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Title: Early Genetic Selection in Douglas-fir: Interactions With Shade, Drought, and Stand Density

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This thesis is concerned with developing techniques for identifying "superior" Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) parent trees based on seedling progeny evaluation. The growth responses of up to 14 open-pollinated families to shade, drought, and stand density were assessed in four experiments. A technique was developed to compare family height growth responses to increasing stand density while accounting for genetic variation in growth rates. Family rankings based on seedling evaluation criteria were compared with 15-year growth records for an earlier cohort from the same parent trees. The significant findings of this study were: (1) fifteen-year field height rankings were related to differences in budset date, height growth rate, and branchiness

among seedlings grown with or without shade or drought stress; (2) seedling-field correlations were inversely related to seedling-seed weight correlations; (3) seedling-field correlations improved with age in the field; (4) family correlations between spaced-plant growth and closed-stand growth were low for measures of seedling size but high for measures of seedling shape, and; (5) there was genetic variation in height growth responses to increasing stand density in single-family seedling plots.

EARLY GENETIC SELECTION IN DOUGLAS-FIR: INTERACTIONS WITH SHADE, DROUGHT, AND STAND DENSITY

by

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To my parents, whose love, understanding, encouragement, and generosity set me on this course and saw me through it: I can never repay your actions with my own, but trust that I have learned from your examples.

Janene, my first love and my partner in life: as important as this thesis is, it's a spit in the wind in comparison to you, to our family, and to our future. Thank you.

PREFACE

This thesis is presented in "manuscript" format. The first manuscript (Chapter Two) describes experiments conducted to test early screening techniques in Douglas-fir. Fifteen-year field data was provided by the Progressive Tree Improvement Program in Douglas-fir. Inasmuch as this program is one of the oldest in the region, and as evaluation plantation data are available for comparisons, this context provided a good chance for obtaining meaningful results.

The second manuscript (Chapter Three) describes a new experimental approach for estimating "relative competitive abilities" of Douglas-fir families. The study was motivated in part by the apparent confusion in the literature over the definition of "competitive ability" and over what constitutes a valid test of genetic variation. Additional motivation for the study was provided by the context of this thesis; the objective in that context was to determine whether early screening programs would need to consider stand density as a parameter when specifying an early screening environment.

Throughout most of this thesis, tables were used in lieu of figures for the presentation of data. This was done because I feel that a thesis should serve as a source document from which numerical data can be readily obtained.

Figures will be substituted for some tables in manuscripts that are submitted for publication.

The data collected for this dissertation reside at the Forest Science Data Bank, College of Forestry, Oregon State University, Corvallis, OR, and may be obtained with permission.

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CHAPTER ONE. INTRODUCTION

The unifying theme of this thesis is that of developing methods for identifying Douglas-fir parent trees that produce fast-growing progeny based on seedling progeny evaluation. Such "screening" techniques could reduce the time required for genetic evaluation and thereby speed the progress of tree improvement programs. Another benefit would be an ability to screen many more parent trees for the same cost. It is not likely that early evaluation will entirely replace current methods; screening might be most useful for eliminating the worst parent trees from longer-term, more costly evaluation.

Previous experiences with early evaluation are limited and have yielded mixed results. Although nurserybed selection has been found unreliable in several studies (Bengston 1963; LaFarge 1975; but see Snyder 1976), selection under simulated field conditions has been more successful (Cannell et al. 1978; Waxler and van Buijtenen 1981; Lambeth et al. 1982). Only Lambeth et al. (1982) have considered Douglas-fir, and they suggested that their test was weakened by an inadequate data base.

Field conditions have been defined in terms of moisture, nutrients, and temperature in early selection studies. However, evidence is accumulating which indicates that stand density can elicit differential genetic responses. Those interactions may result from intergenotypic competition (Adams et al. 1973; Tauer 1975), from inherited "ideotypic" differences (Cannell 1982), or from genetic differences in competitive ability that are independent of growth rate (Sakai et al. 1968; Panetsos 1980). Whatever the explanation, it seems clear that neighbors can have large and variable effects on seedlings in testing environments.

MODEL FOR EARLY EVALUATION

The appropriate framework for gauging the utility of early screening is an extension of the model for correlated response to selection (Falconer 1960, p. 318):

$$G(y/x) = i(x) * h(x) * h(y) * r(x,y) * \sigma(Py)$$

where $G(y/x)$ = the gain in trait y that can be expected based on selection for trait x;

$i(x)$ = the selection intensity for trait x;

$h(x)$ = the square root of the heritability of trait x;

$h(y)$ = the square root of the heritability of trait y;

$r(x,y)$ = genetic correlation between traits x and y, and;

$\sigma(Py)$ = square root of the phenotypic variance of trait y.

If x and y are defined as traits at particular ages in particular environments, then equation (1) can be used to predict the gain from an early evaluation program (Falconer 1960, p. 323; Burdon 1977; Franklin 1979). For example, x may represent seedling height in a test environment, and y the rotation age tree volume in the field.

Ignoring the superiority of early screening in terms of the time required for genetic evaluation, the most important advantage of early screening is that i(x) can be made

arbitrarily large relative to the selection intensity that is practically possible at rotation age in field environments. The disadvantage of early screening is that r(x,y), the genetic correlation between the early screening criterion and the mature tree yield variable, and h(x), the square root of the heritability of the early screening criterion, are usually something less than unity. Thus, while increased selection intensity will tend to increase genetic gain, this potential gain must be balanced against reductions arising from evaluation based upon indirect criteria. For practical application, appropriate early selection criteria are those for which heritabilities and correlations with mature yield are high, and by which large numbers of individuals can be inexpensively evaluated.

GENOTYPE BY ENVIRONMENT INTERACTIONS

Genotype by environment (G x E) interactions refer to the dependence of relative genotype rankings on test environment. When G x E interactions are important, the genetic correlations discussed in the previous section will depend upon the particular environment chosen for early screening and/or upon the particular environment chosen for mature yield evaluation. When the environmental causes of G x E interactions are known, early screening environments can mimic field conditions in order to increase genetic correlations (Cannell et al. 1978). When G x E interactions are important but the environmental causes are not known, early screening can be used to identify genotypes that are "stable" across a range of environments (Waxler and van Buijtenen 1981). Of course, the importance of accounting for G x E interactions largely depends upon whether such interactions are expected to occur in the field, and this in turn depends upon the geographical scope of the particular tree improvement program. Notwithstanding an absence of G x E interactions in the field, early screening techniques must be tested under a variety of environments in order to identify factors that will change relative genotype rankings. Intuitively, early screening will be most effective when G x E interactions are not important in the field or

in early testing environments, and when genetic correlations between field and early test environments are maximized.

OBJECTIVES

The overall objectives of this research were:

1. to investigate the interactions of Douglas-fir seedling growth parameters with test environments characterized by different levels of shade, drought, and density stress;

2. to find early evaluation criteria that are correlated with field performance to age 15 in a typical evaluation program, and;

3. to develop and demonstrate a test for genetic variation in "competitive ability" in Douglas-fir seedlings.

CHAPTER 2. EARLY GENETIC EVALUATION OF OPEN-POLLINATED DOUGLAS-FIR FAMILIES

ABSTRACT

Techniques were explored for identifying, in the seedling stage, open-pollinated Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) families with superior growth potential at older ages. Seedling progeny from 14 parent trees, grown with and without shade and drought stresses, showed significant genetic variation in several growth parameters, but virtually no evidence of genotype by environment interaction. Genetic correlations between seedling growth parameters and field height of an earlier cohort were greatest for those seedling parameters that were least correlated with seed weights. Correlations improved with field age from nine to 15 years. The results encourage the development of early genetic evaluation procedures for Douglas-fir families, provided suitable accounting of differential seed weights and of interactions arising from plantation establishment procedures.

INTRODUCTION

Relatively little work has been reported on the potential of early evaluation for identification of families of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) with superior volume growth at rotation. It is desirable to develop early evaluation techniques that utilize artificial environments for family evaluation at the seedling stage, and then relate seedling parameters to field performance of families measured in progeny tests. Cannell et al. (1978) found that the eight-year volume production of families of loblolly pine was positively correlated with their growth rates as seedlings. When eight-year production on relatively droughty sites was considered, correlations were improved by simulating a droughty evaluation environment, and the shoot-root ratio was negatively correlated with field performance. In contrast, Waxler and van Buijtenen (1981) found that the shoot-root ratio was positively correlated with long-term performance of loblolly pine families. Lambeth et al. (1982) reported that total dry weight of Douglas-fir seedlings was positively correlated with six-year field height. Only the Cannell et al. (1978) study explored phenological evaluation criteria, and, in that study, there was no evidence that seedling budset date was correlated with field performance. Thus, there is evidence that early evaluation is feasible, and that seedling test

environments can be tailored to evaluate performance in environments most like those in the field (where interaction-inducing environmental differences are most likely to occur).

G x E interactions in Douglas-fir may be significant, but generally are not large (Campbell 1972; Ching and Hinz 1978; Lambeth 1979; Silen 1980; White et al. 1981). Controlled environment studies have identified fertility (Lambeth 1979) and temperature (Campbell and Sorenson 1978; Lambeth 1979) as factors that interact with Douglas-fir seedlings. But even if G x E interactions are insignificant in the seedling environment, it is possible that some environmental features will "magnify" genetic differences (Campbell and Sorenson 1978), making genetic differences easier to detect in some environments. This is useful because inferences based upon correlations will be more meaningful when there is clear separation among genotypes at the seedling stage. Therefore it is worthwhile to explore the sources and implications of G x E interactions in seedling evaluation environments.

In this paper, "early genetic evaluation" refers to the identification of superior families by age two years in an artificial environment. In comparison with usual evaluation procedures, early evaluation can reduce generation time and allow screening of larger numbers of genotypes. Recent tests have indicated that early genetic evaluation is

feasible, yet there remain questions regarding the appropriate evaluation criteria, the importance of genotype by environment interactions, and the degree of correlation that can be expected between juvenile and mature trees.

In this chapter, I present the results of a test of early genetic evaluation of 14 open-pollinated Douglas-fir families from a northwest Oregon breeding zone. Three experiments were conducted to assess genetic variation in seedling growth, phenology, and responses to shade and drought stresses. Means of seedling family growth and phenology parameters were then correlated with 9-, 12-, and 15-year family mean heights of an earlier cohort from the same 14 parent trees that were grown in five field evaluation plantations.

MATERIALS AND METHODS

Wind-pollinated seeds were collected in 1981 from 14 Douglas-fir parent trees located within 10 km of Vernonia, Oregon. Progeny arising from those parent trees are hereafter referred to as "families." Trees were selected that are part of the base population for the Vernonia Tree Improvement Program (Silen and Wheat 1979). Seedlings from the base population were planted in 12 progeny test sites, and height growth data was collected periodically through age 15 years (the most recent measurement available). For the 1981 collection, trees were selected to provide a wide range of 15-year height. Because 1981 was a poor seed year in the Vernonia area, the actual range in 15-year height was not the widest possible. Further, cones were collected without regard to position in crown, stage of development, etc.

A random sample of 50 filled seeds from each family were individually weighed. On April 10, 1982 [age 0 days (d)], following stratification at 4°C for 63 d, seeds were sown into sterilized 165 cc Ray Leach plastic tubes (2-3 seeds per tube) with a rooting medium of peat and fine sand (1:1 by volume). Weights of individual seeds were not recorded at planting. The tubes were kept in a controlled environment chamber (20° C and 16-hour daylength) during a 29 d germination period, then weeded to leave one

healthy seedling per tube. Family differences in germination time were not tested, but weeding was conducted to leave seedlings of uniform size where possible. Tubes were then removed to an outdoor, fiberglass-covered cold frame at the Forest Research Laboratory, College of Forestry, Oregon State University, Corvallis, Oregon.

The tubes were watered to field capacity every two to three days, except when experimental protocol dictated otherwise, and except for weekly watering during a 28 d budset induction period in August. Soil fungicide and a complete fertilizer were applied bi-weekly until budset induction, at which time residual fertilizer was leached from the tubes. A 0-10-10 fertilizer was applied twice after budset was complete. Soil acidity varied between pH 5 and pH 6 during the course of the experiments. Mortality due to damping off, insects, and mechanical damage claimed less than five percent of the seedlings during the first year.

Seedlings that were grown longer than one season were kept in sawdust in the cold frame until age 273 d, at which time they were moved to a heated glasshouse, watered every other day, and fertilized weekly with a complete fertilizer. Those seedlings that did not break their terminal bud after 33 d in the glasshouse were presumed dead and were discarded. The "apparent" mortality rate over the winter

was about 30 percent. This rather high rate was probably due to insufficient insulation about the tubes.

The three seedling experiments and the response variables that were used in the analyses are described in Table II.1. The first experiment (experiment I) was conducted to compare budset and budburst dates among families, and to relate height growth rates to seed weights. The experiment was broken into two parts because many seedlings did not survive the winter, and a separate sample of seedlings was required to compare budburst dates. The two parts of this experiment are denoted Ia and Ib (see Table II.1). In experiment III, mild shade and drought stresses were applied in a factorial arrangement to seedlings from age 85 d to 91 d, from age 99 d to 105 d, and from age 107 d to final harvest (ca 180 d). The treatment schedule was intermittent to minimize early budset in the droughted environments (Timmis and Tanaka 1976) and to test the repeatability of stress responses.

"Shaded" environments were created by shade cloth that reduced light intensity to 15 percent of full sun. Light intensity in "unshaded" environments was 50 percent of full sun, the reduction due to the fiberglass cover on the cold frame. On a per-seedling basis, maximum light intensity was above light compensation in the shaded environments, and above light saturation in the unshaded environments (Krueger and Ferrell 1965; Krueger and Ruth 1969). "Droughted"

environments were created by not watering plots for the week-long treatment periods; non-droughted plots were watered at least every three days. An exception was during a budset induction period from age 108 d to 136 d, when all plots were watered only weekly. Pre-dawn xylem water potential (hereafter, "PMS;" Waring and Cleary 1967) was monitored on extra seedlings in each environment. The average difference in PMS between droughted and non-droughted seedlings in unshaded plots was 0.4 MPa.

Height was taken as epicotyl length to the base of either emerging primary needles or terminal buds. Stem diameter was the average of two subcotyledon measurements taken at right angles to each other. Heights were measured with a metal rule, and diameters with a plastic dial caliper. Stem basal area was computed from average stem diameter. Budset was defined as the occasion when brown terminal budscales were first visible, and budburst when green needles were first visible in terminal buds. An "etiolation" index was defined as the ratio of height to basal area, and a "bifurcation" index as the ratio of the number of branches plus buds to height. Harvested seedlings were divided into root (i.e. subcotyledon) and shoot components, dried, and individually weighed.

The statistical analysis follows from the designs outlined in Table 1. An additional statistic, the average

genetic correlation among seedling environments, was computed in experiment III by the formula (Robertson 1959):

$$RG = \sigma^2F/(\sigma^2F + \sigma^2FXE) \quad (1)$$

where σ^2F and σ^2FXE are estimated variance components due to family and to family by environment interaction, respectively. This statistic measures the relative importance of σ^2FXE, and is especially useful for interpretation when interactions are small yet significant. Values of RG close to 1.0 indicate that the interaction term is relatively unimportant.

Parent trees in the base population of the Vernonia Tree Improvement Program were generally selected to sample the road networks of the individual cooperators (Silen and Wheat 1979). Wind-pollinated seeds were collected in the fall of 1966, and seedlings were outplanted in the spring of 1969. Progeny test sites were selected to represent the range of environments in the Vernonia area. Tree heights were measured after 9, 12, and 15 growing seasons. Details of the design for the cooperative progeny tests can be found in Silen and Mandel (1983).

For this study, individual tree height measurement records from 12 plantations were edited to delete dead or damaged trees.[1] After editing, five plantations were

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[1]I wish to thank R. Silen, N. Mandel, and the cooperators in the Vernonia Douglas-fir Tree Improvement Cooperative for making this data available.

retained for analysis; the remainder had too few trees per family to provide a reliable estimate of family means. For those five plantations, mean height was calculated for each family-plantation combination at ages 9, 12, and 15 years (9-year heights were not available for two plantations). Tukey's test of nonadditivity (Steel and Torrie 1980, p. 372) did not detect significant family by plantation interaction at any age, so plantations were equally weighted for computing overall family means at each of the three measurement ages (Table II.2).

RESULTS AND DISCUSSION

Experiment Ia. The average height of all families increased from 0.7 cm at age 45 d to 10.9 cm at age 144 d, and family differences in height were significant ($p < .01$) at each measurement. Family rankings based on mean height generally did not change over time (results not shown). Significant ($p < .01$) differences in relative height growth rate persisted until budset was induced at age 108 d. Family mean seed weights (Table II.3) were not significantly ($p > .10$) correlated with the family means of either height or relative height growth rate at any measurement. However, the correlation between seed weight and height consistently decreased from the first measurement ($r = .45$) until the last ($r = .25$), suggesting that the correlations may have been higher before measurements began.

Differences in budset percentage among the 14 families were significant ($p < .01$) at age 117 d, when overall budset was 12.7 percent, and nine days later, when the overall value was 65.9 percent (Table II.3). By age 135 d, 98.2 percent of the seedlings had set a terminal bud, and family differences were no longer detectable.

Experiment Ib. The overall percentage of trees that had burst bud increased from 21.6 percent at age 285 d to 47.5 percent at age 292 d (Table II.3). Relatively large family differences were not significant at either age,

possibly because of the limited sample sizes. Overall budburst percentage reached 94 percent by age 292 d. The family correlations between seed weights and the budburst or budset percentages were less than r = 0.17 (Table II.3).

Experiment II. The interaction between family and harvest age was significant ($F_{13,476} = 2.97$, $p < .01$) for shoot-root ratio (Table II.4). The family mean correlation between seed weight and the shoot-root ratio was r = 0.27 and r = -0.03 at the two harvests, respectively. When harvests were analyzed separately, there was significant ($p < .01$) family variation in the shoot-root ratio at both ages. Shoot-root ratios may be desirable early evaluation criteria based on the low correlations with seed weight, but the interaction between family and age implies that, in practice, ontological stage would need to be specified in an evaluation program.

Experiment III. Despite highly significant treatment and family effects for all growth parameters, there was virtually no evidence for family by treatment interaction in any growth parameter (Table II.5). In terms of total dry weight, the stress treatments reduced growth by 24 percent to 45 percent, and shade affected dry weight growth more than drought did (Table II.6). The shoot-root ratio decreased with increasing total dry weight. Measures of height increased with shading, in spite of lower total dry weights in those treatments.

Overall family means of the seedling growth parameters are shown in Table II.7. Mean total dry weight varied from 0.86 g to 1.15 g, and height from 9.3 cm to 12.6 cm, illustrating genetic variation in growth rates during the first year. The highest family correlation with seed weight was for total dry weight ($r = 0.50$), but most correlations were less than $r = 0.25$, which suggests that seed weight differences were relatively unimportant to family ranking in these experiments.

Because family by treatment interactions were not important, the relative family rankings did not change much between treatments, and an "optimum" early testing environment could not be chosen based on correlations with field heights. However, early selection efficiency will also depend on family heritability estimates, and these can vary between treatments (Burdon 1977). Assuming perfect genetic correlation between treatments for any growth parameter (i.e. RG = 1.0), the relative family selection efficiency in any treatment is proportional to the relative value of family heritability for that treatment. Therefore, family heritabilities were estimated for each growth parameter in each treatment (Wright 1976, p. 243) (Table II.8). In general, the estimates are relatively stable over treatments (except for the bifurcation index), and no treatment is apparently superior for most of the growth parameters studied. That would indicate difficulty in choosing an

"optimum" testing environment based on the heritability criterion as well.

Correlations Between Seedlings and Field-Grown Trees

The correlations obtained between seedling growth parameters and field heights are shown in Table II.9. Measures of seedling size and morphology are from experiment III only. As shown by experiment II for the shoot-root ratio, it is possible that correlations will change if yet another seedling age is tested. In this analysis, the oldest seedling age was chosen because it was represented by the most complete data set, because better resolution between families was obtained, and because, based on the results of experiment I, seed weight differences would be least important at that age.

Overall, the correlations between seedling parameters and field height are quite low, with some exceptions, especially for 15-year field height. In particular, the youngest budset and youngest budburst percentages were significantly ($p < 0.10$) correlated with 15-year field height. In addition, the signs attached to the correlations were logical in that field height was negatively correlated with budset percentage and positively correlated with budburst percentage. The correlations for the same parameters decreased to much lower r-values at the later seedling phenology measurements. This suggests that if

growing season length is related to future field performance, the best such evaluation criteria would be measures of the tendencies for very early budburst or budset, or alternatively, length of growing season. It is important to note that these results were obtained after frost-damaged trees were deleted from the field data set. In fact, survival and growth rates on frost-prone sites could be higher for families with shorter inherent growing season lengths. This is an example where the choice of early evaluation criteria depends upon the strategy for deployment of selected material.

Fifteen-year field heights were also significantly correlated with seedling height ($p < .05$), relative height growth rate ($p < .10$), and the bifurcation index ($p < .05$). Again, the signs associated with the r-values are logical; field heights were positively correlated with seedling heights and seedling height growth rates and negatively correlated with the bifurcation index. The logic for the latter correlation is that families that divert dry matter to branch production will have less available for leader growth; of course longer-term correlations could be quite different, especially if growth after 15 years depends upon growing space occupied during the first 15 years.

In general, however, the seedling-field correlations were disappointingly low, but two interesting trends were noted that help to explain the low correlations. The first

is the trend of the correlation for any particular seedling growth parameter over field plantation age (Table II.9). In almost every case, the trend with age is towards a higher correlation, and/or, towards a seemingly more logical correlation (in sign). For example, basal area is logically positively correlated with field height. The correlation with field height for that trait was found to be -.20 at age nine years, .07 at age 12 years, and .20 at age 15 years. None of the correlations in that example are significant, but the trend seems to suggest that correlations with field height at later ages will be even higher, and perhaps significant. Other researchers have found that juvenile-mature correlations usually improve as the time interval between ages decreases (Namkoong et al. 1972; Namkoong and Conkle 1976; Lambeth 1980). However, the present results are for different cohorts and not for the same trees as is usually true for calculation of juvenile-mature correlations. In the present study, the improvement in correlations with plantation age may reflect the diminishing effects of earlier size differences in plantations that were due to, for example, nursery culture, site preparation, or early plantation maintenance (Dalmacio 1982). Indeed, the trees in the field plantations were mowed twice while in the nursery, because of constraints imposed by the Cooperative (R. R. Silen, pers. comm.). Further, some of the field plantations experienced severe brush competition and animal

damage (W. T. Adams, pers. comm.). It is possible that without these complications, the correlations obtained between seedling parameters and early field heights would have been higher.

The second interesting trend that was noted was the relationship between seedling-field correlations and seedling-seed weight correlations. For the seedling parameters in Table II.9, excepting the second budset measurements, a higher absolute value for a seedling-seed weight correlation is associated with a lower absolute value for a seedling-field correlation (Figure II.1). It is unclear why the second budset measurement did not follow this apparent trend. Despite the fact that most seedling-seed weight correlations were "nonsignificant" in this study, it appears that differential seed weights may have masked potentially significant seedling-field correlations. Further testing of this apparent trend seems warranted.

There are other possible explanations for the generally poor correlations between field heights and seedling traits. First, relatively large environmental error components may have caused field rankings to be unreliable. Second, different seedlots were used in the field and seedling tests. These potential sources of error can be overcome through better experimental designs.

Given the uncertainty surrounding seed weight effects, future tests of early evaluation should give more emphasis

to minimizing them, perhaps through longer testing periods. Future tests will also have to account for possible G x E interactions, especially when progenies arise from parent trees that represent a wide range of environments.

For practical application of early evaluation techniques, it is necessary to decide upon evaluation criteria and evaluation procedures. Experience will then allow estimation of the magnitude of correlations that can be expected between seedling and mature tree traits. These correlations can be combined with estimates of heritability, costs of early evaluation, costs of long-term genetic testing, and selection intensities in order to analyze the economic feasibility of early evaluation.

SUMMARY AND CONCLUSIONS

This study of open-pollinated seedling progenies of 14 Douglas-fir parent trees from one breeding zone found:

1. genetic variation in most growth and phenology traits measured;
2. evidence of family by age interaction in shootroot ratio during the first growing season;
3. no evidence of family by treatment interactions for any measured trait in response to mid-season shade and drought stresses, and;
4. little evidence that family heritability estimates varied in response to shade and drought stresses.

Analysis of correlations between progeny means for seedling traits and mean heights for open-pollinated progenies from the same trees growing in five genetic test plantations showed:

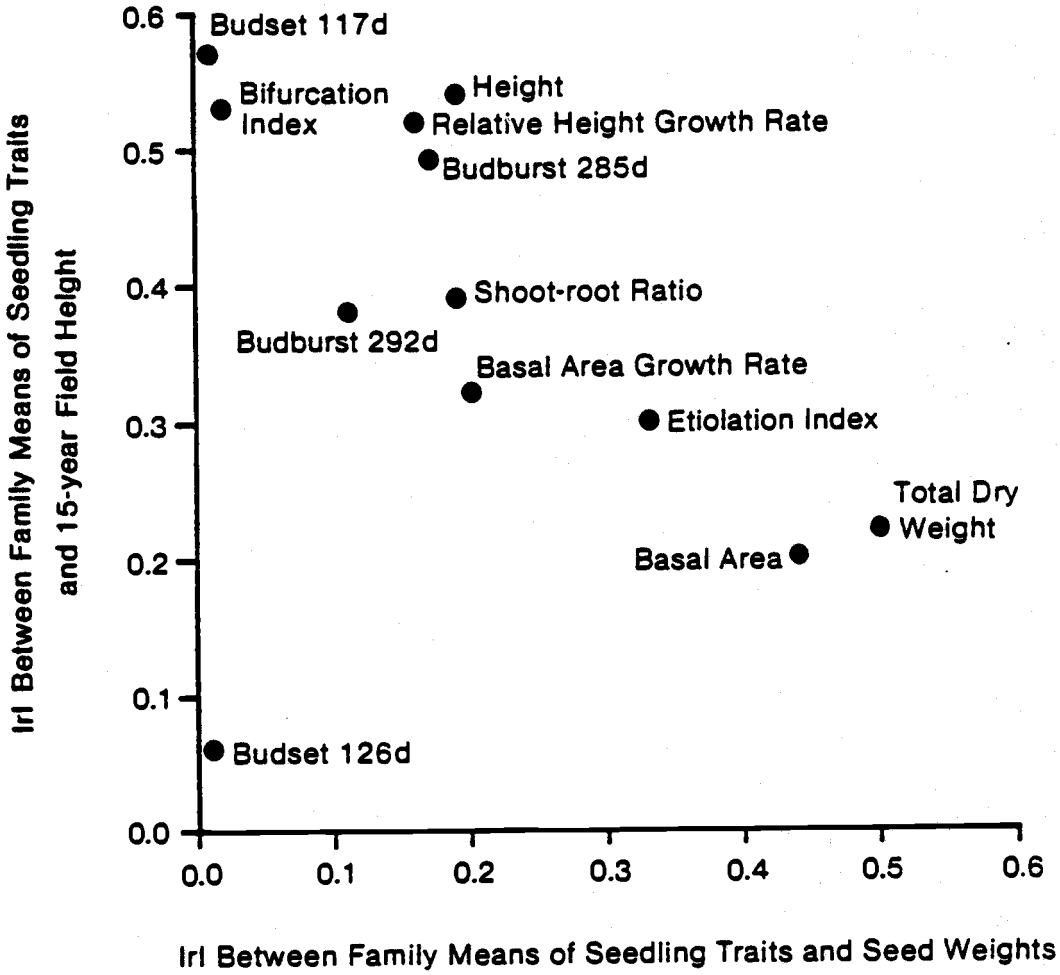
1. seedling growth and phenology traits were at best only weakly correlated with 9-, 12-, and 15-year heights in field plantations;
2. seedling-field correlations improved with field plantation age, probably owing to the diminishing effect of differential responses to early cultural treatments in field plantations;
3. seedling-field correlations seemed to be associated with the effects of seed weight, such that the

highest correlations were obtained for seedling parameters that were least correlated with seed weight, and;

4. 15-year field height was most correlated with first-year budset date, height, and a bifurcation index of seedlings grown in artificial environments.

The results suggest that early genetic evaluation is possible and can be useful in Douglas-fir tree improvement programs. In application, precautions are needed to minimize the confounding effects of seed weight and to ensure that seedling test procedures are standardized.

FIGURE II.I. The Relationship Between Seedling Trait — Field Height Correlations and Seedling Trait — Seed Weight Correlations For 14 Douglas-Fir Families.[1]



[1] Labels on data points are seedling traits in Table 11.9.

TABLE II.1. SUMMARY OF THE THREE EXPERIMENTS CONDUCTED TO COMPARE SEEDLING GROWTH PARAMETERS AMONG 14 DOUGLAS-FIR FAMILIES

	Experiments Ia and Ib	Experiment II	Experiment III
Objective	To relate height growth rates to seed weights and to compare budburst and budset dates among families.	To test family by age interactions in the shoot-root ratio.	To test differential family responses to shade and drought stresses.
Experimental Design	Ia) Four replications in a randomized complete block design. Height analysis based on means of four seedlings per family per replication. Ib) Completely random design with 8 to 15 seedlings per family. (Independent samples were used for Ia and Ib.)	Completely random sample of 16 or 20 seedlings per family each of two ages.	Five replications of a split-plot with four stress treatments (main plots) and 14 families (subplots). Analysis based on means of three seedlings per plot. See text for explanation of treatments.
Measurements (Age in days from sowing)	Ia) Height at 9-d intervals from age 45 through age 144. Budset scored at ages 117, 126, 135, and 144. Ib) Budburst scored at ages 285, 292, 299, and 306.	Shoot and root dry weights at ages 44 and 83.	Height at ages 85, 92, 99, 106, and 169. Stem diameter at ages 115, 145, and 170. Number of branches plus buds (+), and dry weight of shoots and roots at age 180.
Response Variables Used in the Analyses	Ia) At each measurement, height (cm) and relative height growth rate (cm/cm). Percentage budset at ages 117 and 126. Ib) Percentage budburst at ages 285 and 292.	The shoot-root ratio (g/g) at ages 44 and 83.	Height(cm) at age 169. Relative height growth rate (cm/cm) from age 85 to 169. Basal area (mm^2) at age 170. Relative basal area growth rate (mm^2/mm^2) from age 115 to 170. Total dry weight (g), shoot-root ratio (g/g), & bifurcation index (no./cm) at age 180. Etiolation index (cm/mm^2) at age 170 (++).

\+ Number of branches plus buds was measured in three replications only.
++ See text for further explanation.

TABLE II.2. NUMBERS OF TREES AND MEAN HEIGHTS FOR 14 DOUGLAS-FIR FAMILIES AT AGE (FROM SEED) 9, 12, AND 15 YEARS, AVERAGED OVER FIVE EVALUATION PLANTATIONS IN THE VERNONIA DOUGLAS-FIR COOPERATIVE TREE IMRPROVEMENT PROGRAM (+)

Family Number	Number of Trees	Mean Height (cm) in Field at Age		
		9 yr.	12 yr.	15 yr.
1	36	212.6	438.7	705.9
2	35	204.7	450.5	741.7
3	39	209.9	424.9	690.5
4	37	219.7	470.8	760.9
5	44	205.8	445.0	716.3
6	40	208.3	486.6	767.2
7	46	222.0	447.7	725.6
8	42	202.6	448.9	725.7
9	39	212.0	449.5	729.4
10	35	188.7	397.9	683.7
11	31	199.2	428.6	723.5
12	34	210.0	425.9	716.3
13	32	199.6	452.1	744.4
14	39	195.2	424.6	707.7
TOTAL:	529			

+ Each family is represented by an average of 7.6 trees per plantation (range 3-11). Nine-year means are based on three plantations only.

TABLE II.3. DOUGLAS-FIR FAMILY MEAN SEED WEIGHTS AND PHENOLOGICAL RESPONSES IN EXPERIMENT I

Family Number	Seed Weight (mg) (+) Mean	(S.E.)	Budset (%) at age 117 (++)	Budset (%) at age 126 (++)	Budburst (%) at age 285 (+++)	Budburst (%) at age 292 (+++)
1	12.2	(0.23)	20.0	60.0	8.3	25.0
2	11.4	(0.19)	20.0	100.0	10.0	50.0
3	10.9	(0.23)	50.0	81.3	8.3	25.0
4	10.8	(0.19)	6.7	73.3	36.4	45.5
5	8.6	(0.14)	25.0	68.8	30.8	69.2
6	11.1	(0.22)	6.3	68.8	18.2	45.5
7	12.9	(0.29)	6.3	81.3	38.5	76.9
8	9.2	(0.19)	0.0	56.3	25.0	50.0
9	10.3	(0.19)	0.0	66.7	30.8	46.2
10	12.5	(0.19)	18.8	56.2	12.5	37.5
11	10.9	(0.19)	0.0	56.3	13.3	66.7
12	10.8	(0.25)	12.5	62.5	15.4	53.9
13	11.6	(0.26)	0.0	12.5	36.4	72.7
14	11.0	(0.21)	12.5	81.3	16.7	33.3
Overall Percentage			12.7	65.9	21.6	47.5
Homogeneity Chi-Square (13 d.f.)(++++)			35.08*	35.90*	11.24	18.45
Correlation (r) with seed weight			0.01	-0.01	-0.17	-0.11

\+ N = 50 seeds per family
++ N = 15-16 seedlings per family; average 15.7
+++ N = 8-15 seedlings per family; average 11.6
++++ Asterisk denotes significance at p = 0.01

TABLE II.4. MEAN SHOOT-ROOT DRY WEIGHT RATIOS (g/g) FOR 14 DOUGLAS-FIR FAMILIES AT TWO HARVEST AGES

FAMILY NUMBER	Harvest Age 44 d		83 d	
1	1.72	ab (+)	1.73	abc
2	1.59	a	1.81	abc
3	1.79	ab	1.76	abc
4	1.74	ab	1.77	abc
5	1.65	ab	1.84	abc
6	1.80	ab	1.94	abc
7	1.92	b	1.74	abc
8	1.59	a	1.63	ab
9	1.84	ab	1.78	abc
10	1.63	ab	1.61	a
11	1.86	ab	1.98	bc
12	1.77	ab	1.77	abc
13	1.70	ab	2.07	c
14	1.89	ab	1.95	abc
Standard Error of Family Mean	0.09		0.10	
Number of Seedlings per Family	20		16	
Correlation (r) with Seed Weight (13 d.f.)	0.27 ns (++)		-0.03 ns	

+ Numbers in same column followed by different letter are significantly different (protection level = .05) by Duncan's multiple range test.

++ 'ns' indicates nonsignificant at p = .10.

TABLE II.5. SUMMARY OF ANALYSES OF VARIANCE OF GROWTH TRAITS AMONG 14 DOUGLAS-FIR FAMILIES UNDER FOUR TREATMENTS IN EXPERIMENT III

Seedling Growth Parameter (+)	F-Ratio			
D.F.:	Treatments (3,12)	Families (13,208)	Families X Treatments (39,208)	RG (++)
Height (169 d)	26.29* (+++)	12.46*	0.96	1.01
Basal Area (170 d)	88.93*	9.85*	0.99	1.00
Relative Height Growth Rate (85 d - 169 d)	29.87*	7.40*	1.02	0.99
Relative Basal Area Growth Rate (115 d - 170 d)	12.17*	4.95*	1.07	0.95
Total Dry Weight (180 d)	236.35*	8.85*	1.05	0.98
Shoot-Root Ratio (180 d)	39.83*	8.19*	1.02	0.99
Etiolation Index (170 d)	119.74*	10.05*	1.01	1.00
Bifurcation Index (180 d) (++++)	87.74*	3.69*	0.64	1.67

\+ Age at measurement shown in parentheses. See text for description of parameters.
++ Average genetic correlation among seedling environments. See text for details. (Estimates of RG greater than one are the result of negative estimates of the interaction variance component.)
+++ Asterisk denotes significance at p = 0.01.
++++ For this parameter only, d.f. equals (3,6), (13,104), and (39,104) for treatments, families, and interaction, respectively.

TABLE II.6. TREATMENT MEANS OF SEEDLING GROWTH PARAMETERS AVERAGED OVER 14 DOUGLAS-FIR FAMILIES IN EXPERIMENT III

Seedling Growth Parameter (+)	Means for Environments With:				Standard Error of Treatment Mean (++)
	No shade, no drought	Shade only	Drought only	Shade and drought	
Height (cm) (169 d)	10.6 a (+++)	11.3 b	9.53 c	10.3 a	0.141
Basal Area (mm^2) (170 d)	2.86 a	2.13 b	2.43 c	1.82 d	0.047
Relative Height Growth Rate (cm/cm) (85 d - 169 d)	2.57 a	2.77 b	2.29 c	2.47 a	0.037
Relative Basal Area Growth Rate (mm^2/mm^2) (115 d - 170 d)	1.98 a	1.67 b	2.03 a	1.62 b	0.060
Total Dry Weight (g) (180 d)	1.35 a	0.87 b	1.03 c	0.73 d	0.017
Shoot-Root Ratio (g/g) (180 d)	1.07 a	1.35 b	1.18 c	1.54 d	0.033
Etiolation Index (cm/mm^2) (170 d)	3.76 a	5.46 b	4.03 a	5.79 c	0.093
Bifurcation Index (no./cm) (180 d)	1.09 a	0.84 b	1.35 c	1.01 a	0.023

+ Age at measurement is shown in parentheses. See text for description of parameters.
++ D.f. = 12 (6 for bifurcation index).
+++ Numbers in same row followed by different letters are significantly different (protection level = 0.05) by Duncan's multiple range test.

TABLE II.7. FAMILY MEANS OF SEEDLING GROWTH PARAMETERS AVERAGED OVER FOUR TREATMENTS IN EXPERIMENT III

Family Number	Seedling Growth Parameter (+): Height (cm) (169 d)	Basal Area (mm^2) (170 d)	Relative Height Growth Rate (cm/cm) (85 d - 169 d)	Relative Basal Area Growth Rate (mm^2/mm^2) (115 d - 170 d)	Total Dry Weight (g) (180 d)	Shoot-Root Ratio (g/g) (180 d)	Index of: Etiolation (cm/mm^2) (170 d)	Index of: Bifurcation (no/cm) (180 d)
1	10.0 bc (++)	2.07 ab	2.42 b	1.82 bc	0.94 abc	1.27 ab	5.14 e	1.07 abcde
2	10.5 bcde	2.37 d	2.54 bcd	1.76 b	1.01 cdef	1.28 ab	4.62 bcd	1.16 de
3	10.2 bc	2.39 d	2.42 b	1.84 bc	1.03 def	1.23 ab	4.47 abc	1.19 e
4	10.3 bc	2.19 bc	2.62 de	1.89 cd	0.94 abc	1.29 abc	4.90 de	0.95 abc
5	10.0 bc	2.12 ab	2.44 bc	1.82 bc	0.91 ab	1.19 a	5.04 e	0.95 abc
6	11.2 e	2.48 de	2.78 f	1.91 cd	1.06 ef	1.32 bcd	4.72 cd	0.90 a
7	10.7 cde	2.44 de	2.40 ab	1.63 a	1.08 fg	1.23 ab	4.68 bcd	1.00 abcd
8	9.9 ab	1.98 a	2.70 ef	1.79 bc	0.86 a	1.18 a	5.25 e	1.06 abcde
9	9.8 ab	2.38 d	2.50 bcd	1.80 bc	0.95 bcd	1.31 bc	4.32 ab	1.24 e
10	9.3 a	2.31 cd	2.56 bcde	1.77 bc	0.94 abc	1.20 a	4.19 a	1.10 cde
11	11.1 de	2.46 de	2.27 a	1.86 bc	1.04 ef	1.42 de	4.67 bcd	1.10 bcde
12	10.4 bcd	2.11 ab	2.60 cde	1.77 bc	0.98 bcde	1.20 a	5.21 e	1.21 e
13	12.6 f	2.60 e	2.62 de	2.00 d	1.15 g	1.50 e	5.08 e	0.93 ab
14	10.2 bc	2.47 de	2.50 bcd	1.89 bcd	1.07 ef	1.38 cd	4.31 ab	1.10 abcde
Standard Error of Family Mean (+++)	0.223	0.059	0.051	0.038	0.025	0.033	0.114	0.059
Correlation (r) with Family Mean Seed Weight (++++)	0.19	0.44	-0.16	-0.20	0.50*	0.19	-0.33	0.02

\+ Age at measurement shown in parentheses. See text for description of parameters.

++ Numbers in same column followed by different letter are significantly different (protection level = .05) by Duncan's multiple range test.

+++ D.f. = 208 (104 for bifurcation index).

++++ Asterisk denotes significance at p = 0.10.

TABLE II.8. ESTIMATED FAMILY HERITABILITIES (h^2f) FOR SEEDLING GROWTH PARAMETERS AMONG 14 DOUGLAS-FIR FAMILIES IN FOUR TREATMENTS IN EXPERIMENT III (+)

Growth Parameter (++)	Treatment: No shade, no drought	Shade only	Drought only	Shade and drought
Height (169 d)	0.76	0.74	0.73	0.72
Basal Area (170 d)	0.64	0.74	0.54	0.81
Relative Height Growth Rate (85 d - 169 d)	0.68	0.65	0.64	0.46
Relative Basal Area Growth Rate (115 d - 170 d)	0.49	0.60	0.43	0.57
Total Dry Weight (180 d)	0.66	0.80	0.63	0.56
Shoot-Root Ratio (180 d)	0.53	0.58	0.80	0.64
Etiolation Index (170 d)	0.72	0.72	0.65	0.64
Bifurcation Index (180 d)	-0.16	0.55	0.10	0.79

+ $h^2f = \sigma^2F/((\sigma^2E/BN) + (\sigma^2BF/B) + \sigma^2F)$, where B = number of blocks, N = number of trees per block, and σ^2E, σ^2BF, and σ^2F are estimated variance components for error, block X family, and family, respectively, from the randomized block analysis of individual tree measurements in each treatment (Wright 1976, p. 242). (N was estimated by the harmonic mean number of trees per block in each treatment, which ranged from 2.8 to 3.0.)

++ Age at measurement is shown in parentheses. See text for description of parameters.

TABLE II.9. CORRELATION ANALYSIS OF TWO COHORTS OF DOUGLAS-FIR PROGENY: CORRELATIONS OBTAINED BETWEEN SEEDLING GROWTH PARAMETERS AND AVERAGE FIELD HEIGHTS IN FIVE PLANTATIONS AT THREE AGES

Seedling Growth Parameter (+)	Correlation with Field Height at Age: 9 yr.	12 yr.	15 yr.
Experiment I: Budset (117 d)	0.01	-0.38	-0.57** (++)
Budset (126 d)	0.32	0.04	-0.06
Budburst (285 d)	0.40	0.48*	0.49*
Budburst (292 d)	0.11	0.24	0.38
Experiment III: Height (169 d)	0.03	0.42	0.54**
Basal Area (170 d)	-0.20	0.07	0.20
Relative Height Growth Rate (85 d - 169 d)	-0.06	0.50*	0.52*
Relative Basal Area Growth Rate (115 d - 170 d)	-0.32	0.26	0.32
Total Dry Weight (180 d)	-0.06	0.11	0.22
Shoot-Root Ratio (180 d)	-0.24	0.21	0.39
Etiolation Index (170 d)	0.30	0.35	0.30
Bifurcation Index (180 d)	-0.10	-0.58**	-0.53**

+ Age at measurement is shown in parentheses. See text for description of parameters.
++ One and two asterisks denote significance at p = 0.10 and 0.05, respectively.

CHAPTER 3. COMPETITIVE DIFFERENCES AMONG DOUGLAS-FIR FAMILIES AT EARLY STAGES OF STAND DEVELOPMENT

ABSTRACT

Variation in response to mild density stress was studied among eight Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) families. Seedlings were grown for four months as spaced individuals and in single-family stands at three close spacings. The relative height growth rates of stand-grown seedlings were expressed as departures from the expected growth rates based on spaced individuals of the same family; the trends of those departures in relation to average stand height were used to assess "relative competitive abilities" of families. Significant genetic variation in relative competitive ability was found, but it was not associated with more easily measured parameters of growth as spaced individuals. The family correlations between spaced individuals and stand-grown seedlings were generally high for descriptors of seedling shape, but not of seedling size. The lowest such correlations were obtained for the most common genetic evaluation criteria, namely height and basal area.

RATIONALE AND LITERATURE REVIEW

The effect of stand density on tree growth is one of the most studied, yet least understood aspects of forest management. Understanding of density effects is particularly important for genetic selection, since superior genotypes are often selected under density conditions that are quite different from conditions that will be experienced over most of a rotation in operational plantations. This study was undertaken to learn more about density effects on Douglas-fir families during early stages of stand development, with a view towards the development of techniques that would shorten the time required to identify genotypes capable of sustaining high growth rates under conditions of increasing stand density.

The questions addressed in this paper are whether there is a genetic component to the growth response of Douglas-fir seedlings to increasing stand density, and if so, which seedling traits are most useful for so differentiating among families. It is hypothesized that "competitive ability" can be defined in terms of response to changes in stand density (in the broadest sense and not limited to spacing), so that detection of differential responses to changing stand density implies the existence of differences in competitive ability.

One approach to detecting genotypic differences in competitive ability is through "replacement," or "substitutive," experiments. In this design, "competitive ability" can be defined as the difference in yield of a genotype when grown in pure and mixed stands at constant spacings. Examples of this approach in forestry are Adams et al. (1973), Tauer (1975), and Adams (1980).

However, if competitive ability is defined in terms of a response to increasing density stress, then the replacement-type experiment is inappropriate for several reasons. First, variation in growth rate among genotypes makes it difficult to control the "effective" density stress in different stands for the purpose of making statistical comparisons. That leads to three sources of confounding: (1) relatively fast- (or slow-) growing genotypes may be subject to less (or more) density stress in mixed stands than in pure stands at a fixed age; (2) the density stress in pure stands of fast- and slow-growing genotypes is not the same at a fixed age, and; (3) the difference in density stress between pure and mixed stands is not the same for all genotypes at a fixed age.

A second objection is that, in an experimental situation, it is difficult to account for differences in size that arise in mixtures from phenological or maternal differences rather than growth rate or competitive differences. For example, genotypes with larger seeds or those

that germinate or flush earlier may gain an advantage that is unrelated to response to density. These differences may set up the kinds of confounding that have been described earlier. Adjustment for these external factors through covariance analysis (e.g. Tauer 1975) requires an assumption of linearity that is probably not justified.

A second general approach to detecting genotypic differences in competitive ability is through spacing trials. In these designs, competitive ability is defined in terms of response to stand density, and the presence of genotype by spacing interaction can be interpreted as evidence of differences in competitive ability (e.g. Panetsos 1980). However, that inference assumes that a fixed change in growing space per tree represents a fixed change in density stress imposed upon a tree by its neighbors, and that assumption is tenuous in the face of genetic variation in growth rate. Further, statistically significant genotype by spacing interaction may arise from scale changes rather than rank changes (Campbell and Wilson 1973); even "significant" rank changes may not be practically important.

Assessment of response to density within single stands is difficult owing to the confounding effects of size differences that arise from chance environmental factors. Successful analysis requires adjustment of growth rates for differences in initial competitive "status" (e.g. Cannell et al. 1977; Nance et al. 1983). Without such adjustment, the

best "competitors" will likely be genotypes or individuals that, at the time of comparison, happen to display the most leaf area highest in the canopy (Trenbath 1974). This adjustment requires a meaningful estimate of the competitive status of each tree.

Mixed stands are not necessarily required for the detection of competitive differences under the present definitions. Density effects must operate through physical alteration of the seedling environment; the response to density should be independent of the source of the density effect. All that is really important is that density stress and response to density stress be measured in a meaningful way. The simplest approach would be to compare trees of several genotypes grown with and without an artificial constraint, say upon growing space. In that scenario, density stress is presumed to be fixed artificially, and response to density stress is measured in terms of differences in growth relative to individuals grown without the artificial growing space constraint. The obvious objection to that approach is that it requires the researcher to know what environmental parameters determine density stress.

A design that comes close to that approach is common in agronomy studies, where pure stands are grown at several spacings in attempts to find optimum spacings for different varieties. Where growth rates are similar among varieties, it can be reasonably assumed that density stress at any one

spacing is similar among varieties also. All that is lacking is an appropriate standard for detection of the response to density stress. It is more common that varieties have different growth rates, however, and under those conditions, variety by spacing interactions cannot be taken as evidence of differences in response to density stress.

The preceding discussion has emphasized that the major problem associated with tests of competitive ability (when competitive ability is defined in terms of differential responses to increasing stand density in the broadest sense) is the confounding due to variation in inherent growth rate among genotypes. That variation carries two practical implications. First, it is difficult to control the density stress imposed upon genotypes, so that it is difficult to compare genotypes at a fixed density stress. Second, it is difficult to define an appropriate standard for the comparison of growth rates.

Those conclusions led to the design of the present study. The essential features of this design are: (1) single-family ("pure") plots are used to minimize within-stand variation in growth rates and to eliminate intergenotypic effects unrelated to density responses; (2) competitive ability is defined as the reduction in height growth rate, relative to an appropriate control, associated with a fixed increase in stand density; (3) the control for each family is the average growth rate of a sample of trees

grown under no density stress (this feature is discussed more fully below), and; (4) stand density is defined by average stand height. An additional feature is that several spacings were used, not to test family by spacing interaction, *per se*, but to examine the repeatability of the ranking of competitive abilities over a wider range of stand densities than is provided by one spacing alone.

"Open-grown" controls, or trees grown without imposed density stress, have been used by others as "benchmarks" to indicate when density stress first affects the growth of trees in stands (Adams et al. 1973). In a slightly different context, a comparison of the growth rates of open-grown with stand-grown trees has demonstrated competitive differences (Cannell 1982). Thus, the concept of open-grown controls is not new, but the present application is unique in that stand-grown tree growth rate is first adjusted for open-grown growth rate to define density effects; comparison of density effects in relation to a measure of stand density then provides a measure of the relative competitive abilities of different families.

With open-grown controls serving as benchmarks for detecting responses to stand density, relative competitive ability of families should not interact with the spacing of stand-grown trees, provided that the measure of stand density is appropriate. This observation provides a *de facto* test of the utility of the stand density measure.

Additional confidence in the density measure is gained if, at a fixed time, apparent density effects decrease with increased spacing. In any analysis, it is probably impossible to know whether a given measure of density is in fact appropriate, although several measures might be tested for reasonable behavior over spacings through models such as those based on "maximum size-density" relationships (see Curtis 1970).

It is recognized that height growth is not the most robust indicator of a response to density stress. It is less responsive to density stress than diameter growth (Sakai et al. 1968) or leaf area growth. However, height growth was chosen as the basis for comparison because it was a continuous process throughout the experiment (whereas diameter growth was not) and because it was measurable through non-destructive means.

It was mentioned earlier that an additional objective of this study was to provide insights for developing early genetic screening techniques. Such techniques have recently proven useful for identifying "superior" genotypes for rotation volume in the seedling stage (Cannell et al. 1978; Lambeth 1979; Waxler and van Buijtenen 1981; Lambeth et al. 1982). However, those tests have not accounted for potential confounding from differences in stand density between seedling test environments and field environments, or between seedling test environments. Although Campbell

and Wilson (1973) did not find family by spacing interaction in three-year-old Douglas-fir grown at three close spacings, there is evidence that they did not sample a sufficiently wide range of spacings at age three years to provide an adequate test of the hypothesis (Cannell 1982).

One general approach to the probem of incorporating density effects in early evaluation is to use mixtures grown at close spacings to speed up the long-term process of stand development (Franklin 1979, 1983). With this technique, superior genotypes could be identified as survivors of very high density stress after only a few years. However, it is recognized that for some tree species, short- and long-term growth patterns are not identical for different genotypes (Namkoong et al. 1972; Namkoong and Conkle 1976). If survivors of extreme density stress are in fact the largest trees in a stand at the time when subsequent growth depends upon attained size, then genotype by age interactions in growth rate preclude using this technique to predict survival at rotation age at normal spacings. That objection applies mainly to mixed stands, but there are problems with the use of pure stands, as well.

Models of average plant size in relation to spacing in even-aged stands indicate that maximum size may be constrained by spatial limitatiions at high stand density (Yoda et al. 1963; Harper 1977; Gorham 1979; White 1980). This and similar concepts are known to accurately reflect

even-aged forest stand dynamics (Reineke 1933; Drew and Flewelling 1977; 1979; see also Curtis 1970). Wearstler (1979) found no genetic variation in that maximum size-density constraint, and early genetic differences in seedling size became insignificant at high stand densities. Thus, relative tree size at high stand density, at least in pure stands, is an inefficient selection criterion.

The approach taken in the present study was to use close spacing to speed stand development, but to evaluate family differences when density stress was evident but still at a low level. Owing to the inherent difficulties in interpreting genotype by spacing interactions (described earlier), the size and morphology of open-grown individuals were compared to stand-grown seedlings through correlation analyses (see Cannell 1982). Multiple spacings in this study served to reinforce inferences that could have been drawn from one spacing alone. Because long-term evaluation results were available for only four of the eight families tested, this study was limited to identifying seedling parameters that were most sensitive to density stress, and no attempt was made to compare seedling responses with long-term field performance.

In summary, the major problem with most experimental approaches to compare competitive abilities is the inability to control the level of density stress. This results in difficulty in making valid statistical comparisons.

Accounting for genetic variation in growth rate and its effect on stand density, coupled with assessment of growth rate changes per unit of change in stand density, should improve control and allow meaningful interpretations.

Early selection for high growth rate under density stress may be possible under the appropriate experimental conditions. Experience has shown that neither mixed stands nor pure stands grown under extreme density stress can be expected to provide useful evaluation data. Differential responses to mild density stresses, measured by an index of relative competitive ability, may prove to be the basis of a useful early evaluation tool.

MATERIALS AND METHODS

The open-pollinated Douglas-fir trees that provided seeds for this study were from three locations in western Oregon. Cones were collected in 1981 from four trees near Vernonia (elevation ca 300 m), from two trees near Philomath (elevation ca 1200 m), and from two trees near Sisters (elevation ca 1200 m). Because 1981 was generally a poor seed year, the only criterion for selecting trees was that cones were present. These collections are hereafter referred to as "families," and are numbered one through eight, respectively. Following stratification at 4 C for 90 days, seeds were planted in plots in a medium of peat and fine sand (1:1 by volume) in a glasshouse located at the Forest Research Laboratory, Oregon State University, Corvallis, Oregon. Planting locations were defined by templates that were pressed into the rooting medium. Two to three seeds were planted in each planting location, and locations were weeded to leave one healthy tree per location after seed coats were shed. Subsequent mortality trees were replaced using extra seedlings that were planted outside of plots for this purpose. Such replacements were made until one week before measurements began. Over 99 percent of the planting locations produced at least one healthy seedling, and less than two percent of these seedlings had to be replaced. During the remainder of the experiment, 4.6

percent of the seedlings died and were not replaced. Mortality was due to damping off and to a local cutworm infestation.

Plots were constructed as follows. In a split-plot arrangement with five replications (plywood boxes on glasshouse benches), aluminum foil was used to separate the soil between main plots (spacings) and between split plots (families) within main plots. The plots were filled to a depth of 20 cm with rooting media. Except for the aluminum foil soil barrier, plots were contiguous.

Each subplot contained 25 seedlings in a hexagonal planting pattern at one of three spacings. The three spacings correspond to stockings of 161, 323, and 646 seedlings per square meter. Only the inner three-by-three block of seedlings was measured in any plot. In addition, 15 "open-grown" seedlings per family were grown in plastic pots (with 4 l of rooting medium 20 cm deep) located randomly throughout the glasshouse. Pot locations were adjusted slightly throughout the experiment so that seedlings in neighboring pots never touched. A total of 3,120 planting locations were established for this study; 1,200 seedlings were measured and the rest served as buffer trees around plots. Plots and pots were watered to field capacity at least weekly and fertilized at least bi-weekly throughout the experiment. Glasshouse lights were turned on from 6 a.m. until 10 p.m. each day.

Beginning at age (from planting) 55 days (d), and every six days thereafter for 78 d, total height to the base of newly-emerging needles was measured on all seedlings (excluding buffer seedlings). Harvesting was by replication, and was done from age 135 d to 155 d, during which time the glasshouse lights and heat were shut off. At harvest, the following additional seedling parameters were measured:

1. height from cotyledons to the base of newly-emerged primary needles or of the terminal bud;
2. subcotyledon stem diameter (two measurements taken at right angles on each seedling;
3. primary branch heights above cotyledons, and;
4. total length of primary and secondary branches for each primary branch.

Seedlings were separated into root (i.e. subcotyledon), stem, and branch (with attached needles) components. The components for each seedling were then oven-dried and individually weighed. Entire plots were rejected from the analysis if fewer than eight of the nine measured seedlings survived, or if fewer than 22 of the total 25 seedlings per plot survived. In the final analysis, a harmonic mean number of 4.3 plots per family-spacing combination (106 total plots) and 14.2 seedlings per family grown in pots were available.

STATISTICAL ANALYSIS

Data obtained during harvest were analyzed with the "GLM" procedure in the SAS[2] computer package (SAS Institute, Inc. 1979). Height, number of branches, and the dry weights of roots, branches, and shoots (stem plus branches) of open-grown seedlings were analyzed as a completely random design with unequal numbers of seedlings per family. For seedlings grown in stands, plot mean values were analyzed according to a split-plot design. GLM provided least-squares estimates of family-spacing means, adjusted for missing plots.

Branch height and length data was used to estimate parameters of a canopy profile model for each family-spacing combination. To do this, each seedling was divided into 16 height segments, each corresponding to 6.25 percent of total seedling height at final harvest. The percentage of total seedling branch length that appeared in each segment was then calculated. This scaling procedure eliminated differences in seedling heights that arose from family or spacing sources, and allowed pooling of seedling data across replications. Pooling was required to provide a sufficient number of observations for each family-spacing combination for fitting a canopy profile model. The percentage data was

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[2]SAS is registered trademark of SAS Institute, Inc., Cary, NC 27511-8000, USA.

then used to estimate the parameters of the two-parameter cumulative Weibul distribution with a computer program supplied by Zutter et al. (1982). In that distribution, the "b" parameter is a measure of canopy "scale" and the "c" parameter is a measure of canopy "shape." Because the height and branch length data were expressed as percentages of seedling totals, comparisons of scale are largely irrelevant. Comparisons of shape among families are simplified, because any differences in growth rates are accounted for. Because replications were pooled for parameter estimation, no tests of significance were possible, and comparisons were limited to visual inspections of graphs of the fitted distributions.

Pearson correlation coefficients were then computed, for all seedling traits, between family means of open-grown seedlings and adjusted (for missing plots) family means for stand-grown seedlings at each spacing.

A more detailed analysis was made of the seedling height growth data. Consider the following model for the relative height growth rate (RHGR), at time t, of a stand-grown seedling:

$$RHGR(t) = a + b*H(t) + c*D(t) \quad (1) \qquad (1)$$

where $RHGR(t) = \ln(H(t+1)/H(t))$, i.e. the relative height growth rate from time t to time t+1;

$H(t)$ = height at time t;

D(t) = stand "density" at time t, and; a,b,c are parameters.

Equation (1) indicates that the relative height growth rate is affected by three factors: "inherent" growth rate, indicated by the parameter a, an integration of genetic and microsite influences; current height, accounted for by parameter b, and; stand "density," or the effect of neighbors, reflected in the parameter c. This formulation is based on the results of height growth rate data presented by Cannell et al. (1984). Although more complex models of height growth could be formulated, equation (1) can be justified on the basis of simplicity and interpretability.

In an appropriate context, genetic variation in the parameter c (equation 1) can be interpreted as evidence of differential responses to increasing stand density. The appropriate context would require that the measure of stand density is functionally equivalent for all families and that temporal variation in growth rate is unimportant (because not all families would achieve the same stand density at a fixed time). An additional feature that is desirable from a statistical point of view is that H be independent of D; if that were not so, parameter estimates would have inflated variances and perhaps illogical signs.

The use of open-grown individuals as standards for comparisons of density effects is one way to control the effects of temporal variation in growth rate. With

open-grown standards, a density effect can be deduced as the difference in growth rates between open-grown and stand-grown seedlings at the same time of measurement. Although families may have different growth rates, a density effect can be expressed as a "deflection" from the growth curve of open-grown individuals of the same family.

That approach also provides a means to eliminate multicollinearity problems (i.e. correlations between H and D), through removal of H from equation (1). The open-grown individuals can be used to estimate the parameter b, and equation (1) can be rewritten as:

$$ARHGR(t) = a + c*D(t) \qquad (2)$$

where ARHGR(t) = RHGR(t)-bhat*H(t), (i.e. "adjusted" relative height growth rate); "bhat" indicates an estimate of the parameter b from equation (1), and; the other terms are as previously defined.

Since height was repeatedly measured on the same seedlings over time, the open-grown seedling data are time-wise autoregressive and are probably heteroskedastic. To satisfy the assumptions of regression analysis, the parameter b was estimated for each family from the open-grown seedlings following Kmenta (1971, section 12-2). This regression was of the form:

$$RHGR(i,t) = a(i,t) + b*HT(t) \qquad (3)$$

where i and t refer to seedlings and time periods, respectively.

In general, that analysis indicated that inherent growth rate varied among individual seedlings and that the parameter b varied among families but not among individuals within families. The estimates of the parameter b (bhat) from equation (3) were then used to adjust the height growth rates over time of stand-grown seedlings of each family. The analysis was thus reduced to the form shown in equation (2).

The term c*D(t) in equation (2) is interpretable as a density-dependent deflection from an open-grown growth curve, after allowance for inherent growth rate differences. On a per-plot basis in the present design, a comparison of the parameter c among families is a test of differential responses to increasing density.

However, because seedlings within plots are likely to be mutually correlated, the parameters of equation (2) cannot be tested with simple linear regression, even with the procedure cited above. However, the procedure does provide unbiased estimates of regression coefficients, and the three-step procedure described next was used to provide a statistical test.

First, define a set of indicator variables, [V(to)], where V(to) equals unity if t=to and zero otherwise. For each plot, fit the following model of adjusted seedling growth rate:

$$ARHGR(_i,t) = a(_i) + \sum_{t=1}^{13} d(t)*V(to) + e(_i,t) \qquad (4)$$

The subscript ($_i$) again refers to individual trees in plots. Equation (4) is similar to equation (2), except that the estimates of the parameters d(t) (call them "dhat(t)") in (4) represent a set of plot average time-dependent deflections from the open-grown standards, as opposed to density-dependent deflections that are represented by the parameter c in (2). The estimated parameters dhat(t) can then be related to D(t) (stand density) through a second step.

In this step, for each plot assume that D(t) is proportional to plot average height, or Hbar(t). The estimated parameters dhat(t) can be related to Hbar(t) through the simple linear regression.

$$dhat(t) = w + q*Hbar(t) + e(t) \qquad (5)$$

In equation (5), q can be interpreted as the change in plot average deflection in relative growth rate from an open-grown growth curve corresponding to a given change in plot average height (or "density") and therefore as a measure of the average response to increasing density of the seedlings in that plot. (The parameter w is not of interest because measurements began before the onset of density effects. In addition, seedling-to-seedling variation has been removed in step one of this procedure.)

The "three-group resistant" method (Hoaglin et al. 1983) was used to find estimates of the parameter q (call them "qhat") in each stand. That technique is based on group medians of dhat(t) and of Hbar(t), and minimizes the importance of outliers in estimating the slope of a regression line.

The final step is simply to test the parameter estimates (qhat) among spacings and among families. The split-plot design described earlier was used for that purpose. It is important to remember that responses to increasing stand density were estimated for each plot and not across spacings; the comparison of spacings in the split-plot analysis merely serves as a check on the assumption that Hbar(t) is a reasonable surrogate measure of D(t). Confidence is gained if decreased spacing is associated with larger apparent density effects. It is the test of family variation that is of interest, and a significant result is evidence for genetic variation in response to increasing stand density, defined earlier as "competitive ability." In the case where the interaction between families and spacings is significant, it is not possible to compare families except separately for each spacing; family rankings would be expected to vary over spacings. In that case, interactions might be removed through better choice of the measure of stand density.

The above approach, although complex, achieved the objective of obtaining a valid statistical test of differences in response to density among families that was not confounded with growth rate differences among families. One criticism of this approach might be that both "density" and the "response to density" are measured in terms of the same seedling attribute, namely height. Some justification is provided by the common usage of such models in forestry literature, for example in the analysis of "growth versus growing stock" curves. In addition, the response is measured in terms of height growth and density in terms of average height, so the two measures are not strictly the same. Finally, it is the change in height growth, relative to a standard, in relation to the change in plot average height that is the basis for comparison. At this level, it is problematic to sort out the statistical issues, but some reflection will show that any bias will be the result of failing to sample the same range of average height for all families. There are two solutions to their problem. The first would be to pre-specify the relevant range of average height that will be included in the analysis of all families at a given spacing. This solution was not acceptable in the present study because a limited amount of data was available in that case. The second solution would be to use several spacings to provide a wider range of average height for each family than could be obtained with only one spacing. Then,

a density measure could be constructed from both spacing and average height, for example, a measure based on a maximum size-density relationship (see Curtis 1970), and spacings could be ignored in the analysis of variance of response to stand density. These improvements might be considered in future research.

RESULTS AND DISCUSSION

The open-grown seedling harvest data are summarized in Table III.1. There are significant ($p < .01$) family differences for all measured traits except root weight. Note that it was not possible to test the equality of the estimated shape parameter of the Weibul function.

Family means for stand-grown seedlings are shown in Table III.2. The analyses of variance (ANOVA) of the measured traits indicated significant ($p < 0.01$) family differences for all traits and significant ($p < 0.01$) spacing differences for basal area and branch weight (Table III.3). Although spacing did also seem to affect shoot weight and root weight (Table III.2), those differences were not significant in the ANOVA. Height and number of branches were little affected by spacing. Thus, the experimental design did elicit spacing differences, despite the fact that seedlings were grown in small plots with minimal buffering between plots for a relatively short time. Family by spacing interactions were not signficant for any of the traits measured. The lack of interactions in this study agrees with the results of Campbell and Wilson (1973), who found no interactions in Douglas-fir height and basal area when seedlings were grown at several close spacings for three years.

Family mean correlations between open-grown and stand-grown seedlings are shown in Table III.4. In general, the correlations are significant ($p < 0.10$),[3] with some interesting exceptions. Correlations of root weight were not significant for any spacing, probably owing to the lack of family differences in the open-grown seedlings. For the closest spacing, family correlations were not significant for seedling size traits, namely height, basal area, and shoot weight. The results for height and basal area are similar to those reported by Cannell (1982) for Picea sitchensis. If this is true in general, then selection based on these traits will need to account for density effects, if selection is made of open-grown trees. In practice, selection occurs in plantations where trees are both open- and stand-grown for part of their lifetime, and low correlations between the two cases should be considered as a potential problem.

Cannell (1979) and Cannell et al. (1983) suggest that the canopy profile might serve as a useful selection criterion. To be useful, it would be important to be able to measure canopy profiles in such a fashion so as to remove differences arising from variation in seedling size, for example due to spacing effects. In the present study, high

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[3] A different sigificance level was chosen for the correlation analyses because of the reduced sensitivity relative to the other analyses discussed.

correlations were obtained for descriptors of canopy structure (branch weight and number, and the shape parameter of the Weibul distribution) between open-grown and stand-grown seedlings at all spacings. Figure III.1 illustrates the consistency in canopy profiles that were estimated for open-grown seedlings and seedlings grown at the closest spacing. These profiles are graphs of the density functions corresponding to the fitted cumulative distributions. Cannell et al. (1983) suggested specific tree shapes that might have superior growth rates under either high or low density stresses. Although family differences in canopy profile are suggested in Figure III.1, that comparison was not testable in this study.

The analysis of the relative height growth rates of open-grown individuals over time in relation to seedling height (see equation 3) is summarized in Table III.5. For all families. a significant ($p < 0.01$) proportion of variation in growth rate was explained by inherent seedling differences and by current height ($0.54 < r\text{-squared} < 0.93$). Current height was not a significant ($p > 0.01$) term for family number six. The parameter estimates shown in Table III.5 were used to adjust stand-grown seedling growth rates for differences in height.

The results of the "three-step" analytical procedure that was devised to test differences in responses to increasing stand density are summarized in Tables III.6 and

III.7. In the analysis of variance (Table III.6), the response variable is the estimated value of q (qhat; see equation 5) for each plot, i.e. the change in plot average deflection in relative growth rate from an open-grown growth curve in relation to a given change in plot average height, or more simply, "relative competitive ability." Relative competitive ability was significantly ($p < .01$) different among spacings and among families, but the interaction was not significant (Table III.6). Because relative competitive ability is defined in terms of a response to stand density, it is reasonable to find significant spacing effects. That simply indicates that differences in responses were detected among spacings, and does not imply that trees are more or less "competitive" at different spacings. The earlier conclusion that total height was unaffected by spacing (Table III.3) is not inconsistent with the spacing differences in Table III.6; the two conclusions refer to different quantities.

Because greater responses were detected at closer spacings (Table III.7), and because there was no evidence for family by spacing interaction (Table III.6), there is some retrospective justification for the use of stand average height as surrogate measure of stand "density" at a fixed spacing.

Of greatest interest in Table III.6 is the significant ($p < 0.01$) variation in relative competitive ability among

families. Averaged over spacings, there is a four-fold difference in estimated family relative competitive ability between the two extreme families. It is concluded that there is genetic variation in relative competitive ability among Douglas-fir families, at least according to the definitions used in this study.

A question that remains to be answered is: which seedling parameters, as measured on open-grown seedlings, are correlated with relative competitive ability in stands? This question is relevant because techniques need to be developed to identify competitive abilities of trees without having to test them in expensive plantation situations. Of the parameters shown in Table III.1, only average height was significantly ($p < 0.10$) so correlated ($r = 0.724$); families that grew tallest as open-grown individuals tended to suffer less relative reduction in relative height growth rates under conditions of density stress.

Perhaps the most important outcome of this experiment, in terms of application to early evaluation programs, is that stand density needs to be accounted for at two levels. First, it appears to matter whether trees are evaluated as spaced individuals or as members of groups of trees, because of the evidence that family rankings could be different in each case. At another level, when trees are evaluated based on performance when grown in groups of trees, the particular combination of genotypes that surround a particular tree

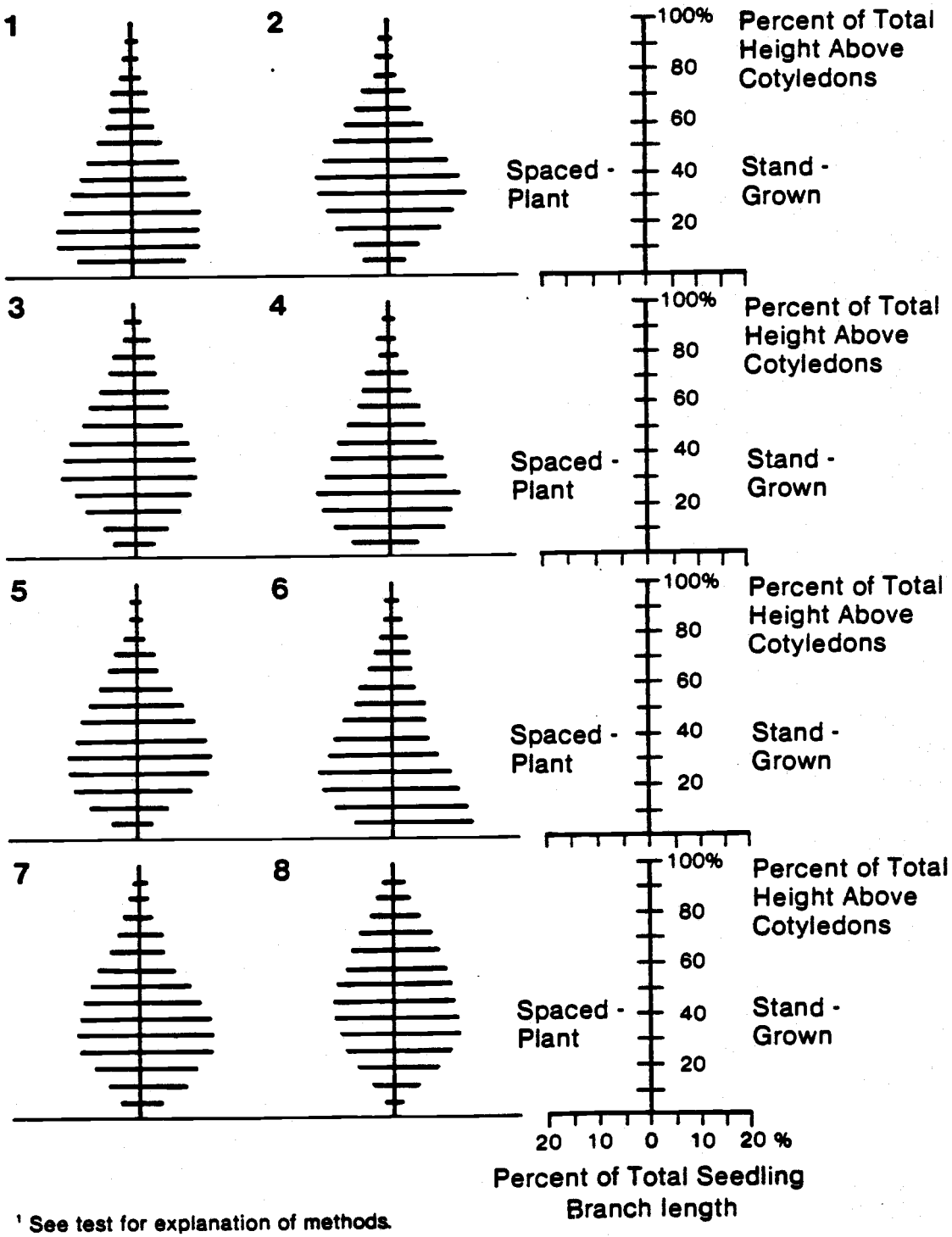
will make a difference in the apparent performance of that tree. This is because of the evidence found in this study for genetic variation in relative competitive ability. Thus some genotypes with exceptionally poor competitive ability might never be selected--not because they don't have fast inherent growth rates, but because they happened to be tested in a group of exceptionally good competitors. Whether that is good or bad depends, in part, upon the strategy for deployment of "superior" genetic material.

SUMMARY AND CONCLUSIONS

This study of seedlings from eight Douglas-fir families grown at several spacings:

1. demonstrated a method for estimating "relative competitive ability," based on height growth responses to increasing stand density, that is independent of growth rates of families and of spacings;
2. found significant genetic variation in relative competitive ability;
3. indicated that correlations based on family means open-grown and stand-grown seedlings were generally higher for descriptors of seedling shape than for descriptors of seedling size, and;
4. suggested that family rankings based on height or on diameter will be different when progeny are grown as spaced individuals versus under conditions of density stress.

FIGURE III.I Canopy Profiles Described by the 2-Parameter Weibul Probability Distribution for Seedlings of Eight Douglas-Fir Families Grown as Spaced Individuals (left) and as Close Spacing (right).[1]



[1] See test for explanation of methods.

TABLE III.1. SUMMARY OF THE ANALYSIS OF OPEN-GROWN SEEDLINGS FROM EIGHT DOUGLAS-FIR FAMILIES

Family Number	Height (cm)	Basal Area (mm^2)	Shoot Weight (mg)	Root Weight (mg)	Branch Weight (mg)	Branch Number (no)	Weibul Shape Parameter(+)
1	19.7 c (++)	4.54 c	1212 c	384 a	589 d	13.1 c	1.51
2	18.7 c	3.98 bc	990 bc	365 a	360 cd	7.7 ab	2.17
3	18.4 c	3.01 ab	835 ab	290 a	296 ab	10.3 bc	2.19
4	19.2 c	3.53 ab	1051 bc	332 a	457 abc	11.6 c	1.73
5	20.0 c	3.70 abc	1012 bc	349 a	452 cd	11.6 c	1.95
6	14.9 ab	3.04 ab	801 ab	301 a	346 abc	10.6 bc	1.76
7	17.4 bc	3.07 ab	790 ab	341 a	242 bc	6.5 a	2.12
8	14.2 a	2.75 a	656 a	282 a	146 a	5.2 a	2.41
Standard Error of Family Mean (+++)	0.9	0.32	101	29	67	1.1	- (++++)
F-Statistic (7,106) (+++++)	5.44*	3.68*	3.26*	1.58	4.47*	6.74*	--

\+ The shape parameter of the cumulative, two-parameter Weibul function estimated for the relationship between cumulative percentage of total seedling branch length and cumulative percentage of total seedling height.

++ Numbers in the same column followed by different letters are significantly different (protection level = .05) by Duncan's multiple range test.

+++ Based on an harmonic mean number of 14.2 seedlings per family.

++++ "--" indicates that the statistic was not available.

+++++ Asterisks indicate significance at p = 0.01.

TABLE III.2. ADJUSTED FAMILY-SPACING MEANS FOR STAND-GROWN SEEDLINGS OF EIGHT DOUGLAS-FIR FAMILIES (+)

Family Number	Height (cm)	Basal Area (mm^2)	Shoot Weight (mg)	Root Weight (mg)	Branch Weight (mg)	Branch Number (no)	Weibul Shape Parameter(++)
			Spacing 1 (161 plants/m^2)				
1	14.0 c (+++)	2.01 ab	488 cdef	149 ab	199 d	8.5 cd	1.65
2	12.9 bc	1.88 ab	415 bcd	163 ab	132 c	5.0 b	1.75
3	13.0 bc	1.68 ab	428 bcde	164 ab	114 bc	6.9 bc	2.01
4	13.8 c	2.07 b	542 f	182 b	217 d	8.9 cd	1.25
5	13.9 c	2.06 b	504 def	167 b	197 d	9.3 d	1.45
6	11.2 b	1.66 a	373 ab	127 a	128 c	6.4 b	1.77
7	12.8 bc	1.83 ab	388 abc	175 b	61 ab	3.0 a	2.40
8	8.8 a	1.68 ab	295 a	131 a	33 a	2.0 a	2.36
Mean	12.5	1.86	429	157	135	6.3	--
			Spacing 2 (323 plants/m^2)				
1	14.9 bc	2.13 b	500 c	150 a	217 d	9.6 e	1.56
2	12.9 b	1.95 ab	370 ab	164 a	85 ab	4.5 bc	1.86
3	13.1 bc	1.56 a	363 ab	134 a	83 ab	5.5 cd	2.29
4	13.9 bc	1.80 ab	436 bc	145 a	166 cd	6.3 cd	1.59
5	15.5 c	1.91 ab	428 bc	131 a	115 bc	7.3 d	2.14
6	12.5 b	1.64 a	364 ab	140 a	101 b	5.3 cd	1.50
7	13.5 bc	1.74 a	390 ab	168 a	61 ab	2.9 ab	2.58
8	9.8 a	1.69 a	293 a	132 a	27 a	2.0 a	2.37
Mean	13.3	1.80	393	146	107	5.4	--

TABLE II.2. ADJUSTED FAMILY-SPACING MEANS FOR STAND-GROWN SEEDLINGS, cont'd.

	Spacing 3 (646 plants/m^2)						
1	13.9 b	1.57 ab	361 a	102 a	112 b	7.5 c	1.62
2	15.2 b	1.84 b	377 a	142 b	85 ab	4.8 b	2.37
3	12.9 ab	1.30 a	278 a	96 a	41 a	5.1 b	1.99
4	13.2 ab	1.37 a	311 a	127 ab	60 ab	5.2 b	1.75
5	12.8 ab	1.37 a	284 a	100 a	74 ab	5.1 b	2.26
6	12.9 ab	1.49 ab	314 a	109 ab	73 ab	5.3 b	1.00
7	14.9 b	1.71 b	383 a	142 b	76 ab	3.4 ab	2.13
8	10.8 a	1.47 ab	298 a	122 ab	40 a	2.1 a	2.27
Mean	13.3	1.52	326	118	70	4.8	--
Standard Error of Family-Spacing Mean (++++)	0.8	0.12	35	12	21	0.7	-- (+++++)

\+ Least-squares means adjusted for missing data.

++ The shape parameter of the cumulative, two-parameter Weibul function estimated for the relationship between cumulative percentage of total seedling branch length and cumulative percentage of total seedling height.

+++ For each spacing, family means in same column followed by different letters are significantly different (protection level = .05) by Duncan's multiple range test, unadjusted for missing data.

++++ Based on an harmonic mean number of 4.3 plots per family at each spacing.

+++++ "--" indicates that the statistic was not available.

TABLE III.3. SUMMARY OF ANALYSES OF VARIANCE OF STAND-GROWN SEEDLING PARAMETERS AMONG EIGHT DOUGLAS-FIR FAMILIES

	F-RATIO		
Seedling Parameter D.F.:	Spacings (2,8)	Families (7,70)	Spacings X Families (14,70)
Height	1.97	10.70* (+)	1.17
Basal Area	9.85*	3.94*	1.32
Shoot Weight	7.24	5.85*	2.02
Root Weight	7.59	4.37*	1.23
Branch Weight	9.59*	13.14*	2.45
Branch Number	1.64	29.14*	1.93

+ Asterisk denotes significance at p = .01.

TABLE III.4. CORRELATIONS BETWEEN OPEN-GROWN AND STAND-GROWN FAMILY MEANS OF EIGHT DOUGLAS-FIR FAMILIES (+)

Seedling Descriptor	Family Correlation Between Open-Grown and Stand-Grown For: Spacing 1 (161 plants/m^2)	Spacing 2 (323 plants/m^2)	Spacing 3 (646 plants/m^2)
Height	0.942	0.873	0.515
Basal Area	0.735	0.941	0.318
Shoot Weight	0.853	0.920	0.256
Root Weight	0.403	0.583	0.183
Branch Weight	0.934	0.958	0.724
Branch Number	0.960	0.951	0.911
Weibul Shape Parameter	0.693	0.802	0.686

+ Correlation coefficients = or > 0.621 are significantly ($p < 0.10$) different from zero (6 d.f.).

TABLE III.5. SUMMARY STATISTICS FOR THE REGRESSION ANALYSIS OF OPEN-GROWN SEEDLING HEIGHT GROWTH DATA FOR EIGHT DOUGLAS-FIR FAMILIES (+)

Family Number	BHAT (*10**3) (++)	S.E. (BHAT) (*10**3)	r-squared
1	-3.76	0.30	0.93
2	-3.65	0.46	0.80
3	-2.85	0.63	0.72
4	-2.42	0.51	0.83
5	-4.54	0.39	0.89
6	-0.52	0.85	0.54
7	-5.11	0.46	0.84
8	-2.61	0.90	0.54

+ Equation 3 in text. The model fitted for each family was: $RHGR_{(i,t)} = a_{(i)} + b*H_{(t)} + e_{(i,t)}$. The subscripts i and t refer to seedlings and time periods, respectively. Thirteen time periods for 13-15 seedlings per family were used in fitting the regression. Adjustments for autoregressive disturbances and heteroskedasdicity followed Kmenta (1971, section 12-2).

++ BHAT is the estimate for the regression coefficient b.

TABLE III.6. ANALYSIS OF VARIANCE OF "RELATIVE COMPETITIVE ABILITY," OR THE ESTIMATED VALUE OF THE PARAMETER q IN EQUATION 5 (+)

Source	D.F.	Mean Square	F	Prob(>F)
Block	4	0.3912	3.43	.065
Spacing	2	1.2019	10.52	.006
Main Plot Error	8	0.1142	1.37	.225
Family	7	0.9038	10.84	<.001
Spacing X Family	14	0.0906	1.09	.385
Split Plot Error	70	0.0834	--	--
TOTAL	105			

+ See text for the derivation of the parameter q.

TABLE III.7. ADJUSTED SPACING AND FAMILY MEANS OF "RELATIVE COMPETITIVE ABILITY" (RCA), OR THE ESTIMATED VALUE OF THE PARAMETER q IN EQUATION 5 (+)

Spacing	RCA	S.E. (RCA)
1 (161 plants/m^2)	-.3400 a (++)	.0482
2 (323 plants/m^2)	-.6008 b	.0512
3 (646 plants/m^2)	-.7018 b	.0507

Family Number	RCA	S.E. (RCA)
1	-.4589 bc (++)	.0948
2	-.4678 bc	.0781
3	-.2346 a	.0816
4	-.5819 cd	.0848
5	-.4969 bc	.0817
6	-.7448 d	.0746
7	-.3446 ab	.0782
8	-1.0509 e	.0746

+ Least-squares means adjusted for missing plots and averaged over other factors. See text for derivation of RCA.

++ Spacing or family means followed by different letters are significantly different (protection level = .05) by Duncan's multiple range test, unadjusted for missing plots. Standard errors for this test were derived from the analysis of variance (.0534 and .0746, respectively, for spacing and family tests).

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