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# First-year height growth of southwestern Oregon Douglas-fir in three test environments[1])

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## Summary

Douglas-fir seedlings from wind-pollinated seed collected from two trees at each of 36 locations throughout southwestern Oregon were grown in three test environments (growth room, greenhouse, and nursery) to assess environmental influence on genetic variation of first-year height growth.

The 36 populations differed markedly in first-year height growth; the estimated variance among populations was about four times greater than both the estimated family-within-population and population × environment variances.

Regression models showed populations originating from higher elevations and southerly latitudes in the sampled areas grew slower in all test environments. While trends were consistent in all environments, the model for the nursery was not as efficient in accounting for variation in population means. This may have resulted from poorer differentiation among populations owing to the shorter nursery growing season


*Key words:* Douglas-fir, genotype × environment interaction, clinal models, genocology.


## Zusammenfassung

Douglasien-Sämlinge *(Pseudotsuga menziesii* MIRB. FRANCO) aus frei abgeblühten Samen, die von je 2 Bäumen an 36 Orten im südwestlichen Oregon stammen, wurden an drei Standorten (Klimaraum, Gewächshaus und Baumschule) angezogen, um den Einfluß der Umwelt auf die genetische Variation der Höhe im Alter 1 abzuschätzen.

Die 36 Populationen differierten markant in diesem Kriterium, die geschätzte Varianz zwischen den Populationen war etwa viermal größer als die Varianzen der Familien innerhalb der Populationen sowie zwischen den Interaktionen von Population und Umwelt.

Regressionsmodelle zeigten, daß Populationen, die aus höheren Lagen oder südlicheren Gebieten stammten, an allen Orten langsamer wuchsen. Während Trends an allen Versuchsorten vorhanden waren, war das Modell für die Baumschule nicht effizient genug, um die Varianten der Populationsmittel zu berechnen. Dies mag aus einer geringeren Differenzierung zwischen Populationen während der kürzeren Baumschul-Wachstumsperiode resultieren.


## Introduction

Many studies have reported geographic variation in juvenile height growth of coastal Douglas-fir *(Pseudotsuga menziesii* [MIRB.] FRANCO). Most of these have sampled provenances from the western portions of British Columbia, Washington, Oregon, (CAMPBELL and SORENSEN 1978, ROWE and CHING 1973) or California (GRIFFIN and CHING 1977, SWEET 1965). Because southern Oregon, an important timber-producing area, has received less attention, we undertook a regional study there in cooperation with the Bureau of Land Management to investigate the patterns of genetic variation in Douglas-fir.

CAMPBELL and SORENSEN (1978) point out that studies to reveal and characterize adaptive genetic variation among plant populations should be initially attempted in environments (common gardens) with high resolution. By reducing environmental variation and by choosing test environments which discriminate among populations, we can better discern the patterns associated with population differences. For example, an environment with long photoperiods will tend to differentiate among populations which do and do not respond to such periods. Because genetic expression can vary in different test environments (genotype × environment interaction), more than one is necessary. We report results of an experiment examining genetic variation in

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first-year height growth of southwestern Oregon Douglas-fir seedlings expressed in three test environments: growth room, greenhouse, and outdoor nursery.

## Materials and Methods

### *Sampling Scheme*

In the fall of 1976, we collected wind-pollinated seed from two parent trees at each of 36 population locations throughout southwestern Oregon *(Figure 1)*. All of the sample locations were between 42.00° and 43.12°N latitude. They ranged from 475 to 1,630 m elevation, from 61 to 162 km from the Pacific Ocean, and from 27 to 43 m (80—130 ft) site index. Site index, in feet at age 100, was determined from 7 to 10 trees at each location as decribed by McArdle *et al.* (1961).

We intended that the 36 locations should represent the range of sites on which Douglas-fir grows in the region. Although slopes and aspects were randomly chosen, constraints on elevation, latitude, and distance from the Pacific ocean ensured a broad regional sample. Because of the region's topography, variables associated with the population locations are not independent *(Table 1)*. The higher elevation sites were located more often in the southern portion of the region and were somewhat further from the Pacific Ocean.

Parent trees were located at least 120 m apart, but were otherwise randomly selected at every location. Because 1976 had only a moderate seed crop, some inadvertent selection may have occurred for seed production.

### *Experimental Designs in the Test Environments*

After extraction and cleaning, we cut open at least 100 seeds from each sample and weighed the filled seed to obtain an average sound seed weight for each of the 72 wind-pollinated families. In mid-March 1977, stratified seeds destined for growth-room and greenhouse tests were individually sown into 45-cm³ tubes (2.5 cm diameter × 10 cm long) containing a 3:2 peat:vermiculite rooting medium.

In the growth room, 35 populations (70 families) were represented, and in the greenhouse, 31 populations (62 families). In both environments, the experiment was organized in a completely randomized design. Each family was represented in the growth room by three row-plots of ten seedlings each and in the greenhouse by eight row-plots of eight seedlings each. Seedlings were watered weekly and fertilized periodically with liquid fertilizer (approximately 10% Hoagland's solution). Growth-room seedlings experienced a 16-hr photoperiod and a 25°/20° C thermoperiod. Photoperiod and thermoperiod were not regulated in the greenhouse.

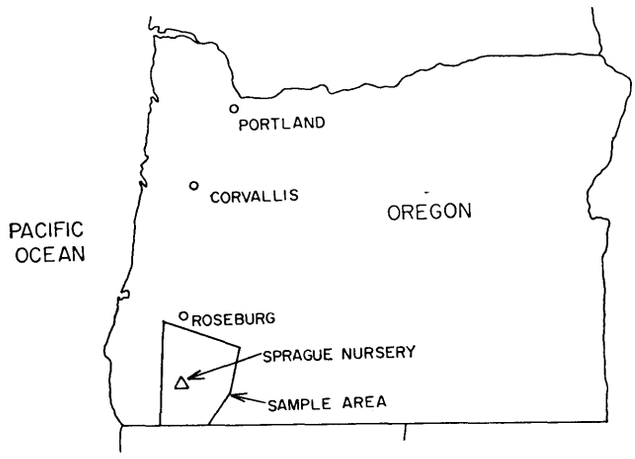


*Figure 1.* — The southwestern area of Oregon sampled in the study.

*Table 1.* — Correlations[a] among the variables associated with the original locations of the 36 populations.

| | Elevation | Latitude | Distance from ocean | Site index | Aspect[b] |
|---|---|---|---|---|---|
| Elevation | 1.0 | -0.80 | 0.44 | -0.34 | -0.16 |
| Latitude | | 1.0 | -0.28 | 0.45 | 0.12 |
| Distance from the ocean | | | 1.0 | 0.04 | 0.02 |
| Site index | | | | 1.0 | -0.14 |
| Aspect | | | | | 1.0 |

a Correlations have 34 degrees of freedom: r = 0.33, significant at P = 0.05; r = 0.42, significant at P = 0.01.

b Aspect = % slope x cosine aspect (Stage 1976).

In mid-April 1977, seeds were sown at the Bureau of Land Management's Sprague Nursery in Merlin, Oregon *(Figure 1)* in a randomized complete block design: row-plots representing 70 families from 35 populations randomly assigned positions in each of four blocks (nursery beds).

At the end of the first growing season, epicotyl length (hereafter, first-year height growth) was measured to the nearest 0.5 cm in each of the three test environments. All seedlings were measured in the growth room and greenhouse; in the nursery, we measured only the first 15 seedlings in each family row-plot.

### *Statistical Analyses*

Individual tree measurements were the basis for analyses of variance of first-year height growth in both growth-room and the nursery test environments. Unfortunately, because trees in the greenhouse were rearranged for another experiment before measurement, an analysis of variance employing individual tree measurements was precluded there and only family means could be obtained.

For the 60 families common to all three test environments, the family means within each environment were the basis for analysis of variance combined over environments. The sum of squares of the population × environment interaction was partitioned into various components by regressing the population mean from a given environment against the mean of all populations in that environment (Finlay and Wilkinson 1963, Mandel 1961). In forestry literature, the rationale behind such a joint regression analysis is discussed by Mergen *et al.* (1974), Morgenstern and Teich (1969), Owino (1977), and Rehfeldt (1979), who describes the further partitioning of the sum of the squares of the slopes into concurrence (convergence) and nonconcurrence (nonconvergence).

Means of height growth from the two families comprising a population were averaged to obtain the population mean. We then regressed the mean height growth of each population against topographic variables associated with the site of origin to relate origin to height growth in the test environment. Models built separately for each test environment and for the populations averaged over test environments used standard techniques for forward and backward

stepwise multiple linear regression. Only variables with significant partial correlation coefficients (P = 0.01) were allowed to enter a model. The independent variables available were elevation, latitude, distance from the Pacific Ocean, site index, aspect, and all first-order interactions. Transforming aspect to a cosine function of the true azimuth in degrees set optimum growth at true north. Weighting by percent of slope ensured that aspects from steeper slopes were given more weight (STAGE 1976).

## Results and Discussion

### *Seed Weight*

An analysis of variance showed that differences in seed weight among the 36 sample populations were significant when tested against the mean square of family-within-population, F = 1.95* with 35 and degrees of freedom. (Throughout this discussion: ns = not statistically significant, * = significant at P = 0.05, ** = significant at P = 0.01, df = of freedom.) Sound seed weight averaged 0.015 g and ranged from 0.011 to 0.019 g per seed among the 72 families. The average population seed weights correlated weakly-to-moderately with the topographic variables of the population locations. Correlations of mean seed weight of a population with elevation, latitude, and distance from the ocean, 0.35*, −0.38*, and 0.47** (34 df), indicate that seed collected from cold parts of the region (high elevation, farther inland) were slightly heavier. Several investigators (BIROT 1972, CHING and BEVER 1960, GRIFFIN and CHING 1977, SWEET 1965) reported similar trends for elevation or distance from the ocean for coastal Douglas-fir.

Differences among the seed weights of populations may be either genetic or environmental. On one hand, we can speculate that faster growth after germination, such as might be conveyed by genetically heavier seed, would benefit seedlings in harsher (for example, colder) environments by allowing more height growth in a shorter growing season. On the other hand, differences in seed weight among the 36 populations and their relation to topographic variables may manifest the different environments in which the seed matured. At any rate, the population differences and topographic trends were not strong.

Family mean seed weight did not correlate strongly with mean height growth in any of the three test environments (growth room r = 0.44** with 68 df, nursery $0.09^{ns}$ with 68 df, and greenhouse $-0.21^{ns}$ with 60 df). The only significant correlation, that in the growth room, indicated decreasing height growth for families with heavier seed. Because seed weight apparently did not influence mean height growth of families, it was not used as a covariate in the following analyses.

### *Influence of Test Environments on Height Growth*

The combined analysis of variance using mean height growth of families in each test environment *(Table 2)* shows, as expected, a marked effect of test environment on first-year height growth. Average heights in the growth room, nursery, and greenhouse were 8.67 cm, 5.62 cm, and 3.52 cm; average height in the growth room was almost 2.5 times that in the greenhouse. With large differences among environments, genotype × environment interaction is potentially large (SHELBOURNE 1972). The estimated variance component associated with differences among populations ($S^2_P$) was about 4 times larger than that associated with the environment × population interaction ($S^2_{EP}$). Population, family-within-population, and the interaction of test en-

*Table 2.* — Combined analysis of variance of first-year height growth based on mean height of families in three test environments.

| Source | Degrees of freedom | Mean square | Intraclass correlation[a] (% $S^2_T$) | Expected mean square |
|---|---|---|---|---|
| Environment (E) | 2 | 383.080** | | |
| Population (P) | 29 | 5.265**[b] | 46.2 | $(K\sigma^2_c + \sigma^2_{EF/P}) + 2\sigma^2_{EP} + 3\sigma^2_{F/P} + 6\sigma^2_P$ |
| Family-within-population (F/P) | 30 | .924** | 10.8 | $(K\sigma^2_c + \sigma^2_{EF/P}) + 3\sigma^2_{F/P}$ |
| Environment x population | 58 | .786* | 12.0 | $(K\sigma^2_c + \sigma^2_{EF/P}) + 2\sigma^2_{EP}$ |
| Slopes | 29 | .827* | | |
| Concurrence | 1 | 14.452** | | |
| Nonconcurrence | 28 | $.340^{ns}$ | | |
| Remainder | 29 | .745* | | |
| Environment x family-within-population | 60 | .477 | 31.0 | $(K\sigma^2_c + \sigma^2_{EF/P})$ |

[a] $S^2_T = S^2_P + S^2_{F/P} + S^2_{EP} + (KS^2_c + S^2_{EF/P})$

Each variance component is estimated by a sample variance component:

$S^2_P$ estimates $\sigma^2_P$ = variance among populations,

$S^2_{F/P}$ estimates $\sigma^2_{F/P}$ = variance among families-within-populations,

$S^2_{EP}$ estimates $\sigma^2_{EP}$ = variance due to the interaction of test environments with populations,

$S^2_{EF/P}$ estimates $\sigma^2_{EF/P}$ = variance due to the interaction of test environments with families-within- populations,

$S^2_c$ estimates $\sigma^2_c$ = composite variance from several families within test-environment sources.

[b] Population mean square was tested using Satterthwaite's Approximate F-Test (ANGERSON and MCCLEAN 1974, p. 117).

vironment × population accounted for 46%, 11%, and 12% of the variance not associated with environment. The component of variance due to the interaction of family-within-population × environment could not be estimated because of other inseparable variance components included in that mean square.

We explored the population × environment interaction by regressing the mean height growth of a given population in a given environment against the mean height of all populations in that environment. For the 30 populations, there were 30 such regressions, each having three points. Each of the three points, through which a line was fitted, represented the average height growth for one population in one environment *(Figure 2)*. The highly significant concurrence, and the lack of nonconcurrence *(Table 2)*, suggest that the 30 lines have a common intersection from which they fan increasingly farther apart in environments with more average height growth. A plot of these lines *(Figure 2)* showed that the point of concurrence is below the mean for the greenhouse, the smallest environmental mean. Thus, the lines tend not to overlap in the inference space. The concurrence mean square is identical to that obtained from Tukey's "one degree of freedom for nonadditivity" (Tukey 1949).

The portion of the interaction of population × environment accounted for by the slopes is best characterized as a scale effect and not as an effect due to population rank changes in different environments. However, a small but significant portion of the interaction (the remainder in *Table 2)* could not be explained in this fashion.

All populations in the study grew faster in more favorable environments; b values ranged from 0.66 to 1.36. A

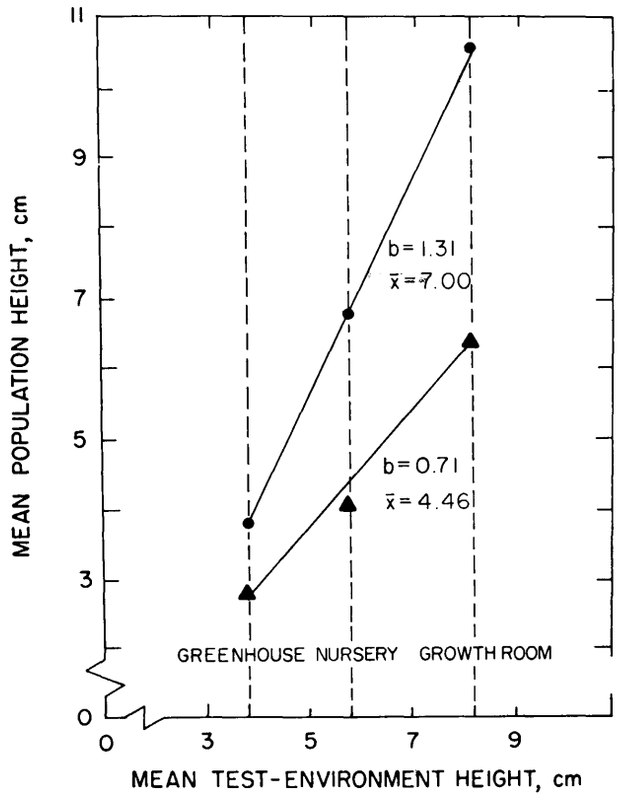


*Figure 2.* — First-year height growth of two Douglas-fir populations plotted against the three test environment means. Test environment means are means over all populations in each environment.

*Table 3.* — Correlations between environments of the means of first-year height growth of families (above diagonal)[a] and of populations (below diagonal)[b].

| Test environment | Growth room | Greenhouse | Nursery |
|---|---|---|---|
| Growth room | 1.00 | 0.81[a] | 0.53[a] |
| Greenhouse | 0.86[b] | 1.00 | 0.54[a] |
| Nursery | 0.71[b] | 0.65[b] | 1.00 |

a For 58 df: r = 0.33, significant at P = 0.01.
b For 28 df: r = 0.46, significant at P = 0.01.

strong correlation (r = 0.78**, 28 df) between population b values and population mean heights averaged over the three test environments shows that taller populations tended to be more responsive to environmental change by growing progressively taller in the better environments. This relationship is identical to that given by the concurrence source of variation in the combined analysis of variance *(Table 2)*. In fact, the coefficient of determination ($R^2 = 0.78^2 = 0.61$) for the relationship between population height and population b values defines the fraction of the sum of squares of the slopes accounted for by concurrence.

Correlation of the mean population height and mean family height among environments *(Table 3)* was significant. Approximately 74% (the coefficient of determination) of the variation in mean population height in the growth room could be accounted for by mean population height in the greenhouse.

### *Clinal Patterns of Population Variation*

The estimated variance among populations ($S^2_P$) was more than 4 times larger than the estimated variance for families-within-populations ($S^2_{F/P}$), a marked genetic differentiation. In other studies of juvenile height growth in western conifers (Campbell 1979, Campbell and Sorensen 1978, Griffin and Ching 1977, Hamrick 1976, Rehfeldt 1974, Rehfeldt 1979), this has been interpreted as the result of adaptive genetic response, natural selection in the populations' original environments.

When populations are strongly differentiated, we attempt to relate population performance to original geography, topography, and climate by developing clinal regression models. In all three test environments (common gardens), mean first-year population height growth correlated most strongly with elevation of place of origin *(Table 4)*; seed collected at higher elevations produced

*Table 4.* — Correlation of mean first-year height growth of populations from three test environments with characeristics of the original population locations.

| Test environment and number of populations[a] | Original location-- Elevation | Latitude | Distance from ocean | Aspect[b] | Site index |
|---|---|---|---|---|---|
| Growth room (35) | -0.868 | 0.777 | -0.531 | 0.161 | 0.347 |
| Greenhouse (31) | - .817 | .709 | - .603 | .197 | .299 |
| Nursery (35) | - .590 | .525 | - .403 | .030 | .222 |
| Combined means (30) | - .855 | .781 | - .563 | .200 | .341 |

a For 33 df: r = 0.33, significant at P = 0.05; and r = 0.42, significant at P = 0.01. For 29 df: r = 0.36, significant at P = 0.05; and r = 0.46, significant at P = 0.01.
b Aspect — percent slope * cosine aspect (Stage 1976).

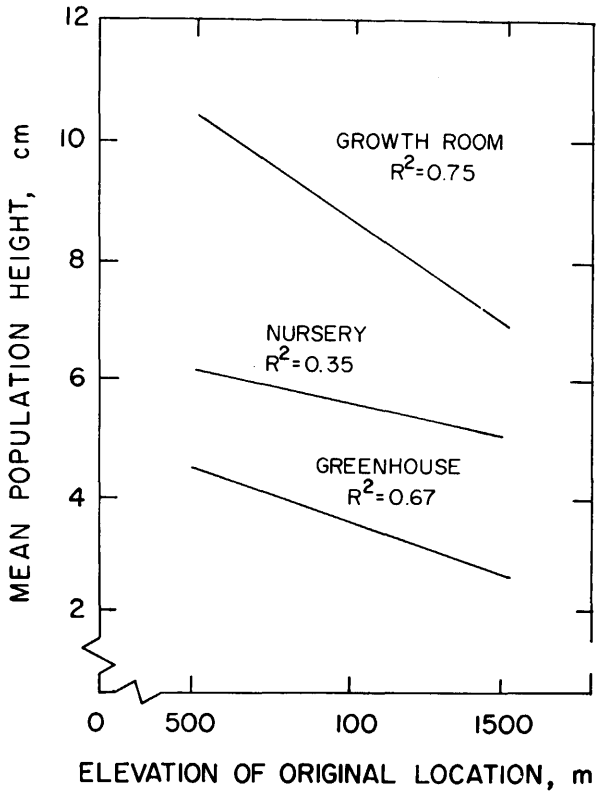


*Figure 3.* — Regressions of first-year height growth of populations in three test environments on the elevation of the original population locations.

shorter seedlings. The multicollinearity between elevation and latitude (r = −0.80**) and between elevation and distance from the ocean (r = 0.44**) implies confounding and makes separation of the influences of the three variables impossible. Indeed, the variables are imperfect substitutes for more fundamental ones such as temperature, photoperiod, and precipitation. Note that the correlations between latitude and height growth of a population reverse those usually reported: shorter seedlings tended to be produced by seed collected in southern or eastern portions of the sampled region. In other investigations (Burley 1966, Campbell and Sorensen 1978, Hamrick and Libby 1972, Morgenstern 1969; see also Wright 1976, p. 255), northern populations were slower growing. We found them faster growing; however, we sampled a smaller latitudinal range (1°) than that in many other provenance tests (6°—20°), and northern populations in our study tended to be at lower elevations and to have more summer precipitation.

Regressions showed that elevation accounted for much of the variation in mean population height in the growth room and greenhouse environments ($R^2$ = 0.75 and 0.67) but for less of the variation in the nursery ($R^2$ = 0.35). Elevation added first to the model for each environment, and after its inclusion, no other variables added significantly. Models including only the elevation variable seemed to account adequately for variation in population means, as shown by tests for lack of fit. In all test environments, populations from higher elevations were shorter *(Figure 3)*, which agrees with reports of Pacific Northwest Douglas-fir (Campbell and Sorensen 1978), California Coastal Douglas-fir (Griffin 1978, Swfet 1965), Rocky Mountain Douglas-fir (Rehfeldt 1974, 1979), and Southern Oregon Douglas-fir (Hermann and Lavender 1968). In these studies, other variables were also sometimes important.

*Effects of Test Environments on Clinal Models and Population Structure*

We can examine similarities among the clinal regression models developed for the three distinct test environments. Overall patterns were similar; however, the efficiencies of the models vary dramatically. Correlations between mean heights and topographic variables for a population were consistently smaller in absolute value for the nursery test environment *(Table 4)* than for other test environments. The regression model for nursery data accounted for only 35% of the variation in mean population height, the model

*Table 5.* — Analyses of variance of first-year height growth in the growth-room and environments.

| Source | Growth room df | Growth room Mean square | Growth room Intraclass[a] correlation (% $S^2_T$) | Nursery df | Nursery Mean square | Nursery Intraclass correlation (% $S^2_T$) | Expected mean square[b] |
|---|---|---|---|---|---|---|---|
| Population | 34 | 12.15** | 22.8 | 34 | $3.76^{ns}$ | 2.8 | $\frac{\sigma^2_w}{K_1} + \sigma^2_R + K_2\sigma^2_{F/P} + K_3\sigma^2_P$ |
| Family-within-population | 35 | 2.98** | 10.2 | 35 | 2.89** | 12.8 | $\frac{\sigma^2_w}{K_1} + \sigma^2_R + K_2\sigma^2_{F/P}$ |
| Row-within-family | 140 | .94** | 8.1 | 207 | .90** | 18.6 | $\frac{\sigma^2_w}{K_1} + \sigma^2_R$ |
| Within-row[c] | 374 | 3.94 | 58.9 | 543 | 2.55 | 65.8 | $\sigma^2_w$[d] |

[a] $S^2_T = S^2_w + S^2_R + S^2_{F/P} + S^2_P$

[b] $K_1$ is the harmonic mean of the number of trees in a row.
For growth room: $K_1$ = 9.9, $K_2$ = 3, $K_3$ = 6. For nursery: $K_1$ = 14, $K_2$ = 4, $K_3$ = 8.

[c] Within-row mean squares were estimated from a random sample of rows.

[d] Each variance component is estimated by a sample variance component:
$S^2_P$ estimates $\sigma^2_P$ = variance among populations,
$S^2_{F/P}$ estimates $\sigma^2_{F/P}$ = variance among families-within-populations,
$S^2_R$ estimates $\sigma^2_R$ = variance among row-plots within families,
$S^2_w$ estimates $\sigma^2_w$ = variance among trees within row-plots.

for growth-room data 75%, and the model for greenhouse data 67%.

To investigate possible reasons the regression model for nursery data was less effective than the model for growth-room data, we ran individual analyses of variance for both test environments *(Table 5)*. Roughly assuming only additive genetic variance, then in each test environment $\sigma^2_{F/P} = 1/3\ \sigma^2_A$, where $\sigma^2_A$ is the additive genetic variance (CAMPBELL 1979, SQUILLACE 1974). Further, $\sigma^2_w = \sigma^2_e + 2/3\ \sigma^2_A$ where $\sigma^2_e$ is the variance due to environmental differences among trees within a rowplot. Our estimate of $\sigma^2_e$ is $S^2_e = S^2_w - 2\ S^2_{F/P}$. If for each test environment $S^2_e$ roughly estimates the error from tree-to-tree within a row and $S^2_R$ estimates the error from row-to-row within a family, $S^2_e + S^2_R$ estimates the total within-block experimental error. For the growth room and nursery, $S^2_e + S^2_R = 47\%$ and 59 % of the total variation. These rough approximations indicate little, if any, more experimental error in the nursery than in the growth-room environment.

Poorer genetic differentiation among populations in the nursery test environment would also lead to a less effective regression model. Differentiation of populations relative to that for families-within populations was 11 times greater in the growth room ($S^2_P/S^2_{F/P} = 2.2$) than in the nursery ($S^2_P/S^2_{F/P} = 0.2$). Possibly, low-elevation populations were better able to take advantage of the longer growing season in the growth room, thus the wider discrimination in that environment. In the shorter growing season of the nursery, low-elevation populations may not have had the advantage, thus the poorer discrimination among the populations.

Both experimental error and less discrimination among populations may explain why the clinal regression model was less effective in the nursery. Our data do not indicate which of the two is more important.

Other investigators have also found clinal regression models to vary with the test environments. In a study of four Northeastern conifers in growth-room environments where trends could be demonstrated, a pattern of decreasing growth with increasing latitude of seed origin was confirmed. However, regression changed with test environments, and in some, no trend could be established between growth and latitude (MERGEN *et al.* 1974). Decreasing height growth of Sitka spruce *(Picea sitchensis)* with increasing latitude was found in some test environments, but correlation was not significant in others (BURLEY 1966). Slightly differing clinal patterns and differing effectiveness of models were also reported for different test environments in a study of juvenile height of Pacific Northwest Douglas-fir (CAMPBELL and SORENSEN 1978).

## Conclusions

This study of first-year height growth of Douglas-fir from southwestern Oregon showed marked genetic variation among the populations within the region. Variation due to population × environment interaction was only one-fourth that of variation due to population differences, and much of this interaction could be interpreted as a scale effect rather than as rank changes. Because the test environments in this experiment were not representative of the range of natural environments, care should be exercised in extrapolating these results. For example, our tests did not include a cold, harsh environment characteristic of higher elevations in this region.

For our three test environments, regression models adequately explained the population differentiation, which indicates that even within this relatively small geographic region, selection has resulted in clinal variation. CAMPBELL (1979) reported clinal variation in Douglas-fir from an even smaller geographic region in the Oregon Cascade Mountains. Strong population differentiation over small geographic areas means that seed transfers within the region must be made with care in order to ensure genetically adapted plantations.


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