

Effect of Natural Inbreeding on Variance Structure in Tests of Wind-Pollination Douglas-Fir Progenies

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ABSTRACT. Studies of the mating habits of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) have shown that wind-pollination families contain a small proportion of very slow-growing natural inbreds.

The effect of these very small trees on means, variances, and variance ratios was evaluated for height and diameter in a 16-year-old plantation by systematically deleting from analyses the shortest individuals in wind-pollination (*W*) and diallel (*D*) progenies of six parent trees. The progenies were growing together in a common field test. The *D* population served as a control (no inbreds).

The low-vigor trees in the *W* population type gave a downward bias to means and an upward bias to within-plot and family \times block variance estimates. Amount of bias differed among *W* families. Before deletion, estimates of additive genetic variance and heritability for height in the *W* test were about one-third and one-sixth the estimates from the *D* test. Deleting the shortest 5 to 8% of the trees from the *W* population did not remove all the discrepancy, but it did result in much closer agreement between *W* and *D* tests. For the *D* test alone, deletion of the smallest trees had a negligible effect on estimates of additive genetic variance and heritability. *FOR. SCI.* 34(1):102-118.

ADDITIONAL KEY WORDS. Diallel mating, genetic variance, heritability, population structure.

RATE OF PROGRESS from breeding programs of forest trees depends, in part, on the ability to rank parents based on their breeding values and to estimate genetic variances. Wind-pollination (*W*) families, obtained by collecting seeds from female parents pollinated by surrounding males, are often used for both these purposes.

When estimating genetic variances, most authors assume members of *W* families are related as half-sibs from a random-mating population (Shelbourne 1969, Evans and Thor 1971, Stonecypher et al. 1973, Rehfeldt 1980, Foster and Lester 1983, McCutchan 1983, Sluder 1983). Then, in the absence of epistasis, the variance among families (σ_f^2) is equal to the covariance of half-sibs and $\sigma_f^2 = \frac{1}{4} \sigma_A^2$; where σ_A^2 is the additive genetic variance. For this to be true, all male and female parents must be unrelated and not inbred, and each female parent must be pollinated by several random males (Squillace 1974).

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Depending on which of these conditions are met, members within a *W* family can be more or less related than half-sibs from a random-mating population (Table 1). Most attention in forestry (Namkoong 1966, Squillace 1974, Snyder and Namkoong 1978, Neale 1985) has been given to problem 5 (Table 1). However, information accumulated on mating systems of forest trees indicates that partial natural inbreeding (number 7, Table 1) may also bias analyses of *W* progenies, particularly analyses of growth traits in species like Douglas-fir that show severe inbreeding depression.

Although predominantly an outbreeder, Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) *W* progenies are reported to have an inbreeding coefficient (*F*) of about 0.035 to 0.05 (Sorensen 1973, El-Kassaby et al. 1981, Shaw and Allard 1982a, Omi 1983, Neale and Adams 1985) at the germinant seedling stage. This inbreeding has been indicated as both predominantly selfing (Shaw and Allard 1982a) and as mixed selfing and matings between relatives (Neale and Adams 1985). If we assume that much natural inbreeding in coastal Douglas-fir is indeed selfing, that $F = 0.04$ at the germinant seedling stage, and that 80% of the inbreds become established in well-tended plantations (Sorensen and Miles 1982), the *W* progenies would have, on the average, $F \approx 0.032$ or about 6.4% self-pollination plants at the stage of crown closure. The *W* population could include two subpopulations; one of cross-pollination plants with $F \sim 0$ and a smaller one of inbred plants with *F* approaching 0.5.

Presence of inbred plants can bias inferences made from *W* families (Robertson 1952, Latter 1965, Mitchell-Olds and Waller 1985). We investigated the bias in estimation of genetic variances, especially within-family variance which is often large in young open-pollination tests (Khalil 1985), in a 16-year-old Douglas-fir plantation containing a mixture of *W* and half diallel (*D*) progenies from six parent trees. The *D* population contains no selfs and serves as a control with which genetic and family rankings obtained from the *W* population are subjectively compared. We also present analyses of *W* and *D* progenies after progressive deletion of about the shortest 12% of the observations from the data sets. The intent is to simulate what might happen to the relative magnitudes of genetic variances and to family rankings as low-vigor inbred plants are lost from the stand because of suppression.

MATERIALS AND METHODS

The parents of the test families were in a 20- to 25-year-old second-growth stand located at about 300-m elevation on the western slopes of the Cascade Range in central Oregon. The stand was divided into 6 "substands" (about 10 to 15 ha each), and one parent was chosen in each substand. Trees that could be climbed (no breakage) and having sufficient male and female reproductive buds were labelled in each substand, and 1 tree per substand selected at random. Trees were mated following a half-diallel design without selfs (method 4 of Griffing 1956). *W* cones as well as cones from the diallel matings were collected in September 1964, a year of moderate to good pollen and cone production in this area.

Pregerminated seeds from each of the 21 families (15*D*, 6*W*) were sown in 7.6-cm "jiffy pots" in the spring of 1965. Experimental design was a randomized complete block with 15 replications of 5-tree, noncontiguous, family plots. All potted plants, both *W* and *D*, were placed at random within replications in nursery beds in early summer. Extra seedlings in jiffy pots were kept in the adjoining bed and replacements made as necessary through

TABLE 1. Potential problems that can influence the genetic variance among families in a test of wind-pollination families.^a

Problem	Assumptions/ comments	Example	Parents inbred? $F_p > 0$? ^b	Progeny inbred? $F_o > 0$? ^b	Parents related? $R_{pp} > 0$? ^b	Composition of family variance ^c	References
1. None	Parents not inbred and not related, many males	Polymix with many males and no inbreeding	No	No	No	$1/4\sigma_A^2$	Kemphorne (1954)
2. Parents inbred	Mates unrelated and all inbred to same degree	Orchard clones inbred but unrelated	Yes	No	No	$0.0\sigma_B^2$ $> 1/4\sigma_A^2$	Cockerham (1963) Cockerham (1961) Cockerham (1963) Squillace (1974)
3. Males related within females	Females not related to each other or to males	Females are in different stands, and males are half-brothers	No	No	Yes	$0.0\sigma_B^2$ $> 1/4\sigma_A^2$	Stuber (1970) Hinkelmann (1969) Fujishima and Fredeen (1972)
4. Females related	Males not related to each other or to females	Polymix with many males applied to related females	No	No	Yes	$< 1/4\sigma_A^2$	Hinkelmann (1969) Fujishima and Fredeen (1972)
5. Few males	May be common in forest trees; full and half-sibs in same family; no inbreeding	Small neighborhood size in natural stands	No	No	No	$0.0\sigma_B^2$ $> 1/4\sigma_A^2$ $> 0.0\sigma_B^2$	Namkoong (1966) Squillace (1974)
6. Assortative mating	Males resemble females to which they are mated	Females in different natural stands and genetic differences among stands; e.g., north and south aspects of same drainage	No	Yes	Yes	Depends on conditions ^d	Falconer (1981)
7. Males related to females	Only problem to result in inbred progeny	Related parents in same natural stand	No	Yes	Yes	Depends on conditions ^e	Cockerham (1963) Stuber (1970) Namkoong (1966)

^a We assume no epistasis, no linkage, and regular diploid inheritance (Cockerham 1963).

^b F = coefficient of inbreeding; p = parental generation; σ = first generation of progeny; R_{pp} = coefficient of genetic relationship between parents.

^c σ_A^2 = additive genetic variance; σ_B^2 = dominance genetic variance.

^d If the reference population to which the σ_A^2 and σ_B^2 estimates apply includes all the stands sampled and if the trees within a stand resemble each other more than trees from other stands, then problems 6 and 7 have the same consequences.

^e The influence of inbred progeny on the composition of variance among families depends on gene frequencies and degree of dominance. At intermediate gene frequencies and modest degrees of dominance, $\sigma_A^2 > 1/4\sigma_B^2$; where, σ_B^2 is the variance among wind-pollination families.

the first growing season. There was no mortality and no replacement during the second season. Nursery spacing was about 7.6 cm. The nursery was located at Corvallis, Oregon, 50 km west of and 225 m lower than the parent stand.

After two years in the nursery, the seedlings were field-planted into a large opening adjacent to and at the same elevation as the parent stand. The same design of 15 replications of 5-tree, noncontiguous, completely randomized family plots was used in the field test. Site preparation consisted of cultivating to break the sod and scalping around the planting spots. Spacing was 3.05 m \times 3.05 m.

For our analyses, data from groups of three original replications have been pooled (after adjustment for an additive replication effect) to form a single new replication. Thus, each of the 5 synthetic blocks had 15-tree noncontiguous plots. Such a grouping allowed deletion of trees to simulate mortality without loss of any family plots. It also provided more trees in each plot to more precisely estimate higher moments (variance and skewness) within plots.

MEASUREMENTS AND ANALYSES

Heights and diameters at 1.37 m were measured after the 16th growing season and individual tree volumes calculated following Bruce and DeMars (1974). Plot means and within-plot variances were calculated for each family plot in each block, and the resulting 6 response variables (height, diameter, volume, and their respective within-plot variances) were subjected to analyses of variance (Table 2).

Analyses were conducted on the data sets containing all living trees and on five sets constructed by progressive deletion of about the shortest 1, 2, 5, 8, and 12% of the trees in each block. The different deletion percentages were chosen to bracket the expected frequencies of inbred plants that might occur in a 16-year-old plantation. Because population sizes differed, deletion percentages differed slightly between the two population types. Percentages also varied slightly from block to block, depending on the number of living trees. The intent was to simulate the effects on genetic variance estimates as the low-vigor trees leave the population via suppression-related mortality (see Matheson and Raymond 1984 for a similar approach). The deletion procedure was applied independently to the *W* and *D* populations. This was done to compare relative effects on the two types of population. More trees were deleted within some families than within others because the shortest trees were eliminated first, without regard to family or block designation.

For each analysis of plot means, the method-of-moments procedure (Milliken and Johnson 1984, p. 233) was used to solve variance components by equating the observed mean squares to their expected values and solving the resulting system of linear equations (Table 2). Method-of-moment estimators are always unbiased and, for most balanced models, these estimators are uniformly minimum variance unbiased (Milliken and Johnson 1984, p. 235). The use of plot means instead of individual tree observations meant that balance was maintained (no missing observations) even with the deletion of as much as 12% of the smallest trees. Plot means were not significantly correlated with within-plot variances either before or after deletion, and no transformations were used. Within-plot variances were estimated separately after analyses of plot means by calculating within-plot sums of squares for each plot and pooling these across all plots.

TABLE 2. Expected mean squares for the three analyses of variance: (A) combined analyses to test the effect of population type; (B) analysis of wind-pollination families; and (C) analysis of diallel families.

Sources of variation	Degrees of freedom	Expected mean squares
(A) Combined analyses^a		
Blocks	4	
Population types (<i>t</i>)	1	$\sigma^2 + 5\sigma_{ft}^2 + 42.8Q^2$
Families-in-population types (<i>ft</i>)	19	$\sigma^2 + 5\sigma_{ft}^2$
Plot error (<i>p</i>)	80	σ^2
(B) Wind-pollination families^b		
Blocks	4	
Families (<i>f</i>)	5	$\frac{\sigma_{w,w}^2}{n_w} + \sigma_{p,w}^2 + 5\sigma_f^2$
Plot error (<i>p</i>)	20	$\frac{\sigma_{w,w}^2}{n_w} + \sigma_{p,w}^2$
Within-plot error (<i>w</i>)	$\sum_{30}^{30} (n_j - 1)^c$	$\sigma_{w,w}^2$
(C) Diallel families^d		
Blocks	4	
GCA (<i>g</i>)	5	$\frac{\sigma_{w,D}^2}{n_D} + \sigma_{p,D}^2 + 5\sigma_s^2 + 20\sigma_g^2$
SCA (<i>s</i>)	9	$\frac{\sigma_{w,D}^2}{n_D} + \sigma_{p,D}^2 + 5\sigma_s^2$
Plot error (<i>p</i>)	56	$\frac{\sigma_{w,D}^2}{n_D} + \sigma_{p,D}^2$
Within-plot error (<i>w</i>)	$\sum_{75}^{75} (n_j - 1)^e$	$\sigma_{w,D}^2$

^a σ^2 = composite plot error.

σ_{ft}^2 = variance among families within population types.

Q^2 = expected value of sum of squared differences among population-type means.

^b $\sigma_{w,w}^2$ = within-plot variance for wind-pollination families.

n_w = harmonic means for number of trees per plot. These values were 13.9, 13.7, 13.6, 13.2, 12.7, and 12.2 when the shortest 0, 1.2, 2.4, 4.8, 8.3, and 11.9%, respectively, of the wind-pollination trees were deleted.

$\sigma_{p,w}^2$ = plot variance for wind-pollination families.

σ_f^2 = variance among wind-pollination families.

^c Degrees of freedom, within-plot, ranged from 330 with 11.9% of trees deleted to 380 with all living trees included.

^d $\sigma_{w,D}^2$ = within plot variance for diallel families.

n_D = harmonic means for number of trees per plot. These values were 14.6, 14.4, 14.2, 13.8, 13.2, and 12.7 when the shortest 0, 0.9, 2.3, 4.6, 8.2, and 11.4%, respectively, of the diallel trees were deleted.

$\sigma_{p,D}^2$ = plot variance for diallel families.

σ_s^2 = variance of general combining ability effects.

σ_g^2 = variance of specific combining ability effects.

^e Degrees of freedom, within-plot, ranged from 884 with 11.4% of trees deleted to 1009 with all living trees included.

Heritability values on an individual-tree basis were calculated as follows for the *W* and *D* families, respectively:

$$h^2 = \frac{\sigma_{A,W}^2}{\sigma_{w,W}^2 + \sigma_{p,W}^2 + \sigma_f^2}$$

$$h^2 = \frac{\sigma_{A,D}^2}{\sigma_{w,D}^2 + \sigma_{p,D}^2 + \sigma_s^2 + 2\sigma_g^2}$$

where $\sigma_{A,W}^2$ and $\sigma_{A,D}^2$ are the estimated additive genetic variances, $\sigma_{w,W}^2$ and $\sigma_{w,D}^2$ are the estimated within-plot variances, and $\sigma_{p,W}^2$ and $\sigma_{p,D}^2$ are the estimated plot variances for the *W* and *D* populations, respectively, and σ_s^2 and σ_g^2 are the estimated specific and general combining ability variances for the *D* population. For the diallel families, $\sigma_{A,D}^2$ was estimated as $4\sigma_g^2$, which assumes that parents were both unrelated and not inbred (Cockerham 1963). The first assumption (unrelatedness) is reasonable because the females came from different substands. Because the parents were vigorous, seed-producing trees, the second assumption (not inbred) also seems reasonable; any violation of the assumption would probably be slight and would affect estimates of σ_A^2 for *W* and *D* families in a similar manner.

For the *W* families, σ_A^2 was estimated as $3.33 \sigma_f^2$. This assumes unrelated and noninbred parents with five equally effective males pollinating each female (Squillace 1974, Neale 1985).

RESULTS AND DISCUSSION

SURVIVAL

Survival was high. Of the original planting of 1,125 *D* and 450 *W* seedlings, 98.6% *D* and 96.0% *W* seedlings were still alive at age 7. Causes of early mortality were mostly not known. At age 12, survival was 97.2% for *D* seedlings and 93.3% for *W*. Almost all mortality between ages 7 and 12 was due to pocket gopher (*Thomomys* sp.). No mortality occurred between ages 12 and 16, when the first plant was lost to suppression. Little of the mortality to age 16 preferentially eliminated low-vigor plants.

COMPARISON OF *W* AND *D* DISTRIBUTIONS AND MEANS

The distributions of individual tree heights (and diameters and volumes) for both *W* and *D* populations have negative skewness (Figure 1). Skewness at age 16 was very much more negative for the *W* than for the *D* type (Figure 2, bottom, zero deletion).

Skewness was calculated as the third moment about the mean (Snedecor and Cochran 1967, p. 86). The more negative values for the *W* distribution are indicative of the longer tail to the left of the distribution. As the shorter trees were progressively deleted, skewness changed little in the *D* population but increased quickly in the *W* population (Figure 2, bottom).

The grand mean of the *D* trees was significantly greater than that of the *W* trees at all levels of deletion (Figure 2, top, gives height as an example). Size differences between the two population types from the same seed parents could be due to (1) low-vigor, self-pollination plants in the *W* families; (2) other inbred offspring in the *W* families; (3) "sampling error" that resulted in the effective pollen parents of the *W* families having smaller breeding values than the six female parents; (4) a portion of the offspring in the *W* families resulting from poor specific combinations between male and female parents; or (5) heavier seed weight from the *D* pollinations (Sorensen and Campbell 1985) (average filled *D* seeds were 18% heavier than the *W* seeds as a consequence of the *D* cones being enclosed in pollen- and insect-isolation bags during development).

Up to a deletion of 5 to 8%, the mean of the *W* population increased faster than that of the *D* population. (For example, the mean height of *D* trees was 3.3% taller at 8% deletion contrasted with 6.1% taller at zero deletion.) This

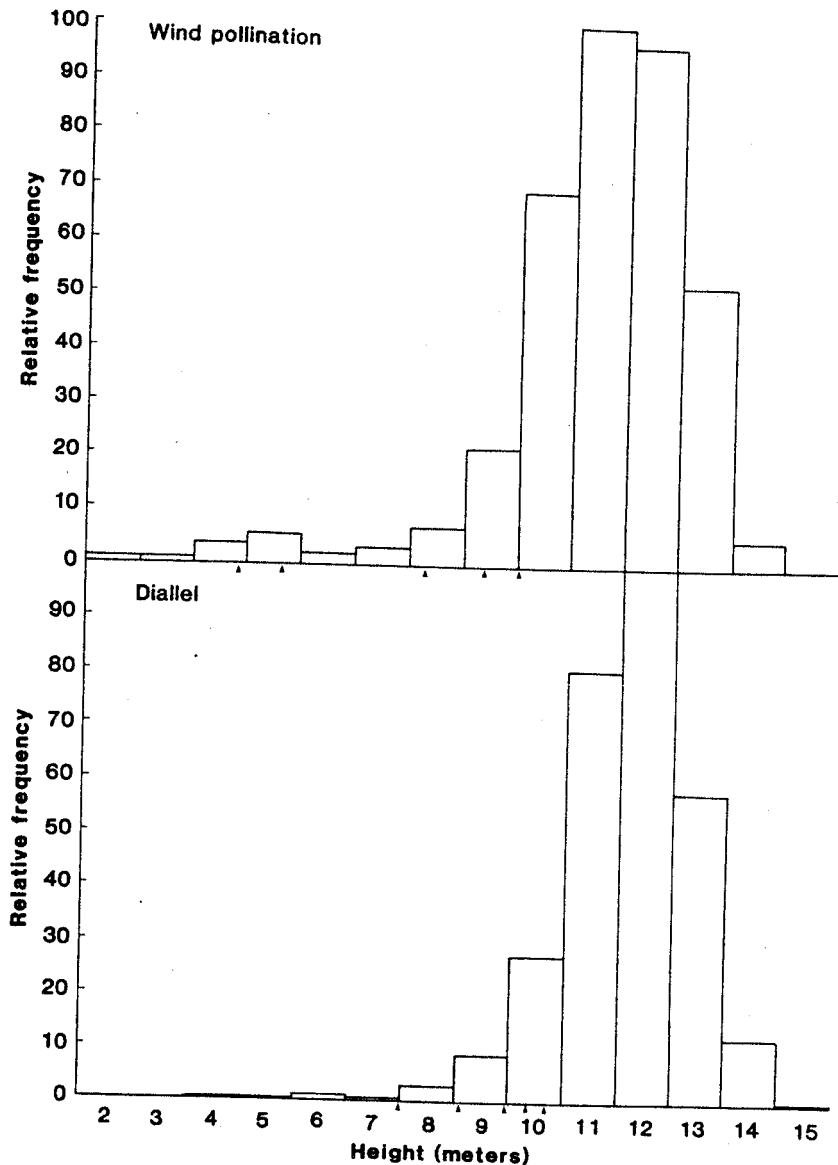


FIGURE 1. Frequency distributions of 16-year heights of trees from two populations. The upper histogram represents the bulked wind-pollination progenies of six parent trees; the lower histogram represents the bulked progenies from half-diallel matings (without selfs) among the same six parents. Midpoints of 1-m-height classes are given on the abscissa. The most frequent class in each population type is set equal to 100. Upper bounds of height groups eliminated by progressive deletion of the shortest trees are indicated by the vertical arrows under each histogram.

increase occurred as the shortest trees were deleted and as skewness of the *W* distribution became rapidly less negative (Figure 2). We believe these trends resulted because the initial deletions from the *W* data set were mostly self-pollination plants.

Above 5 to 8% deletion, the means of the two populations were still significantly different (see Figure 2, top, for height). These differences must result from one or more of the other reasons presented above.

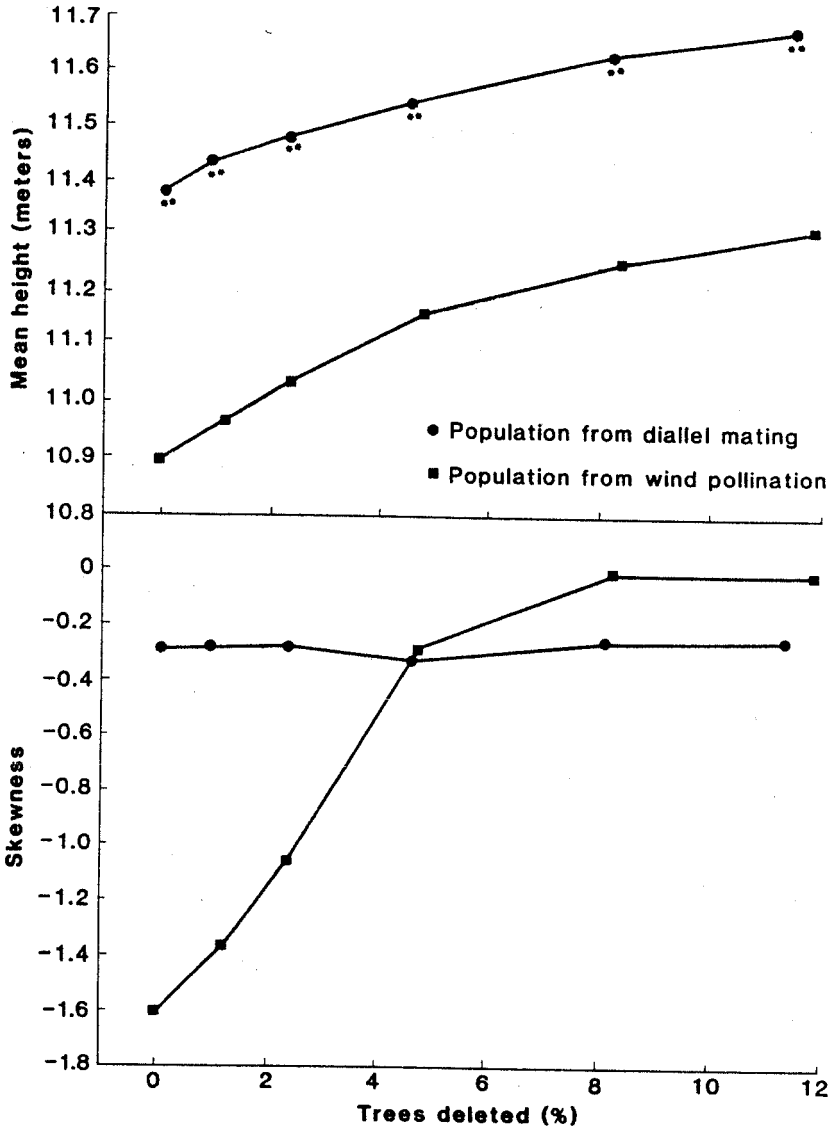


FIGURE 2. Mean heights (top) and skewnesses (bottom) of height distributions after progressive deletion of the shortest trees from the data sets. Differences between the population type means are significant at $P < 0.01$. (**) for all levels of deletion [see Table 2(A) for form of analysis used to compare population types].

COMPARISONS OF W AND D ESTIMATES OF VARIANCE COMPONENTS AND HERITABILITIES

With all living trees present, analyses of the D families showed significant variance of general combining abilities (σ_g^2) for height, diameter, and volume at 16 years (Table 3). Variance of specific combining abilities (σ_s^2) was not significant for height but was significant for diameter and volume. Ratios of σ_s^2/σ_g^2 were 0.07, 0.83, and 0.71 for height, diameter, and volume, respectively. Individual tree heritabilities from the diallel families with all

trees present were 0.23, 0.17, and 0.18 for height, diameter, and volume, respectively. These values are based on a small sample of parents and a single test plantation, but are similar to those reported for a well-maintained, 9-year-old Douglas-fir progeny test of control-pollination families in western Washington (Campbell et al. 1986).

Estimates of σ^2_A in the *W* population type were not biased upward, as expected with few males (Squillace 1974). With all living trees present, family components of variance from the *W* families were nonsignificant for all three traits and heritabilities were near zero (Table 3). The use of 3.33 as a multiplier of $\sigma^2_{f,W}$ (variance among families in the *W* population type) was not appropriate with all plants present. The effect of small inbred individuals on all variances was so powerful that it is doubtful if any one general multiplier could be used. It would depend too much on the mating habits and genetic constitution of the particular parents tested. After deletion, σ^2_A of the two population types was nearly identical if 3.33 and 4 were the multipliers of $\sigma^2_{f,W}$ and $\sigma^2_{f,D}$, respectively (Figure 4, top).

In the *D* test, mean squares and estimates of variance components decreased gradually as short trees were deleted (Figures 3 and 4, top), as is expected when one tail is truncated. Because terms in the numerator and denominator decreased at about the same rate, heritability estimates were nearly stable through the largest deletion (11.4%) (Figure 4, bottom).

For *W* families, on the other hand, the within-plot variances and plot mean squares decreased rapidly up to a deletion of 5 to 8% (Figure 3). At the same time, family mean squares rose slightly, and estimates of additive genetic variance increased markedly (Figure 4, top). Heritability estimates increased as a result of the numerator (σ^2_A) increasing and the denominator (total phenotypic variance) decreasing (Figure 4, bottom). Matheson and Raymond (1984) also found that thinning the smallest trees from a *W* family test of *Pinus radiata* D. Don resulted in lower within-plot variances and higher heritability estimates.

Within-plot variances (σ^2_w) make up more than 95% of the phenotypic variances. Decrease of σ^2_w in the *W* families was a major reason heritability values increase as trees are deleted. With all trees present, within-plot variances of the *W* families were much larger than those of the *D* families (Figure 3, top). Larger within-plot variances were also reported in *W* families compared with control pollination families of *Liriodendron tulipifera* L. (Farmer et al. 1983), but not for seven-year heights of *Pinus pallustris* Mill. (Snyder and Namkoong 1979). Differences between tests and species would be affected by presence or absence of nursery culling, size-related early field mortality, amount of natural inbreeding, proportion of additive to non-additive gene effects, degree of dominance, and size of dominance deviations.

$\sigma^2_{w,W}$ is also expected to be larger than $\sigma^2_{w,D}$ because more additive genetic variance is contained within *W* plots than within true full-sib plots. For height, σ^2_s was not significant and we therefore assumed no dominance variance. If, in addition, epistatic components of variance are small or similar between *D* and *W* population types, the expected values of the two within-plot variances are,

$$\sigma^2_{w,D} = \sigma^2_e + 0.5 \sigma^2_A$$

$$\sigma^2_{w,W} = \sigma^2_e + 0.7 \sigma^2_A$$

where, σ^2_e is the microenvironmental variance within plots. If σ^2_e is as-

TABLE 3. Variance component and individual-tree heritability estimates for 16-year height (m), diameter (cm), and volume (dm^3) from wind-pollination and diallel families after different percentages of the shortest trees have been deleted. Deletion percentages are approximate; see Materials and Methods for actual values.^a Significance levels are ns ($P > 0.10$), + ($P < 0.10$), * ($P < 0.05$), and ** ($P < 0.01$).

Approximate deletion of trees (%)	Wind families				
	Within plot ($\sigma_{w,w}^2$)	Plot ($\sigma_{p,w}^2$)	Additive ^b ($\sigma_{A,w}^2$)	Heritability (h_w^2)	
Height					
0	2.927	-0.009 ^{ns}	0.117 ^{ns}	0.040	(0.047) ^c
1	2.435	-0.021 ^{ns}	0.096 ^{ns}	0.039	(0.045)
2	2.004	-0.008 ^{ns}	0.057 ^{ns}	0.028	(0.042)
5	1.371	-0.026 ^{ns}	0.167**	0.119	(0.082)
8	1.112	-0.024 ^{ns}	0.247**	0.213	(0.126)
12	1.048	-0.021 ^{ns}	0.197**	0.182	(0.114)
Diameter					
0	13.226	-0.028 ^{ns}	0.079 ^{ns}	-0.006	(0.026)
1	11.539	-0.142 ^{ns}	0.189 ^{ns}	0.016	(0.033)
2	10.047	-0.094 ^{ns}	0.116 ^{ns}	0.012	(0.032)
5	7.836	-0.175 ^{ns}	0.189 ^{ns}	0.024	(0.034)
8	6.606	-0.235 ^{ns}	0.573*	0.088	(0.062)
12	5.734	-0.172 ^{ns}	0.424*	0.074	(0.059)
Volume					
0	2608	-19 ^{ns}	-16 ^{ns}	-0.006	(0.024)
1	2480	-34 ^{ns}	13 ^{ns}	0.005	(0.027)
2	2335	-28 ^{ns}	42 ^{ns}	0.018	(0.034)
5	2092	-44 ^{ns}	108 +	0.052	(0.048)
8	1869	-56 ^{ns}	208**	0.111	(0.075)
12	1715	-46 ^{ns}	150**	0.088	(0.066)

^a Significance of variance components was determined from the F-tests in the appropriate analyses of variance. Significance of the additive variance was based on F-test for families in the analyses of wind families and on the F-test for general combining ability in the analysis of diallel families.

^b $\sigma_{A,w}^2 = 3.33 \sigma_f^2$

^c Specific combining ability.

^d $\sigma_{A,D}^2 = 4\sigma_f^2$ (see Table 2).

^e Approximate standard errors of heritability estimates are in parentheses and were calculated by the methods presented in Namkoong (1979, p. 229-234).

sumed to be the same for both family types, $\sigma_{w,w}^2$ would be larger than $\sigma_{w,D}^2$ by $0.2 \sigma_A^2$. Using estimates of σ_A^2 from the *D* test, $0.2 \sigma_A^2$ corresponds to a difference of 0.04 to 0.08 between $\sigma_{w,D}^2$ and $\sigma_{w,w}^2$. $\sigma_{w,w}^2$ still appears much larger than predicted, based solely on differences in additive genetic variance (Figure 3, top).

Further complications involving within-plot variance estimates from the *W* population type were indicated when the within-plot variances themselves were subjected to analysis of variance. Analysis of the *D* population indicated that families from the six parents did not differ significantly for within-plot variances when the plots contained full-sib families. In contrast, within-plot variances differed significantly among the *W* families. Much of this effect was due to a single family (from parent 9) which, for height, had an average within-plot variance 180% larger than the mean of the remaining

TABLE 3. Continued.

Diallel families					
Within plot	Plot	SCA ^c	Additive ^d	Heritability	
($\sigma_{w,D}^2$)	($\sigma_{p,D}^2$)	(σ_s^2)	($\sigma_{A,D}^2$)	(h_b^2)	
1.426	-0.026 ^{ns}	0.006 ^{ns}	0.350**	0.221	(0.123) ^c
1.128	-0.001 ^{ns}	0.001 ^{ns}	0.318**	0.247	(0.139)
1.006	-0.008 ^{ns}	0.002 ^{ns}	0.280**	0.245	(0.140)
0.890	-0.015 ^{ns}	0.003 ^{ns}	0.235**	0.235	(0.138)
0.811	-0.020 ^{ns}	0.005 ^{ns}	0.234**	0.257	(0.152)
0.754	0.027 ^{ns}	0.005 ^{ns}	0.214**	0.255	(0.154)
7.084	-0.018 ^{ns}	0.261**	1.263*	0.159	(0.104)
6.086	0.021 ^{ns}	0.249**	1.042*	0.152	(0.103)
5.494	0.030 ^{ns}	0.252**	0.943*	0.151	(0.106)
4.931	-0.009 ^{ns}	0.246**	0.684+	0.124	(0.096)
4.233	-0.058 ^{ns}	0.219**	0.598+	0.127	(0.098)
3.830	-0.073 ^{ns}	0.204**	0.701+	0.163	(0.115)
2180	-23 ^{ns}	73**	410**	0.168	(0.104)
2055	-13 ^{ns}	73**	366**	0.159	(0.101)
1939	-9 ^{ns}	73*	333**	0.154	(0.100)
1815	-20 ^{ns}	72*	259**	0.130	(0.091)
1649	-34 ^{ns}	69*	243**	0.135	(0.094)
1541	-41 ^{ns}	67*	259**	0.153	(0.102)

five families. As the shortest trees were deleted, the within-plot variance for family 9 \times *W* dropped more rapidly than those of the other families because it contained a higher proportion of very short trees. From other studies, parent 9 was known to have high self-fertility (Sorensen 1971), be a prolific pollen producer (Sorensen, unpublished observations), and give self-pollination progeny with greater than average inbreeding depression in metric traits (Sorensen, unpublished data).

With small tests, such as the one reported here (six parents), the impact of one family can be large, but, even with family 9 excluded, within-plot variance of the *W* families was, before deletion, much larger than the within-plot variance of the *D* families (Figure 3, top).

In addition to biasing within-plot variance estimates, the presence of very small trees in the *W* progenies inflated the estimates of plot mean squares (family \times block interaction). These also dropped rapidly as trees were deleted (Figure 3, bottom). Few trees were very short—only 10 to 15 plants in the *W* test (Figure 1, top). They were not evenly distributed among families, and chance did not distribute them evenly among blocks. Apparently, as they were deleted, family performance became more stable across blocks. Thus, as plot mean squares decreased rapidly, the ability to detect family differences increased as did the estimates of additive genetic variance (Figure 4, top).

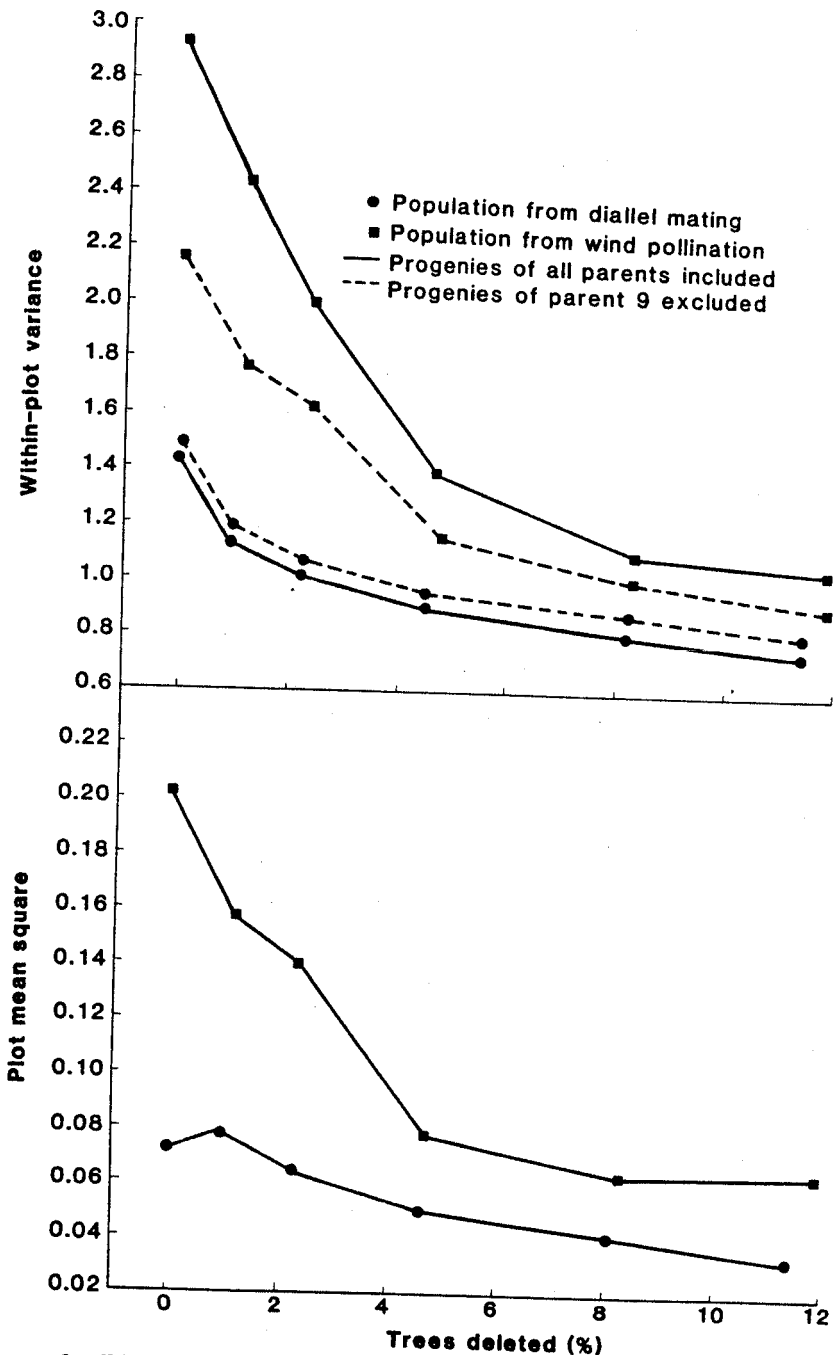


FIGURE 3. Within-plot variances (top) and plot mean squares (bottom) for height in meters from a 16-year-old Douglas-fir test containing wind-pollination and diallel families with all living trees included and after progressive deletion of the shortest trees from the data sets.

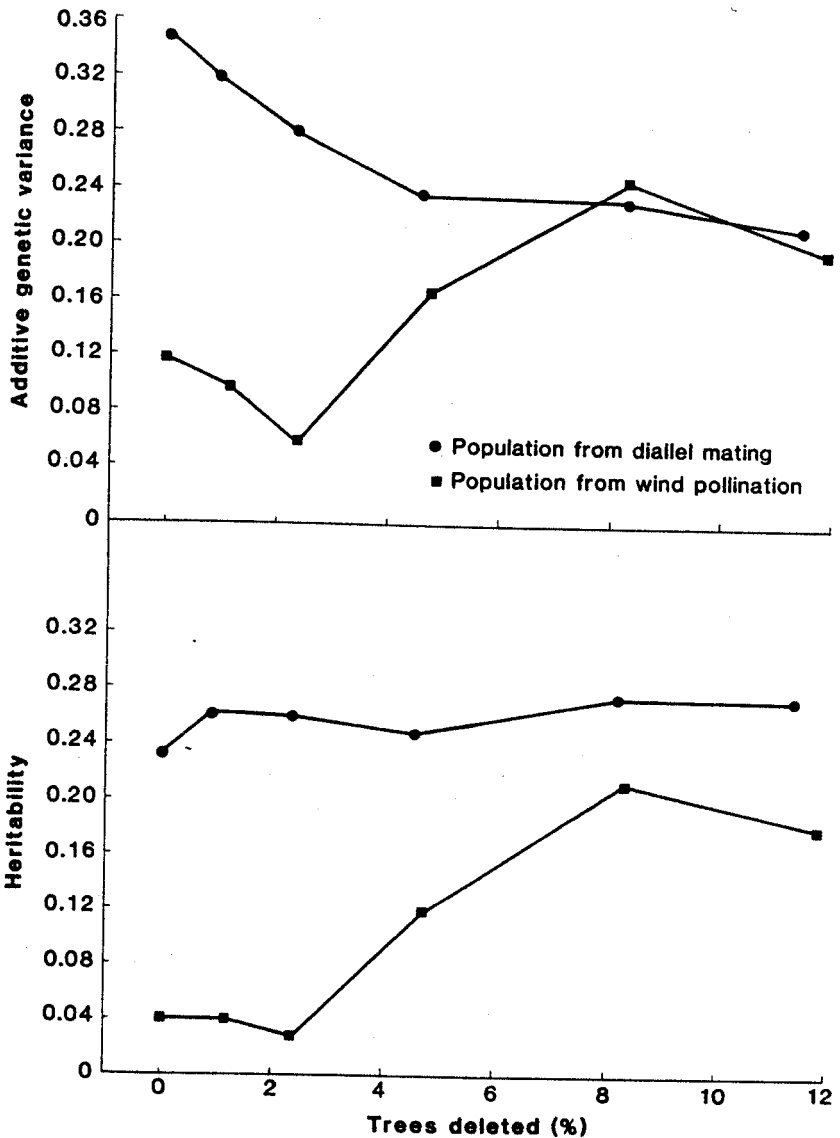


FIGURE 4. Additive genetic variances (top) and heritabilities (bottom) from a 16-year-old Douglas-fir test containing wind-pollination and diallel families with all living trees present and after progressive deletion of the shortest trees from the data sets.

FAMILY MEANS AND COMBINING ABILITIES

W family means underwent important changes as the shortest trees were deleted from the data set (Figure 5, see especially $9 \times W$). The end ranking much more closely agreed with the general combining ability rankings from the *D* test. For height, the correlation between family means from the *W* test with GCAs from the *D* test using all living trees was $r = 0.23$, but it increased to $r = 0.77$ and $r = 0.84$ when 4.8 and 8.3% of the *W* trees were deleted, respectively (values of $r > 0.81$ are significant at $P = 0.05$ with 4 degrees of freedom).

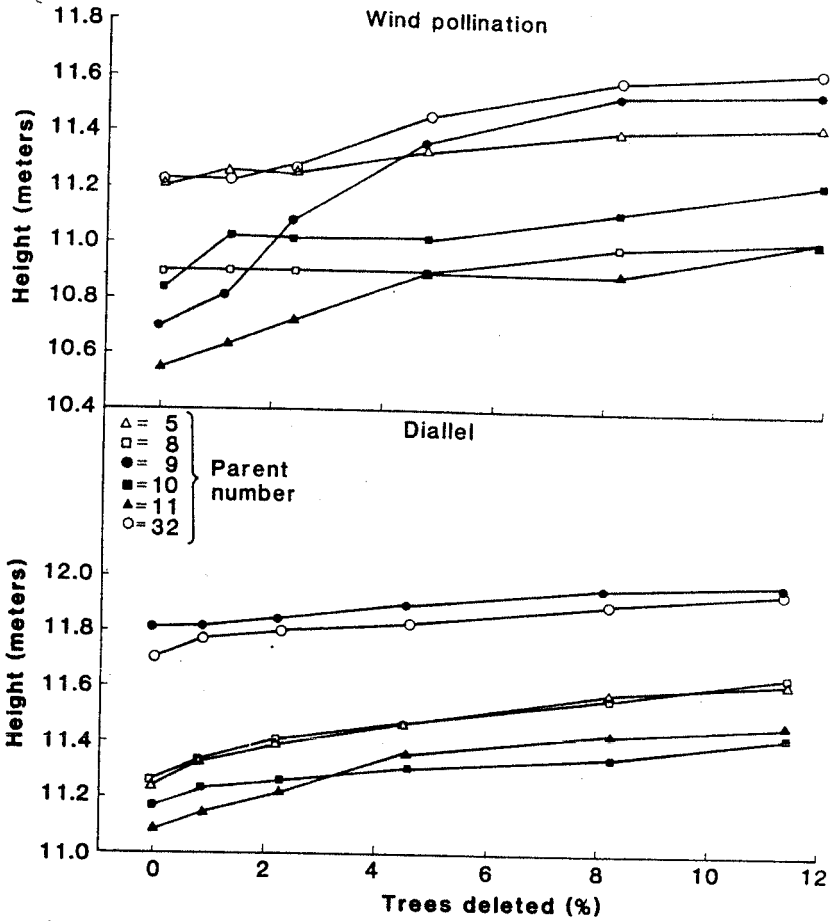


FIGURE 5. Family means (wind pollination, top; diallel, bottom) for 16-year height. Values are based on all living trees and after progressive deletion of the shortest trees. Lines in the top half of the figure represent wind-pollination progenies of six parent trees; lines in the lower half represent progenies from a half-diallel mating of the same six parents.

Parent 9, as noted earlier, had relatively high self-fertility, high potential for natural self-pollination, and inbred progeny with severe vigor depression. It may represent an extreme example. Nevertheless, other results (Sorensen 1971 and unpublished, Shaw and Allard 1982a) show large differences among coastal Douglas-fir in these three aspects of natural inbreeding. This suggests that if small inbred plants are included in the evaluation tests, there can be considerable variation in the accuracy with which true breeding values of parents are estimated by their *W* progenies.

GENERAL DISCUSSION AND CONCLUSION

Natural inbreeding, or the potential for natural inbreeding, and inbreeding depression in metric traits have been reported for many commercial coniferous species. With good nursery culture and good care and maintenance of test plantations, a portion of the inbred plants in the *W* family tests will

become members of the test population. Given this combination of breeding habit and good cultural practices, the *W* population becomes, in fact, a composite of two subpopulations—an outbred group that contributes the bulk of the trees and a much smaller, inbred group. The purpose of this paper has been to give one example of how the small, inbred outliers can affect estimates of variance, heritability, and ranking of parents.

In the analyses of size traits, with all trees present, the *W* and *D* tests seem to represent qualitatively different populations even though presumably they test the same parents and the progenies are tested in a single plantation. If the shortest 5 to 8% of the trees are deleted, much though not all, of the difference disappears. We suggest the differences prior to deletion can be explained by the population structure and natural breeding habits of coastal Douglas-fir.

First, natural mating is not random mating. Of the *W* pollination of coastal Douglas-fir, 40 to 60% is estimated to be self-pollination (Sorensen 1982), and 7 to 10% of the viable seeds may be from self-pollination or equivalent inbreeding (Sorensen 1973, El-Kassaby et al. 1981, Shaw and Allard 1982a, Omi 1983, Neale and Adams 1985). In contrast, controlled mating among trees in different parts of the stand eliminates most or all of the inbreeding.

Second, the weakness and slow growth of inbreds (Orr-Ewing 1957, Sorensen and Miles 1982) are evidence of alleles with large dominance deviations for metric traits. The inbreeding depression is due to directional dominance (Falconer 1981, p. 227) with the recessive homozygotes predominantly associated with the slow growth.

Third, during stand development selection against slow growth and low vigor and therefore against the homozygotes traits is intensive (Shaw and Allard 1982b). As a result, deleterious recessive alleles associated with large dominance deviations in metric traits are present in the adult population at very low frequencies (Mather 1973, pp. 20–21).

We suggest, based on these assumptions, that one of the important distinctions between the *W* and *D* populations is in the expression of dominance effects. Mating for *W* families probably included selfing and other inbreeding, and homozygosity for rare, recessive alleles is much higher than expected under the assumptions of random mating. Even low frequencies in the *W* progenies of homozygotes for recessive alleles with large dominance deviations can strongly affect genetic variances (Robertson 1952, Wright 1952, Falconer 1981, p. 118, Mitchell-Olds and Waller 1985).

In the 4 years after these measurements were taken, 3.8 and 0.4% of the *W* and *D* populations, respectively, were lost. The trees lost were exclusively the shortest outliers. Nature is doing what we were simulating, and this raises the question of how early measurements, particularly of *W* tests, should be handled. Spirek et al. (1981) mention the need "of screening the data to remove outliers (which) should reduce the error terms and result in more significant progeny effects." Our results indicate that one source of very short outliers is natural inbreeding. Outliers from this source violate genetic assumptions of *W* tests and, equally important, are subject to early mortality. To include them in early analyses can result in misleading estimates; to delete data indiscriminately is also a danger. Development of an objective "screening" procedure appears to have value.

As suppression or other causes of mortality eliminate the outliers from the population, estimates and inferences will be less affected by the problems discussed above. However, other problems with *W* family makeup might still result in biases (Table 1).

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Effect of Natural Inbreeding on Variance Structure in Tests of Wind-Pollination Douglas-Fir Progenies

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ABSTRACT. Studies of the mating habits of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) have shown that wind-pollination families contain a small proportion of very slow-growing natural inbreds.

The effect of these very small trees on means, variances, and variance ratios was evaluated for height and diameter in a 16-year-old plantation by systematically deleting from analyses the shortest individuals in wind-pollination (*W*) and diallel (*D*) progenies of six parent trees. The progenies were growing together in a common field test. The *D* population served as a control (no inbreds).

The low-vigor trees in the *W* population type gave a downward bias to means and an upward bias to within-plot and family \times block variance estimates. Amount of bias differed among *W* families. Before deletion, estimates of additive genetic variance and heritability for height in the *W* test were about one-third and one-sixth the estimates from the *D* test. Deleting the shortest 5 to 8% of the trees from the *W* population did not remove all the discrepancy, but it did result in much closer agreement between *W* and *D* tests. For the *D* test alone, deletion of the smallest trees had a negligible effect on estimates of additive genetic variance and heritability. *FOR. SCI.* 34(1):102-118.

ADDITIONAL KEY WORDS. Diallel mating, genetic variance, heritability, population structure.

RATE OF PROGRESS from breeding programs of forest trees depends, in part, on the ability to rank parents based on their breeding values and to estimate genetic variances. Wind-pollination (*W*) families, obtained by collecting seeds from female parents pollinated by surrounding males, are often used for both these purposes.

When estimating genetic variances, most authors assume members of *W* families are related as half-sibs from a random-mating population (Shelbourne 1969, Evans and Thor 1971, Stonecypher et al. 1973, Rehfeldt 1980, Foster and Lester 1983, McCutchan 1983, Sluder 1983). Then, in the absence of epistasis, the variance among families (σ^2_f) is equal to the covariance of half-sibs and $\sigma^2_f = \frac{1}{4} \sigma^2_A$; where σ^2_A is the additive genetic variance. For this to be true, all male and female parents must be unrelated and not inbred, and each female parent must be pollinated by several random males (Squillace 1974).

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Depending on which of these conditions are met, members within a *W* family can be more or less related than half-sibs from a random-mating population (Table 1). Most attention in forestry (Namkoong 1966, Squillace 1974, Snyder and Namkoong 1978, Neale 1985) has been given to problem 5 (Table 1). However, information accumulated on mating systems of forest trees indicates that partial natural inbreeding (number 7, Table 1) may also bias analyses of *W* progenies, particularly analyses of growth traits in species like Douglas-fir that show severe inbreeding depression.

Although predominantly an outbreeder, Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) *W* progenies are reported to have an inbreeding coefficient (*F*) of about 0.035 to 0.05 (Sorensen 1973, El-Kassaby et al. 1981, Shaw and Allard 1982a, Omi 1983, Neale and Adams 1985) at the germinant seedling stage. This inbreeding has been indicated as both predominantly selfing (Shaw and Allard 1982a) and as mixed selfing and matings between relatives (Neale and Adams 1985). If we assume that much natural inbreeding in coastal Douglas-fir is indeed selfing, that $F = 0.04$ at the germinant seedling stage, and that 80% of the inbreds become established in well-tended plantations (Sorensen and Miles 1982), the *W* progenies would have, on the average, $F \approx 0.032$ or about 6.4% self-pollination plants at the stage of crown closure. The *W* population could include two subpopulations; one of cross-pollination plants with $F \sim 0$ and a smaller one of inbred plants with *F* approaching 0.5.

Presence of inbred plants can bias inferences made from *W* families (Robertson 1952, Latter 1965, Mitchell-Olds and Waller 1985). We investigated the bias in estimation of genetic variances, especially within-family variance which is often large in young open-pollination tests (Khalil 1985), in a 16-year-old Douglas-fir plantation containing a mixture of *W* and half diallel (*D*) progenies from six parent trees. The *D* population contains no selfs and serves as a control with which genetic and family rankings obtained from the *W* population are subjectively compared. We also present analyses of *W* and *D* progenies after progressive deletion of about the shortest 12% of the observations from the data sets. The intent is to simulate what might happen to the relative magnitudes of genetic variances and to family rankings as low-vigor inbred plants are lost from the stand because of suppression.

MATERIALS AND METHODS

The parents of the test families were in a 20- to 25-year-old second-growth stand located at about 300-m elevation on the western slopes of the Cascade Range in central Oregon. The stand was divided into 6 "substands" (about 10 to 15 ha each), and one parent was chosen in each substand. Trees that could be climbed (no breakage) and having sufficient male and female reproductive buds were labelled in each substand, and 1 tree per substand selected at random. Trees were mated following a half-diallel design without selfs (method 4 of Griffing 1956). *W* cones as well as cones from the diallel matings were collected in September 1964, a year of moderate to good pollen and cone production in this area.

Pregerminated seeds from each of the 21 families (15D, 6W) were sown in 7.6-cm "jiffy pots" in the spring of 1965. Experimental design was a randomized complete block with 15 replications of 5-tree, noncontiguous, family plots. All potted plants, both *W* and *D*, were placed at random within replications in nursery beds in early summer. Extra seedlings in jiffy pots were kept in the adjoining bed and replacements made as necessary through

TABLE 1. Potential problems that can influence the genetic variance among families in a test of wind-pollination families.^a

Problem	Assumptions/ comments	Example	Parents inbred? $F_p > 0^b$	Progeny inbred? $F_o > 0^b$	Parents related? $R_{pp} > 0^b$	Composition of family variances ^c	References
1. None	Parents not inbred and not related, many males	Polymix with many males and no inbreeding	No	No	No	$1/4\sigma_A^2$	Kemphorne (1954)
2. Parents inbred	Mates unrelated and all inbred to same degree	Orchard clones inbred but unrelated	Yes	No	No	$0.0\sigma_B^2$ $> 1/4\sigma_A^2$	Cockerham (1963) Cockerham (1961) Cockerham (1963) Squillace (1974)
3. Males related within females	Females not related to each other or to males	Females are in different stands, and males are half-brothers	No	No	Yes	$0.0\sigma_B^2$ $> 1/4\sigma_A^2$	Stuber (1970) Hinkelmann (1969) Fujishima and Fredeen (1972)
4. Females related	Males not related to each other or to females	Polymix with many males applied to related females	No	No	Yes	$< 1/4\sigma_A^2$	Hinkelmann (1969) Fujishima and Fredeen (1972)
5. Few males	May be common in forest trees; full and half-sibs in same family; no inbreeding	Small neighborhood size in natural stands	No	No	No	$0.0\sigma_B^2$ $> 1/4\sigma_A^2$ $> 0.0\sigma_B^2$	Fujishima and Fredeen (1966) Namkoong (1966) Squillace (1974)
6. Assortative mating	Males resemble females to which they are mated	Females in different natural stands and genetic differences among stands; e.g., north and south aspects of same drainage	No	Yes	Yes	Depends on conditions ^d	Falconer (1981)
7. Males related to females	Only problem to result in inbred progeny	Related parents in same natural stand	No	Yes	Yes	Depends on conditions ^e	Cockerham (1963) Stuber (1970) Namkoong (1966)

^a We assume no epistasis, no linkage, and regular diploid inheritance (Cockerham 1963).

^b F = coefficient of inbreeding; p = parental generation; σ = first generation of progeny; R_{pp} = coefficient of genetic relationship between parents.

^c σ_A^2 = additive genetic variance; σ_B^2 = dominance genetic variance.

^d If the reference population to which the σ_A^2 and σ_B^2 estimates apply includes all the stands sampled and if the trees within a stand resemble each other more than trees from other stands, then problems 6 and 7 have the same consequences.

^e The influence of inbred progeny on the composition of variance among families depends on gene frequencies and degree of dominance. At intermediate gene frequencies and modest degrees of dominance, $\sigma_A^2 > 1/4\sigma_A^2$; where, σ_B^2 is the variance among wind-pollination families.

the first growing season. There was no mortality and no replacement during the second season. Nursery spacing was about 7.6 cm. The nursery was located at Corvallis, Oregon, 50 km west of and 225 m lower than the parent stand.

After two years in the nursery, the seedlings were field-planted into a large opening adjacent to and at the same elevation as the parent stand. The same design of 15 replications of 5-tree, noncontiguous, completely randomized family plots was used in the field test. Site preparation consisted of cultivating to break the sod and scalping around the planting spots. Spacing was 3.05 m \times 3.05 m.

For our analyses, data from groups of three original replications have been pooled (after adjustment for an additive replication effect) to form a single new replication. Thus, each of the 5 synthetic blocks had 15-tree noncontiguous plots. Such a grouping allowed deletion of trees to simulate mortality without loss of any family plots. It also provided more trees in each plot to more precisely estimate higher moments (variance and skewness) within plots.

MEASUREMENTS AND ANALYSES

Heights and diameters at 1.37 m were measured after the 16th growing season and individual tree volumes calculated following Bruce and DeMars (1974). Plot means and within-plot variances were calculated for each family plot in each block, and the resulting 6 response variables (height, diameter, volume, and their respective within-plot variances) were subjected to analyses of variance (Table 2).

Analyses were conducted on the data sets containing all living trees and on five sets constructed by progressive deletion of about the shortest 1, 2, 5, 8, and 12% of the trees in each block. The different deletion percentages were chosen to bracket the expected frequencies of inbred plants that might occur in a 16-year-old plantation. Because population sizes differed, deletion percentages differed slightly between the two population types. Percentages also varied slightly from block to block, depending on the number of living trees. The intent was to simulate the effects on genetic variance estimates as the low-vigor trees leave the population via suppression-related mortality (see Matheson and Raymond 1984 for a similar approach). The deletion procedure was applied independently to the *W* and *D* populations. This was done to compare relative effects on the two types of population. More trees were deleted within some families than within others because the shortest trees were eliminated first, without regard to family or block designation.

For each analysis of plot means, the method-of-moments procedure (Milliken and Johnson 1984, p. 233) was used to solve variance components by equating the observed mean squares to their expected values and solving the resulting system of linear equations (Table 2). Method-of-moment estimators are always unbiased and, for most balanced models, these estimators are uniformly minimum variance unbiased (Milliken and Johnson 1984, p. 235). The use of plot means instead of individual tree observations meant that balance was maintained (no missing observations) even with the deletion of as much as 12% of the smallest trees. Plot means were not significantly correlated with within-plot variances either before or after deletion, and no transformations were used. Within-plot variances were estimated separately after analyses of plot means by calculating within-plot sums of squares for each plot and pooling these across all plots.

TABLE 2. Expected mean squares for the three analyses of variance: (A) combined analyses to test the effect of population type; (B) analysis of wind-pollination families; and (C) analysis of diallel families.

Sources of variation	Degrees of freedom	Expected mean squares
(A) Combined analyses ^a		
Blocks	4	
Population types (<i>t</i>)	1	$\sigma^2 + 5\sigma_{ft}^2 + 42.8Q_i^2$
Families-in-population types (<i>ft</i>)	19	$\sigma^2 + 5\sigma_{ft}^2$
Plot error (<i>p</i>)	80	σ^2
(B) Wind-pollination families ^b		
Blocks	4	
Families (<i>f</i>)	5	$\frac{\sigma_{w,w}^2}{n_w} + \sigma_{p,w}^2 + 5\sigma_f^2$
Plot error (<i>p</i>)	20	$\frac{\sigma_{w,w}^2}{n_w} + \sigma_{p,w}^2$
Within-plot error (<i>w</i>)	$\sum_{j=1}^{30} (n_j - 1)^c$	$\sigma_{w,w}^2$
(C) Diallel families ^d		
Blocks	4	
GCA (<i>g</i>)	5	$\frac{\sigma_{w,D}^2}{n_D} + \sigma_{p,D}^2 + 5\sigma_s^2 + 20\sigma_g^2$
SCA (<i>s</i>)	9	$\frac{\sigma_{w,D}^2}{n_D} + \sigma_{p,D}^2 + 5\sigma_s^2$
Plot error (<i>p</i>)	56	$\frac{\sigma_{w,D}^2}{n_D} + \sigma_{p,D}^2$
Within-plot error (<i>w</i>)	$\sum_{j=1}^{75} (n_j - 1)^e$	$\sigma_{w,D}^2$

^a σ^2 = composite plot error.

σ_{ft}^2 = variance among families within population types.

Q_i^2 = expected value of sum of squared differences among population-type means.

^b $\sigma_{w,w}^2$ = within-plot variance for wind-pollination families.

n_w = harmonic means for number of trees per plot. These values were 13.9, 13.7, 13.6, 13.2, 12.7, and 12.2 when the shortest 0, 1.2, 2.4, 4.8, 8.3, and 11.9%, respectively, of the wind-pollination trees were deleted.

$\sigma_{p,w}^2$ = plot variance for wind-pollination families.

σ_f^2 = variance among wind-pollination families.

^c Degrees of freedom, within-plot, ranged from 330 with 11.9% of trees deleted to 380 with all living trees included.

^d $\sigma_{w,D}^2$ = within plot variance for diallel families.

n_D = harmonic means for number of trees per plot. These values were 14.6, 14.4, 14.2, 13.8, 13.2, and 12.7 when the shortest 0, 0.9, 2.3, 4.6, 8.2, and 11.4%, respectively, of the diallel trees were deleted.

$\sigma_{p,D}^2$ = plot variance for diallel families.

σ_s^2 = variance of general combining ability effects.

σ_g^2 = variance of specific combining ability effects.

^e Degrees of freedom, within-plot, ranged from 884 with 11.4% of trees deleted to 1009 with all living trees included.

Heritability values on an individual-tree basis were calculated as follows for the *W* and *D* families, respectively:

$$h^2 = \frac{\sigma_{A,W}^2}{\sigma_{w,W}^2 + \sigma_{p,W}^2 + \sigma_f^2}$$

$$h^2 = \frac{\sigma_{A,D}^2}{\sigma_{w,D}^2 + \sigma_{p,D}^2 + \sigma_s^2 + 2\sigma_g^2}$$

where $\sigma_{A,W}^2$ and $\sigma_{A,D}^2$ are the estimated additive genetic variances, $\sigma_{w,W}^2$ and $\sigma_{w,D}^2$ are the estimated within-plot variances, and $\sigma_{p,W}^2$ and $\sigma_{p,D}^2$ are the estimated plot variances for the *W* and *D* populations, respectively, and σ_s^2 and σ_g^2 are the estimated specific and general combining ability variances for the *D* population. For the diallel families, $\sigma_{A,D}^2$ was estimated as $4\sigma_g^2$, which assumes that parents were both unrelated and not inbred (Cockerham 1963). The first assumption (unrelatedness) is reasonable because the females came from different substands. Because the parents were vigorous, seed-producing trees, the second assumption (not inbred) also seems reasonable; any violation of the assumption would probably be slight and would affect estimates of σ_A^2 for *W* and *D* families in a similar manner.

For the *W* families, σ_A^2 was estimated as $3.33 \sigma_f^2$. This assumes unrelated and noninbred parents with five equally effective males pollinating each female (Squillace 1974, Neale 1985).

RESULTS AND DISCUSSION

SURVIVAL

Survival was high. Of the original planting of 1,125 *D* and 450 *W* seedlings, 98.6% *D* and 96.0% *W* seedlings were still alive at age 7. Causes of early mortality were mostly not known. At age 12, survival was 97.2% for *D* seedlings and 93.3% for *W*. Almost all mortality between ages 7 and 12 was due to pocket gopher (*Thomomys* sp.). No mortality occurred between ages 12 and 16, when the first plant was lost to suppression. Little of the mortality to age 16 preferentially eliminated low-vigor plants.

COMPARISON OF *W* AND *D* DISTRIBUTIONS AND MEANS

The distributions of individual tree heights (and diameters and volumes) for both *W* and *D* populations have negative skewness (Figure 1). Skewness at age 16 was very much more negative for the *W* than for the *D* type (Figure 2, bottom, zero deletion).

Skewness was calculated as the third moment about the mean (Snedecor and Cochran 1967, p. 86). The more negative values for the *W* distribution are indicative of the longer tail to the left of the distribution. As the shorter trees were progressively deleted, skewness changed little in the *D* population but increased quickly in the *W* population (Figure 2, bottom).

The grand mean of the *D* trees was significantly greater than that of the *W* trees at all levels of deletion (Figure 2, top, gives height as an example). Size differences between the two population types from the same seed parents could be due to (1) low-vigor, self-pollination plants in the *W* families; (2) other inbred offspring in the *W* families; (3) "sampling error" that resulted in the effective pollen parents of the *W* families having smaller breeding values than the six female parents; (4) a portion of the offspring in the *W* families resulting from poor specific combinations between male and female parents; or (5) heavier seed weight from the *D* pollinations (Sorensen and Campbell 1985) (average filled *D* seeds were 18% heavier than the *W* seeds as a consequence of the *D* cones being enclosed in pollen- and insect-isolation bags during development).

Up to a deletion of 5 to 8%, the mean of the *W* population increased faster than that of the *D* population. (For example, the mean height of *D* trees was 3.3% taller at 8% deletion contrasted with 6.1% taller at zero deletion.) This

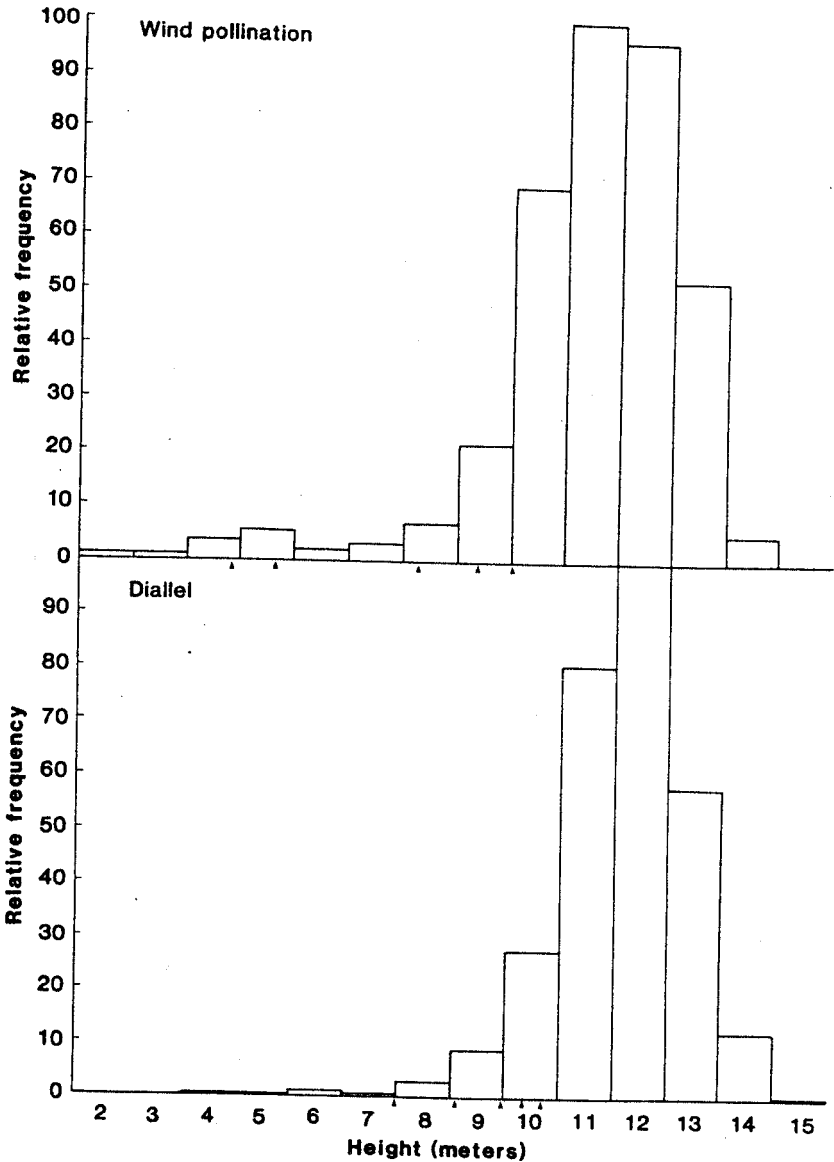


FIGURE 1. Frequency distributions of 16-year heights of trees from two populations. The upper histogram represents the bulked wind-pollination progenies of six parent trees; the lower histogram represents the bulked progenies from half-diallel matings (without selfs) among the same six parents. Midpoints of 1-m-height classes are given on the abscissa. The most frequent class in each population type is set equal to 100. Upper bounds of height groups eliminated by progressive deletion of the shortest trees are indicated by the vertical arrows under each histogram.

increase occurred as the shortest trees were deleted and as skewness of the *W* distribution became rapidly less negative (Figure 2). We believe these trends resulted because the initial deletions from the *W* data set were mostly self-pollination plants.

Above 5 to 8% deletion, the means of the two populations were still significantly different (see Figure 2, top, for height). These differences must result from one or more of the other reasons presented above.

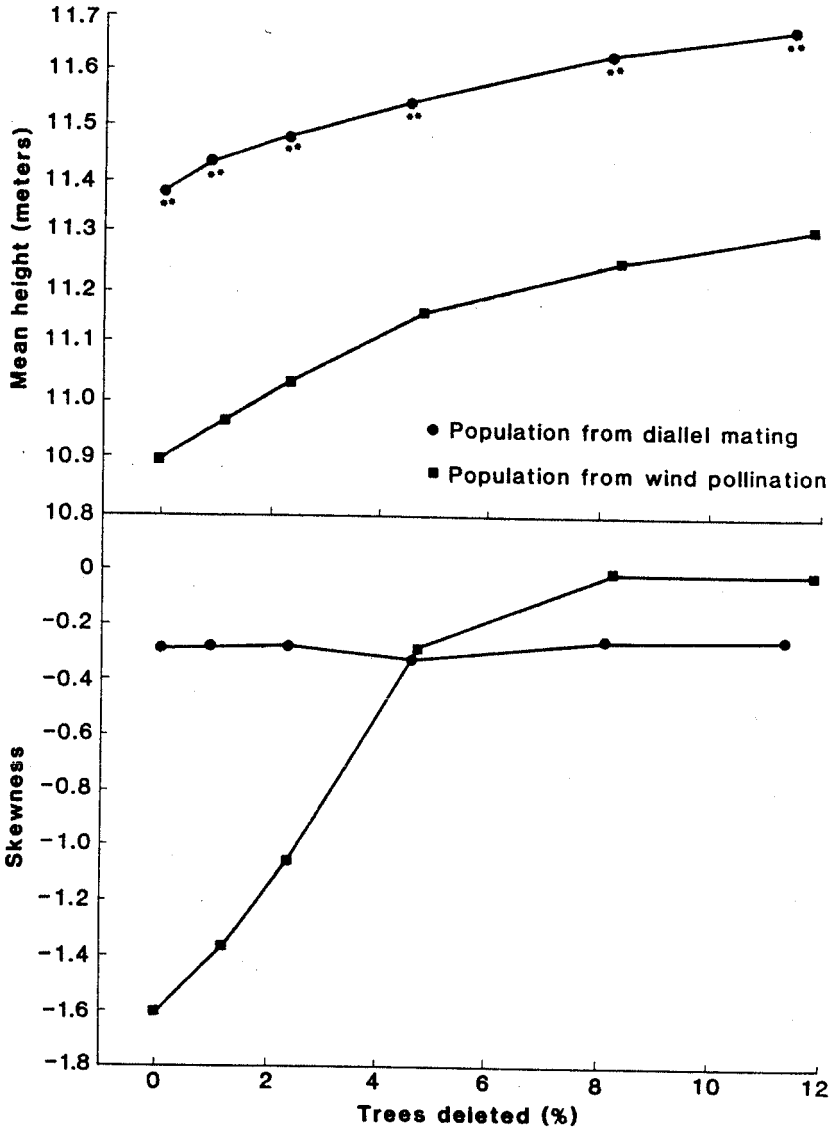


FIGURE 2. Mean heights (top) and skewnesses (bottom) of height distributions after progressive deletion of the shortest trees from the data sets. Differences between the population type means are significant at $P < 0.01$. (**) for all levels of deletion [see Table 2(A) for form of analysis used to compare population types].

COMPARISONS OF W AND D ESTIMATES OF VARIANCE COMPONENTS AND HERITABILITIES

With all living trees present, analyses of the D families showed significant variance of general combining abilities (σ_g^2) for height, diameter, and volume at 16 years (Table 3). Variance of specific combining abilities (σ_s^2) was not significant for height but was significant for diameter and volume. Ratios of σ_s^2/σ_g^2 were 0.07, 0.83, and 0.71 for height, diameter, and volume, respectively. Individual tree heritabilities from the diallel families with all

trees present were 0.23, 0.17, and 0.18 for height, diameter, and volume, respectively. These values are based on a small sample of parents and a single test plantation, but are similar to those reported for a well-maintained, 9-year-old Douglas-fir progeny test of control-pollination families in western Washington (Campbell et al. 1986).

Estimates of σ^2_A in the *W* population type were not biased upward, as expected with few males (Squillace 1974). With all living trees present, family components of variance from the *W* families were nonsignificant for all three traits and heritabilities were near zero (Table 3). The use of 3.33 as a multiplier of $\sigma^2_{f,W}$ (variance among families in the *W* population type) was not appropriate with all plants present. The effect of small inbred individuals on all variances was so powerful that it is doubtful if any one general multiplier could be used. It would depend too much on the mating habits and genetic constitution of the particular parents tested. After deletion, σ^2_A of the two population types was nearly identical if 3.33 and 4 were the multipliers of $\sigma^2_{f,W}$ and $\sigma^2_{f,D}$, respectively (Figure 4, top).

In the *D* test, mean squares and estimates of variance components decreased gradually as short trees were deleted (Figures 3 and 4, top), as is expected when one tail is truncated. Because terms in the numerator and denominator decreased at about the same rate, heritability estimates were nearly stable through the largest deletion (11.4%) (Figure 4, bottom).

For *W* families, on the other hand, the within-plot variances and plot mean squares decreased rapidly up to a deletion of 5 to 8% (Figure 3). At the same time, family mean squares rose slightly, and estimates of additive genetic variance increased markedly (Figure 4, top). Heritability estimates increased as a result of the numerator (σ^2_A) increasing and the denominator (total phenotypic variance) decreasing (Figure 4, bottom). Matheson and Raymond (1984) also found that thinning the smallest trees from a *W* family test of *Pinus radiata* D. Don resulted in lower within-plot variances and higher heritability estimates.

Within-plot variances (σ^2_w) make up more than 95% of the phenotypic variances. Decrease of σ^2_w in the *W* families was a major reason heritability values increase as trees are deleted. With all trees present, within-plot variances of the *W* families were much larger than those of the *D* families (Figure 3, top). Larger within-plot variances were also reported in *W* families compared with control pollination families of *Liriodendron tulipifera* L. (Farmer et al. 1983), but not for seven-year heights of *Pinus pallustris* Mill. (Snyder and Namkoong 1979). Differences between tests and species would be affected by presence or absence of nursery culling, size-related early field mortality, amount of natural inbreeding, proportion of additive to non-additive gene effects, degree of dominance, and size of dominance deviations.

$\sigma^2_{w,W}$ is also expected to be larger than $\sigma^2_{w,D}$ because more additive genetic variance is contained within *W* plots than within true full-sib plots. For height, σ^2_s was not significant and we therefore assumed no dominance variance. If, in addition, epistatic components of variance are small or similar between *D* and *W* population types, the expected values of the two within-plot variances are,

$$\sigma^2_{w,D} = \sigma^2_e + 0.5 \sigma^2_A$$

$$\sigma^2_{w,W} = \sigma^2_e + 0.7 \sigma^2_A$$

where, σ^2_e is the microenvironmental variance within plots. If σ^2_e is as-

TABLE 3. Variance component and individual-tree heritability estimates for 16-year height (m), diameter (cm), and volume (dm³) from wind-pollination and diallel families after different percentages of the shortest trees have been deleted. Deletion percentages are approximate; see Materials and Methods for actual values.^a Significance levels are ns (P > 0.10), + (P < 0.10), *(P < 0.05), and ***(P < 0.01).

Approximate deletion of trees (%)	Wind families				Heritability (h _w ²)
	Within plot (σ _{w,w} ²)	Plot (σ _{p,w} ²)	Additive ^b (σ _{A,w} ²)		
Height					
0	2.927	-0.009 ^{ns}	0.117 ^{ns}	0.040	(0.047) ^c
1	2.435	-0.021 ^{ns}	0.096 ^{ns}	0.039	(0.045)
2	2.004	-0.008 ^{ns}	0.057 ^{ns}	0.028	(0.042)
5	1.371	-0.026 ^{ns}	0.167 ^{**}	0.119	(0.082)
8	1.112	-0.024 ^{ns}	0.247 ^{**}	0.213	(0.126)
12	1.048	-0.021 ^{ns}	0.197 ^{**}	0.182	(0.114)
Diameter					
0	13.226	-0.028 ^{ns}	0.079 ^{ns}	-0.006	(0.026)
1	11.539	-0.142 ^{ns}	0.189 ^{ns}	0.016	(0.033)
2	10.047	-0.094 ^{ns}	0.116 ^{ns}	0.012	(0.032)
5	7.836	-0.175 ^{ns}	0.189 ^{ns}	0.024	(0.034)
8	6.606	-0.235 ^{ns}	0.573 [*]	0.088	(0.062)
12	5.734	-0.172 ^{ns}	0.424 [*]	0.074	(0.059)
Volume					
0	2608	-19 ^{ns}	-16 ^{ns}	-0.006	(0.024)
1	2480	-34 ^{ns}	13 ^{ns}	0.005	(0.027)
2	2335	-28 ^{ns}	42 ^{ns}	0.018	(0.034)
5	2092	-44 ^{ns}	108 ⁺	0.052	(0.048)
8	1869	-56 ^{ns}	208 ^{**}	0.111	(0.075)
12	1715	-46 ^{ns}	150 ^{**}	0.088	(0.066)

^a Significance of variance components was determined from the F-tests in the appropriate analyses of variance. Significance of the additive variance was based on F-test for families in the analyses of wind families and on the F-test for general combining ability in the analysis of diallel families.

^b $\sigma_{A,w}^2 = 3.33 \sigma_p^2$

^c Specific combining ability.

^d $\sigma_{A,D}^2 = 4\sigma_p^2$ (see Table 2).

^e Approximate standard errors of heritability estimates are in parentheses and were calculated by the methods presented in Namkoong (1979, p. 229-234).

sumed to be the same for both family types, $\sigma_{w,W}^2$ would be larger than $\sigma_{w,D}^2$ by $0.2 \sigma_A^2$. Using estimates of σ_A^2 from the *D* test, $0.2 \sigma_A^2$ corresponds to a difference of 0.04 to 0.08 between $\sigma_{w,D}^2$ and $\sigma_{w,W}^2$. $\sigma_{w,W}^2$ still appears much larger than predicted, based solely on differences in additive genetic variance (Figure 3, top).

Further complications involving within-plot variance estimates from the *W* population type were indicated when the within-plot variances themselves were subjected to analysis of variance. Analysis of the *D* population indicated that families from the six parents did not differ significantly for within-plot variances when the plots contained full-sib families. In contrast, within-plot variances differed significantly among the *W* families. Much of this effect was due to a single family (from parent 9) which, for height, had an average within-plot variance 180% larger than the mean of the remaining

TABLE 3. Continued.

Diallel families					
Within plot	Plot	SCA ^c	Additive ^d	Heritability	
($\sigma_{w,D}^2$)	($\sigma_{p,D}^2$)	(σ_s^2)	($\sigma_{\lambda,D}^2$)	(h_b^2)	
1.426	-0.026 ^{ns}	0.006 ^{ns}	0.350**	0.221	(0.123) ^e
1.128	-0.001 ^{ns}	0.001 ^{ns}	0.318**	0.247	(0.139)
1.006	-0.008 ^{ns}	0.002 ^{ns}	0.280**	0.245	(0.140)
0.890	-0.015 ^{ns}	0.003 ^{ns}	0.235**	0.235	(0.138)
0.811	-0.020 ^{ns}	0.005 ^{ns}	0.234**	0.257	(0.152)
0.754	0.027 ^{ns}	0.005 ^{ns}	0.214**	0.255	(0.154)
7.084	-0.018 ^{ns}	0.261**	1.263*	0.159	(0.104)
6.086	0.021 ^{ns}	0.249**	1.042*	0.152	(0.103)
5.494	0.030 ^{ns}	0.252**	0.943*	0.151	(0.106)
4.931	-0.009 ^{ns}	0.246**	0.684+	0.124	(0.096)
4.233	-0.058 ^{ns}	0.219**	0.598+	0.127	(0.098)
3.830	-0.073 ^{ns}	0.204**	0.701+	0.163	(0.115)
2180	-23 ^{ns}	73**	410**	0.168	(0.104)
2055	-13 ^{ns}	73**	366**	0.159	(0.101)
1939	-9 ^{ns}	73*	333**	0.154	(0.100)
1815	-20 ^{ns}	72*	259**	0.130	(0.091)
1649	-34 ^{ns}	69*	243**	0.135	(0.094)
1541	-41 ^{ns}	67*	259**	0.153	(0.102)

five families. As the shortest trees were deleted, the within-plot variance for family $9 \times W$ dropped more rapidly than those of the other families because it contained a higher proportion of very short trees. From other studies, parent 9 was known to have high self-fertility (Sorensen 1971), be a prolific pollen producer (Sorensen, unpublished observations), and give self-pollination progeny with greater than average inbreeding depression in metric traits (Sorensen, unpublished data).

With small tests, such as the one reported here (six parents), the impact of one family can be large, but, even with family 9 excluded, within-plot variance of the W families was, before deletion, much larger than the within-plot variance of the D families (Figure 3, top).

In addition to biasing within-plot variance estimates, the presence of very small trees in the W progenies inflated the estimates of plot mean squares (family \times block interaction). These also dropped rapidly as trees were deleted (Figure 3, bottom). Few trees were very short—only 10 to 15 plants in the W test (Figure 1, top). They were not evenly distributed among families, and chance did not distribute them evenly among blocks. Apparently, as they were deleted, family performance became more stable across blocks. Thus, as plot mean squares decreased rapidly, the ability to detect family differences increased as did the estimates of additive genetic variance (Figure 4, top).

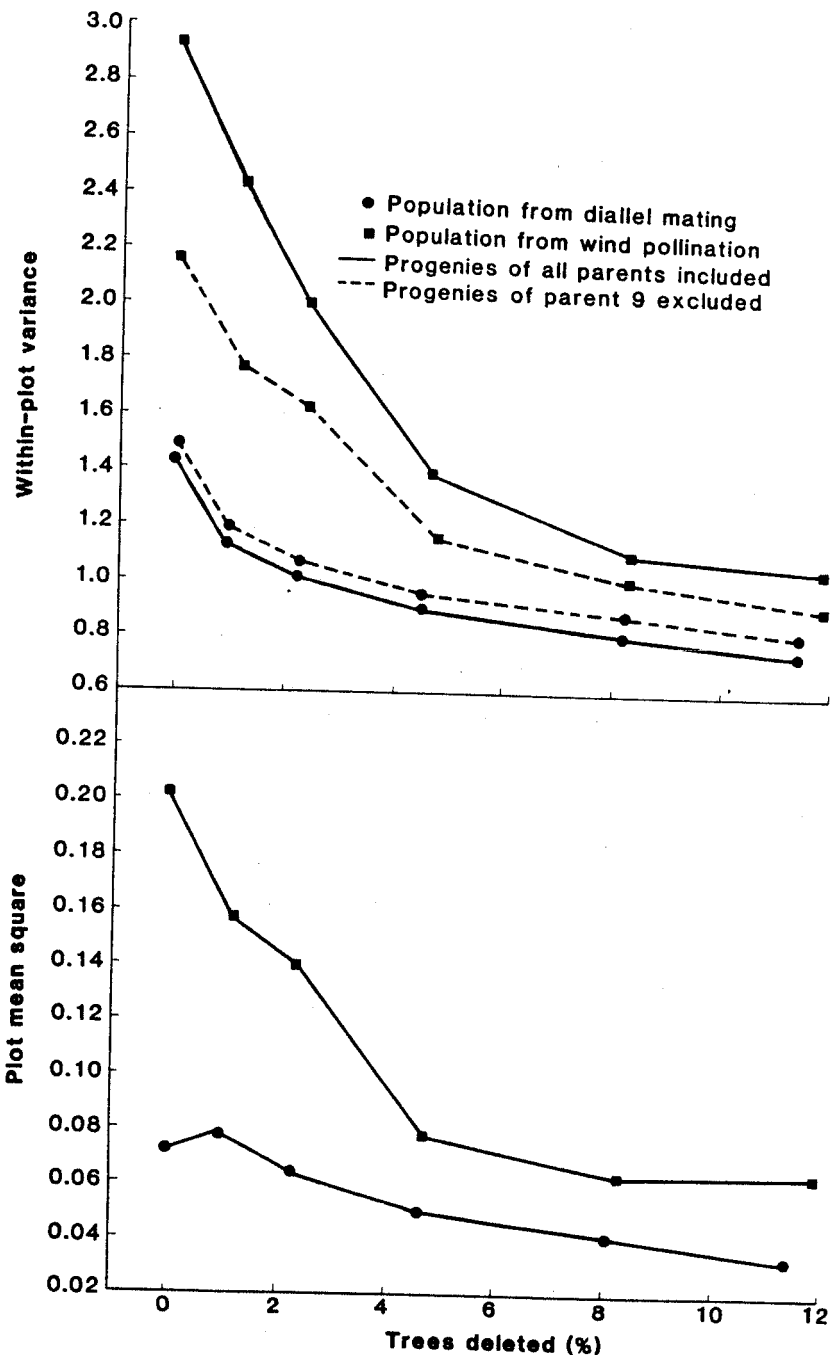


FIGURE 3. Within-plot variances (top) and plot mean squares (bottom) for height in meters from a 16-year-old Douglas-fir test containing wind-pollination and diallel families with all living trees included and after progressive deletion of the shortest trees from the data sets.

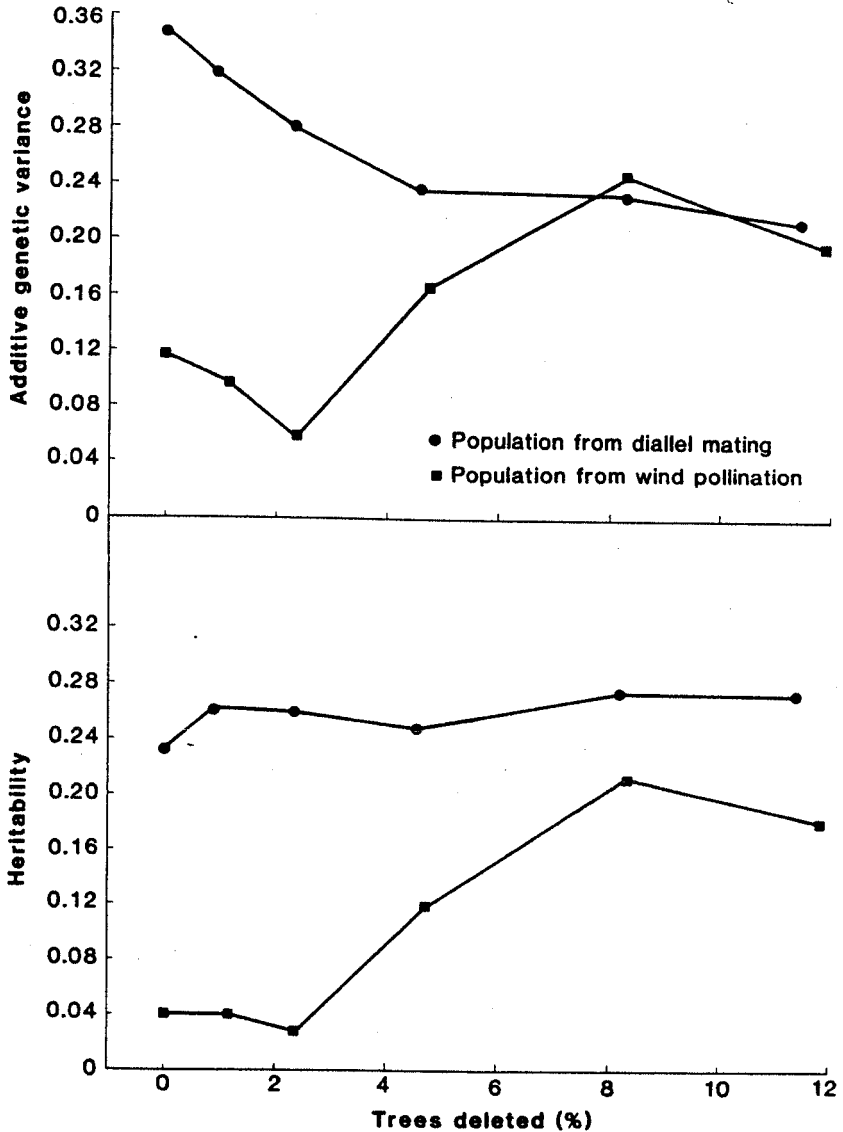


FIGURE 4. Additive genetic variances (top) and heritabilities (bottom) from a 16-year-old Douglas-fir test containing wind-pollination and diallel families with all living trees present and after progressive deletion of the shortest trees from the data sets.

FAMILY MEANS AND COMBINING ABILITIES

W family means underwent important changes as the shortest trees were deleted from the data set (Figure 5, see especially $9 \times W$). The end ranking much more closely agreed with the general combining ability rankings from the *D* test. For height, the correlation between family means from the *W* test with GCAs from the *D* test using all living trees was $r = 0.23$, but it increased to $r = 0.77$ and $r = 0.84$ when 4.8 and 8.3% of the *W* trees were deleted, respectively (values of $r > 0.81$ are significant at $P = 0.05$ with 4 degrees of freedom).

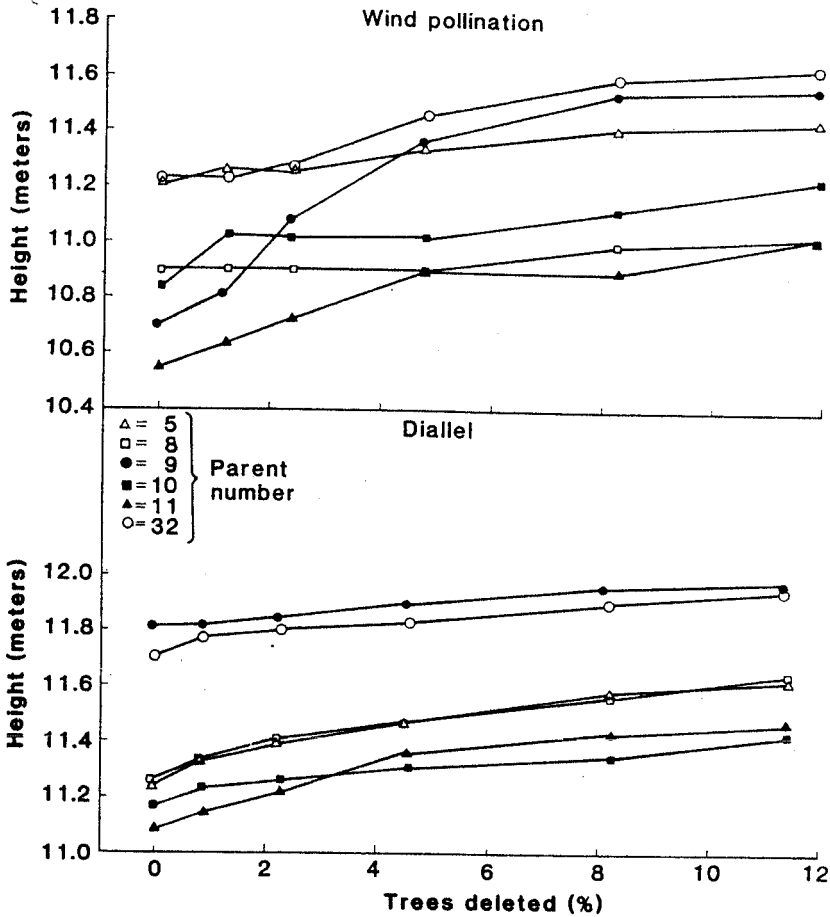


FIGURE 5. Family means (wind pollination, top; diallel, bottom) for 16-year height. Values are based on all living trees and after progressive deletion of the shortest trees. Lines in the top half of the figure represent wind-pollination progenies of six parent trees; lines in the lower half represent progenies from a half-diallel mating of the same six parents.

Parent 9, as noted earlier, had relatively high self-fertility, high potential for natural self-pollination, and inbred progeny with severe vigor depression. It may represent an extreme example. Nevertheless, other results (Sorensen 1971 and unpublished, Shaw and Allard 1982a) show large differences among coastal Douglas-fir in these three aspects of natural inbreeding. This suggests that if small inbred plants are included in the evaluation tests, there can be considerable variation in the accuracy with which true breeding values of parents are estimated by their *W* progenies.

GENERAL DISCUSSION AND CONCLUSION

Natural inbreeding, or the potential for natural inbreeding, and inbreeding depression in metric traits have been reported for many commercial coniferous species. With good nursery culture and good care and maintenance of test plantations, a portion of the inbred plants in the *W* family tests will

become members of the test population. Given this combination of breeding habit and good cultural practices, the *W* population becomes, in fact, a composite of two subpopulations—an outbred group that contributes the bulk of the trees and a much smaller, inbred group. The purpose of this paper has been to give one example of how the small, inbred outliers can affect estimates of variance, heritability, and ranking of parents.

In the analyses of size traits, with all trees present, the *W* and *D* tests seem to represent qualitatively different populations even though presumably they test the same parents and the progenies are tested in a single plantation. If the shortest 5 to 8% of the trees are deleted, much though not all, of the difference disappears. We suggest the differences prior to deletion can be explained by the population structure and natural breeding habits of coastal Douglas-fir.

First, natural mating is not random mating. Of the *W* pollination of coastal Douglas-fir, 40 to 60% is estimated to be self-pollination (Sorensen 1982), and 7 to 10% of the viable seeds may be from self-pollination or equivalent inbreeding (Sorensen 1973, El-Kassaby et al. 1981, Shaw and Allard 1982a, Omi 1983, Neale and Adams 1985). In contrast, controlled mating among trees in different parts of the stand eliminates most or all of the inbreeding.

Second, the weakness and slow growth of inbreds (Orr-Ewing 1957, Sorensen and Miles 1982) are evidence of alleles with large dominance deviations for metric traits. The inbreeding depression is due to directional dominance (Falconer 1981, p. 227) with the recessive homozygotes predominantly associated with the slow growth.

Third, during stand development selection against slow growth and low vigor and therefore against the homozygotes traits is intensive (Shaw and Allard 1982b). As a result, deleterious recessive alleles associated with large dominance deviations in metric traits are present in the adult population at very low frequencies (Mather 1973, pp. 20–21).

We suggest, based on these assumptions, that one of the important distinctions between the *W* and *D* populations is in the expression of dominance effects. Mating for *W* families probably included selfing and other inbreeding, and homozygosity for rare, recessive alleles is much higher than expected under the assumptions of random mating. Even low frequencies in the *W* progenies of homozygotes for recessive alleles with large dominance deviations can strongly affect genetic variances (Robertson 1952, Wright 1952, Falconer 1981, p. 118, Mitchell-Olds and Waller 1985).

In the 4 years after these measurements were taken, 3.8 and 0.4% of the *W* and *D* populations, respectively, were lost. The trees lost were exclusively the shortest outliers. Nature is doing what we were simulating, and this raises the question of how early measurements, particularly of *W* tests, should be handled. Spirek et al. (1981) mention the need “of screening the data to remove outliers (which) should reduce the error terms and result in more significant progeny effects.” Our results indicate that one source of very short outliers is natural inbreeding. Outliers from this source violate genetic assumptions of *W* tests and, equally important, are subject to early mortality. To include them in early analyses can result in misleading estimates; to delete data indiscriminately is also a danger. Development of an objective “screening” procedure appears to have value.

As suppression or other causes of mortality eliminate the outliers from the population, estimates and inferences will be less affected by the problems discussed above. However, other problems with *W* family makeup might still result in biases (Table 1).

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