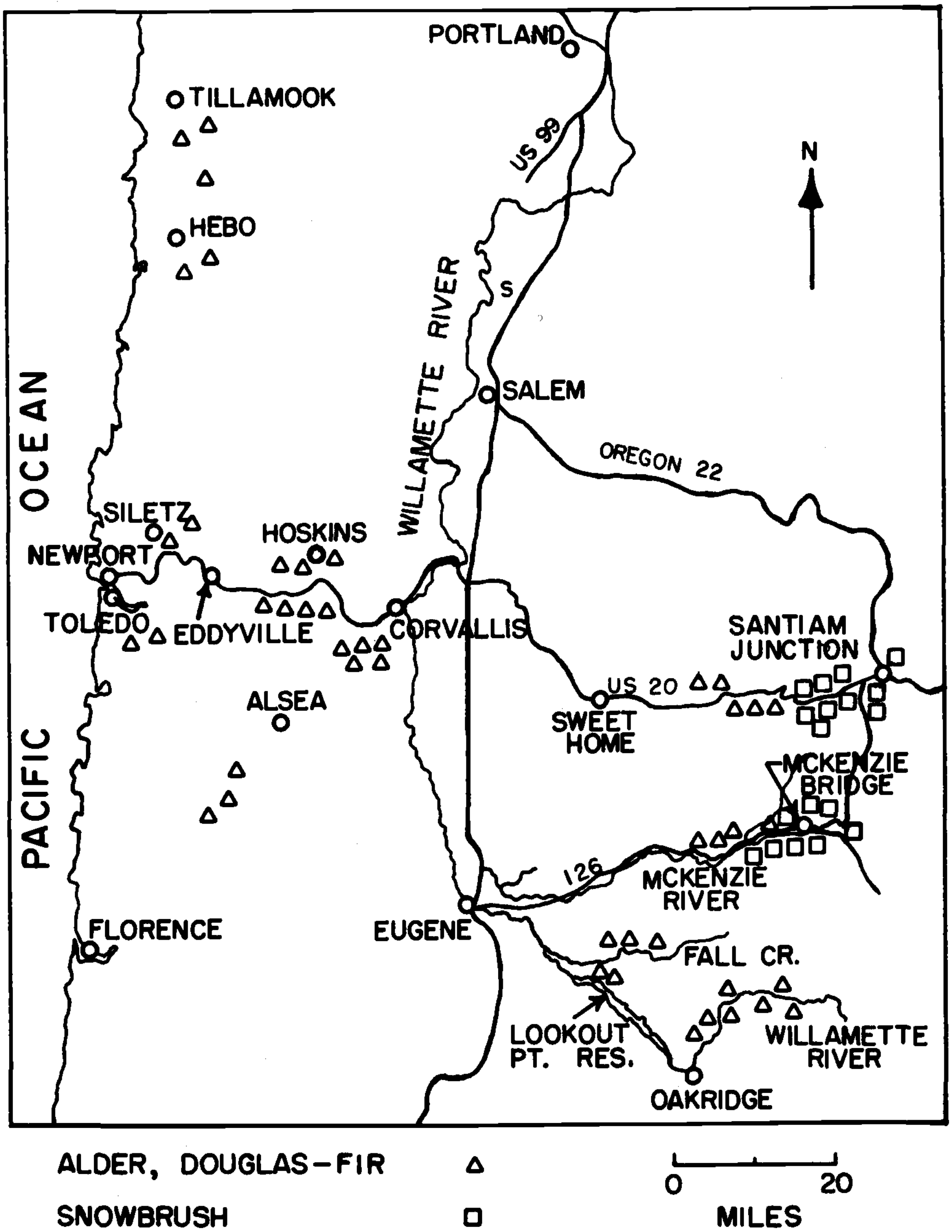

Fig. 1. Map of central western Oregon showing the location of the sample plots.

of 40° F. Details of all climatic data mentioned in this study are summarized from Johnsgard (1963) and are given in the appendix (Table 4). The high annual rainfall--about 80-100 inches--and the high relative humidity in that region result in a cool moist growing season with summer drought periods seldom more than 90 days. Cumulative moisture surplus, occurring during September to May, usually ranges from about 55 to 70 inches. A moisture deficit of four to seven inches often results from excessive evapotranspiration during the months of June, July and August. The soil parent material is composed of igneous intrusive or sedimentary rocks (Franklin, 1965).

Average maximum daily temperature of about 70° F and minimum temperature of 42° F characterize the climate of the Willamette Valley. A maximum daily average temperature of 82° F and a minimum of 33° F usually occur during the hottest and coldest months respectively. The winters are generally mild with some snowfall and the summers are warm. Precipitation ranges from 37 inches in mid-Valley areas to 70 inches in the foot-hills. There is a cumulative moisture surplus of about 25 inches during the months of October to March. A potential evaporation deficit of about 15 inches occurs during May to September (sharpest in July, about five inches).

Cold to very cold winters and warm summers are encountered in the western Cascades. Average maximum daily temperature of

60° F and minimum daily average temperature of about 35° F are typical of this region. Maximum daily average of 87° F and minimum of 25° F are not uncommon during the hottest and coldest months respectively. Fifty to 100 inches cover the range of annual precipitation, which is markedly seasonal and predominantly resulting from snow. Thirty to 60 inches of cumulative moisture surplus occur during the months of October to April. A moisture deficit of ten to 13 inches occurs during June to September (inclusive). Although various watercourses transect the study area in this region, summer drought periods invariably develop and limit the effective growing season. Rugged, well-developed ridge and valley topography with variable slopes and aspects are the dominant land features. Andesitic and basaltic rock in admixture with volcanic ejecta constitute the major parent material (Franklin, 1965).

Vegetation

The common natural tree species, found in association with Douglas-fir and red alder in the western Cascades, are bigleaf maple, vine maple, willows, and Poplars (*Populus* species). *Ceanothus* species are the most common shrubs in certain areas, especially on south slopes and at elevations of 2,500 feet and higher. Horse-tail (*Equisetum* species) and bracken fern (*Pteridium aquilinum* (L.) Kuhn.) are common and rank species in wet sites and along water courses. Trailing blackberry (Rubus vitifolius C. and S.), elderberry (Sambucus callicarpa Greene), thimbleberry (Rubus parviflorus Nutt.), rhododendron (Rhododendron macrophyllum G. Don.), bear grass (Xerophyllum tenax (Pursh) Nutt.), chinkapin (Castanopsis chrysophylla Dougl.) A. DC.) and lupine species (Lupinus species) are also prominent plants. Variation in type, cover and density are encountered as a result of the inequality in elevation, moisture status and possibly because of differences in soil types.

The vegetational cover in the Coast and Valley areas is variable and the discontinuity in distribution is more sharp than in the Cascade region. This variability might be attributed to differences in the magnitude of cumulative moisture surplus or deficit together with other environmental and edaphic factors. Most of the above mentioned plants were found in this study area. Coarse grasses and sedges are dominant in wet habitats and where the shrub cover is not dense. Salal (Gaultheria shallon Pursh) is a common shrub on moist well-drained sites. It is often found in relatively extensive stretches dominating other associated understory species.

Sampling Technique

A general reconnaissance was made for clearcuts supporting at the same time mixtures of red alder and Douglas-fir and open-grown Douglas-fir. Sites where snowbrush and Douglas-fir grow together were selected on the same basis. Lack of random distribution of potential sample sites, and limited availability of suitable stands made random selection among stands impractical, and within-stand random selection of individuals was adopted.

All eligible plots were serially numbered within each Cascade clearcut that qualified according to species composition. Two numbers were drawn at random. The dominant alder tree was felled in each of the randomly selected plots. The age was determined by counting annual rings on stumps as well as by whorl arrangement. Branch whorls were not always very distinct and the trees had to be sectioned at various intervals to avoid errors in some instances. Height was measured at each age and total height was expressed as cumulative one-year growth measurements.

Total height measurements of at least two Douglas-fir directly under the influence of alder (suppressed) and at least two open-grown Douglas-fir were also recorded by annual height growth increments in each plot. Increment borings were taken frequently as a check against the age determined through whorl counting. Eighteen stands were sampled in the Cascades.

Distinct differences were noticed in moisture status between some of the clearcuts, and sometimes within the same clearcut. Areas along or within the vicinity of a creek together with flat or hollow spots that are expected to receive more water from the adjoining steep slopes were classified as wet sites. All other sites were categorized as being non-wet or less wet situations. Almost exclusively, the areas which were classified as wet sites carried a preponderance of moisture-loving species including willows, horsetail and sedges. Although these species were found on some of the non-wet sites, they were either sparsely scattered or limited to small wet pockets.

Variability in moisture status is an important factor regulating growth of red alder, in particular. A more refined scale based on actual soil examination would give more reliable interpretation than binary visual assessment. However, two-class stratification may give insight as to the order of magnitude of moisture effects on relation of growth of Douglas-fir to that of alder, and it is assumed that refinement beyond the present evaluation is not needed for this study.

The above sampling technique was followed in the Coast and Valley regions, but a minor adaptation was required by small differences in structure and distribution of the alder stands. Here, instead of the patchwise distribution pattern encountered in the Cascades, red alder was found in relatively extensive stands. Each stand was divided into a convenient number of approximately equal strata. Two numbers were drawn at random, and within each stratum comparable measurements were carried out on red alder and Douglas-fir. The moisture status was classified as in the

Cascades. Twelve and 11 stands were sampled in the Coast and Valley regions respectively.

The relationship between snowbrush and Douglas-fir was investigated at Foley Ridge and Lava Lake. Total heights of suppressed and open-grown Douglas-fir were analyzed by annual measurements, and canopy height of snowbrush was measured along a transect in each of the clearcuts, after a general survey. At least ten snowbrush clumps, three suppressed and four open-grown Douglas-fir trees were measured in each of the eight transects sampled at Lava Lake and the five transects at Foley Ridge.

Pertinent information, including vegetation, slope, aspect, elevation and stand structure, was recorded at each sample plot. Age of Douglas-fir ranged from four to 25 years. Red alder was of a comparable age. Snowbrush stands ranged from six to 19 years.

STATISTICAL ANALYSIS

The relationship between Douglas-fir and red alder was analyzed with the aid of a multiple regression program. Height and $(\text{height})^2$ were treated as independent variables, and annual height increment as the dependent variable. The following linear model was developed.[2]

$$\Delta H = \alpha + \beta_1 H + \beta_2 H^2 + \varepsilon$$

where ΔH = annual height increment

α, β_1, β_2 = constant terms

H = total height

ε = error term

Numerical integration was carried out through the accumulation of the Δ curve. After the preliminary analysis was carried out, a modification in the model appeared to be necessary. Logarithmic transformation was imposed and the final form of the model was as follows

$$\Delta H = \alpha + \beta_1 \text{ Ln } H + \beta_2 (\text{Ln } H)^2 + \varepsilon$$

The analysis was carried out by a C D C 3300 computer. The

[2] This model was developed by Mr. D. Niess of the Statistics Dept., Oregon State University.

output of the machine included: the adjustment period needed by Douglas-fir to evade suppression by alder, the values for the different constant terms, and standard deviation of annual increment about the height growth curve. Predicted growth patterns and the difference between actual and predicted height were expressed for red alder, suppressed and open-grown Douglas-fir. The age at which red alder is overtaken by Douglas-fir was estimated for some of the plots.

The term adjustment period is a new concept for evaluating performance of species growing on competitive bases. In this study, it is a prediction of time advantage in favor of Douglas-fir required to evade overtopping by red alder. It is an attempt to answer the question: how early should Douglas-fir be established prior to appearance of alder in order that the former species can avoid the hampering effect of the latter? Adjustment periods, from the computer output, were graphed as the function of each of the four variables in the different geographic regions. Preliminary examination indicated that elevation and aspect are inconsequential to the adjustment needed by Douglas-fir, although there exists the possibility of confounding with other factors. A two-way classification analysis of variance was carried out on the unweighted means of the adjustment periods, moisture and on slope. The linear, quadratic and cubic effects of slope were tested for significance.

It should be pointed out that some difficulties were encountered in fitting the data to the previously mentioned model. Some of the sampled stands were only four years old. Prediction or extrapolation from such a young age is difficult owing to the fact that the trend of subsequent development is not yet indicated at this age. Moreover, the model itself was built to describe the growth pattern of the individual tree and not the average of many trees per plot. This same model could have given more valuable results if trees of older age-classes were sampled.

RESULTS

Douglas-fir-Red Alder Association

Adjustment Period

Early establishment of Douglas-fir might be expected to aid its dominance-takeover and allow it to evade suppression by red alder. The predicted values for adjustment periods needed by Douglas-fir covered a range that varied from three to nine years in each region. An average value of four years on non-wet sites and seven years on wet habitats was computed for the Cascade region (table 1).

Table 1. Adjustment period (in years) needed by Douglas-fir to evade alder suppression.

Region	Site	
	Non-wet	Wet
Cascades	4.1	7.2
Coast	6.0	8.0
Valley	4.3	8.0

Coastal Douglas-fir requires an earlier establishment of six and eight years at non-wet and wet sites respectively. The maximum adjustment of eight years is also needed on wet sites in the Valley.

The interpretation of these estimates is as follows: if Douglas-fir in each of these three regions has been established the indicated number of years before the appearance of red alder, the former might not be hampered by the interference of the latter.

Statistical analysis has shown that the moisture effect in the Cascades and the slope effect in both the Cascade and Coast regions are highly significant (Table 2). Moisture effect in the Coast is not significant. In the same region an increase in the degree of slope reduces the adjustment period linearly. This linear trend is highly significant. The relationship between time adjustment and slope in Cascade habitats displays highly significant linear and cubic effects (Fig. 2A).

The adjustment period was plotted against slope. A very slight decrease in this period, for the Cascade plots, accompanies movement from flat areas to sites where the degree of slope is about 10%, thereafter there is a significant increase in time adjustment with increase in slope (Fig. 2A). The disparity between wet and non-wet sites increases with increasing slope both in the Coast and in Cascades at the same rate, but from different base. Douglas-fir growing on wet sites needs to be established earlier than that on drier habitats for the same degree of suppression evasion. The negative correlation between adjustment and slope in the Coast, shows no pronounced difference between wet and non-wet habitats

Table 2. Analysis of variance table for effect of moisture and slope on adjustment period in the Cascades and Coast.

a. Coast

Source	D.F.	S.S.	M.S.	F
Total	7	28.58	4.0828	
Moisture	1	2.64	2.6400	6.4390
Slope	3	25.12	8.3733	20.4227
Error	2[1]	.82	.4100	
Linear	1	23.40	23.40	57.0731
Quadratic	1	1.28	1.28	3.1219
Cubic	1	.44	.44	1.0731

b. Cascades

Source	D.F.	S.S.	M.S.	F
Total	7	17.19	2.4557	
Moisture	1	11.76	11.7600	184.0000
Slope	3	5.40	1.8000	120.0000
Error	2[1]	.03	.0150	
Linear	1	3.90	3.90	260.0000
Quadratic	1	.10	.10	6.6666
Cubic	1	1.40	1.40	93.3333

[1] The missing degree of freedom is for computation of a dummy value.

5% Significance level: F (1, 2) = 18.513   F (3, 2)= 19.164

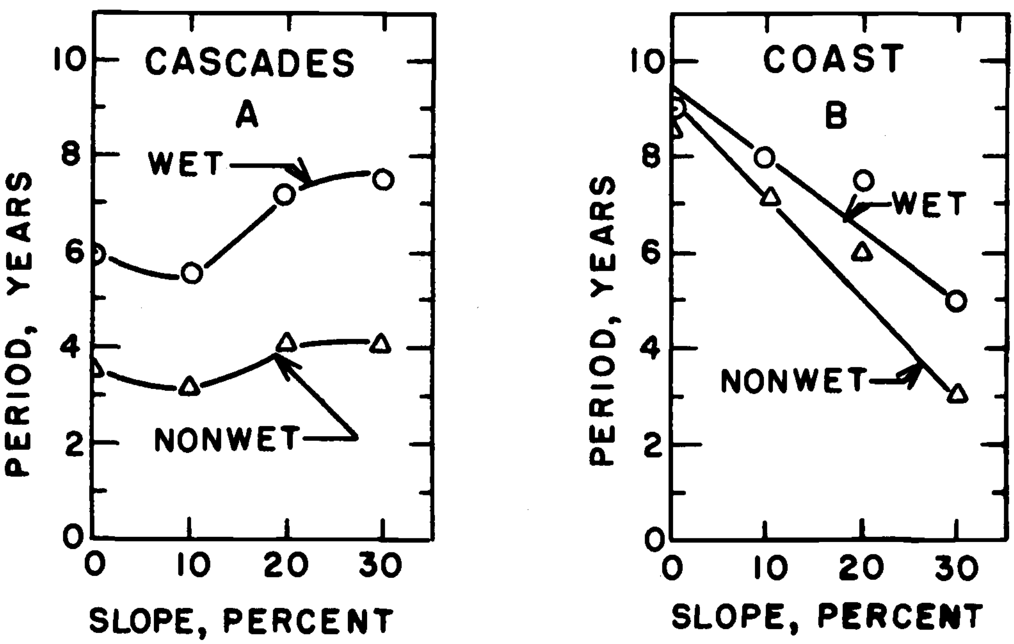

Fig. 2. Relation between adjustment period and slope in the Cascade and Coast regions.

at flat sites. The disparity becomes more distinct with increase in the degree of slope, possibly because differences in drainage become more distinct as slopes increase.

Growth Patterns

Annual height increment for red alder is maximum at the age of three to four years. This has been supported by both actual data and predicted increments. Douglas-fir begins to gain significant annual height increment at this age or a year later, but the increments do not reach a maximum until 10-15 years of age. In view of this consideration, therefore, the predicted adjustment periods are well substantiated.

A compound annual decrease of about 5% in height increment of red alder commences at the age of five years and continues up to about the fifteenth year and thereafter remains constant or drops very gradually. A corresponding percentage increase is exhibited by Douglas-fir prior to the age of ten years. Of course the increment fluctuates annually for each of the two species and the increase or decrease in growth rate reported above is an over-all estimate of the growth pattern.

Results from the present study indicate that during the first three years of development Douglas-fir and red alder bear a ratio of 1:7 for their total heights. This ratio drops to about 2:3 at age 20 years. The rapid juvenile growth rate of red alder is a major threat for the successful establishment of Douglas-fir. Figure 3 shows an example of the comparative size of the two species at age seven years, growing in the open.

Fig. 3. Seven-year-old Douglas-fir (foreground) and red alder (background) saplings.

Dominance-Takeover

The age of equal height for Douglas-fir and alder was estimated. Extrapolation beyond age 30 years was not given in the computer output and precision of estimates is mediocre beyond the age of 15 years. The predicted values for height growth were very comparable to actual data when the latter originated from older trees. The approximate site index was deduced from Worthington et al. (1960) for red alder and from Mc Ardle and Meyer (1949) for Douglas-fir with the aid of the above mentioned sets of information. The original data extended to an average age of 20 years. Extrapolation was carried out from this age up to the point where Douglas-fir overtakes red alder by extending projected growth curves according to yield tables. Then the point of dominance-takeover was estimated for wet and non-wet sites in each of the three regions with the aid of height-age graphs (Figs. 4, 5, and 6). The dotted lines, beyond 20 years, indicate extrapolation from yield tables.

Reference to the above mentioned figures and to Table 3 indicates that the height growth curves intersected at an earlier age on the non-wet sites as compared to wet sites notwithstanding geographic variation. The growth pattern of the two species in the Coast and Valley regions is comparable on similar habitats. Intersection took place at age 40 years on wet sites. Douglas-fir height

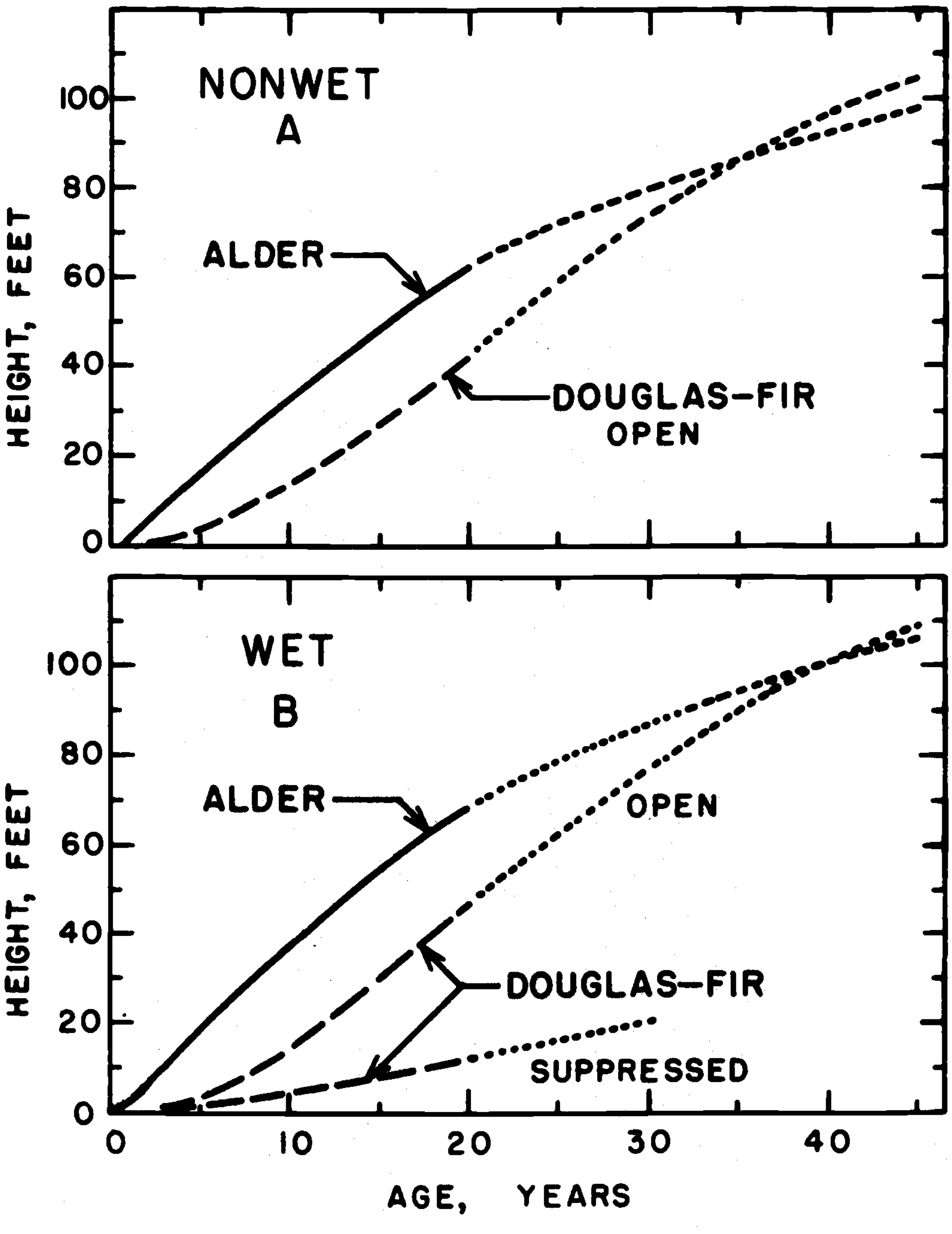

Fig. 4. Height growth of red alder and Douglas-fir on two sites on the coast.

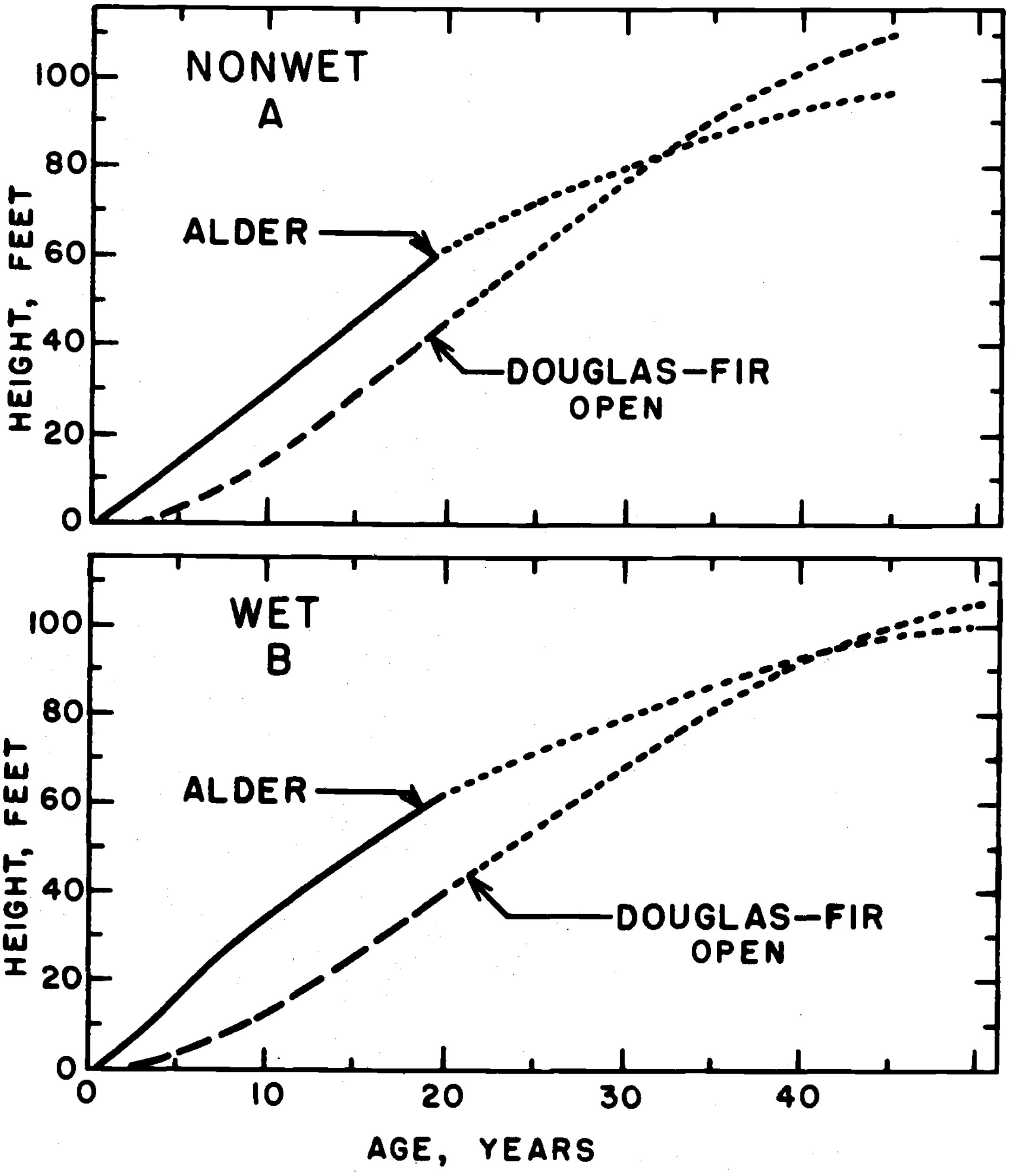

Fig. 5. Height growth of red alder and Douglas-fir on two sites in the Willamette Valley.

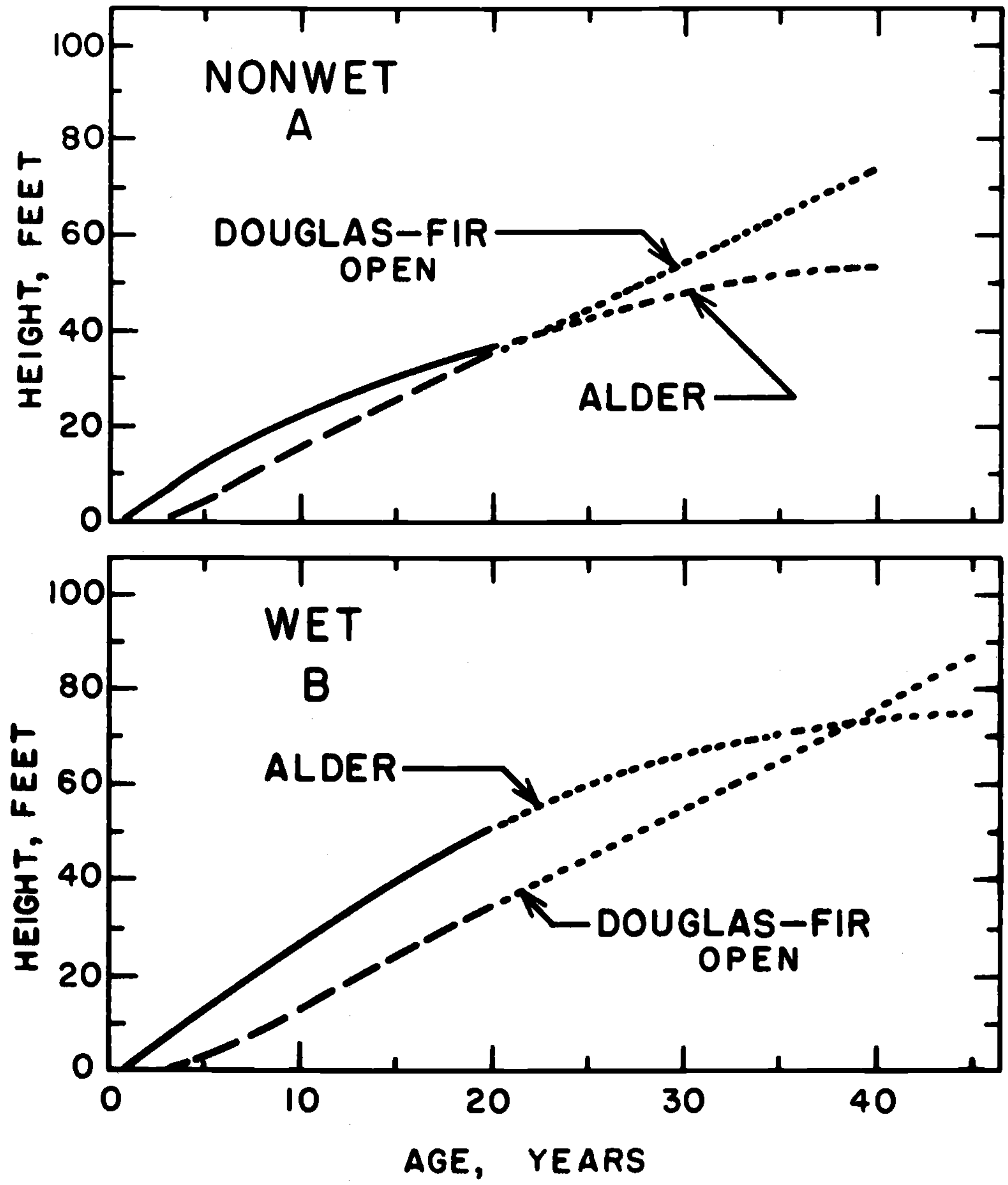

Fig. 6. Height growth of red alder and Douglas-fir on two sites in the Cascade Mountains.

equalled that of red alder at ages 33 and 35 years on non-wet sites of the Valley and Coast respectively.

Table 3. Height and age at which growth curves intersected in the different regions.

Region	Wet		Non-wet		Difference[1]	
	Age years	Ht. feet	Age years	Ht. feet	Age years	Ht. feet
Cascades	38	72	25	40	13	32
Valley	40	92	33	82	7	10
Coast	40	100	35	86	5	14

[1] Difference between wet and non-wet sites at intersection point.

Although dominance-takeover has occurred at about the same age on the wet sites of the three regions, the coastal trees are obviously leading in height growth. There is a difference of about 25 feet in favor of coastal Douglas-fir over Cascade individuals at a comparable age. On dry sites, the growth curves intersected eight to ten years earlier in the Cascades than in the other two regions. The difference in age between wet and non-wet sites at the intersection point is more pronounced in Cascades.

Reference to Tables 1 and 3 shows that Douglas-fir can evade 25-35 years of suppression on non-wet sites if it has been established four to six years before the appearance of alder. An adjustment of seven to eight years on wet habitats will allow the conifer trees to assume their natural development and surpass 40 years of supression. These findings underscore the importance of the adjustment period concept and its bearing on the successful establishment of Douglas-fir on sites where alder competition is a major threat.

Forty years is the average age for intersection in each of the three wet regions. The two species, therefore, grow in direct competition up to this age, with alder able to suppress Douglas-fir. This supports the finding of age of equal height reported by Worthington, Ruth and Matson (1962).

When Douglas-fir is established concurrently with red alder or after its appearance, the former has virtually no chance of survival. Although no quantification was made for the degree of suppression during data collection, all the trees that were categorized as overtopped were predicted to have the same morbid future. The average height for the best trees growing on wet sites in the Coast region is shown on Figure 4B. Relationships for Valley and Cascades sites are identical.

Snowbrush

The impact of snowbrush stands on juvenile development of associated Douglas-fir is different and less complicated than the influence of red alder. Field observations have shown clearly that snowbrush retards the growth of conifers during their first ten years of development. Figure 7 depicts the relationship between Ceanothus and three developmental stages of Douglas-fir. The growth pattern of snowbrush and open-grown Douglas-fir is very similar up to the age of six years, and thereafter the latter species definitely outgrows the former. Associated Douglas-fir does not suppress snowbrush for the first ten years, when they are established concurrently. The brush, however, tends to have an impeding effect on Douglas-fir. Comparing the growth of open-grown with that of snowbrush-associated Douglas-fir a reduction of about 25% in height growth is estimated (Fig. 7). It is doubtful if associated Douglas-fir would eventually compensate for this loss and match the performance of open-grown trees.

Douglas-fir trees that are delayed in establishment definitely suffer from overtopping. They remain in a suppressed position for about ten years and thereafter they may outgrow snowbrush, provided that they survive animal damage and other effects of suppression. Figure 7 shows the trend of development for Douglas-fir appearing five years after snowbrush. The growth curve illustrates the effect of late establishment on the performance of Douglas-fir. The average surviving tree emerges from suppression when snowbrush is 16 years old. This age coincides approximately with the beginning of decadence and the culmination of height for the shrub. Although Douglas-fir might have benefitted from the shelter of the

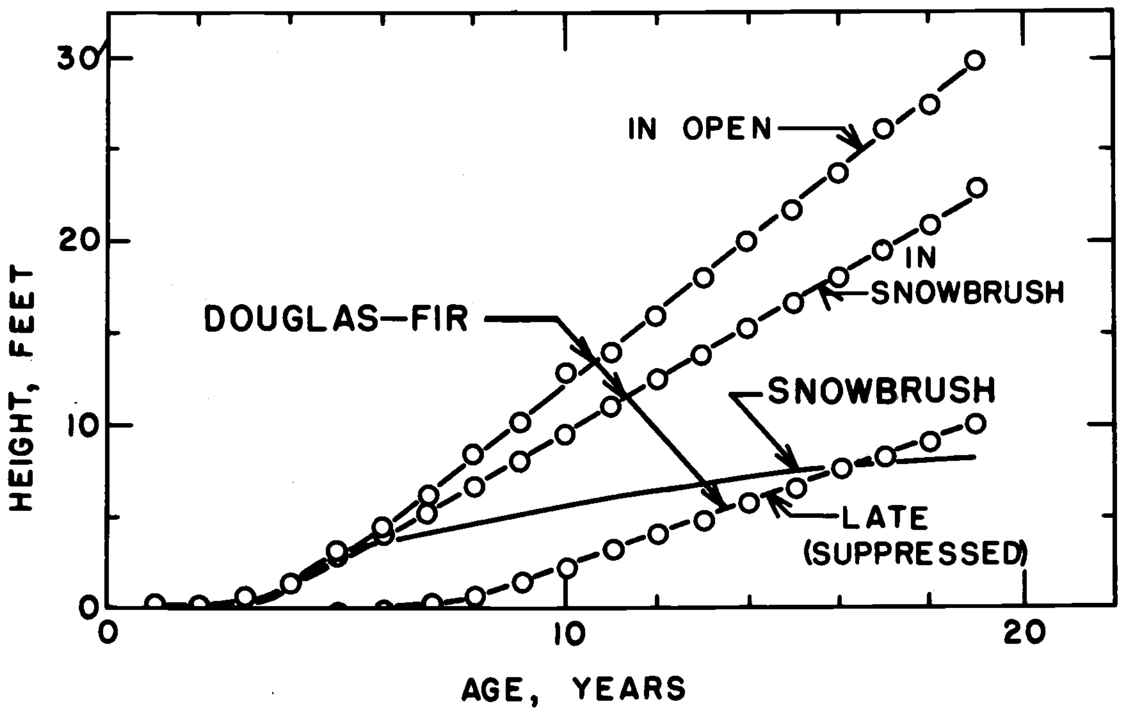

Fig. 7. Height-growth curves of Douglas-fir and snowbrush. The upper two curves are for Douglas-fir that was established concurrently with snowbrush, in the open or in the shrub; the lowest curve is for Douglas-fir that started late in established snowbrush.

shrub cover during germination, it experienced a loss of about 55% in total height as a result of the suppressive effect of the latter species during early stages of development. This loss in total height resulted mainly from late establishment of the coniferous trees. It is expected that the surviving trees will compensate for some of this loss, but they probably never match comparable open-grown Douglas-fir developing under similar conditions.

DISCUSSION

Douglas-fir-Red Alder Association

Results have shown that fast juvenile growth rate of red alder has an important bearing on its capacity to dominate Douglas-fir. Soil moisture status and degree of slope are the most significant factors governing the intricate relationship between the two species in the present study. Reference to Figure 2A shows that a linear and cubic trends are displayed by adjustment period when related to slope. The small decrease in time adjustment accompanying the first slight increase in slope may not be significant, but could be explained by the fact that at flat sites the soil moisture regime is expected to be wetter than on inclined planes. The growth rate of red alder decreases on less-wet habitats and its competitive influence is apparently not as great as on wet sites.

Douglas-fir should be in a favourable position on very steep slopes, according to the above hypothesis. The trend is reversed in the Cascades, however, and Douglas-fir needs a longer adjustment period on steep slopes than on gentle ones in order to evade alder suppression. Even steep slopes occupied by alder in the Cascades were at the lower edges of substantial mountain-slopes, and it is conjectured that seepage may have accounted for rapid development of alder. Consideration of other environmental and edaphic factors might contribute to the understanding of this phenomenon.

Coastal Douglas-fir and alder mixtures display a straightforward relationship in terms of the slope-moisture hypothesis mentioned above. Reference to Figure 2B shows that the adjustment period decreased linearly with increase in the degree of slope, with wet sites being influenced less by slope than non-wet habitats. There is no major elevational effect on effective precipitation among the Coast range stands, with all sites being relatively mesic. It can be inferred that soil moisture run-off from steep slopes tends to deplete the water reserves through excessive drainage, thereby favouring Douglas-fir more than red alder. Thus on steeper slopes an adjustment period of only three years on non-wet sites and five years on wet sites is needed for Douglas-fir as compared to about nine years on flat areas.

Soil moisture tends to be a major factor for the successful development of red alder. Its capacity to dominate associated Douglas-fir trees on wet sites is not affected by locality (Figs. 4, 5, and 6). Preliminary analysis has shown that the same relationship holds true for less-wet sites. Results from the present study, therefore, might be interpreted for general inference on a wider scale.

Snowbrush

It is concluded from the present study that snowbrush impedes juvenile development of Douglas-fir. Time of establishment is a critical factor in this relationship. Some workers claim that snowbrush improves the development of conifers (Wahlenberg, 1930; Wollum, 1962). On the other hand, Zavitkovski (1966) has found that during the first eight years of development no obvious favourable effect can be expected for coniferous species established concurrently with snowbrush. Field observations and results from the present study support this last contention. Figure 8 shows eight-year-old snowbrush and Douglas-fir plants growing on the same site. It is obvious that the annual height increment during these eight years is less than the normal growth of Douglas-fir. Concurrently established coniferous saplings may survive and grow in a codominant position despite the suppressive effect of the shrub, but it is doubtful if their competitive status can be improved by snowbrush. Field observations and growth patterns furnished by the present study indicate that height growth of snowbrush-associated Douglas-fir may never equal that of comparable trees growing in the open under similar conditions.

In view of the above consideration, snowbrush may be expected to contribute to the elimination of Douglas-fir trees associated with

Fig. 8. Eight-year-old Douglas-fir and snowbrush saplings.

it. Substandard planting stock, and seedlings that become established several years after the appearance of the shrub, may suffer serious reduction in height growth or survival rate; under extreme conditions Douglas-fir may be excluded. Sturdy seedlings, however, are expected to assume their natural development when planted as 2-1 stock, or its equivalent, directly after burning.

Ecological Evaluation

The dominance of red alder might lead to elimination of Douglas-fir and its replacement with other species on certain sites. In view of the short life span of alder and the possible presence of trees of greater longevity, it is doubtful if the former would end up in complete equilibrium with its environment as a climax species.

The capacity of red alder to overtop Douglas-fir may control the local environment and modify succession in the direction of pure alder, leading to salmonberry on wet sites and occasional hemlock on drier Coastal habitats. Western red cedar, when established concurrently with alder, can persist well under suppression and end up as a climax species. Presumably the tolerant conifers will eventually emerge as climax species, but only after considerable delay.[3] Alder is not a common type in the Valley, but when present

[3] Michael Newton, Assistant Professor of Forest Management. Oregon State University, Corvallis. Personal Communication.

a similar change in vegetation composition might be expected. It is assumed that the few cedar trees in this latter region would constitute the dominant cover. Salmonberry and occasional hemlock are expected to succeed alder in the Cascade ecologic range and vine maple would be present as a minor species.

It can be inferred that red alder has an important ecological niche which imposes a change on the relative status of species existing in the same ecosystems. Alder is expected to play this role under the existing conditions unless a new trigger factor evolves and offsets the present environmental balance.

The role of snowbrush in succession mechanism has not received much attention from workers involved in ecological studies. Field observations and results from the present study indicate that natural development of snowbrush-associated Douglas-fir is impeded; but the surviving trees may eventually maintain a dominant position if not delayed in establishment for a long period. The suppression of snowbrush by associated conifers has been suggested by Wollum and Youngberg (1965). The shrub decadence starts at about age 15 years and is accelerated by the shading effect of concurrently established coniferous species (Zavitkovski and Newton, 1967).

In view of the above consideration, snowbrush may have a modifying effect on successional status in its habitats. Zavitkovski and Newton report that as a result of the abundant nitrogen-rich litter deposited by the shrub, it might influence plant succession especially on infertile soils. They claim that conifers invariably succeed snowbrush, and hypothesize that Douglas-fir may be excluded and replaced by hemlock trees on sites where the brush can maintain dominance for more than 15 years. The growth patterns of snowbrush and Douglas-fir indicate that the shrub is not expected to contribute greatly to the elimination of early established trees. Delay in establishment of about seven to ten years and the possible buildup of animal population under the shrub cover, however, may lead to the exclusion of Douglas-fir. The theory presented by the latter authors, about a relatively better microenvironment for hemlock, may hold true under the above mentioned conditions. The path toward the hemlock climax, therefore, will likely be shortened by snowbrush, in contrast to the postponement by alder.

SUMMARY

The juvenile development of Douglas-fir, red alder and snowbrush associations was investigated in western Oregon. The relationship between Douglas-fir and red alder was studied and compared in the Coast, Willamette Valley and Cascade regions. Snowbrush-Douglas-fir stands were sampled in the western Cascades. Alder-Douglas-fir relationships were studied on clearcuts supporting at the same time mixtures of alder and Douglas-fir and open-grown Douglas-fir. Sites where snowbrush and Douglas-fir grew together were selected on the same basis. Total heights of alder and Douglas-fir were expressed as cumulative one-year growth measurements. Canopy height of snowbrush was measured at various ages to determine growth rate. Information pertaining to moisture, vegetation, slope, aspect, elevation and stand structure was recorded at each sample plot.

The data were analyzed with the aid of a multiple regression program. Height and $(\text{height})^2$ were treated as independent variables, and annual height increment as the dependent variable.

Results indicate that early establishment of Douglas-fir is expected to aid its dominance-takeover and allow it to evade suppression by red alder. Douglas-fir trees growing on wet sites need to be established earlier than those on drier habitats for the same

degree of suppression evasion. The rapid juvenile growth rate of red alder is a major threat for the successful establishment of Douglas-fir. Height growth curves of the two species intersected at an earlier age on non-wet as compared to wet sites. The two trees grow in direct competition up to about age 40 years on wet habitats, with alder able to suppress Douglas-fir during this period. Douglas-fir has virtually no chance of survival when it is established concurrently with red alder or after its appearance.

Snowbrush retards the growth of Douglas-fir trees during their first ten years of development. Trees that are delayed more than five years in establishment suffer a loss of more than 50% in total height as a result of the suppressive effect of the shrub. It is expected that the trees will compensate for some of this loss, but their growth may never equal that of comparable open-grown Douglas-fir developing under similar conditions.

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APPENDIX

Table 4. Annual temperature, precipitation and water balance for some representative stations.

1. Mc Kenzie Bridge Ranger Station
Lane County

Hot Months		Cold Months		Av. Ann. Pp.	Cum. Surp.		Cum. Deficit	
June	75.1	Nov.	32.5	69.0	Oct.	5.1	June	0.8
July	85.1	Dec.	30.2		Nov.	8.8		
Aug.	84.5	Jan.	27.3		Dec.	11.2	July	4.2
Sept.	78.8	Feb.	29.3		Jan.	10.0		
					Feb.	7.7		
Av. Ann. Temp. °F					Mar.	6.9	Aug	3.7
					Apr.	2.7		
					May	0.6		
						53.0		9.5

Max.	Min.	Av.
63.5	37.6	50.5

2. Oakridge Ranger Station,
Lane County

Hot Months		Cold Months		Av. Ann. Pp.	Cum. Surp.		Cum. Deficit	
June	77.2	Nov.	35.4	43.7	Oct.	1.9	May	0.5
July	84.9	Dec.	32.9		Nov.	5.1	June	1.8
Aug.	86.8	Jan.	30.0		Dec.	6.5	July	4.6
Sept.	81.9	Feb.	31.9		Jan.	6.3	Aug.	4.2
					Feb.	4.4	Sept.	2.1
Av. Ann. Temp.					Mar.	3.7		
					Apr.	1.2		
						29.1		13.2

Max.	Min.	Av.
66.4	40.1	53.2

Table 4. (Continued)

3. Toledo Station, Lincoln County

Hot Months		Cold Months		Av. Ann Pp.	Cum. Surp.		Cum. Deficit	
June	68.6	Dec.	35.4	75.6	Sept.	0.1	June	0.9
July	73.2	Jan.	34.7		Oct.	3.5	July	3.3
Aug.	73.7	Feb.	37.6		Nov.	10.5	Aug.	2.8
Sept.	73.0	Mar.	36.0		Dec.	10.0		
					Jan.	10.4		
Av. Ann. Temp.					Feb.	9.1		
					Mar.	7.8		
Max. Min. Av.					Apr.	4.0		
62.5 41.1 51.8					May	1.0		
						56.6		7.0

4. Tillamook Station, Tillamook County

Hot Months		Cold Months		Av. Ann Pp.	Cum. Surp.		Cum. Deficit	
June	64.7	Dec.	37.3	89.4	Sept.	0.3	July	2.3
July	67.8	Jan.	34.0		Oct.	5.9	Aug.	2.0
Aug.	68.3	Feb.	36.1		Nov.	10.9		
Sept.	67.0	Mar.	36.8		Dec.	14.8		
					Jan.	12.3		
Av. Ann. Temp.					Feb.	10.4		
					Mar.	9.5		
Max. Min. Av.					Apr.	3.7		
59.5 41.5 50.5					May	1.4		
					June	0.2		
						69.3		4.3

Table 4. (Continued)

5. Falls City and Falls City ISW Station, Polk County

Hot Months		Cold Months		Av. Ann. Pp.	Cum. Surp.		Cum. Deficit	
June	72.8	Dec.	33.7	72.7	Oct.	3.8	June	2.0
July	80.5	Jan.	30.4		Nov.	9.9	July	5.9
Aug.	81.8	Feb.	32.8		Dec.	14.1	Aug.	9.2
Sept.	76.1	Mar.	35.6		Jan.	11.8	Sept.	10.6
					Feb.	9.2		
Av. Ann. Temp.					Mar.	7.2		
Max. Min. Av.					Apr.	2.0		
62.7 40.2 51.3						58.0		27.7