Relative family performance and variance structure of open-pollinated Douglas-fir seedlings grown in three competitive environments *

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Summary. Open-pollinated Douglas-fir (*Pseudotsuga menziesii* var '*menziesii*' (Mirb.) Franco) families were tested in three contrasting competitive environments to test the hypothesis that relative performance as measured by total seedling dry weight is dependent upon distance or genotype of neighbors. The three competitive environmnts included (1) a mixture of individuals from all families planted at close spacing, (2) single (pure) family blocks planted at close spacing, and (3) individuals from all families planted at a wide, non-competitive spacing. Despite occasional large changes in rank between competitive environments and only moderate correlations of family means between competitive environments, the family × competitive environment interaction was non-significant. Furthermore, families did not differ significantly in competitive ability or density tolerance. The competitive environment in which seedlings were grown, however, had a large effect on estimates of variance components, which in turn led to large differences in estimates of heritability and genetic gain. Evaluation of families in mixture resulted in the largest estimates of heritability, while evaluation in pure family blocks resulted in the lowest. Analysis of correlated response to selection indicated that testing and selection in mixture result in the largest estimated gain, even if progeny of selected individuals are subsequently grown in a pure or non-competitive environment.

Key words: Intergenotypic competition – Density competition – Genetic variance components – Heritability

Introduction

Competition occurs when the immediate supply of a resource necessary for growth or reproduction falls below the combined demand of all individuals within a community (Donald 1963). Competition is usually assessed by measuring its effects since measuring resources directly is difficult. The effects of competition are dependent upon both the genetic composition and the proximity of neighbors (Sakai 1961). We refer to competition due to the presence of unlike genotypes as intergenotypic competition, whereas competition due to the proximity of neighbors is referred to as density competition.

Three competitive environments may be identified that encompass these two types of competition: (1) a dense mixed community of all genotypes, (2) dense monocultures of each genotype, and (3) individuals of all genotypes grown at a wide. non-competitive spacing. These three competitive environments represent the extremes of genetic composition and proximity. Intermediate competitive environments exist, but all plant communities may be considered to lie "within the triangle" of these three environments (Donald and Hamblin 1976).

Plant ideotypes have been identified to correspond to these three competitive environments (Donald and Hamblin 1976; Cannell 1978). An ideotype is "a biological model which is expected to perform or behave in a predictable manner within a defined environment" (Donald 1968). An isolation ideotype is a model plant that is expected to perform well when grown in isolation (i.e., non-competitive environment); a competition ideotype is a model plant that is expected to perform well when in mixture with other genotypes; and a crop ideotype is a model plant that is expected to perform well when grown in pure stands of genotypes. Crop ideotypes have been identified in several crop species (Donald 1968; Adams

1982; Rasmusson 1987) and in forest trees (Gordon and Promnitz 1976; Cannell 1978; Dickmann 1985; Kärki and Tigerstedt 1985). Hypotheses of forest tree crop ideotypes most often include tall, narrow crowns, compact, fibrous root systems, a phenology that allows full utilization of the growing season, and greater partitioning to the stem.

Crop ideotypes are postulated to lead to the greatest per area yields, provided they are not suppressed by competition ideotypes (Donald 1968; Cannell 1978). They also make the most efficient use of resources per unit area, but are weak competitors since they do not exploit resources from neighbors. This negative relationship of efficiency to exploitation leads to the expectation that performance of genotypes in pure stands will be poorly related to performance in mixture, or to performance at a wide, non-competitive spacing (Donald 1968; Cannell 1978). Furthermore, if exploitation of resources is dependent upon whether a genotype gains the resources from a competing neighbor, or gains them over an unlimited space (in the absence of competition), the relationship between genotypes in mixture and genotypes at a wide spacing may be less than perfect. Thus, one might hypothesize that the relative performance of genotypes is dependent upon competitive environment, such that rankings of genotypes change between competitive environments, genotype × competitive environment interaction is present, and correlations would be less than one between performance in different competitive environments.

Differences in relative family performance between competitive environments would also lead to the expectation that families differ in competitive ability and density tolerance. Competitive ability is defined as the ability to obtain resources in the presence of unlike genotypes, and is measured as the difference between the growth of a family in mixture and in a pure stand (Sakai 1961). Density tolerance is here defined as the response of a genotype to increasing stand density in the absence of interfamily competition, and may be measured by the difference between the growth of a family at wide versus narrow spacing. Family differences in competitive ability and density tolerance could be exploited in breeding programs to develop trees that are less aggressive at exploiting resources from neighboring trees, and more efficient at using available growing space. A crop ideotype would correspond to a genotype with a low competitive ability and a high density tolerance.

The competitive environment in which families are grown may influence the estimation of genetic parameters (Griffing 1967; Gallais 1976; Hamblin and Rosielle 1978; Wright 1982). The estimation of genetic parameters assumes the absence of environmental sources of covariance (Falconer 1981, pp 144–146). Competition presents a case of environmental covariance where variance among relatives may be increased or decreased dependent upon whether competition is primarily between or within families. With interfamily competition, family variance may be magnified if competition between families results in some families experiencing a relatively better microenvironment due to suppression of other families. With intrafamily competition, interactions between members of the same family could magnify any within-family differences, leading to an increase in within-family variance relative to the case of no competition. Increased within-family variance would be reflected by increased within-plot variance since these two sources of variation are confounded. The implications are that increased interfamily competition would result in greater estimates of heritability, and increased intrafamily competition would result in reduced estimates of heritability, when compared to the case of no competition.

Competition may affect the ability to select effectively and efficiently if the competitive environment in which genotypes are tested is not the same as the competitive environment in which progeny from select parents are expected to be grown. The influence of competitive environment on the relative ranking of parental genotypes and on estimates of genetic parameters may lead to inaccurate estimates of expected genetic gains, and may have implications for selection strategies, including decisions of testing in mixed versus pure stands, spacing of tests, and treatment of missing plots. Competitive interactions might also be important when developing an early testing strategy, and might help explain poor juvenile-mature correlations and the dependency of variance components and heritability on age of measurement (Franklin 1979; Lambeth et al. 1983; Foster 1986).

The objectives of this study are: (1) to evaluate the effect of competitive environment on relative family performance, (2) to assess family variation in competitive ability and density tolerance, (3) to evaluate the effect of competitive environment on estimates of genotypic and phenotypic components of variance, heritability, and genetic gain, and (4) to explore the implications of competitive environment on selection strategies.

Materials and experimental design

Open-pollinated seed was collected in the fall of 1985 from 39 Douglas-fir (*Pseudotsuga menziesii* var *menziesii* (Mirb.) Franco) parent trees located in second-growth stands in the Coast Range of west-central Oregon. Parent trees were from selections made within a single breeding zone by the Bureau of Land Management as part of the Umpqua Tree Improvement Cooperative of the Douglas-fir Progressive Tree Improvement Program (Silen and Wheat 1979). In February, 1986, seeds were treated with a fungicide and soaked in tap water for 24 h at room temperature prior to stratification by storage at 3–4 C for 8 weeks.

The study was established in the spring of 1986 in raised nursery beds at the Forest Research Laboratory in Corvallis.

Oregon. The experimental layout was a split-split plot design with three factors. The first factor, competitive environment, included three treatments: (1) individuals from all families planted in random mixture at close spacing, (2) individuals planted in single (pure) family blocks at close spacing, and (3) individuals of all families planted at wide, non-competitive spacing. The close spacing was 4 × 4 cm and was chosen to be as close as possible without incurring much density-related mortality by the end of two growing seasons. The wide spacing was 16 × 16 cm and was chosen to be as close as possible without incurring appreciable competition during the two growing seasons. Competitive environments were assigned at random to each of the three whole plots in each replication.

The second factor was planting-type. Families were either planted as ungerminated seed or as recently germinated "germinants." Planting-type treatments (subplots) were randomly assigned within each competitive environment (whole plot).

The third factor was the 39 open-pollinated families. In the pure blocks, families were represented by square (4 × 4) 16-tree pure family blocks, of which the center 4 trees were measured. The 39 pure family blocks (sub-sub-plots) were located at random within each subplot. In the mix and wide treatments, each family was represented by 4 trees assigned randomly to positions within the subplots (i.e., non-contiguous sub-sub-plots), and all 4 trees were measured.

The ungerminated seed were planted during the first week of April, 1986. Three seeds were planted in each planting position and later randomly thinned to a single seedling per spot. Seed for germinants were germinated on moistened filter paper in petri dishes at a day/night temperature of 30°/20 °C, with a 12-h photoperiod. Germinants were stored at 3°–4 °C to slow elongation of the radical until enough germinants were available to begin planting a replication (stored from 1 to 13 days with most germinants stored for about 7 days). A single germinant was planted into each planting position in the germinant-planted subplots during the third week of April, about the time that seedlings of the seed-planted treatments first began to emerge from the soil.

Some newly emerged seedlings experienced damping off, and many seedlings were lost in May in two replications (nursery beds) due to problems with a root weevil. Fungicides were subsequently used to control damping off, and an insecticide was sprayed to control the root weevil. Replacement seedlings of the same family were transplanted into the empty spots between late May and early July. Late transplants (after May) were excluded from subsequent analyses. Of the original five replications, one full replication and the subplot planted with germinants in another replication, were deleted from further consideration because of high mortality.

In the remaining replications and subplots, some planting locations were missing at the end of the first year despite the attempt to refill them by transplanting. Missing spots are of some consequence at the narrow spacing since they represent loss of competition. The effect was assumed to be inconsequential, however, since the number of missing spots was few (3% in mixtures, 5% in pure blocks), and the surrounding seedlings quickly occupied the open space. During the second year, a few additional trees died (4% in mixture, 2% in pure, 1% in wide). Much of the second-year mortality in mixtures and some in pure blocks appeared to be density related.

During the two growing seasons of the study, seedlings were well watered and fertilized regularly, and thus, competition may be assumed to have been primarily for light. Competition at the close spacing was minimal during the first growing season, but intense during the second growing season, as judged by the amount of crown overlap and the amount of light reaching the soil surface. At the wide spacing, crowns just began to overlap near the end of the second growing season, and thus, competition may be assumed to have been minimal during the course of the experiment.

Measurements and statistical analyses

Trees were harvested after two growing seasons, and several measures of performance were recorded for each seedling. The best measure of the effect of competition is the total yield of plant material, also called the biological yield (Donald and Hamblin 1976), and was measured as the total dry weight of a seedling (referred to as biomass). As an alternative measure of biological yield, we also measured shoot dry weight. Because of the difficulty of measuring roots, many studies analyze only shoot dry weight. It was of interest to determine whether excluding roots affected the results in any way. Preliminary analyses indicated results using shoot dry weight and stem dry weight were similar ($r = 0.97$); thus, we will refer only to total dry weight throughout the rest of the paper.

Measurements of biomass were log-transformed (all log transformations were natural logs) to correct for non-homogeneity of error variances among competitive treatments and among families within competitive treatments (assessed by examination of residual plots). Preliminary analyses of variance (ANOVAs) were done using the split-split plot design with the three full replications left after mortality and transplanting. All interactions involving planting type were non-significant (St. Clair 1989), and, thus, planting type was ignored in subsequent analyses. The three and one-half replications left after mortality and transplanting could then be treated as seven replications (four seed-planted replications and three germinant-planted replications) in a split-plot analysis. Subsequent analyses were of two forms (Table 1). First, an overall analysis of all competitive treatments together was done to test for mean differences between competitive environments and for family × competitive environment interaction. Next, in order to estimate genetic parameters for seedlings grown in each competitive environment, ANOVAs were done separately for each competitive treatment. All analyses were done using least squares procedures (SAS 1987). Competitive environments were treated as a fixed effect, and families were treated as a random effect.

Analyses of covariance were done using seed weight as a covariate in order to adjust for the potential influence of maternal effects due to differential seed size. The relationship between seed weight and 2-year dry weight of seedlings was not strong, and for purposes of comparing competitive environments, results for adjusted values were similar to those for unadjusted values, and are therefore not presented (St. Clair 1989).

The effect of competitive environment on relative family performance (objective 1) was evaluated by considering the statistical significance of the family × competitive environment interaction in the combined ANOVA with all three competitive environments. In addition, family means were determined for each competitive environment, and rank correlations of family means between pairs of competitive environments were calculated.

Family values for competitive ability were calculated as log biomass of seedlings when grown in mixture minus log biomass when grown in pure stands, and density tolerance was calculated as log biomass when grown in pure minus log biomass when grown in wide. A third value, log biomass when grown in mixture minus log biomass when grown in wide, was calculated as a measure of the combined response to interfamily competition and density, here referred to as competitive-density ability. For each family, competitive ability, density tolerance, and competitive-density ability were calculated for each replication separately. For example, the competitive ability of a given family in a

Table 1. Analyses of variance of log e biomass: (A) combined analysis over all competitive treatments; (B–D) analyses for each competitive treatment (mixture, pure blocks, wide spacing) separately

Source	df	MS	F	Probability
(A) Combined				
Block	6	4.2669		
Competitive Environment (CE)	2	898.0452	253.33	0.0001
Whole-plot error	12	3.5449		
Family	38	2.9618	5.98	0.0001
Family × CE	76	0.6283	1.27	0.0701
Split-plot error	684	0.4957		
Within plot	2133	0.5148		
(B) Mixture				
Block (B)	6	0.7444		
Family (F)	38	1.9126	4.15	0.0001
Error (B × F)	228	0.4610		
Within plot	720	0.5425		
(C) Pure blocks				
Block (B)	6	2.3277		
Family (F)	38	1.0621	1.81	0.0032
Error (B × F)	228	0.5732		
Within plot	713	0.5868		
(D) Wide spacing				
Block (B)	6	7.5950		
Family (F)	38	1.1574	2.56	0.0001
Error (B × F)	228	0.4528		
Within plot	700	0.4130		

given replication was calculated as the family mean of log biomass in that replication for the mixture treatment minus the family mean of log biomass in the same replication for the pure treatment. Each measure was then subjected to ANOVA, and the statistical significance of family variation for these traits tested (objective 2).

Variance components for log biomass were determined within each competitive environment on estimates of genetic parameters (objective 3). Variance components were estimated by equating the expected mean squares with the observed mean squares and solving the resulting equations (St. Clair 1989). Standard errors for variance components were estimated as in Becker (1984, p 47).

The influence of competitive environment on potential genetic gain was examined both for selection of progeny based on individual-tree data (mass selection) and for selection of parents based on progeny means (family selection). Individual-tree heritabilities were estimated as:

$$h_I^2 = \frac{\sigma_A^2}{\sigma_P^2}$$

where σ_A^2 = additive genetic variance, $\sigma_P^2 = \sigma_w^2 + \sigma_e^2 + \sigma_f^2$ = phenotypic variance of individual trees, σ_f^2 = family component of variance, σ_e^2 = error component of variance, σ_w^2 = within-plot component of variance.

Family heritabilities were estimated as:

$$h_F^2 = \frac{(1/4)\,\sigma_A^2}{\sigma_F^2}$$

where $\sigma_F^2 = \sigma_w^2\,n\,b + \sigma_e^2\,b + \sigma_f^2$ = phenotypic variance of family means, b = number of replications, n = harmonic mean number of trees per plot.

We assumed that wind-pollinated families are related to a greater extent than half-sibs (Squillace 1974; Sorensen and White 1988), and hence, the additive genetic variance, σ_A^2, was estimated as $3\sigma_f^2$. This estimate of family heritability is appropriate for estimating gain from roguing of a clonal seed orchard. The coefficient of 1/4 occurs because gain is realized by collection and planting of half-sib seed from the seed orchard. Standard errors of estimates of heritabilities were derived by procedures outlined by Osborne and Paterson (1952).

Genetic gain was estimated for individual (mass) selection as (Falconer 1981, p 175):

$$\Delta G_I = i\,h_F^2\,\sigma_P$$

where i = intensity of selection, and for family selection as (Burdon 1977):

$$\Delta G_F = 2\,i\,h_F^2\,\sigma_F$$

Percent genetic gains were determined after back-transformation of the estimated gain and overall means for each competitive environment.

The implications of competitive environment for selection strategies (objective 4) were explored by estimating the effect of testing and selection in one competitive environment on the correlated response when select families are grown in another competitive environment (Burdon 1977; Falconer 1981, p 290–292; Spitters 1984). Correlated response to selection was calculated as:

$$\Delta G_{y \cdot x} = i_x\,h_{Ix}\,h_{Iy}\,r_{Axy}\,\sigma_{Py}$$

where $\Delta G_{y \cdot x}$ = gain in environment y after selection in environment x. r_{Axy} = genetic correlation between environments x and y, and h_{Ix} and h_{Iy} = square-roots of individual-tree heritabilities in environments x and y, respectively.

For family selection, σ_P, is replaced by σ_{Fy}, individual-tree heritabilites are replaced by family heritabilities, and the equation is multiplied by 2 (Burdon 1977). Genetic correlations between competitive environments were calculated as (Burdon 1977):

$$r_{Axy} = \frac{r_{xy}}{(\sigma_{fx}/\sigma_{Fx})\,(\sigma_{fy}/\sigma_{Fy})}$$

where r_{xy} = correlation of family means between environments x and y, σ_{fx} and σ_{fy} = the square-roots of the family variance components in each environment, σ_{Fx} and σ_{Fy} = the square roots of the phenotypic variance of family means.

Percent genetic gains from correlated response to selection were calculated after back-transformation of log values, as before, except the overall mean used to estimate percent gain was the mean of the competitive environment in which trees are expected to be grown.

Results and discussion

Relative family performance in contrasting competitive environments

Results from the ANOVA over all three competitive treatments indicate that although differences between

Table 2. Family means and ranks for log e biomass (g) in three competitive environments

Family	Competitive environment					
	Mixture		Pure		Wide	
	Biomass	Rank	Biomass	Rank	Biomass	Rank
650	1.268	16	1.203	6	2.561	30
653	1.301	14	0.963	28	2.840	14
655	1.451	5	1.398	1	2.998	6
656	1.306	12	1.138	13	2.756	18
658	1.236	19	0.824	33	2.655	24
659	1.111	26	1.292	3	2.830	15
660	0.921	35	0.819	34	2.910	11
663	1.335	11	0.912	30	2.866	13
664	1.489	4	1.046	20	2.961	8
666	1.009	33	1.176	9	2.595	27
667	0.460	38	0.649	36	2.358	39
669	1.305	13	1.143	11	2.418	37
675	1.189	20	1.001	24	2.560	31
676	0.147	39	0.608	37	2.393	38
682	1.411	8	1.093	19	2.881	12
683	1.070	28	1.118	16	2.695	22
684	1.575	1	1.328	2	3.010	5
685	1.014	32	0.975	27	2.739	19
688	1.179	21	0.997	25	2.700	21
692	0.607	37	1.015	22	2.995	7
717	1.103	27	0.890	31	2.665	23
718	1.172	22	1.110	17	2.571	29
720	1.153	24	1.022	21	2.521	35
721	1.024	31	1.142	12	2.541	34
725	0.654	36	0.557	39	2.456	36
726	1.029	30	0.681	35	2.549	32
727	1.297	15	1.232	5	2.776	17
728	1.364	10	1.131	14	2.936	10
729	1.439	7	1.103	18	3.226	1
736	1.167	23	1.012	23	2.655	25
737	1.516	2	1.124	15	3.101	3
740	1.449	6	1.191	7	2.952	9
741	1.387	9	0.832	32	2.543	33
743	1.498	3	1.242	4	3.107	2
744	1.260	17	1.153	10	3.041	4
745	1.146	25	1.191	8	2.594	28
746	0.925	34	0.985	26	2.606	26
749	1.237	18	0.566	38	2.803	16
751	1.055	29	0.939	29	2.733	20
Overall	1.160		1.020		2.746	

Recently, some authors have expressed dissatisfaction with ANOVA as a tool for detecting genotype × environment interaction (Gauch 1985; 1988; Gregorius and Namkoong 1986). By combining the interaction information from all genotypes into a single value (the interaction sums of squares), much valuable information is lost with respect to the response of individual genotypes to changing environments (Gauch 1985). Interactions are of concern to breeders when true means of genotypes change rank between environments (Gregorius and Namkoong 1986; Baker 1988a). In the present study, family ranks based on estimated log biomass means often changed considerably between competitive environments (Table 2). Four families (650, 666, 692, 741) ranked in the top 25% in one competitive environment, while ranking in the bottom 25% in another. Many families, however, were quite stable across competitive environments (e.g., 655, 688, 725, 743). The rank correlation of family means between mixture and pure was $r = 0.52$, between pure and wide, $r = 0.39$, and between mixture and wide, $r = 0.63$. Unfortunately, statistical methods for the detection of true changes in rank are not well developed (Gregorius and Namkoong 1986; Baker 1988a). Baker (1988b) discusses methods to test for statistically significant changes in rank between two genotypes. Extending the analysis to all possible pairs of genotypes, however, runs into problems with respect to comparison-wise versus experiment-wise error rates.

Family variation in competitive ability and density tolerance

Families did not differ significantly in competitive ability ($P = 0.15$), density tolerance ($P = 0.36$), or competitive-density ability ($P = 0.053$), although competitive-density ability approached significance. These results provide additional evidence supporting the hypothesis that relative family performance is independent of competitive environment.

Selection of non-competitive genotypes has been suggested as a method to improve per unit area yields in forest trees (Cannell 1978), and breeding for a high tolerance to crowding has been suggested for corn improvement (Stringfield 1964). The non-significant family differences found in this study, however, indicate that selection and breeding for or against competitive ability, density tolerance, or combined competitive-density ability would be difficult. Studies of intergenotypic competition in forest trees have revealed differences in competitive ability when specific pairwise combinations of loblolly pine families (Adams et al. 1973; Tuskan and van Buijtenen 1986) and poplar clones (Tauer 1975; Adams 1980) have been examined. No studies, however, have shown significant family differences in general competitive ability (i.e., when competition with a large number of

families and between competitive environments were significant (defined as $P \leq 0.05$), the family × competitive environment interaction was not ($P = 0.07$; Table 1 A). Gauch (1988), however, presents an argument for using a higher significance level for the interaction term, for example, $P \leq 0.25$ when the significance level for the main effects is $P \leq 0.05$. Nevertheless, the interaction component of variance was small relative to the family component of variance ($\sigma_{fxe}^2 = 0.005$ versus $\sigma_f^2 = 0.034$). Thus, the ANOVA results suggest that relative family performance is independent of competitive environment.

families or clones is considered). Tuskan and van Buijtenen (1986) computed general competitive ability as the average response of a family over all pairwise mixtures involving that family. Of the five families examined, none were shown to have a general competitive ability significantly different from zero.

Results from previous studies are ambiguous with regards to the presence of genetic variation for density tolerance. Although none of these studies directly estimated density tolerance, many have looked at genetic response to density competition. Campbell and Wilson (1973) emphasized the role of scale effects in contributing to family × spacing interactions. They found a significant family × spacing interaction in three-year diameters of Douglas-fir, but the interaction become non-significant when a square-root transformation was used to correct for non-homogeneity of error variances. Campbell et al. (1986) found a significant family × spacing interaction in nine-year stem volume of Douglas-fir, but also attributed it to scale effects, and noted only minor rank changes of family means between spacings. Riitters (1985) was unable to detect family × spacing interactions in seedlings of Douglas-fir. Malavasi (1984) found a significant family × spacing interaction for log-transformed shoot weight in one-year-old western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), but not in Douglas-fir. Other studies have reported significant genotype × spacing interactions, but it is not clear whether the assumption of homogeneity of error variances was met in the ANOVAs (Panetsos 1980; Reighard et al. 1985). In considering the significance of the family × competitive environment interaction term, we found it necessary to use a transformation to correct for scale effects. The analyses of density tolerance and competitive-density ability was also sensitive to scale effects; if biomass was not log-transformed, the family differences became significant ($P < 0.001$).

Conclusions from studies using regression analyses have been equally ambiguous. While Wearstler (1979) found no family differences in response to increasing density in a nursery test of pure family blocks of loblolly pine, Stonecypher and McCullough (1981) did find significant differences between families in slopes for the regression of eight-year volume on density in a Nelder test of Douglas-fir. In a study of provenance variation in self-thinning trajectories, Schmidtling (1988) found that genetic variation exists with respect to the volume per area that provenances may sustain after self-thinning commences.

Variance structure, heritability, and estimated genetic gain

Competitive environment had a large effect on variance structure, which in turn led to large differences in heritabilities and estimated genetic gains. Using Bartlett's homogeneity test (Steel and Torrie 1980, p 471–472), estimated variances among families were found to be

Table 3. Estimated variance components, heritabilities, and genetic gains[a] for log e biomass in three competitive environments. Estimated genetic gains are for log-transformed biomass, but percent gains are after back-transformation of log e values

	Mixture	Pure	Wide
Variance component:			
Family	0.0602	0.0201	0.0298
Standard error (SE)	0.0178	0.0100	0.0111
Error	−0.0237	−0.0039	0.0118
SE	0.0150	0.0178	0.0141
Within plot	0.5425	0.5868	0.4130
SE	0.0286	0.0310	0.0220
Additive	0.1806	0.0603	0.0895
SE	0.0535	0.0300	0.0333
Phenotypic (Individual-tree basis)	0.6027	0.6069	0.4546
SE	0.0290	0.0275	0.0218
Phenotypic (Family-mean basis)	0.0827	0.0442	0.0490
SE	0.0177	0.0098	0.0110
Individual-tree heritability	0.300	0.099	0.197
SE	0.081	0.049	0.070
Family heritability	0.546	0.341	0.457
SE	0.047	0.098	0.071
Gain from individual-tree			
Selection (g)	0.233	0.077	0.133
Percent	26.2	8.0	14.3
Gain from family			
Selection (g)	0.314	0.144	0.202
Percent	36.9	15.5	22.4

[a] Intensity of selections equals 1.0

significantly heterogeneous among competitive environments ($\chi_2^2 = 11.98$, $P < 0.05$). The percent of the total phenotypic variation among individual trees explained by family was greatest in mixture (10.0%), least in pure family blocks (3.3%), and intermediate at the wide spacing (6.6%) (Table 3). The percent of the total phenotypic variation explained by within-plot differences was greater in pure blocks (96.7%) than in mixture (90.0%) and wide (90.8%). As hypothesized, interfamily competition appears to have magnified family differences, leading to increased family variance and greater estimates of heritability and genetic gain. Intrafamily competition, however, appears to have magnified within-family differences, leading to increased within-plot variances and reduced estimates of heritability and genetic gain. Williams et al. (1983) and Hart (1986) found a similar increase in family variances in progeny tests of loblolly pine when families grown in mixtures were compared to pure family blocks.

When compared to the case of no competition (the wide treatment), the presence of competition appears to have biased estimates of heritability either up or down, depending on whether competition is primarily inter-

family or intrafamily. Which estimate of heritability is appropriate to use for estimating genetic gains, however, depends on the anticipated competitive environment in which improved stock will be grown (mixture versus pure family blocks) (Foster 1989) and the proportion of the time until harvest that trees will be in competition (dependent upon spacing and thinning practices). In addition, estimates of heritability in mixtures may not be entirely appropriate for estimating subsequent gains in mixtures since the composition of the mixture used to estimate heritability will not be the same as that in which selections are grown (Foster 1989).

Concern among tree breeders over the appropriate age for selection has given rise to considerable interest in the importance of age and stand development on variance structure and heritability (Franklin 1979; Lambeth et al. 1983; Foster 1986; Cotterill and Dean 1988). Franklin (1979) proposed a hypothetical model in which stand development was divided into three phases. In the juvenile genotypic phase, additive genetic variance (and family variance) is low, while heritability starts out high and decreases to a low value as trees come into competition. In the mature genotypic phase, additive genetic variance increases steadily, with heritability increasing rapidly at first, then leveling off. The transition between these two phases occurs at the onset of competition. In the third phase, the codominance-suppression phase, both additive genetic variance and heritability decrease as a result of slower growing families catching up to the faster growing families.

The results from the present study indicate that the effect of the onset of competition on variance structure and heritability may depend on the genetic composition of neighbors. If competition is primarily among like genotypes, heritability could, in fact, decrease, rather than increase, after the transition into the mature genotypic phase. Wearstler (1979), using pure family blocks of loblolly pine seedlings, found a declining heritability for height and diameter after the commencement of intrafamily competition, and family differences which were initially statistically significant became non-significant. Foster (1986) found a temporary decrease in heritability for height and diameter after the onset of competition in a loblolly pine progeny test using large pure family blocks. In general, time trend patterns of variances and heritability are not consistent among studies (Franklin 1979; Lambeth et al. 1983; Foster 1986; Tuskan and van Buijtenen 1986; Cotterill and Dean 1988). Some of the inconsistency may be explained by differences in the degree of intergenotypic versus intragenotypic competition. Differences in thinning regimes may be another important factor (Matheson and Raymond 1983). In addition, shifting demand from above-ground to below-ground resources as stands develop may be important to explaining time trend patterns (Namkoong and Conkle 1976).

Table 4. Expected genetic gains[a] in log e biomass (g) of two-year-old seedlings grown in competitive environment y, when individuals or families are selected based on performance in competitive environment x. Percent gains are given in parentheses, and are after back-transformation of log e biomass

		Testing environment x		
		Mixture	Pure	Wide
(A) Gains from individual-tree (mass) selection				
Planting environ- ment y	Mixture	0.233 (26.2)	0.134 (14.3)	0.169 (18.4)
	Pure	0.134 (14.3)	0.077 (8.0)	0.093 (9.9)
	Wide	0.147 (15.8)	0.084 (8.8)	0.133 (14.3)
(B) Gains from family selection				
Planting environ- ment	Mixture	0.314 (36.6)	0.248 (28.1)	0.258 (29.4)
	Pure	0.181 (19.8)	0.144 (15.5)	0.148 (16.0)
	Wide	0.198 (21.9)	0.156 (16.9)	0.202 (22.4)

[a] Intensity of selections equals 1.0

Selection strategies considering competitive environments

Establishment of genetic tests involves decisions of spacing, age at which to select, and experimental design, including whether families are grown in complete mixtures (single-tree or non-contiguous plots), partial mixtures (row plots), or pure stands (large single family plots). Determination of the correlated response to selection in one competitive environment for growth in another competitive environment can shed light on the implications of these decisions.

Estimates of genetic correlations betwen log biomass measured in different competitive environments were very high: $r_A = 0.90$ between mixture and wide, $r_A = 0.89$ between pure and wide, and $r_A = 1.06$ between mixture and pure. Thus, log biomass appears to be under the control of essentially the same set of genes in all three competitive environments. Estimates of correlated response show that selection after testing in mixture would give the greatest expected genetic gains regardless of whether the progeny of selected parents are to be grown in mixture or pure stands (Table 4). In addition, selection of parents whose progenies are to be grown at wide spacing can be done about as effectively when tested in mixture as when tested at wide spacing. Testing in pure stands, however, is expected to result in the lowest gains, irrespective of the planting environment. The superiority of mixtures for genetic testing is the result of the much greater heritability of log biomass in mixture, as well as the large positive genetic correlations between log biomass in mixture and this trait in the other two competitive environments. As pointed out earlier, estimates of heritability in mixture may not be accurate if the mixture of families used to estimate heritability differs markedly from the mixture resulting from the selected parents. If, after selection, the genetic composition of the

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mixture is substantially more uniform than in the test environment (i.e., genotypes in the mixture are more uniform in characteristics that influence competition), heritability estimates may be biased upwards, as well as estimates of genetic gains expected from testing and selection in mixture.

In addition to the question of the appropriate competitive environment for selection and testing, tree breeders are also concerned with the question of how to deploy improved genotypes. Should families or clones be deployed in mixtures or in mosaics of pure blocks? Higher yields, increased phenotypic stability, and a reduced risk of destruction from diseases, insects, and climatic factors are the main hypothesized advantages of heterogeneous stands (Trenbath 1974; Hühn 1985). Although we are unable to address the questions of phenotypic stability and risk, log biomass yield in this study was 16% greater when families were grown in mixture than their average yield when grown in pure blocks ($P<0.001$). Height, diameter, and stem volume were also significantly greater ($P<0.001$) in mixture than in pure blocks – 9% greater in height, 9% greater in diameter, and 24% greater in volume. One might hypothesize that neighboring, like genotypes in pure stands are competing for the same resources in the same space to a greater extent than neighboring, unlike genotypes in mixtures. As a result, available resources are less for families in pure stands, and mutual suppression occurs.

Few studies have reported on the question of yield in mixture versus pure stands in forest trees. Most genetic tests use either mixtures (single-tree or row plots) or pure family blocks, but not both together in a replicated design. Hart (1986) found that for height, diameter, and volume at age eleven, the mean of eight loblolly pine families in mixture was not significantly different from the overall mean of the same eight families grown in pure blocks. Williams et al. (1983) obtained results opposite to ours – in a yield trial of loblolly pine families, four-year height was 3% greater and volume was 9% greater for the mean of 16 families grown in pure blocks than when grown in mixture. They point out, however, that their results are preliminary in that competition had not been strong up to that age. Much research has been done in agriculture comparing the yield of mixtures and monocultures. In a review of the literature, Trenbath (1974) found that, in general, mixtures tend to yield better than the average of the components of the mixtures in monoculture.

biomass measured in the different environments were always strong. Thus, regardless of the intended competitive regime of the planting environment, selection efficiency was greatest in the competitive environment in which the inherent differential growth rates among families were best expressed. This occurred when families were grown in mixture at close spacing. This is an encouraging result for tree breeders, since the prevailing mode of genetic testing in tree improvement programs is family mixtures, although final evaluations may occur at young ages before substantial competition occurs. Tree breeders might consider establishing tests at closer spacings to encourage early competition. Despite the low efficiency of selection in pure stands, they remain the only option for evaluation of families for unit area yields.

We compared only two extremes of intergenotypic competition – competition among a set of diverse genotypes (open-pollinated families) and competition among genotypes within families. Further research is necessary to extend the inference of this study to less diverse mixtures, such as might occur after several generations of selection and breeding, and to more homogeneous pure stands such as pure blocks of full-sib families or clones. Furthermore, this study considered only the effect of competitive environment on seedling growth. Maturation effects, such as the onset of flowering, might affect competition among older trees. Further research is necessary to evaluate effects due to maturation, and to distinguish those effects from effects due to increasing interaction among plants, i.e., stand development.

The seedlings in this study were well watered and fertilized, and thus, competition was assumed to be primarily for light. In a study of genetic variation in height growth of ponderosa pine over 29 years, Namkoong and Conkle (1976) attributed late changes in rank among families to family differences in partitioning between root and shoot. They hypothesized that early in the life of the stand, those families with better crown position were favored, whereas later, those families with large root systems were favored. Further research is necessary to evaluate the effect of competitive environment on family performance when competition is primarily for resources other than light, and to evaluate the effect of shifting demands for different resources.

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Conclusions

Although relative rankings of families for log biomass appeared to differ somewhat in the three competitive environments, estimated genetic correlations between log

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