AN ABSTRACT OF THE THESIS OF

James Hamlin for the degree of Doctor of Philosophy

in Forest Science presented on February 25, 1993.

Title: Quantitative Genetic Structure of Douglas-fir Populations from Southwest Oregon.

Signature redacted for privacy.

Abstract approved: _____

Wesley T. Adams Robert K. Campbell

The major objectives of this study were: (1) to determine the extent to which southwest Oregon populations of Douglas-fir [Pseudotsuga menziesii var menziesii (Mirb.) Franco] differ in quantitative genetic structure (QGS); (2) to determine whether differences in QGS are associated with the environments from which populations originate; and (3) to examine the implications of differences in QGS with regards to expected responses of traits to selection. A two year seedling common garden study was conducted where eight populations (45 families/population), two from each of four major coniferous zones, were sampled.

Variation among populations in QGS was predominately associated with differences in trait means and genetic correlations among traits. The largest differences occurred between the coastal region and the high elevation inland region. The major differences in QGS were associated with differences in correlations between growth and phenology traits in the second growing season.

Differences in QGS were positively associated with the extent of habitat divergence for those comparisons between trait means and genetic correlations. The paired populations within an ecological zone were more similar, in general, than populations from different ecological zones. Three major homogeneous associations, as measured by cluster analysis of both trait means and phenotypic correlation matrices, were found and are geographically aligned to the coastal region, a lower elevation inland region, and a higher elevation inland region of southwest Oregon. Natural selection within these general physiographic regions would appear to be one explanation for the observed patterns in this study.

When selecting for increased height growth in these four major zones, differences among zones in both direct and correlated responses are expected. Expected correlated responses in phenology traits when selection is directed at height growth, while variable among zones, does not appear large enough to adversely affect adaptability to a large degree. Restriction (0% change) of phenology and/or shoot:root ratios in a restricted selection index would severely limit growth response in two of the four zones. Restricted selection indices should be used only when necessary, and their effects should be assessed prior to implementation in an applied breeding program. Knowledge of QGS of populations should be ascertained so that biological impacts of breeding and/or movement of reproductive materials outside of their native habitats can be assessed.

QUANTITATIVE GENETIC STRUCTURE OF DOUGLAS-FIR POPULATIONS FROM SOUTHWEST OREGON

by

JAMES HAMLIN

A THESIS

submitted to

OREGON STATE UNIVERSITY

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed February 25, 1993

Commencement June 1993

ACKNOWLEDGEMENTS

I would like to express my gratitude to the members of my committee: Drs. W. T. Adams, R. K. Campbell, W. Emmingham, J. Hall, W. Hohenboken, and K. Rowe. Their help and assistance throughout the course of the program is greatly appreciated. Indeed, I was fortunate to have this select group as advisors. I am especially indebted to my co-major professors, Drs. W. T. Adams and R. K. Campbell, for their direction, guidance, and time spent in evaluating drafts of the thesis. Their assistance was invaluable.

I appreciate the help provided by the numerous personnel which assisted me throughout the study. I thank the personnel at the USDA Forest Service, Dorena Tree Improvement Center, for their time and effort in packaging of the seedlots. I thank the personnel at the J. Herbert Stone Nursery for their efforts throughout the field portion of the study; from initial establishment through the final lifting and measurement stage. I thank Dr. Ray Steinhoff for his assistance in obtaining the final dry weight measures of the study materials. This study could not have been conducted without the help of these personnel.

I wish to thank the USDA Forest Service for their support, and for the opportunity to pursue the advanced degree while working. In particular, I am very grateful to Ken Roberts and Peter Theisen who originally made it possible.

I appreciate the support of my entire family through the years. I am indebted to my wife, Barbara, for her support. Her encouragement and gentle prodding helped me along in the course of the program.

I also thank my daughter, Tina, for serving as a part-time recorder for those measurements taken at the end of each year.

TABLE OF CONTENTS

	Page
GENERAL INTRODUCTION	1
CHAPTER ONE. DIFFERENCES AMONG POPULATIONS OF DOUGLAS-FIR FROM DIVERSE HABITATS IN QUANTITATIVE GENETIC STRUCTURE	4
ABSTRACT	4
INTRODUCTION	6
MATERIALS AND METHODS	10
RESULTS	20
DISCUSSION AND CONCLUSIONS	30
CHAPTER TWO. IMPLICATIONS OF DIFFERENCES AMONG DOUGLAS-FIR POPULATIONS IN QUANTITATIVE GENETIC STRUCTURE FOR TREE BREEDING	57
ABSTRACT	57
INTRODUCTION	59
MATERIALS AND METHODS	62
RESULTS AND DISCUSSION	70
CONCLUSIONS	79
GENERAL CONCLUSIONS	87
BIBLIOGRAPHY	91
APPENDICES	96
APPENDIX A: Correlations between estimated genetic and phenotypic correlations of traits for the eight study populations	96
APPENDIX B: Estimated phenotypic and genetic correlations for seedling trait pairs	98

LIST OF FIGURES

Figure		Page
I.1	Location of study populations in southwest Oregon.	53
I.2	Seven orthogonal contrasts (CT-#1 to CT-#7) used to compare population means.	54
I.3.	Cluster diagram for eight populations based on dissimilarities of their trait means.	55
I.4.	Cluster diagram for eight populations based on dissimilarities (Dr_m) of their phenotypic correlation matrices.	56

LIST OF TABLES

Table		Page
I.1.	Location and environmental characteristics of southwest Oregon populations.	41
I.2.	Description of traits.	42
I.3.	Forms of the analyses of variance and covariance: (A) All populations together, (B) Individual source populations separately.	43
I.4.	Trait means and coefficients of variation (in parentheses) for the study populations.	44
I.5.	Comparison of population means for individual traits under seven orthogonal contrasts.	45
I.6	Dissimilarity matrix between 8 populations.	46
I.7.	Traits with significant family components of variance (σ^2_f) within populations.	47
I.8.	Estimates of individual heritabilities for nineteen traits in 8 populations.	48
I.9.	Matrix of pairwise combinations of 8 populations showing which combinations differed significantly ($P<.05$) in their phenotypic correlation matrices (indicated by * in upper diagonal); and the percentage of individual correlations which differed significantly over all trait pairs tested (upper diagonal), and for specific subsets (a,b,c) of trait pairs (lower diagonal).	49
I.10.	Pairwise dissimilarities (Dr_m, upper diagonal), and similarities (Sr_m, lower diagonal) between phenotypic correlation matrices of 8 populations.	50
I.11.	Estimates of phenotypic correlations in two Coastal populations (C-1, upper diagonal and C-2, lower diagonal) for a subset of seedling trait pairs.	51
I.12	Estimates of phenotypic correlations in two Western Cascade populations (WC-1, upper diagonal and WC-2, lower diagonal) for a subset of seedling trait pairs.	51

Table		Page
I.13.	Estimates of phenotypic correlations in two Siskiyou populations (S-1, upper diagonal and S-2, lower diagonal) for a subset of seedling trait pairs.	52
I.14.	Estimates of phenotypic correlations in two Mixed-Conifer populations (MC-1, upper diagonal and MC-2, lower diagonal) for a subset of seedling trait pairs.	52
II.1.	Description of traits.	81
II.2.	Form of analyses of variance and covariance for the pooled data sets.	82
II.3.	Estimated genetic correlations (above diagonal) and phenotypic correlations (below diagonal) between seedling traits for populations from each of four ecological zones.	83
II.4.	Estimated means, phenotypic variances (σ^2_p), family components of variance (σ^2_f), family heritabilities (h^2_f), and expected responses to family selection (R_y) per unit of selection intensity ($i = 1.0$), for six seedling traits in populations from each of four ecological zones.	84
II.5.	Estimated direct and correlated responses within populations from each of four ecological zones when selecting for seedling height growth (HT1 or HT2).	85
II.6.	Estimated responses of seedling height (HT1 or HT2) in populations from each of four ecological zones, when restriction selection indices (models 2 - 4) are used to restrict change in correlated traits to zero.	86

LIST OF TABLES IN APPENDICES

Table		Page
A.1.	Correlation between estimated genetic and phenotypic correlations between traits for each of eight populations in southwest Oregon.	97
B.1.	Description of traits in this appendix.	99
B.2.	Estimates of phenotypic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs. Population: C-1.	100
B.3.	Estimates of phenotypic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs. Population: C-2.	101
B.4.	Estimates of phenotypic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs. Population: WC-1.	102
B.5.	Estimates of phenotypic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs. Population: WC-2.	103
B.6.	Estimates of phenotypic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs. Population: S-1.	104
B.7.	Estimates of phenotypic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs. Population: S-2.	105
B.8.	Estimates of phenotypic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs. Population: MC-1.	106
B.9.	Estimates of phenotypic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs. Population: MC-2.	107
B.10.	Estimates of genetic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs. Population: C-1.	108
B.11.	Estimates of genetic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs. Population: C-2.	109

Table		Page
B.12.	Estimates of genetic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs. Population: WC-1.	110
B.13.	Estimates of genetic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs. Population: WC-2.	111
B.14.	Estimates of genetic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs. Population: S-1.	112
B.15.	Estimates of genetic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs. Population: S-2.	113
B.16.	Estimates of genetic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs. Population: MC-1.	114
B.17.	Estimates of genetic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs. Population: MC-2.	115

QUANTITATIVE GENETIC STRUCTURE OF DOUGLAS-FIR POPULATIONS FROM SOUTHWEST OREGON

GENERAL INTRODUCTION

Southwest Oregon represents a region of great diversity in geology, climate, and vegetation associations. Portions of the Siskiyou and Cascade mountain ranges occur in this region where they are separated by a major valley. These mountain ranges, in conjunction with their wide elevation span (sea level to 2894 m) and variable proximity to the Pacific Ocean (range from 0 to 170 km inland), create extreme climatic heterogeneity. A more maritime climate (cooler, moister) exists on the coast while a more mediterranean climate (hotter, dryer) exists inland. These conditions create a great mosaic of plant associations and tree species. Within the region, four major coniferous forest zones are identified: Tsuga heterophylla (Coast range mountains), Tsuga heterophylla (low to mid elevations in Western Cascade mountains), Mixed-Evergreen (Siskiyou mountains), and Mixed-Conifer (high elevations in the Western Cascade and Siskiyou mountains) (Franklin and Dyrness 1973). Douglas-fir [Pseudotsuga menziesii var menziesii (Mirb.) Franco] is an important species component in all four of these zones.

Douglas-fir exhibits a great deal of genetic variation for morphological, physiological, and isozyme traits (Campbell 1987). A number of common garden studies have noted the correlation of genetic patterns of geographic variation with environment of seed source and the apparent adaptive significance of these correlations (Stern and Roche

1974, Silen 1978). The majority of these studies, however, have not examined variation among populations in quantitative genetic structure (QGS), where QGS refers to within population measures of amounts of genetic variation, heritabilities of individual traits, and relationships (covariances and correlations) among traits.

Knowledge of QGS and it's variation among populations provide a conceptual framework from which to quantify potential constraints in the amount and direction of evolutionary change (Mitchel-Olds and Bergelson 1990). In addition, the relative importance of natural selection might be inferred from the degree of association of QGS with specific source environments. If QGS differs among populations, responses of both directly selected and correlated traits in applied breeding programs may also differ, making it necessary to formulate separate breeding strategies for each population.

Published reports on variation in QGS among populations of forest tree species are few, and of those available, the majority have lacked the statistical precision necessary for assessing the biological significance and practical implications of variation in QGS. Two studies specific to Douglas-fir in southwest Oregon (Kaya 1987, Mangold 1988) reported differences among populations in genetic correlation coefficients, suggesting significant geographic variation in QGS may exist in the region. This study follows up on this suggestion, investigating the extent to which Douglas-fir populations from the four major coniferous zones in southwest Oregon differ in QGS.

The remainder of this thesis is composed of two Chapters and a General Conclusions. Chapter 1 investigates the extent to which populations of Douglas-fir in southwest Oregon differ in QGS, and determines whether differences in QGS are associated with environment of origin. Two populations were sampled from each of the four major coniferous zones and differences between populations within zones as well as among zones were tested.

In Chapter 2, implications of differences in QGS for breeding strategies are investigated for the four major zones. Direct responses in first- and second-year height, as well as correlated responses in other (adaptive) traits, were compared. In addition, restricted selection indices were used to explore the extent to which expected response in seedling height (primary trait) is limited, when correlated adaptive traits (secondary traits) are limited to no change.

In General Conclusions, the major findings of the two Chapters are summarized. In addition, some thoughts and recommendations are presented on how future work of this nature can be improved.

CHAPTER ONE

DIFFERENCES AMONG POPULATIONS OF DOUGLAS-FIR FROM DIVERSE HABITATS IN QUANTITATIVE GENETIC STRUCTURE

ABSTRACT

Eight populations of Douglas-fir [Pseudotsuga menziesii var menziesii (Mirb.) Franco], two from each of four ecologically distinct zones in southwest Oregon, were examined for differences in quantitative genetic structure (QGS): differences in trait means, genetic variances, heritabilities, and phenotypic and genetic correlations. Forty-five families from each population were grown in a common garden study for two growing seasons with a total of 22 seedling traits measured. Within populations, genetic and phenotypic (family mean) correlations were strongly associated so that only phenotypic correlations were utilized in population comparisons.

The eight populations varied substantially in estimates of both trait means and phenotypic correlations, but not for genetic variances or heritabilities of traits. The greatest differences in correlations were for trait-pairs where growth phenology was correlated with absolute growth. In general, the degree of differentiation in both trait means and phenotypic correlations were positively related to the extent of habitat divergence of population origins, and geographical patterns of variation appeared to reflect adaptation of populations to their source environments. Differences among populations in QGS have ramifications with regards to expected responses from selection in applied breeding

programs. Thus, it is desirable to evaluate QGS separately for each breeding population, and especially so if populations come from widely different environments.

INTRODUCTION

Patterns of genetic variation associated with population origin have been documented for coastal Douglas-fir [Pseudotsuga menziesii var menziesii (Mirb.) Franco] in a variety of regions throughout its' range (Silen 1978). In southwest Oregon, Douglas-fir grows in a mosaic of environments where strong moisture and temperature gradients extending eastward from the Pacific coast inland, and mountainous topography, create a large variety of communities and plant associations (Franklin and Dyrness 1973). A number of common garden studies have been employed to evaluate geographical patterns of genetic variation in this region for a variety of seedling traits (e.g., Ferrell and Woodward 1966, Hermann and Lavender 1968, Sorensen 1983, Campbell 1986, White 1987, Loopstra and Adams 1989, Kaya et. al. 1989). For many of the traits investigated, genetic patterns of variation appear to be highly correlated with environmental variables as reflected by latitude, longitude, elevation, and topographic features. These correlations suggest that natural selection has played a prominent role in shaping the observed patterns (Endler 1986).

Sampling in common garden studies usually employs a large number of populations each represented by relatively few individuals (ranging from 2 to 25 families in most studies), which are measured for relatively few traits. This sampling scheme is sufficient to meet the major objective of these studies, which is to delineate patterns of variation of individual traits over a large geographic area. Limited sampling of

both traits and individuals within populations, however, makes it difficult or impossible to compare the genetic composition of populations as reflected in their quantitative genetic structure (QGS). QGS is described by quantitative genetic parameters such as means, genetic variances, heritabilities of individual traits, and relationships among traits (i.e., covariances and correlations). The degree to which populations differ in QGS, and the association of QGS with geographic origin, are of great evolutionary and practical significance. To what extent, for example, have populations evolved co-adapted gene complexes, and are QGS's associated with specific source environments?

Differences among populations in QGS could have a number of implications for tree breeding. It is important to know to what extent quantitative genetic parameters derived for one population are applicable to others. If large differences in QGS exist, genetic parameters may have to be estimated separately for different breeding populations and selection strategies tailored for each case. Differences in QGS resulting from adaptation to specific environmental factors need to be recognized and planned for in breeding programs, since correlations between growth/wood properties (e.g., stem volume, branch size, wood density) and other adaptive traits (e.g., timing of budburst and budset, cold hardiness) may differ among populations. The adaptive significance of QGS also has important ramifications when choosing seed sources for reforestation. Seed transfer guidelines for deployment of reforestation stock are based on the premise of genetic adaptation within the transfer limits (Campbell 1986). If adaptation has resulted in co-adapted trait

complexes that are associated with specific source environments, then transfer between habitats that differ appreciably will lead to maladapted plantations.

Variation in QGS among populations within species has been reported for such diverse organisms as frogs (Berven 1987), migratory insects (Dingle et. al. 1988), and perennial grass (Silander 1985). In these cases, variation in QGS was theorized to have resulted, at least in part, from differing selection pressures in the environments of origin. Few published reports on the phenotypic and genetic structure of populations and their association with habitat of origin are available for forest tree species. Limited observations in Douglas-fir, however, suggest that QGS may vary substantially among populations in this species. Genetic structure of 26 populations from the Western Cascade mountains of Washington were assessed in a series of provenance trials established in France (Birot and Christophe 1983). Although the number of families assessed per population was small (≤ 15), estimated genetic correlations between traits and heritabilities of individual traits differed significantly among populations. Two Douglas-fir studies in southwest Oregon also reported variation in QGS. Kaya (1987), employing a sampling intensity of forty families per population, noted that genetic correlations for three pairs of seedling traits differed between coastal and inland populations. Mangold (1988) found that genetic correlations for various trait-pairs differed among three populations (thirty families sampled per population) along an elevational transect, but large standard errors were associated with the estimates. All of the above studies in

Douglas-fir were limited in numbers of families, traits assessed, or populations sampled. Indeed, none of these studies were designed specifically to ascertain the magnitude and degree to which QGS varies among populations.

In the study described in this chapter, a seedling common garden experiment was utilized to: 1) further investigate the extent to which southwest Oregon populations of Douglas-fir differ in QGS, and 2) to determine whether differences in QGS are associated with the environments from which populations originate. Populations were sampled from areas which contrasted strongly in temperature and moisture regimes and plant associations.

MATERIALS AND METHODS

Study Populations

Eight populations, two from each of four ecologically distinct zones in southwest Oregon, were chosen for sampling (Figure I.1). The zones represent the four major coniferous forest types in this region (Franklin and Dyrness 1973): Tsuga heterophylla (Coast range mountains; C-1, C-2), Tsuga hetorophylla (low to mid elevations in Western Cascade mountains; WC-1, WC-2), Mixed-Evergreen (Siskiyou mountains; S-1, S-2), and Mixed-Conifer (high elevations in the Western Cascade and Siskiyou mountains; MC-1, MC-2). The two populations in each ecological zone have very similar plant associations even though they are separated by up to one-half degree in latitude, and differ in elevation, on average, by up to 305 m. The zones differ with respect to location (latitude, longitude, elevation) and environmental characteristics (Table I.1). Latitude, longitude, and elevation have been the variables most highly correlated with genetic variation patterns in previous work, and have been utilized in models for seed transfer guidelines (Adams and Campbell 1981, Campbell 1986). Although the two Tsuga hetorophylla zones from which the Coastal (C-1, C-2) and W. Cascade (WC-1, WC-2) populations were sampled are similar with respect to major tree species and plant associations, they differ in a number of other respects. The Coastal mountain range has higher precipitation, cooler average summer temperatures, longer frost-free growing seasons, and higher productivity (biomass/hectare) than the W. Cascade mountain range (Franklin and

Dyrness 1973). The two Siskiyou (SI-1, SI-2) and two high elevation Mixed-Conifer (MC-1, MC-2) populations are found in more xeric environments where higher summer temperatures, high evapotranspiration rates, and droughty soils abound. These environmental conditions promote a more diverse mixture of conifer species than found in the more mesic Coastal and W. Cascade populations (Table I.1).

Materials

Within each of the designated populations, wind-pollinated seeds had been collected in previous years from individual parent trees for U.S. Forest Service tree improvement programs. Little selection intensity was applied in choosing the parent trees, such that with the exception of exhibiting propensity for cone production during the year of seed collection, the trees were essentially random samples of the population. Parent trees representing each population came from a relatively limited geographic area (39 to 207 km^2) and elevational range (305 to 336 m).

Within each population, seeds (families) from 45 parent trees were sampled from seedlots that were available in storage. The seedlots were collected in 1978, 1980, and 1982. Seedlots were chosen at random except that they were restricted to the same collection year within an individual population and were from parent trees separated from each other by at least 160 m to insure a high probability of non-relatedness between families.

Experimental Methods

After soaking in circulating water for 48 hours and stratifying for 55 days at 2° C, seeds were hand sown (April 16-17, 1985) at the J. Herbert Stone Nursery located in southwest Oregon (latitude - 42° 20' north, longitude - 122° 55' west, elevation - 390 m (Figure I.1). This nursery produces bareroot seedlings for U.S. Forest Service planting programs in the region. The experimental design in the nursery was a randomized complete block with four replications. A five-seedling row plot for each of the 360 families (8 populations X 45 families/population) was allocated at random within each replication. There was a total of 7200 test seedlings (360 families X 5 seedlings/plot X 4 replications). A single-tree border row around the outside edge of the experimental plots was utilized to alleviate edge effects.

Five seeds were sown per planting spot to ensure germination and survival of one tree per spot. In the majority of cases, four or five seeds germinated within twenty days. Each planting spot was thinned randomly to one seedling by June 26, 1985. Final spacing of seedlings was 10 X 10 cm.

Seedlings were grown for two seasons using the standard cultural regime for Douglas-fir in this nursery, except no root pruning was permitted. Seedlings were irrigated at various time intervals through August of each season. This insured survival and growth characteristics typical of 2-0 seedlings produced operationally by the nursery. Irrigation was reduced substantially in September of each season to

promote hardening off. Seedling mortality after the first and second seasons was 0.9 and 1.2 percent, respectively. All family plots had a minimum of three surviving seedlings after two growing seasons.

Measured and Derived Traits

Eighteen traits were measured over the two growing seasons, and four additional traits were derived from the measurements (Table I.2). These traits represent measures of biomass, biomass allocation, growth phenology, and susceptibility to fall frost. In addition, they represent a sample of traits that are perceived as being adaptive singly or in combination with other traits at the seedling stage.

Within-family variation was also considered for analysis. Standard deviations among individuals within family plots were calculated for each population and trait (excluding FL1, FL2, and FR1). Analyses of variance (ANOVAs) indicated that variation among families in within-family standard deviations were not significant ($P > .05$) in most instances (in 89 % of the 152 separate ANOVAs). Therefore, within-plot standard deviations are not considered further as separate traits.

Statistical Analyses

Population means, genetic variances, and individual tree heritabilities for each trait, and genetic and phenotypic correlations between pairs of traits were estimated and compared among populations. Two different types of ANOVAs were utilized in these series of comparisons and statistical procedures. Initially, data (based on plot

means) from all eight populations were analyzed together for the purpose of testing differences among population means (Table I.3, A). An F-test was performed to test for significance of population differences (objective 1). For this and subsequent tests of differences between populations in QGS, differences at $P < .05$ are considered significant unless noted otherwise.

Population means were subjected to two additional procedures in order to assess whether they are associated with the environment of their origin (objective 2). The first procedure subdivided the seven degrees-of-freedom for populations into seven orthogonal single degree-of-freedom contrasts (Figure I.2). The seven contrasts compare mean population differences at three hierarchical levels: populations within zones (CT #1 through CT #4), populations between zones (CT #5 and CT #6) and populations between broad environmental associations (CT #7). If trait means are associated with environment, there should be a greater number of significant differences at the higher hierarchical levels. In the second procedure, a cluster analysis based on a dissimilarity matrix between the eight populations was conducted using the Proc Cluster procedure in SAS (SAS Institute 1988). There exist 28 [(8 x 7)/2] possible pairwise combinations of populations for which means may be compared. These differences between means were represented in a dissimilarity matrix which was used as input for the cluster analysis. The dissimilarity measure between any two populations was calculated as the scaled Euclidean distance (Krzanowski 1988:25):

$[\sum_{i}^{n} (x_{ji} - x_{ki})^2/w_i]^{1/2}$, where x_{ji} and x_{ki} are the estimated means for the

ith pair of traits in the jth and kth populations, respectively, w_i is the pooled within-group variance for the ith trait, and n = 19 (number of traits included in analysis; FL1, FL2, and FR1 were excluded). The cluster analysis should approximate Figure I.2 if the population means are associated in large measure with environments.

Populations were also compared for differences in genetic variance, individual tree heritabilities of traits, and genetic and phenotypic correlations between pairs of traits. In order to estimate these genetic and phenotypic parameters, ANOVA and analysis of covariance (Proc Manova, SAS Institute 1985) were conducted for all traits and all pairs of traits, respectively, in each of the eight populations separately (Table I.3, B). Analyses were based on individual tree data for estimating components of variance needed to calculate individual tree heritabilities, whereas analyses were based on plot means (no within-plot components estimated) for the purpose of estimating the remaining parameters. Statistical tests were conducted for each of the 28 pairwise combinations of populations. Significant differences between populations imply differing QGS (objective 1), whereas if QGS is associated with environment of population origin (objective 2), it is expected that differences will be greater between populations from the more distant hierarchical levels (Figure I.2).

Estimation of Genetic and Phenotypic Parameters

Variance and covariance components were estimated by equating the observed mean squares and cross products to expected values (Table I.3, B). Genetic variance (defined here as the family component of variance) was tested for significance in each of the univariate ANOVAs. Differences between genetic variance estimates for all 28 pairwise combinations of populations were tested by the F-ratio (two-tailed test) of the respective family mean squares. The ratio of the two respective family mean squares can be used to compare family components of variance as long as the data are balanced and error mean squares are homogeneous (Mitchell-Olds and Rutledge 1986).

Individual heritability (h^2_i) was estimated for each trait in each of the eight populations: $h^2_i = 3\ (\sigma^2_f)/[\sigma^2_f + \sigma^2_{fr} + \sigma^2_w]$ where σ^2_f, σ^2_{fr}, and σ^2_w are the components of variance for family, plot, and within-plot, respectively (Table I.3, B). The value of $3\ (\sigma^2_f)$, used in the numerator to estimate the additive genetic variance, reflects the likelihood that offspring from an open-pollinated parent are related to a greater degree than half-sibs (Campbell 1986). Significant differences in heritability estimates between all 28 pairwise combinations of populations were tested with the procedure outlined by Klein (1974). In this procedure, intraclass correlation coefficients $((\sigma^2_f)/(\sigma^2_f + \sigma^2_{fr} + \sigma^2_w))$ associated with the heritability estimate are transformed to z-scores, and the test statistic is calculated as the ratio of the difference of z-scores to the standard error of the difference.

Genetic correlations between traits were estimated as: $r_{g(x,y)} = \sigma_{f(x,y)} / \{[\sigma^2_{f(x)}] \cdot [\sigma^2_{f(y)}]\}^{1/2}$, where $\sigma_{f(x,y)}$ is the family component of covariance between two traits x and y, and $\sigma^2_{f(x)}$ and $\sigma^2_{f(y)}$ are the family components of variance for the respective traits (Falconer 1981). Standard errors of genetic correlations were calculated according to Becker (1984).

Phenotypic correlations between traits were estimated as Pearson product-moment correlations among family means (Namkoong et. al. 1988): $r_{p(x,y)} = MCP_{f(x,y)} / \{[MS_{f(x)}] \cdot [MS_{f(y)}]\}^{1/2}$, where $MCP_{f(x,y)}$ is the family mean cross product between two traits, and $MS_{f(x)}$ and $MS_{f(y)}$ are the family mean squares for the respective traits. Standard errors of phenotypic correlations were calculated according to Mode and Robinson (1959).

Testing Populations for Differences in Correlation Structure

It was of interest to compare populations in terms of genetic correlation coefficients for specific pairs of traits, as well as for genetic correlation structures (i.e., matrices of genetic correlation coefficients for the same set of multiple traits). Large sampling errors and unknown sampling distribution for genetic correlation estimates (Grossman 1970), however, do not permit the application of readily available statistical procedures such as those that can be applied to comparing product-moment correlations (Snedecor and Cochran 1967). The phenotypic correlations calculated in this study (i.e., correlations of family means) are product-moment correlations, and thus are more amenable

to statistical comparisons. Genetic and phenotypic correlations are often similar in sign and magnitude (Searle 1961, Cheverud 1988), and should approach the same value as family size increases (Via 1984). Indeed, genetic and phenotypic correlation coefficients were found to be highly correlated in this study with correlations ranging from 0.89 to 0.96 (mean = 0.93) over the eight populations (Table A.1, Appendix A). Thus, all comparisons of correlations and significance tests were conducted using phenotypic correlations. The results should closely approximate those for the genetic correlation structure, although there exists an unknown bias.

To test the hypothesis that populations differ in correlation structure, two types of statistical tests were conducted for each of the 28 pairwise combinations of populations. First, the entire phenotypic correlation matrices of the two populations were compared by employing the homogeneity test of Jennrich (1970). This test statistic is similar to those employed for testing the equality of two covariance matrices and follows a chi-square distribution. A fortran program (Equorm) provided by the University of Alberta (Harley 1986) was utilized for the calculations. Second, a paired element t-test (Snedecor and Cochran 1967:186) was used to compare individual phenotypic correlation coefficients between corresponding cells of the correlation matrix. This test compliments the homogeneity test by shedding light on specific correlation coefficients which differ between populations. The number of significant differences in correlation coefficients out of the total number tested in each pair of populations, and the specific traits

involved in significant differences, were of interest.

To determine whether the degree of similarity among correlation structures reflects similarity of environments of population origins (objective 2), two different similarity/dissimilarity indices were computed for each of the 28 pairwise combinations of populations. Cluster analyses based on the indices were then conducted using the Proc Cluster procedure in SAS (SAS Institute 1988). The dissimilarity index (Dr_m) was calculated as the Euclidean distance (Krzanowski 1988:25): $[\sum_{i}^{n} (r_{Pji} - r_{Pki})^2]^{1/2}$, where r_{Pji} and r_{Pki} are the estimated phenotypic correlation coefficients for the ith pair of traits in the jth and kth populations, respectively, and n = 171 (number of correlations). This statistic provides a quantitative measure of the magnitude of difference between the population correlation structures (i.e., the larger the value, the greater disparity between matrices). The second index is the product-moment correlation that is calculated from the paired elements in the correlation matrices and is designated the similarity index (Sr_m). All phenotypic correlations were transformed to z-scores prior to computation of Sr_m. Sr_m is a measure of the association of elements between two matrices. Since the cluster analysis utilizes a dissimilarity or distance matrix as input, the Sr_m values were transformed to $1 - Sr_m$. The cluster analyses should approximate Figure I.2 if the correlation structures are associated in large measure with environments.

RESULTS

Trait Means

Means of all traits differed significantly among populations, and patterns of geographic variation, especially for first year traits, often reflected patterns of variation among environments of origin (Table I.4). For example, populations from the milder coastal environments had the greatest height growth (HT1) in the first year, while those from the harsher Mixed-Conifer environments had the least. Coastal seedlings, however, had later budset (FBS1) than Mixed-Conifer seedlings and suffered much greater damage from early fall frosts (FR1) which occurred between October 8-10 in the first year (40% (C-1) and 65% (C-2) damage in Coastal seedlings , vs. 4% in Mixed-Conifer (MC-1, MC-2) seedlings). The large difference in frost damage between the two Coastal populations may be explained by their difference in elevation of origin. Population C-2, which had more frost damage than C-1, comes from a lower elevation (Table I.1), and had seedlings which set bud one-half week later, on average, than those from C-1 (FBS1, Table I.4). The W. Cascade populations also differed in frost damage percent (WC-1 (19%) vs. WC-2 (12%)), again, with the lowest elevation population (WC-1) having the greatest damage and latest average budset. Percentage frost damage of families was moderately to highly correlated to mean budset date for the six populations that incurred the greatest amount of frost damage (mean r_p = .66, range = .58 to .73).

In the second year, budburst (BB2) occurred earliest for the

Coastal and latest for the Mixed-Conifer populations, whereas final budset dates (FBS2) closely followed the same general chronology evident in the first year (Table I.4). Growing season length (GSL2) was closely associated in a positive fashion with FBS2. While frequency of second flushing was low in all populations in the first year (FL1 < 8%), moderate amounts of second flushing (FL2 > 10%) were observed in five of the six inland populations in the second year (Table I.4). FL2 averaged only 3.6% in the Coastal populations.

Growth differences among populations in the second year appeared to be largely influenced by the degree of frost damage they incurred the preceding fall. Despite having the longest growing season length (GSL2), and contrary to expectations based on first year growth rates, the Coastal populations had the smallest trees at the end of the second growing season (HT2). Frost substantially influenced second year growth increment (HT2-HT1), especially in the Coastal populations where growth increment accounted for only 36% (C-2) and 42% (C-1) of total second year height as opposed to 48% to 54% in the remaining populations. In addition, relative growth rates (RGR2) were lowest in the Coastal populations. The Mixed-Conifer populations, however, which had the lowest height growth the first year, but very little (< 4%) frost damage, were taller than Coastal seedlings at the end of the second growing season and had the highest RGR2 of all populations.

Shoot:root ratio (SRR2) was highest for Coastal populations, but lowest for Mixed-Conifer populations (Table I.4). In general, SRR2 was lowest in populations coming from source environments with the hottest,

driest summers.

A large number of traits showed significant differences for those contrasts which exemplify large differences in source habitat (CT #5 - #7, Table I.5); that is, where different ecological zones or environmental associations (Figure I.2) are compared. For contrasts between populations within the same ecological zone, the number of traits which differed significantly between the two Siskiyou (CT #3) and the two Mixed-Conifer (CT #4) populations were few, but were more numerous between the two Coastal (CT #1) and two W. Cascade (CT #2) populations.

To further explore whether differences in population means are associated with environments of origin, a dissimilarity measure was calculated for each pair of populations. The dissimilarity measures represent the scaled Euclidean distance between the respective paired populations (Table I.6), and were used as input for the cluster analysis. The cluster analysis produced groups, where in three out of four cases, the two paired populations within an ecological zone were most similar to each other (Figure I.3). There appear to be three major groups or associations: (A) Coastal populations (C-1, C-2), (B) inland, lower elevation populations which include the W. Cascade and Siskiyou populations (WC-1, WC-2, S-1, S-2), and (C) Mixed-Conifer populations(MC-1, MC-2), with the Coastal populations most distinct from the rest.

Genetic Variability

Significant genetic (family) variability was detected within the majority of the populations for 19 of the 22 traits (Table I.7).

Variation among families for percentage of second flushing (both FL1 and FL2) was significant for only two populations (S-1, S-2), while family variation for percentage of frost damage (FR1) was significant for only three populations (C-1, C-2, S-2), thus, these traits were excluded from further comparisons.

Within population family components of variance (σ^2_f) were compared (F-ratio of respective family mean squares) for all 28 pairwise combinations of populations for each of the 19 traits (for a total of 532 comparisons). Significant differences between family components of variance were found in 17% and 9% of the 532 tests at the .95 and .99 probability levels, respectively. The C-2 population had the largest number of significant differences, and accounted for approximately 25% of all significant differences detected. The majority (63% of total) of significant differences between the C-2 population and remaining populations were associated with final first year and second year budset dates (FBS1, FBS2), growing season length (GSL2), second year bud height (BHT2), and shoot:root ratio (SRR2). When the C-2 population was excluded, the percentage of significant differences was equal to 11% and 4% of the 399 tests (19 traits x 21 pairwise combinations of populations) at the .95 and .99 probability levels, respectively. In this subset of comparisons, a large percentage (44% of total) of significant differences were associated with initial and final first year budset dates (IBS1, FBS1), first year bud height (BHT1), and SRR2. In both series of comparisons, significant differences occurred more often for phenology traits (budset dates or growing season length) and SRR2. In general,

variances among families within the C-2 population were greater than other populations for second year phenology traits and SRR2, in those cases where significant differences were detected. This is probably due, in large part, to the influence of frost, where variation among families in frost damage was high in the C-2 population. In contrast to this trend, no population or zone had consistently higher or lower family components of variance when significant differences were detected (excluding comparisons with the C-2 population).

Heritabilities

Although the magnitudes of heritability estimates for individual traits often differed widely among populations (Table I.8), in no pairwise combination of populations were significant differences between estimates detected. A sample size of at least 200 families would be needed in order to discern significant differences ($P < .05$) between heritabilities where the difference in two estimates approximates the largest difference observed in this study (approximately 0.4). The majority of individual tree heritabilities, when averaged over the eight populations, ranged between 0.20 and 0.30. Traits with average heritability estimates greater than 0.30 were HYHT (.64), FBS1 (.34), HT1 (.39), and DI1 (.33). Four traits had values less than 0.2, on average. Three of these were associated with second year phenology (BB2 (.11), FBS2 (.18), GSL2 (.17)), and the fourth was SRR2 (.16). Heritability estimates were not appreciably different for equivalent first and second year traits. The average heritability for FBS2 (.18), however, was only

about half that for FBS1 (.34). Heritability estimates for HT2 in the W. Cascade populations (.08, .13) were considerably lower than those for HT1 (.50, .47).

Correlation Structure

The chi-square (X^2) tests for homogeneity of correlation matrices indicated heterogeneity ($P < .05$) for 8 of the 28 pairwise combinations of populations (upper diagonal, Table I.9). All eight significant combinations involved comparisons between populations from different zones. While no significant differences were evident for comparisons between populations from the same zone, this statistic provides no information on the magnitude of individual correlation differences associated with the significance level.

The percentage of phenotypic correlation coefficients significantly different (out of 171 total) for each population pair, as determined by t-tests, provides additional information on correlation structure differences between populations (upper diagonal, Table I.9). Four to eight percent of the correlation coefficients were significantly different in the four comparisons of populations from the same zones. For the remaining 24 comparisons, the percentage of significant differences ranged from 4 to 43 percent. The greatest differences among zones, on average, were observed between Coastal populations and populations in the remaining (inland) zones. The differences between Coastal and Mixed-Conifer populations were particularly large and consistent (29% - 43%). Among the inland zones, percentage differences

were small between W. Cascade and both the Siskiyou (4% - 9%) and Mixed-Conifer (7% - 13%) zones, but larger between the Siskiyou and Mixed-Conifer zones (14% - 29%). The t-test results were also summarized for the percentage of significant differences in correlation coefficients involving first year trait- pairs (21 correlations), second year trait-pairs (66 correlations), and first-year-by-second-year trait-pairs (84 correlations), for each respective pairwise combination of populations (lower diagonal, Table I.9). The majority of significant differences were associated with second year trait pairs followed by correlations between first-year by second-year traits.

The t-tests appear to provide a better resolution of differences in correlation structure than the X^2 homogeneity tests. Results from the two tests were only roughly comparable. Although most pairwise comparisons of populations which had more than 20% of the trait pairs with significantly different correlation coefficients, also had significant values for the X^2 homogeneity test, several population combinations with relatively high percentages of significantly different correlation coefficients did not have significantly different correlation matrices (e.g., C-1 vs. MC-1, Table I.9). In addition, two population combinations with low percentages of significant correlation differences (i.e., C-1 vs. WC-2, and S-2 vs. WC-2) had significantly different correlation matrices. In general, both statistical tests indicated a higher degree of homogeneity between populations from the same zone, while showing a range in relative degree of similarity for those comparisons between populations from different zones. By far, the

largest divergence in correlation structure was between populations from the Coastal and Mixed-Conifer zones.

To further explore whether the degree of similarity among correlation structures reflects similarity of environments of population origin, two similarity/dissimilarity indices were calculated for each pair of populations. The dissimilarity index (Dr_m) represents the Euclidean distance between respective populations (upper diagonal, Table I.10). The similarity index (Sr_m) measures the correlation between respective correlation coefficients and increases in value with increasing similarity (lower diagonal, Table I.10). The two measures showed similar patterns and mirror those already seen for the t-test results (upper diagonal, Table I.10).

Cluster analyses based on Dr_m and Sr_m produced similar groupings of populations, so only the results for Dr_m are presented (Figure I.4). The major groups or associations were similar to the cluster analysis based on trait means (Figure I.3), with a coastal group (C-1, C-2), lower elevation inland group (WC-1, WC-2, S-1, S-2), and higher elevation inland group (MC-1, MC-2). The cluster analysis based on correlation structures, however, exhibited less distance between groups relative to the average distance among populations, and the Mixed-Conifer, rather than the Coastal populations, were most distinct from the rest of the populations.

Correlation coefficients between some pairs of traits were similar in magnitude across all populations (Appendix B). For example, moderate correlations (range from .37 to .64) existed between initial (IBS1, IBS2)

and final budset dates (FBS1, FBS2) in the two respective years, and DI2, HT2, SWT2, and RWT2 were all strongly correlated with TWT2 (range from .73 to .99). Further inspection of individual correlation coefficients also revealed where major differences among populations occurred. To illustrate these differences, a subset of seedling trait-pairs (9 of the 19 traits) are highlighted (Tables I.11 - I.14). This subset, which is composed primarily of second year traits, provides a general picture of differences in trait associations between populations within zones (within each Table) as opposed to populations between zones (comparisons between Tables). A large number of differences between populations involve trait pair correlations associated with phenology and growth traits in the second year. For example, IBS2 and GSL2 were essentially uncorrelated with HT2 and TWT2 in the Mixed-Conifer populations (mean = .09, range = -.13 to +.26), whereas low to moderate negative correlations (mean = -.41, range = -.13 to -.68) existed for the remaining populations. In addition, correlations between BB2 and second year biomass traits (HT2, RWT2, TWT2) were negative (range from -.07 to -.24) for the Mixed-Conifer populations as opposed to positive (range from .42 to .65) in the Coastal populations. A closer examination of one population comparison (C-2 vs. MC-2) revealed that approximately 60% of all differences between correlation coefficients were those associated with phenology x growth trait-pairs (Appendix B, Table I.9).

Patterns of variation among populations for correlations between initial budset dates and growth were quite different in the two years. While the correlations between IBS1 and HT1 was positive in all

populations (range from .11 to .43), the correlations between IBS2 and HT2 ranged from near zero in the Mixed-Conifer populations to moderately negative (range from -.40 to -.68) in the remaining populations. This difference between years appears to be the result of differential responses of populations to frost damage at the end of the first growing season. That is, populations which displayed the propensity to set buds latest had the greatest amount of frost damage and moderate negative correlations between IBS2 and HT2 in the second year. In addition, families from the Coastal populations that set bud latest also burst buds sooner the following spring (negative correlation between IBS1 and BB2). Thus, the correlation between BB2 and HT2 was positive in Coastal populations. These traits, however, had weak negative correlations in Mixed-Conifer populations, where frost damage was slight.

DISCUSSION AND CONCLUSIONS

Populations of Douglas-fir in southwest Oregon appear to vary substantially in QGS. This variation is primarily associated with differences in trait means and phenotypic correlations between traits. Since the phenotypic and genetic correlations were highly correlated, variation among populations for genetic correlation structure should be similar to results obtained for phenotypic correlation structure comparisons. Differences in covariance among traits appears to be the primary reason for variation in correlation structure since evidence for among population differences in family components of variance were limited. Homogeneity of variance components among Douglas-fir populations was also reported by Christophe and Birot (1979), Rehfeldt (1983), and Campbell (1986) for various traits. No significant differences were detected for heritabilities of traits in different populations, but the statistical power to detect differences was very poor.

Patterns of variation in trait means among populations reflect adaptation and are generally consistent with earlier findings for Douglas-fir in southwest Oregon (e.g., White 1981, Sorensen 1983, Campbell 1986, Loopstra and Adams 1989). These studies found major genetic gradients associated with east-west transects and large differences between major ecological zones (e.g., coast vs. inland). The genetic gradients, in turn, were correlated with precipitation and temperature gradients that strongly influenced growing season lengths.

While significant differences between populations were observed for a large number of traits in this study, differences in phenology traits were particularly striking. The largest differences occurred between C-2 and MC-2 where means differed by 16 (FBS1), 8 (BB2), 26 (IBS2), 21 (FBS2), and 29 (GSL2) days. These substantial differences reflect differential adaptation to climatic conditions. The populations in the coastal zone have adapted to their environments with later budset dates, and longer growing seasons relative to populations from inland zones, where the harsher environmental conditions necessitate shorter growing seasons. While budburst occurred earlier in the Coastal populations relative to the high elevation Mixed-Conifer populations, the dates were nearly identical between the Coastal and Siskiyou populations. In reference to timing of budburst, differential responses of Douglas-fir from maritime and continental climates have been shown to be substantially influenced by the chilling period and flushing temperatures (Campbell and Sugano 1979). Campbell and Sugano noted that while maritime populations often burst buds later than continental populations, there exist circumstances (e.g., high flushing temperatures) where maritime populations burst buds earlier than continental populations. The nursery environment has a profound influence on the rate and timing of budburst. Budburst dates for a coastal source and W. Cascade source from Oregon differed by only one to two days within each of three nurseries, while mean budburst dates differed by up to 11 days between nurseries (Schuch et. al. 1989). Therefore, while the C-2 population burst buds eight days earlier, on average, than the MC-2 population in

this study, this may not be indicative of differences that might be expressed in other nurseries or years.

Coastal populations typically exhibit higher seedling growth increments when compared to inland populations (e.g., Kaya 1987, Joly et. al. 1989), and the Coastal populations were tallest at the end of the first growing season in this study. In addition, coastal sources have been more susceptible to fall frost events in earlier studies (e.g., Campbell and Sorensen 1973, Loopstra and Adams 1989) due to the later timing of budset inherent in these sources, and this also was the case in this study. In all probability, the Coastal populations would have been the tallest at the end of the second year if the frost event had not occurred.

Populations within the Coastal and W. Cascade zones displayed a greater number and magnitude of differences in trait means than populations within the Siskiyou and Mixed-Conifer zones (Table I.5, Figure I.3). Genetic divergence between the Coastal populations is probably a reflection of the relatively large environmental differences between the two source locations of the sample populations. Population C-1 comes from an environment that is substantially higher in elevation (305 m higher, on average) and drier (50 cm less annual precipitation) than the source environment of population C-2. The harsher environment of C-1 is reflected in the earlier budset, shorter growing season length, but greater resistance of families to early fall frosts relative to those from C-2. The two W. Cascade populations also differed substantially in elevation of source environment (305 m), and the higher elevation

population (WC-2) also set buds earlier (with resultant shorter growing season) and was more frost hardy relative to the lower elevation population (WC-1). The lesser degree of genetic differentiation between populations within the Siskiyou and Mixed-Conifer zones is more difficult to explain. Within these zones, populations also differed with regards to source elevations, although they differed less in total annual precipitation (Table I.1). Perhaps, the environments in these harsher (drier) climatic zones impose limiting factors which, in effect, limit the range of responses to a greater extent than those found in other climatic zones (e.g., mesic environment). For example, even though two Mixed-Conifer populations differed by 305 m in average elevation of source environments, growing season length differed by only two days. This is in contrast to a difference of 11 days in growing season length between the two Coastal populations. Factors such as drought stress and high summer temperatures in the harsher climatic zones may impose quite different constraints on the growth patterns (response functions) of populations in comparison to other climatic zones. Thus, these factors, in combination with other environmental factors, may cause response functions to differ appreciably from those of other zones. Differences in elevation, for example, may not cause similar changes in trait responses among zones due to the influence of other environmental factors within any one zone.

Patterns of variation among populations in correlation structure differed somewhat from patterns observed in trait means. Differences among zones relative to differences between populations within zones were

greater for trait means (Figures I.3 - I.4). Thus, populations appear to be less differentiated in terms of correlation structure than for trait means. Trait means may be more sensitive to environmental variation and be a more sensitive measure of environmental factors important to adaptation. Correlation structures, however, may be less variable within certain environmental ranges. Major differences in growth patterns (as caused by very different environmental stress factors) may be necessary to affect the relative correlation structures to an appreciable degree.

Patterns of variation based on both trait means and correlation structures were not entirely as predicted on the basis of habitat groupings that were originally envisioned (Figures I.3 - I.4). Instead of four, three relatively distinct groupings were identified, which are geographically associated with the coastal zone (C-1, C-2), a lower elevation inland zone (WC-1, WC-2, S-1, S-2) and a high elevation inland zone (MC-1, MC-2). The environmental characteristics of the source locations and growth patterns observed for the populations within each of these three climatic zones are quite distinct. Major climatic differences among these zones influence growth patterns and phenology of Douglas-fir, and adaptation to these macro-climates is probably, at least partially, responsible for the patterns observed. The Coastal zone experiences a more maritime climate and longer growing season as opposed to the inland populations where a continental climate (hot-dry summers) and shorter growing seasons exist. The high elevation zone is distinguished by very short growing seasons, cooler temperatures, and a

large proportion of precipitation in the form of snow.

Differences among populations from different zones in correlations between second year phenology and biomass traits (i.e., HT2, SWT2, RWT2, TWT2) were quite prominent, and contributed in large measure to the overall differences in correlation structure among populations. The observed correlations between phenology and biomass traits, however, were not always those expected based on adaptation. This was especially so for the Coastal populations. While the longer growing season of Coastal population families is as expected, the negative correlation between growing season length and HT2 (Table I.11) appears to be counter to an efficient accumulation of height, and the adaptation of these populations to a mild climate. The negative correlation between growing season length and HT2, however, seems to be a frost related artifact. A later budset date in the first year was correlated with a later budset date in the second year, which in turn was highly correlated to the growing season length in the second year. Later budset in year one coincided with greater frost damage to terminal leaders. The more damaged families subsequently grew less in the second growing season and accumulated less overall biomass in year two (e.g., correlation between second year height increment and total accumulated height (HT2) averaged 0.93 for the Coastal populations). Thus, there was a negative correlation between growing season length and biomass accumulation in populations which suffered the greatest amounts of frost damage in year one.

In a previous study, Kaya (1987), using similar families from the same two Coastal populations, estimated the genetic correlation between

second year height increment and second year budset date as r_g = 0.42, which indicates a positive association between biomass and growing season length for the coastal zone. There was no fall frost event in Kaya's study, and the large difference in correlations in the two studies is undoubtedly due to the response of the Coastal populations to the presence or absence of frost. Numerous studies in other species have also shown changes in correlation structure when populations were subjected to different environmental conditions (Schlichting 1986). Consequently, inferences from this study are necessarily limited to comparisons on the basis of a single test environment, and any one specific correlation coefficient must be viewed in the context of the particular study environment only.

The W. Cascade and Siskiyou populations also had low to moderate negative correlations (range from -.13 to -.68, Tables II.12-13) between growing season length, or initial budset date, and HT2 in the second year. The fact that these populations also incurred a moderate amount of frost damage (range from 12% to 19% (within family plots)) may partially explain these negative correlations. Other explanations may also be plausible. Kaya (1987) examined genetic structure in an inland population, which combined families from the S-1 and MC-1 populations in this study. He found second year height increment in inland families to be primarily a function of predetermined growth. He also found a negative genetic correlation (-.43) between predetermined growth and budset timing, and near zero genetic correlation between second year increment and budset timing. Thus, in inland zones, height growth may

rely less on growing season length. Relative fitness and growth rates in lower elevation inland populations may also be dependent on ability to survive drought stress and high summer heat loads. Physiological attributes (e.g., stomatal closure, growth cessation) that permit the trees to survive and prosper may occur sporadically during the growing season, and there may not necessarily be a positive correlation between growing season length (or budset date) and height growth in a particular year.

In contrast to the other populations, there existed zero to low positive correlations (0.0 to .26 range) between growing season length and biomass traits (HT2, RWT2, TWT2) in the Mixed-Conifer populations. Frost damage in Mixed-Conifer populations was only slight, and thus, the large differences in correlation structure between this zone and other zones may be principally due to this fact. These populations, however, also had a tendency to second flush at higher frequencies in the second year, and this characteristic may provide opportunities to extend the growing season (and growth) under favorable climatic conditions. In addition, the high elevation populations have been shown to be more drought tolerant than lower elevation populations in this region, although this may be an indirect result of their earlier budset dates (White 1987). These factors in combination, however, suggest that these populations have adapted patterns of growth quite distinct from other zones.

The relative similarity of correlation structures between populations within each of the three general climatic zones may, in part,

be the result of natural selection where a specific integrated trait complex is favored in similar environments. Natural selection can occur only if there is phenotypic variation among individuals and fitness differences among inherited traits (Endler 1986). These two conditions necessary for natural selection indeed exist for Douglas-fir in southwest Oregon as indicated by the genetic and phenotypic variation shown in this study, and previously. Whether fitness differences exist among correlation structures is not easily determined. The total phenotype has been referred to as the unit upon which natural selection acts (Cheverud 1982), and a logical extension of this proposal suggests that phenotypic structure of populations might also be shaped by selective forces. It is generally accepted that specific traits have different fitness values in different environments. Major differences exist between the coastal, low elevation inland, and high elevation inland zones with regards to general growth patterns, environmental extremes, and plant associations (Franklin and Dyrness 1973). The fact that correlation structures are associated with habitat divergence implies that the environments have influenced character covariation (Thorpe 1976). Natural selection results from differences in adaptation (Endler 1986), and these differences will be evident in the covariance structures. The fact that differences in correlation structure increase with increasing difference in source environment strengthens the inference that selection plays a prominent role in determination of the structures. It is difficult to prove that selection is the primary process that molds the covariance (or correlation) structure. For example, the relative geographic proximity

of the paired populations may result in substantial gene flow between populations which would contribute to their similarity. Discrimination between selection and gene flow explanations (and composite effects of both) is not possible in this study because similarity of habitats and distance between populations are confounded (i.e., most similar populations were also the closest geographically). The results of this study, however, lend support to the idea that selection plays an important role in determining QGS, including interrelationships among traits.

Differences in QGS among populations have practical ramifications with regards to seed transfer and selective breeding. As observed for trait means in this and previous studies, correlation structures also differ among populations and test environments. In addition, quantitative structures appear to deviate to a greater extent when the environments of their origin also differ to a large degree in harshness and growing season length. Substantial differences among populations in genetic correlation structure implies that differences in correlated responses can be expected when the populations are subjected to natural and/or artificial selection. One cannot make broad generalizations about the magnitude (and sign) of interrelationships between traits, especially when populations come from very diverse environments. Thus, there may be a need to estimate the degree of genetic control and interrelationships among traits separately for each breeding population. For example, when selection is applied to growth traits, correlated responses for timing of budburst and budset might vary substantially

among populations. Changes in phenology might drastically affect the adaptive characteristics associated with cold hardiness (Campbell and Sorensen 1973) and frost avoidance (Rehfeldt 1989) that have evolved in specific environments. However, populations from similar environments appear to be less differentiated on basis of genetic correlation structures, than for trait means. This suggests that populations may be pooled for breeding purposes if environmental differences are not too great, and there exists the possibility to breed for broadly adapted genotypes for the environments in question. Therefore, the QGS and biology of the species must be understood when seed transfers and breeding plans are implemented. Biological ramifications of gene resource management can only be understood when the magnitude of differences among genetic structures are understood.

Table I.1. Location and environmental characteristics of southwest Oregon populations.

Zone/ (Pop[n])	Latitude/ Longitude	Elevation (meters)	Precipitation[a/] Annual (cm)	Precipitation[a/] Summer (cm)	Temperature[b/] Jan. (°C)	Temperature[b/] July (°C)	Forest Type[c/]
Coastal							
(C-1)	42° 40′/ 124° 05′	457-762	280	33	2	25	Tsuga[d/] heterophylla
(C-2)	42° 10′/ 124° 10′	152-457	330	35	3	22	"
W. Cascade							
(WC-1)	43° 40′/ 122° 45′	427-762	127	18	-1	28	"
(WC-2)	43° 25′/ 122° 40′	731-1067	152	21	-1	28	"
Siskiyou							
(S-1)	42° 30′/ 123° 40′	305-610	146	17	0	31	Mixed-[e/] Evergreen
(S-2)	42° 20′/ 123° 35′	457-762	127	13	0	31	"
Mixed-Conifer							
(MC-1)	42° 30′/ 122° 20′	1067-1372	120	17	-6	28	Mixed-[f/] Conifer
(MC-2)	42° 05′/ 122° 55′	1372-1677	114	14	-3	31	"

a/ Average annual precipitation and average dry season (Summer) precipitation (May through September) from 1960-1980 (Oregon State Univ. 1982a, 1982b).

b/ January mean minimum temperatures and July mean maximum temperatures (Franklin and Dyrness 1973).

c/ General forest zone classification (Franklin and Dyrness 1973).

d/ Western hemlock (Tsuga heterophylla) is the climax species while Douglas-fir (Pseudotsuga menziesii var meniesii) is the major sub-climax species.

e/ Douglas-fir, sugar pine (Pinus lambertiana Dougl.) , tanoak (Lithocarpus densiflora), and various schlerophyll hardwoods constitute the major species.

f/ Douglas-fir, sugar pine, ponderosa pine (Pinus ponderosa Dougl.), incense-cedar (Libocedrus decurrens Torr.), and white fir (Abies concolor (Gord. and Glend) Lindl.) are the major species components.

Table I.2. Description of traits.

Code	Trait	Units
I. First Growing Season:		
HYHT	Hypocotyl height	cm
#COT	Number of cotyledons	number
IBS1	Initial budset date[a/]	weeks after August 21, 1985
FBS1	Final budset date[a/]	weeks after August 21, 1985
HT1	First year height	cm
BHT1	Length of terminal bud	mm
DI1	First year diameter[b/]	mm
FL1	Percent seedlings in a family plot with multiple flushing	arcsin √%
FR1	Percent seedlings in a family plot damaged by October 8-10, 1985 frost event	arcsin √%
II. Second Growing Season:		
HT2	Total height (2-years)	cm
BHT2	Length of terminal bud	mm
DI2	Second year diameter[b/]	mm
SWT2	Shoot dry weight	gms (X 10)
RWT2	Root dry weight	gms (X 10)
BB2	Budburst date[c/]	days after January 1, 1986
IBS2	Initial budset date[a/]	days after January 1, 1986
FBS2	Final budset date[a/]	days after January 1, 1986
SRR2	Shoot:Root ratio	ln(SWT2)/ln(RWT2)
GSL2	Growing season length (FBS2 - BB2)	days
RGR2	Relative growth rate	[ln(HT2)-ln(HT1)]/GSL2
TWT2	Total dry weight (SWT2 + RWT2)	gms (X 10)
FL2	Percent seedlings in a family plot with multiple flushing	arcsin √%

[a/] Initial budset date denotes time of initial budset (time when terminal bud scales occurred). Final budset date refers to budset after any second flush. Final budset date equals initial budset date if second flushing did not occur. Budset was recorded once per week.

[b/] Diameters were taken directly below the cotyledon scar.

[c/] Budburst date was recorded twice a week; time when needles first became visible in the opening terminal bud.

Table I.3. Forms of the analyses of variance and covariance:

(A) All populations together, (B) Individual source populations separately.

Source of variation	Degrees of freedom	Expected mean squares[a/]
(A)		
Replications	3	
Populations (P)	7	$\sigma^2_e + 4\ \sigma^2_{f(p)} + 25.714\ K^2_p$
Families/Pop [F(P)]	352	$\sigma^2_e + 4\ \sigma^2_{f(p)}$
Error	1077	σ^2_e
(B)		
Replications (R)	3	
Families (F)	44	$\sigma^2_w + n\ \sigma^2_{fr} + 4n\ \sigma^2_f$
F x R	132	$\sigma^2_w + n\ \sigma^2_{fr}$
Error	[(N-1)-(179)]	σ^2_w

[a/] (A): K^2_p = fixed effect due to populations; $\sigma^2_{f(p)}$ = variance among open-pollinated families within populations; σ^2_e = error variance; where analysis is based on family plot means.

(B): σ^2_f = variance among open-pollinated families; σ^2_{fr} = variance of family x replication (plot); σ^2_w = within plot error variance; n = harmonic mean number of trees per plot; N = total number of trees; where analysis was based on individual tree basis. When analysis is based on family plot means, there is no estimate of within plot error. Plot error (F X R) then equals the error variance, σ^2_e, while family (F) mean squares equal $\sigma^2_e + 4\ \sigma^2_f$. Covariance (ANCOVA) components have the same form when expected mean squares are replaced with expected cross-products.

Table I.4. Trait means and coefficients of variation (in parentheses) for the study populations.

	Population							
	Coastal		W.Cascade		Siskiyou		Mixed-Conifer	
Traits[a/]	C-1	C-2	WC-1	WC-2	S-1	S-2	MC-1	MC-2
HYHT	9.33	9.37	9.71	9.54	9.46	9.42	9.05	9.06
	(8.4)	(8.7)	(8.7)	(8.3)	(7.6)	(7.6)	(8.2)	(8.5)
#COT	6.96	6.77	6.95	6.96	6.76	6.78	6.73	6.78
	(5.9)	(5.6)	(6.0)	(6.5)	(5.6)	(5.5)	(5.8)	(6.0)
IBS1	5.16	5.66	4.53	4.04	4.09	4.33	3.70	3.42
	(14.2)	(14.6)	(17.3)	(18.5)	(18.2)	(18.8)	(19.8)	(21.8)
FBS1	5.45	6.02	4.85	4.29	4.48	4.56	3.90	3.71
	(10.9)	(10.4)	(14.7)	(16.9)	(17.8)	(15.8)	(19.3)	(20.4)
HT1	26.2	27.1	25.8	24.1	23.8	24.2	22.0	21.6
	(11.2)	(11.4)	(11.4)	(11.2)	(11.7)	(11.3)	(11.5)	(11.8)
BHT1	3.32	2.39	4.21	4.75	4.30	4.32	5.21	5.17
	(30.1)	(36.1)	(23.4)	(17.8)	(24.0)	(21.7)	(14.5)	(15.3)
DI1	5.29	5.34	5.46	5.29	5.12	5.27	5.02	5.03
	(8.0)	(8.0)	(8.2)	(8.8)	(8.1)	(8.6)	(8.4)	(7.6)
FL1	5.2	6.1	5.9	5.6	7.8	4.6	4.4	6.3
	(186)	(189)	(141)	(218)	(184)	(182)	(191)	(171)
FR1	39.6	64.7	18.6	12.0	19.4	18.8	3.9	3.8
	(44)	(66)	(28)	(13)	(27)	(27)	(23)	(13)
HT2	44.9	42.6	49.5	48.4	46.1	46.8	47.5	46.1
	(14.4)	(15.1)	(15.2)	(13.8)	(14.6)	(13.2)	(9.1)	(10.0)
BHT2	8.10	7.49	8.85	8.92	8.88	8.74	9.18	9.06
	(7.5)	(10.3)	(7.7)	(7.1)	(7.1)	(6.8)	(6.8)	(6.0)
DI2	8.74	8.43	9.68	9.21	8.89	9.18	8.75	8.50
	(10.2)	(12.1)	(11.0)	(10.6)	(10.5)	(10.2)	(8.9)	(8.7)
SWT2	16.7	15.0	20.5	19.0	17.2	18.0	16.7	15.7
	(24.5)	(29.3)	(23.4)	(23.7)	(24.3)	(21.4)	(20.1)	(20.1)
RWT2	5.0	4.4	6.3	5.9	5.7	6.0	5.6	5.4
	(24.5)	(28.3)	(22.7)	(22.4)	(23.2)	(21.0)	(23.3)	(36.5)
BB2	97.7	95.1	100.6	100.5	97.5	97.3	102.3	103.2
	(4.4)	(3.1)	(4.2)	(4.6)	(4.1)	(4.3)	(4.6)	(4.2)
IBS2	176.7	185.9	172.8	166.6	169.1	172.3	161.5	159.6
	(4.2)	(4.9)	(4.2)	(5.0)	(4.4)	(4.2)	(4.5)	(4.2)
FBS2	178.4	186.5	175.0	171.8	173.7	175.5	167.3	166.0
	(3.5)	(4.8)	(3.7)	(4.0)	(3.3)	(3.4)	(4.1)	(4.2)
SRR2	3.40	3.49	3.31	3.26	3.13	3.05	3.06	3.03
	(3.1)	(3.9)	(2.6)	(2.6)	(2.9)	(3.0)	(3.9)	(3.9)
GSL2	80.7	91.5	74.5	71.2	76.3	78.2	65.1	62.8
	(9.9)	(10.7)	(11.6)	(12.4)	(10.0)	(10.2)	(12.9)	(13.1)
RGR2	.254	.186	.347	.371	.314	.307	.427	.420
	(40.1)	(42.4)	(32.2)	(23.6)	(26.3)	(26.1)	(19.6)	(18.9)
TWT2	21.7	19.4	26.8	24.9	22.9	24.0	22.4	21.2
	(24.6)	(28.9)	(22.9)	(23.2)	(23.6)	(20.9)	(19.7)	(19.2)
FL2	5.4	1.9	7.6	17.5	16.9	11.6	21.7	22.5
	(217)	(341)	(96)	(74)	(128)	(150)	(91)	(81)

[a/] Trait means presented in original units of measure. See Table I.2. for trait description and units of measure. See Table I.1 and Figure I.1 for location of populations.

Table I.5. Comparison of population means for individual traits under seven orthogonal contrasts.

Trait[b/]	Contrast[a/] 1	2	3	4	5	6	7
HYHT	NS	NS	NS	NS	*	**	**
#COT	**	NS	NS	NS	NS	NS	**
IBS1	**	**	NS	*	**	**	**
FBS1	**	**	NS	NS	**	**	**
HT1	*	**	NS	NS	**	**	**
BHT1	**	**	NS	NS	**	**	**
DI1	NS	*	*	NS	NS	**	**
HT2	*	NS	NS	NS	**	NS	NS
BHT2	**	NS	NS	NS	**	**	**
DI2	*	**	NS	NS	**	**	**
SWT2	**	*	NS	NS	**	**	**
RWT2	**	NS	NS	NS	**	*	**
BB2	**	NS	NS	NS	**	**	**
IBS2	**	**	**	NS	**	**	**
FBS2	**	**	NS	NS	**	**	**
SRR2	**	NS	NS	NS	**	NS	**
GSL2	**	**	NS	NS	**	**	**
RGR2	**	**	NS	NS	**	**	**
TWT2	**	*	NS	NS	**	**	NS
FL1	NS	NS	**	*	NS	NS	NS
FL2	NS	**	**	NS	**	**	**
FR1	**	**	NS	NS	**	**	**

a/ See Figure I.2. for description of contrasts. Each contrast represents a single degree of freedom F-test with 1, 352 degrees of freedom. NS = non-significant, * = $P < .05$, ** = $P < .01$.

b/ See Table I.2. for trait descriptions and units of measure.

Table I.6. Dissimilarity matrix between 8 populations.[a/]

Population	Coastal		W.Cascade		Siskiyou		Mixed-Conifer	
	C-1	C-2	WC-1	WC-2	S-1	S-2	MC-1	MC-2
C-1		3.19	3.37	4.26	3.36	3.05	6.08	6.52
C-2			6.29	7.31	6.25	5.90	9.06	9.46
WC-1				1.96	2.32	1.82	4.27	4.92
WC-2					1.66	1.94	2.46	3.07
S-1						0.96	3.18	3.73
S-2							3.81	4.42
MC-1								0.89
MC-2								

[a/] Dissimilarity is equal to the scaled Euclidean distance: $[\sum_{i}^{n} (x_{ji} - x_{ki})^2/w_i]^{1/2}$, where x_{ji} and x_{ki} are the estimated means for the ith pair of traits in the jth and kth populations, w_i is the pooled within-group variance for the ith trait, and n = 19 (number of traits).

Table I.7. Traits with significant family components of variance (σ^2_f) within populations.[a/]

	Population							
	Coastal		W.Cascade		Siskiyou		Mixed-Conifer	
Traits[b/]	C-1	C-2	WC-1	WC-2	S-1	S-2	MC-1	MC-2
I. First Growing Season								
HYHT	**	**	**	**	**	**	**	**
#COT	**	**	**	**	**	**	**	NS
IBS1	**	NS	*	**	**	**	**	**
FBS1	**	**	**	**	**	**	**	**
HT1	NS	**	**	**	**	**	**	**
BHT1	**	**	*	**	**	**	**	*
DI1	**	**	**	*	**	**	**	**
II. Second Growing Season								
HT2	**	**	NS	NS	**	**	**	**
BHT2	**	**	**	**	**	*	**	**
DI2	**	**	**	*	**	**	**	**
SWT2	**	**	**	**	**	**	**	**
RWT2	**	**	**	**	**	**	*	**
BB2	*	**	NS	NS	NS	NS	**	*
IBS2	*	**	**	NS	**	**	**	**
FBS2	*	**	**	c/	**	*	**	**
SRR2	**	**	NS	*	**	**	*	**
GSL2	**	**	**	NS	**	NS	**	**
RGR2	**	**	c/	**	**	**	**	**
TWT2	**	**	**	**	**	**	**	**

a/ Significance based on F-test with 44, 132 degrees of freedom; NS = non-significant, * = $P < 0.05$, ** = $P < 0.01$.

b/ See Table I.2 for trait descriptions and units of measure. See Table I.1 and Figure I.1 for locations of populations.

c/ Non-significant due to negative component of variance estimate.

Table I.8. Estimates of individual heritabilities for nineteen traits in 8 populations.[a/]

	Population								
	Coastal		W.Cascade		Siskiyou		Mixed-Conifer		Mean
Traits[b/]	C-1	C-2	WC-1	WC-2	S-1	S-2	MC-1	MC-2	
I. First Growing Season									
HYHT	.49	.45	.68	.69	.84	.77	.65	.59	.65
#COT	.18	.29	.27	.21	.39	.20	.19	.05	.22
IBS1	.13	.09	.13	.47	.50	.19	.30	.41	.28
FBS1	.29	.21	.24	.48	.40	.38	.30	.39	.34
HT1	.13	.26	.50	.47	.60	.41	.47	.32	.39
BHT1	.24	.45	.14	.21	.35	.38	.21	.15	.27
DI1	.27	.35	.39	.20	.43	.37	.18	.43	.33
II. Second Growing Season									
HT2	.33	.32	.08	.13	.34	.25	.30	.33	.26
BHT2	.23	.46	.19	.26	.40	.14	.30	.17	.27
DI2	.27	.35	.39	.20	.37	.27	.23	.36	.29
SWT2	.24	.34	.21	.19	.40	.29	.24	.24	.27
RWT2	.19	.40	.17	.15	.30	.24	.10	.22	.22
BB2	.12	.32	.04	.04	.06	.03	.19	.11	.11
IBS2	.17	.23	.26	.07	.31	.27	.19	.37	.23
FBS2	.14	.22	.26	b/	.13	.11	.16	.24	.18
SRR2	.22	.34	.06	.11	.14	.15	.12	.17	.16
GSL2	.16	.33	.16	.02	.14	.05	.23	.28	.17
RGR2	.22	.34	b/	.25	.22	.27	.18	.30	.25
TWT2	.23	.35	.22	.18	.39	.27	.21	.30	.27

a/ See Table I.2. for trait descriptions and units of measure. See Table I.1 and Figure I.1 for locations of populations. Standard errors of estimates ranged from 0.05 - 0.21.

b/ No estimate of individual heritability due to negative family component of variance estimate.

Table I.9. Matrix of pairwise combinations of 8 populations showing which combinations differed significantly (P<.05) in their phenotypic correlation matrices (indicated by * in upper diagonal)[a/];and, the percentage of individual correlations which differed significantly over all trait pairs tested (upper diagonal)[b/], and for specific subsets (a,b,c) of trait pairs (lower diagonal)[c/].

	Coastal		W.Cascade		Siskiyou		Mixed-Conifer	
Population	C-1	C-2	WC-1	WC-2	S-1	S-2	MC-1	MC-2
C-1		8 %	8%	* 11%	6%	6%	29%	* 32%
C-2	a. 0% b.18% c. 2%		26%	* 22%	16%	* 20%	* 41%	* 43%
WC-1	a. 0% b. 3% c.14%	0% 52% 13%		5%	4%	7%	8%	13%
WC-2	a. 0% b.23% c. 5%	5% 42% 11%	5% 6% 5%		4%	* 9%	9%	7%
S-1	a. 5% b. 3% c. 8%	0% 29% 11%	0% 6% 4%	0% 5% 4%		8%	14%	19%
S-2	a. 5% b. 9% c. 5%	5% 35% 12%	0% 9% 7%	5% 8% 11%	5% 0% 13%		27%	* 29%
MC-1	a. 5% b.45% c.23%	5% 71% 26%	10% 17% 1%	0% 18% 5%	0% 32% 4%	14% 42% 18%		4%
MC-2	a.19% b.48% c.23%	14% 70% 30%	10% 27% 2%	10% 11% 4%	10% 41% 5%	10% 39% 25%	0% 8% 2%	

a/ Chi-square test with 171 degrees of freedom in all cases (Jennrich 1970).

b/ Based on t-tests of 171 trait-pairs per pairwise combination of populations.

c/ Based on t-tests of trait-pairs which numbered for each subset: a. 21 first-year trait-pair combinations, b. 66 second-year trait-pair combinations, and c. 84 first-year-by-second-year trait-pair combinations.

Table I.10. Pairwise dissimilarities (Dr_m, upper diagonal), and similarities (Sr_m, lower diagonal) between phenotypic correlation matrices of 8 populations.[a,b/]

Population	Coastal C-1	Coastal C-2	W.Cascade WC-1	W.Cascade WC-2	Siskiyou S-1	Siskiyou S-2	Mixed-Conifer MC-1	Mixed-Conifer MC-2
C-1		2.21	2.49	2.81	2.30	2.88	4.24	4.65
C-2	.95		3.58	3.63	2.94	3.33	5.19	5.47
WC-1	.93	.89		2.30	2.00	2.90	2.70	3.18
WC-2	.91	.87	.93		2.17	2.68	3.07	2.95
S-1	.94	.91	.95	.95		2.59	3.13	3.73
S-2	.93	.91	.91	.92	.93		4.23	4.29
MC-1	.80	.74	.90	.88	.89	.80		2.55
MC-2	.75	.70	.86	.88	.83	.78	.90	

a/ Dr_m is equal to the Euclidean distance: $[\sum_{i}^{n} (r_{Pji} - r_{Pki})^2]^{1/2}$, where r_{Pji} and r_{Pki} are the estimated phenotypic correlation coefficients for the ith pair of traits in the jth and kth populations, and n = 171 total pairs.

b/ Sr_m is the product-moment correlation between r_{Pji} and r_{Pki} (z-transformed correlation coefficients) over all n trait pairs.

Table I.11. Estimates of phenotypic correlations in two Coastal populations (C-1, upper diagonal and C-2, lower diagonal) for a subset of seedling trait pairs.

Seedling Trait	IBS1	HT1	HT2	RWT2	BB2	IBS2	SRR2	GSL2	TWT2
IBS1		.11	-.52	-.39	-.44	.60	.35	.62	-.36
HT1	.33		.26	.37	.15	-.03	-.15	-.11	.38
HT2	-.32	.44		.78	.48	-.56	-.31	-.63	.82
RWT2	-.43	.29	.82		.44	-.28	-.57	-.46	.95
BB2	-.20	.32	.56	.65		-.32	-.28	-.69	.42
IBS2	.37	-.02	-.40	-.57	-.55		.15	.85	-.30
SRR2	.46	-.08	-.46	-.75	-.47	.57		.23	-.33
GSL2	.34	-.12	-.50	-.67	-.74	.96	.61		-.46
TWT2	-.38	.36	.88	.97	.63	-.48	-.63	-.59	

See Table I.2. for trait descriptions, and Table I.1 for location of populations. Correlations greater than ± .28 are significantly different ($P < .05$) than zero.

Table I.12 Estimates of phenotypic correlations in two Western Cascade populations (WC-1, upper diagonal and WC-2, lower diagonal) for a subset of seedling trait pairs

Seedling Trait	IBS1	HT1	HT2	RWT2	BB2	IBS2	SRR2	GSL2	TWT2
IBS1		.22	-.25	-.24	-.03	.55	.21	.44	-.23
HT1	.37		.64	.41	.31	-.11	-.06	-.24	.46
HT2	-.30	.38		.68	.34	-.44	-.12	-.49	.77
RWT2	-.29	.48	.69		.16	-.16	-.50	-.15	.96
BB2	-.21	-.15	-.13	-.01		-.19	-.06	-.56	.14
IBS2	.54	.24	-.40	-.29	-.36		.04	.86	-.19
SRR2	.32	.08	-.27	-.65	-.16	.20		.06	-.27
GSL2	.35	.22	-.13	-.22	-.78	.65	.31		-.19
TWT2	-.26	.56	.74	.96	-.09	-.28	-.44	-.14	

See Table I.2. for trait descriptions, and Table I.1 for location of populations. Correlations greater than ± .28 are significantly different ($P < .05$) than zero.

Table I.13. Estimates of phenotypic correlations in two Siskiyou populations (S-1, upper diagonal and S-2, lower diagonal) for a subset of seedling trait pairs.

Seedling Trait	IBS1	HT1	HT2	RWT2	BB2	IBS2	SRR2	GSL2	TWT2
IBS1		.39	-.24	-.25	.05	.52	.18	.40	-.23
HT1	.16		.56	.47	.23	.06	.03	-.07	.53
HT2	-.48	.19		.81	.28	-.44	-.23	-.51	.83
RWT2	-.51	-.02	.72		.13	-.34	-.42	-.36	.97
BB2	-.06	-.02	.07	-.02		-.20	-.11	-.69	.13
IBS2	.61	.01	-.68	-.54	-.13		.37	.73	-.27
SRR2	.53	.24	-.37	-.60	.10	.49		.39	-.24
GSL2	.49	.07	-.53	-.49	-.56	.77	.38		-.31
TWT2	-.41	.13	.76	.94	.00	-.50	-.34	-.46	

See Table I.2. for trait descriptions, and Table I.1 for location of populations. Correlations greater than ± .28 are significantly different ($P < .05$) than zero.

Table I.14. Estimates of phenotypic correlations in two Mixed-Conifer populations (MC-1, upper diagonal and MC-2, lower diagonal) for a subset of seedling trait pairs.

Seedling Trait	IBS1	HT1	HT2	RWT2	BB2	IBS2	SRR2	GSL2	TWT2
IBS1		.39	.09	-.02	.07	.40	.05	.26	-.01
HT1	.43		.69	.30	.12	-.11	.26	-.04	.52
HT2	.10	.65		.59	-.08	-.13	.07	.00	.76
RWT2	.02	.46	.53		-.10	.06	-.52	.21	.82
BB2	-.16	-.19	-.20	-.12		-.18	.12	-.73	-.07
IBS2	.59	.24	-.03	-.02	-.22		.08	.65	.10
SRR2	.30	-.11	-.21	-.78	-.10	.24		-.09	.03
GSL2	.52	.15	.13	.08	-.65	.71	.25		.19
TWT2	.12	.64	.73	.83	-.24	.11	-.44	.26	

See Table I.2 for trait descriptions, and Table I.1 for location of populations. Correlations greater than ± .28 are significantly different ($P < .05$) than zero.

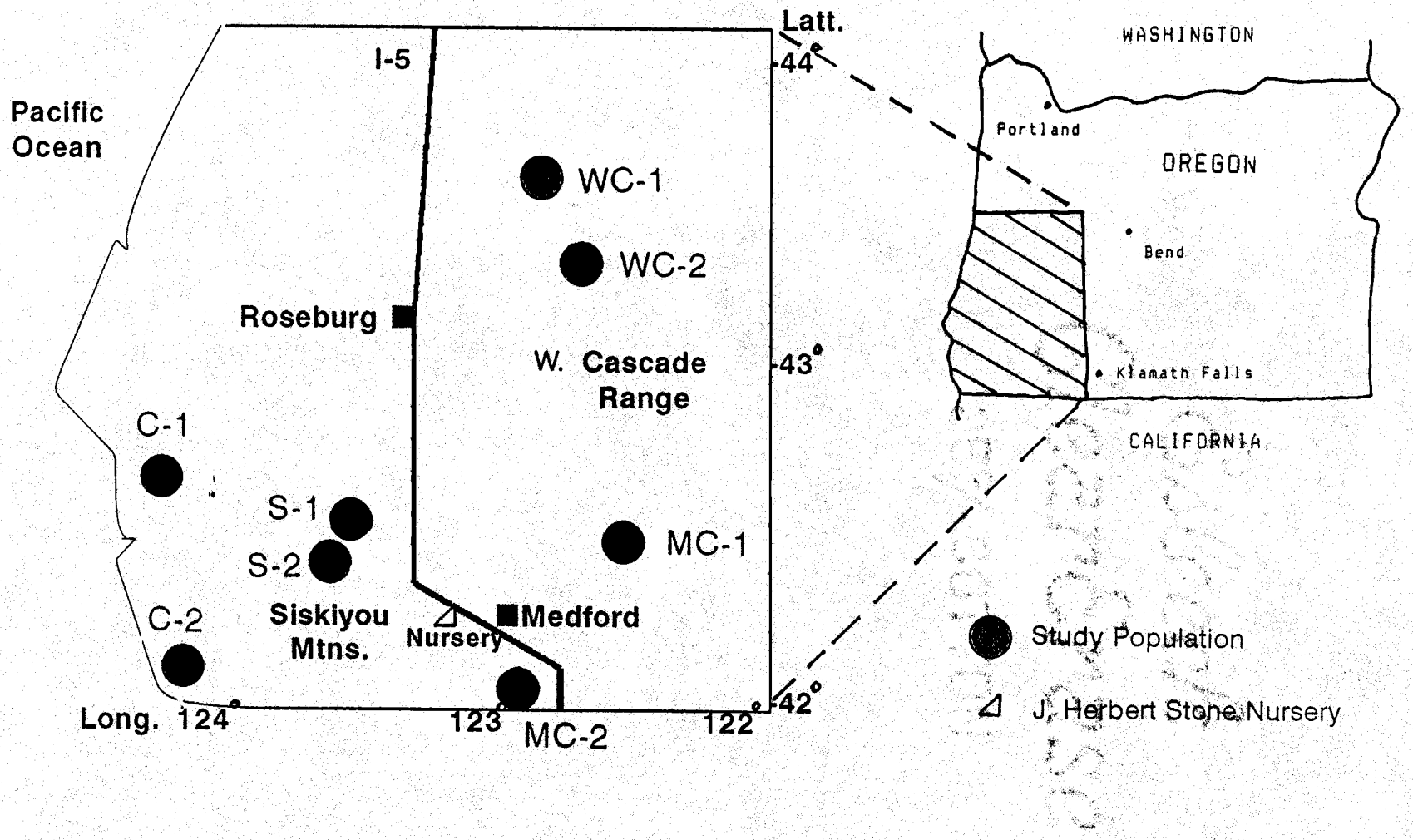

Figure I.1. Location of study populations in southwest Oregon.

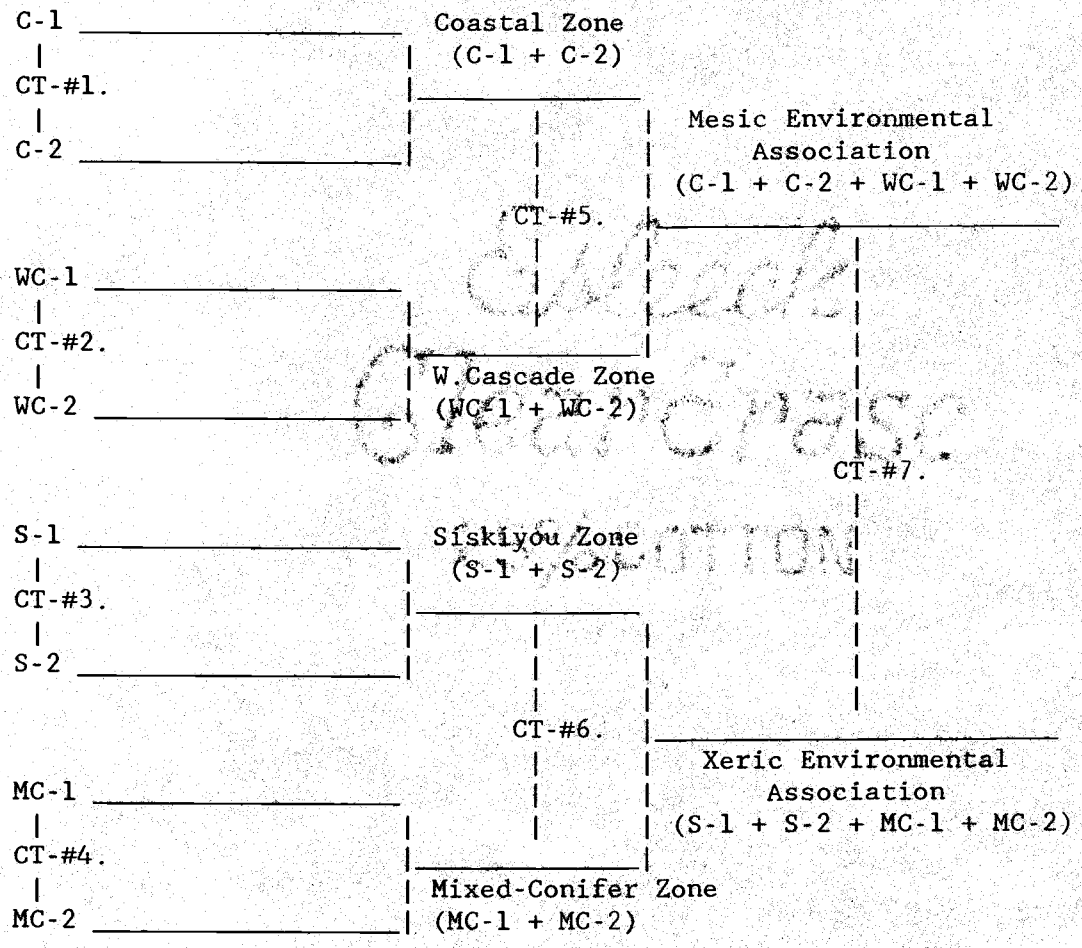

Figure I.2. Seven orthogonal contrasts (CT-#1 to CT-#7) used to compare population means. See Table I.1 for descriptions of populations, and Figure I.1 for locations of populations.

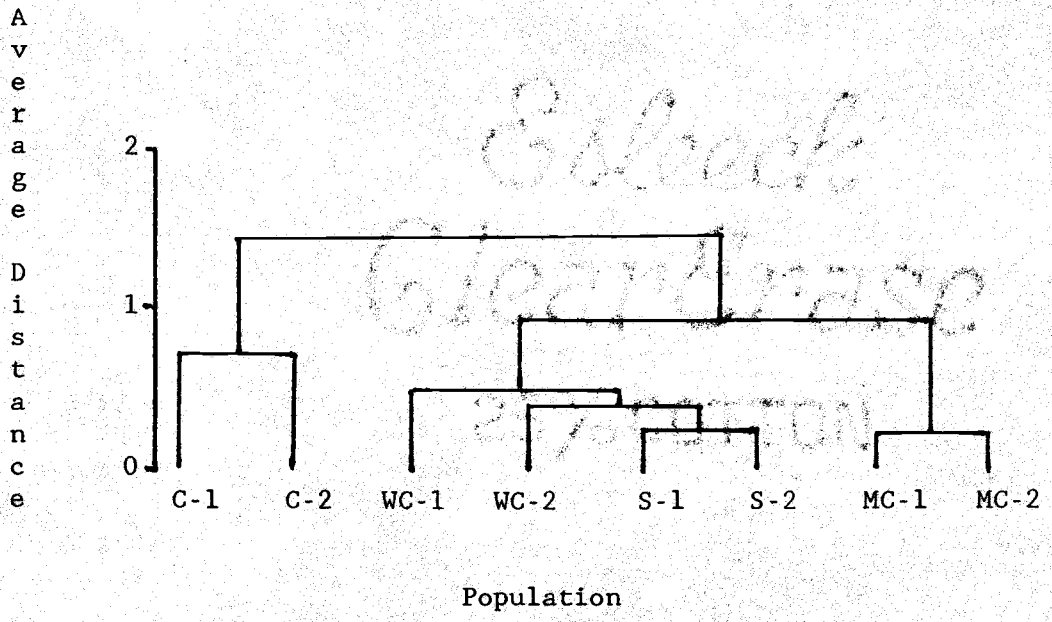

Figure I.3. Cluster diagram for eight populations based on dissimilarities of their trait means. See Table I.1 and Figure I.1 for locations and descriptions of populations.

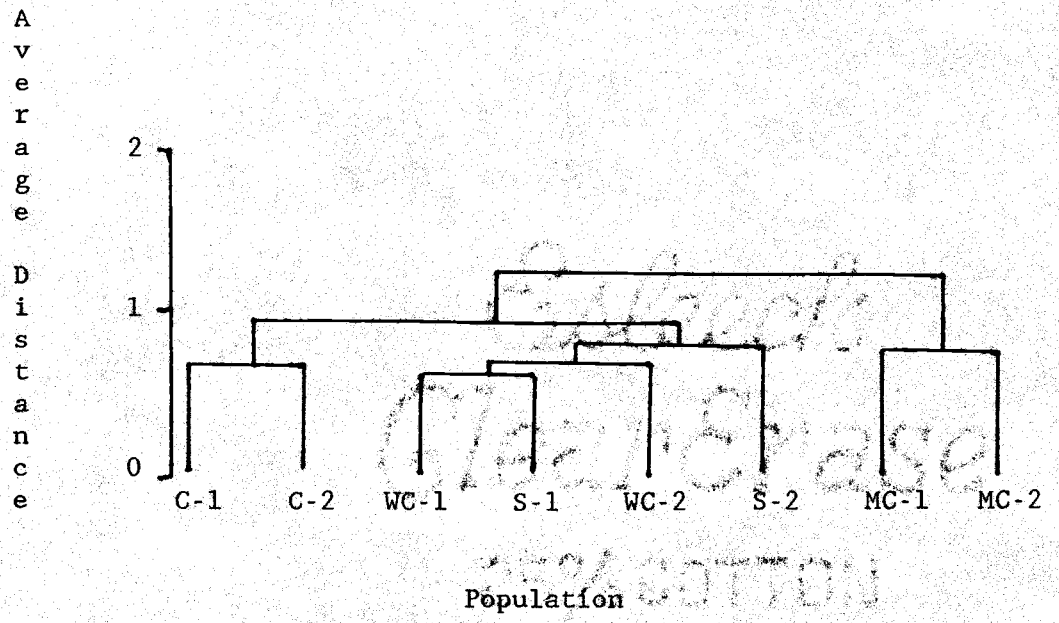

Figure I.4. Cluster diagram for eight populations based on dissimilarities (Dr_m) of their phenotypic correlation matrices. See Table I.1 and Figure I.1 for locations and descriptions of populations.

CHAPTER TWO

IMPLICATIONS OF DIFFERENCES AMONG DOUGLAS-FIR POPULATIONS IN QUANTITATIVE GENETIC STRUCTURE FOR TREE BREEDING

ABSTRACT

Expected responses of seedling traits to selection were investigated in order to assess the effects of differences in quantitative genetic structure (QGS) of Douglas-fir (Pseudotsuga menziesii var menziesii (Mirb.) Franco) populations on tree breeding. QGS varied substantially among populations from 4 ecological zones in southwest Oregon. In particular, genetic correlations between seedling height and other adaptive traits (e.g., phenology traits, and shoot:root ratio) differed among zones. Responses under two types of selection in the different zones were of interest: 1) correlated responses in adaptive traits when univariate selection is applied to stem height; and 2) responses in stem height, when restricted selection indices are utilized to limit change in adaptive traits to zero (multi-trait selection).

Correlated responses in adaptive traits are expected to be either favorable or unfavorable, depending upon within which of the four zones selection for stem height occurs. The magnitude of unfavorable responses, however, are expected to be quite limited, such that adaptation should not be negatively impacted in any large degree. The use of restricted selection indices had variable influence on height growth response in the different zones. Influences ranged from very limited in one zone to quite strong in others, where height growth would be

appreciably reduced. Restrictions, of course, would be necessary only when expected correlated responses are expected to be unfavorable. To optimize productivity, tree breeders need to tailor selection methods according to the QGS of populations and the intended environments to be reforested with the improved population.

INTRODUCTION

Genetic gains from an applied breeding program depend on the quantitative genetic structure (QGS) of the reference population and the selection strategies (models) that are implemented. QGS refers to trait means, the amounts of genetic variation and heritabilities of individual traits, and covariance and correlations between traits. If QGS differs substantially in different breeding populations, it will be necessary to utilize different selection strategies in order to optimize genetic gains. In addition, correlated responses between selected and non-selected traits, some of which may be undesirable, will differ in different breeding populations. The biological impacts and practical consequences of applying selection need to be assessed and understood prior to implementation.

In Chapter 1 of this thesis, QGS was compared among eight populations of Douglas-fir (Pseudotsuga menziesii var menziesii (Mirb.) Franco) from four ecologically distinct zones in southwest Oregon. Two populations each from the Coast mountain range, lower elevations in the Western Cascade range, Siskiyou mountains, and higher elevations in the Western Cascade/Siskiyou mountains were sampled. Substantial differences in QGS were observed among populations, particularly in trait means and genetic correlations between traits. The extent of differentiation in both trait means and genetic correlations between traits was positively associated with the extent of differences in source habitats. Differences among populations in correlations between second year

phenology (e.g., timing of budburst and budset) and growth traits (e.g., stem height) were especially striking, and occasionally were of opposite sign. For example, the genetic correlation between second year height and budset date was estimated to be -.59 in the Coastal zone, but +.09 in the high elevation Western Cascade/Siskiyou mountain zone. The majority of differences among populations in correlation coefficients appeared to be related to differential responses of the populations to damage from an early frost at the end of the first growing season.

Most tree breeding programs emphasize improvement in stem growth. It is important to assess the implications of selection for improved growth on adaptive characteristics of trees. For example, if improved growth comes at the expense of extended growing seasons or increased shoot:root ratios, susceptibility to damage from early fall frost or summer drought might be increased (Rehfeldt 1983, White 1987, Kaya et. al. 1989). Differences in QGS observed in Chapter 1 suggest that populations from the four diverse zones will respond differently under the same selection regimes. The implications of these differences, however, cannot be fully appraised until direct and correlated responses of various traits are compared under different selection methods. Estimated responses to selection are dependent on numerous factors. Parameters such as genetic correlations between traits, heritabilities, and genetic and phenotypic variances influence the magnitude of direct and correlated responses. In addition, numerous selection methodologies (e.g., univariate vs. index selection) are available, each with their own consequences with regards to response.

The goal of this chapter is to examine the implications of the differences in QGS observed in Chapter 1 with regards to responses to selection. Two types of selection are investigated. First, univariate selection for growth was assessed in terms of both direct response in growth and correlated responses in adaptive traits. Second, restricted selection indices including both growth and adaptive traits were used to assess the implications of restricting changes in adaptive traits, with regards to expected responses in growth. The practical and biological significance of the various response patterns in the different zones are discussed.

MATERIALS AND METHODS

Materials

Details on materials used in this study, nursery growing conditions, and traits measured are given in Chapter 1. A brief overview of the methods and specific information pertinent to this Chapter follow. The four ecological zones from which populations were sampled are designated in Chapter 1 as the Coastal, W. Cascade, Siskiyou, and Mixed-Conifer zones, respectively. Two populations were sampled within each zone, each occupying a different elevational subzone (average elevational differences between zones ranged from 152 to 305 m). The subzones correspond to what have been identified by tree breeders as distinct Douglas-fir breeding populations for southwest Oregon (Wheat and Silen 1984). In this case, elevational subzones within zones have similar environments and plant associations, relative to larger differences between zones. The Coastal zone has more than twice the average annual precipitation (305 cm) than the Mixed-Conifer zone (117 cm), while the W. Cascade (139 cm) and Siskiyou (137 cm) zones have values intermediate between the other two (Oregon State Univ. 1982a). The difference between average mean minimum January temperature and average mean maximum July temperature is smaller in the Coastal zone (2°C (Jan.), 23°C (July)), in comparison to the W. Cascade (-1°C, 28°C), Siskiyou (0°C, 31°C), and Mixed-Conifer (-4°C, 29°C) zones (Franklin and Dyrness 1973).

Each population was represented by 45 parent trees. Wind-pollinated seeds collected from each parent were sown in a U.S. Forest Service

nursery located in Central Point, Oregon and seedlings grown under operational conditions for two years. The experimental design in the nursery was a randomized complete block with four replications. A five-seedling row plot for each of the 360 families (8 populations X 45 families/population) was allocated at random within each replication. Twenty-two traits were measured over the two growing seasons. The traits represented measures of biomass (e.g., stem height and diameter, dry weight), biomass allocation (e.g., shoot:root ratio), and shoot phenology (e.g., dates of budset and budburst, percentage of second flushing). In addition, following an early October frost event at the end of the first growing season, the percentage of seedlings within family plots damaged by frost was recorded. Frost damage was most severe among seedlings in the Coastal populations (average of 52% of seedlings within families damaged), while in the remaining inland zones, damage was 19% (Siskiyou), 15% (W. Cascade), and 4% (Mixed-Conifer). Frost damage significantly affected second year growth, as well as QGS in the Coastal, W. Cascade, and Siskiyou zones.

Among the 22 traits evaluated, 6 traits were selected for analysis of selection response (Table II.1). These traits included measures of seedling growth each year (HT1, HT2), as well as traits directly related to adaptability of seedlings, including measures of phenology in each year (FBS1, BB2, IBS2), and shoot:root ratio (SRR2). Combinations of shoot growth and phenology traits were of particular interest, because differences in their correlations were responsible, in large measure, for the observed variation among populations in QGS. Seedling growth and

phenology traits also appear to be of practical significance for early testing (e.g., nursery tests) of Douglas-fir families in tree improvement programs (Adams and Aitken 1991). Initial budset (IBS2) was chosen in lieu of final budset as a phenology trait in the second year because a negative family component of variance was estimated for final budset in one of the populations. In addition, the genetic correlation between IBS2 and final budset was very high in all populations (mean = .98; range = .89 to 1.00).

Two different subsets of these traits were utilized in subsequent analyses. First year traits were not affected by the frost event and were included along with shoot:root ratio in the first subset. Second year shoot growth and phenology traits were included along with shoot:root ratio in the second subset. The second subset was of particular interest because second year traits were affected to various degrees in the different zones by the frost event that occurred in the first year. In addition, comparison of results in Chapter 1 with earlier findings (Kaya 1987) for the same populations indicated that correlations between growth and phenology traits are quite different in the absence of fall frost in first year. SRR2 was included in both subsets since the change in correlation between SRR2 and height in the two respective growing seasons was quite consistent among populations where a more negative correlation existed in year two as opposed to year one, despite the fact that some populations were damaged more by frost (Chapter 1). In addition, mean SRR2 was comparable to other studies, where higher ratios are associated with milder climates (e.g., Coastal) and lower

ratios with harsher climates (e.g., inland habitats). Thus, SRR2 was deemed not to have been as much affected by the frost event as other second year traits, and was included in both subsets. In each subset, seedling height (HT1 or HT2) represented the primary trait of interest for selection, while the remaining traits were considered secondary traits.

Estimation of Parameters

Previous analyses indicated that both estimated genetic variances of individual traits and genetic correlations between traits were similar for the two populations from the same zone (Chapter 1). Therefore, mean squares calculated for each population separately were pooled by zone for the analyses in this chapter. This created four populations (zones) for comparison and increased the precision of population parameter estimates (i.e., now based on data from 90 families rather than 45). Analyses of variance and covariance were conducted on plot means. Components of variance and covariance were estimated from the pooled data sets by equating the observed mean squares and cross-products to expected values (Table II.2). To standardize notation in this chapter, $\sigma_{(xy)}$ refers to the covariance between traits x and y, while $\sigma^2_{(x)}$ and $\sigma^2_{(y)}$ refer to the variances of trait x and y, respectively. For illustrative purposes, the open-pollinated family is utilized as the unit of selection in this study. Additive genetic variances and covariances were estimated as the family component of variance for traits x and y ($\sigma^2_{f(x)}$ or $\sigma^2_{f(y)}$), and family component of covariance between traits x and y ($\sigma_{f(xy)}$),

respectively. Phenotypic covariances were estimated as: $\sigma_{p(xy)} = \sigma_{f(xy)} + \sigma_{e(xy)}/r$, where $\sigma_{e(xy)}$ is the estimated error component of covariance, and r=4 (number of replications). In like fashion, phenotypic variances ($\sigma^2_{p(x)}$, $\sigma^2_{p(y)}$) were estimated, but utilizing components of variance rather than covariances.

Genetic correlations between traits were estimated as: $r_{g(xy)} = \sigma_{f(xy)} / \{[\sigma^2_{f(x)}] \cdot [\sigma^2_{f(y)}]\}^{1/2}$. Standard errors of genetic correlations were calculated according to Becker (1984). Phenotypic (family mean) correlations between traits were estimated as: $r_{p(xy)} = \sigma_{p(xy)} / \{[\sigma^2_{p(x)}] \cdot [\sigma^2_{p(y)}]\}^{1/2}$. Standard errors of phenotypic correlations were calculated according to Mode and Robinson (1959). Family heritabilities ($h^2_{f(x)}$) were estimated as $h^2_{f(x)} = \sigma^2_{f(x)}/\sigma^2_{p(x)}$, and their standard errors by the approximation given in Dickerson (1969). These genetic and phenotypic parameter estimates were utilized as input in the various selection models.

Analytical Procedures

The four zones were compared for selection response under two general selection procedures. Response in both growth and adaptive traits in each subset, respectively, were estimated when selection is directed towards height growth (HT1 or HT2) only. This represents a univariate selection procedure where selection is applied directly to an individual trait based on information for that one trait only, and is referenced as model 1. The objective is to evaluate the consequences for adaptation in each zone, when improved growth is the sole selection

criterion. In the second selection procedure, response in growth traits (HT1 or HT2) were estimated when various combinations of growth and adaptive traits are included in restricted selection indices (models 2-4). In models 2-4, height growth (HT1 or HT2) was included in the index as an unrestricted trait, along with one or more adaptive traits (i.e., phenology traits and/or shoot:root ratio), which were restricted to zero response (i.e., the restricted traits). Comparisons between the expected responses in these models (2-4) with model 1 make it possible to assess the biological significance (and trade-offs) of selection directed towards improving growth traits, with or without restrictions on adaptive traits.

Both direct and correlated responses under model 1 can be calculated with the formula (Baradat 1976):

$R_y = [i][CGP_{(xy)}][(\sigma^2_{p(y)})^{1/2}]$,where R_y is the expected genetic response in trait y, i is the selection intensity, $CGP_{(xy)}$ is the coefficient of genetic prediction and $(\sigma^2_{p(y)})^{1/2}$ is the phenotypic standard deviation of trait y. The coefficient of genetic prediction is the amount of change in trait y (in standard deviation units) expected when trait x is changed by one standard deviation unit. When trait y is directly selected (i.e., x and y are the same trait), $CGP_{(xy)} = h^2_{f(y)}$. When selection is applied to trait x, $CGP_{(xy)} = [h_{f(x)}][h_{f(y)}][r_{g(xy)}]$. In all cases, expected responses are presented per unit of selection intensity (i=1.0) applied.

Models 2 through 4 are variations of the restricted selection index, where two or more traits are used in the index (Baker 1986:117). The restricted selection index model can accommodate any specific number of

traits ,with or without restrictions, in the index. Selection is applied to index values (I) calculated for each family by the equation $I = b_1T_1 + b_2T_2 + \ldots + b_mT_m$, where b represents the index coefficient for each trait, T the respective trait phenotypic value for the family, and m is the number of traits in the index. The index coefficients (b) are estimated by the following formula presented in matrix notation: $b = P^{-1}G_r'(G_rP^{-1}G_r')^{-1}k$, where r equals the number of traits to be restricted in their change by some specific amount (restricted traits), k = r x 1 vector of desired changes in the restricted traits, P = matrix of phenotypic covariances among the m traits, and G_r = r x m matrix of genotypic covariances between the r restricted traits and all m traits in the index. In models 2-4, height growth (either HT1 or HT2) is not constrained while the other traits included in the index are constrained to 0% change (i.e., zero response when selection index is applied).

In model 2, both height growth and phenology traits were considered jointly in the model specifications for each respective subset of traits. Thus, HT1 and FBS1 were included in one restricted index, while HT2, BB2, and IBS2 were included in a second restricted index. For model 3, selection was directed towards improving height growth in each respective subset (HT1 or HT2), while maintaining no change in mean SRR2. Model 4 incorporates all traits in each respective subset into a restricted index (i.e., (HT1, FBS1, SRR2), or (HT2, BB2, IBS2, SRR2)). Comparing model 4 with models 2 and 3 makes it possible to assess the effects of restrictions on additional adaptive traits, on expected response in growth.

Expected responses (R_y) in HT1 or HT2 for models 2 through 4 were calculated according to Baker (1986): $R_y = (i/\sigma_I)(\sigma_{G(j)I})$, where i is the selection intensity, σ_I is the square root of variance of the index ($\sigma^2_I = b'Pb$), and $\sigma_{G(j)I}$ is the covariance between the index (I) and genotypic value of the jth trait. Again, responses are presented in units of selection intensity ($i = 1.0$). The correlation ($r_{GP(I)}$) between the genotypic value and the phenotypic value of the selected trait (index in this case) is estimated as: $r_{GP(I)} = b'G'/[\sigma_I][\sigma^2_{f(x)}]^{1/2}$, where G represents a 1 x m vector of genetic covariances between the selected trait and all m traits, $\sigma^2_{f(x)}$ is the genetic variance of the selected trait, and b and σ_I represent terms described previously. The correlation ($r_{GP(I)}$) is an estimate of the accuracy of predicting genetic values on the basis of index values.

RESULTS AND DISCUSSION

Genetic Variation and Parameter Estimates

Significant variation ($P < .05$) was observed among families for all 6 traits in all zones, with two exceptions. The two exceptions involved budburst date (BB2), where family variation approached significance in the Siskiyou ($P < .08$) and W. Cascade ($P < .10$) zones. In the first subset of traits (HT1, FBS1, SRR2), none of the estimated phenotypic correlations (Table II.3) differed significantly among zones on the basis of a heterogeneity chi-square test (Snedecor and Cochran:186), while significant differences in phenotypic correlation coefficients were found for three (HT2-BB2, SRR2-BB2, SRR2-IBS2) of the six pairs of traits in the second subset (HT2, BB2, IBS2, SRR2). The largest differences in estimated correlation coefficients were between the Coastal and Mixed-Conifer zones (Table II.3).

In general, estimated genetic correlation coefficients were of the same sign, but larger in magnitude than corresponding phenotypic correlation coefficients (Table II.3). In addition, the range among populations in genetic correlations was generally greater than that for corresponding phenotypic correlations. Genetic correlations between HT2 and SRR2, for example, ranged from 0.00 (Mixed-Conifer) to - 0.53 (Coast), while correlations between HT2 and BB2 ranged from -0.53 (W.Cascade) to 0.73 (Coast). Of the six pairs of traits in the second subset, in only one, BB2-IBS2, was the estimated genetic correlation the same sign in all four zones (range from -.08 (Siskiyou) to -.72 (Coast)).

Standard errors of phenotypic correlation estimates were substantially less (mean = .09, range = .07 to .10), on average, than standard errors of genetic correlation estimates (mean = .25, range = .13 to .73).

As in Chapter 1, where correlation structures of the populations were compared for 19 traits, the Mixed-Conifer population differed substantially from the other three populations for the subset of traits that included second year traits. The Mixed-Conifer population, in general, had correlation coefficients of lower magnitude in comparison to the other three populations. In addition, while the genetic correlation between HT2 and IBS2 was near zero (.09) in the Mixed-Conifer population, it was moderately negative (range from -.35 to -.59) in the remaining populations. In contrast to this pattern, the genetic correlation between HT1 and FBS1 was positive for all populations (range from .11 (Coast) to .35 (W. Cascade)). These differences in correlations between height and budset in the two growing seasons are probably due to the effects of frost which occurred in the first growing season. Kaya (1987) sampled two zones (Coastal and inland) in southwest Oregon, and in the absence of frost damage, estimated near zero to moderately positive (.42) genetic correlations between second year height increment and budset date in the inland and Coastal zones, respectively. The occurrence of frost damage in this study affected the correlation estimates in the following manner. Families (populations) which set buds latest sustained greater damage from frost, and second year growth was substantially reduced. Thus, a more negative correlation existed between budset and growth after the second growing season in those populations

which sustained a high amount of frost damage in the first growing season.

Differences among zones in magnitudes of the estimates of phenotypic variances, genetic variances, and family heritabilities were also evident (Table II.4). Estimated variances differed substantially between the Coastal population and remaining populations, and especially so for second year traits, where variances were generally greater in the Coastal zone. The larger variances observed for the Coastal zone may reflect more the variation in frost resistance among families as opposed to any differences among families in inherent growth rate per se. Family heritabilities were low to moderate (range from .36 to .65, Table II.4) for the majority of traits and zones. Family heritability estimates, however, were especially low for BB2 in the W.Cascade (.19) and Siskiyou (.20) zones.

Direct and Correlated Responses to Selection

While direct responses of HT1 and HT2 to univariate selection were of primary interest (model 1), direct responses of all traits were calculated for comparison (Table II.4). Expected genetic responses due to direct selection ranged, depending on the trait, two- to three-fold among the zones investigated. The Coastal zone had the highest expected responses for HT2 and SRR2 and was due primarily to the large family variances for these traits. In contrast, the W. Cascade population had the lowest expected responses for these traits, which in large measure is due to the lower heritabilities of HT2 and SRR2 in this zone.

Selection for HT1 and HT2 in the Coastal zone, and to a lesser extent in the W. Cascade and Siskiyou zones, may in fact be selecting for different inherent characteristics in the two growing seasons; where taller families in the first season represent an inherent growth efficiency, while taller families in the second season represent greater ability to withstand the first year's frost event. Expected responses for BB2 were quite small relative to both FBS1 and IBS2. The combination of low phenotypic variance of BB2 in all zones, and its generally low heritability resulted in these reduced responses.

A wide range among zones in correlated responses is expected when selection is applied to height only (Table II.5). Expected correlated responses in SRR2 and FBS1 are small when selection is directed at HT1. While the expected change in SRR2 is quite small in the Siskiyou and Mixed-Conifer zones, the trend to a more positive value could result in decreased hardiness to drought. A positive increase in FBS1 is expected in all zones when selection is directed at HT1. This change to later budset may be detrimental, since improved populations would presumably be more susceptible to damage from early fall frosts and late summer drought. The magnitude of the expected responses, however, is quite small (< 1 day).

When HT2 is selected, no change is expected in SRR2 for the Mixed-Conifer zone, while a reduction is expected in the remaining zones(Table II.5). Reduced SRR2 appears beneficial, especially so for the zones within the harsher inland environments. Direction and magnitude of correlated responses in both budburst and budset in year two varied among

zones, but in no instance is the correlated response expected to have a large negative impact on adaptability. Budburst is expected to occur later by approximately one day in the Coastal zone, while expected responses in the remaining zones were considerably less (range from 0.1 to - 0.6 days). Earlier budsets (< 2 days) are projected for three of the four zones, while a delay in budset (0.3 days) is expected in the Mixed-Conifer zone. In the cases where the correlated responses were largest (e.g., Coastal zone), the direction was favorable (i.e., later BB2 or earlier IBS2), and absolute magnitudes were relatively small.

In terms of impacts on adaptability, the expected correlated responses in phenology following family selection for HT2 within zones, are minor relative to the movement of populations (i.e., propagules) outside of native zones for reforestation. For example, zone means differed by 11 days (e.g., Coast vs. Siskiyou or W. Cascade zones, Table II.4) in IBS2, while correlated responses in budset of only a few days, at most, are expected when selection is directed at HT2 within any single zone. Movement of populations from the coast to an inland environment (e.g., Siskiyou zone) is expected to have very negative implications for adaptation, because Coastal populations would be more susceptible than the native populations to early fall frosts since they are expected to set bud later. In addition, Coastal populations are expected to be less drought hardy than native inland populations (Ferrell and Woodward 1966, Joly et. al. 1989).

The estimates of direct and correlated responses (model 1) in Tables II.4 and II.5 were based on QGS of the respective zones as

revealed in a single test environment. Trait responses may differ considerably in different test environments. As an example of how environments (and year effects) may affect trait responses, the results of this study can be compared to a previously reported seedling common garden experiment which utilized the same Coastal zone populations (C-1, C-2) and two inland populations (S-1, MC-1)(Kaya 1987). Kaya's common garden was in Corvallis, Oregon where the growing conditions were more moderate than in this study. This is not only reflected by the lack of a frost event in Kaya's study, but by the longer second year growing seasons of the coastal (13 days) and inland (6 days) sources in Corvallis. Kaya calculated expected correlated responses in phenology traits when selection was directed at second year height increment. Like the results for the W. Cascade and Mixed-Conifer zones in this study, Kaya found little or no effect on phenology when inland families are selected for height growth in the second year. For the Coastal populations, however, Kaya predicted selection for second year height would result in both earlier budburst (-.32 days, for i = 1.0) and later budset (.56 days), both responses opposite in sign to those found in this study (i.e., later budburst (1.1 days) and earlier budset (-1.9 days)). Although these expected responses are opposite in sign, they are either favorable in direction or of small magnitude, such that, selection for height alone would not be expected to have much of a negative impact on adaptation.

Expected responses in HT1 or HT2 when using a restricted selection index varied among models (Table II.6). Effects on height growth

response (i.e., decrease in response compared to model 1, Table II.5) were, on average, greatest for model 4 which had the largest number of traits restricted. As more restrictions are placed on correlated traits, the response of the primary traits should also be more restricted (Baker 1986).

In general, HT2 responses were affected (i.e., decreased) to a greater extent than HT1 responses when the specified restricted indices were employed (Table II.6). The use of restricted selection indices (models 2-4) is expected to have only a minor impact (slight decrease) on expected response of HT1. Even when both FBS1 and SRR2 (model 4) were restricted in the index, HT1 still approached at least 75% of the respective responses estimated per zone under model 1. These results are not unexpected, since relatively weak genetic correlations (< .36) were found between HT1 and the other traits in the same subset (Table II.3). In contrast, restrictions on correlated traits often had considerable impacts on expected responses in HT2, where severe reductions (in comparison to model 1 responses) were estimated for the Coastal and W. Cascade zones under models 2 and 4. Restricting phenology in models 2 and 4 severely limited the potential for advancing height growth (HT2) in these two zones. Expected gains in HT2 were least impacted in the Mixed-Conifer zone. This is expected due to the low genetic correlations (< .38 in absolute magnitude) that exist within this second subset of traits in this zone (Table II.3). Model 3 had the least detrimental effect on HT2 response of any restricted index.

Selection indices may not provide very precise estimates of response if parameters are estimated with large sampling errors or if a large number of traits are included in the index (Baker 1986). In addition, restricted indices will reduce the efficiency of selection as opposed to multi-trait indices with no restrictions. The imposed restrictions, in effect, reduce the correlation ($r_{GP(I)}$) between the index (restricted) and estimated genotypic values of the selected trait as opposed to an index with no restrictions (Ronningen and Van Vleck 1985). Correlations ($r_{GP(I)}$) were moderate (mean = .69, range = .54 to .78) between the restricted indices (models 2-4) and genotypic values for HT1 (among all zones). Excluding the W. Cascade zone, correlations were also moderate (mean = .57, range = .42 to .77) between the restricted indices and genotypic values for HT2. For the W. Cascade zone, $r_{GP(I)}$ was equal to .16, .45, and .09 for models 2, 3, and 4, respectively. Therefore, except for the W. Cascade zone, the estimate of responses and relative differences among both zones and models within zones would appear to be of moderate accuracy. Correlations ($r_{GP(I)}$) were also calculated for similar multi-trait selection indices, where restrictions were not specified for any trait. In all cases, $r_{GP(I)}$ was higher for those indices where restrictions were not specified: HT1 (mean = .75, range = .63 to .79), HT2 excluding W. Cascade zone (mean = .77, range = .73 to .79), HT2 for W. Cascade zone (.58, .50, .59 for models 2, 3, and 4, respectively). Thus, the relative accuracy of restricted selection indices may indeed be quite lower in some cases as opposed to the more standard (no restrictions) selection indices.

Restricted indices are only necessary when correlated responses are deemed unfavorable. Thus, restricted indices may or may not be beneficial in a specific breeding program and should only be utilized when predicted biological responses warrant their use. It is advisable to evaluate the various options that are possible with restricted and unrestricted indices in order to achieve the expected goals (Cotterill and Jackson 1981). Given the QGS of the Coastal zone in this study, for example, selection for HT2 is expected to result in both later budburst and earlier budset in the next generation. Since both of the predicted correlated responses are favorable, there would be no reason to use restricted selection indices to limit change in phenology, since their use would result in less HT2 gain.

CONCLUSIONS

The major findings from this study indicate that direct and correlated responses to selection for height are expected to vary among zones from southwest Oregon which differ in QGS. These findings support previous results where variation among populations in QGS have been demonstrated (e.g., Cannell and Willett 1976, Birot and Christophe 1983, Rehfeldt 1983), and the effect of these different quantitative structures have been noted (e.g., Christophe and Birot 1983, Rehfeldt 1983).

In the conditions of this study, unfavorable correlated responses for timing of budburst and budset could be expected in some zones. The expected magnitude of these correlated responses, however, were not large. Movement of seed from one zone to another would appear to have a much larger detrimental impact on adaptive traits relative to expected responses to selection within zones.

Restricted selection indices provide an effective tool for limiting changes in adaptive traits, but such indices were found in this study to have variable effects on responses of growth traits in the different zones. Such indices, however, may cause severe reductions in expected gains in growth. Their use may not be warranted in those situations where expected changes in both traits of interest (primary traits) and adaptive traits are favorable in relation to meeting the aggregate goals of the breeder. Thus, use of restricted indices and other selection strategies need to be evaluated prior to finalizing any multi-trait selection strategy.

Test environments can have a profound effect on the genetic expression of traits and QGS. Thus, predictions of expected responses and development of the most appropriate selection strategies are dependent on both the inherent genetic composition of populations and test conditions that the populations have been exposed to. Estimates of QGS and expected responses may have limited application if based on a limited sampling of both populations and test environments. If sampling is severely limited, inferences pertaining to a wider range of populations and environments may not be advisable.

Knowledge of the QGS of populations is needed prior to formulating the most efficient selection strategies for any particular population. As previously noted by Thorpe (1976), estimation of quantitative genetic parameters must be specific to the natural population or deme. The correlation between expected genetic changes and realized changes (after selection) in a breeding program will likely be highest when the QGS is estimated for those particular populations and environmental zones in which selection is to be applied.

Table II.1. Description of traits.

Code	Trait	Units
I. First Growing Season:		
FBS1	Final budset date[a/]	weeks after August 21, 1985
HT1	First year height	cm
II. Second Growing Season:		
HT2	Total height (2-years)	cm
BB2	Budburst date[a/]	days after January 1, 1986
IBS2	Initial budset date[b/]	days after January 1, 1986
SRR2	Shoot:Root ratio	ln(SWT2)/ln(RWT2)[c/]

a/ Budburst scored twice a week; was recorded as the date when needles first became visible in the opening terminal bud.

b/ Initial budset date denotes date on which terminal bud scales were first observed. Final budset date refers to budset date after any second flushing. Final budset equals the initial budset date if second flushing did not occur. Budset scored once per week.

c/ SWT2 is dry weight of shoot and RWT2, dry weight of root, both in gms (X 10). The ratio of ln(SWT2)/ln(RWT2) was used instead of the ratio of absolute weights in order to conform to assumptions of the analysis of variance.

Table II.2. Form of analyses of variance and covariance of the pooled data sets.

Source of variation	Degrees of freedom	Expected mean squares[a/]
Blocks	6	
Families (f)	88	$\sigma^2_e + 4\ \sigma^2_f$
Error (e)	264	σ^2_e

a/ σ^2_f = variance among open-pollinated families; σ^2_e = error variance; where analysis is based on family plot means. Covariance (ANCOVA) components have the same form when expected mean squares are replaced with expected cross-products.

Table II.3. Estimated genetic (above diagonal) and phenotypic correlations (below diagonal) between seedling traits for populations from each of four ecological zones.

Zone	Trait[a/]			Trait[a/]			
	HT1	SRR2	FBS1	HT2	SRR2	BB2	IBS2
Coast							
HT1		-.27	.11	HT2	-.47	.73	-.59
SRR2	-.10		.54	SRR2	-.39	-.61	.59
FBS1	.26	.41		BB2	.52	-.39	-.72
				IBS2	-.46	.44	-.44
W. Cascade							
HT1		-.09	.35	HT2	-.33	-.53	-.35
SRR2	.01		.55	SRR2	-.20	-.06	-.05
FBS1	.42	.32		BB2	.10	-.11	-.36
				IBS2	-.42	.12	-.27
Siskiyou							
HT1		.14	.27	HT2	-.53	.13	-.63
SRR2	.13		.71	SRR2	-.30	.03	.73
FBS1	.37	.44		BB2	.19	-.01	-.08
				IBS2	-.55	.43	-.17
Mixed-conifer							
HT1		.27	.26	HT2	.00	-.36	.09
SRR2	.09		.37	SRR2	-.08	-.03	.28
FBS1	.38	.21		BB2	-.13	.02	-.37
				IBS2	-.07	.17	-.20

[a/] See Table II.1 for description of traits.

Phenotypic correlations from two different zones are significantly different ($P < .05$) if their absolute difference (z-transformed basis) exceeds 0.30. Individual phenotypic correlation coefficients are significantly different from 0 if their absolute difference exceeds 0.20.

Table II.4. Estimated means, phenotypic variances (σ^2_p), family components of variance (σ^2_f), family heritabilities (h^2_f), and expected responses to family selection (R_y) per unit of selection intensity (i = 1.0), for six seedling traits in populations from each of four ecological zones.

Zone	Trait[a/]	Mean[b/]	σ^2_p	σ^2_f	h^2_f	R_y	% R_y/i[c/]
Coast	HT1	26.7	3.7	1.4	.38	.74	2.8
	FBS1	5.7	0.2	0.1	.55	.25	4.4
	HT2	43.7	26.1	15.64	.60	3.06	7.0
	SRR2	3.45	.001	.0009	.62	.23	6.7
	BB2	96.4	7.2	3.9	.54	1.45	1.5
	IBS2	181.3	34.3	17.1	.50	2.90	1.6
W.Cascade	HT1	25.0	5.3	3.3	.62	1.43	5.7
	FBS1	4.6	0.4	0.2	.65	.40	8.6
	HT2	48.9	16.8	4.1	.25	1.01	2.1
	SRR2	3.3	.0004	.0001	.30	.06	1.8
	BB2	100.5	6.0	1.2	.19	.50	0.5
	IBS2	169.7	24.8	9.6	.39	1.94	1.1
Siskiyou	HT1	24.0	5.0	3.1	.62	1.39	5.8
	FBS1	4.5	0.4	0.3	.53	.34	7.6
	HT2	46.4	21.9	11.5	.53	2.47	5.3
	SRR2	3.09	.0006	.0003	.44	.11	3.6
	BB2	97.4	5.3	1.1	.20	.49	0.5
	IBS2	170.7	31.0	17.6	.57	3.24	1.9
Mixed-conifer	HT1	21.8	3.8	2.2	.58	1.13	5.2
	FBS1	3.8	0.4	0.2	.63	.39	10.3
	HT2	46.8	12.4	7.4	.60	2.11	4.5
	SRR2	3.04	.0009	.0004	.36	.11	3.6
	BB2	102.7	9.1	4.0	.44	1.34	1.3
	IBS2	160.5	26.7	14.7	.55	2.89	1.8

[a/] See Table II.1 for description of traits.

[b/] Means presented in original units of measure per Table II.1.

[c/] % R_y/i expressed as percentage of original population mean per unit of selection intensity.
Response (R_y) calculated as: $R_y = (i)(h^2_f)(\sigma_p)$.

Table II.5. Estimated direct and correlated responses within populations from each of four ecological zones when selecting for seedling height growth (HT1 or HT2).

I. Selection for HT1

Zone	Responding Trait[a/]		
	HT1	SRR2	FBS1
Coastal	0.74(2.8)	-.05(1.5)	.02(0.4)
W.Cascade	1.43(5.7)	-.01(0.3)	.14(3.0)
Siskiyou	1.39(5.8)	.02(0.7)	.11(2.4)
Mixed-Conifer	1.13(5.2)	.04(1.3)	.10(2.6)

II. Selection for HT2

Zone	Responding Trait[a/]			
	HT2	SRR2	BB2	IBS2
Coastal	3.06(7.0)	-.11(3.2)	1.11(1.2)	-1.88(1.0)
W.Cascade	1.01(2.1)	-.02(0.6)	-.28(0.3)	-.53(0.3)
Siskiyou	2.47(5.3)	-.06(1.9)	.10(0.1)	-1.93(1.1)
Mixed-Conifer	2.11(4.5)	.00(0)	-.57(0.6)	.27(0.2)

[a/] See Table II.1 for description of traits. Absolute responses, and responses as percentage of original zone mean (in parentheses), are per unit selection intensity (i = 1.0) in the original units of measurement. Selection unit is the open-pollinated family.

Table II.6. Estimated responses of seedling height (HT1 or HT2) in populations from each of four ecological zones, when restriction selection indices (models 2-4) are used to restrict change in correlated traits to zero.

I. Selection for HT1[a/]

Zone	Model[b/] 2	3	4
Coastal	0.74(2.8)	0.68(2.6)	0.64(2.4)
W.Cascade	1.37(5.5)	1.41(5.6)	1.08(4.3)
Siskiyou	1.37(5.7)	1.37(5.7)	1.37(5.7)
Mixed-Conifer	1.12(5.1)	1.02(4.7)	1.05(4.8)

II. Selection for HT2[a/]

Zone	Model[b/] 2	3	4
Coastal	1.67(3.8)	2.57(5.9)	1.67(3.8)
W.Cascade	0.32(0.6)	0.91(1.9)	0.18(0.4)
Siskiyou	1.75(3.8)	1.77(3.8)	1.71(3.7)
Mixed-Conifer	1.77(3.8)	2.11(4.5)	1.77(3.8)

a/ See Table II.1 for description of traits.

b/ Absolute responses, and responses as percentage of original zone mean (in parentheses), are per unit selection intensity (i = 1.0) in the original units of measurement. Selection unit is the open-pollinated family. Models: 2. Restricted index where FBS1 (I), or IBS2 and BB2 (II) are restricted to 0% change, while HT1 (I) or HT2 (II) is selected; 3. Restricted index where SRR2 is restricted to 0% change, while HT1 (I) or HT2 (II) is selected; 4. Restricted index where FBS1 and SRR2 (I), or BB2 and IBS2 and SRR2 (II) are restricted while HT1 (I) or HT2 (II) is selected.

GENERAL CONCLUSIONS

Populations of Douglas-fir in southwest Oregon varied substantially in quantitative genetic structure (QGS). This variation was primarily associated with differences in trait means and genetic correlations between traits. Significant differences among populations in genetic variances were limited and no differences were detected for heritabilities of traits. Paired populations within the Coast and W. Cascade zones differed significantly in means for large numbers of individual traits, but had correlation coefficients which were quite similar. Paired populations from the harsher Siskiyou and Mixed-Conifer zones, however, showed limited differentiation in both trait means and correlation coefficients.

Populations appear to be less differentiated in terms of correlation structure than for trait means as measured by Euclidean distances (cluster analyses). The magnitudes of population differentiation for both trait means and correlation structure, however, were positively associated with the relative extent of habitat divergence. Three relatively homogenous groupings of populations were identified and were geographically associated with the coastal zone, a lower elevation inland zone (< 1067 m), and a high elevation inland zone (> 1067 m). It is hypothesized that Douglas-fir has adapted to these macro-climates where selection has significantly influenced relative biomass and growth phenology and, in turn, the populations have differentiated in QGS. This relative grouping into three geographic

regions follows general trends which have been reported earlier with regards to genetic gradients in southwest Oregon.

Their existed major differences among populations in correlations between growth and phenology traits in the second growing season. These differences were largely due to differential responses of populations to frost damage at the end of the first growing season which affected the subsequent year's growth patterns. The degree of frost damage expressed by populations was associated with their environment of origin, where populations from milder environments (e.g., Coast populations) sustained the greatest damage. Frost was greatest in families with the latest date of budset. These conditions led to moderately negative correlations between height (age 2) and budset date in the second growing season in six of eight populations. In contrast to the estimated negative correlations between height and budset in this study, positive correlations between height and budset in the second year were found in an earlier investigation of similar populations when no frost was experienced in the first year (Kaya 1987). Thus, QGS can vary substantially when the test environment differs.

As expected, differences in QGS among zones causes different expectations in both direct and correlated responses from selection. Practical significance of these differences, however, must be explored in terms of whether expected responses are favorable or unfavorable, and whether the magnitude of unfavorable responses are large enough to be of practical concern. Restricted indices provide a technique to limit change (expected response) in some traits, while allowing response in

others. The use of restricted indices (selection for height) caused differential responses among the four zones, and estimated height growth response was severely limited in two zones. Differences among populations in QGS must be recognized, and implications of alternative selection strategies should be assessed prior to application in breeding programs.

Further assessments of variation in QGS should be pursued in Douglas-fir and other species. The magnitude of differences in QGS between populations and the relationship of variation in QGS to environmental patterns of variation must be understood in order to assess optimal strategies for breeding and long-term gain. These studies will also further refine our understanding of the amounts of variation among populations and the biological significance of this variation in relation to evolution and forest management.

Limitations in resources and time necessitate that experiments be conducted as efficiently as possible. The following suggestions might provide for more efficient experiments in at least some cases. Genetic parameter estimates are imprecise unless sample sizes are large. It may be better to sample fewer populations with a larger number of genetic entries (e.g., > 100 families) per population in any one experiment in order to obtain the precision desirable for making inferences. In addition, taking measurements on multiple traits which are highly correlated (e.g., $r > .90$) may not provide additional information of substance, yet will add unnecessarily to the workload of the experiment. In many instances, past studies provide information on which traits are

highly correlated. Future investigators may also wish to include more direct measurements on those traits which have a large influence on adaptation. For example, traits such as cold hardiness in spring and fall and drought tolerance could be directly measured along with various growth traits in suitably designed tests (Blum 1988).

Both juvenile and mature traits in the same populations need to be assessed in order to determine the extent to which QGS changes over various life cycle stages. The majority of older established tests (e.g., provenance or progeny tests) were not designed with adequate sample sizes to estimate quantitative genetic parameters precisely. Thus, it is desirable to design some new long-term tests where nursery seedlings (juvenile life stage) are subsequently planted in the field for further long-term evaluations (into mature life stage). The tests should be designed so that adequate sample sizes are in place throughout the useful life of the experiment. Also, the test environments need to be given careful consideration, since populations react differentially to various environmental stimuli. In order to evaluate the plasticity of parameter estimates, it would be very beneficial if these experiments were conducted in a minimum of two environments.

BIBLIOGRAPHY

Adams, W. T. and Campbell, R. K. 1981. Genetic adaptation and seed source specificity. In: Hobbs, S. D., and Helgerson, O. T., eds., Reforestation of skeletal soils: Proceedings of a workshop, Medford, Or., November 17-19, 1981. Forest Research Laboratory, Oregon State University, Corvallis, Or., p. 78-85.

Adams, W. T. and Aitken, S. 1991. Annual report 1990-91, Pacific northwest tree improvement research cooperative, Forest Research Laboratory, Oregon State University, Corvallis, Or., 22 pp.

Baker, R. J. 1986. Selection indices in plant breeding. CRC Press, Inc., Boca Raton, Fl., 218 pp.

Baradat, Ph. 1976. Use of juvenile-mature relationships and information from relatives in combined multitrait selection. In: Procedings of the I.U.F.R.O. joint meeting of genetic working parties on advanced generation breeding, Bordeaux 1976, I.N.R.A., France, p. 121-138.

Becker, W. A. 1984. Manual of quantitative genetics. 4th edn., Academic Enterprises, Pullman, Wa., 186 pp.

Berven, K. A. 1987. The heritable basis of variation in larval developmental patterns within populations of the wood frog (Rana Sylvatica). Evolution. 41(5): 1088-1097.

Birot, Y. and Christophe, C. 1983. Genetic structures and expected genetic gains from multitrait selection in wild populations of Douglas-fir and Sitka spruce. Silvae Genet. 32: 141-151.

Blum, A. 1988. Plant breeding for stress environments. CRC Press, Inc., Boca Raton, Fl., 223 pp.

Campbell, R. K. 1986. Mapped genetic variation of Douglas-fir to guide seed transfer in southwest Oregon. Silvae Genet. 35: 85-95.

Campbell, R. K. 1987. Biogeographical distribution limits of Douglas-fir in southwest Oregon. For. Ecol. Manage. 18: 1-34.

Campbell, R. K. and Sorensen, F. C. 1973. Cold-Acclimation in seedling Douglas-fir related to phenology and provenance. Ecology. 54: 1148-1151.

Campbell, R. K. and Sugano, A. I. 1979. Genecology of bud-burst phenology in Douglas-fir: Response to flushing temperature and chilling. Bot. Gaz. 140: 223-231.

Cannell, M. G. R. and Willett, S. C. 1976. Shoot growth phenology, dry matter distribution and root:shoot ratios of provenances of Populus trichocarpa, Picea sitchensis and Pinus contorta growing in Scotland. Silvae Genet. 25: 49-59.

Cheverud, J. M. 1982. Phenotypic, genetic, and environmental morphological integration in the cranium. Evolution 36(3): 499-516.

Cheverud, J. M. 1988. A comparison of genetic and phenotypic correlations. Evolution 42(5): 958-968.

Christophe, C. and Birot, Y. 1979. Genetic variation within and between populations of Douglas-fir. Silvae Genet. 28: 197-206.

Christophe, C. and Birot, Y. 1983. Genetic structures and expected genetic gains from multitrait selection in wild populations of Douglas-fir and Sitka spruce. II. Practical application of index selection on several populations. Silvae Genet. 32: 173-181.

Cotterill, P. and Jackson, N. 1981. Short note: Index selection with restrictions in tree breeding. Silvae Genet. 30: 106-108.

Dickerson, G. E. 1969. Techniques for research in quantitative animal genetics. In: Techniques and Procedures in Animal Production Research, Am. Soc. Anim. Prod., Champaign, IL., p. 36-79.

Dingle, H., Evans, K. E., and Palmer, J. O. 1988. Responses to selection among life-history traits in a nonmigratory population of milkweed bugs (Oncopeltus fasciatus). Evolution. 42: 79-92.

Endler, J. A. 1986. Natural selection in the wild. Princeton Univ. Press, Princeton, New Jersey, 336 pp.

Falconer, D. S. 1981. Introduction to quantitative genetics. Longman Inc., New York, N.Y., 340 pp.

Ferrell, W. K. and Woodward, E. S. 1966. Effects of seed origin in drought resistance of Douglas-fir. Ecology 47: 499-503.

Franklin, J. F. and Dyrness, C. T. 1973. Natural vegetation of Oregon and Washington. USDA For. Ser. Gen. Tech. Rep. PNW-8, PNW Forest and Range Experiment Station, Portland, Or., 417 pp.

Grossman, M. 1970. Sampling variance of the correlation coefficients estimated from analyses of variance and covariance. Theor. and Appl. Genetics. 40: 357-359.

Harley, D. 1986. Equorm: A program to test the homogeneity of a set of correlation matrices. The Amer. Stat. 40: 51.

Hermann, R. K. and Lavender, D. P. 1968. Early growth of Douglas-fir from various altitudes and aspects in southern Oregon. Silvae Genet. 17: 143-151.

Jennrich, R. L. 1970. An asymptotic test for the equality of two correlation matrices. J. Amer. Statist. Assoc. 65: 904-912.

Joly, R. J., Adams, W. T., and Stafford, S. G. 1989. Phenological and morphological responses of mesic and dry site sources of coastal Douglas-fir to water deficit. Forest Science. 35: 987-1005.

Kaya, Z. 1987. Genetic variation in shoot-growth patterns of Douglas-fir populations from southwest Oregon. Ph.D. Diss., Oregon State Univ., Corvallis, Or., 123 pp.

Kaya, Z., Campbell, R. K., and Adams, W. T. 1989. Correlated responses of height increment and components of increment in 2-year-old Douglas-fir. Can. J. For. res. 19: 1124-1130.

Klein, T. W. 1974. Heritability and genetic correlation: statistical power, population comparisons, and sample size. Behav. genet. 4: 171-189.

Krzanowski, W. J. 1988. Principles of multivariate analysis: A user's perspective. Oxford University Press, New York, N.Y., 563 pp.

Loopstra, C. A. and Adams, W. T. 1989. Patterns of variation in first-year seedling traits within and among Douglas-fir breeding zones in southwest Oregon. Silvae genet. 38: 235-243.

Mangold, R. 1988. Genetic variation and phenotypic stability among three elevational sources of coastal Douglas-fir from southwest Oregon. Ph.D. Diss., Oregon State Univ., Corvallis, Or., 107 pp.

Mitchel-Olds, T. and Rutledge, J. J. 1986. Quantitative genetics in natural plant populations: a review of the theory. Am. Nat. 127: 379-402.

Mitchel-Olds, T. and Bergelson, J. 1990. Statistical genetics of an annual plant, Impatiens capensis. I. Genetic basis of quantitative variation. Genetics. 124: 407-415.

Mode, C. G. and Robinson, H. F. 1959. Pleiotropism and the genetic variance and covariance. Biometrics 15:518-537.

Namkoong, G., Kang, H. C., and Brouard, J. S. 1988. Tree breeding: principles and strategies. Springer-Verlag, New York, NY., 180 pp.

Oregon State University. 1982a. Average annual precipitation, 1960-1980, in southwest Oregon. Extension Publication EM 82:20, Nov. 1982, Oregon State U., Corvallis, Or.

Oregon State University. 1982b. Average dry-season precipitation, in in southwest Oregon, May through September. Extension Publication EM 82:26, Dec. 1982, Oregon State U., Corvallis, Or.

Rehfeldt, G. E. 1983. Genetic variability within Douglas-fir populations: implications for tree improvement. Silvae Genet. 32: 9-14.

Rehfeldt, G. E. 1989. Ecological adaptations in Douglas-fir (Pseudotsuga menziesii var glauca): A synthesis. For. Ecol. Management. 28: 203-215.

Ronningen, K. and Van Vleck, L. D. 1985. Selection index theory with practical applications. In: Chapman, A. B., ed., World Animal Science, A4, General and Quantitative Genetics, Elsevier Science Publishers, New York, N.Y., p. 187-225.

SAS Institute Inc. 1985. SAS/STAT guide for personal computers, version 6 edition. Cary, NC:SAS Institute Inc., 378 pp.

SAS Institute Inc. 1988. SAS/STAT user's guide, release 6.03 edition. Cary, NC:SAS Institute Inc., 1028 pp.

Schlichting, C. D. 1986. The evolution of phenotypic plasticity in plants. Ann. Rev. Ecol. Syst. 17:667-693.

Schuch, U. K., Duryea, M. L., and Fuchigami, L. H. 1989. Dehardening and budburst of Douglas-fir seedlings raised in three Pacific Norhwest nurseries. Can. J. For. Res. 19: 198-203.

Searle, S. 1961. Phenotypic, genetic, and environmental correlations. Biometrics 17: 474-480.

Silander, J. A. 1985. The genetic basis of the ecological amplitude of Spartina Patens. II. Variance and correlation analysis. Evolution 39(5): 1034-1052.

Silen, R. R. 1978. Genetics of Douglas-fir. USDA For. Serv. Res. Pap. WO-35, 34 pp.

Snedecor, G. W. and Cochran, W. G. 1967. Statistical methods, 6th edn., Iowa State University Press, Ames, IA., 593 pp.

Sorensen, F. C. 1983. Geographic variation in seedling Douglas-fir from the western Siskiyou mountains of Oregon. Ecology. 64: 696- 702.

Stern, K. and Roche, L. 1974. Genetics of forest ecosystems. Springer-Verlag, New York, NY., 330 pp.

Thorpe, R. S. 1976. Biometric analysis of geographic variation and racial affinities. Biol. Rev. 51: 407-452.

Via, S. 1984. The quantitative genetics of polyphagy in an insect herbivore. II. Genetic correlations in larval performance within and among host plants. Evolution. 38: 896-905.

Wheat, J. and Silen R. 1984. Progress report for the IFA-PNW cooperative tree improvement programs. Industrial Forestry Assoc., Portland, Or., 51 pp.

White, T. L. 1981. Genecology of Douglas-fir from southwestern Oregon. Ph.D. Diss., Oregon State Univ., Corvallis, Or., 103 pp.

White, T. L. 1987. Drought tolerance of southwestern Oregon Douglas-fir. Forest Science. 33: 283-293.

APPENDICES

APPENDIX A: Correlations between estimated genetic and phenotypic correlations of traits for the eight study populations.

Table A.1. Correlation between estimated genetic and phenotypic correlations between traits for each of eight populations in southwest Oregon.

Population	Correlation[a/]
Coast	
C-1	0.94 ; N = 160.
C-2	0.96 ; N = 162.
W.Cascade	
WC-1	0.90 ; N = 146.
WC-2	0.89 ; N = 140.
Siskiyou	
S-1	0.96 ; N = 165.
S-2	0.92 ; N = 159.
Mixed-Conifer	
MC-1	0.95 ; N = 170.
MC-2	0.93 ; N = 162.

[a/] N is the number of trait-pairs included in each correlation calculation. Only trait pairs for which the estimates of the respective genetic correlations were between -1.0 and + 1.0 were included in the analyses (out of 171 total N trait-pairs). The genetic and phenotypic correlations were transformed to z-scores prior to calculating the correlations.

APPENDIX B: Estimated phenotypic and genetic correlations for seedling trait pairs.

Table B.1. Description of traits in this appendix.

Code	Trait	Units
I. First Growing Season:		
HYHT (1)	Hypocotyl height	cm
#COT (2)	Number of cotyledons	number
IBS1 (3)	Initial budset date[a/]	weeks after August 21, 1985
FBS1 (4)	Final budset date[a/]	weeks after August 21, 1985
HT1 (5)	First year height	cm
BHT1 (6)	Length of terminal bud	mm
DI1 (7)	First year diameter[b/]	mm
II. Second Growing Season:		
HT2 (8)	Total height (2-years)	cm
BHT2 (9)	Length of terminal bud	mm
DI2 (10)	Second year diameter[b/]	mm
SWT2 (11)	Shoot dry weight	gms (X 10)
RWT2 (12)	Root dry weight	gms (X 10)
BB2 (13)	Budburst date[c/]	days after January 1, 1986
IBS2 (14)	Initial budset date[a/]	days after January 1, 1986
FBS2 (15)	Final budset date[a/]	days after January 1, 1986
SRR2 (16)	Shoot:Root ratio	ln(SWT2)/ln(RWT2)
GSL2 (17)	Growing season length (FBS2 - BB2)	days
RGR2 (18)	Relative growth rate	[ln(HT2)-ln(HT1)]/GSL2
TWT2 (19)	Total dry weight (SWT2 + RWT2)	gms (X 10)

a/ Initial budset date denotes time of initial budset (time when terminal bud scales occurred). Final budset date refers to budset date after any second flush. Final budset date equals the initial budset date if second flushing did not occur. Budset was recorded once per week.

b/ Diameters were taken directly below the cotyledon scar.

c/ Budburst date was recorded twice a week; time when needles first became visible in the opening terminal bud.

Table B.2. Estimates of phenotypic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs.

Population : C-1

Seedling Trait	HYHT (1)	#COT (2)	IBS1 (3)	FBS1 (4)	HT1 (5)	BHT1 (6)	DI1 (7)	HT2 (8)	BHT2 (9)	DI2 (10)	SWT2 (11)	RWT2 (12)	BB2 (13)	IBS2 (14)	FBS2 (15)	SRR2 (16)	GSL2 (17)	RGR2 (18)	TWT2 (19)
HYHT (1)		.36	-.29	-.17	.75	.30	.62	.43	.17	.62	.55	.58	.45	-.16	-.19	-.31	-.37	.11	.57
#COT (2)	.13		-.19	-.16	.11	.24	.34	.24	.24	.43	.35	.40	.20	-.13	-.08	-.25	-.16	.21	.37
IBS1 (3)	.13	.14		.84	.11	-.63	-.19	-.52	-.31	-.42	-.36	-.39	-.44	.60	.52	.35	.62	-.64	-.36
FBS1 (4)	.14	.14	.04		.18	-.74	-.19	-.52	-.20	-.41	-.31	-.28	-.57	.66	.58	.22	.73	-.73	-.29
HT1 (5)	.06	.15	.15	.14		.01	.66	.26	.05	.45	.37	.37	.15	-.03	-.05	-.15	-.11	-.20	.38
BHT1 (6)	.13	.14	.09	.07	.15		.33	.78	.44	.70	.63	.57	.66	-.63	-.58	-.23	-.77	.84	.61
DI1 (7)	.09	.13	.14	.14	.08	.13		.37	.12	.72	.57	.55	.27	-.16	-.24	-.27	-.32	.09	.57
HT2 (8)	.12	.14	.11	.11	.14	.06	.13		.60	.77	.83	.78	.48	-.56	-.51	-.31	-.63	.85	.82
BHT2 (9)	.14	.14	.13	.14	.15	.12	.14	.09		.43	.52	.55	.14	-.37	-.33	-.24	-.32	.54	.53
DI2 (10)	.09	.12	.12	.12	.12	.07	.07	.06	.12		.93	.88	.48	-.37	-.38	-.32	-.53	.56	.93
SWT2 (11)	.10	.13	.13	.13	.13	.09	.10	.05	.11	.02		.92	.42	-.32	-.33	-.27	-.46	.62	.99
RWT2 (12)	.10	.12	.12	.14	.13	.10	.10	.06	.10	.03	.02		.44	-.28	-.31	-.57	-.46	.58	.95
BB2 (13)	.12	.14	.12	.10	.14	.08	.14	.11	.14	.11	.12	.12		-.32	-.23	-.28	-.69	.56	.42
IBS2 (14)	.14	.14	.09	.08	.15	.09	.14	.10	.13	.13	.13	.14	.13		.93	.15	.85	-.66	-.30
FBS2 (15)	.14	.15	.11	.10	.15	.10	.14	.11	.13	.13	.13	.13	.14	.02		.11	.86	-.60	-.32
SRR2 (16)	.13	.14	.13	.14	.14	.14	.14	.13	.14	.13	.14	.10	.14	.14	.15		.23	-.26	-.33
GSL2 (17)	.13	.14	.09	.07	.15	.06	.13	.09	.13	.11	.12	.12	.08	.04	.04	.14		-.74	-.46
RGR2 (18)	.15	.14	.09	.07	.14	.04	.15	.04	.10	.10	.09	.10	.10	.08	.09	.14	.07		.61
TWT2 (19)	.10	.13	.13	.13	.13	.09	.10	.05	.11	.02	.00	.01	.12	.13	.13	.13	.12	.09	

See Table B.1 for description of traits.

Table B.3. Estimates of phenotypic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs.

Population : C-2

Seedling Trait	HYHT (1)	#COT (2)	IBS1 (3)	FBS1 (4)	HT1 (5)	BHT1 (6)	DI1 (7)	HT2 (8)	BHT2 (9)	DI2 (10)	SWT2 (11)	RWT2 (12)	BB2 (13)	IBS2 (14)	FBS2 (15)	SRR2 (16)	GSL2 (17)	RGR2 (18)	TWT2 (19)
HYHT (1)		.16	-.06	.04	.71	.19	.50	.59	.22	.54	.55	.50	.30	.02	.05	-.27	-.06	.18	.55
#COT (2)	.14		-.17	-.21	-.02	.16	.26	.10	.01	.26	.24	.29	.14	-.10	-.09	-.40	-.11	.15	.25
IBS1 (3)	.15	.14		.80	.33	-.49	.04	-.32	-.30	-.34	-.37	-.43	-.20	.37	.34	.46	.34	-.61	-.38
FBS1 (4)	.15	.14	.05		.34	-.74	-.08	-.36	-.52	-.45	-.47	-.57	-.41	.55	.55	.58	.56	-.71	-.49
HT1 (5)	.07	.15	.13	.13		.02	.56	.44	.27	.37	.37	.29	.32	-.02	-.02	-.08	-.12	-.12	.36
BHT1 (6)	.14	.14	.11	.07	.15		.27	.70	.74	.69	.72	.77	.63	-.71	-.72	-.60	-.77	.84	.73
DI1 (7)	.11	.14	.15	.15	.10	.14		.53	.33	.76	.68	.65	.48	-.17	-.20	-.40	-.31	.29	.68
HT2 (8)	.10	.15	.13	.13	.12	.07	.11		.62	.83	.87	.82	.56	-.40	-.41	-.46	-.50	.80	.88
BHT2 (9)	.14	.15	.13	.11	.14	.07	.13	.09		.61	.63	.67	.55	-.71	-.73	-.62	-.76	.62	.65
DI2 (10)	.10	.14	.13	.12	.13	.08	.06	.05	.09		.95	.95	.58	-.42	-.44	-.65	-.53	.72	.96
SWT2 (11)	.10	.14	.13	.11	.13	.07	.08	.03	.09	.01		.95	.61	-.44	-.46	-.57	-.56	.75	.99
RWT2 (12)	.11	.14	.12	.10	.13	.06	.08	.05	.08	.02	.01		.65	-.57	-.58	-.75	-.67	.79	.97
BB2 (13)	.13	.14	.14	.12	.13	.09	.11	.10	.10	.10	.09	.08		-.55	-.53	-.47	-.74	.58	.63
IBS2 (14)	.15	.15	.13	.10	.15	.07	.14	.12	.07	.12	.12	.10	.10		.99	.57	.96	-.60	-.48
FBS2 (15)	.15	.15	.13	.10	.15	.07	.14	.12	.07	.12	.12	.10	.11	.00		.57	.96	-.61	-.49
SRR2 (16)	.14	.12	.12	.10	.15	.09	.12	.12	.09	.08	.10	.07	.11	.10	.10		.61	-.56	-.63
GSL2 (17)	.15	.15	.13	.10	.14	.06	.13	.11	.06	.10	.10	.08	.07	.01	.01	.09		-.67	-.59
RGR2 (18)	.14	.14	.10	.08	.14	.05	.13	.06	.09	.07	.07	.06	.10	.10	.10	.10	.08		.77
TWT2 (19)	.10	.14	.13	.11	.13	.07	.08	.03	.09	.01	.00	.01	.09	.11	.11	.09	.10	.06	

See Table B.1 for description of traits.

Table B.4. Estimates of phenotypic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs.

Population : WC-1

Seedling Trait	HYHT (1)	#COT (2)	IBS1 (3)	FBS1 (4)	HT1 (5)	BHT1 (6)	DI1 (7)	HT2 (8)	BHT2 (9)	DI2 (10)	SWT2 (11)	RWT2 (12)	BB2 (13)	IBS2 (14)	FBS2 (15)	SRR2 (16)	GSL2 (17)	RGR2 (18)	TWT2 (19)
HYHT (1)		.30	-.23	-.04	.79	.12	.47	.76	.39	.60	.59	.61	.31	-.38	-.33	-.25	-.41	.20	.60
#COT (2)	.13		-.14	.13	.16	-.14	.25	.19	-.04	.28	.42	.39	-.15	.04	.06	-.01	.11	-.03	.42
IBS1 (3)	.14	.14		.82	.22	-.66	-.10	-.25	-.19	-.21	-.23	-.24	-.03	.55	.51	.21	.44	-.62	-.23
FBS1 (4)	.15	.14	.05		.37	-.79	-.05	-.13	-.09	-.15	-.11	-.16	-.07	.47	.43	.25	.40	-.64	-.11
HT1 (5)	.06	.14	.14	.13		-.19	.49	.64	.31	.48	.46	.41	.31	-.11	-.13	-.06	-.24	-.18	.46
BHT1 (6)	.14	.14	.08	.05	.14		.13	.31	.24	.20	.21	.20	.16	-.66	-.62	-.09	-.59	.70	.20
DI1 (7)	.11	.14	.15	.14	.11	.14		.55	.24	.80	.71	.62	.08	-.30	-.28	-.14	-.27	.13	.69
HT2 (8)	.06	.14	.14	.14	.09	.13	.10		.39	.78	.79	.68	.34	-.44	-.41	-.12	-.49	.52	.77
BHT2 (9)	.13	.15	.14	.15	.13	.14	.14	.12		.28	.29	.27	.07	-.24	-.23	.02	-.22	.15	.29
DI2 (10)	.09	.14	.14	.14	.11	.14	.05	.06	.14		.93	.85	.17	-.31	-.27	-.21	-.29	.38	.92
SWT2 (11)	.09	.12	.14	.15	.12	.14	.07	.05	.13	.02		.91	.15	-.22	-.18	-.17	-.22	.33	.99
RWT2 (12)	.09	.13	.14	.14	.12	.14	.09	.08	.14	.04	.03		.16	-.16	-.10	-.50	-.15	.28	.96
BB2 (13)	.13	.14	.15	.15	.13	.14	.15	.13	.15	.14	.14	.14		-.19	-.17	-.06	-.56	.35	.14
IBS2 (14)	.13	.15	.10	.11	.15	.08	.13	.12	.14	.13	.14	.14	.14		.93	.04	.86	-.68	-.19
FBS2 (15)	.13	.15	.11	.12	.14	.09	.14	.12	.14	.14	.14	.15	.14	.02		.04	.91	-.67	-.16
SRR2 (16)	.14	.15	.14	.14	.15	.15	.14	.14	.15	.14	.14	.11	.15	.15	.15		.06	-.15	-.27
GSL2 (17)	.12	.15	.12	.12	.14	.10	.14	.11	.14	.13	.14	.14	.10	.04	.02	.15		-.71	-.19
RGR2 (18)	.14	.15	.09	.09	.14	.08	.14	.11	.14	.13	.13	.14	.13	.08	.08	.15	.07		.31
TWT2 (19)	.09	.12	.14	.15	.12	.14	.08	.06	.13	.02	.00	.01	.14	.14	.14	.14	.14	.13	

See Table B.1 for description of traits.

Table B.5. Estimates of phenotypic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs.

Population : WC-2

Seedling Trait	HYHT (1)	#COT (2)	IBS1 (3)	FBS1 (4)	HT1 (5)	BHT1 (6)	DI1 (7)	HT2 (8)	BHT2 (9)	DI2 (10)	SWT2 (11)	RWT2 (12)	BB2 (13)	IBS2 (14)	FBS2 (15)	SRR2 (16)	GSL2 (17)	RGR2 (18)	TWT2 (19)
HYHT (1)		.38	-.28	-.20	.66	.20	.49	.50	.04	.66	.73	.69	-.06	-.14	-.07	-.20	-.02	-.11	.74
#COT (2)	.13		-.26	-.15	.20	.11	.17	.31	.08	.29	.35	.34	.05	-.12	-.20	-.18	-.16	.21	.35
IBS1 (3)	.14	.14		.93	.37	-.65	.12	-.30	-.15	-.25	-.24	-.29	-.21	.54	.36	.32	.35	-.66	-.26
FBS1 (4)	.14	.14	.02		.47	-.73	.19	-.26	-.01	-.19	-.18	-.25	-.23	.59	.42	.36	.40	-.69	-.21
HT1 (5)	.08	.14	.13	.11		-.20	.60	.38	.17	.48	.57	.48	-.15	.24	.21	.08	.22	-.55	.56
BHT1 (6)	.14	.15	.09	.07	.14		.18	.54	.19	.42	.39	.47	.34	-.75	-.50	-.46	-.52	.72	.41
DI1 (7)	.11	.14	.14	.14	.10	.14		.43	.12	.64	.62	.58	.03	.02	-.05	-.17	-.05	-.12	.62
HT2 (8)	.11	.13	.13	.14	.13	.10	.12		.23	.76	.75	.69	-.13	-.40	-.30	-.27	-.13	.41	.74
BHT2 (9)	.15	.15	.14	.15	.14	.14	.14	.14		.27	.22	.30	.09	-.05	.01	-.46	-.04	.07	.22
DI2 (10)	.08	.13	.14	.14	.11	.12	.09	.06	.14		.91	.90	-.07	-.24	-.28	-.49	-.15	.21	.92
SWT2 (11)	.07	.13	.14	.14	.10	.13	.09	.07	.14	.03		.93	-.12	-.26	-.26	-.37	-.11	.12	.99
RWT2 (12)	.08	.13	.13	.14	.11	.11	.10	.08	.13	.03	.02		-.01	-.29	-.33	-.65	-.22	.22	.96
BB2 (13)	.15	.15	.14	.14	.14	.13	.15	.14	.15	.15	.14	.15		-.36	-.37	-.16	-.78	.41	-.09
IBS2 (14)	.14	.14	.10	.10	.14	.06	.15	.12	.15	.14	.14	.14	.13		.67	.20	.65	-.73	-.28
FBS2 (15)	.15	.14	.13	.12	.14	.11	.15	.13	.15	.14	.14	.13	.13	.08		.34	.86	-.74	-.28
SRR2 (16)	.14	.14	.13	.13	.15	.12	.14	.14	.12	.11	.13	.09	.14	.14	.13		.31	-.41	-.44
GSL2 (17)	.15	.14	.13	.12	.14	.11	.15	.14	.15	.14	.15	.14	.06	.09	.04	.13		-.71	-.14
RGR2 (18)	.15	.14	.09	.08	.10	.07	.15	.12	.15	.14	.14	.14	.12	.07	.07	.13	.07		.14
TWT2 (19)	.07	.13	.14	.14	.10	.12	.09	.07	.14	.02	.00	.01	.15	.14	.14	.12	.14	.14	

See Table B.1 for description of traits.

Table B.6. Estimates of phenotypic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs.

Population : S-1

Seedling Trait	HYHT (1)	#COT (2)	IBS1 (3)	FBS1 (4)	HT1 (5)	BHT1 (6)	DI1 (7)	HT2 (8)	BHT2 (9)	DI2 (10)	SWT2 (11)	RWT2 (12)	BB2 (13)	IBS2 (14)	FBS2 (15)	SRR2 (16)	GSL2 (17)	RGR2 (18)	TWT2 (19)
HYHT (1)		.19	-.25	-.16	.70	.33	.58	.73	.43	.73	.79	.74	.25	-.25	-.26	-.09	-.32	.11	.78
#COT (2)	.14		-.16	-.10	.07	.26	.21	.26	.16	.24	.31	.33	-.10	-.08	-.16	-.26	-.07	.17	.32
IBS1 (3)	.14	.14		.90	.39	-.69	.21	-.24	-.61	-.15	-.21	-.25	.05	.52	.57	.18	.40	-.66	-.23
FBS1 (4)	.14	.15	.03		.42	-.79	.23	-.27	-.54	-.11	-.17	-.26	.00	.60	.58	.32	.44	-.73	-.20
HT1 (5)	.07	.15	.12	.12		-.11	.68	.56	.05	.56	.55	.47	.23	.06	.06	.03	-.07	-.35	.53
BHT1 (6)	.13	.14	.08	.05	.15		.08	.54	.60	.39	.42	.45	.18	-.59	-.63	-.24	-.56	.73	.43
DI1 (7)	.10	.14	.14	.14	.08	.15		.51	.12	.76	.70	.61	.12	-.01	.02	.01	-.04	-.16	.69
HT2 (8)	.07	.14	.14	.14	.10	.10	.11		.53	.81	.83	.81	.28	-.44	-.50	-.23	-.51	.51	.83
BHT2 (9)	.12	.14	.09	.10	.15	.09	.14	.11		.41	.49	.48	-.04	-.46	-.59	-.20	-.42	.54	.50
DI2 (10)	.07	.14	.14	.15	.10	.12	.06	.05	.12		.94	.91	.20	-.29	-.34	-.17	-.36	.28	.94
SWT2 (11)	.06	.13	.14	.14	.10	.12	.07	.05	.11	.02		.95	.13	-.24	-.30	-.17	-.29	.28	.99
RWT2 (12)	.07	.13	.14	.14	.11	.12	.09	.05	.11	.03	.01		.13	-.34	-.40	-.42	-.36	.37	.97
BB2 (13)	.14	.15	.15	.15	.14	.14	.14	.14	.15	.14	.14	.14		-.20	-.29	-.11	-.69	.31	.13
IBS2 (14)	.14	.15	.11	.09	.15	.10	.15	.12	.12	.13	.14	.13	.14		.84	.37	.73	-.71	-.27
FBS2 (15)	.14	.14	.10	.10	.15	.09	.15	.11	.10	.13	.13	.12	.13	.04		.45	.89	-.80	-.33
SRR2 (16)	.15	.14	.14	.13	.15	.14	.15	.14	.14	.14	.14	.12	.15	.13	.12		.39	-.41	-.24
GSL2 (17)	.13	.15	.12	.12	.15	.10	.15	.11	.12	.13	.13	.13	.08	.07	.03	.13		-.75	-.31
RGR2 (18)	.15	.14	.08	.07	.13	.07	.14	.11	.10	.14	.14	.13	.13	.08	.06	.13	.07		.30
TWT2 (19)	.06	.13	.14	.14	.11	.12	.08	.05	.11	.02	.00	.01	.14	.14	.13	.14	.13	.13	

See Table B.1 for description of traits.

Table B.7. Estimates of phenotypic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs.

Population : S-2

Seedling Trait	HYHT (1)	#COT (2)	IBS1 (3)	FBS1 (4)	HT1 (5)	BHT1 (6)	DI1 (7)	HT2 (8)	BHT2 (9)	DI2 (10)	SWT2 (11)	RWT2 (12)	BB2 (13)	IBS2 (14)	FBS2 (15)	SRR2 (16)	GSL2 (17)	RGR2 (18)	TWT2 (19)
HYHT (1)		.23	-.38	-.21	.73	-.01	.34	.37	-.05	.29	.40	.27	.11	-.17	-.10	.04	-.14	-.17	.37
#COT (2)	.14		-.16	-.05	.08	-.36	.03	-.18	.17	.03	.08	.14	-.06	.11	.09	-.09	.11	-.20	.10
IBS1 (3)	.13	.14		.89	.16	-.59	.08	-.48	-.34	-.34	-.37	-.51	-.06	.61	.55	.53	.49	-.58	-.41
FBS1 (4)	.14	.15	.03		.29	-.73	.11	-.48	-.42	-.35	-.38	-.56	-.05	.66	.64	.57	.56	-.68	-.43
HT1 (5)	.07	.15	.14	.13		-.37	.51	.19	-.18	.15	.18	-.02	-.02	.01	.07	.24	.07	-.54	.13
BHT1 (6)	.15	.13	.10	.07	.13		-.02	.61	.39	.38	.39	.50	.13	-.68	-.56	-.45	-.53	.79	.43
DI1 (7)	.13	.15	.15	.15	.11	.15		.34	.04	.68	.58	.39	-.25	-.05	-.08	.08	.06	-.12	.54
HT2 (8)	.13	.14	.11	.11	.14	.09	.13		.26	.70	.76	.72	.07	-.68	-.59	-.37	-.53	.69	.76
BHT2 (9)	.15	.14	.13	.12	.14	.12	.15	.14		.31	.26	.30	-.03	-.30	-.40	-.22	-.32	.38	.28
DI2 (10)	.13	.15	.13	.13	.14	.13	.08	.08	.13		.92	.86	-.13	-.45	-.53	-.32	-.37	.48	.92
SWT2 (11)	.12	.15	.13	.13	.14	.12	.10	.06	.14	.02		.90	.01	-.47	-.52	-.25	-.43	.51	.99
RWT2 (12)	.14	.14	.11	.10	.15	.11	.12	.07	.13	.04	.03		-.02	-.54	-.61	-.60	-.49	.62	.94
BB2 (13)	.15	.15	.15	.15	.15	.14	.14	.15	.15	.14	.15	.15		-.13	-.06	.10	-.56	.21	.00
IBS2 (14)	.14	.15	.09	.08	.15	.08	.15	.08	.13	.12	.11	.10	.14		.85	.49	.77	-.65	-.50
FBS2 (15)	.15	.15	.10	.09	.15	.10	.15	.10	.12	.11	.11	.09	.15	.04		.52	.86	-.66	-.55
SRR2 (16)	.15	.15	.10	.10	.14	.12	.15	.13	.14	.13	.14	.09	.15	.11	.11		.38	-.47	-.34
GSL2 (17)	.14	.15	.11	.10	.15	.10	.15	.11	.13	.13	.12	.11	.10	.06	.04	.13		-.66	-.46
RGR2 (18)	.14	.14	.10	.08	.10	.05	.14	.08	.12	.11	.11	.09	.14	.08	.08	.11	.08		.55
TWT2 (19)	.13	.15	.12	.12	.14	.12	.10	.06	.14	.02	.00	.02	.15	.11	.10	.13	.12	.10	

See Table B.1 for description of traits.

Table B.8. Estimates of phenotypic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs.

Population : MC-1

Seedling Trait	HYHT (1)	#COT (2)	IBS1 (3)	FBS1 (4)	HT1 (5)	BHT1 (6)	DI1 (7)	HT2 (8)	BHT2 (9)	DI2 (10)	SWT2 (11)	RWT2 (12)	BB2 (13)	IBS2 (14)	FBS2 (15)	SRR2 (16)	GSL2 (17)	RGR2 (18)	TWT2 (19)
HYHT (1)		.20	-.22	-.20	.70	.54	.61	.72	.47	.54	.64	.44	.05	-.28	-.17	.15	-.15	-.03	.63
#COT (2)	.14		-.07	-.01	.17	.03	.17	.23	.30	.27	.25	.20	-.17	-.12	.02	.09	.10	-.12	.26
IBS1 (3)	.14	.15		.93	.39	-.60	-.02	.09	-.24	.02	.01	-.02	.07	.40	.41	.05	.26	-.47	-.01
FBS1 (4)	.14	.15	.02		.36	-.66	.02	.05	-.27	.04	.03	.02	.07	.41	.42	.03	.27	-.49	.01
HT1 (5)	.07	.14	.12	.13		.10	.50	.69	.33	.50	.55	.30	.12	-.11	.04	.26	-.04	-.34	.52
BHT1 (6)	.10	.15	.09	.08	.15		.43	.33	.43	.18	.26	.18	-.01	-.62	-.50	.00	-.35	.39	.26
DI1 (7)	.09	.14	.15	.15	.11	.12		.43	.20	.64	.63	.47	.05	-.13	.00	.13	-.03	-.15	.62
HT2 (8)	.07	.14	.15	.15	.08	.13	.12		.45	.65	.76	.59	-.08	-.13	-.05	.07	.00	.06	.76
BHT2 (9)	.11	.13	.14	.14	.13	.12	.14	.12		.38	.37	.20	.02	-.24	-.31	.18	-.23	.22	.36
DI2 (10)	.10	.14	.15	.15	.11	.14	.09	.08	.13		.90	.73	-.10	.14	.27	.07	.25	-.18	.91
SWT2 (11)	.09	.14	.15	.15	.10	.14	.09	.06	.13	.03		.71	-.05	.11	.20	.19	.17	-.09	.98
RWT2 (12)	.12	.14	.15	.15	.13	.14	.11	.10	.14	.07	.07		-.10	.06	.22	-.52	.21	-.07	.82
BB2 (13)	.15	.14	.15	.15	.14	.15	.15	.15	.15	.15	.15	.15		-.18	-.29	.12	-.73	.48	-.07
IBS2 (14)	.14	.14	.12	.12	.15	.09	.14	.14	.14	.14	.15	.15	.14		.78	.08	.65	-.50	.10
FBS2 (15)	.14	.15	.12	.12	.15	.11	.15	.15	.13	.14	.14	.14	.13	.06		-.04	.87	-.74	.21
SRR2 (16)	.14	.15	.15	.15	.14	.15	.14	.15	.14	.15	.14	.11	.14	.15	.15		-.09	-.03	.03
GSL2 (17)	.14	.15	.14	.14	.15	.13	.15	.15	.14	.14	.14	.14	.07	.08	.04	.15		-.78	.19
RGR2 (18)	.15	.14	.12	.11	.13	.12	.14	.15	.14	.14	.15	.15	.11	.11	.07	.00	.06		-.09
TWT2 (19)	.09	.14	.15	.15	.11	.14	.09	.06	.13	.03	.00	.05	.15	.15	.14	.15	.14	.15	

See Table B.1 for description of traits.

Table B.9. Estimates of phenotypic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs.

Population : MC-2

Seedling Trait	HYHT (1)	#COT (2)	IBS1 (3)	FBS1 (4)	HT1 (5)	BHT1 (6)	DI1 (7)	HT2 (8)	BHT2 (9)	DI2 (10)	SWT2 (11)	RWT2 (12)	BB2 (13)	IBS2 (14)	FBS2 (15)	SRR2 (16)	GSL2 (17)	RGR2 (18)	TWT2 (19)
HYHT (1)		-.18	-.20	-.23	.65	.35	.50	.68	.07	.65	.58	.52	-.12	-.24	-.27	-.38	-.16	.08	.62
#COT (2)	.14		.27	.21	-.11	-.24	.00	-.16	-.03	.08	.03	.04	-.03	.23	.31	.14	.26	-.22	.03
IBS1 (3)	.14	.14		.94	.43	-.54	.16	.10	.12	.16	.16	.02	-.16	.59	.57	.30	.52	-.70	.12
FBS1 (4)	.14	.14	.02		.41	-.62	.09	.07	.04	.10	.15	-.03	-.22	.61	.60	.37	.57	-.74	.09
HT1 (5)	.08	.15	.12	.12		-.11	.62	.65	.15	.68	.64	.46	-.19	.24	.09	-.11	.15	-.42	.64
BHT1 (6)	.13	.14	.10	.09	.14		.12	.26	.13	.11	.03	.12	.20	-.66	-.53	-.30	-.50	.63	.06
DI1 (7)	.11	.15	.14	.15	.09	.14		.46	.03	.83	.67	.65	-.06	-.03	.02	-.36	.04	-.14	.73
HT2 (8)	.08	.14	.15	.15	.08	.14	.12		.27	.73	.74	.53	-.20	-.03	.05	-.21	.13	.03	.73
BHT2 (9)	.15	.15	.14	.15	.14	.14	.15	.14		.19	.15	.14	-.25	.10	.03	.05	.13	-.07	.15
DI2 (10)	.08	.15	.14	.15	.08	.15	.05	.07	.14		.87	.79	-.17	.07	.12	-.42	.17	-.16	.92
SWT2 (11)	.10	.15	.14	.14	.09	.15	.08	.07	.14	.04		.61	-.29	.16	.26	-.20	.33	-.25	.95
RWT2 (12)	.11	.15	.15	.15	.12	.14	.08	.11	.14	.06	.09		-.12	-.02	.03	-.78	.08	-.04	.83
BB2 (13)	.14	.15	.14	.14	.14	.14	.15	.14	.14	.14	.13	.14		-.22	-.29	-.10	-.65	.52	-.24
IBS2 (14)	.14	.14	.10	.09	.14	.08	.15	.15	.15	.15	.14	.15	.14		.78	.24	.71	-.75	.11
FBS2 (15)	.14	.13	.10	.09	.15	.11	.15	.15	.15	.14	.14	.15	.13	.06		.26	.92	-.77	.20
SRR2 (16)	.13	.14	.13	.13	.15	.13	.13	.14	.15	.12	.14	.06	.15	.14	.14		.25	-.28	-.44
GSL2 (17)	.14	.14	.11	.10	.14	.11	.15	.14	.14	.14	.13	.15	.08	.07	.02	.14		-.83	.26
RGR2 (18)	.15	.14	.07	.07	.12	.09	.14	.15	.15	.14	.14	.15	.11	.06	.06	.14	.05		-.20
TWT2 (19)	.09	.15	.14	.15	.09	.15	.07	.07	.14	.02	.01	.05	.14	.14	.14	.12	.14	.14	

See Table B.1 for description of traits.

Table B.10. Estimates of genetic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs.

Population : C-1

Seedling Trait	HYHT (1)	#COT (2)	IBS1 (3)	FBS1 (4)	HT1 (5)	BHT1 (6)	DI1 (7)	HT2 (8)	BHT2 (9)	DI2 (10)	SWT2 (11)	RWT2 (12)	BB2 (13)	IBS2 (14)	FBS2 (15)	SRR2 (16)	GSL2 (17)	RGR2 (18)	TWT2 (19)
HYHT (1)		.57	-.51	-.26	1.01	.48	.65	.51	.18	.75	.68	.76	.88	-.23	-.21	-.41	-.58	.28	.71
#COT (2)	.23		-.48	-.39	.29	.53	.61	.37	.46	.66	.46	.58	.55	-.29	-.22	-.30	-.42	.42	.50
IBS1 (3)	.25	.35		1.09	-.44	-.97	-.60	-.83	-.54	-.74	-.60	-.66	-.90	1.19	1.08	.53	1.20	-.97	-.61
FBS1 (4)	.22	.29	.11		-.12	-.83	-.46	-.70	-.25	-.56	-.39	-.32	-.96	1.01	.99	.18	1.16	-.98	-.37
HT1 (5)	.20	.44	.56	.40		.59	.75	.54	.15	.80	.73	.90	.84	-.23	-.05	-.53	-.45	.43	.78
BHT1 (6)	.22	.31	.20	.11	.51		.63	.91	.57	.93	.78	.64	1.03	-.88	-.83	-.21	-1.08	.96	.74
DI1 (7)	.15	.27	.34	.26	.21	.26		.43	.06	.85	.66	.75	.67	-.28	-.36	-.50	-.58	.32	.68
HT2 (8)	.18	.27	.22	.17	.35	.09	.23		.76	.78	.84	.80	.74	-.73	-.62	-.34	-.80	.97	.84
BHT2 (9)	.23	.29	.28	.25	.39	.22	.28	.15		.45	.59	.66	.25	-.60	-.42	-.29	-.41	.72	.61
DI2 (10)	.13	.23	.25	.20	.31	.12	.11	.10	.21		.94	.93	.83	-.46	-.44	-.32	-.71	.66	.95
SWT2 (11)	.15	.25	.26	.22	.34	.15	.17	.08	.18	.03		.94	.69	-.35	-.36	-.25	-.59	.70	1.00
RWT2 (12)	.15	.25	.27	.24	.39	.19	.18	.10	.18	.05	.04		.74	-.19	-.22	-.55	-.52	.57	.96
BB2 (13)	.24	.36	.31	.21	.56	.19	.32	.22	.31	.24	.25	.25		-.59	-.40	-.48	-.77	.71	.72
IBS2 (14)	.28	.36	.29	.18	.48	.19	.33	.20	.27	.26	.28	.32	.34		1.04	-.02	1.01	-.84	-.29
FBS2 (15)	.28	.38	.31	.22	.48	.22	.32	.22	.29	.27	.28	.32	.37	.05		-.07	.89	-.73	-.30
SRR2 (16)	.22	.30	.28	.26	.42	.28	.26	.24	.26	.24	.25	.20	.30	.35	.35		.19	-.19	-.31
GSL2 (17)	.23	.34	.27	.17	.46	.13	.28	.16	.27	.20	.22	.24	.18	.09	.09	.31		-.86	-.57
RGR2 (18)	.27	.34	.20	.13	.57	.08	.33	.07	.20	.19	.17	.21	.23	.19	.22	.31	.14		.71
TWT2 (19)	.15	.25	.27	.23	.35	.16	.17	.08	.18	.03	.00	.02	.25	.29	.30	.25	.23	.18	

See Table B.1 for description of traits.

Table B.11. Estimates of genetic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs.

Population : C-2

Seedling Trait	HYHT (1)	#COT (2)	IBS1 (3)	FBS1 (4)	HT1 (5)	BHT1 (6)	DI1 (7)	HT2 (8)	BHT2 (9)	DI2 (10)	SWT2 (11)	RWT2 (12)	BB2 (13)	IBS2 (14)	FBS2 (15)	SRR2 (16)	GSL2 (17)	RGR2 (18)	TWT2 (19)
HYHT (1)		.22	-.07	.11	.79	.33	.52	.75	.28	.64	.63	.57	.43	.07	.11	-.34	-.06	.37	.63
#COT (2)	.23		-.36	-.48	-.07	.24	.34	.08	-.01	.33	.28	.33	.20	-.19	-.20	-.59	-.21	.20	.29
IBS1 (3)	.35	.37		1.31	.43	-1.02	-.09	-.80	-.52	-.69	-.78	-.84	-.25	.80	.76	.92	.63	-1.20	-.79
FBS1 (4)	.27	.28	.28		.31	-1.01	-.39	-.62	-.76	-.73	-.74	-.83	-.54	1.06	1.10	.87	.97	-1.04	-.76
HT1 (5)	.12	.29	.38	.30		.25	.50	.58	.51	.52	.49	.44	.65	.03	.03	-.17	-.19	.16	.50
BHT1 (6)	.21	.23	.33	.12	.28		.37	.86	.93	.79	.84	.87	.73	-.96	-1.02	-.78	-.97	.95	.85
DI1 (7)	.17	.23	.38	.30	.21	.21		.56	.50	.86	.78	.79	.74	-.21	-.25	-.56	-.42	.49	.79
HT2 (8)	.14	.26	.38	.24	.23	.11	.18		.78	.84	.91	.88	.73	-.54	-.58	-.58	-.66	.88	.92
BHT2 (9)	.20	.23	.31	.18	.24	.08	.19	.13		.73	.75	.76	.68	-.96	-.99	-.72	-.94	.74	.77
DI2 (10)	.15	.22	.33	.20	.23	.11	.09	.07	.12		.97	.98	.74	-.54	-.59	-.78	-.67	.79	.98
SWT2 (11)	.15	.22	.34	.20	.23	.10	.12	.05	.12	.02		.96	.77	-.58	-.62	-.67	-.70	.86	.99
RWT2 (12)	.15	.21	.31	.16	.23	.08	.12	.07	.10	.02	.02		.80	-.75	-.81	-.85	-.85	.89	.98
BB2 (13)	.20	.23	.33	.21	.25	.12	.17	.15	.14	.13	.12	.10		-.79	-.79	-.68	-.90	.67	.79
IBS2 (14)	.25	.26	.36	.22	.31	.11	.25	.21	.11	.20	.19	.15	.16		1.00	.80	.98	-.82	-.63
FBS2 (15)	.25	.27	.37	.24	.31	.12	.26	.22	.11	.19	.19	.15	.17	.01		.84	.98	-.85	-.68
SRR2 (16)	.21	.19	.33	.17	.28	.13	.19	.18	.12	.12	.14	.08	.16	.16	.16		.83	-.73	-.73
GSL2 (17)	.23	.24	.33	.19	.28	.08	.21	.17	.08	.15	.14	.11	.09	.02	.02	.13		-.84	-.75
RGR2 (18)	.23	.25	.34	.15	.32	.06	.23	.08	.13	.11	.10	.08	.15	.16	.16	.16	.13		.87
TWT2 (19)	.15	.22	.33	.19	.23	.09	.11	.05	.11	.02	.00	.01	.12	.18	.18	.13	.13	.09	

See Table B.1 for description of traits.

Table B.12. Estimates of genetic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs.

Population : WC-1

Seedling Trait	HYHT (1)	#COT (2)	IBS1 (3)	FBS1 (4)	HT1 (5)	BHT1 (6)	DI1 (7)	HT2 (8)	BHT2 (9)	DI2 (10)	SWT2 (11)	RWT2 (12)	BB2 (13)	IBS2 (14)	FBS2 (15)	SRR2 (16)	GSL2 (17)	RGR2 (18)	TWT2 (19)
HYHT (1)		.43	-.31	-.01	.90	.06	.42	1.43	.62	.66	.66	.73	.71	-.49	-.43	-.58	-.62	--	.67
#COT (2)	.20		-.22	.25	.25	-.23	.43	.59	-.15	.49	.80	.73	-.71	.15	.08	.09	.28	--	.78
IBS1 (3)	.26	.32		1.00	-.02	-1.24	-.38	-.67	-.53	-.34	-.40	-.35	.10	.98	.95	.43	.89	--	-.37
FBS1 (4)	.23	.28	.10		.26	-1.12	-.29	-.07	-.28	-.21	-.11	-.17	.09	.56	.55	.49	.50	--	-.12
HT1 (5)	.07	.25	.32	.24		-.29	.35	1.30	.48	.53	.54	.59	.92	-.25	-.23	-.50	-.49	--	.54
BHT1 (6)	.28	.34	.28	.15	.31		.07	-.63	.46	-.14	-.20	-.16	-.51	-.78	-.76	.27	-.58	--	-.19
DI1 (7)	.18	.24	.32	.28	.21	.32		.74	.30	.88	.76	.74	.15	-.48	-.42	-.41	-.45	--	.75
HT2 (8)	.54	.50	.55	.47	.51	.95	.32		.69	.90	.90	.82	.32	-.40	-.37	-.07	-.45	--	.87
BHT2 (9)	.22	.31	.37	.32	.26	.36	.28	.45		.25	.24	.21	-.35	-.40	-.34	.42	-.23	--	.25
DI2 (10)	.14	.24	.30	.27	.19	.37	.08	.21	.28		.93	.87	-.01	-.30	-.19	-.16	-.18	--	.92
SWT2 (11)	.15	.23	.32	.29	.20	.41	.13	.19	.30	.04		.94	-.19	-.12	-.03	-.10	.02	--	.99
RWT2 (12)	.14	.25	.33	.29	.22	.41	.16	.26	.31	.07	.05		-.08	-.02	.08	-.40	.10	--	.98
BB2 (13)	.42	.57	.57	.49	.53	.78	.44	.70	.61	.45	.53	.52		.07	.03	.15	-.27	--	-.15
IBS2 (14)	.20	.29	.24	.22	.26	.18	.24	.39	.30	.25	.29	.30	.50		1.01	-.34	.96	--	-.09
FBS2 (15)	.20	.28	.25	.22	.25	.20	.24	.39	.29	.26	.29	.30	.48	.03		-.23	.96	--	-.01
SRR2 (16)	.43	.49	.56	.47	.54	.67	.48	.81	.61	.44	.49	.40	.85	.57	.52		-.27	--	-.24
GSL2 (17)	.22	.32	.31	.27	.28	.26	.28	.42	.35	.29	.35	.36	.48	.07	.05	.62		--	.04
RGR2 (18)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--		--
TWT2 (19)	.14	.23	.31	.28	.20	.39	.13	.21	.29	.04	.01	.02	.51	.28	.28	.45	.34	--	

See Table B.1 for description of traits.
-- = No estimate of genetic correlation due to negative component of variance (σ^2_f) estimate.

Table B.13. Estimates of genetic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs.

Population : WC-2

Seedling Trait	HYHT (1)	#COT (2)	IBS1 (3)	FBS1 (4)	HT1 (5)	BHT1 (6)	DI1 (7)	HT2 (8)	BHT2 (9)	DI2 (10)	SWT2 (11)	RWT2 (12)	BB2 (13)	IBS2 (14)	FBS2 (15)	SRR2 (16)	GSL2 (17)	RGR2 (18)	TWT2 (19)
HYHT (1)		.57	-.38	-.28	.70	.17	.56	.67	-.01	.83	.96	.99	-.10	-.20	--	-.34	.05	-.18	.99
#COT (2)	.21		-.52	-.34	.31	.28	.40	1.07	.32	.83	.91	.91	.08	-.51	--	-.44	-.70	.53	.92
IBS1 (3)	.18	.24		1.00	.30	-.91	.01	-.86	-.19	-.56	-.55	-.60	-.62	1.15	--	.53	1.07	-.90	-.58
FBS1 (4)	.19	.26	.02		.44	-.94	.10	-.71	.04	-.47	-.44	-.51	-.65	1.14	--	.58	1.06	-.90	-.47
HT1 (5)	.11	.27	.20	.18		-.40	.51	.21	.20	.42	.63	.58	-.54	.63	--	.18	1.02	-.84	.62
BHT1 (6)	.23	.32	.14	.11	.26		.03	.62	.09	.47	.40	.63	.79	-1.35	--	-.94	-.93	.89	.46
DI1 (7)	.19	.35	.28	.27	.21	.34		.03	-.03	.48	.52	.56	.16	.37	--	-.23	.27	-.37	.54
HT2 (8)	.24	.50	.38	.36	.34	.28	.49		.14	.78	.77	.79	-1.27	-.32	--	-.49	1.20	.20	.77
BHT2 (9)	.22	.31	.23	.24	.25	.28	.32	.37		.16	.07	.17	.00	.06	--	-.70	.48	-.15	.06
DI2 (10)	.14	.36	.27	.27	.24	.28	.27	.19	.31		.90	.97	-.62	-.38	--	-.75	.31	.04	.93
SWT2 (11)	.12	.33	.25	.26	.19	.27	.24	.19	.30	.06		.96	-.93	-.59	--	-.52	.38	-.11	1.00
RWT2 (12)	.15	.35	.26	.26	.22	.25	.25	.22	.30	.06	.04		-.62	-.57	--	-.75	.09	.04	.98
BB2 (13)	.40	.55	.49	.49	.52	.53	.59	1.10	.49	.70	.78	.73		-1.15	--	-.19	-1.66	.43	-.82
IBS2 (14)	.37	.56	.49	.45	.46	.46	.59	.57	.46	.51	.50	.49	.87		--	.26	.62	-1.01	-.62
FBS2 (15)	--	--	--	--	--	--	--	--	--	--	--	--	--	--		--	--	--	--
SRR2 (16)	.27	.37	.26	.25	.32	.29	.38	.44	.25	.28	.31	.21	.60	.55	--		.52	-.55	-.58
GSL2 (17)	.48	.82	.88	.83	.96	.63	.77	1.69	.78	.84	.82	.74	1.06	.60	--	.67		-.82	.30
RGR2 (18)	.22	.29	.12	.11	.16	.12	.32	.36	.28	.32	.31	.32	.40	.28	--	.28	.37		-.07
TWT2 (19)	.12	.33	.25	.26	.19	.27	.24	.19	.31	.06	.00	.02	.76	.50	--	.29	.80	.32	

See Table B.1 for description of traits.

-- = No estimate of genetic correlation due to negative component of variance (σ^2_f) estimate.

Table B.14. Estimates of genetic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs.

Population : S-1

Seedling Trait	HYHT (1)	#COT (2)	IBS1 (3)	FBS1 (4)	HT1 (5)	BHT1 (6)	DI1 (7)	HT2 (8)	BHT2 (9)	DI2 (10)	SWT2 (11)	RWT2 (12)	BB2 (13)	IBS2 (14)	FBS2 (15)	SRR2 (16)	GSL2 (17)	RGR2 (18)	TWT2 (19)
HYHT (1)		.29	-.31	-.24	.76	.44	.62	.94	.52	.87	.94	.92	.47	-.33	-.35	-.15	-.45	.20	.93
#COT (2)	.19		-.22	-.12	.18	.38	.40	.43	.28	.40	.48	.52	.03	-.12	-.39	-.49	-.30	.32	.49
IBS1 (3)	.17	.20		1.00	.35	-.87	.22	-.38	-.85	-.20	-.28	-.30	.02	.70	1.04	.16	.77	-.95	-.29
FBS1 (4)	.19	.22	.04		.34	-.92	.24	-.45	-.75	-.12	-.23	-.34	.00	.80	1.09	.49	.83	-1.05	-.27
HT1 (5)	.09	.22	.18	.20		-.02	.68	.72	.07	.69	.67	.63	.40	.03	.19	-.04	-.02	-.38	.66
BHT1 (6)	.18	.22	.10	.08	.24		.06	.54	.82	.36	.42	.48	.04	-.61	-.94	-.40	-.73	.76	.44
DI1 (7)	.13	.22	.20	.22	.12	.24		.52	.13	.85	.80	.71	.08	.08	.25	.04	.16	-.33	.77
HT2 (8)	.10	.23	.22	.23	.16	.19	.19		.68	.84	.84	.89	.41	-.45	-.60	-.44	-.61	.36	.85
BHT2 (9)	.16	.22	.12	.15	.22	.14	.22	.17		.44	.55	.54	-.31	-.62	-.98	-.24	-.61	.76	.55
DI2 (10)	.08	.21	.20	.23	.14	.21	.09	.08	.18		.96	.93	.24	-.26	-.39	-.13	-.39	.13	.96
SWT2 (11)	.07	.20	.20	.22	.15	.20	.10	.08	.17	.02		.98	.04	-.21	-.38	-.19	-.30	.11	1.00
RWT2 (12)	.08	.20	.20	.21	.17	.19	.14	.08	.17	.04	.02		.07	-.36	-.59	-.35	-.47	.27	.99
BB2 (13)	.30	.36	.32	.36	.34	.38	.36	.36	.37	.34	.35	.36		-.23	-.47	-.27	-.74	.20	.04
IBS2 (14)	.20	.24	.15	.14	.24	.17	.25	.22	.18	.23	.23	.22	.36		1.01	.63	.85	-.79	-.26
FBS2 (15)	.23	.28	.21	.22	.29	.18	.30	.23	.19	.25	.26	.24	.41	.09		1.00	.94	-1.06	-.44
SRR2 (16)	.24	.25	.24	.24	.28	.27	.28	.29	.26	.27	.27	.24	.43	.25	.31		.86	-.72	-.24
GSL2 (17)	.22	.29	.23	.24	.29	.20	.30	.23	.22	.25	.27	.25	.22	.13	.07	.31		-.88	-.35
RGR2 (18)	.24	.26	.14	.13	.24	.13	.27	.26	.18	.27	.27	.26	.41	.14	.12	.27	.13		.15
TWT2 (19)	.07	.20	.19	.22	.15	.20	.11	.07	.16	.02	.00	.01	.35	.23	.25	.26	.26	.26	

See Table B.1 for description of traits.

Table B.15. Estimates of genetic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs.

Population : S-2

Seedling Trait	HYHT (1)	#COT (2)	IBS1 (3)	FBS1 (4)	HT1 (5)	BHT1 (6)	DI1 (7)	HT2 (8)	BHT2 (9)	DI2 (10)	SWT2 (11)	RWT2 (12)	BB2 (13)	IBS2 (14)	FBS2 (15)	SRR2 (16)	GSL2 (17)	RGR2 (18)	TWT2 (19)
HYHT (1)		.37	-.60	-.23	.85	-.12	.31	.38	-.18	.25	.40	.25	.15	-.13	.05	.10	.00	-.31	.37
#COT (2)	.22		-.39	-.06	.12	-.66	-.07	-.39	.40	.02	.13	.26	-.14	.13	.15	-.08	.24	-.31	.18
IBS1 (3)	.20	.31		.97	-.28	-.85	-.22	-.99	-.53	-.72	-.74	-.96	-.32	1.05	1.22	1.02	1.56	-.71	-.82
FBS1 (4)	.19	.26	.05		.18	-.91	.00	-.76	-.67	-.56	-.61	-.88	-.20	.97	1.24	.96	1.54	-.87	-.69
HT1 (5)	.09	.28	.34	.24		-.58	.36	.05	-.42	-.02	.02	-.23	-.35	.10	.39	.38	.60	-.72	-.05
BHT1 (6)	.21	.23	.17	.09	.21		-.19	.65	.44	.36	.37	.59	-.23	-.81	-.82	-.81	-.87	.92	.43
DI1 (7)	.19	.29	.31	.25	.22	.25		.26	.03	.76	.59	.36	-1.29	.13	.20	.20	.77	-.20	.53
HT2 (8)	.20	.29	.25	.19	.28	.16	.26		.17	.64	.73	.75	-.42	-.86	-.72	-.65	-.67	.68	.74
BHT2 (9)	.26	.33	.30	.23	.31	.25	.32	.32		.29	.19	.28	-.71	-.38	-.61	-.43	-.43	.44	.23
DI2 (10)	.20	.28	.26	.21	.27	.22	.13	.16	.29		.94	.88	-1.05	-.47	-.62	-.33	-.30	.46	.93
SWT2 (11)	.17	.27	.24	.19	.26	.20	.17	.12	.29	.03		.92	-.52	-.53	-.66	-.32	-.56	.55	1.00
RWT2 (12)	.20	.27	.21	.16	.27	.18	.22	.13	.28	.06	.04		-.57	-.65	-.91	-.65	-.84	.76	.95
BB2 (13)	.50	.67	.74	.59	.72	.69	1.33	.85	1.07	1.20	.83	.85		.20	.57	.54	.26	-.16	-.53
IBS2 (14)	.22	.29	.19	.13	.27	.12	.28	.13	.29	.21	.19	.17	.72		1.00	.84	1.09	-.72	-.57
FBS2 (15)	.29	.37	.33	.28	.37	.22	.37	.22	.33	.24	.23	.21	1.11	.10		1.29	.94	-.82	-.74
SRR2 (16)	.25	.33	.25	.20	.29	.23	.30	.27	.35	.27	.27	.18	.86	.23	.39		1.29	-.83	-.41
GSL2 (17)	.41	.54	.91	.84	.64	.43	.73	.39	.53	.43	.40	.45	1.69	.38	.17	.81		-.90	-.65
RGR2 (18)	.22	.28	.18	.12	.18	.08	.27	.15	.27	.21	.19	.14	.74	.15	.18	.24	.35		.61
TWT2 (19)	.18	.27	.23	.18	.26	.20	.18	.12	.29	.03	.00	.03	.83	.19	.22	.26	.40	.17	

See Table B.1 for description of traits.

Table B.16. Estimates of genetic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs.

Population : MC-1

Seedling Trait	HYHT (1)	#COT (2)	IBS1 (3)	FBS1 (4)	HT1 (5)	BHT1 (6)	DI1 (7)	HT2 (8)	BHT2 (9)	DI2 (10)	SWT2 (11)	RWT2 (12)	BB2 (13)	IBS2 (14)	FBS2 (15)	SRR2 (16)	GSL2 (17)	RGR2 (18)	TWT2 (19)
HYHT (1)		.32	-.30	-.27	.78	.74	.75	.80	.57	.56	.74	.59	.05	-.35	-.10	.32	-.09	-.10	.74
#COT (2)	.23		-.04	.09	.32	-.13	.38	.30	.51	.44	.40	.37	-.26	-.15	.29	.30	.31	-.40	.45
IBS1 (3)	.20	.28		1.01	.32	-.88	-.31	.18	-.31	.04	.01	.02	-.10	.50	.61	-.08	.43	-.59	-.02
FBS1 (4)	.21	.29	.03		.27	-.83	-.17	.16	-.30	.11	.04	.16	-.06	.48	.62	-.20	.42	-.55	.02
HT1 (5)	.10	.27	.21	.22		.31	.36	.84	.41	.52	.63	.34	.07	-.25	.15	.51	.06	-.38	.58
BHT1 (6)	.16	.33	.16	.14	.27		.71	.34	.58	.17	.35	.34	-.11	-.71	-.58	-.01	-.31	.22	.38
DI1 (7)	.15	.33	.31	.31	.24	.26		.40	.22	.69	.74	.75	-.08	-.08	.33	.18	.25	-.31	.74
HT2 (8)	.10	.27	.24	.25	.11	.25	.25		.54	.60	.86	.75	-.17	.04	.18	.29	.20	-.18	.87
BHT2 (9)	.16	.26	.23	.23	.21	.22	.29	.19		.40	.40	.06	-.02	-.42	-.35	.58	-.21	.29	.37
DI2 (10)	.16	.27	.25	.26	.18	.28	.17	.16	.22		.93	.82	-.28	.41	.76	.36	.61	-.48	.94
SWT2 (11)	.12	.27	.25	.26	.16	.26	.17	.09	.22	.05		.82	-.21	.19	.46	.43	.40	-.24	.99
RWT2 (12)	.24	.38	.34	.35	.30	.37	.31	.22	.35	.16	.17		-.25	.30	.84	-.16	.65	-.31	.88
BB2 (13)	.24	.31	.28	.29	.27	.32	.34	.28	.28	.29	.29	.39		-.33	-.60	.07	-.86	.61	-.25
IBS2 (14)	.23	.33	.24	.24	.28	.19	.35	.30	.28	.30	.30	.42	.32		.89	.03	.72	-.38	.20
FBS2 (15)	.25	.36	.23	.23	.29	.24	.38	.31	.27	.31	.30	.46	.30	.12		-.26	.92	-.84	.55
SRR2 (16)	.29	.39	.34	.35	.30	.38	.39	.34	.35	.36	.34	.47	.38	.40	.41		-.20	.00	.34
GSL2 (17)	.22	.30	.23	.24	.26	.26	.33	.27	.25	.26	.26	.38	.12	.17	.07	.35		-.83	.47
RGR2 (18)	.23	.31	.20	.20	.23	.28	.31	.28	.25	.27	.27	.38	.22	.26	.13	.00	.11		-.25
TWT2 (19)	.13	.28	.27	.27	.18	.28	.18	.10	.24	.04	.01	.12	.31	.32	.31	.38	.27	.29	

See Table B.1 for description of traits.

Table B.17. Estimates of genetic correlations (upper diagonal) and associated standard errors (lower diagonal) for seedling trait pairs.

Population : MC-2

Seedling Trait	HYHT (1)	#COT (2)	IBS1 (3)	FBS1 (4)	HT1 (5)	BHT1 (6)	DI1 (7)	HT2 (8)	BHT2 (9)	DI2 (10)	SWT2 (11)	RWT2 (12)	BB2 (13)	IBS2 (14)	FBS2 (15)	SRR2 (16)	GSL2 (17)	RGR2 (18)	TWT2 (19)
HYHT (1)		-.45	-.29	-.34	.74	.50	.51	.76	-.04	.71	.65	.74	-.34	-.29	-.32	-.65	-.13	.08	.68
#COT (2)	.44		.93	.82	-.17	-1.13	.05	-.32	-.14	.19	.31	-.19	.39	.74	1.01	.73	.65	-.59	.15
IBS1 (3)	.19	.61		1.03	.34	-.87	.11	.02	.20	.14	.17	-.10	-.43	.78	.89	.64	.82	-.94	.08
FBS1 (4)	.20	.59	.03		.27	-.83	.02	.05	.04	.08	.21	-.15	-.60	.76	.92	.81	.90	-.97	.08
HT1 (5)	.13	.51	.22	.24		-.05	.62	.75	.11	.81	.82	.54	-.76	.31	.22	-.02	.42	-.57	.72
BHT1 (6)	.24	.82	.21	.17	.35		.10	.24	.13	.10	-.09	.32	.31	-.85	-.69	-1.02	-.63	.77	.03
DI1 (7)	.16	.45	.22	.23	.16	.30		.46	-.09	.92	.76	1.02	-.26	-.02	.10	-.69	.16	-.21	.84
HT2 (8)	.11	.47	.23	.24	.15	.30	.19		.19	.78	.91	.61	-.63	.13	.31	-.25	.45	-.23	.80
BHT2 (9)	.25	.54	.26	.27	.31	.35	.28	.27		.00	-.11	.01	-.74	.14	.13	.34	.34	-.30	-.10
DI2 (10)	.11	.44	.21	.22	.13	.29	.06	.10	.27		.93	1.02	-.49	.11	.23	-.59	.34	-.31	.95
SWT2 (11)	.15	.52	.24	.24	.15	.33	.13	.10	.32	.05		1.07	-.76	.20	.40	-.48	.56	-.42	1.01
RWT2 (12)	.19	.60	.29	.29	.26	.38	.18	.21	.35	.11	.21		-.52	.05	.16	-.70	.30	-.25	1.03
BB2 (13)	.28	.69	.30	.31	.39	.39	.31	.34	.37	.30	.33	.41		-.45	-.61	-.15	-.80	.75	-.66
IBS2 (14)	.20	.55	.13	.13	.25	.16	.24	.25	.28	.23	.25	.30	.30		.95	.45	.87	-.89	.15
FBS2 (15)	.21	.65	.16	.15	.29	.22	.25	.27	.30	.24	.25	.32	.31	.09		.51	.97	-.82	.32
SRR2 (16)	.24	.71	.28	.28	.36	.44	.27	.31	.38	.24	.33	.18	.41	.29	.31		.44	-.48	-.54
GSL2 (17)	.22	.50	.16	.15	.28	.22	.24	.26	.28	.23	.23	.31	.17	.10	.03	.30		-.88	.46
RGR2 (18)	.22	.51	.11	.10	.22	.17	.24	.27	.29	.23	.24	.31	.22	.09	.10	.30	.07		-.36
TWT2 (19)	.13	.46	.22	.23	.15	.31	.10	.11	.30	.03	.02	.10	.32	.24	.24	.24	.23	.23	

See Table B.1 for description of traits.