AN ABSTRACT OF THE THESIS OF

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<u>Two-Year Performance of Open-Pollinated Douglas-Fir Families</u>

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Ungerminated seed and recent germinants from 39 open-pollinated Douglas-fir (Pseudotsuga menziesii var. menziesii (Mirb.) Franco) families were planted in each of three competitive environments in order to determine the degree to which growth differences among families are influenced by competitive environment, seed weight, and date of emergence. The three competitive environments were a mixture of individuals from all families planted at a narrow spacing (4x4 cms), single (pure) family blocks planted at a narrow spacing (4x4 cms), and individuals from all families planted at a wide, non-competitive spacing (16x16 cms). Despite some large changes in the relative ranking of families between competitive environments for total dry weight, the family x competitive environment interaction was nonsignificant (p<0.05). Furthermore, families did not differ significantly in competitive ability or density tolerance. Competitive environment, however, had a large effect on estimates of variance components, heritability, and genetic gain. Analysis of correlated

response to selection indicated that testing and selection in mixture would result in the largest estimated gains in seedling dry weight, irrespective of the competitive environment anticipated for outplanting.

Families differed significantly in seed weight, total percent emergence, and rate of emergence. Nevertheless, correlations between seed weight and rate of emergence, seed weight and seedling size, and rate of emergence and seedling size were not strong. The magnitude of the correlation between seed weight and seedling size of families was no less when germinants were used than when ungerminated seed was used. Thus, using germinants did not appear to be useful for controlling seed weight effects in this study. In addition the magnitude of the correlation between seed weight and seedling size was not influenced by interfamily competition.

Genetic variation in seedling architecture (the form and structure of a seedling's crown, stem, and root system, as well as the proportion of total biomass partitioned to each) was assessed in order to explore the potential for realizing gains from ideotype breeding. Families differed significantly for all traits and estimates of heritability were mostly moderate (ranging from $h^2=0.07$ to 0.49). Relative family performance for traits of seedling architecture was dependent upon the density at which families were grown for all traits except crown width relative to height, but intergenotypic competition did not affect relative family performance. Phenotypic relationships among traits of seedling architecture and seedling size were generally consistent across competitive environments, but genetic relationships did depend to some extent on competitive environment. These results using seedlings indicate that the potential exists to realize gains from ideotype breeding. However, relative family performance for seedling architecture traits may depend upon the density at which families are grown. Correlated responses to selection as determined by genetic correlations between traits may also depend upon competitive environment. EFFECTS OF SEED CHARACTERS AND COMPETITIVE ENVIRONMENT ON TWO-YEAR PERFORMANCE OF OPEN-POLLINATED DOUGLAS-FIR FAMILIES

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TABLE OF CONTENTS

CHAPTER I. GENERAL INTRODUCTION

CHAPTER II. EFFECT OF COMPETITIVE ENVIRONMENT ON RELATIVE FAMILY PERFORMANCE AND VARIANCE STRUCTURE IN A NURSERY TEST OF OPEN-POLLINATED DOUGLAS-FIR FAMILIES	5
Abstract Introduction Literature Review Materials and Experimental Design Measurements and Statistical Analyses Results and Discussion Conclusions	5 7 10 20 24 31 43
CHAPTER III. EFFECTS OF SEED WEIGHT AND RATE OF EMERGENCE ON EARLY GROWTH OF OPEN-POLLINATED DOUGLAS-FIR FAMILIES	54
Abstract	54
Introduction	55
Materials and Methods	59
Results and Discussion	64
Conclusions	73
CHAPTER IV. GENETIC VARIATION IN SEEDLING ARCHITECTURE OF TWO-	70
YEAR-OLD DOUGLAS-FIR GROWN IN THREE COMPETITIVE ENVIRONMENTS	79
Abstract	79
Introduction	81
Materials and Methods	86
Results and Discussion	91
Conclusions	105
CHAPTER V. GENERAL CONCLUSIONS	115

LITERATURE CITED

APPENDIX

129

120

LIST OF TABLES

<u>Table</u>	<u>Cable</u>					
Chapter	II					
II.1.	Form of the analyses of variance.	47				
II.2.	Analyses of variance for log biomass.	48				
II.3.	Family means and ranks for log biomass in three competitive environments. 49					
II.4.	Analyses of variance for family differences in competitive ability, density tolerance, and competitive-density ability.	50				
II.5.	Estimated variance components, heritabilities, and estimate genetic gains in three competitive environments.	ed 51				
II.6.	Expected genetic gains in log-transformed biomass when progeny of parent trees are tested in competitive environme x, but are intended for planting in competitive environment y.	ent 52				
11.7.	Efficiency of selection when progeny are tested at competitive environment x, but intended for planting in competitive environment y.	53				
Chapter III						
III <i>.</i> 1	Family variation in seed weight, emergence, and germination.	75				
III.2 <i>.</i>	Correlations between family means for seed weight and seedling size, and rate of emergence and seedling size, within each competitive environment and planting type.	76				
III.3.	Partitioned chi-square test of homogeneity of correlation coefficients among six combinations of planting types and competitive environment treatments.	77				
III.4.	Estimated family heritabilities and expected gains from parental selection based on progeny performance, before and after adjusting for seed weight.	78				
Chapter	IV					
IV.1.	Forms of the analyses of variance when data for individual					

competitive environments are analyzed, and when pairs of competitive environments are analyzed.

IV.2.	Means, statistical significance of differences among families, and estimated individual-tree heritabilities for size and seedling architecture traits in three competitive environments.	109
IV.3.	Correlations of family means between pairs of competitive environments for seedling architecture traits.	110
IV.4.	F-values for family x competitive environment interaction mean squares, and their probabilities, for seedling architecture traits when competitive environments are analyzed in pairs.	111
IV.5.	Estimated phenotypic and genotypic correlations among size and seedling architecture traits in three competitive environments.	112
Appendix		
A.1.	Analyses of variance using other variables as measures of performance.	130
A.2.	Analyses of variance for log biomass including planting type.	136
A.3.	Analyses of variance within each competitive environment for total dry weight.	138
A.4.	Variance components, heritabilities, and estimated genetic gains in three competitive environments for total dry weight.	139
A.5.	Analyses of covariance for log biomass using first-year height as the covariate.	140
A.6.	Analyses of variance in which log biomass is adjusted for family differences in seed weight by regressing mean log biomass on mean seed weight, and then using predicted valu subtracted from observed values from the regression in the analysis of variance.	les 141
A.7.	Analyses of variance to test interaction of families between pairs of competitive environments.	142
A.8.	Family values for competitive ability, density tolerance, and competitive-density ability.	143
A.9.	Correlations between family values for competitive ability density tolerance, and competitive-density ability.	, 144
A.10.	Overall means for mix, pure, and wide competitive environments for several measures of performance, and percent differences between measures of performance for mix and pure competitive environments.	145

A.ll Means and statistical significance of means between three competitive environments for seedling architecture traits.

EFFECTS OF SEED CHARACTERS AND COMPETITIVE ENVIRONMENT ON TWO-YEAR PERFORMANCE OF OPEN-POLLINATED DOUGLAS-FIR FAMILIES

CHAPTER I

GENERAL INTRODUCTION

The overall objective of this study is to determine the degree to which growth differences among families of two-year-old Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) are influenced by competitive environment, seed weight, and rate of emergence. Three competitive environments are considered: (1) a mixture of all families planted at a narrow spacing, (2) single (pure) family blocks planted at a narrow spacing, and (3) individuals from all families planted at a wide, non-competitive spacing. The narrow spacing was 4x4 cms, and the wide spacing was 16x16 cms. These three competitive environments represent the extremes of the two types of competition - competition due to the proximity of neighbors, referred to as density competition, and competition due to the presence of unlike genotypes, referred to as intergenotypic competition.

The study has been divided into three parts corresponding to the three chapters which follow. In Chapter II, the effect of competitive environment on relative family performance and estimation of genetic parameters is considered. It is hypothesized that relative family performance as measured by total dry weight of seedlings is not consistent in different competitive environments. Large differences in relative performance when families grown in mixture versus pure stands would indicate family variation in intergenotypic competitive ability, while large differences between performance at a wide, non-competitive spacing and a narrow spacing in pure stands would indicate family variation in density tolerance. It is also hypothesized that competitive environment will affect the magnitude of differences between families, such that the family variance component will be increased by interfamily competition in mixtures, while the within-plot component of variance will be increased by intrafamily competition in pure stands. Consequently, estimates of heritability and genetic gain should be greatest in mixed plantings at narrow spacing, least in pure family blocks at narrow spacing, and intermediate at wide spacing. The implications of competitive environment on selection strategies are explored by estimating the effect of testing and selection in one competitive environment on correlated response when progeny of selected parents are grown in another competitive environment.

In Chapter III, the effect of seed weight and rate of emergence on early growth of Douglas-fir families is investigated. It is hypothesized that families with heavier seed will emerge faster and produce larger seedlings. In addition the influences of interfamily competition, and of using ungerminated versus germinated seed, on the relationships among seed weight, seedling emergence, and seedling size are explored. Interfamily competition is expected to magnify early growth differences among families that are due to seed weight differences, and using germinants is expected to reduce seed effects on early seedling size.

In Chapter IV, genetic variation in traits of seedling

architecture is investigated. Seedling architecture refers to the form and structure of a tree's crown, stem, and root system, and the relative proportions of total biomass that make up the different components of tree structure (i.e., biomass partitioning). Assessment of genetic variation in seedling architecture is useful for evaluating the potential for progress from ideotype breeding. Ideotype breeding implies identification and selection of traits that may be important for increasing product value, and may be most useful when traits included as part of the ideotype are traits thought to enhance unit area yields, but not necessarily individual tree yield (e.g., narrow crowns). Seedling architecture traits considered in this study include crown form traits and biomass partitioning. In this chapter, I also consider the phenotypic and genetic relations among traits of seedling architecture, and the degree to which seedling architecture depends on the competitive environment in which trees are grown.

Results from these studies have implications both for the management of improved families in nurseries and tree improvement strategies. When families are grown in mixtures at close spacing, as is commonly done in nurseries, seed effects and interfamily competition may lead to increased differences among families in the numbers and size of seedlings. Families with small seed growing in mixed-family blocks may be much smaller at the time of lifting, and be differentially culled from outplanting mixtures, an undesirable consequence if seed weight and early growth are not associated with subsequent performance in the field, or if the genetic diversity of seedling mixtures is greatly reduced. If seed effects or interfamily competition do lead to increased differential growth of families, nursery managers might consider growing families separately in the nursery. Growing families in pure blocks in the nursery would reduce interfamily competitive effects, and would allow greater control of the composition of outplanting mixtures.

Seed effects and interfamily competition may also have important consequences for genetic testing. The validity of inference on family performance based on seedling studies to performance of families in older stands may depend in part upon the influence of competitive environment and seed effects. Assessment of the degree to which competitive environment and seed effects influence the outcome of seedling studies may be useful in designing more effective early genetic tests. Furthermore, if one assumes that seedling studies are a useful model for investigating competitive effects in older stands, results from these studies may be helpful for evaluating the influences of competitive regime on genetic testing in the field. Finally, evaluation of seedling architecture, and the influence of competitive environment on seedling architecture, may be important as a first step in assessing the potential for ideotype breeding to improve forest productivity in Douglas-fir.

CHAPTER II

EFFECT OF COMPETITIVE ENVIRONMENT ON RELATIVE FAMILY PERFORMANCE AND VARIANCE STRUCTURE IN A NURSERY TEST OF OPEN-POLLINATED DOUGLAS-FIR FAMILIES

ABSTRACT

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 environments included a mixture of individuals from all families planted at close spacing, single (pure) family blocks planted at close spacing, and 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 x competitive environment interaction was nonsignificant. 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 wide competitive environment.

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 proximity of neighbors. Competition due to the presence of unlike genotypes is referred to as intergenotypic competition, whereas competition due to the proximity of neighbors is referred to as density competition. When the family is the genetic entity of interest, three competitive environments may be identified that encompass these two types of competition: (1) a mixture of individuals from all families planted at a close spacing, (2) single (pure) family blocks planted at a close spacing, and (3) individuals from all families planted at a wide, non-competitive spacing. Competitive ability is defined as the performance of a family in mixture relative to its performance in pure blocks, and density tolerance is defined as the performance of a family at a narrow spacing in pure blocks relative to its performance at a wide, non-competitive spacing. Thus, a family of high competitive ability does relatively better under competition from neighbors of different genotypes when compared to performance in pure stands, and a family of high density tolerance is least affected by proximity of neighbors when grown in pure stands. Performance is here defined as total dry weight of seedlings, a measure of an individual's ability to capture and utilize

resources.

The effect of intraspecies competition on genetic evaluation of forest trees has been studied relatively little. Competitive environment may influence both the relative performance of genotypes, and the degree to which genotypes differ. 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. To accomplish these objectives, seed and germinants of 39 open-pollinated Douglas-fir (Pseudotsuga menziesii var. menziesii (Mirb.) Franco) families were planted in the three contrasting competitive environments - in mixture at close spacing, in pure family blocks at close spacing, and at a wide, non-competitive spacing. Trees were harvested after two years in the nursery, and dry weights, heights, and diameters were recorded.

Results from this study have implications both for the management of improved families in nurseries and tree improvement strategies. Interfamily competition may lead to increased differences between families in seedling size as better families suppress poorer families. As a result, culling at the time of lifting may lead to representations of families in mixtures much different than intended at the time of sowing. If interfamily competition does lead to increased differential growth of families, nursery managers might consider growing families

separately in the nursery in order to exercise control over the composition of outplanting mixtures. Competitive effects may also be important in genetic testing. The correlation between juvenile and mature performance may depend in part on planting density, as well as whether competition is primarily interfamily or intrafamily. Thus, competitive interactions may be important to consider when developing an early testing strategy. Furthermore, if one assumes that seedling studies are a useful model for investigating competitive effects in older stands, results from this study may be helpful for evaluating the influence of competitive regime on genetic testing in the field.

LITERATURE REVIEW

Studies of intergenotypic competition manipulate the number and proportion of competing genetic types (species, varieties, families, or clones) in plantings. Two common experimental designs are the replacement series and the diallel experiment. In replacement series, two genetic types are grown in mixed plantings, where the proportion of one type ranges from zero to 100 percent and overall density is maintained at a constant level (de Wit 1960; Harper 1977; Radosevich 1987). Replacement series studies, however, become extremely large when many genotypes are compared, or when comparisons are extended beyond pairwise mixtures. Diallel experiments involve growing individuals of two genetic entities in pure stands and in mixed stands of usually a single, equal proportion, while maintaining overall density constant (Radosevich 1987). Because a wide range of proportions are not considered, diallel experiments involve less plantings, and thus, make it more feasible to study a greater number of genetic entities. Diallel experiments are still cumbersome, however, when comparisons beyond pairwise mixtures are included. A more useful design for studies of intergenotypic competition involving a large number of genotypes is to grow all genotypes together in a single mixture, and separately in pure stands. The advantage of the replacement series and diallel experiment is that they allow investigation of specific competitive effects between two genotypes, while the advantage of the latter design is that it provides a means of estimating the general (average) competitive ability of genotypes, and

allows investigation of a greater number of genotypes.

Intergenotypic competition, the interaction among individuals of unlike genotypes, has been studied extensively in short-lived, selfpollinating cultivars of field crops (reviewed by Trenbath 1974, 1976; Adams 1980). Forest trees offer an opportunity to study competition among families or clones of long-lived, outcrossing species. Intergenotypic competition in forest trees, however, has been studied relatively little.

Replacement series and competition diallels have been used to study interactions among seedlings or young plants of loblolly pine families (Adams et al. 1973; Tuskan and Van Buijtenen 1986) and poplar clones (Tauer 1975; Adams 1980). In these studies, significant competitive effects were detected for specific combinations of families or clones, and some of these combinations were overcompensatory, i.e., yields in mixtures exceeded the mean of the components in pure stands. Identification of specific competitive interactions may be useful for increasing yield by planting overcompensatory pairs of genotypes, but outplanting mixtures are more likely to involve many genotypes. Assessment of genetic variation for general competitive ability, the average performance of a genotype when in mixture with several genotypes compared to its pure stand performance, may be useful for evaluating selection for non-competitive genotypes in tree improvement programs. Non-competitive genotypes are thought to lead to increased per unit area yields (Cannell 1978).

Studies of density competition look at the effect of plant density or spacing on growth or reproduction. The effect of density on growth

and mortality within a species forms the basis of such well known maxims as the law of constant final yield, the reciprocal yield law, and the -3/2 power rule of self-thinning (Harper 1977). Genetic variation in response to density, however, has received little attention. Relative ranking of genotypes of agricultural species have been found to differ when plants are grown at very wide and very narrow spacings (reviewed by Campbell and Wilson 1973; Cannell 1978). Results from studies of forest trees are ambiguous. Two general approaches have been used to study genetic variation in density response in forest trees - analyses of variance which consider the statistical significance of the family x spacing interaction, and regression analyses to test for differential response of families to increasing density.

One of the primary assumptions of the analysis of variance is homogeneity of error variance (Steel and Torrie 1980, p. 161). Nonhomogeneity of error variance is likely to be a problem when treatments result in large differences in scale. Campbell and Wilson (1973) emphasized the role of scale effects in contributing to family x spacing interactions. They found a significant family x spacing interaction in three-year diameter growth of Douglas-fir, but the interaction became 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 x spacing interaction in nineyear stem volume of Douglas-fir, but also attributed it to scale effects, and noted only minor rank changes of families between spacings. Malavasi (1984) found a significant family x density interaction for log-transformed shoot weight in one-year-old western hemlock, but not in Douglas-fir. Riitters (1985) also was unable to detect family x density interactions in seedlings of Douglas-fir. In other studies, significant genotype x spacing interactions have been reported in forest trees, but it is not clear whether the assumption of homogeneity of error variances was met in the analyses of variance (Panetsos 1980; Reighard et al. 1985).

Conclusions from studies using regression analyses have been equally ambiguous. While Wearstler (1980) 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. An approach that is similar to the regression approach is consideration of the magnitude of family rank correlations between performance in very wide and very narrow spacings. Cannell (1982) found poor rank correlations between ten families and two provenances grown at a wide, non-competitive spacing versus a narrow spacing, and concluded that progenies may be ranked very differently when evaluated at the different spacings.

The inconsistent conclusions from genetic studies of density response may be due to several factors. First, density effects may have been confounded with effects due to intergenotypic competition. Pure stands were not used in some studies, and family responses may have been partially a response to increasing intergenotypic competition. Second, the outcome of studies might depend upon the

actual range of densities or spacings used. The interaction of families with spacing may be minor over a small range of densities, but more pronounced between very wide and very narrow spacings. Third, a significant interaction may be due to scale effects; the assumption of homogeneity of error variances should be tested. Fourth, the response of families to spacing depends on the specific trait considered. Diameter, for example, is much more responsive to increasing density than height (Sakai et al. 1968; Stonecypher and McCullough 1981). Finally, the results might depend on the experimental and analytical techniques used. Results from studies using analysis of variance may differ from studies using regression analysis or correlations. The statistical precision and power should also be considered.

Another type of study that has been used to investigate both intergenotypic competition and density competition is the neighborhood experiment. In neighborhood studies, the performance of an individual plant is recorded as a function of the number, distance, spatial arrangement, and size of its neighbors (Radosevich 1987). Neighborhood procedures have been used extensively on a phenotypic level in forestry to develop competition indices for growth and yield studies (Bella 1971; Daniels et al. 1986). In genetic studies, Sakai et al. (1968) and Hühn (1970) used correlations between neighboring trees to investigate genetic components of competition. Weyerhaeuser Company developed a neighborhood procedure using regression analysis to use in the selection of parents for their first generation tree improvement program (personal communication, R.K. Campbell). Recently, neighborhood procedures have been developed to adjust for bias due to competition in

genetic tests (Cooper and Ferguson 1977; Tuskan and McKinley 1984; Land and Nance 1987; Magnussen and Yeatman 1987).

In characterizing genetic variation in competitive response, the term "competitive ability" has been used both in intergenotypic competition studies and density studies, and its use in both types of studies leads to confusion. Here, competitive ability of a genotype is defined as the ability to obtain resources in the presence of unlike genotypes. Competitive ability is measured either by the difference between growth of a family in mixture and in pure stands (Sakai 1961), or by the regression of growth on the proportion of unlike neighboring genotypes when density is held constant (Schutz and Brim 1967). I suggest the term "density tolerance" to indicate the response of a genotype to increasing stand density in the absence of intergenotypic competition. Density tolerance may be measured either by the difference between growth of a family at wide spacing versus narrow spacing, or by the regression of growth on density in pure stands. Density tolerance measures the response of a genotype to increasingly limited space when available resources per unit area remain constant. A genotype of high density tolerance is more efficient at resource extraction, whereas a genotype of high competitive ability is better able to exploit resources from neighboring, unlike genotypes.

Donald and Hamblin (1976) identified three competitive environments which are useful to consider in plant breeding. An "isolation environment" is an environment in which plants grow at a wide, non-competitive spacing. A "competition environment" is one in which plants grow within a dense mixed community. A "crop environment" is one in which plants grow in a dense monoculture. In forest trees, true monocultures in an agricultural sense are rarely achieved, except in rare clonal plantations. But "pure" plantings of families or species may be considered monocultures for the purpose of studying competition in tree species. In that case, "crop environment" is somewhat of a misnomer for forestry, since forest tree crops are most often grown as a mixture of genotypes, not monocultures. Still the concept of three competitive environments is useful. These three competition, 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).

The competitive environment concept is closely related to the plant ideotype concept. An ideotype is "a biological model which is expected to perform or behave in a predictable manner within a defined environment" (Donald 1968). Ideotypes are most often identified to correspond to specific competitive environments. An isolation ideotype is a model plant that is expected to perform well when grown in isolation. A competition ideotype is a model plant that is expected to perform well when in mixtures of genotypes. 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). Forest tree crop ideotypes are most often characterized by 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). Crop ideotypes make the most efficient use of resources per unit area, but are weak competitors since they do not exploit resources from neighbors. A 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 over an unlimited space (in the absence of competition), or gains them from a competing neighbor, 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 x competitive environment interaction is present, and correlations would be less than one between performance in different competitive environments. Furthermore, differences in relative family performance between competitive environments would lead to the expectation that families differ in competitive ability and density tolerance. Family differences in competitive ability and density tolerance could be exploited in breeding programs to develop trees that are more or less aggressive at

exploiting resources, or more efficient at using available growing space.

The competitive environment in which families are grown may also 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 intragenotypic competition, interactions between members of the same family would magnify any within-family differences, leading to an increase in within-family variance. Increased within-family variance would be reflected by increased within-plot variance since these two sources of variation are confounded. The implications are that interfamily competition would result in greater estimates of heritability, and 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 estimates of genetic parameters and the relative ranking of parental genotypes, 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 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).

MATERIALS AND EXPERIMENTAL DESIGN

Open-pollinated seed was collected in the fall of 1985 from 39 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). Elevations of parent trees ranged between 500 and 1500 feet.

In February, 1986, seeds were treated with a fungicide and soaked in tapwater for 24 hours at room temperature prior to stratification by storage at 3-4°C for eight 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 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 4x4 cms, and was chosen to be as narrow as possible without incurring much density-related mortality by the end of two growing seasons. The wide spacing was 16x16 cms, and was chosen to be as narrow as possible without incurring 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-

emerged germinants. Planting-type treatments (subplots) were randomly assigned within each competitive environment (Figure II.1). The third factor was the 39 open-pollinated families. Each family was represented by four trees in each subplot. The four trees per family in the pure blocks formed the center of a 16-tree pure family stand (Figure II.1). The four trees per family in the mix and wide treatments were randomly assigned to positions within the subplots (i.e., non-contiguous plots). Five replications were planted in all, with each replication occupying a different raised bed.

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 planting germinants were germinated on moistened filter paper in petri dishes at a day/night temperature of $30/20^{\circ}$ C, with a 12-hour photoperiod. Germination was recorded for each family (defined as when the radical had just penetrated the seed coat), and germinants stored at $3-4^{\circ}$ C to slow elongation of the radical until enough germinants were available to begin planting a replication (stored from one to thirteen days with most germinants stored for about seven 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.

Emergence (i.e., epicotyl penetration through the surface of the soil) from seeds of both planting types was recorded every three days. Some newly-emerged seedlings experienced damping off, and many seedlings were lost in May in two replications 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 subplots 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 percent in mixtures, 5 percent in pure blocks), and the surrounding seedlings quickly occupied the open space. During the second year, a few additional trees died (4 percent in mixture, 2 percent in pure, 1 percent in wide). Much of the secondyear mortality in mixtures, and some in pure blocks, appeared to be density-related.

During the two growing seasons, seedlings were well watered and fertilized regularly, so that little, if any, competition was likely to have occurred among roots. Thus, competition may be assumed to have been primarily for light. Competition at the narrow 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). Biological yield is an integrated measure of the success of a plant at capturing resources. Biological yield was measured as the total dry weight of a seedling (referred to as biomass), and results reported in subsequent sections are concerned primarily with this measure of performance. As an alternative measure of biological yield, I also recorded 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 biases the results in any way. Another measure of performance is economic yield, or yield of that portion of the plant that is of economic value. In forest trees, economic yield is most often the weight or volume of the stem. When selecting genotypes in tree improvement programs, however, height, diameter, or stem volume estimated from height and diameter measurements, are often used to select for economic yield. In this study, four different measures of economic yield were considered: stem weight, height, diameter, and stem volume (where volume was approximated by height x (diameter)²).

Preliminary analyses indicated results using shoot dry weight, stem dry weight, stem volume, and diameter were similar to results using total dry weight (see Appendix Table A.1) (alternative traits

were highly correlated with total dry weight - r>0.77). The only notable exception was two-year height. While in all the other traits mean values were greatest in the non-competitive environment, mean height was unaffected by competition. In addition, the family x competitive environment interaction was significant for height. Thus, assessment of relative family performance for height was dependent upon the competitive environment in which seedlings were grown.

Further preliminary analyses of variance were carried out for each competitive environment separately, and for all three combined into a single analysis, using the three full replications left after mortality and transplanting (see Appendix Table A.2). In no case was the family x planting type interaction significant, so for purposes of the competition analyses, planting type was ignored, leaving a total of seven replications for each competitive treatment (four seed-planted replications and three germinant-planted replications). The analyses then took two forms. First, an overall analysis of all competitive treatments together (Table II.1A) was done to test for mean differences between competitive environments and for family x competitive environment interaction. Next, in order to estimate genetic parameters for seedlings grown in each competitive environment, analyses of variance were carried out separately for each competitive treatment (Table II.1B). All analyses were done with the GLM procedure of SAS using Type III sums of squares (SAS 1987). Type III sums of squares are adjusted for imbalance in the number of observations per plot. Observations for biomass, diameter, and volume were log-transformed to correct for non-homogeneity of error variances. Scale effects before

log-transformation were particularly large between the narrow and wide treatments in the combined analysis, but error variances were also heterogeneous over families for analyses done for each competitive environment separately (see Appendix Tables A.3 and A.4 for a comparison of results based on non-log-transformed biomass).

Analyses of covariance were done using seed weight and first-year height as covariates in order to adjust for the potential influence of maternal effects due to differential seed size or condition (see Appendix Tables A.5 and A.6). Results from adjusted analyses were similar to the analyses of variance of unadjusted values, and are therefore not presented. Other analyses indicate that the relationship between seed weight and two-year dry weight of seedlings is not strong (see Chapter III).

The effect of competitive environment on relative family performance (objective 1) was evaluated by consideration of the statistical significance of the family x competitive environment interaction in the combined analysis of variance 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, 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 intergenotypic competition and density, called 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 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. Calculation of competitive abilities, density tolerances, and competitive-density abilities for each family in each replication made it possible to subject each measure to analysis of variance so that the statistical significance of family differences for these traits could be tested (objective 2).

Variance components for log biomass were determined within each competitive treatment to evaluate the effect of competitive environment on estimates of genetic parameters (objective 3). For each analysis of variance done separately for each competitive treatment, variance components were estimated by equating the expected mean squares with the observed mean squares and solving the resulting equations (Table II.1B). The expected means squares as shown in Table II.1 are not strictly correct when imbalance exists with respect to the number of observations within plots. Plot sizes in this study, however, were approximately balanced, and alternative procedures for estimating variance components differed little from those presented. Standard errors for variance components were estimated as in Becker (1984, p. 47). Individual-tree heritabilities were estimated as:

$$h_{I}^{2} = \frac{\sigma_{A}^{2}}{\sigma_{P}^{2}}$$
(1)
where σ_A^2 = additive genetic variance,

$$\begin{split} \sigma_{\rm P}^2 &= \sigma_{\rm W}^2 + \sigma_{\rm e}^2 + \sigma_{\rm f}^2 = {\rm phenotypic \ variance \ of \ individual \ trees,} \\ \sigma_{\rm f}^2 &= {\rm family \ component \ of \ variance,} \\ \sigma_{\rm e}^2 &= {\rm error \ component \ of \ variance,} \\ \sigma_{\rm W}^2 &= {\rm within-plot \ component \ of \ variance.} \end{split}$$

Family heritabilities were estimated as:

$$h_{\rm F}^2 = \frac{(1/4)\sigma_{\rm A}^2}{\sigma_{\rm F}^2}$$
 (2)

where $\sigma_F^2 = \sigma_w^2/nb + \sigma_e^2/n + \sigma_f^2$ = phenotypic variance of family means, b = number of replications,

n = harmonic mean number of trees per plot.

The additive genetic variance, σ_A^2 , was estimated as $3\sigma_f^2$ since openpollinated families are assumed to be related to a greater extent than half-sibs (Squillace 1974; Sorensen and White 1988). The above estimate of family heritability is appropriate to use for estimating gain from the progeny of a clonal seed orchard after roguing of clones based on performance of their open-pollinated families in progeny tests. 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 follows (Falconer 1981, p.175):

$$\Delta G_{I} = i h_{I}^{2} \sigma_{P} \tag{3}$$

where i = intensity of selection,

and for family selection as follows:

$$\Delta G_{\rm F} = 2 \mathrm{i} h_{\rm F}^2 \sigma_{\rm F} \tag{4}$$

The coefficient of 2 in equation 4 occurs because the selected parents will be intermated rather than mated back to the original, unselected base population. Percent genetic gains were determined after backtransformation 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 follows:

$$\Delta G_{\mathbf{y}\cdot\mathbf{x}} = \mathbf{i}_{\mathbf{x}} \mathbf{h}_{\mathbf{I}\mathbf{x}} \mathbf{h}_{\mathbf{I}\mathbf{y}} \mathbf{h}_{\mathbf{A}\mathbf{x}\mathbf{y}} \sigma_{\mathbf{P}\mathbf{y}} \tag{5}$$

where $\Delta G_{\mathbf{y},\mathbf{x}}$ = 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_{Py} is replaced by σ_{Fy} in equation 6, individualtree heritabilities are replaced by family heritabilities, and the equation is multiplied by 2 for reasons given earlier (see equation 4). Genetic correlations between competitive environments were calculated as follows (Burdon 1977):

$$r_{Axy} = \frac{r_{xy}}{(\sigma_{fx}/\sigma_{Fx})(\sigma_{fy}/\sigma_{Fy})}$$
(6)

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,
- $\sigma_{\rm F\,x}$ and $\sigma_{\rm F\,y}$ = 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. Efficiency of selection in one competitive environment for predicting performance in another competitive environment was calculated by dividing the correlated response to selection by the expected genetic gain given that trees are selected and grown in a single environment.

RESULTS AND DISCUSSION

Relative Family Performance in Contrasting Competitive Environments

The hypothesis of interest is whether family performance is dependent upon competitive environment. A test of this hypothesis is provided by the significance of the family x competitive environment interaction in the combined analysis of variance (Table II.2A). Results indicate that although differences between families and between competitive environments were significant (defined as p<0.05), the family x competitive environment interaction was not (p=0.07). Gauch (1988), however, presents an argument for using a higher significance level for the interaction, for example, p<0.25 when the significance level for the main effects is p<0.05. In such a case, one might conclude that the interaction was significant. Nevertheless, the interaction component of variance was small relative to the family component of variance ($\sigma_{fxe}^2 = 0.005$ versus $\sigma_{f}^2 = 0.034$). The interaction sums of squares was also non-significant when each pairwise combination of competitive environments was analyzed (p=0.15 for the interaction between mix and pure, p=0.07 between mix and wide, and p=0.21 between pure and wide; see Appendix Table A.7).

Recently, some authors have expressed dissatisfaction with analysis of variance as a tool for detecting genotype x 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, estimated family means often changed rank considerably between competitive environments (Table II.3). Family 741, for example, ranked in the top 25 percent in mixture, but ranked in the bottom 20 percent in the pure and wide competitive environments. Other families, however, were quite stable across competitive environments (e.g. family 743). The rank correlation of family means between mixture and pure was r=0.52, between pure and wide was r=0.39, and between mixture and wide was 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 experimentwise error rates.

Family Variation in Competitive Ability and Density Tolerance

Families did not differ significantly in competitive ability, density tolerance, or competitive-density ability (Table II.4; see also Appendix Tables A.8 and A.9), although competitive-density ability approached significance (p=0.053). The analysis was sensitive to scale effects between the wide and narrow treatments; if biomass was not logtransformed, the family differences for density tolerance and competitive-density ability became highly significant (p<0.001).

Competitive ability, density tolerance, and competitive-density ability are additional measures of family variation in response to competitive environment. The finding that family differences are nonsignificant is in accord with results from the combined analysis of variance showing a non-significant family x competitive environment interaction, providing additional evidence against the hypothesis that relative family performance is dependent upon 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 crop plants and forest trees demonstrate a genetic basis for competitive interactions (Sakai 1961; Adams et al. 1973; Adams 1980; Tuskan and Van Buijtenen 1986), but effective selection for or against general competitive ability or density tolerance has not been demonstrated. Few studies present evidence for genetic variation in general competitive ability, or estimate its heritability. In forest trees, 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. Although the response of a family in specific combination with another family was in some cases quite large, when averaged over all families the magnitude of the response (general competitive ability) was small. General competitive abilities have not been reported in other studies of forest trees. Results from genetic studies of density response in forest trees have been ambiguous, as pointed out earlier. The findings of Schmidtling (1988), however, suggest that, at least at the provenance level, genetic variation exists with respect to the volume per area that genotypes may sustain after self-thinning commences.

Donald (1968) hypothesized that mutual suppression of highly competitive individuals when grown in pure stands may result in a negative relationship between competitive ability and pure stand performance. When competitive ability is measured as the difference in growth between mixture and pure, a negative relationship between competitive ability and pure stand performance may be expected purely as a result of the method used to measure competitive ability. This can be shown as follows:

By definition, the correlation between competitive ability (CA) and pure stand performance (P) is

$$\mathbf{r}_{CA,P} = \frac{COV (CA,P)}{\sigma_{CA}\sigma_{P}} , \qquad (7)$$

where COV (CA,P) is the covariance between competitive ability and pure stand performance, and σ_{CA} and σ_{P} are the standard errors for competitive ability and pure stand performance, respectively. σ_{CA} and $\sigma_{\rm P}$ must both be positive, so the question is whether the covariance is expected to be negative. Given that CA = M-P, where M represents performance in mixture, then

$$COV(CA, P) = COV(M-P, P) = COV(M, P) - \sigma_P^2 .$$
(8)

Since

$$r_{M,P} = \frac{COV (M,P)}{\sigma_M \sigma_P} , \qquad (9)$$

rearranging gives $COV(M, P) = r_{M, P} \sigma_M \sigma_P$. (10) Substituting equation 10 into equation 8 yields

$$COV(CA, P) = r_{M, P} \sigma_M \sigma_P - \sigma_P^2 .$$
(11)

If one assumes $\sigma_M^2 = \sigma_P^2$, as is the usual assumption in the analysis of variance (i.e., homogeneous variances), then

$$COV(CA, P) = r_{M, P} \sigma_{P}^{2} - \sigma_{P}^{2} = \sigma_{P}^{2}(r_{M, P} - 1).$$

Under these circumstances, COV(CA,P), and thus, $r_{CA,P}$, must always be less than or equal to zero, since $r_{M,P}$ cannot take a value greater than one. In other words, competitive ability and pure stand yield are not mathematically independent. The same argument may be used to demonstrate the expectation of a positive relationship between density tolerance and pure stand performance. The relationship of interest to tree breeders is not that between competitive ability or density tolerance and pure stand performance, however. Instead, it is the relationship between performance in mixture and performance in pure stands, and between performance in pure stands at a narrow spacing and performance at a wide, non-competitive spacing. These relationships were the topic of the previous section. 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 test for homogeneity of variances (Steel and Torrie 1980, p. 471-472), estimated variances among families were significantly heterogeneous between competitive environments (p<0.05 for χ^2 =11.98 with 2 d.f.). The percent of the total phenotypic variation explained by family was greatest in mixture, least in pure family blocks, and intermediate at the wide spacing (Table II.5). The percent of the total phenotypic variation explained by within-plot differences was greater in pure blocks than in mixture and wide. 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. Hart (1986) found a similar increase in family differences in progeny tests of loblolly pine in which families were grown in mixtures compared to pure family blocks. Interestingly, the overall phenotypic variation among individual trees remained the same whether seedlings were grown in pure blocks or in mixture (Table II.5). Thus, growing seedlings in pure stands in the nursery would not necessarily decrease the overall variation among seedlings coming out of the nursery.

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 interfamily 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) and the proportion of the rotation in which trees will be in competition. In addition, estimates of heritability in mixtures may not be entirely appropriate for estimating 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.

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 grow. 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 intragenotypic 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).

Selection Strategies Considering Competitive Environments

I have shown that genetic gains are expected to be greatest when

families are selected and grown in mixture. I have also shown that the phenotypic correlation between family means in different competitive environments is less than perfect. I now pose the question of the effect of selection in one competitive environment on the expected genetic gain when trees are grown in another competitive environment, and the related question of which competitive environment is best for selection. 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 noncontiguous 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 between 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. Genetic correlations may be expected to be high since the same trait is measured in each competitive environment. For example, the high genetic correlation between mixture and pure indicates that biomass is controlled by the same set of genes in the two competitive environments. The narrow and wide environments differ some in the amount of light received per plant, and thus, the genetic correlation between mix and wide, and between pure and wide are somewhat less than one, but still high. Genetic control of biomass at wide spacing may differ slightly from the control of this trait at narrow spacing.

Results of estimates of correlated response to selection show that selection after testing in mixture gave the greatest expected genetic gains irrespective of the competitive environment in which progeny of selected individuals are grown (Table II.6). The smallest genetic gains may be expected after testing in pure stands irrespective of the planting environment. Individual-tree selection after testing in mixture resulted in estimated genetic gains for growth in pure stands that were 1.7 times greater than gains expected in pure stands after selection in pure stands (Table II.7). Family selection after testing in mixture resulted in estimated genetic gains for growth in pure stands that were 1.3 times greater than gains in pure stands after selection in pure stands. Estimated genetic gains for growth in a competition-free (wide spacing) environment were slightly larger after testing and selection in mixture for individual-tree selection, and about the same for family selection, when compared to gains after selection in a wide competitive environment. Thus, the best competitive environment for evaluation and selection is a mixture at a narrow spacing, even if progeny from select genotypes are expected to be grown in pure stands or in a non-competitive environment.

The superiority of mixtures for genetic testing is largely a result of the much greater heritability in mixture, as well as the large positive genetic correlations of biomass in mixture with biomass in the other two competitive environments. As pointed out earlier, estimates of heritability in mixture may not be accurate if the mixture used to estimate heritability is not similar to the mixture in which selections are grown. If, after selection, the genetic composition of

the mixture becomes much more uniform, i.e., genotypes in the mixture are more uniform in characteristics that influence competition, the mixture in which select genotypes is grown may be somewhat closer to a pure stand. In such a case, heritability may be biased upward, and gains estimated for testing and selection in mixture may likewise be biased upward.

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 I am unable to address the questions of phenotypic stability and risk, results from this study indicate that the yield in mixture was greater than the average yield of all families when grown in pure blocks (see Appendix Table A.10). Average biomass in mixture was 16 percent greater than the average biomass of the families in pure blocks (p=0.0001). Height, diameter, and stem volume were also significantly greater (p=0.0001) in mixture than in pure blocks - 9 percent greater in height, 9 percent greater in diameter, and 24 percent 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 been done to look at the question of yield in mixture versus pure stands in forest trees. Most genetic tests use either mixtures (single-tree or multiple-tree, non-contiguous 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 of mine - in a yield trial of 16 half-sib loblolly pine families, four-year height was 3 percent greater and volume was 9 percent greater in pure blocks than in mixture. They point out, however, that results are preliminary in that competitive influences were not 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.

CONCLUSIONS

The effect of competitive environment on relative family performance remains unclear. Despite large changes in rank between competitive environments for some families and only moderate correlations of family means between competitive environments, the family x competitive environment interaction was not significant at the p=0.05 level. The implications of competitive environment on selection strategies, however, is clear. The high genetic correlations for biomass between different competitive environments indicate that selection in one competitive environment is expected to be effective for genetic gains in another competitive environment. The heritability of biomass was greatest when families were grown in mixture at narrow spacing, and genetic gain for biomass was greatest when selections were made in this competitive environment, regardless of the intended competitive regime of the planting environment. These results imply that selection is most efficient when families are evaluated in mixture. Furthermore, early selection may be more effective when trees are evaluated at a close spacing. Franklin (1979) set forth a similar proposition, but did not consider the implications of intergenotypic competition (mixed versus pure stands). Although mixtures were the best competitive environment for distinguishing family differences, and although pure stands resulted in a lower average yield than a mixture of the same families, pure stands remain the only option for evaluating family variation in unit area yield.

Family differences in seedling size were magnified by interfamily

competition. Increased family differences would lead to a greater likelihood that large proportions of poorer families would be culled from nursery mixtures at the time of lifting. Differential culling of families from nursery mixtures may be undesirable if early growth is not associated with subsequent performance in the field, or if the genetic diversity of outplanting mixtures is greatly reduced. Growing families in pure blocks in the nursery would reduce family differences in seedling size, leading to less likelihood that poorer families would be largely culled. In addition, growing families in pure blocks would give nursery managers control over the composition of mixtures to be outplanted. However, further research is necessary to assess the effect of culling on composition of outplanting mixtures when families are grown in mixture using standard nursery practices.

I 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 considers only the effect of competitive environment on seedling growth, and ignores any maturation effects that may occur during 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 of 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.



Figure 1. Layout of study.

Table II.1. Form of the analyses of variance; (A) combined analysis with all three competitive environments; (B) analysis within each competitive environment separately.

Source of variation	df	Expected mean squares ^a
Block Competitive Envir. Whole-plot error Family Family x CE Split-plot error Within plot	6 (CE) 2 12 38 76 684 2133 ^b	$\sigma_{w}^{2} + n\sigma_{e}^{2} + nc\sigma_{g}^{2} + ncf\sigma_{b}^{2}$ $\sigma_{w}^{2} + n\sigma_{e}^{2} + nc\sigma_{g}^{2} + nbf(\Sigma C^{2}/C-1)$ $\sigma_{w}^{2} + n\sigma_{e}^{2} + nc\sigma_{g}^{2}$ $\sigma_{w}^{2} + n\sigma_{e}^{2} + nbc\sigma_{f}^{2}$ $\sigma_{w}^{2} + n\sigma_{e}^{2} + nb\sigma_{fc}^{2}$ $\sigma_{w}^{2} + n\sigma_{e}^{2}$

(A) Combined analysis

(B) Analysis within each competitive environment

Source of variation	df	Expected mean squares ^a
Block Family Plot error Within plot	6 38 228 Σ(n _j -1)°	$\sigma_{w}^{2} + n\sigma_{e}^{2} + nf\sigma_{b}^{2}$ $\sigma_{w}^{2} + n\sigma_{e}^{2} + nb\sigma_{f}^{2}$ $\sigma_{w}^{2} + n\sigma_{e}^{2}$ $\sigma_{w}^{2} - \dots - $

^a σ_w^2 , σ_e^2 , σ_g^2 , σ_f^2 , σ_b^2 are the within-plot error, split-plot error, whole-plot error, family, and block variance components, respectively; C is the competitive environment effect; n is the harmonic mean number of trees per plot; b,f,c are the numbers of replications, families, and competitive environments, respectively.

 $^{\rm b}$ Within plot degrees of freedom are less than ${\rm bfc}({\rm n-l})$ due to missing individuals within plots.

° n, is the number of trees in plot j.

Table II.2. Analyses of variance of log biomass; (A) combined analysis over all competitive treatments; (B-D) analyses for each competitive treatment (mixture, pure blocks, wide spacing) separately.

(A) Combined	·				
Source	df	SS	MS	F	probability
Block	6	25 61	4.2669		
Comp. Envir. ((CE) 2	1796.09	898.0452	253.33	0.0001
Whole-plot erro	or 12	42.54	3.5449		
Family	38	112.55	2.9618	5.98	0.0001
Family x CE	76	47.75	0.6283	1.27	0.0701
Split-plot erro	or 684	339.05	0.4957		
Within plot	2133	1098.09	0.5148	<u> </u>	
(B) Mixture					
Source	df	SS	MS	F	probability
Block	6	4.47	0.7444	, 15	0 0001
Family	38	72.68	1.9126	4.15	0.0001
Error	228	105.12	0.4610		
Within plot	720	390.61	0.5425		
(C) Pure block	s				
Source	df	SS	MS	F	probability
		10.07			
Block	6	13.97	2.3277	1 01	0 0033
Family	38	40.36	1.0621	1.01	0.0052
Error	228	130.69	0.5/32		
Within plot	/13	418.41	0.5868		
(D) Wide spaci	ng				
Source	df	SS	MS	F	probability
		/ = = 7	7 5050	_	
BLOCK	b 20	43.37	1 157/	9 56	0 0001
Family Former	۵C	43.98	1.13/4	2.00	0.0001
Error	228	103.24	0.4328		
within plot	/00	289.07	0.4130		

	Competitive Environment						
	Mixtu	ire	Pur	Pure		Wide	
Family	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	
720	1 297	15	1 232	5	2 776	17	
728	1 364	10	1 131	14	2 936	10	
720	1,504	7	1 103	18	3 226	1	
725	1 167	23	1 012	23	2 655	25	
730 727	1.107	25	1 1 2 4	15	3 101	25	
757	1.510	6	1 101	7	2 952	q	
740	1 207	0	0 832	32	2.552	22	
/4⊥ 7/2	1 /00/	2	1 242	JZ /i	3 107	2	
743	1 260	כ דו	1 153	10	3 0/1	2 /i	
/44 7/5	1.20U	1/ 25	1 101	δ 10	2.041 2.504	-+ 2 2	
745	1.140	37	1.131	26	2.534	20	
740 740	0.925	10	0.905	20	2.000	16	
749	1.055	29	0.939	29	2.733	20	
Overall	1 160		1,020		2,746		

Table II.3. Family means and ranks for log biomass (g) in three competitive environments.

Table II.4. Analyses of variance for family differences in competitive ability, density tolerance, and competitive-density ability.

 (A) Analy	ysis to	r competiti	ve ability		
 Source	df	SS	MS	F	probability_
Block	6	2.981	0.4968		
Family	38	15.099	0.3973 ·	1.27	0.15
Error	228	71.593	0.3140		

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(B) Analysis for density tolerance

Source	df	SS	MS	F	probability_
Block Family Error	6 38 228	21.286 12.979 106.653	3.5477 0.3415 0.3175	1.08	0.36

(C) Analysis for competitive-density ability

Source	df	SS	MS	F	probability
Block	6	11.889	1.9815		
Family	38	16.121	0.4242	1.45	0.053
Error	228	66.711	0.2926		

Table II.5. Estimated variance components, heritabilities, and genetic gains in three competitive environments. Percents of total phenotypic variance of individual trees are given for the family, plot, and within-plot components. Estimated genetic gains are for logtransformed biomass, but percent gains are after back-transformation of log values.

	Mixture	Pure	Wide
Verieres component:			
Variance component:	0 0(0)	0 0201	0 0208
ramily	0.0602	0.0201	0.0296
Standard error (SE)	10.0178	0.0100	0.0111
Percent	10.0	3.3	0.0
Plot	-0.0237	-0.0039	0.0118
SE	0.0150	0.0178	0.0141
Percent	0	0	2.6
1010000	-	-	2.0
Within plot	0.5425	0.5868	0.4130
SE	0.0286	0.0310	0.0220
Percent	90.0	96.7	90.8
Additive	0.1806	0.0603	0.0895
SE	0.0535	0.0300	0.0333
Phenotypic (Indiv-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
Heritability:			
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
Estimated genetic gain ^a :			
Gain from individual-tree			
selection (grams)	0.233	0.077	0.133
Percent	26.2	8.0	14.3
Gain from family			
selection (grams) ^{a,b}	0.314	0.144	0.202
Percent	36.9	15.5	22.4

^a Intensity of selection to equal 1.0.

^b Gains from family selection are gains expected from roguing of seed orchard clones based on family performance in progeny tests.

Table II.6. Expected genetic gains^a in log-transformed biomass (g) when progeny of parent trees are tested in competitive environment x, but are intended for planting in competitive environment y. Percent gains are given in parentheses, and are after back-transformation of log biomass.

		Testing environment x				
		Mixture	Pure	Wide		
	Mixture	0.233 (26.2)	0.134 (14.3)	0.169 (18.4)		
Planting environment	Pure	0.134 (14.3)	0.077 (8.0)	0.093 (9.9)		
У	Wide	0.147 (15.8)	0.084 (8.8)	0.133 (14.3)		

(A)	Gains	from	individua	l-tree	(mass)) se	lecti	lon.
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(B) Gains from family selection $^{\rm b}$.

		Testing environment x				
		Mixture	Pure	Wide		
	Mixture	0.314 (36.6)	0.248 (28.1)	0.258 (29.4)		
environment	Pure	0.181 (19.8)	0.144 (15.5)	0.148 (16.0)		
У	Wide	0.198 (21.9)	0.156 (16.9)	0.202 (22.4)		

^a Intensity of selections assumed to equal 1.0.

^b Gains from family selection are gains expected from roguing of seed orchard clones based on family performance in progeny tests.

Table II.7. Efficiency of selection^a (relative to testing in the same environment as that intended for planting) when progeny are tested at competitive environment x, but intended for planting in competitive environment y.

		Testing environment x				
		Mixture	Pure	Wide		
D1	Mixture	1.00	0.58	0.73		
environment	Pure	1.73	1.00	1.20		
У	Wide	1.10	0.63	1.00		

(A) Individual-tree (mass) selection.

(B) Family selection^b.

		Testing environment x		
		Mixture	Pure	Wide
Planting environment y	Mixture	1.00	0.79	0.82
	Pure	1.26	1.00	1.03
	Wide	0.98	0.77	1.00

^a Intensity of selections assumed to equal 1.0.

^b Gains from family selection are gains expected from roguing of seed orchard clones based on family performance in progeny tests.

CHAPTER III

EFFECTS OF SEED WEIGHT AND RATE OF EMERGENCE ON EARLY GROWTH OF OPEN-POLLINATED DOUGLAS-FIR FAMILIES

ABSTRACT

Seed weight, time of emergence, and several measures of seedling size were recorded for 39 open-pollinated Douglas-fir (Pseudotsuga menziesii var. menziesii (Mirb.) Franco) families in order to assess genetic variation in seed weight and emergence, and the influence of seed weight and rate of emergence on early growth. Families were planted both as ungerminated seed and as recent germinants to test whether using germinants minimized seed effects on early growth. To evaluate the effect of competition on the relations of seed weight and rate of emergence to seedling size, individuals of families were planted in mixed-family blocks at a narrow spacing, in single (pure) family blocks at a narrow spacing, and at a wide, non-competitive spacing. Results indicate that families differed significantly in seed weight, total percent emergence, and rate of emergence; nevertheless, the correlations of seed weight to rate of emergence, and seed weight and rate of emergence to seedling size were not strong. Using germinants was ineffective in diminishing seed effects, and interfamily competition was of minor importance in magnifying seed effects.

INTRODUCTION

Variation in the average weight of seed collected from different female parents is thought to be largely a consequence of variation in the environmental conditions experienced by those parents (Sorensen and Franklin 1977; Silen and Osterhaus 1979; Shen and Lindgren 1981; Sorensen and Campbell 1985). The female parent also influences to a great extent the size and quality of seeds in gymnosperms since the seed coat is diploid maternal tissue, and the gametophyte is haploid maternal tissue (Perry 1976). This disproportionate contribution of the female parent to seed characters is known as a maternal effect (Falconer 1981, p.124).

Maternal effects as expressed through seed characters are hypothesized to contribute to family differences in early growth of forest tree progenies (Perry 1976; Wilcox 1983). Because maternal effects represent a non-heritable source of variation, their presence can reduce the accuracy of genetic studies, leading to poor estimates of variance components and inaccurate genetic ranking of parents. As a result, the validity of inference from genetic studies using seedlings may be reduced. For example, maternal effects may contribute to poor juvenile-mature correlations, thereby reducing the effectiveness of early testing.

The degree to which maternal effects contribute to the nonheritable differences between families may be assessed by reciprocal crosses in which the mean performance of progenies from a specific cross depends upon which parent was used as the female. Perry (1976)

estimated that the female parent accounted for 88 percent of the total variation in seed weight among crosses of *Pinus taeda*. Wilcox (1983) found that seed size differences between reciprocal crosses of *Pinus radiata* led to significant height differences after six months in the nursery and up to two years in the field. The effect of seed size on height growth, however, diminished with time. Sorensen and Campbell (1985) demonstrated a non-genetic effect of seed weight on seedling size in Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) by leaving some developing cones unbagged, while enclosing others in kraftpaper bags for two different durations to produce seed of varying weights at the same crown position within individual trees. They found that a 10.7 percent increase in seed weight led to a 9.1 percent increase in first-year epicotyl length and a 4.0 percent increase in second-year height, a seed size effect that also diminished with time.

Seed size effects on early growth differences among families may operate through differential rate of germination and emergence. Germination refers to the penetration of the seed coat by the root tip, whereas emergence refers to penetration of the soil surface by a recently germinated seedling. Dunlap and Barnett (1983) found that the size advantage of seedlings derived from large seeds was a consequence of their more rapid germination. Their study, however, did not include a genetic component. Bramlett et al. (1983) found a strong maternal influence on germination properties of five full-sib families of *Pinus virginiana*. If seed size effects on early growth differences operate through earlier germination, seed size effects might be minimized by planting recent germinants rather than ungerminated seed, thereby reducing variation in the time of emergence.

The effect of seed size on early growth may also be influenced by competitive regime. Differential growth among families due to seed size differences may be magnified when individuals from different families are grown in mixtures at close spacing versus in pure family blocks at close spacing, or at a wide, non-competitive spacing. Furthermore, competitive interactions among seedlings of families planted in mixture may magnify the advantages of seedlings from larger seed germinating and emerging earlier (Black 1958; Williams et al. 1968). Thus, the correlations of seed size and rate of emergence with seedling size may be greatest when families are planted in mixture at close spacing.

The influence of seed characters on early seedling growth may be important to the management of improved families in the nursery. If family differences in seed characters are large, and if the relationship of seed characters to seedling size is strong, seedling size differences among families at the time of lifting may be magnified, particularly in mixed-family plantings. As a result, individuals from families with small seed may be largely culled due to transitory maternal effects rather than growth potential as determined by the genetic worth of the embryo. Furthermore, differences among families in total percent emergence may affect the family composition of nursery mixtures. Large differences between families in the number emerged and the number culled may affect the genetic gain realized from nursery mixtures of improved families, and reduce genetic diversity of outplantings. If the change in genetic composition of nursery mixtures is large, nursery managers may wish to control composition by planting single family blocks.

In the study described in this chapter, the extent to which seed weight influences the rate of emergence and early growth of 39 openpollinated families of coastal Douglas-fir was investigated. Because full-sib seed with reciprocal crosses was not used, I was unable to assess the degree to which seed effects were of maternal origin. The use of open-pollinated seed instead of full-sib seed, however, allows better inference to what might be expected in populations of improved seed from tree improvement programs. The objectives of this study were: (1) to assess the degree to which open-pollinated families of Douglas-fir differ in seed characters, (2) to determine the degree to which family differences in seedling size are related to differences in seed weight and rate of emergence, (3) to evaluate the effect of interfamily competition on the relations of seed weight and rate of emergence to seedling size, and (4) to evaluate the effectiveness of planting germinants to minimize seed effects on family differences in seedling growth.

To accomplish these objectives, ungerminated seed and recent germinants were planted in mixed family blocks at a narrow spacing, in pure family blocks at a narrow spacing, and at a wide, non-competitive spacing. Analysis of variance was carried out to test whether families differed significantly in seed characters. The relations between seed weight and rate of emergence, seed weight and seedling size, and rate of emergence and seedling size were assessed by determining the correlation of family means between each.

MATERIALS AND METHODS

This study was conducted as part of a larger investigation of the effect of competitive environment on relative family performance and estimation of genetic parameters. Details of the experimental design are given in Chapter II. Only a brief summary of methods will be presented here.

Open-pollinated seed was collected in fall of 1985 from 39 parent trees located in second-growth stands between elevations of 500 and 1500 feet 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). Thus, families used in this study are representative of material in tree improvement programs.

Seed weight was recorded for each family. The experimental design for analysis of family differences in seed weight was a randomized block design with three replicates of 35 seeds each. Seed was stratified by storage at 3-4°C for eight weeks beginning in February, 1986. In April, 1986, the families were planted in raised nursery beds as ungerminated seed and as recent germinants in each of five replications of three competitive environments: (1) a mixture of all families, with individuals planted at a narrow spacing (4x4 cms), (2) single (pure) family blocks, with individuals planted at a narrow spacing (4x4 cms), and (3) individuals of all families planted at a wide, non-competitive spacing (16x16 cms). The experimental layout was

a split-split-plot design, with the three competitive treatments assigned randomly to whole plots and the two planting treatments (i.e., ungerminated seed and recent germinants) assigned randomly to subplots. In the mixture and wide treatments, each family was represented by four individuals assigned at random to each of four spots within each subplot (i.e., four-tree, non-contiguous sub-subplots). In the pure competitive environment, each family sub-subplot was represented by a sixteen tree square plot in which only the inner four trees were used in the analyses of seedling size.

The germinants used in this study were obtained by germinating seeds on moistened filter paper in petri dishes located in a laboratory germinator. The germinator was set to a day/night temperature of 30/20°C, with a 12-hour photoperiod. Germination data was recorded for each family in order to assess family differences in germination, and compare percent and rate of germination to that of emergence. A seed was considered germinated once the root tip penetrated the seed coat. Each family was represented by five petri dishes of approximately 60 to 90 seeds each. The experimental design for analysis of family differences in germination characters was a randomized block design in which each of the five petri dishes represented one replication. As seeds germinated, they were removed from the petri dishes and stored at 3-4°C to slow elongation of the radical until enough germinants were available to plant a replication. The length of cold storage was from one to thirteen days, with most germinants being stored around seven days.

Three seeds per planting location were planted into the

"ungerminated seed" subplots during the first week of April, 1986, while one germinant per location was planted into the "recent germinant" subplots approximately two weeks later. Individuals planted as ungerminated seed and individuals planted as germinants emerged at approximately the same time - the mean dates of emergence differed by only one day. Beginning in late May, seedlings were transplanted to spots which were empty due to lack of emergence and mortality, and spots in which more than one seedling emerged were thinned to a single individual.

The number emerged in each family was recorded every three days until the end of May in the pure competitive treatment whole plots. This data was used to estimate total percent emergence, and traits related to speed of emergence of each family in each planting type. The experimental design for analysis of emergence characters was a randomized block design with five replications. Speed of emergence traits, as well as traits related to speed of laboratory germination, were estimated using a procedure described by Campbell and Sorensen (1979). Their procedure first transforms cumulative percentages of emergence or germination to probits, and then fits a straight line to probits regressed on rates (1/days). The slope and intercept of the regression line may then be used to estimate various properties of emergence or germination. This procedure was used to obtain estimates for rate of emergence or germination, and days to 50 percent emergence or germination. Rate of emergence is equal to the inverse of days to 50 percent emergence (with rounding error). I present both because rate of emergence is used to explore the relationship of speed of

germination with seedling size, but time to 50 percent emergence is easier to conceptualize. Total percent emergence, rate of emergence, and days to 50 percent emergence were estimated for each family in each of the five replications of the pure competitive treatment and subjected to analysis of variance to test for family differences (objective 1). Total percent germination, rate of germination, and days to 50 percent germination were similarly estimated for each of the five replications in the laboratory germinator, and analysis of variance carried out.

The relations between seed weight, rate of emergence, and early seedling growth were assessed for each competitive environment by planting type treatment (objective 2) by calculating the correlations of family means between seed weight and rate of emergence, seed weight and seedling size, and rate of emergence and seedling size. Seedling size was measured as total two-year dry weight, and one- and two-year height. Homogeneity of correlation coefficients over the different competitive environment by planting type treatments was investigated by chi-square (χ^2) analysis (Steel and Torrie 1980, pp. 278-282). The five degrees of freedom (df) among the six treatment combinations were partitioned in order to test separately the heterogeneity associated with competitive environments (2 df), planting types (1 df), and their interaction (2 df). By comparing correlation coefficients over the three competitive environments, the effect of interfamily competition on the relationships between seed traits and seedling size can be evaluated (objective 3). By comparing correlation coefficients between planting types, the effect of planting germinants to reduce the

influence of seed effects can be assessed (objective 4).

A positive relationship between seed weight and seedling size would magnify family differences in seedling size over what would be expected if all families had equal seed weights. If seed weight differences mostly reflect maternal effects, then increased family differences in seedling size would result in upwards biases of estimates of heritability and genetic gain. I investigated the degree to which heritability and genetic gain may be overestimated by comparing estimates based on variance components corrected and uncorrected for seed weight. The method used to correct for seed weight was to regress family means for seedling size on family means for seed weight, and then subtract predicted seedling size values from observed values to obtain adjusted values. Variance components were calculated from the analysis of variance of adjusted values, and used to estimate adjusted heritabilities and genetic gains. Because I only had family means for seed weight, I was able to estimate only family heritability and gain from reselection of parent trees, and not individual-tree heritability and gain from mass selection.
RESULTS AND DISCUSSION

Family Differences in Seed Characters

Families differed significantly (defined as p≤0.05) in seed weight, and in total percent emergence, mean rate of emergence, and days to 50 percent emergence when planted as ungerminated seed (Table III.1). Total percent emergence ranged widely among families (40 to 94 percent) (Table III.1). Families also differed significantly for emergence traits when planted as germinants, with the exception of total percent emergence (Table III.1). Family differences in emergence when planted as germinants, however, were less, as indicated by the smaller F-values (comparable between planting types since degrees of freedom are equal) and intraclass-correlation coefficients (ratio of family variance to family plus error variance). Families also differed significantly in total percent germination, mean rate of germination, and days to 50 percent germination in the laboratory (Table III.1). Significant family differences in seed characters indicate that the potential exists to affect family differences in early growth.

Influence of Planting Ungerminated Versus Germinated Seeds

Planting germinants reduced the time to 50 percent emergence from about 27 to 16 days (Table III.1). Families that emerged early when planted as ungerminated seed were to some extent the same families that emerged early when planted as germinants - the correlation of family means for days to 50 percent emergence was r=0.66 (note that r≥0.27 is significantly greater than zero at p=0.05 for all correlations presented). The correlation of family means between time of emergence when planted as seed and time of germination in the laboratory test, however, was weaker (r=0.42). Time to emergence is a function of both time of germination in the soil and time to grow to the soil surface. The poor correlation between family means for time to germination and time to emergence may be due to family differences in time to grow to the soil surface after germination, and/or a poor relation between time to germinate in the soil versus time to germinate in the germination chamber where environmental conditions are much different.

The relationship between seed weight and total percent emergence of families was weak, whether individuals were planted as ungerminated seed (r=0.17) or as recent germinants (r=0.30). The relationship between seed weight and total percent germination in the laboratory was also weak (r=0.20). Heavier seed did not appear to germinate or emerge more completely.

Total percent germination of families in the laboratory was strongly related to total percent emergence when seeds were planted ungerminated (r=0.79). Total percent emergence of families when planted as ungerminated seed, however, was not related to total percent emergence when planted as germinants (r=0.02). Surprisingly, mean total emergence over all families was nearly the same, regardless of whether seeds were planted ungerminated (75.5 percent) or as germinants (77.1 percent) (Table III.1). Total percent emergence when seed is

planted ungerminated is a function of the potential to germinate and the potential to survive to emergence, whereas total percent emergence when planted as germinants is only a function of the potential to survive to emergence. If one assumes that percent germination in the germination test is a measure of the potential to germinate in the nursery, then the potential to survive to emergence was relatively good for individuals planted as ungerminated seed as compared to individuals planted as germinants (since 84.5 percent of the ungerminated seed were expected to germinate, and of these, 89 percent (i.e., 75.5 percent/84.5 percent) emerged, as compared to only 77 percent emergence of the those individuals planted as germinants). Perhaps planting germinants stressed individuals to a greater degree such that they were more susceptible to damping-off diseases or other misfortunes. In such a case, total percent emergence of seed planted ungerminated becomes more a measure of the potential to germinate, whereas total percent emergence of germinants is more a measure of the ability to survive to emergence. The poor correlation between percent emergence when planted as ungerminated seed and percent emergence when planted as germinants might then be explained by these traits being controlled by very different factors. Damping-off diseases may have indeed been a factor in this study, since the weather during the time of germination and emergence study was initially warm, but then became cool and wet, conditions which may have favored damping-off diseases.

The relation between family means for seed weight and rate of emergence when planted as ungerminated seed was positive, as expected, but was relatively weak (r=0.37); family differences in seed weight explained only 14 percent of the family differences in rate of emergence (as given by the square of the correlation coefficient - r^2). Furthermore, using germinants did not weaken the relationship between seed weight and rate of emergence - the estimated correlation was, in fact, larger (r-0.46), although not significantly different from the correlation based on seeds planted ungerminated. The correlation between seed weight and rate of germination in the laboratory was not significantly different from zero (r=0.12). Thus, using germinants did not diminish the effect of seed weight on rate of emergence, largely because of the apparent lack of relationship between family seed weight and germination rate.

Influence of Seed Traits on Family Differences in Seedling Size

In exploring the relations between seed weight and seedling size, and rate of emergence and seedling size, three measures of seedling size were considered - first year height, second year height, and second-year dry weight. As expected, the relation between seed weight and seedling size was positive (Table III.2). The strength of the relation depended on the measure of seedling size - the relation was stronger when seedling size was measured as dry weight than when it was measured as total height. Also, the strength of the relation diminished with time as indicated by larger correlation coefficients for first year height as compared to second year height.

The relation of rate of emergence to seedling size was weaker than

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

Many studies have reported a positive relation between seed weight and seedling size, but often these studies compare only seed from widely different seed classes in which family structure is not considered (Burgar 1964; Griffin 1972; Dunlap and Barnett 1983; Belcher et al. 1984). In some of these studies, a significant relationship between these traits was not found (Lavender 1958; Dumroese and Wenny 1987). Studies that considered family structure are equally ambiguous. Robinson and Van Buijtenen (1979) report significant positive correlations between seed weight and volume up to age 15 in loblolly pine (r=0.30). Other studies with loblolly pine, however, found no detectable correlation between seed weight and seedling size (Perry and Hafley 1981; Shear and Perry 1985), or found only a transitory relation that was non-significant after 24 weeks (Waxler and Van Buijtenen 1981). In seedling studies of Douglas-fir, correlations of family means between seed weight and seedling size have been either of a similar magnitude as those found in the present study, or weaker and non-significant (Bell et al. 1979 - r=0.004 between seed weight and 14week dry weight; Lambeth et al. 1982 - r=0.50 between seed weight and 1-year dry weight; Mangold 1987 - r=0.15 between seed weight and firstyear height; Loopstra and Adams 1989 - r=0.34 between seed weight and first year height). Silen and Osterhaus (1979) found no significant

correlation between seed weight and 10-year height or diameter in Douglas-fir.

Inconsistent findings on the effect of seed weight on seedling size may be due, in part, to the influence of environmental factors on seed characters. For example, variation among families in seed weight may depend on variation in environmental conditions experienced by different female trees during the period of seed development. Furthermore, if cones are picked at various stages of maturity, the weight and physiological condition of seeds may vary greatly between female trees. Thus, the magnitude of family differences in seed weight may vary greatly between studies. Larger differences among families in seed weight increase the probability of finding a strong relation between seed weight and seedling size.

Family variation in seed characters and the relation between seed characters and seedling size may also depend on length of stratification and on spring weather conditions during germination and emergence. Length of stratification affects family variation in time of emergence and early growth (Campbell and Sorensen 1984). Short stratification periods, particularly when combined with cool weather conditions during germination and emergence, will increase variability in time of emergence among families. If family differences in time of emergence are large due to short stratification periods or cool spring weather, the relations between seed characters and seedling size may be stronger.

Effect of Competitive Environment and Planting Type on Relationships Between Seed Traits and Seedling Size

None of the χ^2 values in the partitioned χ^2 test of homogeneity of correlation coefficients were significant (Table III.3). Thus, the relations between seed weight and seedling size, and between rate of emergence and seedling size did not differ significantly between competitive environments or between planting types. Although none of the comparisons were significant, it still may be useful to examine the individual correlation estimates to see whether their values differ in the directions hypothesized.

Using germinants was hypothesized to lead to a weaker relation between seed weight and seedling size. The correlation coefficients, however, were very nearly equal for both planting types, except, perhaps, the difference between planting types for the correlation between seed weight and first-year height at the wide spacing (Table III.2). Using germinants also did not affect the relation between rate of emergence and seedling size. Once again, however, the relationship involving first year height at a wide spacing may be an exception.

Interfamily competition did not appear to increase the strength of the relation between seed weight and seedling size. The correlation coefficients were nearly equal for all three competitive environments (Tables III.2). Interfamily competition, however, may have had an effect on the relation between rate of emergence and seedling size. The correlation coefficient for second-year dry weight was much greater in mixture than in wide or pure. The correlation coefficient for

second-year height was also greater in mixture than in wide or pure, although the difference was not as large.

Influence of Seed Weight Differences Among Families on Estimates of Heritability and Genetic Gain

Although families differed significantly in seed weight, the relation between seed weight and seedling size was not strong. For example, the correlation between family means for seed weight and seedling dry weight in a wide competitive environment planted with ungerminated seed (such as might be the typical situation for genetic studies using seedlings) was r=0.48 (Table III.2). Thus, in this case, family variation in seed weight explained only 23 percent of the variation in dry weight of seedlings. Assuming, however, that seed weight effects are maternal, the observed relationship may, in fact, still represent an important source of bias in genetic studies. Estimated family heritabilities for dry weight and height of seedlings planted as ungerminated seed and grown at a wide spacing decreased after adjusting for seed weight in the analysis of variance (Table III.4). Although the decrease in heritability was small, the influence of the concomitant decrease on estimated genetic gains seemed substantial in two of the three seedling size traits. Assuming that the estimated gains after adjusting for seed weight are closer to the true values, the estimated gains before adjustment represent upwardly biased estimates. The degree to which gains were biased upward were 32

percent for two-year dry weight, 10 percent for two-year height, and 44 percent for one-year height. Note that the amount of bias depends on the trait measured as indicated by the difference between two-year height and dry weight. Also, the decrease in bias between the first and second year heights suggests that the bias is diminishing quickly. Geneticists need only be concerned about bias due to seed weight effects if the genetic study is of short duration. Such is the case in the early testing studies where selections are based on one or two year performance in the nursery or greenhouse. In an analysis of early testing data in Douglas-fir, the correlation between family means for 12-year height and seedling height improved considerably when family means for seedling height were first adjusted for seed weight (W.T. Adams, personal communication).

CONCLUSIONS

Significant family differences were found in seed traits, but the relationships between seed weight, rate of emergence, and seedling size were not strong, and appeared to diminish from one- to two-year old seedlings. Nevertheless, adjusting for seed weight may be useful for improving the precision of estimates of genetic potential of families for seedling growth and for reducing bias in genetic parameter estimation. The greatest potential benefits of adjusting for seed size may be in early testing when genotypes are evaluated after less than two years of age.

Although emergence occurred faster when germinants were planted, the relationships between family means for seed weight and rate of emergence and for seed weight and seedling size did not diminish when germinants versus ungerminated seed were planted, presumably because of a lack of relationship between family seed weight and rate of germination. Thus, using germinants does not appear to be useful for reducing seed size effects in nursery tests. However, family variation in rates of germination and emergence may be magnified by shorter stratification periods and cooler spring weather. Further research is necessary to assess the effect of using germinants for diminishing seed size effects under a variety of conditions.

An influence of competitive environment on the relationships between seed weight and seedling size and rate of emergence and seedling size could not be detected statistically in this study. Nevertheless, correlations tended to be greatest when families were

grown in mixtures at a close spacing, particularly the correlations between rate of emergence and different measures of seedling size.

Large differences among families in total percent emergence indicate that the composition of family mixtures at the time of lifting may differ considerably from that at the time of planting in nurseries. Family variation in seed weight and rate of emergence, however, probably has only a minor influence on family composition of nursery mixtures. The relationships between seed weight, rate of emergence, and seedling size were not particularly strong in our study materials, and not strongly influenced by competitive regime. Inherent growth differences between families, however, may still lead to large changes in family composition after standard nursery culling practices.

Sowing seed by size classes has been suggested to promote more uniform germination in the nursery, leading to more uniform seedling density in the seedbed and thus, more uniform seedling sizes (Belcher et al. 1984). However, large family differences in seed weight, such as those found in this study, suggest that sizing of bulked seedlots with the exclusion of small seed prior to sowing may lead to reduced genetic variation of nursery mixtures (Hellum 1976; Silen and Osterhaus 1979). If this is a concern, nursery managers may want to avoid seed sizing practices.

Character ^a	Mean	Range among families	F	probability	t ^b
Seed weight	0.42	0.32-0.56	64.53	0.0001	0.95
<u>Nursery:</u>					
Ungerminated seed plante Total emergence Rate of emergence Time to 50% emergence	ed: 75.5 0.037 27.2	40.1-93.8 0.031-0.045 22.4-35.1	8.89 3.70 3.39	0.0001 0.0001 0.0001	0.73 0.35 0.32
Germinants planted: Total emergence	77.1	46.9-96.9	1.59	0.0783	0.11
Rate of emergence Time to 50% emergence	15.9	14.2 - 18.6	1.70 1.74	0.0131	0.12
<u>Laboratory:</u>					
Total germination Rate of germination Time to 50% germinatio	84.5 0.176 on 5.9	42.5-98.5 0.121-0.233 4.3-8.2	40.37 57.91 58.45	0.0001 0.0001 0.0001	0.93 0.95 0.95

Table III.1. Family variation in seed weight, emergence, and germination.

^a Seed weight measured as g per 35 seed; total emergence and germination as percent; rate as 1/(number of days to 50 percent emergence); time as days.

^b t = intraclass correlation coefficient = ratio of family to family plus error variance.

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

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

^a $r \ge 0.21$ is significantly greater than 0 at the 10% probability level. $r \ge 0.27$ is significantly greater than 0 at the 5% probability level. $r \ge 0.37$ is significantly greater than 0 at the 1% probability level.

Relationship	Planting Types (P) (1 df ^b)	Competitive Environments (C) (2 df)	P x C Interaction (2 df)	Overall (5 df)		
Seed weight with:	:					
2-yr dry weight 2-yr height 1-yr height	0.001 0.002 0.079	1.097 0.061 0.158	1.692 1.065 2.734	2.790 1.128 2.971		
Rate of emergence with:						
2-yr dry weight 2-yr height 1-yr height	0.053 0.189 0.564	2.442 1.372 0.658	2.833 2.154 2.057	5.329 3.715 3.278		

Table III.3. Partitioned chi-square test of homogeneity of correlation coefficients among six combinations of planting types and competitive environment treatments^a.

^a All χ^2 values are non-significant at the 5% probability level.

^b df = degrees of freedom.

Measure of seedling size		h	2 F	G ^b		
	r°	before	after	before	after	bias ^d
2-yr dry weight (g)	0.48	0.65	0.56	3.02	2.29	32%
2-yr height (mm)	0.35	0.70	0.67	33.8	30.7	10%
l-yr height (mm)	0.52	0.66	0.54	8.4	5.8	44%

Table III.4. Estimated family heritabilities (h_F^2) and expected genetic gains (G) from parental selection based on progeny performance, before and after adjusting family means for seed weight^a.

^a Data from treatment in which ungerminated seed was planted at a wide, non-competitive spacing.

^b Intensity of selection assumed to equal 1.0.

° Correlation between seed weight and seedling size.

^d Bias = <u>gain before adjustment</u> - <u>gain after adjustment</u> x 100 gain before adjustment

CHAPTER IV

GENETIC VARIATION IN SEEDLING ARCHITECTURE OF TWO-YEAR-OLD DOUGLAS-FIR GROWN IN THREE COMPETITIVE ENVIRONMENTS

ABSTRACT

Seedling architecture refers to the form and structure of a seedling's crown, stem and root system, and the proportion of total biomass partitioned to each. Ideotype breeding has been proposed as a method to improve forest productivity by selection of trees with architectures that use available growing space efficiently, and partition more biomass to the stem. Assessment of genetic variation in seedling architecture is useful to assess the potential for realizing gains from ideotype breeding.

Significant family differences and favorable estimates of heritability were found in Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) for branch angle, branch number, crown width relative to height, height relative to stem diameter, and partitioning to roots, stem, branches, and foliage. Thus, progress may be achieved from selection and breeding for these traits. Relative family performance for all traits except relative crown width was sensitive to seedling density, but was unaffected by the presence or absence of interfamily competition (i.e., pure stands versus mixed family plantings at the same density). Phenotypic relationships among traits of seedling architecture and seedling size were generally consistent across competitive environments; trees with greater total dry weight generally allocated more to branches and stem and less to roots. Genetic relationships among traits, however, did depend to some extent on competitive environment. Differences in estimates of genetic correlations between traits when trees are grown in different competitive environments may be explained either by different sets of genes controlling the same trait in different competitive environments, or by interactions among genotypes affecting the estimates of the components of variance and covariance differentially, or both.

INTRODUCTION

Ideotype breeding has been proposed as a method to improve per area yields in forest trees (Cannell 1978). An ideotype is a model plant comprised of a collection of component traits that are thought to enhance yield (Rasmusson 1987). Seedling architecture traits hold the most promise for achieving gains from ideotype breeding. Seedling architecture refers to the number, size, shape, structure, arrangement, and display of plant parts (Adams 1982).

The concept of ideotype breeding is useful because traits associated with individual-plant yield are not always the same traits associated with increased yield as a community (Cannell 1978). Success of an individual depends on the ability to capture resources, often by exploiting resources from neighboring plants. Aggregate yield, however, depends on effective utilization of resources as a community, where efficient sharing of resources by individuals becomes important. For example, trees with wide crowns may produce maximum yields as individual trees, but trees with tall, narrow crowns may be more productive on a per unit area basis.

Ideotypes may also incorporate traits that enhance product value or product recovery. Product value may be enhanced by breeding for traits that increase stem quality, such as smaller branches, flatter branch angles, and decreased taper in the lower stem. Product recovery may be enhanced by increased partitioning of the total biomass to the stem (as well as by increased stem quality). Stem wood represents the economic portion of a forest tree. The ratio of the economic portion

of a plant (stem wood in forest trees) to the total biomass is known as the harvest index. Selection for increased harvest index has been advocated as a useful method to increase per area yields in forest trees (Cannell 1978; Shepherd 1984; Velling and Tigerstedt 1984). In agricultural species, progress from genetic improvement is generally recognized to be primarily a result of increases in harvest index, and not a result of improvements in photosynthetic efficiency (Donald and Hamblin 1976; Gifford and Evans 1981; Gifford et al. 1984).

Ideotypes are most often identified to correspond to three competitive environments (Donald and Hamblin 1976; Cannell 1978). An isolation ideotype is a model plant designed to grow well at a wide, non-competitive spacing. A competition ideotype is a model plant designed to grow well when competing with unlike neighbors in a mixed community. A crop ideotype is a model plant designed to grow well when in mixture with other crop ideotypes, such as would occur in a pure family stand. Crop ideotypes are hypothesized to make the most efficient use of resources per unit area, and thus, lead to the greatest unit area yields. Crop ideotypes proposed for forest trees are characterized by tall, narrow crowns, compact, fibrous root systems with a strongly developed taproot, a phenology that allows full utilization of the growing season, and greater harvest index (Gordon and Promnitz 1976; Cannell 1978; Dickman 1985; Kärki and Tigerstedt 1985). Isolation and competition ideotypes, on the other hand, are thought to have wide, spreading crowns and root systems.

Three steps are involved in ideotype breeding (Rasmusson 1987). First, the specific characters to be included in an ideotype must be

identified. This may involve working with physiologists and ecologists to identify characters important to increasing community productivity. For example, models of canopy photosynthesis based on light interception theory have played a role in demonstrating the importance of narrow crowns to increased unit area productivity at competitive spacings (Jahnke and Lawrence 1965; Kellomäki et al. 1985).

The second step is assessment of genetic variation of the proposed ideotype traits. Traits that do not vary or traits with high environmental variation relative to genetic variation (i.e., low heritability) are of little value in a breeding program. Furthermore, the genetic relationships among traits must be understood. Selection for some traits may have unfavorable correlated responses in other traits. For example, selection for increased partitioning to the stem (greater harvest index) may lead to reduced root biomass, which may lead to a reduction in drought tolerance.

The third step is to conduct the breeding program and monitor progress from selection, i.e., verify ideotype models. Do hypothesized ideotypes perform as expected? Substantiating gains from ideotype breeding may be a difficult task, particularly in forest trees. Tree breeders must show that increased productivity of forest stands is a consequence of breeding and not just improved cultural practices. Moreover, tree breeders must demonstrate that selection for ideotype characters resulted in greater unit area gains than selection for individual tree yield alone.

The present study is primarily concerned with the second step of ideotype breeding. Results will be important in assessing the

potential to achieve progress from ideotype breeding. Seedlings are used to serve as a model for processes in older stands, and as such, are a useful first approximation to what may be expected in applied tree breeding programs. The objectives are: (1) to assess genetic variation and inheritance of seedling architecture traits that may be included in ideotype breeding, (2) to determine the degree to which relative family performance for seedling architecture traits is dependent upon the competitive environment in which trees are grown, and (3) to explore the phenotypic and genetic relationships among traits of seedling architecture and seedling size. Assessment of seedling architecture was accomplished by growing 39 open-pollinated Douglas-fir (Pseudotsuga menziesii var. menziesii (Mirb.) Franco) families in each of three competitive environments: (1) individuals from all families grown in mixture at close spacing (4x4 cm), (2) individuals grown in single (pure) family blocks at close spacing (4x4 cm), and (3) individuals from all families grown at a wide, noncompetitive spacing (16x16 cm). Seedlings were harvested after two growing seasons, and measured for stem height and diameter, crown width, branch angle, branch number, and dry weights of roots, stem, branches, and needles. Consideration of competitive environment is important because families may be tested under one competitive regime, but deployed in another. For example, assessment of ideotype traits may be done at a wide spacing before competition has commenced, but in production plantations, trees may be grown in competition either in mixtures or in pure stands for the majority of the rotation. Special emphasis is given to evaluation of harvest index, because of its

importance to improvements in productivity in agriculture. I also discuss breeding for increased partitioning to stem diameter growth versus height growth, a trait that has been suggested to decrease logging and milling costs, and increase volume and quality of the valuable lower logs (Libby 1987).

MATERIALS AND METHODS

The 39 open-pollinated families used in this study were from parent trees located in second-growth stands of west-central Oregon. The 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). Details of seed treatment, establishment of nursery tests, and experimental layout have been described in detail previously (Chapter II).

Families were planted in the spring of 1986 in each of three competitive environments: (1) mixture of individuals from all families at a close spacing (4x4 cm), (2) single (pure) family blocks with individuals at a close spacing (4x4 cm), and (3) individuals from all families planted at a wide, non-competitive spacing (16x16 cm). The experimental layout was a split-split-plot design, with the three competitive treatments assigned randomly to whole plots. Two planting types were assigned randomly to subplots - individuals from all families were planted either as ungerminated seed or as recent germinants. Preliminary analyses found no planting type x competitive environment interaction, so for purposes of the competition analyses, planting types were ignored and treated as separate replications. Problems with damping off disease and a root weevil reduced the number of replications from ten to seven. In the mixture and wide competitive environments, four individuals from each of the 39 families were planted at random locations within each subplot (i.e. four-tree non-

contiguous sub-subplots), whereas in the pure competitive environment, sixteen individuals were planted in a square sub-subplot, with the inner four seedlings being the study trees.

Crowns and roots of seedlings overlapped considerably at the close spacing by the end of the two growing seasons, but because seedlings were fertilized and watered regularly, competition is assumed to have been primarily for light. At the wide spacing, crowns had just began to overlap by the end of the second growing season, and thus, competition was assumed to be minimal during the duration of the study.

Seedlings were harvested after two growing seasons, and measured for stem height and diameter, crown width, branch angle, branch number, and dry weights of roots, stem, branches, and needles. Harvesting was done between November and January, after roots had stopped growing. Stem height (mm) was measured from the soil surface to the base of the terminal bud. Stem diameter (0.01 mm) was measured at the root collar. Crown width (mm) was measured as the widest horizontal distance between the terminal buds of two opposing branches. Branch angle was measured as the angle (to the nearest 10°) from the main stem of the largest branches in the lower crown. Branch number was the total number of branches originating from the stem that were 10 mm or longer. Dry weights (0.01 g) of plant parts were determined after drying each seedling in a paper bag for two to three days at 70°C. Seedlings were then separated into needles, branches, stem, and roots (divided at the root collar), and each component weighed separately.

Based on the above measurements, ten traits were selected for analysis, including two measures of size - total dry weight (a measure of overall performance) and dry weight of the stem (a measure of the economic portion of a forest tree) - and several measures of seedling architecture - branch angle, branch number, relative crown width (measured as crown width divided by height), stem slenderness (measured as height divided by diameter - Velling and Tigerstedt 1984), and proportions of total biomass partitioned to roots, stem, branches, and foliage (dry weight of component divided by total seedling dry weight). Analyses of variance for each trait were carried out for each competitive environment separately in order to test whether families differed significantly within each competitive environment, and to estimate components of phenotypic and genetic variance (objective 1). The form of the analysis of variance for individual competitive environments is given in Table IV.1B. Individual-tree heritabilities were computed for each competitive environment as follows:

$$h_{I}^{2} = \frac{\sigma_{A}^{2}}{\sigma_{P}^{2}}$$
(1)

where σ_A^2 = additive genetic variance,

 $\sigma_{\rm P}^2 = \sigma_{\rm w}^2 + \sigma_{\rm e}^2 + \sigma_{\rm f}^2 = {\rm phenotypic \ variance \ of \ individual \ trees},$ $\sigma_{\rm f}^2 - {\rm family \ component \ of \ variance},$

- $\sigma_{\rm e}^2$ = error component of variance,
- σ_w^2 = within-plot component of variance.

The additive genetic variance, σ_A^2 , was estimated as $3\sigma_f^2$ since openpollinated families are assumed to be related to a greater extent than half-sibs (Squillace 1974; Sorensen and White 1988). Standard errors of estimates of heritabilities were derived by procedures outlined by Osborne and Paterson (1952). Two procedures were followed to evaluate the influence of competitive environment on relative family performance for seedling architecture traits (objective 2). First, correlations of family means between pairs of competitive environments were determined. I also determined correlations of family ranks between pairs of competitive environments, but results were similar to correlations of family means, and thus, only the later are presented. Second, combined analyses of variance were carried out on the seedling data for pairs of competitive environments, and the statistical significance of the family x competitive environment interaction component determined. The form for the combined analyses of variance is given in Table IV.1B. The combined analyses of variance were also used to test significance of the difference between overall means between pairs of competitive environments in order to test the overall effect of competitive regime on seedling architecture.

Phenotypic relationships among traits of seedling architecture and seedling size were explored by calculating simple phenotypic correlations between traits as measured on individual trees (objective 3). Genetic relationships between traits were investigated by subjecting pairs of traits to covariance analysis. Again, each competitive environment was treated separately, with the form of the analysis being the same as in Table IV.IA, but with expected cross products replacing expected variances. Genetic correlations were calculated as:

$$\mathbf{r}_{A\mathbf{x},\mathbf{y}} = \frac{\sigma_{f\mathbf{x},\mathbf{y}}}{(\sigma_{f\mathbf{x}})(\sigma_{f\mathbf{y}})}$$
(2)

where $r_{Ax,y}$ = genetic correlation between traits x and y,

 $\sigma_{\rm fx,y}$ = family component of covariance between traits x and y,

 $\sigma_{\rm fx}$ and $\sigma_{\rm fy}$ = square-roots of the family components of

variance for traits x and y, respectively.

Standard errors of estimates of genetic correlations were determined by procedures outlined by Becker (1984, pp. 116-117).

RESULTS AND DISCUSSION

Mean Differences between Competitive Environments

Large differences in overall means for seedling architecture and size traits were found between seedlings grown in pure family blocks and seedlings grown at a wide, non-competitive spacing (Table IV.2). Analyses of variance indicated that all differences were statistically significant (defined as $p \leq 0.05$; see Appendix Table A.11). Besides being much larger, seedlings grown in the absence of competition had flatter branches, more branches, wider crowns, less slenderness (more taper), and more partitioning to roots and branches and less partitioning to stems and foliage as compared to seedlings grown in pure family blocks. Thus, density competition had a large effect on seedling architecture, as well as seedling size.

Significant differences in overall means were also found between seedlings grown in mixture at close spacing and seedlings grown in pure family blocks at close spacing for relative crown width and partitioning to roots, stem, and branches (Table IV.2). Seedlings grown in mixtures had wider crowns, and partitioned more to stems and branches and less to roots, as compared to seedlings grown in pure family blocks.

Genetic Variation in Seedling Architecture Traits

Families differed significantly for all traits in all three competitive environments with the exception of relative crown width (crown width/height) as measured in pure family blocks (Table IV.2). Estimates of heritability ranged from low (0.07) to relatively high (0.49). The frequently wide range in family means and at least moderate estimates of heritability indicate that the potential exists to achieve significant progress from breeding for seedling architecture traits.

Estimates of heritability seemed to depend upon the competitive environment in which families were grown. Heritability estimates for total weight, stem weight, branch number, relative crown width, and partitioning to roots and branches were lower for seedlings grown in pure family blocks as compared to mixed family blocks or at a wide spacing (Table IV.2). Heritability of branch angle, however, was higher in pure family blocks than in the other two competitive environments, while heritabilities of slenderness (height/diameter) and partitioning to the stem and foliage were relatively high in all three competitive environments.

Intrafamily competition (in pure blocks) may have influenced the ability of a seedling to express its genetic potential for traits of seedlings size, and crown and root form. Individuals from families with the potential for large size, wide crowns, many long branches, and large root systems may be mutually suppressive when grown together in pure family blocks. Meanwhile, individuals from families of small

size, narrow crowns, and less partitioning to branches and roots will grow relatively better in pure family stands, where they are not in competition with individuals of more competitive families. Thus, family differences may be reduced in the presence of intrafamily competition, resulting in lower estimates of heritability.

Effect of Competitive Environment on Relative Family Performance

Relative family performance for most seedling architecture traits appeared to be dependent upon the density at which families were grown. Correlations of family means between the pure and wide competitive environments were low for many traits (Table IV.3), and the family x competitive environment interaction was often statistically significant when the combined analysis of variance involved these two competitive environments (Table IV.4). The one notable exception was relative crown width - the correlation of family means was fairly strong and the interaction component was not significant.

Relative family performance of seedling architecture traits did not appear to depend upon intergenotypic competition to any strong degree. Correlations of family means between the mix and pure competitive environments were moderate to strong (Table IV.3), and for every trait, the family x competitive environment interaction component involving these two competitive environments was non-significant (Table IV.4).

Correlations between Traits

Consideration of the relationships among traits may involve exploring either phenotypic or genetic correlations. Examination of phenotypic correlations between traits of seedling architecture and seedling size of individual trees may identify architecture traits that are of key importance to the success of an individual (success is considered to be the ability to fix carbon as measured by total dry weight of the plant). The primary interest in genetic correlations, however, is to determine the degree to which traits are under the control of the same genes, and thus, are likely to respond together when selection is applied to one of the traits.

The phenotypic relationships among traits were generally consistent across the three competitive environments (Table IV.5). Total dry weight and weight of stem were highly correlated, as expected, since the stem comprises a large portion (approximately 1/3) of the total weight. Thus, conclusions about total dry weight apply to stem weight. Greater total dry weight was associated with greater partitioning to branches, greater number of branches, greater crown widths, and slightly steeper branch angles - all traits that may be expected to increase an individual's ability to capture light, whether as an isolated plant or in competition with other plants.

A positive correlation is expected between relative crown width and total dry weight in mixtures, since individuals with relatively wide crowns are expected to be larger as a result of their ability to shade individuals with relatively narrow crowns. Although a positive correlation was found between relative crown width and total dry weight, it was not strong (Table IV.5C). The correlation between relative crown width and total dry weight in pure family blocks is expected to be weaker than the correlation in mixtures, since genotypes of relatively narrow crowns are grouped together, and are expected to compete less and produce greater biomass than if they were in competition with genotypes of relatively wide crowns. The correlation in pure blocks, however, is of the same magnitude as the correlation in mixture. This result might be explained by the presence of considerable within-family variation in crown widths within openpollinated families. Thus, a relatively wide crown is still of great importance to individual trees for achieving a large size in pure family blocks.

Increased total dry weight was associated phenotypically with less partitioning to the roots and more partitioning to the stem (Table IV.5). Consequently, a negative correlation was found between root proportion and stem proportion, and also between root proportion and branch proportion and number. Large trees partitioned more to the photosynthetic half of the seedling, and less to the water and nutrient gathering half. This is expected because soil factors were not expected to be limiting to growth since a generous water and fertilizer regime was used.

Interestingly, despite a positive association between total dry weight and both crown width and proportion stem, a weak negative correlation was found between crown width and proportion stem (Table IV.5). Thus, narrow-crowned seedlings tended to partition relatively

more biomass to the stem, as compared to wide-crowned seedlings. Hamilton (1969) and Assmann (1970, pp. 120-122) reported findings in which the most efficient producers of stem wood volume per unit area of crown projection were narrow-crowned trees.

Partitioning to foliage was associated with slightly reduced dry weights (Table IV.5). This may seem counter-intuitive, since one might expect that trees that partition more to photosynthetic tissue would be larger. As trees become larger, however, more and more of the total weight of the tree is found in the woody component. Thus, negative correlations are found between the proportion of foliage and the proportions of roots and stem. Because roots and stem comprise a large portion of the tree, a negative association between proportion of foliage and dry weight is not surprising. In other words, a small proportion of foliage reflects the past success of a tree at capturing light.

Like phenotypic correlations, genetic correlations between total dry weight and stem dry weight were very high in all three competitive environments. Thus, the two traits seem to be largely controlled by the same set of genes, and will not be considered separately here.

Estimated genetic correlations between traits measured in the wide competitive environment were often similar to their phenotypic correlations (Table IV.5); the average absolute difference between genetic and phenotypic correlation coefficients was 0.15. This was especially true for the positive genetic correlations between total dry weight and number of branches, crown width, and proportions of branches and stem, and the negative correlation between total dry weight and

proportion of roots. The negative genetic correlation between dry weight and branch angle, however, was much stronger than the corresponding phenotypic correlation between these two traits. Thus, selection for larger trees, or larger stems, would result in greater partitioning to the branches and stem, less partitioning to the roots, and steeper branches. Greater partitioning to the stem is desirable, but greater partitioning to branches and increased branch angle may have undesirable consequences for wood quality, and reduced partitioning to the roots may have undesirable consequences for maintaining drought tolerance.

In the pure competitive environment, genetic correlations were less similar to phenotypic correlations than in the wide competitive environment (Table IV.5); the average absolute difference between genetic and phenotypic correlation coefficients was 0.36. Furthermore, the magnitude and sign of genetic correlations were often different from those in the wide competitive environment. Although total dry weight was still positively correlated with proportions branches and stem, and negatively correlated with proportion roots, the correlations with proportion branches and roots were weaker, and the correlation with proportion stem was stronger. Furthermore, the estimated genetic correlations between total dry weight and two branching traits (branch number and branch angle) were opposite in sign to those observed at the wide spacing. Large differences in correlation coefficients among traits of seedling architecture were also found (e.g., between branch angle and branch number, between branch angle and proportion roots, and between branch number and proportion roots). Differences between

genetic correlations of traits measured in the pure family blocks and the same traits measured in seedlings grown at wide spacing indicate that density competition may affect the genetic relationships among traits.

In the mixed competitive environment, genetic correlations were once again similar to phenotypic correlations; the average absolute difference between genetic and phenotypic correlation coefficients was 0.13. Large differences between genetic correlations of traits measured on seedlings grown in the mixed family environment versus pure family blocks indicate that interfamily competition may also affect genetic relationships between traits (Table IV.5). For example, the estimated genetic correlation between total dry weight and branch number went from weakly negative in pure stands to strongly positive in mixture. The positive genetic correlation between dry weight and proportion branches and the negative genetic correlation between total dry weight and slenderness were stronger in mixture than in pure stands, while the positive genetic correlation between dry weight and proportion stem appeared to be weaker.

Intrafamily competition (pure competitive environment) appears to influence both the degree to which genetic correlations are similar to phenotypic correlations, and the magnitude and direction of genetic correlations among traits of seedling size and seedling architecture. The differences between estimates of genetic correlations in different competitive environments may be due to: (1) experimental error (i.e., correlations are actually the same, but estimates vary as a result of sampling error); (2) genetic causes (i.e., traits are wholly or

partially determined by different genes in different competitive environments); or (3) environmental bias (i.e., competitive interactions among like or unlike genotypes result in a repeatable environmental influence on estimates of genetic covariance and variance).

An analogous situation to the third possibility given above has been described by Falconer (1980, pp. 146) in which intrafamily competition may reduce the resemblance between relatives such that the family component of variance is decreased, while the within-family component of variance is increased. I considered this as an explanation for the decreased estimate of heritability for total dry weight in the pure competitive environment as compared to the mixture or wide competitive environments (Chapter II). Similarly, competitive interactions among like or unlike genotypes may influence the family component of covariance between two traits. For example, when individuals from families with the potential for greater partitioning to branch size and number are grown in pure stands, the interaction between crowns may lead to mutual suppression and a decrease in overall seedling size within a family, resulting in a reduced family component of covariance between branch traits and total dry weight compared to that in wide or mixed competitive environments. Recall that genetic correlations are estimated as the ratio of the family component of covariance to the square-root of the product of the family components of variance (equation 2). If, as a result of intrafamily competition, the component of covariance between two traits is reduced to a greater degree than the components of variance of each trait, the estimate of
the genetic correlation coefficient may be reduced. Thus, the reduction in positive genetic correlation of total weight with branch number or proportion branches found in the pure competitive environment when compared to the wide and mixed competitive environments (Table IV.5) may be a consequence of intrafamily competition affecting the estimates of covariance and variance, and not a consequence of different genes involved in expression of the trait in different competitive environments. The appropriate estimate of genetic correlation to use for predicting correlated response to selection, however, depends on the anticipated competitive environment in which progeny from select genotypes will be deployed. If selection is done in one competitive environment for deployment in another competitive environment, the correlated response to selection may not be predictable.

Breeding for Harvest Index

Breeding for harvest index in forest trees is of special interest because of the importance of increases in harvest index to achieving greater productivity in agricultural species (Donald and Hamblin 1976). Results from the present study indicate that the potential exists for progress from selection for harvest index in Douglas-fir. Harvest index is here defined as the proportion of total biomass due to the stem. Families differed significantly in harvest index, and heritabilities were relatively high in all three competitive environments - $h^2=0.35$ in wide, $h^2=0.36$ in pure, and $h^2=0.29$ in mix (Table IV.2). Family means for harvest index ranged from 0.21 to 0.27 in wide, from 0.25 to 0.34 in pure, and from 0.30 to 0.37 in mixture.

Relative family performance for harvest index appears to depend to some extent on seedling density, and to a lesser degree on intergenotypic competition (Tables IV.3 and IV.4); families that allocate relatively more to the stem at close spacing do not necessarily allocate relatively more to the stem at wide spacing.

Harvest index had a positive genetic correlation with both total dry weight and dry weight of the stem, although the correlations were relatively weak in the wide and mixture treatments (Table IV.5). Thus, selection for harvest index would result in either an increase or no change in tree or stem size, and selection for tree or stem size would likewise result in increases or no change in harvest index. Genetic correlations of harvest index with other traits of seedling architecture varied somewhat between competitive environments. In general, selection for harvest index would result in a decrease in relative crown widths, a decrease or no change in number and proportion of branches, a decrease or no change in proportion of roots, and a decrease in proportion of foliage. A narrow crown and reduced allocation to branches are traits associated with a non-competitive crop ideotype. The addition of harvest index as a selection criterion may be one option for incorporating non-competitive ideotypes in a breeding program without sacrificing gains in individual-tree yield. Reduced allocation to roots, however, may be of concern for maintaining drought tolerance. Reduced allocation to foliage is not necessarily of

concern, since this relation may just be a consequence of larger trees having greater wood biomass, as discussed earlier.

Results from other studies with older trees support the conclusion that genetic variation exists for harvest index. Matthews et al. (1975) found significant family differences in biomass partitioning among 20 half-sib families of Virginia pine at age eight. The proportion of stem wood to total above-ground wood ranged from 0.32 to 0.43 among families. Estimated heritability was greater than one, which was explained as due to the parents not being selected at random. Van Buijtenen (1978) found non-significant differences in biomass partitioning among 15 half-sib families of 14-year-old loblolly pine, but found significant differences among nine clones of 7- to 11- year old slash pine. The proportion of stem wood to total above-ground biomass ranged from 0.58 to 0.66 among the loblolly pine families, and from 0.30 to 0.47 among the slash pine clones. Broad-sense heritability of harvest index among the slash pine clones was 0.53. Cannell et al. (1983) found large differences in allocation to stem wood relative to total above-ground biomass among seven clones of 8year-old Sitka spruce (ranging from 0.26 to 0.48) and among seven clones of 8-year-old lodgepole pine (ranging from 0.21 to 0.31). Clones with a higher harvest index were more sparsely branched. Velling and Tigerstedt (1984) found significant family differences in stem weight relative to above-ground biomass among 30 full-sib families of 16-year-old Scots pine. Family means ranged from 0.43 to 0.57, and heritability was estimated as 0.52. As in the present study, correlations of family means of harvest index with height, diameter,

and fresh weight of the stem were positive, and correlations with relative crown width were negative. The results from previous studies, as well as those from the present study, indicate that selection for harvest index may be a promising method for increasing forest productivity.

Breeding for Stem Form

Libby (1987) suggested that one goal of tree breeding should be to breed for allocation to stem diameter growth versus height growth; i.e., breed for shorter, fatter trees. The advantages of short, fat trees are reduced logging and milling costs per volume of wood, increased volume in the valuable lower logs, reduced taper in the lower logs resulting in increased recovery at the mill, and an increased proportion of mature wood in lower logs. He recognizes that diameter and height are positively correlated, but suggests selection of "correlation breakers" should be possible. He also recognizes that short, fat trees may be at a competitive disadvantage, but suggests deployment of such trees in pure stands in order to avoid differences in competitive ability.

Results from this study indicate that the potential exists for progress from selection for allocation to stem diameter versus height growth. Families differed significantly in slenderness (height/diameter), and heritabilities were favorable in all three competitive environments - $h^2=0.36$ in wide, $h^2=0.20$ in pure, and $h^2=0.24$ in mixture (Table IV.2). As expected, both the genetic and phenotypic correlations between height and diameter were strongly positive (phenotypic correlations were between 0.66 and 0.74 over the three competitive environments, and genetic correlations were between 0.74 and 1.00). Genetic correlations between slenderness and total dry weight, and between slenderness and dry weight of the stem were small in the wide and pure competitive environments, but were strongly negative in mixture (Table IV.5). Thus, selection for decreased slenderness would result in either very little correlated response in tree size, or a concomitant increase in tree size if the competitive environment in which trees are tested and grown is a mixture. Genetic correlations of slenderness with other seedling architecture traits were to some extent dependent on competitive environment. In general, selection for short, fat trees would not affect allocation to stem wood, but would result in increased allocation to roots. In the mixed competitive environment, selection for short, fat trees would result in an increase in branch number and allocation to branches, while in the wide competitive environments, selection for short, fat trees would result in a decrease in branch number.

CONCLUSIONS

Based on results of this study using seedlings, the potential to realize gains from ideotype breeding is good. Significant family differences and favorable heritabilities for traits of crown form and biomass partitioning indicate that adequate genetic variation exists to achieve progress from selection for these traits. The ability to evaluate family performance for seedling architecture, however, depends to some extent upon the density at which families are grown. Relative family performance for branch angle, branch number, slenderness (stem height relative to diameter), and partitioning to roots, stem, branches, and foliage appeared to differ when seedlings were grown at wide versus narrow spacings. Relative family performance was highly consistent only between densities for only a single trait, relative crown width.

Phenotypic relationships among traits of seedling architecture and seedling size were generally consistent across competitive environments. Seedlings with greater total dry weight generally allocated more biomass to branches and stem and less to roots. Genetic correlations between traits, however, often appeared to be influenced by competitive environment. In particular, estimates of genetic correlations differed from phenotypic correlations in the pure competitive environment to a greater extent than they did in the other two competitive environments. Differences in the genetic relationships between traits when trees are grown in different competitive environments may be explained either by different sets of genes controlling the same trait in different competitive environments, or because competitive interactions among genotypes affect estimates of components of variance and covariance differentially, or both.

Selection for larger trees may have undesirable consequences for correlated responses in seedling architecture traits. Genetic correlation estimates in this study indicate that selection for greater total biomass when seedlings are grown at wide spacing would result in trees with decreased partitioning to roots, and more and steeper angled branches. Decreased partitioning to roots may lead to decreased drought tolerance, whereas more and steeper branches may reduce wood quality. Interestingly, relative crown width would not be expected to increase after selection for total biomass in the wide treatment. Τf selection for total biomass was done after testing in mixture, branch number would be expected to increase, but allocation to roots and branch angle would not be expected to change. Crown width, however, would be expected to increase, an undesirable consequence if narrow crowns were included as part of a desirable ideotype. Selection for total biomass in the pure treatment would result in a strong correlated response for increased partitioning to the stem, a favorable response if increased harvest index is included as part of a desirable ideotype.

Seedling studies may serve as a model for processes in older stands, and as such, are useful as a first approximation to what may be expected in applied tree breeding programs. Caution should be exercised, however, in extrapolating results from seedling studies to those of older stands. Poor inference to older stands may be a consequence of two factors. First, the environment in which seedlings

are grown may be sufficiently different from the environment in which improved trees are grown that genotype x environment interaction becomes important. The present study apparently considered the response of genotypes primarily to competition for light. Inference of my results to older stands assumes that competition for water and nutrients is of minor importance to determining relative family performance, as compared to competition for light. Water or nutrient stress may affect partitioning between shoot and root (Keyes and Grier 1981; Ledig 1983), but whether it affects the relative performance of genotypes for size or partitioning traits is unclear. Second, inference of seedling studies to older materials may be affected if different genes are involved in the expression of traits at different ages. For example, partitioning to various plant parts may involve expression of different sets of genes after the onset of flowering. Allocation to reproductive structures may involve a considerable portion of the carbon budget of a tree (Ledig 1983; Cannell 1985), and evidence suggests that genetic variation exists with respect to flowering (Longman 1985). However, the phenotypic and genetic relationships between allocation to flowering, allocation to other plant parts, and overall size are unknown.

Table IV.1. Forms of the analyses of variance when data for individual competitive environments are analyzed (A), and when pairs of competitive environments are analyzed (B).

Source of variation	dfª	Expected mean squares ^b
Block Family Plot error Within plot		$\sigma_{w}^{2} + n\sigma_{e}^{2} + nf\sigma_{b}^{2}$ $\sigma_{w}^{2} + n\sigma_{e}^{2} + nb\sigma_{f}^{2}$ $\sigma_{w}^{2} + n\sigma_{e}^{2}$ σ_{w}^{2}

(A) Analysis for a single competitive environment

(B) Combined analysis for pairs of competitive environments

Source of variation	dfª	Expected mean squares ^b
Block Comp. Envir. Whole-plot error Family Family x CE Split-plot error	6 1 6 38 38 456	$\sigma_{w}^{2} + n\sigma_{e}^{2} + nfc\sigma_{b}^{2}$ $\sigma_{w}^{2} + n\sigma_{e}^{2} + nbf(\Sigma C^{2}/C-1)$ $\sigma_{w}^{2} + n\sigma_{e}^{2} + nc\sigma_{f}^{2}$ $\sigma_{w}^{2} + n\sigma_{e}^{2} + nbc\sigma_{f}^{2}$ $\sigma_{w}^{2} + n\sigma_{e}^{2} + nb\sigma_{fc}^{2}$ $\sigma_{w}^{2} + n\sigma_{e}^{2}$
Within plot	$\Sigma(n_i - 1)^d$	$\sigma_{\rm w}^2$

^a n_j is the number of trees in plot j.

^b σ_w^2 , σ_e^2 , σ_f^2 , σ_b^2 are the within-plot, error, family, and block variance components, respectively; C is the competitive environment effect; n is the harmonic mean number of trees per plot; b,f,c are the numbers of replications, families, and competitive environments, respectively.

^c With the exception of branch angle, within-plot degrees of freedom were 720, 717, and 700 in the mixture, pure, and wide competitive environments, respectively. Degrees of freedom for branch angle were 573, 541, and 587, respectively.

^d With the exception of branch angle, within-plot degrees of freedom were 1436, 1418, and 1415 for the mixture versus pure, mixture versus wide, and pure versus wide analyses, respectively. Degrees of freedom for branch angle were 1113, 1159, and 1127, respectively. Table IV.2. Means, statistical significance of differences among families, and estimated individual-tree heritabilities (h_I^2) for size and seedling architecture traits in three competitive environments; (A) families planted at a wide, non-competitive spacing; (B) families planted in pure blocks at a narrow spacing; (C) families planted in mixture at a narrow spacing.

		Differences am			
O [.] Trait ^a	verall mean	Range	F probability	h_T^2	$SE(h_T^2)$
(A) Wide Spacing					
(A) wide spacing					
Total weight (g)	19.34	12.59 - 27.22	3.18 0.0001	0.25	0.08
Stem weight (g)	4.66	2.78 - 6.53	3.23 0.0001	0.25	0.08
Branch angle (10°)	5.57	4.96 - 6.11	2.41 0.0001	0.18	0.07
Branch number	15.8	10.2 - 20.0	1.85 0.0034	0.12	0.06
Crown width/height	0.563	0.473 - 0.690	2.65 0.0001	0.22	0.07
Slenderness ^a	0.477	0.400 - 0.566	3.99 0.0001	0.36	0.10
Proportion roots	0.363	0.326 - 0.397	3.24 0.0001	0.29	0.09
Proportion stem	0.236	0.214 - 0.274	3.83 0.0001	0.35	0.10
Proportion branches	0.100	0.075 - 0.129	3,46 0,0001	0.29	0.09
Proportion foliage	0.301	0.272 - 0.345	5.14 0.0001	0.41	0.10
(B) Pure Blocks					
Total weight (g)	3.58	2.24 - 4.82	1.62 0.0177	0.05	0.04
Stem weight (g)	1.11	0.59 - 1.65	1.91 0.0021	0.12	0.06
Branch angle (10°)	5.10	4.26 - 6.23	2.93 0.0001	0.28	0.09
Branch number	9.9	6.6 - 14.2	1.72 0.0086	0.08	0.04
Crown width/height	0.236	0.187 - 0.287	1.41 0.0675	0.07	0.06
Slenderness ^a	1.01	0.85 - 1.16	2.18 0.0002	0.20	0.08
Proportion roots	0.307	0.263 - 0.357	1.56 0.0260	0.11	0.07
Proportion stem	0.298	0.248 - 0.342	3.07 0.0001	0.36	0.11
Proportion branches	0.037	0.025 - 0.050	1.92 0.0020	0.12	0.05
Proportion foliage	0.358	0.317 - 0.413	4.74 0.0001	0.49	0.12
(C) Mixture					
Total weight (g)	4.13	1.75 - 6.08	3.43 0.0001	0.26	0.08
Stem weight (g)	1.42	0.59 - 2.14	3.30 0.0001	0.25	0.07
Branch angle (10°)	4.95	4.30 - 5.64	2.32 0.0001	0.15	0.06
Branch number	11.0	6.7 - 15.0	2.84 0.0001	0.19	0.06
Crown width/height	0.245	0.202 - 0.299	2.90 0.0001	0.21	0.07
Slenderness ^a	1.06	0.84 - 1.26	3.03 0.0001	0.24	0.08
Proportion roots	0.267	0.236 - 0.310	3.12 0.0001	0.23	0.07
Proportion stem	0.334	0.301 - 0.370	3.88 0.0001	0.29	0.08
Proportion branches	0.045	0.030 - 0.063	2.66 0.0001	0.17	0.06
Proportion foliage	0.354	0.323 - 0.397	3.84 0.0001	0.32	0.09

a Height (mm)/diameter (0.01mm)

Trait	Mix and Pure	Mix and Wide	Pure and Wide
Breen also an also	0 (7	0.47	0.20
Branch angle	0.67	0.47	0.30
Branch number	0.57	0.47	0.29
Crown width/height	0.66	0.48	0.62
Slenderness ^a	0.44	0.41	0.23
Proportion roots	0.55	0.36	0.16
Proportion stem	0.65	0.45	0.41
Proportion branches	s 0 .49	0.44	0.37
Proportion foliage	0.84	0.66	0.61
-			

Table IV.3. Correlations of family means between pairs of competitive environments for seedling architecture traits.

^a Height (mm)/diameter (0.01mm)

		air				
	Mix	Mix vs Pure		vs Wide	Pur	e vs Wide
Trait	Fp	robability	F	probability	F	probability
Branch angle	0.99	0.48	1.48	0.04	2.05	<0.01
Branch number	1.16	0.24	1.53	0.03	1.65	0.01
Crown width/heightª	0.64	0.95	1.22	0.17	0.79	0.82
Slenderness ^{a,b}	1.40	0.06	2.20	<0.01	2.10	<0.01
Proportion roots	1.08	0.34	2.06	<0.01	2.00	<0.01
Proportion stem	1.37	0.07	2.22	<0.01	2.27	<0.01
Proportion branches ^a	1.03	0.42	1.30	0.12	1.52	0.03
Proportion foliage	0.84	0.75	1.56	0.02	2.02	<0.01

Table IV.4. F-values for family x competitive environment interaction means squares, and their probabilities, for seedling architecture traits when competitive environments are analyzed in pairs.

^a Observations were log-transformed prior to analysis of variance in order to meet the assumption of homogeneity of variance.

^b Height (mm)/diameter (0.01mm)

Table IV.5. Estimated phenotypic (above diagonal) and genotypic (below diagonal) correlations between size and seedling architecture traits^a in three competitive environments; (A) families planted at a wide, non-competitive spacing; (B) families planted in pure blocks at a narrow spacing; (C) families planted in mixture at a narrow spacing. Phenotypic correlations which were not significantly different from zero are indicated by "ns". All other phenotypic correlations were statistically significant at p<0.05. Standard errors of genetic correlations are given in parentheses.

	WT	WTST	BA	BN	CWHT	SLN	RT	ST	BR	LF
WT	-	0.96	-0.10	0.71	0.19	-0.02 ns	-0.46	0.22	0.70	-0.07
WTS:	0.97 (0.01)	-	-0.11	0.66	0.09	0.07	-0.50	0.42	0.61	-0.13
BA	-0.58 (0.22)	-0.48 (0.22)	-	-0.12	0.38	-0.12	0.24	-0.13	-0.16	-0.12
BN	0.77 (0.14)	0. 62 (0.16)	-0.40 (0.25)	-	0.08	0.13	-0.55	0.09	0.63	0.24
CWHI	0.0 <mark>6</mark> (0.24)	-0.12 (0.24)	0.50 (0.20)	0.09 (0.27)	-	-0.46	0.04 ns	-0.33	0.43	-0.08
SLN	0.10 (0.22)	0.16 (0.22)	-0.04 (0.23)	0.34 (0.23)	-0.41 (0.19)	-	-0.48	0.39	-0.18	0.46
RT	-0.39 (0.19)	-0.39 (0.19)	0.32 (0.23)	-0.68 (0.15)	0.00 (0.24)	-0.66 (0.14)	-	-0.47	-0.54	-0.60
ST	0.18 (0.22)	0.42 (0.19)	-0.16 (0.23)	-0.18 (0.24)	-0.62 (0.16)	0.18 (0.21)	-0.05 (0.22)	-	-0.05	-0.20
BR	0.50 (0.16)	0.32 (0.20)	-0.28 (0.23)	0.63 (0.16)	0.52 (0.18)	-0.15 (0.21)	-0.42 (0.18)	-0.44 (0.18)	-	0.06 ns
LF	-0.05 (0.21)	-0.13 (0.21)	-0.03 (0.22)	0.44 (0.20)	0.16 (0.22)	0.63 (0.13)	-0.72 (0.11)	-0.46 (0.17)	0.14 (0.21)	-

^a Key to traits: WT=total dry weight; WTST=dry weight of stem; BA=branch angle; BN=branch number; CWHT=crown width relative to height; SLN=slenderness (height/diameter); RT=proportion roots; ST=proportion stem; BR=proportion branches; LF=proportion foliage.

(A) Wide

Table IV.5. (cont.)

(B)	Pure	Blocks
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	WT	WTST	BA	BN	CWHT	SLN	RT	ST	BR	LF
WT	-	0.97	-0.17	0.76	0.36	-0.30	-0.37	0.37	0.69	-0.20
WTS	0.97 (0.02)	-	-0.17	0.72	0.28	-0.22	-0.45	0.52	0.62	-0.23
BA	0.29 (0.27)	0.33 (0.29)	-	-0.23	0.26	-0.07	0.23	-0.14	-0.23	-0.05 ns
BN	-0.20 (0.58)	0.03 (0.35)	0.19 (0.30)	-	0.31	-0.13	-0.47	0.26	0.76	0.04 ns
CWH	0.24 (0.46)	0.07 (0.44)	0.72 (0.27)	0.62 (0.36)	-	-0.49	0.01 ns	-0.13	0.51	-0.10
SLN	-0.14 (0.35)	-0.12 (0.31)	0.44 (0.27)	0.18 (0.30)	0.20 (0.48)	-	-0.36	0.21	-0.25	0.40
RT	-0.11 (0.44)	-0.24 (0.36)	-0.59 (0.34)	-0.04 (0.39)	-0.38 (0.52)	-0.68 (0.27)	-	-0.66	-0.40	-0.51
ST	0.81 (0.19)	0.93 (0.11)	0.25 (0.24)	-0.24 (0.28)	-0.24 (0.36)	-0.13 (0.27)	-0.20 (0.31)	-	0.11	-0.23
BR	0.18 (0.37)	0.03 (0.35)	-0.35 (0.26)	0.86 (0.11)	0.37 (0.37)	0.10 (0.32)	0.04 (0.41)	-0.24 (0.29)	-	-0.01 ns
LF	-0.73 (0.22)	-0.70 (0.18)	0.22 (0.22)	0.06 (0.25)	0.37 (0.35)	0.52 (0.19)	-0.44 (0.25)	-0.76 (0.13)	-0.04 (0.26)	-

Table IV.5. (cont.)

(C) Mi	xture
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	WT	WTST	BA	BN	CWHT	SLN	R T	ST	BR	LF
		· · · · ·								
WT	-	0.98	-0.16	0.69	0.38	-0.56	-0.22	0.25	0.60	-0.30
WTST	0.98 (0.01)	-	-0.16	0.65	0.33	-0.50	-0.31	0.41	0.54	-0.34
BA	0.01 (0.26)	-0.26 (0.24)	-	-0.19	0.22	0.03 ns	0.17	-0.10	-0.23	0.01 ns
BN	0.63 (0.15)	0.58 (0.14)	-0.14 (0.24)	-	0.30	-0.37	-0.32	0.12	0.63	-0.04 ns
CWHT	0.41	0.34 (0.21)	0.39 (0.23)	0.38 (0.20)	-	-0.54	0.01 ns	-0.11	0.50	-0.15
SLN	-0.80 (0.10)	-0.75 (0.12)	0.44 (0.23)	-0.28 (0.21)	-0.47 (0.19)	-	-0.20	0.08	-0.46	0.39
RT	-0.06 (0.23)	-0.16 (0.22)	-0.05 (0.25)	-0.36 (0.20)	0.12 (0.24)	-0.33 (0.22)	-	-0.61	-0.27	-0.44
ST	0.33 (0.20)	0.52 (0.17)	-0.34 (0.23)	0.06 (0.22)	-0.14 (0.22)	-0.14 (0.22)	-0.53 (0.16)	-	-0.04 ns	-0.34
BR	0.58 (0.16)	0.52 (0.18)	-0.25 (0.26)	0.74 (0.12)	0.69 (0.15)	-0.56 (0.18)	-0.19 (0.23)	0.04 (0.23)	-	-0.11
LF	-0.50 (0.17)	-0.58 (0.16)	0.50 (0.21)	0.02 (0.22)	-0.23 (0.22)	0.67 (0.15)	-0.36 (0.19)	-0.64 (0.15)	-0.23 (0.23)	-

CHAPTER V

GENERAL CONCLUSIONS

This study investigated the degree to which growth differences among families were influenced by competitive environment, seed weight, and rate of emergence. Genetic variation in traits of seedling architecture was also explored, as well as the phenotypic and genetic relationships between seedling architecture traits and seedling size. The three competitive environments were individuals from all families planted in mixture at close spacing, individuals planted in single (pure) family blocks at close spacing, and individuals from all families planted at a wide, non-competitive spacing. Individuals were planted both as ungerminated seed and as recent germinants.

The effect of competitive environment on relative family performance as measured by total dry weight of seedlings was not clear. Despite large changes of rank between competitive environments for some families and only moderate correlations of family means between competitive environments, the family x competitive environment interaction was not significant (at the p=0.05 level). Furthermore, families did not differ significantly in competitive ability or density tolerance. Competitive environment, however, had a large effect on estimates of variance components, which, in turn, lead to large differences in estimates of heritability and genetic gain. Family differences were magnified by testing individuals from all families in mixture, with the result that estimates of heritability and genetic

gain were greatest in that environment. Analysis of correlated response to selection indicated that testing and selection in mixture result in the greatest estimated gain, even if progeny of selected individuals are subsequently grown in a pure or wide competitive environment.

Significant family differences were found in seed weight, total percent germination and emergence, and rate of germination and emergence. Despite large family differences, the relationships among seed weight, rate of emergence, and seedling size were not strong and appeared to diminish from one- to two-year-old seedlings. Using germinants was ineffective in diminishing seed effects, and interfamily competition was of minor importance in magnifying seed effects.

Significant family differences and favorable estimates of heritability were found for seedling architecture traits, indicating that the potential exists to achieve significant progress from breeding for these traits. Evaluation of relative family differences for seedling architecture traits appeared to be dependent upon the density at which families were grown for all traits except relative crown width, but intergenotypic competition did not appear to affect relative family performance. Phenotypic correlations among traits of seedling architecture and seedling size were generally consistent across competitive environments. Seedlings of greater total biomass generally allocated more biomass to branches and stem and less to roots. Genetic correlations among traits appeared to depend on the competitive environment in which seedlings were grown. For example, the genetic correlations between total dry weight and branch number were strongly

positive when seedlings were evaluated at wide spacing $(r_a=0.77)$ or in mixture at narrow spacing $(r_a=0.63)$, but was negative when seedlings were evaluated in pure family blocks at narrow spacing $(r_a=-0.20)$. Differences in genetic relationships between competitive environments may be explained either by different genes controlling the same trait in different competitive environments, or by interactions among genotypes affecting the estimates of the components of variance and covariance differentially, or both.

Results from this study have implications to the management of improved families in the nursery. Relative to growth in pure stands, growing mixtures of families at narrow spacing appears to magnify family differences in seedling size. Thus, growing families in mixture magnifies the likelihood that poorer families would be culled from nursery mixtures at the time of lifting. Differential culling of families from nursery mixtures may be undesirable if early growth is not associated with subsequent field performance, or if genetic diversity is greatly reduced. Nursery managers may chose to grow families in pure blocks in order to decrease family differences, and to have greater control over the composition of outplanting mixtures. Pure family blocks, however, resulted in somewhat smaller seedlings and no more overall uniformity than mixed sowings. Further research is necessary to assess the degree to which family differences in emergence and growth in operational nurseries affect the family composition of outplanting mixtures following standard culling practices.

Seed weight and rate of emergence were not strongly related to seedling size of families and, thus, are probably of minor importance

in determining the family composition of nursery mixtures. The relationships among seed weight, rate of emergence, and seedling size, however, may depend upon the length of stratification of seed and environmental conditions at the time of germination and emergence. Families did differ greatly in total percent emergence, which may be important in determining family composition of nursery mixtures. Further research is necessary to extend the inference from this study to different conditions of stratification and environment during germination and emergence.

Results from this study also have implications for genetic testing. My findings suggest that growing families in mixture at close spacing is the best procedure to evaluate genetic differences among families for biomass production at a young age. Thus, early genetic testing may be most effective when families are grown in mixtures at close spacing. Inference of results of this seedling study to field testing in older stands depends on additional factors, including maturation effects, increased environmental heterogeneity in field tests, and the role of competition for water and nutrients. Further research is necessary to extend the inference of this study to field testing.

Although seed weight was not strongly related to two-year total dry weight of seedlings, adjusting for seed weight in the analysis of variance for seedling size may be useful for improving the precision of estimates of genetic potential of families for seedling growth and reducing bias in estimates of heritability and genetic gain. Because seed weight effects appear to diminish quickly, the greatest benefit in

adjusting for seed size would be in young seedlings, i.e., early testing. In general, the correlations between seed weight and seedling size and between rate of emergence and seedling size did not decrease when germinants were used. Thus, using germinants to minimize effects due to family differences in seed weight or rate of emergence did not appear to be a particularly useful practice under the conditions of this study.

Further research is needed to assess the importance of various tree form and biomass partitioning traits to increased forest productivity on a unit area basis. Progress from ideotype breeding depends upon knowledge of which traits are associated with increased community productivity, and should, therefore, be included in an ideotype. Furthermore, knowledge of the importance of individual traits to per unit area productivity is important to determine the relative weightings each trait should be given in selection indices. This study looked at the importance of competitive regime under simplified conditions in which competition among seedlings was primarily for light. Further research is necessary to consider competition in the root zone for water and nutrients, and under more realistic field conditions. In addition, this study dealt only with competition among open-pollinated families. The consequences of competition among full-sib families and clones also needs to be studied.

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APPENDIX

Table A.1. Analyses of variance using other variables as measures of performance.

Measure of performance = 2-yr height

Combined analysis

Source	df	SS	F	probability
Block Comp. Envir. Whole-plot error Family Family x CE Split-plot error Within plot	6 2 12 38 76 684 2133	1005373 479539 2564537 1778762 912591 4909127	1.12 6.52 1.67	0.3575 0.0001 0.0005

Analysis of families in mixture

Source	df	SS	F	probability
Block Family Error Within plot	6 38 228 720	484679 688387 1017923 4056045	4.06	0.0001

Analysis of families in pure blocks

Source	df	SS	F	probability
Block Family Error Within plot	6 38 228 713	880347 546992 1866897 3881437	1.76	0.0065

Source	df	SS	F	probability
Block Family Error Within plot	6 38 228 700	2028568 1332989 2024907 5853895	3.95	0.0001

Table A.1. (cont.)

Measure of performance = 1-yr height

Combined analysis

Source	df	SS	F	probability
Block	6	145636		
Comp. Envir.	2	150435	9.60	0.0032
Whole-plot error	12	94069		
Family	38	203417	6 .50	0.0001
Family x CE	76	72812	1.16	0.1707
Split-plot error	684	562943		
Within plot 2	2133			

Analysis of families in mixture

Source	df	SS	F	probability
Block Family Error	6 38 228	75681 82955 163426	3.05	0.0001
Within plot	720	577131		

Analysis of families in pure blocks

Source	df	SS	F	probability
Block Family	6 38	47320 80337	2.02	0.0009
Error	228	239179		
Within plot	713	453900		

Source	df	SS	F	probability
Block Family Error Within plot	6 38 228 700	99981 105805 160339 483304	3.96	0.0001

Table A.1. (cont.)

Source	df	SS	F	probability
Block	6	3.0120		
Comp. Envir.	2	370.8524	541.62	0.0001
Whole-plot error	12	4.1083		
Family	38	22.7375	6.88	0.0001
Family x CE	76	7.7437	1.17	0.1601
Split-plot error	684	59.4523		
Within plot	2133			

Measure of performance = log of 2-yr diameter

Analysis of families in mixture

Source	df	SS	F	probability
Block Family Error Within plot	6 38 228 720	1.4727 13.8236 20.3711 74.7412	4.07	0.0001

Analysis of families in pure blocks

Source	df	SS	F	probability
Block Family Error	6 38 228	1.7449 8.4899 21.4853	2.37	0.0001
Within plot	713	/0.2648		

Analysis of families at wide spacing

Source	df	SS	F	probability
Block Family Error Within plot	6 38 228 700	3.7723 7.7342 17.5959 49.9545	2.64	0.0001

Table A.1. (cont.)

Source	df	SS	F	probability
Block	6	26.3245		
Comp. Envir.	2	1454.1373	112.42	0.0001
Whole-plot error	12	77.6225		
Family	38	165.1171	6.87	0.0001
Family x CE	76	57.1202	1.19	0.1412
Split-plot error	684	432.7435		
Within plot	2133			

Measure of performance = log of 2-yr volume

Analysis of families in mixture

Source	df	SS	F	probability
Block Family Error Within plot	6 38 228 720	14.9482 90.5020 129.2630 496.8072	4.20	0.0001

Analysis of families in pure blocks

Source	df	SS	F	probability
Block Family Error Within plot	6 38 228 713	18.0834 58.4604 159.5362 496.0884	2.20	0.0002

Source	df	SS	F	probability
Block Family Error Within plot	6 38 228 700	66.2329 67.7206 143.9444 405.5826	2.82	0.0001

Table A.1. (cont.)

Source	df	SS	F	probability
Block	6	60.7485		
Comp. Envir.	2	1255.5843	101.61	0.0001
Whole-plot error	12	74.1438		
Family	38	149.8412	6.46	0.0001
Family x CE	76	57.3270	1.24	0.0943
Split-plot error	684	417.7161		
Within plot 2	2133			

Measure of performance = log of stem weight

Analysis of families in mixture

Source	df	SS	F	probability
Block Family Error Within plot	6 38 228 720	13.2622 88.0869 122.7791 467.0989	4.30	0.0001

Analysis of families in pure blocks

Source	df	SS	F	probability
Block Family Error Within plot	6 38 228 713	32.2279 63.9149 178.7617 504.1289	2.15	0.0003

Source	df	SS	F	probability
Block Family Error Within plot	6 38 228 700	81.4796 50.0096 116.1753 320.2899	2.58	0.0001

Table A.1. (cont.)

Source	df	SS	F	probability
Block	6	44.4979		
Comp. Envir.	2	1572.7415	137.51	0.0001
Whole-plot error	12	68.6220		
Family	38	119.0402	5.58	0.0001
Family x CE	76	55.55 2 7	1.30	0.0501
Split-plot error	684	383.8975		
Within plot 2	2133			

Measure of performance = log of shoot weight

Analysis of families in mixture

Source	df	SS	F	p ro bability
Block Family Error Within plot	6 38 228 720	9.2078 76.3016 113.1378 420.8001	4.05	0.0001

Analysis of families in pure blocks

Source	df	SS	F	p r ob a bility
Block Family Error Within plot	6 38 228 713	26.7713 43.5879 154.1431 466.9248	1.70	0.0101

Source	df	SS	F	p ro bability
Block Family Error Within plot	6 38 228 700	70.2904 49.8715 116.6166 322.9762	2.57	0.0001
Table A.2. Analyses of variance for log biomass including planting type; (A) all three competitive environments combined; (B-D) analyses within each competitive environment.

Source	df	SS	MS	F	probability
Block	2	20.8844	10.4422		
Comp. Envir.	(CE) 2	1585.4936	792.7468	113.14	0.0003
Whole plot en	cror 4	28.0272	7.0068		
Planting Type	e(PT) 1	1.3168	1.3168	1.80	0.2284
CE x PT	2	4.1480	2.0740	2.83	0.1360
Split plot en	cror 6	4.3922	0.7320		
Family	38	106.4124	2.8003	5.42	0.0001
Family x CE	76	43.6627	0.5745	1.11	0.2558
Family x ST	38	26.7421	0.7037	1.36	0.0780
Family x CE >	c PT 76	32.5969	0.4289	0.83	0.8399
Split-split	456	235.3352	0.5161		
Within plot	1828	982.8980	0.5377		

(A) Competitive environments combined

(B) Analysis of families in mixture

Source	df	SS	MS	F	probability
		0.0111	1 / 700		Ē
Block	2	2.9444	1.4/22		
Planting Type(P	T) 1	0.1678	0.1678	0.25	0.6687
Whole-plot erro	r 2	1.3613	0.6807		
Family	38	67.9675	1.7886	3.70	0.0001
Fam x PT	38	20.5021	0.5395	1.12	0.3141
Split-plot erro	r 152	73.4526	0.4832		
Within plot	612	353.4460	0.5775		

(C) Analysis of families in pure blocks

	16		NO.		
Source	dI	55	MS	r	probability
Block	2	4.9330	2.4665		
Planting Type(P	r) 1	0.0019	0.0019	0.00	0.9743
Whole-plot error	c 2	2.8824	1.4412		
Family	38	41.2536	1.0856	1.72	0.0114
Fam x PT	38	18.2325	0.4798	0.76	0.8358
Split-plot error	r 152	95.7393	0.6299		
Within plot	612	379.4334	0.6200		

Table A.2. (cont.)

Source	df	SS	MS	F	probability
Block	2	38.8013	19.4007		
Planting Type(PT) 1	4.6521	4.6521	72.41	0.0135
Whole-plot err	or 2	0.1285	0.0643		
Family	38	37.2241	0.9796	2.24	0.0003
Fam x PT	38	20.7447	0.5459	1.25	0.1733
Split-plot err	or 152	66.3253	0.4364		
Within plot	612	250.0186	0.4085		

(D) Analysis of families at wide spacing

Table A.3 Analyses of variance within each competitive environment for total dry weight (non-log-transformed). These analyses are for comparison with log-transformed analyses, but are not appropriate due to heterogeneity of error variance.

Source	df	SS	MS	F	probability
Block	6	117.41	19.5688	2 / 2	0,0001
Family Error	228	876.41 1531.49	6.7171	5.45	0.0001
Within plot	720	5219.96	7.2499		

(A) Analysis of families in mixture

(B) Analysis of families in pure blocks

Source	df	SS	MS	F	prob a bility
Block Family Error Within plot	6 38 228 717	79.31 367.35 1363.59 4013.34	13.2180 9.6672 5.9807 5.5974	1.62	0.0177

(U) Analysis	OI Lamil	ies at wide	spacing		
Source	df	SS	MS	F	probability
Block Family Error Within plot	6 38 228 700	9507.93 12753.03 24056.15 75186.05	1584.6543 335.6060 105.5094 107.4086	3.18	0.0001

(C) Analysis of families at wide spacing

Table A.4. Variance components, heritabilities, and estimated genetic gains in three competitive environments for total dry weight (non-log-transformed). Standard errors (SE) and coefficients of variation (CV) are given below each variance component. These analyses are for comparison with log-transformed analyses, but are not appropriate due to heterogeneity of error variance.

	Mixture	Pure	Wide
Variance component:			
Family	0 6779	0 1514	9.7430
CF	0 2154	0 0917	3 2048
SE CU	0 1070	0 1085	0 1609
CV	0.1979	0.1005	0.1009
Plot	-0.1547	0.1102	-0.5629
SE	0.2129	0.1814	3.3752
CV	0	0.0925	0
Within plot	7.2499	5.5974	107.4086
SE	0.3786	0.2952	5.7330
CV	0.6473	0.6596	0.5342
Additive	2.0337	0.4543	29.2290
SE	0.6463	0.2751	9.6143
CV	0.3428	0.1879	0.2787
Phenotypic (Indiv-tree basis) 7.9278	5.8590	117.1516
SE	0.3786	0.2665	5.7111
CV	0.6768	0.6748	0.5579
Phenotypic (Fam-mean basis)	0.9785	0.3971	14.2910
SE	0.2139	0.0888	3.1776
CV	0.2378	0.1757	0.1949
Heritability:			
Individual-tree heritability	0.257	0.078	0.249
SE	0.076	0.046	0.077
Pauila basitability	0 520	0 286	0 511
Family heritability	0.520	0.200	0.011
SE	0.054	0.112	0.057
Estimated genetic gain:			
Coin from individual-tree			
celection (grame)	0 724	0 189	2 695
Democratic (grams)	17 /	5 3	13 0
retcent	1/.4	ر.ر	13.7
Gain from family			
selection (grams)	1,029	0.360	3.864
Percent	24.7	10.0	19.9

Table A.5. Analyses of covariance for log biomass using first-year height as the covariate; (A) combined analysis to test family x competitive environment interaction; (B-D) analyses within each competitive environment.

Source df SS F probability Block 6 21.1357 339.35 0.0001 Whole-plot error 12 32.4822 5.37 0.0001 Family 38 37.0164 5.37 0.0001 Split-plot error 683 123.9582 0.0 0 (B) Analysis of families in mixture	(A) Combined	analysis			
Source df SS F probability Block 6 21.1357 339.35 0.0001 Whole-plot error 12 32.4822 5.37 0.0001 Family 38 37.0164 5.37 0.0001 Sourcate 1 215.0893 1185.13 0.0 Split-plot error 683 123.9582 0.0 0.0 Block 6 25.4655 5 5 Family 38 16.1119 2.92 0.0001 Error 228 33.0890 0.0001 0.0001 Govariate 1 290.9887 0.0001 0.0001 Error					
Block 6 21.1357 Comp. Envir. 2 1837.1381 339.35 0.0001 Whole-plot error 12 32.4822 Family 38 37.0164 5.37 0.0001 Family 38 37.0164 5.37 0.0001 Family X CE 76 16.3281 1.18 0.1461 Covariate 1 215.0893 1185.13 0.0 Split-plot error 683 123.9582 0.0001 (B) Analysis of families in mixture Source df SS F probability Block 6 25.4655 5 5 Family 38 16.1119 2.92 0.0001 Error 228 33.0890 0 0.0001 Covariate 1 290.9887 1 1 Within plot 719 99.6249 0.0001 1 Block 6 21.9179 1 1 1 Block 6 21.9179 1 1 0.0001 Error 2	Source	df		F	probability
Block 0 2 11.1537 Gomp. Envir. 2 1837.1381 339.35 0.0001 Whole-plot error 12 32.4822	Block	. 6	21 1357		
Whole-plot error 12 32.4822 Family 38 37.0164 5.37 0.0001 Family XCE 76 16.3281 1.18 0.1461 Covariate 1 215.0893 1185.13 0.0 Split-plot error 683 123.9582 0.0 (B) Analysis of families in mixture Source df SS F probability Block 6 25.4655 5 5 Family 38 16.1119 2.92 0.0001 Error 228 33.0890 0.0001 Covariate 1 290.9887 0.0001 Within plot 719 99.6249 0.0001 (B) Analysis of families in pure 5 S F probability Block 6 21.9179 12.12.8101 0.0001 Error 228 57.6343 0.0001 112.8101 (B) Analysis of families in wide (B) Analysis of families in wide 100.0001	Comp Envir	2	1837 1381	339 35	0.0001
Image: Solution of the second seco	Whole-plot er	ror 12	32 4822	557.55	0.0001
Family x CE 76 16.3281 1.18 0.1461 Covariate 1 215.0893 1185.13 0.0 Split-plot error 683 123.9582 0.0 (B) Analysis of families in mixture Source df SS F probability Block 6 25.4655 5 5 Family 38 16.1119 2.92 0.0001 Error 228 33.0890 0.0001 Covariate 1 290.9887 0.0001 Within plot 719 99.6249 0.0001 (B) Analysis of families in pure 50 5 5 Source df SS F probability Block 6 21.9179 5 0.0001 Error 228 57.6343 0.0001 5 Error 228 57.6343 0.0001 Error 228 57.6343 0.0001 Covariate 1 305.5994 0.0001 (B) Analysis of families in wide (B) Analysis of families in wide 0.0001 <td>Family</td> <td>38</td> <td>37 0164</td> <td>5 37</td> <td>0.0001</td>	Family	38	37 0164	5 37	0.0001
The formation of the second se	Family v CE	76	16 3281	1 18	0.1461
Source in a construction of the second secon	Covariate	, 0	215,0893	1185.13	0.0
(B) Analysis of families in mixtureSourcedfSSFprobabilityBlock625.46552.920.0001Error22833.08902.920.0001Covariate1290.98870.0001Within plot71999.62499(B) Analysis of families in pureSourcedfSSFprobabilityBlock621.91792.140.0001Error22857.63432.140.0001Error22857.63432.140.0001Error1305.59940.0001Within plot712112.81010.0001	Split-plot er	ror 683	123.9582	1100.10	
(B) Analysis of families in mixtureSourcedfSSFprobabilityBlock625.46552.920.0001Error22833.08902.920.0001Covariate1290.9887 \cdot \cdot Within plot71999.624999.6249 \cdot (B) Analysis of families in pureSourcedfSSFprobabilityBlock621.91792.140.0001Error22857.63432.140.0001Error22857.63432.140.0001Error22857.6343 \cdot \cdot (B) Analysis of families in wide(b) Analysis of families in wide \cdot \cdot					
(B) Analysis of families in mixtureSourcedfSSFprobabilityBlock625.46552.920.0001Error22833.08902.920.0001Covariate1290.9887					
Source df SS F probability Block 6 25.4655 2.92 0.0001 Error 228 33.0890 2.92 0.0001 Covariate 1 290.9887	(B) Analysis	of famili	les in mixtur	e	
Source df SS F probability Block 6 25.4655 2.92 0.0001 Error 228 33.0890 2.92 0.0001 Error 228 33.0890 2.92 0.0001 Covariate 1 290.9887 2.92 0.0001 Within plot 719 99.6249 2.92 0.0001 (B) Analysis of families in pure 50 50 50 50 Source df SS F probability Block 6 21.9179 2.14 0.0001 Error 228 57.6343 2.14 0.0001 Error 228 57.6343 2.14 0.0001 (B) Analysis of families in wide (B) Analysis of families in wide 2.14 0.0001					
Block 6 25.4655 Family 38 16.1119 2.92 0.0001 Error 228 33.0890 0 0 Covariate 1 290.9887 0 0 Within plot 719 99.6249 0 0 (B) Analysis of families in pure 0 0 0 0 Source df SS F probability Block 6 21.9179 0 0 0 Family 38 20.5435 2.14 0 0 Error 228 57.6343 0 0 0 0 (B) Analysis of families in wide 1 305.5994 0 0 0 0 (B) Analysis of families in wide 0 0 0 0 0 0 0	Source	df	SS	F	probability
Block 6 25.4633 Family 38 16.1119 2.92 0.0001 Error 228 33.0890 0 0 Covariate 1 290.9887 0 0 Within plot 719 99.6249 0 0 (B) Analysis of families in pure 0 0 0 0 Source df SS F probability Block 6 21.9179 0.0001 0 Family 38 20.5435 2.14 0.0001 Error 228 57.6343 0 0 Covariate 1 305.5994 0 0 Within plot 712 112.8101 0 0	D11-	(
Family 36 16.1119 2.92 0.0001 Error 228 33.0890 0.0001 Covariate 1 290.9887 0.0001 Within plot 719 99.6249 0.0001 (B) Analysis of families in pure 0.0001 0.0001 Source df SS F Block 6 21.9179 Family 38 20.5435 2.14 Error 228 57.6343 Covariate 1 305.5994 Within plot 712 112.8101	BLOCK	0 20	25.4055	2 92	0 0001
Error 226 53.0890 Covariate 1 290.9887 Within plot 719 99.6249 (B) Analysis of families in pure	Family	20	22 0000	2.92	0.0001
Covariate1250.9887Within plot71999.6249(B) Analysis of families in pureSourcedfSSFBlock621.9179Family3820.54352.14Error22857.6343Covariate1305.5994Within plot712112.8101	EIIOI	220	22.0090		
Within plot71339.0249(B) Analysis of families in pureSourcedfSSFBlock621.9179Family3820.54352.14Error22857.6343Covariate1305.5994Within plot712112.8101	Uithin plot	710	290.9007		
(B) Analysis of families in pureSourcedfSSFprobabilityBlock621.91792.140.0001Family3820.54352.140.0001Error22857.63432.140.0001Covariate1305.59944Within plot712112.81014(B) Analysis of families in wide	within piot	/19	<u> </u>		
(B) Analysis of families in pureSourcedfSSFprobabilityBlock621.9179Family3820.54352.140.0001Error22857.63430.0001Covariate1305.59940.0001Within plot712112.81010.0001					
Source df SS F probability Block 6 21.9179 2.14 0.0001 Family 38 20.5435 2.14 0.0001 Error 228 57.6343 5994 5994 Within plot 712 112.8101 112.8101 112.8101	(B) Analysis	of famili	les in pure		
Source df SS F probability Block 6 21.9179 2.14 0.0001 Family 38 20.5435 2.14 0.0001 Error 228 57.6343 - - Covariate 1 305.5994 - - Within plot 712 112.8101 - -	(2)		F		
Block 6 21.9179 Family 38 20.5435 2.14 0.0001 Error 228 57.6343 0.0001 Covariate 1 305.5994 0.0001 Within plot 712 112.8101 0.0001	Source	df	SS	F	probability
Block 6 21.9179 Family 38 20.5435 2.14 0.0001 Error 228 57.6343 0.0001 Govariate 1 305.5994 0.0001 Within plot 712 112.8101 0.0001					
Family 38 20.5435 2.14 0.0001 Error 228 57.6343 0.0001 Covariate 1 305.5994 0.0001 Within plot 712 112.8101 0.0001 (B) Analysis of families in wide 0.0001 0.0001	Block	6	21.9179		
Error 228 57.6343 Covariate 1 305.5994 Within plot 712 112.8101 (B) Analysis of families in wide	Family	38	20.5435	2.14	0.0001
Covariate1305.5994Within plot712112.8101(B) Analysis of families in wide	Error	228	57.6343		
Within plot 712 112.8101 (B) Analysis of families in wide	Covariate	1	305.5994		
(B) Analysis of families in wide	Within plot	712	112.8101		
(B) Analysis of families in wide					
(B) Analysis of families in wide	<i></i>				
	(B) Analysis	of famili	les in wide		
Source of SS F probability	Courses	AF	CC	F	nrobability
Source at SS r probability	Source	<u></u>		<u>r</u>	probability
Block 6 18,0063	Block	6	18,0063		
Family $38 16.1649 2.32 0.0001$	Family	38	16,1649	2.32	0.0001
Error 228 41.8332	Error	228	41.8332	2.52	
Covariate 1 159.2170	Covariate	1	159.2170		
Within plot 699 129,8492	Within nlot	699	129.8492		
	proo				

Table A.6. Analyses of variance in which log biomass is adjusted for family differences in seed weight by regressing mean log biomass on mean seed weight, and then using predicted values subtracted from observed values from the regression in the analysis of variance.

ÿ					
Source	df	SS	MS	F	prob a bility
Block Family Error	6 38 228	4.8366 50.3588 105.1171	0.8061 1.3252 0.4610	2.87	0.0001

Analysis of families in mixture

Analysis of families in pure

Source	df	SS	MS	F	probability
Block Family Error	6 38 228	14.3526 30.7645 130.6738	2.3921 0.8096 0.5732	1.41	0.0660

Source	df	SS	MS	F	probability
Block Family Error	6 38 228	48.9128 33.8549 103.2386	8.1521 0.8909 0.4528	1.97	0.0013

Analysis of families in wide

Table A.7. Analyses of variance to test interaction of families between pairs of competitive environments; (A) between mix and pure; (B) between pure and wide; (C) between mix and wide.

Source	df	SS	MS	F	probability	
Block	6	13.65	2,2753			
Comp. Envir.	1	10.89	10.8860	21.05	0.0001	
Whole-plot error	6	5.71	0.9519			
Family	38	90.82	2.3900	4.62	0.0001	
Family x CE	38	24.63	0.6482	1.25	0.1487	
Split-plot error	456	235.81	0.5171			
Within plot	1436	809.02	0.5646			

(A) Analysis with mix and pure as competitive environments

(B) Analysis with pure and wide as competitive environments

Source	df	SS	MS	F	probability
Block	6	25.59	4.2652		
Comp. Envir.	1	1464.15	1464.1515	233.71	0.0001
Whole-plot error	6	37.59	6.2648		
Family	38	64.05	1.6856	3.29	0.0001
Family x CE	38	23.23	0.6112	1.19	0.2067
Split-plot error	456	233.93	0.5130		
Within plot	1418	707.48	0.5007		
-					

(C) Analysis with mix and wide as competitive environments

df	SS	MS	F	probability
6	33.29	5.5499		
1	1228.46	1228.4601	358.27	0.0001
6	20.57	3.4289		
38	93.72	2.4664	5.40	0.0001
38	24.10	0.6342	1.39	0.0664
456	208.36	0.4569		
1415	679.68	0.4786		
	df 6 38 38 456 1415	df SS 6 33.29 1 1228.46 6 20.57 38 93.72 38 24.10 456 208.36 1415 679.68	dfSSMS633.295.549911228.461228.4601620.573.42893893.722.46643824.100.6342456208.360.45691415679.680.4786	dfSSMSF633.295.549911228.461228.4601620.573.42893893.722.46643824.100.6342456208.360.45691415679.680.4786

Family	CA	Rank	DT	Rank	CD	Rank
650	0 065	27	-1 358	2	-1 203	з
653	0.005	27	-1.558	30	-1.295	20
655	0.550	29	-1.070	12	-1.555	20
656	0.052	18	-1.533	13	-1.547	10
658	0.100	5	-1.831	27	-1.40	7
659	-0 181	36	-1.538	27	-1 719	31
660	0 102	24	-2 091	37	-1 988	37
663	0.102	4	-1 954	34	-1 531	19
664	0.444	- 	-1 916	33	-1 472	12
666	-0 167	35	-1 420	5	-1 586	26
667	-0.189	37	-1 709	18	-1 898	36
669	0 162	19	-1 275	1	-1,113	1
675	0 181	17	-1 559	10	-1.378	5
676	-0 461	39	-1.785	23	-2.245	38
682	0.318	10	-1.788	24	-1.469	11
683	-0 048	32	-1.577	11	-1.625	28
684	0 247	13	-1.683	16	-1.435	8
685	0 040	30	-1.764	21	-1.725	32
688	0.181	16	-1.703	17	-1.522	18
692	-0.408	38	-1.980	36	-2.388	39
717	0.213	15	-1.775	22	-1.563	22
718	0.062	28	-1.461	6	-1.399	6
720	0.131	21	-1.499	7	-1.368	4
721	-0.118	34	-1.398	3	-1.516	16
725	0.097	25	-1.899	32	-1.802	35
726	0.348	7	-1.869	29	-1.520	17
727	0.065	26	-1.544	9	-1.479	13
728	0.233	14	-1.805	26	-1.572	24
729	0.336	9	-2.123	38	-1.787	34
736	0.156	20	-1.643	15	-1.487	14
737	0.392	6	-1.976	35	-1.584	25
740	0.258	11	-1.761	20	-1.504	15
741	0.555	2	-1.711	19	-1.156	2
743	0.256	12	-1.866	28	-1.610	27
744	0.107	23	-1.888	31	-1.781	33
745	-0.044	31	-1.403	4	-1.448	9
746	-0.060	33	-1.620	14	-1.681	30
749	0.672	1	-2.237	39	-1.566	23
751	0.115	22	-1.794	25	-1.679	29

Table A.8. Family values for competitive ability (CA), density tolerance (DT), and competitive-density ability (CD).

	CA	DT	CD
CA	1.00000	-0.42707 0.0067	0.58460 0.0001
DT		1.00000	0.48395 0.0018
CD			1.00000

Table A.9. Correlations between family values for competitive ability (CA), density tolerance (DT), and competitive-density ability (CD).

Table A.10. Overall means for mix, pure, and wide competitive environments for several measures of performance, and percent difference between measures of performance for mix and pure competitive environments.

Measure	Mix	Pure	Wide	Percent	Difference
Log biomass (g)	1.18	1.02	2.76	15.5	
Biomass (g)	4.16	3.59	19.40	15.9	
2-yr height (mm)	369	338	352	9.4	
l-yr height (mm)	110	93	100	18.8	
Diameter (mm)	3.68	3.47	7.51	6.0	
Volume (mm ³)	6029	4848	23415	24.4	
Stem weight (g)	1.43	1.12	4.68	27.7	
Shoot weight (g)	3.08	2.55	12.67	21.1	

	Means			F-values			
Trait	Mixture	Pure	Wide	M vs P	M vs W	P vs W	
Branch angle	4.94	5.11	5.57	1.13	31.69***	5.74**	
Branch number	11.0	9.9	15.8	5.81*	18.03***	16.96***	
Crown width/height	0.245	0.236	0.563	6.05**	709.56***	1538.83**	
Height/diameter	1.06	1.01	0.48	1.44	686.30***	179.62**'	
Proportion roots	0.267	0.307	0.363	13.50**	51.58***	7.18**	
Proportion stem	0.334	0.298	0.236	26.78***	220.10***	33.53**'	
Proportion branches	s 0.045	0.037	0.100	18.19***	370.52***	234.63**'	
Proportion foliage	0.353	0.358	0.301	1.17	71.07***	53.55**'	

Table A.11. Means and statistical significance of means between three competitive environments for seedling architecture traits.

significantly different at p=0.01

significantly different at p=0.05significantly different at p=0.10