terdependent. All the models address the optimum selection time, but the criteria used to evaluate the time vary. The basic model, extended time model and multiple cycle model use the expected annual genetic gain as the measure for determining the time for $\triangle G^*_{max}$, or when $\triangle G^*_x = \triangle G^*_T$. The MFN uses the expected genetic gain $\triangle G_{max}$. The expected genetic gain migh be a better measure than the annual genetic gain for economic analysis of early selection.

The annual genetic gain is a relative quantity, like heritability, and is useful for comparing different populations, but the relative nature itself makes it difficult to interpret the validity of $x_{max}$ evaluated in the models. As discussed in the introduction to the MFN section, the division of the expected genetic gain by x could lead to a nonsense value for maximum point for cases with high genetic juvenile mature correlations. It was also shown in *Table 2* and *Figure 2* that the reduction in x to obtain smallest $x_{max}$ requires an extremely large increase in the intercept (A) of the heritability ratio, g.

Obviously, there must be a point where the reduction in x is accompanied by fast decrease in the correlation, r. The log functions in *Figure 3* show that any of the curves may indeed be approximated by two linear functions of different slopes. The point where such division occurs might be the point where the loss of correlation does not justfy the reduction in x. For the log function, the point is where the slope of the curve (or r = dr/dx) is 1, or x = B. Any reduction of x below x = B will cause faster reduction in r than in x. Despite the faster reduction in r, the annual genetic gain will continue to increase as x decreases beyond B until it reaches $x_{max}$.

An alternate way of defining $x_{max}$ with respect to annual genetic gain is to apply the restriction that $x_{max}$ be defined between $B \leq x \leq 1$. When $x_{max}$ does not exist within the range, then x = B is taken as $x_{max}$. If g(x) = 1, the basic model has no intermediate $x_{max}$, and y is maximum when x = B. In extended models the addition of

constants in the denominator delays the $x_{max}$, and increases the chance that the $x_{max}$ will fall between B and 1.

The problems associated with interpreting the concept of annual genetic gain and defining the $x_{max}$ suggest that it is not necessarily correct to equate the optimum selection age and $x_{max}$. In the basic model x = B could be the optimum selection age even though the annual genetic gain is not maximum at this point. In multiple cycle model. and in the basic model, earliest x which generates y = 1 could be considered as optimum selection age.

The multiple cyle model presented here does not generate any information that is significantly different from the basic model, except that the x is translated into n. However, the model is important because it defines a reference point which can connect the single cycle models and multiple cycle models.

### Acknowledgement

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# Provenance Study of Douglas-Fir in the Pacific Northwest Region IV. Field Performance at Age 25 Years*)

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### Summary

Twenty-five-year results are reported for 14 Pacific Northwest provenances of Douglas-fir growing in 5 thinned, fast-growing plantations. In all plantations, the southern Oregon provenance was the poorest performer for all response variables (height, diameter at breast height, height: diameter ratio, volume per hectare, and site index). It produced 30 percent less volume than the average of the other provenances. Differences among the other 13 provenances were smaller and often not statistically significant. Provenance $\times$ plantation interactions were generally not significant when the southern Oregon source was omitted from the analyses. These results seemingly contradict experiments with seedlings and young plantations which indicate an extremely tight adaptation of Douglas-fir populations to the local environment in which they evolved. Of the several possible explanations for the apparent discrepancies, the most likely is a lack of experimental precision in the present study.

*Key words:* Douglas-fir, provenance, yield, genotype $\times$ environment interaction.

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## Zusammenfassung

Es wird über die Entwicklung von 14 aus dem pazifischen Nordwesten der USA stammenden Douglasien-Provenienzen auf 5 durchforsteten Schnellwuchsplantagen im Alter 25 berichtet. In allen Plantagen war eine Herkunft aus Oregon am schlechtesten, was die untersuchten Merkmale, Höhe, Durchmesser in Brusthöhe, das Höhe:Durchmesser Verhältnis, das Volumen pro ha und den Standort-Index betrifft. Diese Herkunft hatte im Durchschnitt 30% weniger Holzmasse produziert, als im Durchschnitt von den anderen Provenienzen erreicht wurde. Die Unterschiede unter den anderen 13 Provenienzen waren geringer und oft nicht statistisch abzusichern. Die Interaktion zwischen Herkunft und Standort war generell nicht signifikant, wenn die Herkunft „Südoregon" aus der Analyse herausgenommen wurde. Diese Resultate scheinen anderen Ergebnissen aus Anbauversuchen mit Sämlingen und jüngeren Pflanzungen zu widersprechen, die eine extrem enge Anpassung der Douglasien-Populationen an die örtlichen Standortgegebenheiten, unter denen sie aufwachsen, zeigen. Von einigen möglichen Erklärungen für die auftretenden Diskrepanzen ist die wahrscheinlichste diejenige eines Mangels an Präzision in der vorliegenden Studie.

## Introduction

Knowledge of magnitudes and patterns of genetic differentiation among seed sources is useful for delimiting both seed collection zones for operational reforestation and breeding units for tree improvement programs. Delimitation can be based upon knowledge of genetic differentiation of seed or seedling populations growing in controlled environments or upon genetic differentiation among seed sources in field experiments at or near harvest stage (ADAMS and CAMPBELL 1981).

Studies of seedlings and young plantations indicate that, within the Pacific Northwest (PNW), the process of natural selection has apparently resulted in close adaptation of Douglas-fir (Pseudotsuga menziesii (MIRB.) FRANCO) to the local environment in which it evolved (CAMPBELL 1979, SILEN and MANDEL 1983). In the absence of substantiative data from long-term field studies, this information has been used to confirm relatively small seed collections zones (WESTERN FOREST TREE SEED COUNCIL 1973) and delimit extremely small (sometimes only a few km wide)

Table 1. — Geographic areas and cooperative owners of provenance seed sources and planting locations.

| Provenance designation[a] | | Location | Latitude | Elevation (m) | Coastal (C) or Mountain (M) | Cooperator |
|---|---|---|---|---|---|---|
| BRITISH COLUMBIA | | | | | | |
| 4 | A | Nimpkish Forest, Vancouver Island | 50° 31' | 150 | C | Canadian Forest Products, Ltd. |
| 2 | B | Courtenay Area, Vancouver Island | 49° 45' | 460 | C | Crown Zellerbach CDA, Ltd. |
| 1 | C | Sugar Loaf Mt., Vancouver Island | 49° 10' | 840 | C | MacMillan & Bloedel, Ltd. |
| 3 | D | Masachie Lake, Vancouver Island | 48° 50' | 200 | C | British Columbia Forest Service |
| 15 | E[b] | Haney | 49° 10' | 180 | C | University of British Columbia |
| WASHINGTON | | | | | | |
| 16 | F[b] | Snoqualmie National Forest | 47° 30' | 1,200 | C | Weyerhaeuser Co. |
| 6 | G | Shelton area | 47° 15' | 90 | C | Simpson Timber Co. |
| 5 | H | Elbe area | 46° 45' | 590 | M | State Department of Natural Resources |
| OREGON | | | | | | |
| 7 | I | Tillamook area | 45° 30' | 580 | C | State Board of Forestry |
| 9 | J | Clackamas Tree Farm, Molalla | 45° 10' | 580 | M | Crown Zellerbach Corp. |
| 10 | K | Clackamas Tree Farm, Molalla | 45° 10' | 1,070 | M | Crown Zellerbach Corp. |
| 8 | L | Willamette Valley, Salem | 44° 50' | 60 | C | Jack Stump and Kenneth McCrae |
| 11 | M | McDonald Forest, Corvallis | 44° 30' | 580 | C | Oregon State University |
| 12 | N | Oakridge area | 43° 45' | 580 | M | USDA Forest Service |
| 13 | O | High Prairie, Oakridge | 43° 45' | 840 | M | USDA Forest Service |
| 14 | P | Butte Falls | 42° 20' | 910 | ($\frac{c}{-}$) | Medford Corporation |
| CALIFORNIA | | | | | | |
| | Q | Korbel | 41° 00' | 680 | | Simpson Timber Co. |

a A, E, L, M, and Q are the thinned plantation locations reported on here. Q is only a plantation location, not a seed source. A, B, C, E, F, K, L, M, O, and Q are the plantation locations reported for 20-yr field performance by CHING and HINZ (1978).

b Data from sources E and F are 1 yr younger and omitted from analysis.

c P is the southern Oregon source and is neither Coastal nor Mountain.

geographic breeding units for cooperative Douglas-fir tree improvement programs (SILEN 1966, SILEN and WHEAT 1979). However, patterns and magnitudes of genetic differentiation are known to change as stands age (NAMKOONG et al. 1972, NAMKOONG and CONKLE 1976), and long-term field studies are needed to confirm such tight patterns of adaptation in economically important characteristics.

The cooperative Douglas-fir regional provenance study initiated in 1954 is based on seed collected from 16 locations west of the Cascade Mountain summit in the Pacific Northwest. In 1959, 2-year-old seedlings of these provenances were outplanted in a reciprocal planting design (CHING 1965) in plantations established at or near each seed collection site. The stated objectives were " . . . to detect genetic variation in this widely distributed variety, and to correlate the existence of distinct races if any, with geographical variables such as altitude and latitude" (CHING and BEVER 1960). Earlier results from ages 1, 2, 5, 9, and 20 years have emphasized that provenances differ significantly in height and diameter at breast height (DBH) but that provenance × location interactions are of only minor practical significance (CHING and BEVER 1960, CHING 1965, ROWE and CHING 1973, CHING and HINZ 1978). In particular, three of the four provenances from Vancouver Island (Provenances B, C, D in *Table 1*) have consistently been among the tallest sources in most plantations, while the southern Oregon provenance (P) and a mountain source (N) have been below-average performers.

The present report describes patterns of 25-year growth of the various provenance trees in five mild-climate, fast-growing plantations. These data, from large field plots at approximately one-half rotation age, provide some direct measures of provenance differentiation in economically important traits such as yield per unit area and site index.

## Materials and Methods

### Seed source locations and field designs

Details of seed source (provenance) locations, sampling schemes, nursery procedures, and field plantations have been presented earlier (CHING and BEVER 1960, ROWE and CHING 1973). Briefly, cones were collected from 14 to 89 trees within a 40-km radius at 16 seed sources scattered throughout the west side of the Cascade Mountains in the Pacific Northwest *(Table 1)*. Seedlings were grown for 2 years in a bareroot nursery and outplanted at each of the 16 seed source locations and at a 17th planting location (Q). Seedlings from provenances E and F were 1 year younger and outplanted 1 year later; their data are omitted from this report. At each of the original 16 locations, two blocks of provenance plots were established in each of two nearby plantations (a total of four blocks of 16 provenance

plots = 64 plots at each location). At location Q only two blocks were planted. Each square provenance plot consisted of 121 trees from the same seed source; the trees were planted at a spacing of 2.44 m × 2.44 m The innermost 49 trees of each plot made up the measurement plot, with the two outer rows serving as buffers.

### 25-year measurements

The five fast-growing plantations (A, E, L, M, and Q) reported on here were thinned after either the 1976 or 1977 growing season to release 25 (out of 49) final crop trees on each measurement plot. Twenty-five well-spaced, vigorous trees were chosen in each plot. On some plots, survivors numbered fewer than 25 and no thinning was done.

Each tree was measured for height and DBH after the 1981 growing season (25 years from seed). In addition, three variables were derived from these measurements: tree taper, calculated as height/DBH (H:D ratio); cubic volume per hectare, calculated from a small-log volume equation (BRUCE and DEMARS 1974) for each tree and summed over all trees on a plot; and site index, obtained by averaging site index (50-year index age, KING 1966) of the five tallest trees on each plot.

### Analyses

All analyses of the five variables were based on plot means of untransformed values; analyses assumed that blocks and locations were random effects and that provenances were fixed effects. Analyses of variance for each location assumed a randomized block design. Locations A, E, and M had four blocks, while locations L and Q contained two blocks. Q began with two blocks; however, for L, data from two of the original four blocks were eliminated because obvious intrablock variability in site quality caused tremendously high error variances. Analyses of variance pooled across locations were based on the unweighted means method (COCHRAN and COX 1957, p. 558).

In addition to the general analyses of variance, two single-degree-of-freedom contrasts were of a priori interest. First, earlier work (LAVENDER et al. 1968, LAVENDER and OVERTON 1972) had shown southern Oregon sources to be slower growing than other PNW sources of Douglas-fir; that difference made the contrast of "provenance P vs. all others" of particular interest. Second, the "C vs. M" contrast was tested because the five Cascade Mountain (M) provenances might average slower growth than the eight more Coastal (C) sources *(Table 1)* (see CAMPBELL and SORENSEN 1978). Other statistical methods were employed to detect and characterize provenance × location interaction, and these are discussed as the results are presented.

## Results and Discussion

### Preliminary analysis

Regressions of plot means of 25-year growth variables on 14-year survival in the same plots (before thinning) showed the same positive relationships previously reported (CHING and HINZ 1978); faster growth was positively correlated with early survival. As before (CHING and HINZ 1978), early survival was interpreted as a proxy variable for site quality and effectiveness of site preparation at time of planting; plots with better site preparation had better early survival and, thus, better growth.

This interpretation suggests that plot means adjusted for survival would be a better measure of growth because they would "average out" the spurious effects of differential site preparation and brush competition. Thus, for each

Table 2. — Twenty-five-year stand statistics for the five thinned plantations.

| Location | Survival[a] (%) | Site quality | | DBH (cm) | Volume (m³/ha) |
|---|---|---|---|---|---|
| | | King's index (m at 50 yr) | Site class | | |
| A | 94 | 33.7 | III+ | 18.1 | 145.2 |
| E | 90 | 40.5 | II+ | 21.0 | 227.4 |
| L | 79 | 40.9 | II+ | 22.1 | 262.2 |
| M | 50 | 25.9 | IV | 15.0 | 71.3 |
| Q | 68 | 28.8 | III- | 14.6 | 77.3 |

[a] Survival was measured at 14 years, the last assessment prior to thinning.

growth variable, an analysis of covariance resulted in a common slope (common to all planting locations), which was used to adjust the plot means to the average survival at each location. These adjusted plot means were the basis of all analyses and means reported here for all response variables except H:D ratio. In actuality, adjustment had little impact on trends or rankings, but it did increase precision to some degree.

### Performance by individual planting locations

The five thinned plantations reported here (A, E, L, M, and Q) are faster growing than the five remaining unthinned locations. At age 20, A, E, L, and Q had the tallest average heights of the 10 plantations reported (CHING and HINZ 1978). Two of these sites (E and L) exhibit extremely high site quality for Douglas-fir in the PNW (Table 2).

Analyses of variance showed significant[1]) provenance differences for volume production only at location A (Table 3). Height and site index varied significantly among provenances at locations A, E, and L (the three sites with highest site index). Provenance G (Shelton, WA) was tallest at each of these locations. The contrast of the performance of provenance P with the average of the other 13 provenances was significant for height, DBH, volume production, and site index at three of the five locations and significant for stockiness (low H:D ratio) in four of the five.

In general, for all response variables, analyses of variance by individual locations were fairly insensitive even to relatively large differences among provenance means. For example, 95 percent LSD's (least square differences) indicate that, depending upon the location, differences in provenance means of 10 to 25 percent for height and 25 to 50 percent for volume were not significantly different. Thus, while the large differences between provenance P and the others were usually statistically significant, some large differences among remaining provenances were not.

### Performance across planting locations

Analyses of variance conducted across planting locations showed significant provenance differences for all response variables (Table 4). These differences are not surprising in view of the consistently poor performances of N and P at all planting locations and the relatively good performances of A and G in a number of locations. Even though ranking changed across locations for most response variables, overall provenance × location interaction was not significant for any response variable.

Orthogonal contrasts were partitioned to provide a closer look at the makeup of the provenance and provenance × location terms (Table 4). As expected, the southern Oregon provenance (P) differed significantly from the average of the other 13 provenances for all response variables. This single contrast (PO) accounted for 60 to 80 percent of the total provenance sum of squares for all response variables except H:D ratio (where $r^2 = 0.47$). This relationship was consistent over locations (PO × L was not significant for any response variable). The southern Oregon provenance is truly slower growing and across all five locations produced some 30 percent less volume/ha than the average of the other 13 provenances.

The remaining 12 provenances (after P is omitted) fall into one of two group designations, Coastal or Mountain (Table 1). Comparisons of the average performances of Mountain provenances with those of more Coastal provenances (CM contrast, Table 4) were not consistent but indicated that Coastal sources were taller and more slender

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[1]) Throughout the text of this paper, "significant" means statistically significant at P ≤ 0.05.

Table 3. — Means and significances of provenance effects at five locations (provenances ranked left to right by decreasing height at each location).

| Location and variable | | | | | | Provenance means | | | | | | | | | Provenance effects[a] | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | | | | With Prov. P | Without Prov. P | Prov. P vs. Others |
| **A** | G | C | A | B | O | H | K | M | J | I | L | D | N | P | | | |
| Height (m) | 15.7 | 15.6 | 15.6 | 15.0 | 14.9 | 14.8 | 14.8 | 14.6 | 14.1 | 14.0 | 13.8 | 13.7 | 12.2 | 11.9 | ** | * | ** |
| DBH (cm) | 18.7 | 19.4 | 17.8 | 19.3 | 19.4 | 19.0 | 18.2 | 18.9 | 18.0 | 17.9 | 17.6 | 16.7 | 16.7 | 16.3 | + | ns | * |
| Volume (m³/ha × 10⁻¹) | 16.5 | 17.5 | 14.6 | 17.1 | 17.2 | 16.1 | 14.9 | 16.6 | 13.7 | 13.7 | 12.8 | 11.5 | 10.8 | 10.1 | * | ns | * |
| Site index (m) | 36.4 | 36.0 | 35.9 | 35.0 | 34.6 | 34.7 | 34.6 | 35.0 | 33.2 | 32.3 | 33.1 | 31.9 | 29.8 | 28.6 | ** | * | ** |
| H:D ratio (m/cm × 10²) | 85.1 | 82.0 | 88.8 | 79.6 | 78.8 | 79.2 | 82.1 | 78.3 | 80.0 | 79.7 | 79.2 | 83.1 | 74.8 | 75.2 | ** | ** | ** |
| **E** | G | A | K | I | D | C | H | O | J | B | L | N | M | P | | | |
| Height (m) | 18.2 | 17.9 | 17.4 | 17.4 | 17.1 | 16.9 | 16.9 | 16.8 | 16.8 | 16.7 | 16.7 | 16.5 | 16.3 | 14.8 | ** | ns | ** |
| DBH (cm) | 22.5 | 22.0 | 21.6 | 21.1 | 21.4 | 21.3 | 20.7 | 21.0 | 20.2 | 20.8 | 21.2 | 21.4 | 19.8 | 19.3 | ns | ns | * |
| Volume (m³/ha × 10⁻¹) | 25.8 | 24.9 | 23.2 | 23.9 | 23.8 | 24.1 | 23.0 | 21.9 | 21.8 | 21.9 | 23.1 | 23.5 | 20.5 | 17.0 | ns | ns | ** |
| Site index (m) | 42.9 | 41.7 | 42.1 | 40.8 | 40.1 | 39.7 | 41.0 | 40.6 | 39.6 | 40.7 | 40.4 | 38.9 | 40.4 | 37.7 | ** | * | ** |
| H:D ratio (m/cm × 10²) | 85.2 | 83.5 | 85.7 | 86.6 | 85.0 | 83.7 | 85.8 | 82.8 | 88.2 | 86.3 | 84.2 | 80.3 | 88.7 | 80.3 | ns | ns | + |
| **L** | G | L | D | O | M | I | A | J | C | K | H | N | B | P | | | |
| Height (m) | 20.1 | 18.9 | 18.7 | 18.7 | 18.7 | 18.7 | 18.6 | 18.6 | 18.5 | 18.2 | 18.0 | 17.9 | 17.7 | 15.3 | * | ns | ** |
| DBH (cm) | 23.5 | 21.9 | 22.2 | 22.3 | 23.5 | 22.7 | 22.3 | 22.7 | 22.0 | 22.3 | 21.3 | 22.6 | 21.1 | 19.1 | ns | ns | * |
| Volume (m³/ha × 10⁻¹) | 31.2 | 26.9 | 27.0 | 28.4 | 29.4 | 27.4 | 26.9 | 27.3 | 25.4 | 26.2 | 23.3 | 26.2 | 23.1 | 18.5 | ns | ns | ** |
| Site index (m) | 43.8 | 42.3 | 41.1 | 41.9 | 40.8 | 41.0 | 41.2 | 41.6 | 41.7 | 40.3 | 40.0 | 40.0 | 40.1 | 37.4 | * | + | ** |
| H:D ratio (m/cm × 10²) | 86.2 | 89.1 | 87.2 | 86.8 | 81.6 | 84.0 | 84.7 | 83.6 | 85.4 | 83.2 | 86.8 | 80.2 | 85.3 | 77.2 | ns | ns | * |
| **M** | C | D | M | H | O | K | A | B | L | J | I | G | N | P | | | |
| Height (m) | 11.9 | 11.7 | 11.4 | 11.1 | 11.0 | 10.9 | 10.8 | 10.8 | 10.8 | 10.8 | 10.6 | 10.5 | 10.5 | 9.3 | ns | ns | ** |
| DBH (cm) | 15.6 | 16.3 | 16.0 | 14.9 | 15.0 | 15.0 | 14.5 | 15.0 | 15.8 | 15.0 | 14.5 | 14.6 | 14.6 | 13.4 | ns | ns | * |
| Volume (m³/ha × 10⁻¹) | 8.2 | 9.0 | 7.9 | 8.0 | 7.5 | 6.9 | 6.3 | 6.3 | 7.2 | 7.6 | 6.5 | 6.7 | 6.2 | 5.8 | ns | ns | + |
| Site index (m) | 28.2 | 28.4 | 25.5 | 27.3 | 26.9 | 26.3 | 26.6 | 25.1 | 24.9 | 25.5 | 25.9 | 23.8 | 25.0 | 22.5 | ns | ns | ** |
| H:D ratio (m/cm × 10²) | 80.3 | 75.0 | 68.9 | 76.4 | 76.2 | 78.1 | 80.2 | 73.4 | 71.9 | 74.0 | 79.3 | 68.8 | 74.7 | 66.8 | * | ns | * |
| **Q** | J | A | M | O | I | H | G | B | K | L | C | D | N | P | | | |
| Height (m) | 13.0 | 13.0 | 12.7 | 12.4 | 12.1 | 11.9 | 11.7 | 11.6 | 11.6 | 11.3 | 11.2 | 10.8 | 10.5 | 10.3 | ns | ns | ns |
| DBH (cm) | 15.9 | 14.5 | 16.1 | 15.8 | 15.2 | 14.8 | 14.4 | 14.1 | 14.5 | 14.2 | 13.5 | 14.0 | 13.7 | 13.5 | ns | ns | ns |
| Volume (m³/ha × 10⁻¹) | 10.0 | 8.7 | 10.9 | 8.8 | 8.5 | 9.6 | 7.3 | 6.6 | 7.8 | 7.1 | 6.1 | 6.1 | 6.0 | 5.0 | ns | ns | ns |
| Site index (m) | 31.5 | 31.0 | 29.8 | 30.0 | 28.7 | 30.0 | 28.8 | 27.7 | 28.9 | 28.6 | 27.8 | 27.3 | 26.8 | 25.8 | ns | ns | + |
| H:D ratio (m/cm × 10²) | 83.1 | 87.8 | 79.4 | 81.1 | 81.0 | 79.6 | 84.2 | 85.2 | 79.6 | 82.0 | 85.6 | 82.2 | 78.5 | 78.8 | ** | ** | * |

[a] ns = not statistically significant at P ≤ 0.10; + = significant at P = 0.10; * = significant at P = 0.05; ** = significant at P = 0.01.

87

Table 4. — Mean squares and significances from analyses of variance of the 25-year-old Douglas-fir regional provenance study representing 14 provenances planted in 5 locations.

| Source of variation | Degrees of freedom | Mean square[a] | | | | |
|---|---|---|---|---|---|---|
| | | Height | DBH | Volume/ha | Site index | H:D Ratio |
| Locations (L) | 4 | -- | -- | -- | -- | -- |
| Provenances | 13 | 28.76** | 0.285** | 1,170** | 89.7** | 0.188** |
| Prov. P vs. others (PO) | 1 | 255.60** | 2.861** | 11,038** | 731.7** | 1.158** |
| Coastal vs. Mountain (CM) | 1 | 13.56+ | .018ns | 134ns | 12.1ns | .210* |
| Within Coastal (WC) | 7 | 7.00ns | .070ns | 378ns | 22.5ns | .092ns |
| Within Mountain (WM) | 4 | 13.93* | .084ns | 348ns | 66.2** | .108+ |
| Provenances × Location | 52 | 4.08ns | .096ns | 346ns | 16.5ns | .051ns |
| PO × L | 4 | 5.06ns | .088ns | 723+ | 9.9ns | .027ns |
| CM × L | 4 | 2.13ns | .057ns | 144ns | 16.7ns | .074ns |
| WC × L | 28 | 4.71ns | .113ns | 365ns | 19.7ns | .066ns |
| WM × L | 16 | 3.22ns | .078ns | 269ns | 12.5ns | .025ns |
| Pooled error | 143 | 4.25 | .123 | 333 | 17.4 | .049 |

[a] ns = not statistically significant at $P \leq 0.05$; + = significant at $P = 0.10$; * = significant at $P = 0.05$; ** = significant at $P = 0.01$.

(larger H:D ratios). This relationship did not vary across locations (CM × L was not significant), with Coastal sources averaging 0 (at location Q) to 4 percent (at location A) taller. There were no indications of statistical differences of any kind among the eight coastal provenances (WC and WC × L contrasts, Table 4). The five provenances within the Mountain group varied in height and site index (and in H:D ratio at $P = 0.10$). There was no statistical indication of provenance × location interaction among the five provenances within the Mountain group (WM × L contrast, Table 4). The poor performance of provenance N at all locations probably accounts for most of the difference among Mountain provenances.

### Clinal trends in provenance performance

Analyses correlating provenance performance for a given response variable with climatic and topographic variables associated with provenance origin were conducted with and without provenance P. Climatic and topographic variables included latitude, elevation, longitude, summer precipitation (May—July), January mean temperature, date of last spring frost, and length of frost-free growing season (see WHITE et al. 1979 for a complete listing of these variables for each provenance).

Significant linear correlations were found between provenance latitude and mean provenance performance (averaged over all five locations) for height ($r = 0.55*$), H:D ratio ($r = 0.80**$), and site index ($r = 0.58*$). When provenance P was excluded, only H:D ratio remained significantly correlated with provenance latitude ($r = 0.76**$), indicating that more northerly provenances produce more slender trees.

Correlation analyses conducted by individual planting location (with and without provenance P) indicated that different clinal expressions might be exhibited in different plantation environments. For example, the relationship between H:D ratio and latitude (provenance P excluded) varied from strongly positive at locations A and Q to very small and nonexistent at locations E, M, and L (Fig. 1). Statistical analysis of this changing relationship, however, indicated that the slopes of the lines were not significantly different (the latitude × location interaction with 4 df was not significantly larger than the pooled error with 143 df);

thus, experimental error may be confusing the issue of truly different clinal expressions in different test environments.

### Performance through time

On the basis of provenance means (averaged over all five planting locations), correlations (with and without provenance P) among pairs of measurement years indicated significant correspondence through time (Table 5). Overall correlations (excluding provenance P) between provenance means at 9 and 25 years were 0.84** for location A, 0.73** for E, 0.38ns for L, 0.58* for M, and 0.68* for Q. Again, these differences may be due to experimental error or actually represent different trends at different locations.


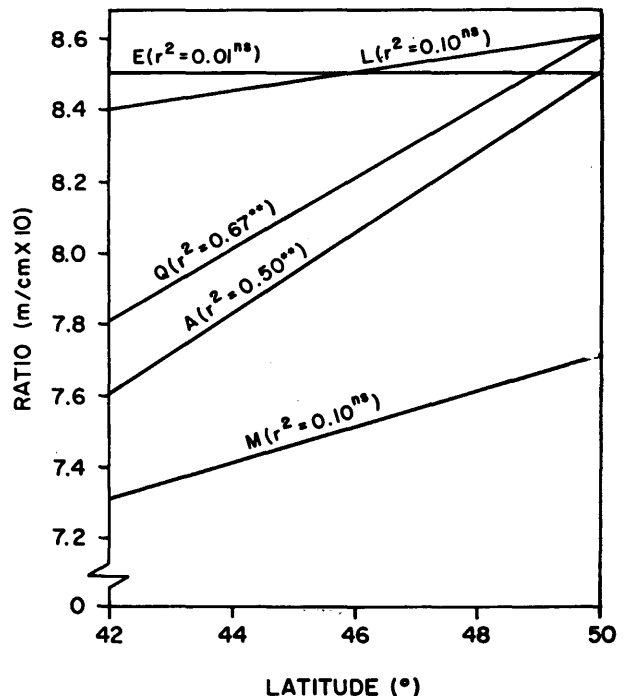
Figure 1. — Regression equations relating provenance latitude to H:D ratio for each location ($r^2$ values have 11 df, provenance P excluded).

Table 5. — Correlations among provenance means for height at ages 5, 9, 14, 20, and 25 years (all 14 provenances included above diagonal; provenance P excluded below diagonal). [a, b]

| Age | 5 | 9 | 14 | 20 | 25 |
|---|---|---|---|---|---|
| 5 | | 0.92 | 0.81 | 0.70 | 0.52 |
| 9 | 0.91 | | 0.93 | 0.83 | 0.68 |
| 14 | 0.83 | 0.95 | | 0.97 | 0.88 |
| 20 | 0.75 | 0.87 | 0.97 | | 0.95 |
| 25 | 0.48 | 0.68 | 0.84 | 0.88 | |

[a] Means from ages 20 and 25 are based on trees remaining after thinning.

[b] Above diagonal:  r = 0.53, significant at P = 0.05
  r = 0.66, significant at P = 0.01.
Below diagonal:  r = 0.55, significant at P = 0.05
  r = 0.68, significant at P = 0.01.

A final observation regarding performance through time involves provenance A, which, since age 9, has risen from consistently poor performance at all five locations (see Table 3 in Rowe and Ching 1973) to above-average or superior performance at every location. Its rise at location L may be one reason for the low correlation between the 9- and 25-year heights (0.38).

## Conclusions

Results of this experiment confirm those of previous seedling tests that southern Oregon provenances have slower growth than do other, more mesic PNW provenances (Lavender et al. 1968, Lavender and Overton 1972). In the nursery phase of this experiment (Ching and Bever 1960), the southern Oregon provenance burst bud earlier, set bud earlier, and had a shorter growing cycle than did the other provenances. That volume production in the southern Oregon provenance was 30 percent less than the average of the other provenances at age 25 may be due to natural selection for genotypes with earlier bud set, slower growth rates, or higher drought resistance in the dry southern Oregon environment (see Heiner and Lavender 1972).

Differences among the remaining 13 provenances from the more mesic PNW areas were of much smaller magnitude. Contrasts between the averages of the Coastal and Mountain provenances were inconsistent and mostly nonsignificant. No differences among the eight Coastal provenances were detectable, while differences among the five Mountain provenances were due mainly to the consistently poor performance of provenance N from Oakridge, Oregon. Furthermore, provenance X location interactions were nonsignificant or extremely small for all response variables. These results apparently conflict with those of seedling tests reporting tight adaptation of Douglas-fir to narrow climatic and ecological zones in the PNW (Campbell and Sorensen 1978, Campbell 1979, White et al. 1981, Silen and Mandel 1983). There are several possible reasons for these apparent discrepancies:

1. Statistical power (sensitivity) of many of the hypotheses tested was probably reduced because of experimental error. While critical to the important questions regarding harvest yield, the size of the field plots coupled with variability in early brush competition and animal damage introduced considerable amounts of such error.
2. The thinning conducted in 1976 and 1977 truncated the distribution of trees remaining on a given measurement plot. Results reported thus apply to a phenotypically superior fraction of each provenance. Because both spacing and tree size were used as thinning criteria, different plot volumes may have been removed, thus reducing differences among provenances.
3. Population buffering may be occurring. Families within provenances are not identified, and interaction between families within provenances and location may be present even though provenance X location interaction is small. Families adapted to different environments may have been represented within a single provenance: seed collection areas were large (5,000 km²) relative to distance within which large genetic differentiation has been previously reported for PNW Douglas-fir (Campbell 1979, White et al. 1981). A broad genetic mix of families within each seed source might tend to make seed sources more similar and reduce provenance X location interaction.
4. Ontogenetical changes in gene expression as trees age may result in different patterns of genetic variation as trees progress from seedling to mature stages (Namkoong 1969, Namkoong et al. 1972, Conkle 1973, Namkoong and Conkle 1976). Genetic expression measured during the seedling stage may differ from that of later years.
5. The planting locations reported here represent mild, fast-growing sites that have had few extreme climatic disturbances through the course of the study. On mild sites, expression of provenance differences and provenance X location interactions may depend on rare climatic events (that have not yet occurred at these five locations) or may show up as growth loss over time, especially as inter-tree competition intensifies (Adams and Campbell 1981).

The large chance of type 2 errors makes it important to look for trends in the data. For instance, in the 16-year period from age 9 to 25, the local provenances have greatly increased their height rankings for the three locations at which local sources are present (A, L, and M) (see Table 3, Rowe and Ching 1973). In these three locations, the local source has risen from near the bottom to near the top of the rankings. Perhaps provenance differences and evidence of tight adaptation to planting location will become more evident as these tests approach rotation age.

The need to field test hypotheses developed on seedlings growing in artif.cial environments is apparent both because genotype X environment interaction may occur between the artificial and field environments and because of the possibility of ontogenetical changes as trees age (reason 4 above). The lack of confirmation by the present study of hypotheses developed on seedlings is disturbing; however, the present results lack the precision needed to refute these hypotheses soundly.

Long-term field tests with large plots are costly, difficult to carry out effectively, and yet, in our opinion, imperative. Future field tests must have hypotheses (probably developed from seedling experiments) that are clearly delineated so that statistical, genetic, and field designs can

be effectively formulated. Finally, those field test sites which are inevitably "lost" because of rare climatic events such as drought, ice storms, frost, and wind storms must be closely scrutinized for the information they provide.

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# Flowering in Norway Spruce Seed Orchards

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### Summary

Female and male flowering have been assessed during ten years in six Norway spruce seed orchards, and during three years in a clonal archive. A large variation in flowering is observed between sites, between years within each site, between provenances, and between clones of the same provenance within the orchard. Depending on environmental conditions for flowering, a certain percentage of the clones in each orchard can be expected to have none, or very modest, flowering most years. Flowering is also affected by latitudinal and altitudinal transfers of the clones.

Key words: Picea abies, flowering, seed orchards.

### Zusammenfassung

In einer Periode von 10 Jahren wurde auf sechs norwegischen Fichten-Samenplantagen das männliche und weibliche Blühverhalten bonitiert. Das gleiche wurde in einem Klon-Archiv vorgenommen, jedoch nur über einen Zeitraum von drei Jahren. Es wurden zwischen den verschiedenen Standorten, zwischen den Jahren innerhalb der einzelnen Standorte, zwischen den Provenienzen und zwischen den Klonen ein und derselben Provenienz große Unterschiede im Blühen festgestellt. In Abhängigkeit von den Umweltbedingungen zeigt sich, daß in den meisten Jahren ein bestimmter Prozentsatz der Klone auf jeder Plantage nur gering oder gar nicht blüht. Einfluß auf das Blühen hat auch ein Verbringen der Klone in andere Breitengrade oder andere Höhenlagen.

## Introduction

Frequent and abundant flowering of a large proportion of the clones is essential for the success of a clonal seed orchard breeding program. With Norway spruce (Picea abies (L.) KARST.), flowering in seed orchards has been variable, and seed yields have, with few exceptions, been low compared to other species (SAMUELSON, 1979). The observed variation in flowering parallels to the variability found in natural stands. Norway spruce flowers at irregular intervals with large regional differences. Within the Nordic countries, the amount of seed produced in a stand decreases from south to north, and from low to high altitudes (SARVAS, 1957; HAGNER, 1965). Differentiation of reproductive buds is affected by favourable environmental conditions, and temperature is one significant factor influencing this process (TIREN, 1935; BRØNDBO, 1970; LINDGREN et al., 1977). Other environmental variables, such as light intensity, water conditions, and nutritional status are also important. A recent review of the flower induction process in Norway spruce is provided by DUNBERG (1979).

The present paper reports results from ten years of flowering assessments in six Norwegian seed orchards, compri-