Effects of Seed Weight and Rate of Emergence on Early Growth of Open-Pollinated Douglas-Fir Families

J.B. St. Clair
W.T. Adams

ABSTRACT. Seed weight, time of emergence, and three measures of seedling size were recorded for 39 open-pollinated Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco) families in order to assess family variation in seed weight and emergence, and the influence of these seed traits on early growth. Families were planted both as ungerminated seed and as recent germinants to test whether using germinants minimized seed effects on early growth. To evaluate the effect of competition on the relationships of seed weight and rate of emergence to seedling size, individuals of families were planted in mixed-family blocks at close spacing, in single (pure) family blocks at close spacing, and at a wide, noncompetitive spacing. Families differed significantly in seed weight, total percent emergence, and rate of emergence. Nevertheless, correlations of seed weight to rate of emergence, and seed weight and rate of emergence to seedling size were not strong. Using germinants was ineffective in diminishing seed effects, and interfamily competition had only a minor influence on magnifying seed effects. FOR. SCI. 37(4):987–997.
ADDITIONAL KEY WORDS. Maternal effects, germinants, competition, heritability, genetic gain.

IN CONIFERS, VARIATION IN THE AVERAGE WEIGHT of seed collected from different female parents is a consequence of three factors: (1) the mean diploid genotype of the embryo, (2) the mean haploid genotype of the megagametophyte, and (3) environmental effects common to the mother tree. The latter two factors are maternal effects. Evidence suggests that family differences in seed weight and other seed traits are largely due to maternal effects. For example, Perry (1976) estimated that the female parent accounted for 88% of the total variation in seed weight among crosses of *Pinus taeda*, and Bramlett et al. (1983) found a strong maternal influence on germination properties of five full-sib families of *Pinus virginiana*. In addition, several studies indicate that environmental conditions of the female parent can have a strong influence on seed weight (Sorensen and Franklin 1977, Silen and Osterhaus 1979, Shen and Lindgren 1981, Sorensen and Campbell 1985).

Maternal effects as expressed through seed weight differences may contribute to family differences in early growth of forest tree progenies. Wilcox (1983) found that seed size differences between reciprocal crosses of *Pinus radiata* led to significant height differences after 6 months in the nursery and up to 2 years in the field; the effect of seed size on height growth, however, diminished with time. Sorensen and Campbell (1985) separated environmental effects of seed weight on

seedling size from genetic effects by leaving some developing cones unbagged, while enclosing others in kraft-paper bags, to produce seed of varying weights within individual Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) trees. They found that a 10.7% increase in seed weight led to a 9.1% increase in first-year epicotyl length and a 4.0% increase in second-year height.

These studies indicate that effects of seed weight on seedling size are primarily maternal in origin and strongly influenced by the environment of the mother tree. Therefore, maternal effects contribute error to the genetic analysis of seedling growth traits, leading to biased estimates of variance components and inaccurate genetic ranking of parents. The degree to which maternal effects contribute error in genetic testing depends on the strength of the relationship between seed weight and seedling size, as well as the extent to which maternal effects are repeatable in different seed years or when maternal genotypes are moved to different environments, and the degree to which the mother trees used in the genetic test are used as mothers in producing the next generation.

Seed weight effects on early growth differences among families may operate through differential rates of germination and emergence (Waller 1985). Dunlap and Barnett (1983) found that the size advantage of seedlings derived from large seeds was a consequence of their more rapid germination and emergence. Their study, however, did not include a genetic component. If the effect of seed weight on early growth is primarily the result of differences in germination and emergence rate (i.e., heavier seeds germinate and emerge earlier), planting recent germinants rather than ungerminated seed is expected to lead to weaker relationships between seed weight and seedling size and between rate of emergence and seedling size.

The effect of seed weight on early growth may be influenced by the competitive environment in which seedlings are grown. Competitive interactions among seedlings of families planted in mixture may magnify the advantages of seedlings from heavier seed germinating and emerging earlier (Black 1958, Williams et al. 1968, Waller 1985). Thus, it may be hypothesized that correlations of seed weight and rate of emergence with seedling size will be larger when families are planted in mixture at close spacing than when families are planted in pure blocks or at a wide spacing.

In the study described in this paper, the extent to which seed weight influences the rate of emergence and early growth of 39 open-pollinated families of coastal Douglas-fir was investigated. The objectives were: (1) to assess the degree to which open-pollinated families of Douglas-fir differ in seed characters (seed weight, germination, and emergence), (2) to determine the degree to which family differences in seedling size are related to differences in seed weight and rate of emergence, (3) to evaluate the effectiveness of planting germinants to minimize seed effects on family differences in seedling growth, and (4) to evaluate the effect of competitive environment on the relationships of seed weight and rate of emergence to seedling size. To accomplish these objectives, ungerminated seed and recent germinants were planted into nursery plots in mixed family blocks at close spacing, in pure family blocks at close spacing, and at a wide, noncompetitive spacing. Correlations between family means for seed weight and rate of emergence, seed weight and seedling size, and rate of emergence and seedling size were then compared between planting types (ungerminated seed versus recent germinants) and competitive environments.

Open-pollinated seeds were collected in fall of 1985 from 39 parent trees located in second-growth stands between elevations of 150 and 500 m in the Coast Range of west-central Oregon. Parent trees were from selections within a single breeding zone (approximately 35 × 50 km) of the Umpqua Tree Improvement Cooperative of the Progressive Tree Improvement Program (Silen and Wheat 1979). Cones were collected only after they were ripe, as indicated by color and fully developed embryos of seed from a sample of cones. All seedlots were treated equally after collection. Seeds were dewinged and cleaned, then stored at 0°C. In the process of cleaning, most of the empty seeds were removed, resulting in only minor differences in percentage filled seed among families. Cutting seed that did not germinate in later germination tests indicated that overall 97% of the seed was filled, with a range among families of 86 to 100% (the second lowest family was 94%). In addition, the percentage filled seed in each family was uncorrelated with seed weight, germination rate and percent, and emergence rate and percent.

Three independent samples of 35 seeds were drawn from each family seedlot and weighed. The experimental design for seed weight was a completely random design with three replicates. Seed was stratified at 3–4°C for 8 weeks beginning in February 1986.

The present study was part of a larger investigation of the effect of competitive environment on relative family performance and estimation of genetic parameters in Douglas-fir seedlings (St. Clair 1989). In April 1986, seeds and germinants were planted to a depth of 8 mm in a split-split plot design in raised nursery beds. Main plots were three competitive environments: (1) a mixture of individuals from all families at close (4 × 4 cm) spacing, (2) single (pure) family blocks, with individuals planted at the same close spacing, and (3) individuals of all families planted at a wide (16 × 16 cm), noncompetitive spacing. The two planting types (ungerminated seed and recent germinants) were subplots. In environments (1) and (3), each family was represented by four individuals assigned at random to each of four spots within each subplot (i.e., four-tree, noncontiguous sub-subplots). In the pure competitive environment, each family sub-subplot was represented by a 16-tree square plot in which all 16 spots were measured for emergence, but only the inner four seedlings were measured for growth traits. The design was replicated in five complete blocks. However, one full replication, and the subplot planted with germinants in another replication, were excluded from measurements of seedling size due to high mortality from disease (*Fusarium* sp.) and a weevil (*Barypeithes pellucidus*).

The germinants were obtained by germinating seeds on moistened filter paper in petri dishes located in a laboratory germinator set to a day/night temperature of 30/20°C and a 12-hr photoperiod. Numbers germinated were recorded at variable time intervals (more frequently during peak germination; Campbell and Sorensen 1979) in order to assess family differences in germination percent and rate (objective 1), and to assess their relationships with emergence. A seed was considered germinated once the root tip penetrated the seed coat. Each family was represented by five petri dishes of approximately 60 to 90 seeds each. The experimental design for analysis of family differences in germination characters was a randomized complete block design in which one dish from each family was present in each replication, and each replication was a separate shelf in the

germinator. As seeds germinated, they were removed from the petri dishes and stored at 3–4°C to slow elongation of the radical until enough germinants were available to plant a replication in the nursery. The length of cold storage was from 1 to 13 days, with most germinants being stored around 7 days.

Rate of germination was estimated using the procedure described by Campbell and Sorensen (1979). In their procedure, cumulative percentages of germination to each measurement time are first transformed to probits and then linearly regressed on the inverse of the time to that measurement. Mean germination rate is estimated using the slope and intercept of the resulting regression line. Time to 50% germination was also estimated using equations given by Campbell and Sorensen (1979) (approximately equal to the inverse of rate of germination).

Three seeds per planting location were planted into the "ungerminated seed" subplots during the first week of April 1986, while one germinant per location was planted into the "recent germinant" subplots approximately 2 weeks later. Emergence (defined as when the seedling first broke the soil surface) was recorded every 3 days until the end of May in the five replications of the pure competitive environment whole plots. Individuals planted as ungerminated seed and individuals planted as germinants emerged at approximately the same time; the mean dates of emergence differed by only 1 day. Total percent, rate, and time to 50% emergence were estimated for each family by planting type combination in each replication (using the same probit procedure as used to estimate germination), and subjected to analyses of variance to test the significance of family differences and planting type on emergence traits (objective 1).

Beginning in late May, seedlings were transplanted to spots which were empty due to lack of emergence and mortality (20.0% of the spots were transplanted), and spots in which more than one seedling emerged were randomly thinned to a single individual. Early transplants were not different in size from nontransplants. Late transplants (after May), however, were much smaller than nontransplants, and were excluded from further analyses (3.1% of the spots). Transplants came from adjacent transplant beds which were planted at the same time as the experiment or from the excluded replication.

The relationships between seed weight and rate of emergence, seed weight and seedling size, and rate of emergence and seedling size were assessed for each of the six pairwise treatment combinations of the three competitive environments and two planting types by calculating correlations of family means (objective 2). Three measures of seedling size were evaluated: total dry weight of 2-year-old seedlings, and 1- and 2-year height. Homogeneity of correlation coefficients over treatment combinations was investigated by chi-square (χ^2) analysis (Steel and Torrie 1980, pp. 278–282), with the five degrees of freedom (df) partitioned in order to test separately the heterogeneity associated with planting types (1 df; objective 3), competitive environments (2 df; objective 4), and their interaction (2 df). Examination of residual plots from regression analyses indicated that a linear model of untransformed variables was adequate to describe all relationships.

A positive relationship between seed weight and seedling size magnifies family differences in seedling size over what would be expected if all families had equal seed weights. Thus, if seed weight differences mostly reflect nonheritable maternal effects, estimates of heritability of seedling size traits and expected genetic gains in these traits will be upwardly biased. We investigated the degree to which heritability and genetic gain of seedling size traits may be overestimated by

comparing estimates based on variance components before and after adjusting seedling size for seed weight. Linear regression was used to relate family means for each seedling size trait to mean family seed weight. The predicted seedling size for each family was then subtracted from observed plot means to obtain adjusted values for each family in each replication. Analyses of variance for size traits were done before and after adjustment, and variance components from each analyses were used to calculate heritabilities of family means and expected genetic gains from parental selection using procedures in Namkoong (1979, p. 72).

RESULTS AND DISCUSSION

FAMILY VARIATION IN SEED CHARACTERS

Families differed significantly (defined as $P \leq 0.05$) in seed weight, and in total percent emergence, mean rate of emergence, and days to 50% emergence when planted as ungerminated seed (Table 1). Total percent emergence ranged widely among families (40 to 94%). When planted as recent germinants, families differed significantly in rate of emergence and days to 50% emergence, but not total percent emergence (Table 1). Family differences in emergence when planted as germinants were less than when planted as ungerminated seed, as indicated by the smaller F-values (comparable between planting types since degrees of freedom are equal) and intraclass-correlation coefficients. In addition, planting germinants reduced the time to 50% emergence from 27 to 16 days (Table 1). The

TABLE 1.

Variation among 39 open-pollinated families of coastal Douglas-fir in seed weight, laboratory germination, and emergence after planting germinated and ungerminated seeds in the nursery.

Character[a]	Mean	Range among families	F[b]	Probability	t[c]
Seed weight	0.42	0.32–0.56	65.77	0.0001	0.95
Laboratory					
Total germination	84.5	42.5–98.5	40.37	0.0001	0.93
Rate of germination	0.176	0.121–0.233	57.91	0.0001	0.95
Time to 50% germination	5.9	4.3–8.2	58.45	0.0001	0.95
Nursery					
Ungerminated seed planted					
Total emergence	75.5	40.1–93.8	8.89	0.0001	0.73
Rate of emergence	0.037	0.031–0.045	3.70	0.0001	0.35
Time to 50% emergence	27.2	22.4–35.1	3.39	0.0001	0.32
Germinants planted					
Total emergence	77.1	46.9–96.9	1.59	0.0783	0.11
Rate of emergence	0.064	0.054–0.073	1.70	0.0131	0.12
Time to 50% emergence	15.9	14.2–18.6	1.74	0.0100	0.15

[a] Seed weight measured as g per 35 seed; total emergence and germination as percent; rate as 1/(number of days to 50% emergence); time as days.
[b] F-value for testing significance of differences among family means, with (38,76) degrees of freedom for seed weight, and (38,152) degrees of freedom for germination and emergence traits.
[c] t = intraclass correlation coefficient = ratio of family to family plus error variance.

correlation of family means for days to 50% emergence when planted as ungerminated seed with days to 50% emergence when planted as germinants was $r = 0.66$ (note that $r \geqslant 0.27$ is significantly greater than zero at $P = 0.05$ for all correlations presented). Thus, families that emerged early when planted as ungerminated seed were to some extent the same families that emerged early when planted as germinants.

Families also differed significantly in total percent germination, mean rate of germination, and days to 50% germination in the laboratory (Table 1). Total percent germination of families in the laboratory was strongly related to total percent emergence when seeds were planted ungerminated ($r = 0.79$). The correlation between family means for time of germination in the laboratory test and time of emergence when planted as seed, however, was not strong ($r = 0.42$).

RELATIONSHIPS BETWEEN SEED WEIGHT AND EMERGENCE OR GERMINATION

The relationship between seed weight and total percent emergence was weak, whether individuals were planted as ungerminated seed ($r = 0.17$) or as recent germinants ($r = 0.30$). The relationship between seed weight and total percent germination in the laboratory was also weak ($r = 0.21$). Families of heavier seed did not appear to germinate or emerge more completely.

The correlation between family means for seed weight and rate of emergence when seeds were planted was positive, as expected, but was relatively weak ($r = 0.37$); thus, family differences in seed weight explained only 14% of the family variation in rate of emergence (i.e., $r^2 = 0.14$). Furthermore, using germinants did not weaken the relationship between seed weight and rate of emergence; the estimated correlation was, in fact, larger ($r = 0.46$), although not significantly different from the correlation based on seeds planted ungerminated. The correlation between seed weight and rate of germination in the laboratory was not significantly different from zero ($r = 0.13$). Thus, using germinants did not diminish the effect of seed weight on rate of emergence, largely because of the apparent lack of relationship between mean family seed weight and germination rate. Lack of a significant correlation between seed weight and rate of emergence has also been reported in other conifer species (Perry and Hafley 1981, Mikola 1984).

RELATIONSHIPS BETWEEN SEED CHARACTERS AND SEEDLING SIZE

As expected, correlations between seed weight and seedling size were positive, although not particularly strong (Table 2). For example, the correlation between family means for seed weight and seedling dry weight in the wide competitive environment planted with ungerminated seed (such as might be the typical situation for genetic studies using seedlings) was $r = 0.48$. Thus, in this case, family differences in seed weight explained only 23% of the variation in dry weight of seedlings.

The strength of the relationship between mean family seed weight and seedling size depended on the measure of seedling size; mean family seed weight was

TABLE 2.

Correlations (r) between family means for seed weight and seedling size (2-yr dry weight, 2-yr height, 1-yr height), and rate of emergence and seedling size, within each competitive environment and planting type.[a]

| | Planting type | | | | | | |
| | Ungerminated seed | | | Germinants | | | Overall mean correlation |
Relationship	Wide	Pure	Mix	Wide	Pure	Mix	
Seed weight with							
2-yr dry weight	0.48	0.34	0.50	0.39	0.35	0.59	0.44
2-yr height	0.35	0.20	0.22	0.17	0.24	0.33	0.25
1-yr height	0.52	0.37	0.33	0.26	0.29	0.49	0.38
Rate of emergence with							
2-yr dry weight	0.16	0.15	0.47	0.20	0.05	0.38	0.23
2-yr height	−0.03	−0.06	0.25	−0.14	−0.06	0.07	0.01
1-yr height	0.30	0.18	0.29	0.09	−0.04	0.21	0.17

[a] $r \geq 0.21$ is significantly greater than 0 at the 10% probability level.
$r \geq 0.27$ is significantly greater than 0 at the 5% probabillity level.
$r \geq 0.37$ is significantly greater than 0 at the 1% probability level.

more strongly correlated with dry weight than with total height. In addition, the relationship between seed weight and seedling size may be expected to diminish with time as indicated by the weaker correlation of seed weight with second-year height than with first-year height.

The relationship between rate of emergence and seedling size was weaker than between seed weight and seedling size, and in most cases, the correlation coefficient was not significantly greater than zero (Table 2). The strength of this relationship depended on the measure of seedling size and age of measurement in a manner similar to the relationship between seed weight and seedling size.

Positive relationships between seed weight and seedling size have been reported for many studies in conifers (Burgar 1964, Griffin 1972, Dunlap and Barnett 1983, Belcher et al. 1984), but these studies often compare only seed from widely different seed classes in which family structure is not considered. In other studies, significant relationships between these traits were not found (Lavender 1958, Dumroese and Wenny 1987). Discrepancies may be due, in part, to differences in composition of the seed classes. Studies utilizing family structure have been equally ambiguous. Robinson and van Buijtenen (1979) reported significant positive correlations between mean family seed weight and volume up to age 15 in *Pinus taeda* ($r = 0.30$). Other studies in the same species, however, found no detectable correlations between these traits (Perry and Hafley 1981, Shear and Perry 1985), or found only a transitory relationship that became nonsignificant when the seedlings were greater than 10 weeks old (Waxler and van Buijtenen 1981). In seedling studies of Douglas-fir, correlations of family means between seed weight and seedling size have been of a similar magnitude to those found in the present study, or weaker and nonsignificant (Bell et al. 1979, Lambeth et al. 1982, Mangold 1987, Loopstra and Adams 1989).

The lack of consistent relationships between seed weight and seedling size may be due, in part, to the influence of environmental factors on seed characters. For

example, variation among families in seed weight may depend on variation in environmental conditions experienced by different female trees during the period of seed development. Furthermore, if cones are picked at various stages of maturity, the weight and physiological condition of seeds may differ greatly among female trees. Larger differences among families in seed weight increase the likelihood of finding a strong relationship between seed weight and seedling size.

Family variation in seed characters and relationships between seed characters and seedling size may also depend on the length of stratification and on spring weather conditions during germination and emergence. Length of stratification affects family variation in time of emergence and early growth (Campbell and Sorensen 1984). Short stratification periods, particularly when combined with cool spring weather conditions during germination and emergence, will increase variability in time of emergence among families. Larger differences among families in time of emergence could lead to stronger relationships between seed characters and seedling size.

Although the relationships between mean family seed weight and seedling size do not appear to be strong in Douglas-fir, they still may represent an important source of bias in genetic studies using seedlings. Estimated family heritabilities for dry weight and height of seedlings planted as ungerminated seed and grown at wide spacing decreased after these traits were adjusted for seed weight (Table 3). Although the decreases in estimated heritabilities were small, the concomitant decreases in estimated genetic gains seemed substantial in two of the three seedling size traits. The decrease in bias between the first- and second-year heights, however, suggests that the bias diminishes quickly as trees increase in age. Since at least a portion of the family differences in seed weight are due to the diploid genotypes of embryos (i.e., nonmaternal causes), the method used to adjust seedling size for seed weight will also remove some of the additive genetic variance for seedling size traits. Thus, heritabilities and genetic gains calculated from adjusted data are probably underestimates, with the true values actually lying somewhere between the adjusted and unadjusted values. However, because a large proportion of the variation in seed weight is probably environmental in origin and nonrepeatable, the true values are probably closer to estimates derived from the adjusted values.

TABLE 3.

Estimated family heritabilities (h_F^2) for seedling size traits and expected genetic gains (G) from parental selection based on progeny performance, before and after adjusting family means for seed weight.[a]

Measure of seedling size	r[c]	h_F^2		G[b]		
		before	after	before	after	bias[d]
2-yr dry weight (g)	0.48	0.65	0.56	3.02	2.29	32%
2-yr height (mm)	0.35	0.70	0.67	33.8	30.7	10%
1-yr height (mm)	0.52	0.66	0.54	8.4	5.8	45%

[a] Data from treatment in which ungerminated seed was planted at a wide noncompetitive spacing.
[b] Intensity of selection assumed to equal 1.0.
[c] Correlation between mean family seed weight and seedling size.
[d] Bias = gain before adjustment − gain after adjustment/gain after adjustment × 100.

Effect of Competitive Environment and Planting Type on Relationships between Seed Characters and Seedling Size

It was hypothesized that interfamily competition would lead to stronger relationships between seed weight and seedling size and between rate of emergence and seedling size, and that planting germinants rather than ungerminated seed would lead to weaker relationships between these traits. The correlations, however, did not differ significantly among competitive environments or between planting types; none of the χ^2 values in the partitioned χ^2 test of homogeneity of correlation coefficients were significant (Table 4). In addition, correlations did not differ significantly in any pairwise comparisons of competitive environments.

The homogeneity of correlation coefficients among competitive environments indicates that interfamily competition did not magnify seed effects to a strong degree, despite large differences between spacings in mean dry weight of seedlings (19.4 g at the wide spacing as compared to 4.2 g at the narrow spacing when families are in mixture and 3.6 g when in pure blocks). The estimated correlation between rate of emergence of ungerminated seed and seedling dry weight, however, was three times larger in the mixed treatment ($r = 0.47$; Table 2), than in either the pure stands ($r = 0.15$) or at the wide spacing ($r = 0.16$), and in both cases, the difference in correlation coefficients approached statistical significance ($P = 0.06$ and 0.07, respectively).

The homogeneity of correlation coefficients between planting types indicates that using germinants was ineffective in reducing the influences of seed weight and rate of emergence on seedling size, presumably because germination rate is only weakly associated with seed weight in this study. However, when seed is stratified for only a short period and then germinated in especially cool weather, family differences in time of germination and emergence may be magnified (Campbell and Sorensen 1984). Under these conditions, seed size effects on germination, emergence, and early growth may be stronger, and using germinants may be more effective in reducing the influences of seed weight and rate of emergence on seedling size.

TABLE 4.

Partitioned chi-square test of homogeneity of correlation coefficients among six combinations of planting types and competitive environment treatments.[a]

Relationship	Planting types (P) (1 df[b])	Competitive environments (C) (2 df)	$P \times C$ interaction (2 df)	Overall (5 df)
Seed weight with				
2-yr dry weight	0.001	1.097	1.692	2.790
2-yr height	0.002	0.061	1.065	1.128
1-yr height	0.079	0.158	2.734	2.971
Rate of emergence with				
2-yr dry weight	0.053	2.442	2.833	5.329
2-yr height	0.189	1.372	2.154	3.715
1-yr height	0.564	0.658	2.057	3.278

[a] All χ^2 values are nonsignificant at the 5% probability level. Estimates of correlations are in Table 2.

[b] df = degrees of freedom.

LITERATURE CITED

BELCHER, E.W., G.N. LEACH, and H.H. GRESHAM. 1984. Sizing slash pine seeds as a nursery procedure. Tree Plant. Notes 35:5–10.

BELL, H.E., R.F. STETTLER, and R.W. STONECYPHER. 1979. Family × fertilizer interaction in one-year-old Douglas-fir. Silvae Genet. 28:1–5.

BLACK, J.N. 1958. Competition between plants of different initial seed sizes in swards of subterranean clover (*Trifolium subterraneum* L.) with particular reference to leaf area and the light microclimate. Aust. J. Agric. Res. 9:299–318.

BRAMLETT, D.L., T.R. DELL, and W.D. PEPPER. 1983. Genetic and maternal influences on Virginia pine seed germination. Silvae Genet. 32:1–4.

BURGAR, R.J. 1964. The effect of seed size on germination, survival, and initial growth in white spruce. For. Chron. 40:93–97.

CAMPBELL, R.K., and F.C. SORENSEN. 1979. A new basis for characterizing germination. J. Seed Tech. 4:24–34.

CAMPBELL, R.K., and F.C. SORENSEN. 1984. Genetic implications of nursery practices. P. 183–191 *in* Forest nursery production of bareroot seedlings, Duryea, M.L., and T.D. Landis (eds.). Martinus Nijhoff/Dr W. Junk Publishers, The Hague.

DUMROESE, R.K., and D.L. WENNY. 1987. Sowing sized seed of western white pine in a containerized nursery. West. J. Appl. For. 2:128–130.

DUNLAP, J.R., and J.P. BARNETT. 1983. Influence of seed size on germination and early development of loblolly pine (*Pinus taeda* L.) germinants. Can. J. For. Res. 13:40–44.

GRIFFIN, A.R. 1972. The effects of seed size, germination time and sowing density on seedling development in radiata pine. Aust. For. Res. 5:25–28.

LAMBETH, C.C., R.W. STONECYPHER, and B.J. ZOBEL. 1982. Early testing of Douglas-fir in phytotron environments—the effect of selection trait and genotype-environment interaction. P. 137–148 *in* Proc. 7th North Am. For. Biol. Workshop, Lexington, KY.

LAVENDER, D.P. 1958. Effect of seed size on Douglas-fir seedlings. Oreg. For. Lands Res. Cent. Res. Note 32.

LOOPSTRA, C.A., AND W.T. ADAMS. 1989. Patterns of variation in first-year seedling traits within and among Douglas-fir zones in southwest Oregon. Silvae Genet. 38:235–243.

MANGOLD, R.D. 1987. Genetic variation and phenotypic stability among three elevational sources of coastal Douglas-fir from southwest Oregon. Ph.D. diss., Oregon State Univ., Corvallis, OR.

MIKOLA, J. 1984. Relationships between height growth differences of scots pine full-sib families and variation in seed size, annual growth rhythm, and some foliage characteristics. P. 233–243 *in* Crop physiology of forest trees, Tigerstedt, P.M.A., P. Puttonen, and V. Koski (eds.). Helsinki University Press, Helsinki, Finland.

NAMKOONG, G. 1979. Introduction to quantitative genetics in forestry. USDA For. Serv. Tech. Bull. No. 1588.

PERRY, T.O. 1976. Maternal effects on the early performance of tree progenies. P. 474–481 *in* Tree physiology and yield improvements, Cannell, M.G.R., and F.T. Last (eds.). Academic Press, New York.

PERRY, T.O., and W.L. HAFLEY. 1981. Variation in seedling growth rates: Their genetic and physiological bases. P. 288–301 *in* Proc. 16th South. For. Tree Improv. Conf., Blacksburg, VA.

ROBINSON, J.F., AND J.P. VAN BUIJTENEN. 1979. Correlation of seed weight and nurserybed traits with 5- , 10- , and 15-year volumes in a loblolly pine progeny test. For. Sci. 25:591–596.

ST. CLAIR, J.B. 1989. Effects of seed characters and competitive environment on two-year performance of open-pollinated Douglas-fir families. Ph.D. diss., Oregon State Univ., Corvallis, OR.

SHEAR, T.H., and T.O. PERRY. 1985. Predicting loblolly pine seedling performance from seed properties. P. 226–233 *in* Proc. 18th South. For. Tree Improv. Conf., Long Beach, MS.

SHEN, H.H., and D. LINDGREN. 1981. An example of variation in seed weight within a clone. Sver. Lantbruksuniv. Inst. Skoglig Genet. Vaextfysiol. Umea, Int. Rapp. No. 35.

SILEN, R.R., and C. OSTERHAUS. 1979. Reduction of genetic base by sizing of bulked Douglas-fir seed lots. Tree Plant. Notes 30:24–30.

SILEN, R.R., and J.G. WHEAT. 1979. Progressive tree improvement program in coastal Douglas-fir. J. For. 77:78–83.

SORENSEN, F.C., and R.K. CAMPBELL. 1985. Effect of seed weight on height growth of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*) seedlings in a nursery. Can. J. For. Res. 15:1109–1115.

SORENSEN, F.C., AND J.F. FRANKLIN. 1977. Influence of year of cone collection on seed weight and cotyledon number in *Abies procera*. Silvae Genet. 26:41–43.

STEEL, R.G.D., and J.H. TORRIE. 1980. Principles and procedures of statistics. McGraw-Hill, New York.

WALLER, D.M. 1985. The genesis of size hierarchies in seedling populations of *Impatiens capensis* Meerb. New Phytol. 100:243–260.

WAXLER, M.S., and J.P. VAN BUIJTENEN. 1981. Early genetic evaluation of loblolly pine. Can. J. For. Res. 11:351–355.

WILCOX, M.D. 1983. Reciprocal cross effects in *Pinus radiata*. N. Z. J. For. Sci. 13:37–45.

WILLIAMS, W.A., J.N. BLACK, and C.M. DONALD. 1968. Effect of seed weight on the vegetative growth of competing annual trifoliums. Crop Sci. 8:660–663.

AUTHORS AND ACKNOWLEDGMENTS

J.B. St. Clair is currently with the USDA Forest Service, PNW Research Station, Forest Science Laboratory, 3200 SW Jefferson Way, Corvallis, OR 97331.

W.T. Adams is with the Dept. of Forest Science, College of Forestry, Oregon State University, Corvallis, OR, U.S.A. 97331. This is Paper No. 2671 of the Forest Research Laboratory, Oregon State University. The authors gratefully acknowledge the Pacific Northwest Tree Improvement Research Cooperative for the financial support which made this research possible.