Comparison of selected Douglas-fir seed sources for cambial and leader growth patterns in four western Oregon environments[1]

WILLIAM H. EMMINGHAM
School of Forestry, Oregon State University, Corvallis, OR, U.S.A. 97331

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The leader and cambial growth of sapling Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) from both inland and coastal varieties followed a definite pattern in four western Oregon environments. Generally, buds became active first and cambial growth became active soon after. Leader growth stopped in August, long before cambial growth, which continued into October. Phenology, total seasonal growth, and growth pattern for trees from coastal sources from Vancouver Island, B.C., to southern Oregon were more similar than for trees from inland sources from British Columbia to Idaho and Arizona. Most of the differences among populations in one season's growth were related to growth rate rather than growth duration.

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La croissance de la flèche terminale et la croissance cambiale de jeunes Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) de variétés de l'intérieur et de variétés côtières ont suivi un patron défini dans quatre environnements de l'ouest de l'Orégon. Règle générale, le gonflement des bourgeons était suivi de près par l'activité de croissance cambiale. La croissance en hauteur s'est arrêtée en août, bien avant la croissance radiale, laquelle s'est poursuivie jusqu'en octobre. La phénologie, la croissance saisonnière totale et le patron de croissance se rapprochaient davantage chez les arbres de provenance côtière, depuis l'Ile de Vancouver jusqu'au sud de l'Orégon, que chez les arbres de provenances intérieures originant de la Colombie Britannique à l'Idaho et l'Arizona. La plupart des différences entre les populations au plan de la croissance d'une saison étaient attribuables au taux de croissance plutôt qu'à la durée de croissance.

[Traduit par le journal]

Introduction

Provenance trials have identified differences in long-term height growth among populations of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Rowe and Ching 1974). Superior height growth of seedlings in the nursery (Ching and Bever 1960) and saplings in plantations (Ching 1965) was correlated with location of seed source.

Major questions remained concerning how duration and rate of growth of various provenances change with environment. Also, questions were raised as to whether superior height growth resulted from longer growth period or greater rate of growth.

These questions prompted a detailed study for one season of cambial and leader growth of sapling Douglas-fir from several seed sources. Four plantations in differing environments were chosen to show how growth responses varied with climate. Plant-response models were used to define more clearly the environment at each site. The major objectives were to describe seasonal cambial and leader growth of sapling Douglas-fir from various sources at four plantations, to identify whether differences in growth rate and duration were genetically or environmentally caused, and to quantify environments of the plantations for comparison.

Douglas-fir is noted for variation in both appearance and physiology. Two distinct varieties are generally recognized (Little 1952), a coastal form (*P. menziesii* var. *menziesii*) and a Rocky Mountain or inland form (*P. menziesii*

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var. *glauca*). Kung and Wright (1972) recognized several races, and Flous (1935) divided inland Douglas-fir into several species. In addition, marked genetic variations in trees of the coastal variety (Hermann and Lavender 1968) and in trees of the inland variety (Rehfeldt 1974) have been shown to occur within a few kilometres and to be associated with distinct local microclimates.

This genetic variability, along with habitat diversity caused by rapid change in slope, aspect, and elevation, may account for the variability of management success in some areas. A better understanding of how one forest site differs environmentally from other sites and of how trees from various sources respond to environmental differences could help make management results more predictable.

Recent advances in physiological research have provided new tools for identifying subtle genetic differences in plant responses, such as photosynthesis (Krueger and Ferrell 1965; Pope 1973), or in chemical makeup (Rudloff 1972), but the factors *driving* genetic selection are not yet assessed easily. Field trials are able to show only that a given population or genotype is adapted to a given test location. In this study, therefore, I sought to quantify the environment at each plantation for comparison with other areas.

Methods

Environmental Classification

In ecological studies, Waring (1969) and Waring *et al.* (1972) showed that quantitative gradients of moisture and temperature were helpful for understanding natural distribution of flora. Gradients of evaporative demand (Reed and Waring 1974) and photosynthetic potential (Emmingham and Waring 1977) appear useful in understanding variation in productivity. The same environmental factors may be important in driving genetic selection.

Because the link between these gradients and recurring natural forest communities has been demonstrated (Zobel *et al.* 1974), extrapolation of results from a study area to other locations is possible.

To quantify the environment of each study site, the microclimate was measured for 1 year. The measurements were then evaluated with plant response models. In this way, the effect of daily moisture, temperature, and light conditions could be summarized as indices for the growing season (temperature) or year (photosynthesis).

Soil moisture limitations were appraised by measuring predawn plant water potential on reference trees at each site (Waring and Cleary 1967). The maximum predawn water potential found during the summer was used as an index to drought at a site. Trees on well-watered sites did not rise above 5 bars but those on a dry site rose to 20 bars by late summer.

The combined effect of air and soil temperature was estimated for each day during the growing season with procedures outlined by Cleary and Waring (1969). The procedures were based on a generalized growth response of Douglas-fir to a variety of soil and air temperatures (Lavender and Overton 1972). Where Douglas-fir grew, the index (summation of each day's values) ranged from 30 on cool sites to 100 on warm sites.

An estimate of daily photosynthesis (mg $CO_2\,dm^{-2}\,day^{-1}$) in a few fully exposed needles was made from knowledge of Douglas-fir's response to air temperature, solar radiation, drought, frost, and cold soils (Emmingham 1974). Daily totals, based on climatic data from each site, were summarized to produce an index of yearly photosynthesis for each site (Emmingham and Waring 1977). In the present study, the index ranged from 7000 to 12 000 mg $CO_2\,dm^{-2}\,year^{-1}$.

Study Areas

Four genetics plantations in western Oregon were chosen for study and are designated as the Coast Range, Cascade Mountain, Willamette Valley (Salem), and Willamette Valley (Corvallis) plantations (Table 1). The first three were chosen from 10 plantations available in a regional provenance study started in 1958 (Ching 1965; Ching and Bever 1960; Rowe and Ching 1974). The fourth was from a breeding archive established in 1960 (Irgens-Moller 1963).

The Coast Range plantation 8 km northwest of Corvallis, Oregon, is on a warm, dry, southeast slope. Trees on this site experienced summer drought because of high evaporation and strong vegetative competition for soil moisture. The moisture, temperature, and photosynthesis coordinates were 9, 87, and 9350.

The Cascade Mountain plantation, located on a rocky slope at 1050 m in the Cascade Mountains 20 km east of Molalla, Oregon, is cool and moist. Its environmental coordinates were 6, 62, and 7200, which indicate a short growing season that could restrict productivity.

The Willamette Valley (Salem) plantation is located on a deep, clay–loam soil in the Willamette Valley 20 km east of Salem, Oregon. This is a warm, moist site with high photosynthetic potential (coordinates 6.5, 94, and 11 700).

The Willamette Valley (Corvallis) plantation is located 8 km north of Corvallis, Oregon, in much the same physiography and climate as the Salem plantation (coordinates 7.5, 100, 11 400). It is slightly warmer and drier than the Salem plantation.

These four locations provided contrast in plant environment. The Cascade Mountain plantation is similar to the valley in moisture available during summer but has a permanent snowpack in winter. The short growing season (June–September) is reflected in the temperature index, which is 25 units cooler than at low-elevation sites. Photosynthesis was restricted in the Cascade Mountains by low temperatures and in the Coast Range by moisture stress. The productivity

TABLE 1. Plantation and seed source names, locations, geographic positions, and elevations

Seed source	Location	Latitude	Longitude	Elevation, m
Northern	Vancouver Island, B.C.	49°10′	123°55′	840
Mountain	Cascade Mountains* (Molalla, OR)	45°10′	122° 0′	1050
Coast Range	Coast Range* (Corvallis, OR)	44°30′	123°40′	570
Southern	Butte Falls, OR	42°20′	122°20′	915
Victoria	Vancouver Island, B.C.	48°40′	123°45′	61
Idaho	St. Maries, ID	46°20′	115°40′	792
Northern Arizona	Flagstaff, AZ	34°50′	111°40′	2438
Southern Arizona	Tucson, AZ	32°20′	110°40′	2377
†	Willamette Valley* (Salem, OR)	44°50′	123°20′	70
†	Willamette Valley* (Corvallis, OR)	44°40′	123°15′	75

*Study plantation.
†No seed source from this site was examined.

of the areas correlates well with the photosynthesis index (Emmingham and Waring 1977).

Sources

At each of the first three plantations, trees from 16 seed sources had been planted in blocks of 121 trees each. For this study, I chose 4 of the 16 established groups. A population from Vancouver Island, B.C., was selected because it grew best on 9 out of 10 sites (Rowe and Ching 1974). Stock of a southwestern Oregon source was included because it grew slowly on all plantations. Trees of the other two sources, the Coast Range and Cascade Mountain sites, were intermediate in height growth. These four groups were designated Northern (NO), Southern (SO), Coast Range (CR), and Mountain (MT) seed sources (Table 1).

At the breeding archive, trees from various geographic locations had been planted in a random pattern (Irgens-Moller 1963). I chose a Victoria, Vancouver Island, B.C. (VIC), source for comparison with the northern stock of the other three plantations. Northern Idaho (ID), northern Arizona (NO AZ), and southern Arizona (SO AZ) seed sources were selected from inland varieties.

Although the trees from inland sources were the same age as those from the coastal source at Victoria, they were generally less than half the size and were less vigorous.

Field Measurement

Throughout the growing season of 1971, intense sampling was conducted at the four plantations. At each location, air and soil temperature, humidity, and shortwave incoming radiation were recorded continuously. At the time of the study, the trees in the provenance trials were saplings 13 years old. Trees averaged 323, 421, and 952 cm in height at the Mountain, Coast Range, and Salem plantations. Trees at the genetics archive were 11 years old and ranged from 200 to 600 cm in height.

Three trees from each selected population at each site were sampled periodically for stomatal aperture, plant moisture stress (Emmingham 1974), phenology, and cambial and leader growth. A larger sample would have benefited some of the comparisons presented in this paper, but the scope of the original study, which included climatic measurements and physiological and ecological aspects, precluded more intense sampling.

Growth was measured at about 10-day intervals from before bud swell until fall, when cambial cell divisions were infrequent. Terminal growth was measured to the nearest centimetre with a metre stick held adjacent to the leader.

Cambial growth was marked by inserting a small pin into the cambium about 40 cm above ground level (Wolter 1968). Each pin caused wound tissue to form for a few weeks. After the growing season, the marked portion of the xylem was removed and carefully sectioned for microscopic examination. Total ring width and the distance from the end of the previous year's latewood to the start of wound tissue was measured. Accuracy of determination was within 10 cells, or to 0.05 mm.

Latewood formation was judged to have started when the cell wall thickness was equal to the radial width of the cell lumen. This was determined on three cross sections chosen at random from the many available for each tree.

Analysis of Growth Data

Growth measurements were analyzed in three ways. First, phenology, including initiation and cessation of both cambial and leader activity, was examined. Second, total cambial growth and leader growth were evaluated. Finally, patterns of seasonal cambial activity were compared.

Growth pattern was compared by computing and plotting the cumulative growth as a percentage of the year's total (percentage growth). This standardizes the end point at 100% so that timing is emphasized.

Typically, seasonal cambial or leader growth follows

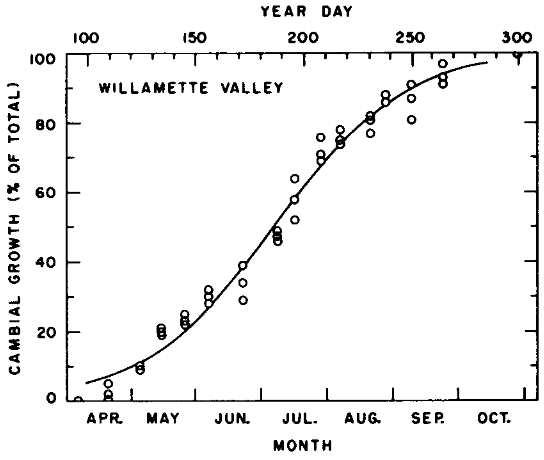

FIG. 1. A nonlinear least squares curve fit of percentage cambial growth of three trees from a single population at the Willamette Valley (Salem, Oregon) plantation. Each point represents a single observation.

a pattern that can be fitted with a logistics curve of the form

$$Y = B_1/B_2 + B_3 e^{B_1 X},$$

where Y is growth, X is time in days, and B's are constants. B_1 is related to the Y intercept when time is 0, B_2 is related to total seasons growth, and B_3 is related to the slope of the curve at the inflection point.

Because the pattern of growth could not be fitted by a linear regression, the hypothesis that all populations were similar was tested by a method analogous to the additional sum of squares method (Draper and Smith 1966; W. S. Overton (1975), Oregon State University, Corvallis, personal communication). Data for cambial growth of each population were fitted by iterative least squares until the best fit was obtained (Fig. 1). This was analogous to fitting a reduced model. Next, data for all the trees from each area were fitted in the same manner to produce a general model. Finally, the sums of squared deviations for the reduced models were compared with the sum of squared deviations for the general model. An F test determined whether more of the variation was explained by the general model or by the reduced models.

Results

Phenology

Bud swelling (BS) and the initiation of cambial cell divisions (SCD) began in April at the three low-elevation areas but not until early June at the Cascade Mountain site (Fig. 2). In most instances, bud swelling preceded cambial cell division by a few days. Bud burst (BB) generally occurred from 10 to 15 days after bud swelling.

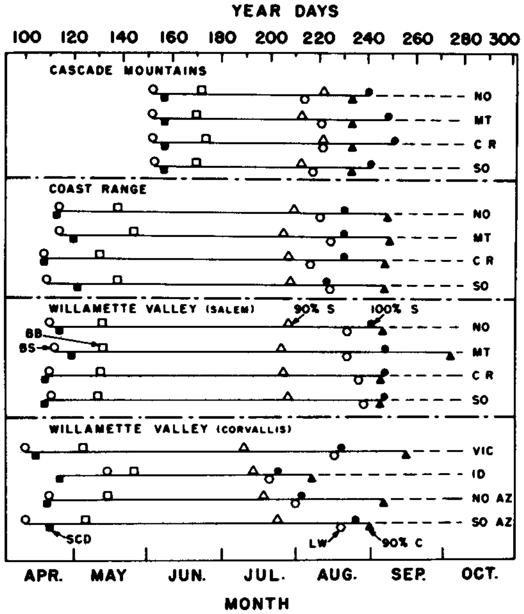

FIG. 2. A comparison of phenology of four populations (at right of figure) at three locations, and of an additional four populations at a fourth location. Shoot growth phenology is shown above the line: bud swell (BS), bud break (BB), 90% completion of extension (90% S), and 100% completion of extension (100% S). Cambial growth is shown below the line: start of cambial cell divisions (SCD), beginning of latewood formations (LW), and 90% completion of cambial growth (90% C). The broken line indicates continued growth of the cambium. NO, Northern; MT, Mountain; C R, Coast Range; SO, Southern; VIC, Victoria, B.C.; ID, northern Idaho; NO AZ, northern Arizona; SO AZ, southern Arizona.

For trees from coastal sources, bud swell occurred when soil temperature rose to about 5 °C at a depth of 20 cm (Emmingham 1974). Uniform growth initiation at the Mountain plantation was associated with a rapid warming of soils during warm weather after snowmelt. Soil temperature rose from 1 °C on May 18 to 7 °C on June 5. During the same period, buds of trees from all sources began to swell. The correlation between soil temperature and bud swelling has been observed in a wide variety of Oregon plant communities. The Idaho source was an exception to this general observation, as its buds did not become active until long after soil temperature was above 5 °C.

Leader growth was nearly completed by the end of August at all areas. Shoot growth was 90% complete before the end of July at low-elevation sites and, by mid-August at the Cas-

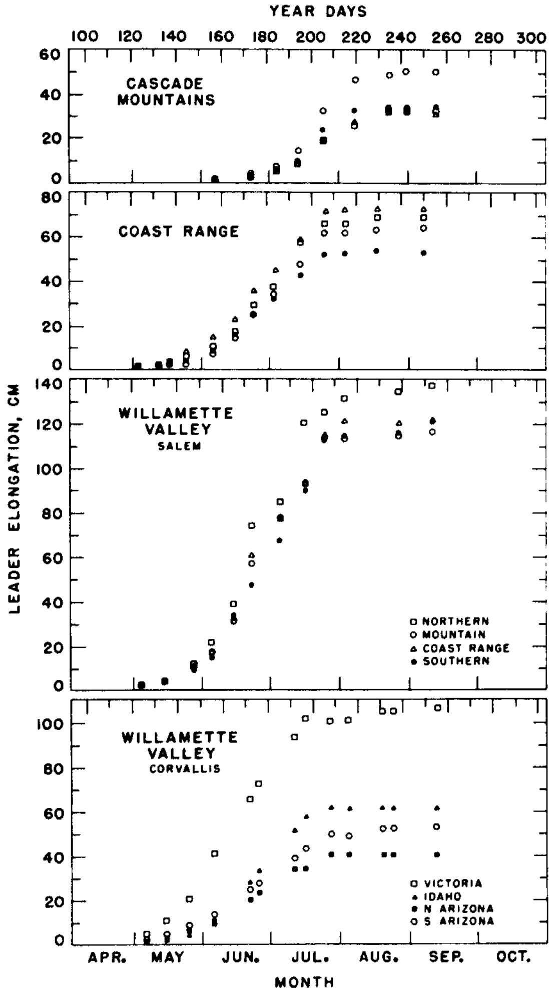

FIG. 3. A comparison of leader growth of eight populations of Douglas-fir at four locations in western Oregon. Each point is the average of three trees.

cade Mountain plantation. Drought, as measured by night xylem water potential (Scholander *et al.* 1965), was most severe in the Coast Range and Corvallis plantations, where shoot growth stopped first. There was no second flushing of shoots at any of the areas despite a partial recharge of soil moisture after a 5-cm rainfall at the end of August.

Latewood formation generally began between 90% completion of leader growth and 90% completion of cambial growth (Fig. 2). After the August rain, cambial growth rate increased slightly and cell walls were not as thick; however, they were thick enough to be considered latewood.

Cambial growth continued after leader growth ceased. Cambial growth was 90% complete in the Cascade Mountain plantation before the end of August, but in the Coast Range and at Salem it was not 90% complete until 10–15 days later. At the archive, cambial growth of Idaho-source trees was 90% complete by mid-August, but the trees of other sources did not reach the same point until early September.

Cambial cell divisions continued at a slow pace until sampling was terminated in late September at the Cascade Mountain location and until the end of October at the Coast Range and valley plantations. Although several killing frosts occurred before sampling, there was no apparent damage to the cambium.

Growth of the shoot slowed and stopped before cessation of cambial growth. Shoots stopped growing when cambial growth was about 90% complete. At the drier locations (Coast Range and Corvallis) shoot growth ceased before 90% completion of cambial growth, but the reverse was true at the more moist and cool mountain site.

In general, phenological events in different sources at provenance trial plantations occurred within a 10-day period. Differences were pronounced, however, among trees from coastal and inland sources at the genetics archive. There, the source trees from Victoria started both cambial and bud activity early in April, but trees from Idaho began bud swell more than a month later and, surprisingly, long after the cambium was actively dividing.

Leader Growth

Average leader growth (Fig. 3, Table 2) in the mountains was nearly 40 cm, at the Salem plantation 121 cm. In the Coast Range, growth ranged from 54 to 70 cm.

Total leader growth of Northern-source trees was greatest in the valley, next greatest in the Coast Range, and least in the Cascade Mountains. Trees of the Mountain source showed least growth in the valley, most growth at their home location, and intermediate growth in the Coast Range. Analysis of variance showed that no one population had a clear superiority in growth at all three locations; the local source tended to be better, as exhibited by the Mountain and Coast Range sources in their plantations.

TABLE 2. Comparison of average growth rate (linear phase), duration of growth, and total growth for cambium and leader of sapling Douglas-fir in western Oregon plantations

	Cambial growth			Leader growth		
Plantation and source	Rate,* mm day^{-1}	Duration,† days	Total, mm	Rate,* cm day^{-1}	Duration,‡ days	Total, cm
Cascade Mountains						
Northern	0.0273	77	2.44	0.66	130	34
Mountain	0.0402	77	3.05	0.98	135	50
Coast Range	0.0322	77	2.56	0.66	135	33
Southern	0.0493	77	3.50	0.66	136	35
Mean	0.0373	77	2.89	0.76	134	38
Coast Range						
Northern	0.0538	132	7.08	1.00	94	70
Mountain	0.0476	128	6.51	1.00	88	65
Coast Range	0.0472	139	6.45	1.14	100	73
Southern	0.0429	125	5.48	0.86	87	54
Mean	0.0479	131	6.38	1.00	92	66
Willamette Valley (Salem, OR)						
Northern	0.0744	134	10.77	2.09	79	138
Mountain	0.0509	156	6.82	2.00	87	107
Coast Range	0.0710	139	10.38	2.00	87	120
Southern	0.0507	139	9.97	2.00	80	120
Mean	0.0618	142	9.49	2.02	83	121
Willamette Valley (Corvallis, OR)						
Victoria	0.0615	153	9.91	1.53	110	106
Idaho	0.0433	107	4.29	1.10	60	60
N. Arizona	0.0354	141	4.77	0.53	80	40
S. Arizona	0.0547	134	8.85	0.63	115	52

*Slope of growth curve for leader and cambium taken from Figs. 3 and 4.
†Time from initiation of cell divisions to completion of 90% of growth (Fig. 1).
‡Time from bud burst to growth cessation (Fig. 1).

At the Willamette Valley (Corvallis) plantation, the Victoria-source trees grew about 102 cm while those from Idaho, and southern and northern Arizona grew 61, 56, and 40 cm.

Total elongation depends on rate and duration of growth. Differences in total growth at the Coast Range and Willamette Valley plantations resulted mainly from unequal growth rates (1 compared with 2 cm/day) during the linear growth phase (Fig. 3, Table 2). Both rate and duration of growth were less at the Mountain site. Leader elongation was completed in a shorter time at sites with greater drought or low temperatures.

At the Corvallis site, the rate of leader elongation was greatest for trees from the Victoria source (1.53 cm/day), next greatest for Idaho trees (1.1 cm/day), and least for trees from Arizona sources (0.53 and 0.64 cm/day). The Victoria-source trees not only grew for a longer time (Fig. 3) but had a much faster growth rate. The long growth period (115 days) of trees from the Arizona source did not compensate for their slow growth rate.

The correlation between total leader growth and growth rate was 0.97, and between growth and duration, 0.53. In a multiple regression, little additional variation in growth was explained by adding duration.

Cambial Growth

The average cambial growth of coastal-source trees for the growing season of 1971 varied greatly with location (Fig. 4, Table 2). In the Cascade Mountains, total growth was from 2 to 3.5 mm in radius, but in the Willamette Valley (Salem), growth ranged from 7 to 11 mm. Cambial expansion of the Mountain-source trees was only two-thirds that for trees of the Northern and Coast Range source at the Salem plantation. Mean growth at the Coast Range site was 6.4 mm, and at the genetics archive, it ranged from 5 to 10 mm.

A simple *t* test revealed a significantly

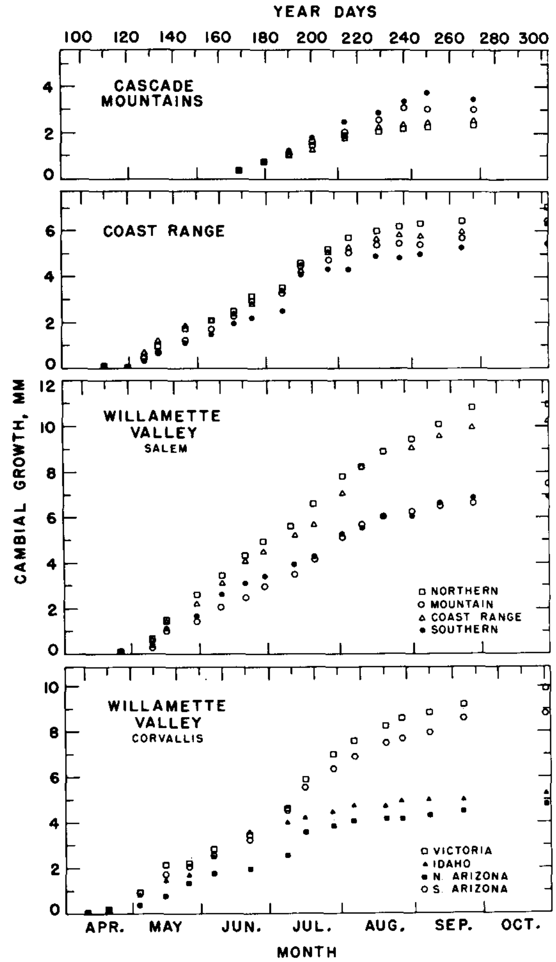

FIG. 4. A comparison of seasonal cambial growth of eight populations of Douglas-fir at four locations in western Oregon. Each point represents the average of three trees. Growth was determined by a pinning technique.

greater cambial growth at the Willamette Valley (Salem) plantation for trees from Northern and Coast Range sources than for those from the Mountain and Southern source. A two-way analysis of variance, which included the four coastal sources at three genetics plantations, revealed no persistent trend by population. That is, trees of no one source grew better or worse at all locations. Instead, there was a trend for the Northern and Coast Range stock to do better at the milder Coast Range and Salem locations. At the Cascade Mountain site, Mountain and Southern stock grew best. At the Willamette Valley (Corvallis) plantation, the Idaho and northern Arizona stock grew less than that from Victoria and southern Arizona; however, these trees were smaller at the beginning of the growing season.

Cambial growth continued at a nearly constant rate from the start of cambial cell division until about 90% of growth was complete (Fig. 4). A growth rate for each tree was computed for this growth phase. There was 0.88 correlation between total growth and growth rate. A multiple linear regression showed that 89% of the variation in total growth was explained by rate (77%) and duration (12%) of growth.

At the three provenance trial plantations where only coastal sources were represented, the fitted curves for all populations were quite similar (Fig. 5). Conversely, patterns of growth were easily separated at the genetics archive.

Although the curves for the four populations at the Coast Range and Salem plantations appear to be similar (Fig. 5), tests for pooling of the data indicated that at least one of the populations had a significantly different growth pattern. Careful examination of the parameters computed for each population's growth curve indicated that Northern and Coast Range stock had similar growth patterns at the Coast Range plantation. The duration of the active linear growth phase (Table 2) was from 5 to 17 days longer for trees from those sources than for others At the Salem plantation, Mountain-source trees had a longer active growth period but less total growth.

Differences in pattern, like those in growth totals, were not persistent among locations. For example, in the Coast Range, the Mountain-source population responded to good growing conditions during the fall more than did other populations. In the valley, however, it was the first to complete 90% of its cambial growth.

In the genetics archive, differences in pattern among populations were striking. Idaho-source trees started cambial growth at the same time as trees of other sources but stopped at the end of August. In contrast, trees of both the Victoria and southern Arizona sources put on more than 10% of the season's growth after the end of August.

Discussion

Timing of growth is important because of interaction between growth periods and en-

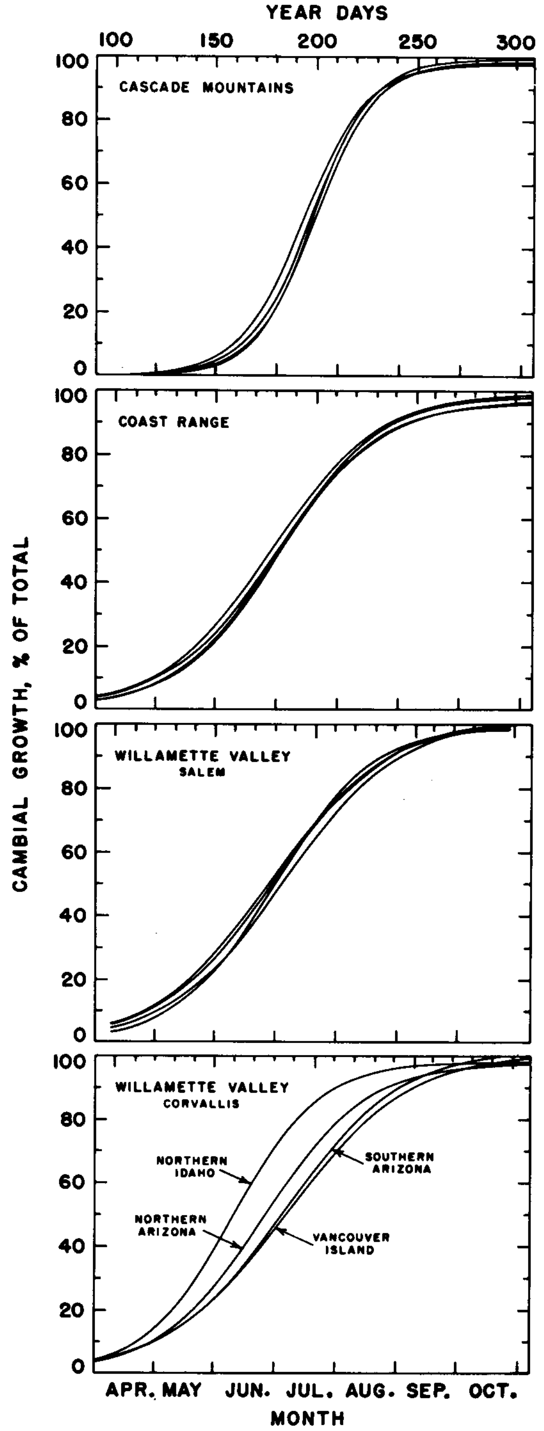

FIG. 5. Comparison of the pattern of percentage cambial growth for eight populations of Douglas-fir at four locations. Each line represents the least squares curve fit of the data for one population.

vironmental extremes such as frost (Dietrichson 1968) or summer drought (Fritts 1974). Plants can grow only when conditions are generally favorable. For example, trees in the Mountain plantation began growth immediately after snowmelt and completed growth in about 60 days, before severe fall frosts became a threat. In the Coast Range, trees began growth a month earlier than at the Mountain plantation, but slowed as moisture stress became severe. Responses to photoperiod were genetically fixed, as illustrated by stock from the Idaho source in this study, and by coastal-source Douglas-fir in the studies of Irgens-Moller (1958, 1968).

Cambial growth generally started after buds began swelling. Lavender *et al.* (1969) also found that active cambial growth followed bud growth. The only marked exception to this rule was Idaho-source stock, which initiated cambial growth nearly 3 weeks before active bud swell. Irgens-Moller (1968) suggested that such inconsistencies may be due to lack of adequate chilling for stock from northern sources in the mild Willamette Valley. Worrall (1971) noted in laboratory studies of Douglas-fir seedlings that cambial growth began before bud break when chilling requirements were not fulfilled.

The correlation between soil temperature and bud swell is supported by work of Lavender *et al.* (1973), who found that initiation of growth in Douglas-fir was controlled by hormones produced in the roots. They noted that the inhibiting effect of cold soil could be relieved by applying gibberellic acid to shoots. It follows that predictions of bud burst based on air temperature sums (Campbell 1974; Campbell and Sugano 1975) may be improved by including a root-temperature threshold in prediction equations.

Although cessation of shoot growth in coastal-source trees can undoubtedly be hastened by drought, the slowing of growth while temperature and moisture conditions were still favorable (at Salem and Cascade Mountain sites) suggests that cessation of shoot growth was keyed to shorter day length. At the genetics archive, trees from Idaho started late but finished early, completing 90% elongation in 60 days, although other sources took from 90 to 100 days. Irgens-Moller (1967) also found that trees from continental climates slowed growth earlier than those from maritime sources.

The fact that cambial activity generally continued at a slow pace into late fall is consistent with observations by Worrall (1971), who found that the cambium of Douglas-fir had no required rest or dormant stage. Studies of coniferous nursery stock showed substantial increases in girth of seedlings during the fall season (Hagem 1947). Thus, cambial growth does not appear to be restricted under short-day conditions, and Douglas-fir trees from a wide variety of sources were capable of taking advantage of favorable autumn growing conditions.

Some sources may yield trees better adapted to continue cambial growth in the fall (for example, the Mountain source in the Coast Range). Such adaptation could be useful in increasing forest production in irrigated plantations.

The uniformity in phenophases for coastal-source trees in the provenance trial plantations is not surprising because of the overriding effect of Pacific storm systems on the climate of western British Columbia, Washington, and Oregon. The distinct phasing of growth in the genetics archive is correlated to the separation of sources in both distance and climate.

Because rate of growth during the linear phase rather than duration of growth was most important in determining differences in total growth of both cambium and leader, growth rate may be a better predictor of superior growth characteristics than the measures of phenology generally used. Leader growth rate is measured more easily than cambial growth rate and is correlated to it ($R^2 = 0.52$; $F = 15.4$). Therefore, measurement of leader growth rate should be considered in genetics studies for correlations between juvenile and mature behavior.

Because populations that grew best in 1971 were not always the ones that were tallest after 9 years (Rowe and Ching 1974), we would approach juvenile–mature correlations cautiously. The small sample size in the present study may not be sufficient to characterize the population's response, especially as differences among populations in any 1 year may be small. Other explanations, however, should be considered. A second possibility is that growth of all populations is similar in years with low moisture stress such as 1971 but is different for high-stress years.

A third explanation is suggested by the data of Rowe and Ching (1974). In the Willamette Valley plantation, trees from all populations are growing in proportion to their size, and accumulated differences have resulted from early advantages in leader growth by superior stock. The shorter trees from more droughty southern locations may have put energy into root growth at the expense of top growth, as shown by Hermann and Lavender (1968) for other seed sources in southwest Oregon. Once trees become well established, they may be able to buffer environmental stress, and grow in proportion to their size.

At other plantations in the provenance trial, however, trees from fast growing populations continued to increase their lead over trees from slow growing populations, and conversely, other populations that grew slowly for the first 13 years have since gained in comparative standings (K. K. Ching (1975), Oregon State University, Corvallis, personal communication). Perhaps still others will prove best adapted for growth once stands have closed. Clearly, interactions between a particular stock and competition could be an important consideration in selecting sources for intensive forest-management options.

Trees from the Northern and Coast Range sources tended to react the same in both cambial and leader growth. They did well in the Coast Range and Salem plantations but poorly in the Cascade Mountains. Conversely, trees from the Southern and Mountain sources grew most in the Cascade Mountains and least at low elevation. Without further quantification of Northern- and Southern-source environments, statements about selection pressure would be speculative.

Evaluation of microclimate through measurement of plant water potential and models of tree growth and photosynthesis could provide a standard procedure for comparing seed source and plantation locations.

Development of indexing techniques (see Methods) suggests a partial solution to the problem of maintaining widespread provenance trials. A variety of local environments could be used for provenance plantations and compared with more distant areas with indexing methods.

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