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THEORETICAL AND EXPERIMENTAL EVALUATION OF EARLY SELECTION IN LODGEPOLE PINE (*PINUS CONTORTA* SPP. *LATIFOLIA* Englm.)

BY

XIAMING WU

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

DEPARTMENT OF FOREST SCIENCE

EDMONTON, ALBERTA

SPRING 1993

ISBN 0-315-82039-X

Canada

UNIVERSITY OF ALBERTA

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NAME OF AUTHOR: XIAMING WU

TITLE OF THESIS: THEORETICAL AND EXPERIMENTAL EVALUATION OF EARLY SELECTION IN LODGEPOLE PINE (*PINUS CONTORTA* SPP. *LATIFOLIA* Englm.)

DEGREE: DOCTOR OF PHILOSOPHY

YEAR THIS DEGREE GRANTED: 1993

Xiaming Wu

4008-Aspen Drive West
Edmonton, Alberta
Canada T6J 2B3

March 19th 1993

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled THEORETICAL AND EXPERIMENTAL EVALUATION OF EARLY SELECTION IN LODGEPOLE PINE (*PINUS CONTORTA* SPP. *LATIFOLIA* Englm.) submitted by XIAMING WU in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Forest Science.

F. C. Yeh (Superviser)

B. P. Dancik

J. Hoddinot

for SET John

S. E. T. John

S. J. Titus

W. T. Adams (External Examiner)
Oregon State University, USA

Date Mar. 17/97

Dedicated to

my mother and father.

ABSTRACT

The theoretical results of genetic gain from indirect early selection for mature traits under different early selection approaches (selection from single early trait, selection from multiple early traits, index selection based on early and mature traits, two-stage selection based on early and mature traits, and multi-generation selection based on early traits) were investigated. The performances of 28 seedling traits for two growth periods in the greenhouse and nine-year tree heights in the four field sites were evaluated in lodgepole pine (*Pinus contorta* spp. *latifolia* Englm.) and relationships between seedling traits and tree height in the field sites were examined. The efficiencies of indirect selection based on single and multiple seedling traits, indices combining seedling traits and nine-year tree height, two-stage selection based on seedling traits and nine-year tree height, and multi-generation selection based on seedling traits, were investigated using the genetic parameters derived from greenhouse and field tests.

A two-stage selection theory was developed to determine the optimal allocation of early and mature selection intensities based on the genetic parameters of early and mature traits. This theory can quantitatively evaluate advantages of early selection through increase in the overall selection intensity. The genetic theory of multi-generations of indirect selection was developed under the assumption of effectively infinite loci. This theory can assess genetic gains from several generations of early selection within one conventional breeding cycle. Results of the multi-generations of indirect early selection indicate: (1) genetic correlation between early and mature traits will decline after each generation of early selection and will

approach a fixed value as the number of generations approaches infinity, (2) genetic and phenotypic variances, and heritabilities of both early and mature traits, will decline after each generation of early selection and the reduction of genetic variance in the mature trait will be slower than the reduction in the early trait, (3) selection responses in both early and mature traits will decline after each generation of early selection and soon will reach a limiting value, and the decline of selection response in the mature trait is slower than that of the early trait.

Family effects were significant at the 1% probability level in all 28 seedling traits during the two growth periods in the greenhouse. Seed weight was not a major contributor to family differentiation. Estimates of individual heritabilities (0.543±0.103 to 0.949±0.137) and family heritabilities (0.721±0.044 to 0.837±0.026) were highest for seedling height. Selection for higher harvest index in lodgepole pine would result in increased stem productivity, tolerance to drought, and narrow and compact seedlings.

Significant family differences at the 5% level of probability were detected in nine-year tree height on all four field sites. Family-by-site interaction was highly significant, the result of rank change of the families across sites. Estimates of individual heritabilities (0.1203±0.030 to 0.1773±0.041) and family heritabilities (0.2779±0.021 to 0.3924±0.031) in nine-year tree height were significantly lower than estimated heritabilities of height traits in the greenhouse.

Twenty-four seedling traits had significant genetic correlations with nine-year tree height on the most productive (site B) of the four sites, but no seedling traits were correlated with nine-year tree height on site C. The remaining two sites (A and

D) each had four seedling traits correlated with nine-year tree height. Five seedling traits were correlated with mean nine-year tree height across all sites.

Shoot-root biomass ratio (SR) was the most efficient seedling trait for indirect selection of nine-year tree height across sites, while seedling height and diameter were the most efficient traits for indirect selection of nine-year height on site B. However, indirect selection of individual seedling traits was not as efficient as direct selection for nine-year tree height. Indirect selection of nine-year height on site B based on two seedling traits was, on average, 34% more efficient than indirect selection based on individual seedling traits. Index selection based on one seedling trait and nine-year tree height on site B was on average 40% more efficient than selection based on nine-year tree height alone.

Under two-stage selection for height growth performance on site B, 20 percent of the families in the greenhouse could have been culled on the basis of basal diameter at lifting (D8) with no negative impact on the genetic gain in nine-year height expected if all families had been field tested.

Under multi-generations of early selection scheme, two generations of early selection based on seedling height after two growing seasons in the greenhouse would produce expected genetic gain similar to that obtained by direct selection of nine-year tree height on site B. The application of early selection for shortening the breeding cycle and for increasing overall selection intensity or reducing long-term test size is discussed for lodgepole pine.

ACKNOWLEDGEMENT

Many individuals contributed to the completion of this study. First of all, I would like to thank Dr. Francis Yeh, my guiding professor for his persistent encouragement, assistance and friendship during last few years. I express my sincere thanks to the members of my graduate committee for their valuable advices and comments during preparation of this thesis.

The study would have been impossible without the help from Dr. Narinder Dhir at the Alberta Forest Service, who kindly provided the seeds and the data from his field genetic trials of lodgepole pine.

I am indebted to Dr. Israel Jiang for his assistance and guidance on the establishment of greenhouse experiment.

Thanks also go to Mr. Kumbongsi Dyx and Miss Elizabeth Marshall for their enthusiasm in helping me to measure and harvest all seedlings. I would like to thank Dr. Ian Dymock at Northern Forest Centre, Forest Canada, for providing facilities to complete the biomass study.

Finally, I would like to thank my wife Hong Zheng for all the help and support along the way.

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CHAPTER ONE

INTRODUCTION AND LITERATURE REVIEW

1. INTRODUCTION

For several decades, long generation intervals and breeding cycles have been obstacles to progress in breeding of commercial tree species. The time span required for trees to reach sexual maturity and the advanced age at which a reliable genetic evaluation of selected material can be made are two major contributing factors to the long breeding cycle. Reducing one or both of these time spans is essential to forest geneticists for speeding up breeding progress and increasing genetic gains per unit time.

Many biological and cultural approaches have been developed to achieve sexual maturity at an early age. The application of plant hormones, such as gibberellin, water stress and out-of-phase dormancy are some methods used to induce early flowering (Greenwood 1978, 1981, Pharis et al. 1987). Even more important to tree geneticists is the fact that final evaluation or harvesting of selected trees is performed many years after the trees have reached reproductive age. A common recommendation is that final evaluation and selection in progeny tests be delayed until trees reach approximately one-half the projected rotation age (Zobel and Talbert 1984, Lowe and van Buijtenen 1989). For most conifers, the attainment of

half rotation age takes several decades, and waiting for such a long period to select breeding material is unacceptable for many operational tree breeding programs. Consequently, there is great need for developing procedures to select individual trees or genetic entries (such as provenances, clones) at an early age. Early selection is based on the premise of a higher genetic gain per unit time. However, an increased rate of genetic improvement can only be realized through early testing and selection if genetic relationships exist between the early and mature traits (Magnussen 1988). Because the efficiency and effectiveness of early selection depend on the genetic relationship between early and mature traits, considerable research in the past two decades has examined this early-mature relationship (Talbert et al. 1985).

The concept of early selection is very confusing in the tree breeding literature (Jiang 1985). It is believed that Schmidt (1963) was the first systematic user of juvenile-mature correlations and early selection (Sziklai 1974). Strictly speaking, any selection before rotation age should be called early selection. However, in operational tree breeding, one usually refers to selection before half-rotation age as early selection. Lambeth (1983) defined early testing or selection as a process in which trees are selected after being grown at close spacing in a greenhouse, growth chamber or nursery for one or two years. In this thesis, conventional selection age (half-rotation age) or reference age (any age older than age of early selection) will be referred to as the mature age and ages younger than this will be referred to as early or juvenile age.

In the literature of forest genetics, there are two approaches to studying the

effectiveness of early selection. The first is comparative studies, in which seedlings are grouped into fast-growing and slow-growing groups (or groups based on other distinguishing factors) to observe the effectiveness of this classification in later stages (Waxler et al. 1980), or in which super-seedlings are selected and comparisons with average (or check) seedlings are made in later stages to evaluate the effectiveness of early selection (King et al. 1965, Overton and Ching 1978, Hans Nienstaedt 1981). The second approach is through quantitative genetic studies in which early testing and selection are carried out in a population and the effectiveness of early selection quantified in terms of genetic gain. In this contribution, only the second approach will be reviewed and discussed.

2. LITERATURE REVIEW AND DISCUSSION

Early selection studies focus mainly on the estimation of juvenile-mature correlations and its implications for early selection. Some theories have also been developed for early selection.

2.1 Theory

To compare the effectiveness or efficiency of selection at early and mature ages, measurement of genetic gain is required. The basic theoretical work on genetic gain of early selection was developed by Nanson (1967b, 1968, 1976), who applied the

principle of indirect selection (Lerner 1958, Searle 1965) and regarded genetic gain of mature traits upon early selection as correlated gain. This correlated genetic gain (Falconer 1981, Nanson 1988) is expressed as

$$\begin{aligned} E_x(G_y) &= i_x\, r_G\, h_x\, h_y\, \sigma_y \\ &= i_x\, r_G\, h_x\, \sigma_{G_y} \\ &= i_x\, CGP\, \sigma_y \quad , \end{aligned} \tag{1}$$

where $E_x(G_y)$ is the expected genetic value G_y of mature trait Y under selection of early trait X. Traits X and Y are not necessarily the same traits at the different ages.

i_x is the selection intensity in the early trait X.

h_x is the square root of the heritability of early trait X.

h_y is the square root of the heritability of mature trait Y.

r_G is the genetic correlation between early trait X and mature trait Y.

σ_y is the phenotypic standard deviation of mature trait Y.

σ_{G_y} is the genetic standard deviation of mature trait Y.

$CGP = r_G \cdot h_x \cdot h_y$, which is the coefficient of genetic prediction (Baradat 1976).

When one assumes the covariance between genetic value and environmental value at early and mature stage is zero [$Cov(G_y E_x) = Cov(G_x E_y) = 0$], then correlated genetic gain is

$$E_x(G_y) = i_x\, r_{x.G_y}\, \sigma_{G_y} \quad , \tag{2}$$

where r_{xG_y} is genophenotypic correlation between genetic value of mature trait Y and phenotypic value of early trait X. If one sets $e_x^2 = 1 - h_x^2$, $e_y^2 = 1 - h_y^2$, the correlated

genetic gain can be written as

$$E_x(G_y) = i_x(r_P - e_x e_y r_E)\sigma_y \quad , \qquad (3)$$

where r_P is phenotypic correlation between early trait X and mature trait Y and r_E is environmental correlation between early trait X and mature trait Y. When r_E is zero,

$$E_x(G_y) = i_x \, r_P \, \sigma_y \quad . \qquad (4)$$

Nanson (1970) extended this correlated genetic gain to genotypic gain based on selection of "genotypic elements". He defined "genotypic elements" as the basic unit for testing and selection. The "genotypic element" can be provenance, stand, family, clone and variety as well as individual breeding values. From this context, the quantitative genetic gain concept can be applied to different "genetic elements". Thus, the parameters in the gain prediction should be "genotypic element" parameters.

Genetic or genotypic gain ($E_y(G_y)$) from direct selection is expressed as:

$$E_y(G_y) = i_y \, h_y^2 \, \sigma_y \quad , \qquad (5)$$

where i_y is selection intensity applied to mature trait (Falconer 1981, Namkoong 1979). The efficiency of early selection ($R_{x,y}$) can be estimated from the gain ratio of indirect selection to direct selection as:

$$R_{x,y} = \frac{E_x(G_y)}{E_y(G_y)} = \frac{i_x}{i_y} \, \frac{h_x}{h_y} \, r_G \quad . \qquad (6)$$

If one considers the total time required for a breeding cycle under early and mature

selection, $R_{x,y}$ will increase due to the time saving of early selection. The gain ratio of indirect early selection to direct mature selection per unit time ($R'_{x,y}$) is given as:

$$R'_{x.y} = \frac{E_x(G_y)}{E_y(G_y)} \frac{T_y}{T_x} = \frac{i_x}{i_y} \frac{h_x}{h_y} r_G \frac{T_y}{T_x} \qquad (7)$$

where T_y = number of years (or unit time) to complete a breeding cycle with mature selection

T_x = number of years to complete a breeding cycle with early selection (Nanson 1967b, 1988, Lambeth 1980).

From equation 6, it can be seen that with equal selection intensity ($i_x=i_y$), early selection will yield greater genetic gain than mature selection if $h_x r_G > h_y$. If one considers the shortened breeding cycle with early selection (equation 7), r_G does not need to be very large to justify early selection. Lambeth (1983) demonstrated that a juvenile-mature correlation of only 0.2 is sufficient to make age-2 selection as effective as age-35 selection under equal selection intensities and heritabilities in loblolly pine (*Pinus taeda* L.).

Besides increasing genetic gain per unit time, another major application of early selection is to reduce size of field tests or to increase selection intensity (Lambeth 1980, Magnussen 1988, Adams et al. 1989, 1991). Early testing results could be used for culling families with the poorest performance before field tests are established. The results would be smaller, more efficient, and cost-effective field tests (Adams et al. 1989). If field test size is fixed, early selection can increase genetic gain in mature tree by increasing the overall selection intensity.

2.2 Experimental studies

Experimental studies on early selection in the last three decades have provided information in three areas: (1) early-mature correlations, (2) optimal early selection age, and (3) early selection strategies. The results of these studies are reviewed and discussed in the following three sections.

2.2.1 Early-mature correlations

Several authors have reviewed or summarized early-mature correlation studies (Nanson 1968, Sziklai 1974, Waxler and van Buijtenen 1981, Lambeth 1982, Jiang 1985, Gill 1987). Waxler and van Buijtenen grouped most of the works into three categories: (1) assessing the value of nurserybed selection by correlating nursery growth with later field performance, (2) utilizing provenance and progeny test data in an attempt to statistically relate growth at an early stage to growth at a later stage, and (3) comparing juvenile growth under simulated field conditions to actual field performance at a later stage. Lambeth classified early testing into two categories: (1) retrospective studies, where the performance of genetic groups already in field tests is related to measures of the same genetic groups established retrospectively into early tests using stored or reconstructed seedlots, and (2) selection studies, in which early selections are followed for several years, such as after super-seedling selection or early selection of families.

It is difficult, based on the literature, to extract general trends of early-mature

correlations and to make comparisons among the studies. The results vary widely and are often controversial due primarily to differences among species, sample size, the time interval considered, test environments, design, and silvicultural treatments. In addition, the indiscriminate use of phenotypic and genetic correlations in the studies has added to the confusion.

To have a clearer understanding of the interpretation of early-mature correlations reported in these studies, the degree to which these correlations reflect genetic (or genotypic) correlations needs to be understood. Let us suppose the phenotypic values of the early and mature traits are X and Y, respectively. These phenotypic values have genetic and environment components and can be expressed as follows:

$$\begin{aligned} X &= \mu_x + G_x + E_x \\ Y &= \mu_y + G_y + E_y \quad , \end{aligned} \tag{8}$$

where μ_x and μ_y are population means of X and Y respectively, G_x and G_y are genotypic values of X and Y, respectively, and E_x and E_y are environmental values of X and Y, respectively. The covariance between X and Y has four components as shown in the numerator in equation 9. The correlations between X and Y, between G_x and G_y and between E_x and E_y are the phenotypic (r_P), genetic (r_G) and environmental (r_E) correlations, respectively. Phenotypic correlation has been defined by Searle (1961) as:

$$r_P = \frac{cov(G_x\ G_y) + cov(G_x\ E_y) + cov(G_y\ E_x) + cov(E_x\ E_y)}{\sqrt{(\sigma^2_{G_x} + \sigma^2_{E_x})\ (\sigma^2_{G_y} + \sigma^2_{E_y})}}\ , \qquad (9)$$

since covariances cov(G_x E_x) and cov(G_y E_y) are equal to zero in the designed experiments. Depending on the relationship between early and mature testing environments, the covariances cov(G_x E_y), cov(G_y E_x) and cov(E_x E_y) in equation 9 may also be zero. Thus, early-mature correlation studies may be grouped by considering possible differences between early testing and mature testing in (1) testing macrosite and (2) genotypic element. There are three groups of early-mature correlation studies:

(1) Early and mature testing on the same macrosite with the same trees or genotypic elements. An example is studying the same individual jack pine (*Pinus banksiana* Lamb.) over time on the same field site (Riemenschneider 1988).

(2) Early and mature testing in different macrosites but with the same individuals or genotypic elements. An example is studying the same individual lodgepole pine in the nursery and in the field over time (Ying et al. 1989).

(3) Early and mature testing in different macrosites with different but related trees or genotypic elements. An example is a retrospective study in loblolly pine in which seedlings from families in field tests are studied in the greenhouse (Williams 1989).

The results of these three groups are detailed below.

2.2.1.1 Early and mature testing on the same macrosite with the same trees or genotypic elements (age-age correlation studies)

This approach utilizes existing provenance, progeny, clone and other field trial data to observe relationships of growth at early ages to growth at maturity in the same trees or the same genotypic elements on the same site. Because individual trees are fixed in the same microenvironment from juvenile to mature stages, the covariances cov(G_x E_y), cov(G_y E_x) and cov(E_x E_y) in equation 9 are not likely to equal zero, and the genetic covariance (cov(G_x G_y)) cannot be estimated independently of other covariances in the analysis of variance. The experiments reported below include different genetic levels.

I. Provenance level

Different correlations were reported and compared in the literature. To understand the relationships among them, assume G_x and G_y in the equation 8 represent the provenance elements in the early and mature stages, respectively. A provenance test with b blocks and an n-tree plot has the following linear model:

$$\begin{aligned} X &= \mu_x + G_x + B_x + I_x + R_x \\ Y &= \mu_y + G_y + B_y + I_y + R_y \ , \end{aligned} \qquad (10)$$

where μ, B, I and R represent grand mean, block effect, interaction effect of provenance with block and the residual effect. Different correlations can be estimated utilizing variance and covariance components estimated from analyses of variance and covariance. The provenance correlation (r_{pr}) is

$$r_{pr} = \frac{cov(G_x\ G_y)}{\sigma_{G_x}\sigma_{G_y}} \quad . \qquad (11)$$

The provenance mean correlation ($r_{\overline{pr}}$) is

$$r_{\overline{pr}} = \frac{cov(G_x\ G_y) + \frac{cov(I_x\ I_y)}{b} + \frac{cov(R_x\ R_y)}{bn}}{\sqrt{(\sigma^2_{G_x} + \frac{\sigma^2_{I_x}}{b} + \frac{\sigma^2_{R_x}}{bn})\ (\sigma^2_{G_y} + \frac{\sigma^2_{I_y}}{b} + \frac{\sigma^2_{R_y}}{bn})}} \quad . \qquad (12)$$

The within-provenance correlation (r_{prw}) is

$$r_{prw} = \frac{cov(I_x\ I_y) + cov(R_x\ R_y)}{\sqrt{(\sigma^2_{I_x} + \sigma^2_{R_x})\ (\sigma^2_{I_y} + \sigma^2_{R_y})}} \quad . \qquad (13)$$

The plot mean correlation ($r_{\overline{pl}}$) is

$$r_{\overline{pl}} = \frac{cov(G_x\ G_y) + cov(I_x\ I_y) + \frac{cov(R_x\ R_y)}{n}}{\sqrt{(\sigma^2_{G_x} + \sigma^2_{I_x} + \frac{\sigma^2_{R_x}}{n})\ (\sigma^2_{G_y} + \sigma^2_{I_y} + \frac{\sigma^2_{R_y}}{n})}} \quad . \qquad (14)$$

The residual correlation (within plot r_R) is

$$r_R = \frac{cov(R_x\ R_y)}{\sigma_{R_x}\sigma_{R_y}} \quad . \qquad (15)$$

The provenance phenotypic correlation (r_{prp}) after adjustment for block effects is

$$r_{prp} = \frac{cov(G_x\ G_y) + cov(I_x\ I_y) + cov(R_x\ R_y)}{\sqrt{(\sigma^2_{G_x} + \sigma^2_{I_x} + \sigma^2_{R_x})\ (\sigma^2_{G_y} + \sigma^2_{I_y} + \sigma^2_{R_y})}} \quad . \qquad (16)$$

Provenance mean correlation and plot mean correlation can be estimated without analysis of variance and covariance, but the correlations will include a fraction of

block variance and covariance. There are two points to emphasize from these correlation formulae. First, these formulae clearly indicate different correlation estimates have different components. Since we are only interested in the provenance correlation in early provenance selection, application of the other correlation estimates is suspect. Second, the covariance analysis used to estimate these correlations is no longer valid because provenance effects at one stage are not independent of the block, interaction and residual effects at the other stage. Thus, correlation estimation using the covariance method can only be considered approximate.

Steinhoff (1974) studied correlations of ponderosa pine (*Pinus ponderosa* Laws) provenances from age five to age 50 for height and age 20 to 50 for diameter at breast height (DBH). He found between-provenance correlations were high (r_{pr} > 0.74) and significantly different from zero after age twelve. Nanson (1987) calculated provenance mean correlations in an international Norway spruce (*Picea abies* (L.) Karst.) provenance test at two sites. The correlation between age nine and 40 was greater than 0.54 on one site and the correlation between age nine and 35 was greater than 0.76 on another site. Provenance mean correlations based on 30 sources were estimated by Ying et al. (1989) in lodgepole pine from age four to age eighteen. The correlations at one site were high and stable (above 0.65) over time, but on another site the correlations were low and unstable until age nine.

These studies indicate early-mature correlations at the provenance level are usually high and provenance selection at an early age should be considered.

However, the extrapolation of an early-mature correlation from one macrosite may not be very applicable to other macrosites as Ying's result indicated. This is because there may be large provenance-environment interactions, as many tests have revealed (Wellendorf 1987).

II. Family level

The majority of early-mature correlations reported in the literature have been based on families. With family structure, additive genetic variance and covariance can be estimated. Thus, additive genetic correlations and correlated genetic gain under random mating in the base population or in a seed orchard can be estimated. Different correlations have been used. Again, it is often misleading to compare among the different correlations as they have different components. For clarity, the relationship among correlations often found in the literature can be demonstrated from a linear model for family (f) in block (b) with an n-tree plot. The model is identical to the provenance model of equation 10 except that G_x and G_y here represent family effects in the early and mature stages. By analysis of variance and covariance, family correlation (r_f) denotes genetic correlation in the half-sib and full-sib family structure. It is of the form

$$r_f = \frac{cov(G_x\ G_y)}{\sigma_{G_x}\sigma_{G_y}} \quad . \qquad (17)$$

The formulations of family mean correlation ($r_{\bar{f}}$), the within-family correlation (r_{fw}), the plot mean correlation ($r_{\bar{pl}}$), the residual correlation (within plot r_R), and phenotypic correlations (r_p) are similar to equations 12 to 16, respectively. Here, G_x

and G_y are family elements for X and Y, respectively. Family mean correlation and plot mean correlation can be estimated without analysis of variance and covariance, but the correlations will include a fraction of block variance and associated covariance. As for the provenance case, these correlation estimates are approximations due to the existence of cross-stage G x E, and E x E covariances.

Correlation estimates in this category which have appeared in the literature are listed in Appendix 1.1 along with sources and sample size. From these data, the following trends can be extracted:

(1) With the exception of a few reports (Namkoong 1972, 1976, Riemenschneider 1988), most tests have small sample sizes (< 20 families). If one considers the large sampling error for estimating correlations (Reeve 1955, Robertson 1959, Lambeth 1983), these correlations are estimated with very low precision, and thus, are of limited value.

(2) The majority of correlations (genetic, family mean or phenotypic) reported are positive, except in four cases. In two of these cases (Namkoong 1972, Giertych 1974), family effects were not significant. In the third report of negative correlations (Gill 1987), only nine half-sib families were included; thus a negative early-mature correlation estimate is not surprising if considering the small family size. The fourth negative early-mature correlation was reported by Namkoong (1976), who attributed the result to varying competitive effects during different stages of tree growth.

(3) Genetic correlation estimates are usually larger than phenotypic correlations (Lambeth et al. 1983, Loo and Tauer 1984, Cotterill and Dean 1988, and

Riemenschneider 1988).

(4) Correlations increased as the time interval between the two measurements decreased.

III. Individual level

Correlations between individual trees can be estimated in designed experiment, but many confounding effects other than genetics contribute to the correlations. Equation 18 is an expression for individual correlation when the model of family level is assumed for a randomized block design:

$$r_I = \frac{cov(G_x\ G_y) + cov(B_x\ B_y) + cov(I_x\ I_y) + cov(R_x\ R_y) + cov(G_i\ B_i)}{\sqrt{(\sigma^2_{G_x}+\sigma^2_{B_x}+\sigma^2_{I_x}+\sigma^2_{R_x})\ (\sigma^2_{G_y}+\sigma^2_{B_y}+\sigma^2_{I_y}+\sigma^2_{R_y})}} + \frac{cov(G_i\ I_j) + cov(G_i\ R_j) + cov(B_i\ I_j) + cov(B_i\ R_j) + cov(I_i\ R_j)}{\sqrt{(\sigma^2_{G_x}+\sigma^2_{B_x}+\sigma^2_{I_x}+\sigma^2_{R_x})\ (\sigma^2_{G_y}+\sigma^2_{B_y}+\sigma^2_{I_y}+\sigma^2_{R_y})}} \quad (18)$$

where i, j=x, y, but i≠j. Since individual trees are positioned in same spots from the early to the mature stages, the cross stage genotype-by-environment covariances such as cov(G_x R_y) are unlikely to be zero. Thus, one should avoid using individual correlation to predict efficiency of early selection due to many noise components. However, for many old experiments only individual correlations can be estimated due to a lack of replication and randomization (Nanson 1976). Wakeley (1971) estimated individual age-age correlations of four pine species from 21 subunit plantations. He found age-age correlations between age three and 30 were positive, but that slash pine (*Pinus elliottii* Engelm.) was better correlated at an early age with mature performance, than the other three species. Wakeley also found that trees with

superior size at age 30 could be identified with a high degree of certainty at age 20, and in some situations at age fifteen. He suggested that selections could be made between age ten and fifteen to establish second-generation seed orchards. Gonzalez and Richards (1988) investigated age-age correlations of wood density by examining total-stem density of 50-year old trees and their breast-height density from age five to age 30. They found that linear regression and rank correlations improved as age increased from age five to fifteen years, but there was no significant further improvement between fifteen and 30 years. Thus, they concluded that selection for wood density at age 50 could be made between ages ten and fifteen years.

IV. Clone level

The genotypic correlation among clones at different ages can be estimated in replicated experiments when it is assumed that covariances of clones and environments at different ages are zero. Such genotypic correlations have been extensively studied in Europe with Norway spruce. Bentzer et al. (1989) using 75 clones, found large genotypic correlations between age ten and earlier ages for height, diameter and volume. Their result suggested that clonal selection for height could be effective as early as age four. In another study, Roulund (1987) examined age-age correlations in three experiments. In the first experiment with seven clones, all age-age correlations for ages ranging four to thirteen were significantly different from zero ($r > 0.75$), with the exception of correlations at ages four and seven with age thirteen. In another experiment with 116 clones, age-age correlations for ages ranging from six to ten were all high ($r > 0.68$). In his third experiment, all age-age

correlations of height were significant and above 0.48 from age one to ten. Huehn (1989) estimated the phenotypic correlations of five clones in Norway spruce. The age-age correlations showed a good agreement with Lambeth's empirical age-age correlation curve (Lambeth 1980). Wilkinson (1972) estimated phenotypic and genetic age-age correlations in hybrid clones of poplar (*Populus* L.). The genotypic correlations were systematically larger than the phenotypic correlations and selection at age nine for a fifteen-year rotation was concluded to be very reliable.

2.2.1.2 Early and mature testing in different macrosites with the same tree or genotypic elements

In this approach, evaluation is first conducted in the nursery or other controlled environments, followed by field evaluation for the same trees. A typical example involves seedlings raised in the nursery and then randomized in a field experiment. With this approach the covariances $cov(G_x E_y)$, $cov(G_y E_x)$ in equation 9 are zero. The environmental covariance $cov(E_x E_y)$ is not equal to zero, when the environmental effect on early stage is carried over to the mature stage. The $cov(E_x E_y)$ is equal to zero when the environmental effect on early stage is not carried over to the mature stage. Therefore, the covariance of the early trait with the mature trait has one component ($cov(G_x G_y)$) or two components ($cov(G_x G_y)$ and $cov(E_x E_y)$). Some typical results are listed below.

I. Provenance level

Ying et al. (1989) found for nineteen provenances of lodgepole pine that provenance mean correlations of height between a nursery and plantation sites decreased as the age of plantation trees increased, except in one nursery-plantation pair where nursery-field correlations increased over time. Ying's study showed that nursery growth was not a good predictor of provenance field performance. Nienstaedt (1984) investigated nursery-field correlations in a black spruce (*Picea mariana* (Mill) B.S.P.) test of 108 provenances and in another test with a subsample of 48 of these provenances. The results were mixed. Nursery characters (dates of flushing, dates of growth cessation and height) were significantly correlated with field performance on two sites for all 108 provenances. But in the 48 provenance subsample, nursery characters were not correlated with the field tests, except for flushing at two years.

Based on 26 provenances in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), Christophe and Birot (1979) found that the correlation of provenance means for total height at age two (nursery) with field height at age eight was 0.82, the correlation of family means within provenances averaged 0.66, and both were significantly different from zero. Nanson (1987) in two Norway spruce provenance tests demonstrated that heights at ages 35 and 40 were well correlated not only with length of growing season but also with seed weight and fresh weight of one-year old seedlings.

II. Family level

La Farge (1975) studied age-age correlation of height in slash pine and loblolly pine with nine to 56 families from poly-crosses and single-cross family tests. Correlations of seventeen family means at age five in the field with age one in the nursery were poor. This study suggested that nursery evaluation of growth traits did not provide useful data for slash and loblolly pines. Nienstaedt and Riemenschneider (1985) studied 55 families of white spruce (*Picea glauca* (Moench) Voss) and found significant family mean correlations between nursery and field height. Nursery height at age two had correlations of 0.507 and 0.603, respectively, with heights at age fifteen on two sites. A significant, positive nursery-field correlation of height was also found in twenty-nine loblolly pine families (Robinson et al. 1984). Correlations of nursery height with height and diameter after five years of growth in a plantation were significant (> 0.63) and suggested that seedling selection in the nursery would be effective for 5-year growth in the field.

Mikola (1988) reported nursery-field correlations in a Norway spruce provenance and family study. The results indicated that nursery-field height correlations of fifteen families were positive, but generally non-significant, and nursery height only weakly related to subsequent volume production at age fourteen in the field. But the relationship between nursery height and field volume was much stronger at the provenance level. Mikola concluded that direct selection in the nursery for growth rate might be misleading for families, but the potential for provenances was better.

2.2.1.3 Early and mature testing in different macrosites with different but related tree or genotypic elements

This approach is often referred as retrospective studies in the literature because of the use of seeds from related genotypes to test the performance of trees already being grown in field tests. Seedling performance at early ages (usually between three months to two years) in controlled environments is correlated with field performance of related genotypes to determine the effectiveness of early selection (Lambeth 1982). Retrospective studies have received much attention in recent years and many results have been reported. From a statistical point of view, the cross-stage G x E interaction covariances cov(G_x E_y), cov(G_y E_x) and the cross-stage environment covariance cov(E_x E_y) in equation 9 can be regarded as zero because they are not correlated in retrospective studies. If pre-conditioning effects such as seed size or nutrition affect only the early stage, the cross-stage cov(E_x E_y) is still zero. Thus the covariance between early trait X and mature trait Y consists only of genetic covariance, cov(X Y)=cov(G_x G_y). If pre-conditioning effects affect both the early and mature stages, their covariance is confounded with genetic covariance. In retrospective studies, entities can be at different genetic levels, e.g. provenance, clone, sibs. However, in most studies reported, the genetic entities are usually expressed in terms of half-sib, full-sib, and parent-progeny.

I. Half-sib retrospective studies

Due to a consistent positive relationship between shoot dry weight at age one and field performance in a group of western Gulf loblolly pine families over a wide

range of greenhouse conditions (Miller 1982 and Davison 1984), Williams (1987, 1988) studied eighteen half-sib loblolly families to find the best test procedure and the best growth conditions in the greenhouse for predicting field performance. The results indicated seedling growth in an accelerated short-term genetic test was poorly correlated with field performance, but a non-accelerating treatment with no light supplement offered promise for early genetic testing. Williams also concluded that length of the shoot beyond first budset (cyclic growth length) was the best juvenile indicator of eight-year height in the field.

In two other loblolly pine early selection studies, Cannell et al. (1978) found that seedling growth rate of well-watered seedlings was positively correlated with 8-year volumes, especially for families field tested on a poorly drained site. For families tested on a better-drained site, the correlations with seedling height growth rates were significant only when the seedlings were subjected to mild water stress; that is, families which produced the greatest 8-year volumes grew fastest under mild water stress as seedlings. Waxler and van Buijtenen (1981) found that shoot-root ratio correlated positively with long-term field performance of loblolly pine families.

Riiter and Perry (1987) investigated fourteen open-pollinated families of Douglas-fir. Growth and phenology of seedlings in the greenhouse were significantly correlated with field height at ages nine, twelve and fifteen. Carter et al. (1990) grew 20 half-sib families of jack pine for sixteen to 21 months in two different greenhouse regimes (one with natural photoperiod and another with controlled temperature and extended photoperiod to accelerate growth) and found heights in both regimes at the

end of the second growth cycle to be positively correlated with seven-year field height. The greenhouse measurements correctly classified the majority of families into upper and lower groups based on field height. In another jack pine study, Magnussen and Yeatman (1986) showed that nursery height of half-sib families at age four was correlated (r=0.61) with field height of age twelve at field site. It should be emphasized that above inconsistent early-mature correlations were likely caused by the small sample size of the studies. Adams et al. (1989) studied correlations between seedling performance in four nursery environments (age two) and field (ages twelve and thirteen) performance of 71 open-pollinated families of Douglas-fir. Genetic correlations between growth traits in seedling and field-grown trees (height, diameter and branch length) were moderate to strong, for example, seedling height at two years significantly correlated with bole diameter (r=0.78), stem sinuosity (r=0.44), and branch length (r=0.76). Diameter and stem sinuosity in the nursery also significantly correlated with branch length in field trees, and nursery stem sinuosity was significantly correlated with branch angle in field trees. In the same study, they found that family mean correlations of height, branch angle and sinuosity between nursery and field were greater than 0.30, and recommended that the use of early testing for low-level culling of families could be effective for height growth, branch angle and stem sinuosity.

II. Full-sib

Lambeth (1982) grew sixteen full-sib families of Douglas-fir in twelve greenhouse and growth chamber environments, under varying moisture, nutrition,

temperature and light conditions, to study whether seedling test environments influence the ability to predict field performance. Performance of families grown in seven greenhouse environments correlated better with field performance than those grown in growth chambers. Correlations between field performance and total seedling dry weights were higher than with seedling height, suggesting it might be possible to make early selections with the proper choice of traits and testing environments.

Jiang (1988) studied correlations of greenhouse growth with field growth of 34 lodgepole pine families, when seedlings were grown under two nutrition regimes and water stress treatments. Performance of seedlings grown under the normal condition was better correlated with field growth than when grown under water stress. There was a significant correlation between six-year field height and seedling dry weight and basal stem diameter, but height in the greenhouse was weakly correlated with field height. In 36 full-sib families of *Pinus sylvestris* L., Jiang (1988) found the mean length of stem units was most promising as an explanatory variable for variation of tree height in the field. Jonsson et al. (1990) studied nutrition effects on correlations between juvenile and field performance. Seedling general combining ability (GCA) estimates were correlated with GCA estimates from two field trials, and the greatest correlations were obtained when seedlings were grown under the highest nutrition treatment.

III. Parent-offspring

Early-mature correlation can also be estimated from genetic relationship

between parent (mature) and progeny (early). If the pollen pool is common to all parents, the genetic correlation between juvenile and mature stages can be estimated by the covariance between progeny (juvenile) and parent (mature), because this covariance estimates half the juvenile-mature genetic covariance. Genetic variances in the progeny and parent populations also must be estimated in order to estimate juvenile-mature genetic correlation. It should be pointed out that the relationship between parents and their juvenile offspring is not only a measure of juvenile-mature genetic correlation, but also parent-offspring correlations. When parents and progenies are tested at same age, parent-offspring genetic correlation is expected to be unity, since at same age, genetic variance of progeny in the half-sib families estimates a quarter of genetic variance of parents and parent-offspring covariance estimates half genetic variance of parent.

Franklin and Squillace (1973) estimated juvenile-mature genetic correlations using parent-offspring genetic relationship in two studies. Low genetic correlation between offspring at age three and parents at age nineteen ($r=0.18$) was found for oleoresin yield, but moderate to strong correlations were found between offspring at age three and parents at age 25 for other traits ($r=0.56$ for height, $r=0.43$ for volume, $r=0.71$ for turpentine, $r=0.43$ for specific gravity, $r=0.38$ for ethanol-benzene extractives and $r=0.34$ for moisture content) .

From the literature cited above, most correlations estimated in retrospective studies are not genetic, but are based on family means. Thus, prediction is biased when family mean correlations are used to estimate early-selection gain or efficiency

in early mass selection.

After reviewing juvenile-mature correlation studies, the following trends are apparent:

(1) Early provenance selection is more promising than early family and individual selection, as indicated by Steinhoff (1974), Ying et al. (1989), Nanson (1970), Christophe and Birot (1979).

(2) In retrospective studies, the choice of suitable early traits and testing environments appears crucial. Thus, under the appropriate choice of early traits and early testing environments there is potential promise to reliably predict mature performance as indicated by Cannell et al. (1978), Lambeth et al. (1983), Williams (1987,1988), Riiter and Perry (1987), Jiang (1988), and Jonsson (1990).

(3) Conflicting results on the effectiveness of early selection may have been caused by the small size of many studies. Thus, there is the need to critically examine the effectiveness of early selection based on large numbers of genetic entries. The number of families and individuals within families are extremely critical in detecting the true relationship between family performance in early and field tests (Lambeth 1983).

2.2.2 Optimal early selection age

The optimum early selection age is the age when annual genetic gain through early selection is maximized. The annual genetic gain due to early selection is expressed as

$$\Delta E_x(G_y) = \frac{i_x h_x(t)\ h_y r_G(t) \sigma_y}{t + t_B}\ , \qquad (19)$$

where $h_x(t)$ is square root of heritability of juvenile trait X at early age t, t_B is additional years needed to complete the breeding and $r_G(t)$ is the genetic correlation between trait X at an early age t and trait Y at mature age. The optimum selection age can be evaluated by comparing the annual genetic gain of early selection when early selection is implemented at different ages. For constant early selection intensity i_x and fixed mature selection age, the parameters i_x, h_y, and σ_y remain unchanged. The parameters changing with early age are $h_x(t)$ and $r_G(t)$. Thus, if information on these two parameters at different ages were available, it would be relatively simple to find the optimal early selection age. If one considers the cost of early selection, there would be two optimum selection ages: biologically and economically optimum selection ages (McKeand 1988). The optimum economical selection age is the age when the present value of genetic gain per year is maximized and this age will be somewhat greater than the biological optimum, because the turnover of each generation will incur certain costs (Burdon 1988).

From published results, there is no clear trend in heritability patterns of different traits over age. Some studies have shown that heritability increases with age at juvenile stage. For example, Huehn (1988) studied clone heritability of height in Norway spruce and indicated a tendency of increasing in h^2 from age one to fourteen. The initial range of heritability in tree height was between 0.16 to 0.29, and the final range was between 0.37 to 0.43 (Huehn 1988). Cotterill and Dean (1988) observed

heritability of basal area in a thinned population, and heritability of height in an unthinned population of radiata pine (*Pinus radiata* Don.) increased from age four to sixteen. Gill (1987) found heritability of height very high in sitka spruce (*Picea sitchensis* (Bong) Carr.) at time of planting (h^2=0.91) and decreased to 0.75 ten years after planting. Heritability patterns are also irregular within species. For example, for height and volume of loblolly pine, Foster (1986) found heritability dipped around age seven or eight while McKeand (1988) found heritability peaked at age eight to twelve. Lambeth et al. (1983) observed that heritability of height increased from age five to 20 on one site, but in another site, heritability decreased with age increase while remained three sites did not show clear pattern in heritability estimate. Similarly equivocal results were found for volume.

Franklin (1979) proposed a hypothetical growth model to explain long-term trends in genetic variance and heritability, based on data from four conifers (slash pine, loblolly pine, Douglas-fir and ponderosa pine). In his model, stand development was divided into juvenile-genotype, mature-genotype and codominace-suppression phases. The model suggests heritability reaches a rather high level during early stand development, then decrease markedly, declining to its lowest point at about the time of stand closure. After this, the additive genetic variance and heritability increase again and reaches a maximum around the middle of the second phase. In the third phase, heritability declines. Franklin's model also indicates a trend of strongly positive age-age correlations within phases and generally weak or negative correlations between phases. Hence, little or no genetic gain would be

produced from juvenile selection in these populations, and under typical stand conditions selection should be deferred until about half of rotation age. Nevertheless, not all patterns of stand development confirm Franklin's trends (Foster 1986, Cotterill 1987).

In most reports on early-mature correlations, correlations between early and mature stages seems more predictable. Age-age correlations are often positive and increase as the age of the early stage approaches the mature age. Lambeth (1980) analyzed juvenile-mature correlations of height in several pine species, and found age-age correlations (r), except when the early ages were between one to three years, could be estimated with reasonable accuracy by the following regression:

$$r = a + b \log_e\left(\frac{juvenile\ age}{mature\ age}\right), \qquad (20)$$

where a and b are estimated intercept and regression coefficient, respectively. By applying his model to loblolly pine, Lambeth concluded that selection at ages of five and six was optimal for a rotation age of 20-years and selection at ages of seven and eight was optimal for a rotation age of 50-years.

Kang (1985) developed four different juvenile-selection models on the basis of the Lambeth model. When a linear function was used to represent juvenile-mature heritability ratio and a linear or logarithmic function was used to predict juvenile-mature correlation, large differences in optimum selection ages were found for the four models.

Optimum selection ages estimated from experiments include: age three for

height at age 30 in jack pine (Riemenschmeider 1988), age six for age sixteen-year height and basal area in radiata pine (Cotterill and Dean 1988), age ten for slash pine (Squillace and Gansel 1974), ages from six to eight for rotation age 25 in loblolly pine (McKeand 1988), and age one for volume gain at age seven in loblolly pine (NeBgen and Lowe 1985). These optimum selection ages were estimated without considering breeding time t_B. If time effect is included, optimum selection age should be greater. These age-age correlations and optimal early selection ages are quite encouraging for early selection.

2.2.3 Early selection strategy

One of main objectives of early selection is to increase genetic gain per unit time in the mature trait. Most studies have looked at early selection based on a single trait at an early age. There are two other ways to increase genetic gain of mature trait from early selection: multi-trait early selection and multi-stage selection.

2.2.3.1 Multi-trait early selection

Most early selection studies reported have dealt with one juvenile trait. However, early selection can include a multiplicity of traits if additional traits provide useful information on mature performance. Multiple early traits at the same early stage can be combined into a selection index. Burdon (1989) indicated the measurements of a single trait at different ages can be treated as several traits. Using the matrix of phenotypic and genetic variances and covariances of each early

trait with the mature trait, such an index takes into account all available information, namely, heritability, variance, and both genetic and nongenetic correlations between traits. Provided there is good information on genetic parameters, employing selection indices with several early traits should give at least as much genetic gain as selection based on a single trait at the early age, and in some situations the use of multiple traits could substantially increase the efficiency of early selection. The efficiency of an index of indirect early selection can be increased substantially by adding traits that are either weakly correlated with early traits already in the index and strongly correlated with mature traits or strongly correlated with early traits in the index and weekly correlated with mature traits (White and Hodge 1991).

Several multi-trait early selection results have been reported. Selection for a combination of height and survival can be practised as early as age three in loblolly pine with little loss (19%) in relative efficiency, compared to direct selection for plot volume at age fifteen (Foster 1986). Cotterill and Dean (1988) built a restricted index combining height and basal area increments to 6.5 years and expected to produce over 60% more genetic gain per year in volume at age sixteen compared with later direct selection on volume 16 itself. At age eight after planting, an index combining total height and square girth procured 90% of direct genetic gain in volume at age fifteen (Bastien and Roman-Amat 1990). In slash pine, De Souza et al.(1992) reported that indices of greenhouse traits after inoculation of fusiform rust fungus (*Cronartium quercuum* Miyabe ex Shirai f. sp *fusiforme*) on seedlings could partially predict breeding value of disease resistance of field trees.

2.2.3.2 Multi-stage selection

Multi-stage selection offers an opportunity to increase overall gain at the mature stage by increasing overall selection intensity while maintaining a constant test size for mature tests, and to incorporate early testing into an operational tree improvement program (Talbert et al. 1985). Multi-stage selection applicable to early selection has the following sequence: (1) individual or family selection in the nursery or other controlled environments, (2) field testing of the selected material and (3) selection of best individual or family based on field plus nursery performance. Two-stage selection can either increase population size for early selection while keeping field test constant (increasing selection intensity) or decrease population size for field testing (Adams et al. 1992). Decreasing population size will reduce costs of testing and increase the precision of field testing, because the test is more compact.

Cotterill and James (1984) suggested using early selection in a young genetic test to establish a seed orchard. Final roughing of the orchard could be delayed until mature evaluation of those selections was conducted in the same genetic test. Their results indicated that expected genetic progress would be greater under two-stage independent culling, than it would be for single-stage selection alone, unless the heritability of the first-stage trait was much greater than that of the second-stage trait. In this case, greatest progress would come from single-stage selection at the first stage. Predicted gain was always greatest when the trait with the highest heritability was used in the first stage. Pacques (1984) considered operational costs of selection, breeding, and seed production in two-stage independent culling selection in loblolly

pine and found that predicted genetic progress reached a maximum when selection intensity was greatest at the first stage. Namkoong (1970) developed two-stage selection theory to optimize selection intensity allocations to maximize the ratio of gain to cost. Adams et al. (1989) applied two-stage selection theory to reduce the number of height measurements in tests (second stage) by culling progenies on the basis of DBH measurement at the first stage. Their results for a family selection scenario indicated that if as many as 60 to 65 percent of the families were removed from consideration based on DBH ranking in the first stage, nearly the same gain in bole volume would result after two-stage selection as would be expected from bole volume selection only in a single stage. When they applied this theory to two-stage progeny selection, the results showed that as many as 90 percent of the progeny individuals could be deleted from consideration in the first stage, without negatively affecting final gains in the bole volume. In a recent report, Adams et al. (1992) reported that 20-30% of the families under testing could have been culled on the basis of one-year height in a nursery test, with little or no negative impact on genetic gains in tree height at age fifteen that would have been obtained if all families had been field tested. They also calculated the financial advantage due to early selection.

3. FURTHER WORK NEEDED

To thoroughly understand the advantage of practising early selection in forest tree breeding, there is a need to investigate theoretically and empirically early

selection efficiency with different early traits and under different early selection approaches for the species of interest.

3.1 Theoretical

The most important advantage of early selection is to shorten the breeding cycle such that instead of one mature breeding cycle, one can have several breeding cycles of early selection. Thus, expected genetic gain derived from several early breeding cycles is of unique interest to the tree breeder. The only theory developed for genetic gain prediction of early selection is indirect selection theory. This is strictly valid only for one generation of early selection and cannot be used reliably to assess multi-generation gain because genetic parameters (heritability, genetic correlation) probably change with each generation of selection. To predict genetic gain after multiple generations of early selection, a quantitative genetic theory of multi-generation indirect selection needs to be developed.

Another advantage of early selection is that it can easily increase total selection population size for greater selection intensity and genetic gain. On the other hand, early selection can also reduce the population size for field testing. Thus, quantitative genetic method to quantify the increase of genetic gain due to this early selection needs to be addressed. Chapter two will deal with these theoretical problems.

3.2 Empirical

Experiments are needed to provide knowledge pertaining to early-mature genetic correlations, genetic variance and heritability trends for specific tree species, especially in the following areas:

(1) What is best early trait or best combination of early traits to predict mature performance.

(2) What is best early test environment which can efficiently predict mature performance.

(3) What is the sample size needed in early tests to generate meaningful early-mature genetic correlations.

(4) What is G x E effect on genetic correlations and early selection efficiency.

(5) How can early selection be used as first-stage selection in two-stage selection approaches.

Chapters Three, Four, Five and Six will address some of the problems stated above using lodgepole pine. Chapter Three deals with a greenhouse experiment to assess early traits and chapter Four assesses the tree performance at age nine in the field. The correlation of greenhouse and field performance was investigated in chapter Five. Chapter Six evaluates the best early selection traits and optimum combination of early traits for early selection, and efficiencies of two-stage selection and of multi-generations of early selection in lodgepole pine.

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CHAPTER TWO

GENERAL THEORY OF EARLY SELECTION

In this chapter, the theory of direct and indirect selection will be reviewed. Theories of two-stage selection and multi-generation indirect selection pertaining to early selection will be developed. The objective is to create a general and unified theory for early selection under the assumption detailed below in order to evaluate the outcome of different early selection strategies. Equations preceded or followed with references relate to existing theories, and equations without references are derivations derived by the author.

1. GENERAL ASSUMPTION

Assume in a large base population, Y is a mature trait with genetic value G_y, and X_1, X_2, ... X_p are early traits at an earlier stage with genetic values G_{x_1}, G_{x_2}, ... G_{x_p}, respectively. Before selection, the genetic values of G_y, G_{x_1}, G_{x_2}, ... G_{x_p} are assumed to follow a multinormal distribution with frequency function $f(G_y\ G_{x_1}\ G_{x_2}$ ... $G_{x_p})$, and following parameters in the base population:

(1) Genetic variances $\sigma_{G_y}^2$ and $\sigma_{G_{x_i}}^2$, i=1, 2, ... p.

(2) Genetic correlations $r_{y\cdot x_i}$ and $r_{x_i\cdot x_j}$, i, j=1, 2, ... p.

The multinormal distribution is justified if one assumes the early and mature traits

are each controlled by many loci with pleiotropic effects (Bulmer 1980). The phenotypic values of Y and X_1, X_2, ... X_p are composed of genetic values G_y, G_{x_1}, G_{x_2}, ... G_{x_p} and environmental effects E_y, E_{x_1}, E_{x_2}, ... E_{x_p} according to the simple relationships:

$$Y=G_y + E_y$$

$$X_i=G_{x_i} + E_{x_i} \quad i=1, 2, \ldots p.$$

Elements in the phenotypic array Y, X_1, X_2, ... X_p are multinormally distributed with frequency function $f(Y, X_1, X_2, \ldots X_p)$, and the following population parameters assuming that environmental values are normally distributed:

(1) Phenotypic variances σ_y^2 and $\sigma_{x_i}^2$, i=1, 2, ... p.

(2) Phenotypic correlations ρ_{y,x_i} and ρ_{x_i,x_j}, i, j=1, 2, ... p.

(3) Heritabilities h_y^2 and $h_{x_i}^2$, i=1, 2, ... p.

In this base population, different selection methods will be implemented and their effect on genetic gain of the mature trait will be evaluated. First, we will consider results from one generation of early and mature selection. This will be followed by multiple generation results of selection. Standardized variates of Y and X_i will be used in all following derivation.

2. ONE GENERATION RESULTS

Selection in one generation for mature gain can be at different stages from seedling to harvest. This can be:

(1) One-stage direct selection for gain in mature trait.

(2) One-stage indirect early selection for gain in mature trait.

(3) Two-stage selection for gain in mature trait (early selection is followed by mature selection).

(4) Index selection for gain in mature trait (an index of multiple early traits or an index of early and mature traits).

Results of these different selection approaches are separately investigated and discussed below.

2.1 One-stage mature selection

In this approach, selection is postponed until the mature stage is reached. The consequence of one-stage mature selection can be described by considering the marginal distribution of the mature variable Y, in the multinormal distribution. The standard marginal probability distribution of Y, f(y), is a univariate normal distribution (Kendall et al. 1987):

$$f(y) = \frac{1}{\sqrt{2\pi}} \exp^{-.y^2} \quad . \qquad (1)$$

Because individuals with the best Y values are selected, the population is truncated at a point b of Y such that the selected proportion is p(b) with

$$p(b) = \int_b^{\infty} f(y)\,dy = \int_b^{\infty} \frac{1}{\sqrt{2\pi}} \exp^{-\frac{y^2}{2}}\,dy \quad . \tag{2}$$

The expected phenotypic mean of Y, ($E_y(y)$) in the selected population is

$$E_y(y) = \int_b^{\infty} y\ \frac{1}{\sqrt{2\pi}} \exp^{-\frac{y^2}{2}} dy \ / \ \int_b^{\infty} \frac{1}{\sqrt{2\pi}} \exp^{-\frac{y^2}{2}} dy \quad . \tag{3}$$

By integration, the numerator is

$$e^{-\frac{b^2}{2}} \frac{1}{\sqrt{2\pi}} \ , \tag{4}$$

which is the height of the coordinate of the normal curve at the truncation point b. The equation 3 of expected mean of mature trait Y is known as the selection intensity (Namkoong 1979, Falconer 1981).

The genetic gain (or genotypic gain) of mature selection $E_y(G_y)$ is the expected phenotypic values of offspring of the selected parents after random mating or the average breeding (genetic) values of the selected parents, and can be obtained from bivariate normal distribution theory (Weiler 1959, Kendall et al. 1987) as

$$\begin{aligned} E_y(G_y) &= \rho_{y.G_y}\ E_y(y)\ \ \sigma_{G_y} \\ &= h_y\ E_y(y)\ \ \sigma_{G_y} \\ &= h_y^2\ E_y(y)\ \ \sigma_y \quad . \end{aligned} \tag{5}$$

Here, Y and G_y are distributed as bivariate normal with a correlation of $\rho_{y.G_y}$ under the linear model $Y=G_y + E_y$. This is the standard gain formula for direct selection presented by Falconer (1981). It also has broader application because it can be used in additive genetic gain prediction and genotypic element gain prediction such as

provenance and clonal selection.

2.2 One-stage early (juvenile) selection

In this case selection is carried out at the early stage on one trait, X, and will affect mature trait Y due to the genetic relationship between these traits (e.g. pleiotrophic effects between X and Y). If genetic and phenotypic correlations are r and ρ, respectively, the effect of early selection for X on mature trait Y can be described as the effect of truncating one variable on another variable in the bivariate normal distribution. By bivariate normal distribution theory, the expected phenotypic mean of Y after truncating X at the point a is

$$E_x(y) = \rho\, E_x(x) = \rho \frac{\frac{1}{\sqrt{2\pi}} e^{-\frac{a^2}{2}}}{\int_a^{\infty} \frac{1}{\sqrt{2\pi}} e^{-\frac{x^2}{2}} dx} \quad . \tag{6}$$

The genetic gain of Y upon selection of X can be derived from equation 7, which is the expected genetic (genotypic) value of mature trait in the early selected population

$$\begin{aligned} E_x(G_y) &= r\, E_x(G_x)\ \sigma_{G_y} \\ &= r\, h_x\, E_x(X)\ \sigma_{G_y} \\ &= r\, h_x\, h_y\, E_x(X)\ \sigma_y \\ &= i_x \frac{Cov(G_x\, G_y)}{\sigma_x} \quad , \end{aligned} \tag{7}$$

where $E_x(G_x)$ is the expected mean of genetic value of X in early selection, $E_x(X)$ is

the expected mean of early phenotypic value of the selected population, $cov(G_x, G_y)$ is the genetic covariance of X and Y, and $i_x=E_x(X)$ is the intensity of early selection. This expression for genetic gain is identical to the standard indirect selection gain equation given in Falconer (1981) and has frequently been used in early selection of forest tree species by Nanson (1968, 1976, 1988) and others (Lambeth 1980).

2.3 Comparison of one-stage mature selection with one-stage early selection

The ratio $R_{x,y}$ of genetic gain in Y from indirect selection on X over genetic gain from direct selection on Y was given in Chapter one (equation 5). Two special situations are considered here:

(1) When intensities of early and mature selection are the same, i.e. $i_x = i_y$, the ratio $R_{x,y}$ becomes $(r \bullet h_x)/h_y$ and the necessary condition of equal or greater gain by indirect early selection as stated in Chapter one is

$$r \bullet h_x \geq h_y ;$$

i.e., the product of genetic correlation and square root of early trait heritability is equal to or greater than the square root of mature trait heritability.

(2) When heritabilities of X and Y are the same, i.e. $h_x^2 = h_y^2$, then the gain ratio is $(r \bullet i_x)/i_y$. The necessary condition of equal or greater genetic gain by indirect early selection relative to direct selection requires that i_x to be equal to or greater than i_y/r.

The ratio of i_x to i_y required to achieve identical genetic gain of a mature trait from one-stage of early selection and from one-stage of mature selection, is a

function of the early-mature genetic correlation (r), and the ratio of the heritabilities of the early (h_x^2) and mature (h_y^2) traits (Table 2.1).

2.4 Early and mature two-stage selection

In this approach, selection is allocated in two stages: an early stage (for example in the nursery), followed by further selection in the truncated population at a mature stage. Assume a proportion p(a) is selected with truncation point, a, of early trait X in the early stage, and another proportion p(b | a) with truncation point, b, is selected for mature trait Y in the population remaining after truncation at the early stage. The total proportion selected is p(a)•p(b | a). By the bivariate normal distribution, the total proportion selected can be expressed as

$$p(a) * p(b|a) = p(a\ b:\rho) = \int_a^{\infty}\int_b^{\infty} \frac{1}{2\pi\sqrt{1-\rho^2}} \exp\left[-\frac{1}{2(1-\rho)^2}(x^2-2\rho xy+y^2)\right] dx\ dy\ . \tag{8}$$

From this proportion, the expected phenotypic mean of mature trait Y after two-stage selection has the following estimate (Weiler 1959):

$$E_{xy} = \frac{\left(\frac{1}{\sqrt{2\pi}} e^{-\frac{b^2}{2}} \int_{\frac{(a-\rho b)}{\sqrt{1-\rho^2}}}^{\infty} \frac{1}{\sqrt{2\pi}} e^{-\frac{x^2}{2}} dx + \rho \frac{1}{\sqrt{2\pi}} e^{-\frac{a^2}{2}} \int_{\frac{(b-\rho a)}{\sqrt{1-\rho^2}}}^{\infty} \frac{1}{\sqrt{2\pi}} e^{-\frac{y^2}{2}} dy\right)}{p(a\ b:\rho)}\ . \tag{9}$$

This expected phenotypic mean is a function of the allocation of selection intensities at the early and mature stages.

The genetic (genotypic) gain after two-stage selection will be developed by the following consideration. At the early stage we select a proportion p(a) with corresponding selection intensity i_x and correlated response of mature trait Y, $E_x(G_y)$. This expected genetic gain in Y due to selection on X is

$$E_x(G_y) = i_x \, h_x \, h_y \, r \, \sigma_y \quad . \tag{10}$$

After early selection, phenotypic and genetic variances and heritabilities of X and Y are altered. If the base population is large and early selection intensity is not strong, the early selected population still has a normal distribution. Assuming the altered phenotypic and genetic variances and heritability of Y are $\sigma_y^{2'}$, $\sigma_{G_y}^{2'}$ and $h_y^{2'}$, respectively, the two-stage selection genetic gain $E_{xy}(G_y)$, after a second-stage of mature selection with proportion p(b | a), and corresponding selection intensity i_y', is

$$E_{xy}(G_y) = i_x \, h_x \, h_y \, r \, \sigma_y + i_y' \, h_y^{2'} \, \sigma_y' \quad . \tag{11}$$

To estimate two-stage selection genetic gain $E_{xy}(G_y)$, we must first estimate $\sigma_y^{2'}$ and $h_y^{2'}$. The phenotypic variance of Y ($\sigma_y^{2'}$) after selection on X can be obtained from bivariate normal distribution theory (Cochran 1951, Weiler 1959):

$$\sigma_y^{2'} = (1-\rho^2 \, k) \, \sigma_y^2 \, , \tag{12}$$

where $k = i_x(i_x - a)$. To estimate $h_y^{2'}$, the genetic variance $\sigma_{G_y}^{2'}$ must be first obtained from the early selected population as detailed in Appendix 2.1 and is

$$\sigma_{G_y}^{2'} = (1-r^2 \, h_x^2 \, k) \, \sigma_{G_y}^2 \quad . \tag{13}$$

Thus, $h_y^{2'}$ is

$$h_y^{2'} = h_y^2 \left(\frac{1 - r^2 \, h_x^2 \, k}{1 - \rho^2 \, k} \right) \quad . \tag{14}$$

Genetic gain from two-stage selection can be expressed as

$$E_{xy}(G_y) = \left(i_x \, h_x \, h_y \, r + i_y' \cdot \frac{1 - r^2 \, h_x^2 \, k}{\sqrt{1 - \rho^2 k}} h_y^2 \right) \sigma_y \quad . \tag{15}$$

Therefore, the gain $E_{xy}(G_y)$ of two stage selection can be evaluated by equation 11 or 15. Under the condition that genetic parameters are available for only the base population, one can use equation 15. However, if genetic parameters in the early selected population are also known, one can use equation 11.

Young and Weiler (1961) derived another form of selection response in two correlated traits by independent culling. Their selection response is

$$\begin{aligned} E_{xy}(G_y) = & \left(\frac{h_{xy} - \rho \, h_y^2}{1 - \rho^2} \, i_x + \frac{h_y^2 - \rho \, h_{xy}}{1 - \rho^2} \, i_y \right) \sigma_y \\ & - \left[(i_x - \rho \, i_y) \frac{r \, h_x \, h_y}{1 - \rho^2} + (i_y - \rho \, i_x) \frac{h_y^2}{1 - \rho^2} \right] \sigma_y \, , \end{aligned} \tag{16}$$

where

$$h_{xy} = \frac{Cov(G_x \, G_y)}{\sigma_x \, \sigma_y} = r \, h_x \, h_y \quad . \tag{17}$$

Equation 16 collapses into equation 5 when only a single stage of selection on the mature trait is assumed (i.e. $i_x = 0$) since in this case, the early trait has no effect on expected genetic gain in the mature trait (so ρ must equal zero). Thus, gain after two-stages of selection can also be estimated from equation 16, but i_y is the selection intensity of the mature trait in the base population. This is different from i_y' in

equations 11 and 15, which is the selection intensity of the mature trait in the population after truncation due to early selection. The i_y' can be estimated as

$$i_y' = \frac{\int_b^{\infty} y \frac{1}{2\pi\sqrt{1-\rho^2 k}} \exp\left[-\frac{(y-\rho\, i_x)^2}{2(1-\rho^2 k)}\right] dy}{p(b \mid a)} \qquad (18)$$

or approximated by the univariate selection intensity if we know the selection proportion in the mature stage ($p(b \mid a)$). When the mature trait in the population after truncation due to early selection is still normally distributed, the approximation is exact.

Equations 15 and 16 can be used to study the effect of different allocations of early and mature selection intensities on genetic gain of a mature trait. Only equation 16 will be used here because the relationship of i_x and i_y with the corresponding truncation points a and b in the base bivariate normal population are well documented in Pearson's table (1931) and Weiler's charts (1959) and Williams and Weiler's charts (1964).

Different allocations of selection intensities in two-stage selection will result in different genetic gain, but for each set of parameters ($r\ \rho\ h_x\ h_y$) in the base population, there will be only one globally optimal allocation of selection intensities. This optimal allocation can be evaluated by maximizing $E_{xy}(G_y)$.

To derive the optimal two-stage selection intensity allocation, the genetic gain in equation 16 is rewritten as

$$E_{xy}(G_y) = \frac{h_y^2}{p(a\ b:\rho)}\left[r\cdot\frac{h_x}{h_y}\ Z(a)\ Q(A)+Z(b)\ Q(B)\right]\sigma_y - \frac{h_y^2}{p(a\ b:\rho)}\ f(a,b)\ \sigma_y\ , \tag{19}$$

where Z(a) and Z(b) are the coordinates of the standardized normal curve corresponding to abscissas, a and b, respectively; $A=(b-\rho a)/\sqrt{(1-\rho^2)}$; $B=(a-\rho b)/\sqrt{(1-\rho^2)}$; $Q(A)=p(A\ -\infty:\rho)$; $Q(B)=p(-\infty\ B:\rho)$ and

$$f(a,b) = r\cdot\frac{h_x}{h_y}\ Z(a)\ Q(A)+Z(b)\ Q(B)\quad . \tag{20}$$

Maximizing $E_{xy}(G_y)$ is equivalent to maximizing function f(a,b) under condition p(a b:ρ). With expansion of function f(a,b), we have

$$f(a,b) = r\cdot\frac{h_x}{h_y}e^{-\frac{a^2}{2}}\frac{1}{\sqrt{2\pi}}\int_{\frac{b-\rho a}{\sqrt{1-\rho^2}}}^{\infty}\frac{1}{\sqrt{2\pi}}e^{-\frac{x^2}{2}}dx + e^{-\frac{b^2}{2}}\frac{1}{\sqrt{2\pi}}\int_{\frac{a-\rho b}{\sqrt{1-\rho^2}}}^{\infty}\frac{1}{\sqrt{2\pi}}e^{-\frac{y^2}{2}}dy\quad . \tag{21}$$

Thus, the optimal selection truncation points a and b or equivalent selection intensities i_x and i_y can be estimated by differentiating f(a,b) with corresponding a and b under condition p(a b:ρ) and solving the differential equations. Unfortunately, explicit solutions of these differential equations do not exit. Thus numerical methods should be applied to estimate optimal selection intensity allocation under different sets of genetic parameters. As an example, the optimal truncation points for a 5% final selection proportion in a population with phenotypic and genetic correlation $\rho=r=0.5$ and heritabilities of early and mature traits of 0.6 and 0.3, respectively, are 1.36 for early and 0.7 for mature traits. These translate into a selection intensities

of 1.82 and 1.29, respectively.

Precise estimation of optimal selection intensity requires numerical integration of the multivariate normal distribution. Numerous computer programs have been developed to estimate general optimal independent culling levels in animal breeding based on such an algorithm (Schervish 1984), or by using other approximate methods (Baxton 1989, Xu and Muir 1991a and 1991b). These programs can be adapted to estimate early and mature optimal selection allocations in tree selection.

2.5 Application of two-stage selection

Many authors have contended that one of the major advantages of early selection prior to long-term progeny testing is that more individuals can be screened relative to long-term progeny testing alone, and consequently, expected genetic gain may be greater (Lambeth 1980, Riiter and Perry 1988, Adams, et al. 1989). Yet, quantitative genetic methods have not been developed to evaluate this claim of greater expected genetic gain. Methods to do this based on two-stage selection theory are presented below.

We assume test size at the mature stage is the same with or without early testing and the final number of selected individuals is n after both selection schemes. Consider the situation that the total base population size is N with early selection, and after first stage early selection, M individuals are selected and subjected to long term testing. Thus, the final selection proportion is

$$p_{xy}=\frac{n}{N}=\frac{M}{N}\times\frac{n}{M}=p(a)\ P(b\mid a)\ , \qquad (22)$$

and with corresponding selection intensities i_x and i_y'. In one stage mature selection, M individuals are tested and n individuals selected. The selection proportion in this case is

$$p_y=\frac{n}{M}=p(b')=p(b\mid a)\ , \qquad (23)$$

thus, $i_y=i_y$'.

Using equations 5 and 15, the ratio of genetic gain of two-stage early plus mature selection to mature stage selection only is

$$R_{xy.y}=\frac{E_{xy}(G_y)}{E_y(G_y)}=\frac{i_x}{i_y}\ \frac{h_x}{h_y}\ r+\frac{1-r^2\ h_x^2\ k}{\sqrt{1-\rho^2 k}}\ . \qquad (24)$$

The first part of equation 24 is the ratio of indirect genetic gain due to early selection only under two-stage selection to direct gain under one-stage mature selection. With different genetic parameters and selection intensities, the advantage of early plus mature stage selection to mature selection only can be evaluated. Here, we consider the following conditions:

(1) $\rho = r \cdot h_x$. This is an example where the phenotypic correlation (ρ) is less than the genetic correlation (r) when heritability of early traits is less than unity. The condition of $\rho < r$ is common for correlations between early and mature traits (see point 3 of page 14).

Under this condition, the genetic gain ratio is

$$R_{xy.y} = \frac{i_x}{i_y} \frac{h_x}{h_y} r + \sqrt{1-\rho^2 k} \quad . \qquad (25)$$

By definition, k is always less than unity because $k=i_x(i_x - a)$. When ρ is small (say $\rho<0.5$), the second term, $\sqrt{(1-\rho^2 k)}$ approximates unity such that the genetic gain ratio is

$$R_{xy.y} \approx 1 + \frac{i_x}{i_y} \frac{h_x}{h_y} r \quad . \qquad (26)$$

Thus, the increase in genetic gain with two-stage selection over one-stage mature selection only is approximated by the proportion, $(i_x \cdot h_x \cdot r)/(i_y \cdot h_y)$. The values of the second term $\sqrt{(1-\rho^2 k)}$ when $\rho=0.5$, for example, depend on the early selection proportion (intensity), but most are above 0.90 (Table 2.2).

(2) $i_x = i_y$ and $h_x \cdot r = h_y$. In this example, selection intensities of the early and mature traits are identical and heritability of the early trait is greater than heritability of the mature trait when the genetic correlation is less than unity.

Under these conditions, the genetic gain ratio is

$$R_{xy.y} = 1 + \frac{1-r^2 h_x^2 k}{\sqrt{1-\rho^2 k}} \quad , \qquad (27)$$

and the increase of genetic gain under two-stage selection over one-stage mature selection is the proportion, $(1-r^2 h_x^2 k)/\sqrt{(1-\rho^2 k)}$.

(3) Both conditions 1 and 2 above are met.

The genetic gain ratio is $R_{xy.y}=1+\sqrt{(1-\rho^2 k)}$ and the genetic gain under two-stage selection over one-stage mature selection is significantly greater than that in

conditions (1) and (2) above. Some ratios are calculated in Table 2.3. In most cases, genetic gain with two-stages of selection is almost twice compared to genetic gain without early selection.

Equations 15 and 16 can also be used to address the following additional questions regarding gains from two-stage selection: (1) are there conditions when any selection at the early stage will result in less gain than if all selection is at the mature stage only; (2) under what conditions is there more gain when both early and mature selection are practised than when selection is practised at the mature stage only; (3) under what conditions can two-stage selection be used to reduce the size of field testing without any loss in ultimate gains for the mature trait. The necessary relationships among the parameters which satisfy the conditions in question 1 are:

$$E_{xy}(G_y) < i_y h_y^2 \sigma_y \qquad (28)$$

Substituting equation 15 into 28,

$$i_x h_x r + i_y' \cdot \frac{1-r^2 h_x^2 k}{\sqrt{1-\rho^2 k}} h_y < i_y h_y. \qquad (29)$$

The necessary relationships among the parameters which satisfy the conditions in question 2 are:

$$i_x h_x r + i_y' \cdot \frac{1-r^2 h_x^2 k}{\sqrt{1-\rho^2 k}} h_y > i_y h_y. \qquad (30)$$

The answer to the third question can be found by setting the left term in equation (30) equal to the right term.

2.6 Index selection

Previous discussion of early selection has been limited to a single early trait. However, early selection can be applied to several traits simultaneously and they can form an index to predict mature performance. In another way, early traits can serve as additional information for the prediction of mature genetic value.

Theory of standard index selection is well established in the literature (Henderson 1963, Lin 1978, Bulmer 1980, Wrick and Weber 1986). Two papers have described the application of selection indices to early forest tree selection (Burdon 1988, White and Hodge 1991). All of the standard selection index theory applicable to direct selection also applies to indirect selection (White and Hodge 1991). Thus, there is no special need to restate the theory of indirect index selection. However, some special properties and application of this theory to early selection will be examined for forest trees.

2.6.1 Selection of a single mature trait with the aid of early traits

An index for mature selection which includes early traits has the form

$$I = aY + b_1X_1 + b_2X_2 + \ldots + b_pX_p \quad , \qquad (31)$$

where Y is the mature trait, X_1, X_2, ... X_p are early traits and a, b_1, ... b_p are index coefficients of the mature trait and early traits, respectively. This index, I, is a single predictor of mature genotypic value (or breeding value). Selection index theory indicates that the coefficient vector (a, b_1, b_2, ... b_p) in an index is the vector of partial

regression coefficients (Cochran 1951) and is estimated as

$$\boldsymbol{b}=\boldsymbol{P}^{-1}\boldsymbol{G} \quad , \tag{32}$$

where $\mathbf{b}'=(a, b_1, b_2, \ldots b_p)$, **P** is a p+1 order symmetric matrix of estimated phenotypic variances, and covariances in the p+1 traits of Y, X_1, X_2, ... X_p as:

$$\boldsymbol{P}=\begin{bmatrix} \sigma^2_y & cov(y\ x_1) & \cdots & cov(y\ x_p) \\ cov(x_1\ y) & \sigma^2_{x_1} & \cdots & cov(x_1\ x_p) \\ \cdots & & & \\ cov(x_p\ y) & cov(x_p\ x_1) & \cdots & \sigma^2_{x_p} \end{bmatrix} \quad , \tag{33}$$

and **G** is a p+1 order vector of estimated genetic variances of Y and covariances of Y with X as:

$$\boldsymbol{G}=[\sigma^2_{G_y}\ cov(G_y\ G_{x_1})\ cov(G_y\ G_{x_2}) \ldots cov(G_y\ G_{x_p})] \quad , \tag{34}$$

The expected response to selection based on index (I) is predicted by the equation (Falconer 1981 and Henderson 1984):

$$R_I=i_I\ \sigma_{G_y}\ r_{G_y.I} \quad , \tag{35}$$

where i_I is standardized selection differential of I, and r_{G_yI} is the correlation between the genotypic value for Y and the index value. We can study the genetic gain ratio between index selection and mature selection by comparing the expected response of this index selection to the expected response of direct mature selection under the same selection intensity. This ratio is

$$R_{I.Y}=\frac{r_{G_y.I}}{h_y}=\frac{[b'G]\,\sigma_y}{\sqrt{[b'Pb]}\,\sigma^2_{G_y}}=\frac{\sigma_I\,\sigma_y}{\sigma^2_{G_y}}=\frac{\sqrt{[b'G]}}{\sigma_{G_y}\,h_y}\quad , \tag{36}$$

where σ_I is the standard error of I. From equation 36, the relative efficiency of index selection can be judged. Whether or not an early traits should be included in the index can be determined by the value of R_{LY}.

One special case is when only one early trait is included in index (I). The index coefficient vector b'=[a b] and its estimator is

$$\begin{bmatrix}a\\b\end{bmatrix}=\frac{1}{\sigma^2_x\,\sigma^2_y-\sigma^2_{xy}}\begin{bmatrix}\sigma^2_x\,\sigma^2_{G_y}-\sigma_{xy}\,\sigma_{G_x.G_y}\\ \sigma^2_y\,\sigma_{G_x.G_y}-\sigma_{xy}\,\sigma^2_{G_y}\end{bmatrix}\quad , \tag{37}$$

where $\sigma_{G_xG_y}$ are covariances between genetic values of early and mature traits. Thus, the efficiency ratio between this special index selection and mature-trait selection alone is

$$R_{I.y}=\sqrt{\frac{\sigma^2_x\,\sigma^2_{G_y}-\sigma_{xy}\,\sigma_{G_x.G_y}+\frac{(\sigma^2_y\,\sigma^2_{G_x.G_y}-\sigma_{xy}\,\sigma^2_{G_y}\,\sigma_{G_x.G_y})}{\sigma^2_{G_y}}}{(\sigma^2_x\,\sigma^2_y-\sigma^2_{xy})\,h^2_y}}\quad , \tag{38}$$

which can be simplified to

$$\begin{aligned}R_{I.y}&=\sqrt{\frac{1-2\rho\;r\;\frac{h_x}{h_y}+r^2\frac{h^2_x}{h^2_y}}{1-\rho^2}}\\ &=\sqrt{1+\frac{(\rho-r\frac{h_x}{h_y})^2}{1-\rho^2}}\quad .\end{aligned} \tag{39}$$

Since $-1 \le \rho \le 1$, the term

$$\frac{(\rho - r\,\frac{h_x}{h_y})^2}{1-\rho^2} \qquad (40)$$

will always be positive. Thus, R_{Ly} is always greater or equal to unity. This suggests the inclusion of early trait information into mature trait will result in greater genetic gain relative to selection based on mature trait alone. As a numerical example, conditions for R_{Ly} to be $\sqrt{2}$ or greater are:

(1) When $r=\rho$, (which indicates genetic correlation is equal to phenotypic correlation), heritabilities of early and mature traits must satisfy:

$$h_x > h_y\left(1+\sqrt{\frac{1-\rho^2}{\rho^2}}\right) \quad or$$
$$h_x < h_y\left(1-\sqrt{\frac{1-\rho^2}{\rho^2}}\right) \quad . \qquad (41)$$

(2) When $h_x=h_y$, (which indicates heritabilities are equal for early and mature traits), the genetic correlation (r) and phenotypic correlation (ρ) must satisfy:

$$r > \rho+\sqrt{1-\rho^2} \quad or$$
$$r < \rho-\sqrt{1-\rho^2} \quad . \qquad (42)$$

2.6.2 Indirect early index

Multiple early traits can be used to form an index for early selection to maximize genetic gain in one or more mature traits. This is the Binet type of index (Binet 1965) for indirect selection. If the genetic correlation between the mature trait

and this early index is greater than with individual early traits, the expected genetic gain in the mature trait is greater by this early index approach than early selection based on any single trait alone. This index has the form

$$I = b_1X_1 + b_2X_2 + \cdots + b_pX_p \quad . \tag{43}$$

If genetic correlations or covariances between the mature trait and early traits are known, the optimal index coefficient vector $\mathbf{b}' = (b_1\ b_2 \cdots b_p)$ is estimated as (Lin 1978)

$$\boldsymbol{b} = \boldsymbol{P}^{-1}\ \boldsymbol{G} \tag{44}$$

with

$$\boldsymbol{P} = \begin{bmatrix} \sigma^2_{x_1} & \sigma_{x_1 \cdot x_2} & \cdots & \sigma_{x_1 \cdot x_p} \\ \sigma_{x_1 \cdot x_2} & \sigma^2_{x_2} & \cdots & \sigma_{x_2 \cdot x_p} \\ \cdots & & & \\ \sigma_{x_p \cdot x_1} & \sigma_{x_p \cdot x_2} & \cdots & \sigma^2_{x_p} \end{bmatrix} \tag{45}$$

and

$$\boldsymbol{G} = [\sigma_{G_y \cdot G_{x_1}}\ \sigma_{G_y \cdot G_{x_2}} \cdots \sigma_{G_y \cdot G_{x_p}}] \quad . \tag{4}$$

The expected response of the mature trait upon selection based on the early i. value is

$$
\begin{aligned}
E_I(G_y) &= i_I \, r_{I.G_y} \, \sigma_{G_y} \\
&= i_I \, \frac{Cov(I\ G_y)}{\sigma_I \, \sigma_{G_y}} \sigma_{G_y} \\
&= i_I \, \sigma_I \\
&= i_I \, \frac{\boldsymbol{b'G}}{\sqrt{\boldsymbol{b'Pb}}} \quad .
\end{aligned}
\tag{47}
$$

To compare the efficiency of the early index selection with individual early trait selection, the genetic gain from early selection of a single early trait is modified from equation (7) to

$$E_x(G_y) = i_x \, \rho_{x.G_y} \, \sigma_{G_y} \tag{48}$$

where ρ_{xG_y} is the correlation of phenotypic value of early trait X with the genetic value of mature trait, Y. Thus, under the same selection intensity, the gain ratio of early index selection to single early trait selection is

$$R_{I.x} = \frac{r_{I.G_y}}{\rho_{x.G_y}} \quad . \tag{49}$$

This shows that when the correlation of the early index and mature genetic values is greater than the correlation of a single early trait and mature genetic values, early index selection is more efficient.

Now let us look at the effectiveness of early selection when a second early trait X_2 is added to the early trait X_1. The correlation of each early trait with the genetic value of the mature trait can be written as

$$\rho_{x_i \cdot G_y} = r_{x_i \cdot y} \, h_{x_i} \quad \text{and}$$

$$r_{I \cdot G_y} = \frac{\sqrt{b'Gb}}{\sigma_{G_y}} \,, \tag{50}$$

where $r_{x_i y}$ is the genetic correlation between early trait X_i and mature trait Y. By expansion as in section 2.6.1, the ratio of genetic gain due to the addition of X_2 to X_1 is

$$R_{I \cdot x_1} = \frac{r_{I \cdot G_y}}{\rho_{x_1 \cdot G_y}} = \sqrt{1 + \frac{\left(\rho_{x_1 \cdot x_2} - \frac{\rho_{x_2 \cdot G_y}}{\rho_{x_1 \cdot G_y}}\right)^2}{1 - \rho^2_{x_1 \cdot x_2}}} \,, \tag{51}$$

where $\rho_{x_1 \cdot G_y}$ and $\rho_{x_2 \cdot G_y}$ are correlations of phenotypic values for X_1 and X_2, respectively, with the genetic value of mature trait Y. In theory, inclusion of an additional early trait increases the expected genetic gain of the mature trait because the second term in equation 51 is always greater than or equal to zero when $|\rho_{x_1 x_2}| \leq 1$.

When applying early index selection or combined index selection of mature and early traits, if one only considers genetic gain, inclusion of additional early traits will, in theory, always incur more genetic gain. In practice, however, genetic correlation, genetic variance and heritability used to build the index are estimators, not the true population parameters. They have large standard errors (Harris 1963, 1964, Nordskog 1978) and often result in inconsistent estimates of the variance-covariance matrix (Hayes and Hill 1981). Thus, standard error of selection index will dramatically increase when more early traits are added into the index and to a certain degree will outweigh the increase of genetic gain (Williams 1962a, 1962b, Sale and

Hill 1976).

3. MULTI-GENERATION RESULTS OF EARLY SELECTION

So far, we have only dealt with the results from one generation of early selection. However, within a conventional breeding cycle, say, of twenty-five years, one option is to have several selective breeding cycles based solely on results from early tests. Thus, genetic gain due to early selection over several generations must be considered. Currently, no theory has been developed to estimate genetic gain of correlated traits for multi-generation selection. The study of the genetic consequences of several generations of selection on correlated traits (early selection is a special case) is important to the theory of indirect selection and evolution. It is also important in breeding programs for evaluating total genetic gain of correlated traits, especially for economic and feasibility analysis of early selection.

If a conventional breeding cycle takes T_M years with selection age, S_M, and breeding time, B_M, then $T_M=S_M+B_M$. In early selection and breeding, breeding cycle T_J has early selection age, S_J, and breeding time, B_J, such that $T_J=S_J+B_J$. The selection age S_M is much greater than S_J. However, breeding time B_J may or may not take longer than B_M. If a tree at age S_J cannot be induced to reproduce, then $B_J>B_M$ (Lambeth 1980 and Lowe 1988). Age difference between early and mature selection is often much greater than the time required to induce flowering after early selection. Thus, when $T_M>>T_J$, there are t breeding cycles within one conventional breeding

cycle T_M, with

$$c = \frac{T_M}{T_J} \quad . \tag{52}$$

The question that must be addressed is the total genetic gain of correlated mature trait Y after t generations of selection on early trait X. This total genetic gain of Y after t generations of early selection on X can be used to assess early selection by comparing it with the genetic gain of direct selection on Y in the same time framework. The total genetic gain of multiple-generation selection in either X or Y is not a simple multiplicity of the gain estimated for a single generation. As noted earlier, selection alters genetic parameters. Bulmer (1971) studied the effect of multiple-generations of direct selection on genetic variances and gain. Under the assumption that there is an effectively infinite number of unlinked loci controlling the trait under direct selection, change in genetic variance is due to correlation between pairs of loci, i.e. joint linkage disequilibrium. This correlation leads to a reduction in the genetic variance under directional selection (such as early selection). Thus, genetic gain would be reduced in the next generation of selection. Under continuing direct selection, contribution of linkage disequilibrium to the genetic variance would rapidly reach a limiting value. Correspondingly, reduction of response to selection would also reach a limiting value. When selection ceases and the population mates at random, the correlation rapidly disappears as the joint equilibrium at pairs of loci is reestablished and variance returns to its original value. Therefore, selection would not change gene frequency and would not cause any permanent change of genetic

variance. Under finite numbers of gene loci, however, selection changes gene frequency and causes permanent change in genetic variance. The simulation results of Bulmer (1976) indicate that for a trait under direct selection and controlled by twelve gene loci, gene frequencies change and go to fixation under intensive multi-generation direct selection. However, simulated results also showed that the effect of joint linkage disequilibrium is more important than the slower and less dramatic effect caused by changes in gene frequencies. In addition, simulated results indicated that changes of genetic variance due to selection under finite gene loci was in good agreement with predicted on theoretical grounds under infinite gene loci in the first several generations (Bulmer 1976).

Selection affects not only phenotypic and genetic variances of traits under direct selection (early trait), but also the phenotypic and genetic variances of correlated traits (mature trait) and their phenotypic and genetic correlations with the directly selected traits (Bohren, Hill and Robertson 1965, Sheridan and Barker 1974a, 1974b). To study genetic variances and genetic gain of a correlated trait under continuing directional selection, we need to derive the theory which predicts these changes.

3.1 Theoretical results of multiple generation indirect selection on genetic parameters and genetic gain

The phenotypic and genetic variances of the correlated mature trait in the

base population after truncation selection at the early-stage are given in equations 12 and 13. For multiple generations, the notation should be different; with the base population now referred to as generation 0 and equations 12 and 13 rewritten as

$$\sigma_y^{2'}(0) = [1-\rho^2(0)\,k]\,\sigma_y^2(0) \qquad \textit{and}$$
$$\sigma_{G_y}^{2'}(0) = [1-r^2(0)\,h_x^2(0)\,k]\,\sigma_{G_y}^2(0) \quad , \tag{53}$$

where $\sigma_{G_y}^2(0)$ and $\sigma_y^2(0)$ are the base (0) population genetic and phenotypic variances, respectively; $\sigma_{G_y}^{2'}(0)$ and $\sigma_y^{2'}(0)$ are genetic and phenotypic variances, respectively, after early selection in the base population; $\rho(0)$, $r(0)$ and $h_x^2(0)$ are phenotypic and genetic correlations and the heritability of the early trait before early selection in the base population, respectively. Only additive genetic variance and covariance are considered for a random mating population. Before deriving the result for correlated traits, let us first look at the results for directly selected traits.

The effect of early-trait direct selection on phenotypic variance was derived by Cochran (1951) and Weiler (1959):

$$\sigma_x^{2'}(0) = (1-k)\,\sigma_x^2(0) \quad , \tag{54}$$

and the direct selection effect on genetic variance was given by Robertson (1976)

$$\sigma_{G_x}^{2'}(0) = [1-k\,h_x^2(0)]\,\sigma_{G_x}^2(0) \quad . \tag{55}$$

The genetic covariance between the early and mature traits after early-stage selection can be derived in the same manner as in Appendix 2.1:

$$cov'(G_x(0)\ G_y(0)) = cov(G_x(0)\ G_y(0))\,[1-h_x^2(0)\,k] \quad . \qquad (56)$$

Similarly, the phenotypic covariance is

$$cov'(X(0)\ Y(0)) = cov(X(0)\ Y(0))\,(1-k) \quad . \qquad (57)$$

If mating in the truncated population is assumed to be at random, and the environmental variance does not change, the genetic and phenotypic variances of the directly selected trait (early trait X) in the next generation are (Bulmer 1980):

$$\sigma^2_{G_x}(1) = \frac{1}{2}\,[1-h_x^2(0)\,k]\,\sigma^2_{G_x}(0) + \frac{1}{2}\sigma^2_{G_x}(0) - \sigma^2_{G_x}(0)\,[1-\frac{1}{2}h_x^2(0)\,k] \quad , \qquad (58)$$

and

$$\sigma^2_x(1) = \sigma^2_x(0) - \frac{1}{2}h_x^4(0)\,k\ \sigma^2_x(0) - \sigma^2_x(0)\,[1-\frac{1}{2}h_x^4(0)\,k] \quad . \qquad (59)$$

Thus, heritability in generation one is

$$h_x^2(1) = h_x^2(0) \cdot \frac{1-\frac{1}{2}h_x^2(0)\,k}{1-\frac{1}{2}h_x^4(0)\,k} \quad . \qquad (60)$$

Using some of the above results, Bulmer (1971) derived a recurrent relationship for the mean and variance of a directly selected trait under continuing truncation selection, with the same selection intensity each generation. Bulmer's results showed after n generations of selection, the genetic variance is

$$\sigma^2_{G_x}(n) = \sigma^2_{G_x}(0) - D_x(n) \quad , \tag{61}$$

and phenotypic variance is

$$\sigma^2_x(n) = \sigma^2_x(0) - D_x(n) \quad , \tag{62}$$

where

$$D_x(n) = \frac{k}{2} h^2_x(n-1)\,\sigma_{G_x}(n-1) + \frac{k}{4} h^2_x(n-2)\,\sigma^2_{G_x}(n-2) + \cdots + \frac{k}{2^n} h^2_x(0)\,\sigma^2_{G_x}(0) \quad . \tag{63}$$

Under Fisher's infinitesimal genetic model (Fisher 1918), the genetic variance of the directly selected trait X will decline under continuing selection and rapidly reach a limiting value. The limiting value is

$$\sigma^2_{G_x}(n) = \sigma^2_{G_x}(0) - D_x(\infty) \quad , \tag{64}$$

with

$$D_x(\infty) = \frac{\sigma^2_x(0)\{2kh^2_x(0) + 1 + [1 + 4kh^2_x(0)\,(1 - h^2_x(0))]^{\frac{1}{2}}\}}{2(1+k)} \quad . \tag{65}$$

Correspondingly, the expected selection response declines in the first few generations and then becomes stable (Bulmer 1971).

To derive the genetic variance and selection response of the correlated mature trait, we assume that the genetic values of the early and mature traits are distributed as a bivariate normal distribution in the base population, and thus, have a linear regression relationship

$$G_y(0) = a\ G_x(0) + E_y(0) \quad . \tag{66}$$

After early stage selection in the base population the genetic variance of correlated mature trait, Y, is given in the equation 58. Under random mating, correlated genetic variance of the mature trait in the next generation is reduced to the following (see Appendix 2.2)

$$\begin{aligned} \sigma^2_{G_y}(1) = &\frac{1}{2}\left[1 - h^2_x(0)\, k\, r^2(0)\right]\sigma^2_{G_y}(0) + \frac{1}{2}\sigma^2_{G_y}(0) \\ &- \sigma^2_{G_y}(0)\left[1 - \frac{1}{2}h^2_x(0)\, k\, r^2(0)\right] \quad . \end{aligned} \tag{67}$$

If we assume the same linear regression of early and mature genetic values still exist in the next generation under random mating, the covariance of two genetic values in the next generation is

$$cov(G_y(1)\ G_x(1)) = \frac{cov(G_y(0)\ G_x(0))}{\sigma^2_{G_x}(0)}\sigma^2_{G_x}(1) \quad , \tag{68}$$

and correspondingly the genetic correlation is

$$r(1) = r(0)\sqrt{\frac{1 - \frac{1}{2}h^2_x(0)\, k}{1 - \frac{1}{2}h^2_x(0)\, k\, r^2(0)}} \quad . \tag{69}$$

Under random mating and constant environmental variance, the correlated phenotypic variation of mature trait, Y, in the next generation is (see Appendix 2.3)

$$\begin{aligned} \sigma^2_y(1) = &\frac{1}{2}\left[1 - h^2_x(0)\, h^2_y(0)\, k\, r^2(0)\right]\sigma^2_y(0) + \frac{1}{2}\sigma^2_y(0) \\ &- \sigma^2_y(0) - \frac{1}{2}h^2_x(0)\, k\, r^2(0)\, \sigma^2_{G_y}(0) \quad . \end{aligned} \tag{70}$$

Thus, the theoretical responses of both directly selected and correlated traits when selection is practised in the next generation (generation one) can be derived as follows:

(1) Direct selection response of selection for X

$$E_x(G_x)(1) = i_x(1)\, h_x(1)\, \sigma_{G_x}(1)$$

$$= E_x(G_x)(0)\frac{1-\frac{1}{2}h_x^2(0)\,k}{\sqrt{1-\frac{1}{2}h_x^4(0)\,k}} \qquad (71)$$

if selection intensity is the same as in the previous generation $i_x(0)$.

(2) Direct selection response of selection for Y

$$E_y(G_y)(1) = i_y(1)\, h_y(1)\, \sigma_{G_y}(1)$$

$$= E_y(G_y)(0)\frac{1-\frac{1}{2}h_x^2(0)\,kr^2(0)}{\sqrt{1-\frac{1}{2}h_x^2(0)\,h_y^2(0)\,kr^2(0)}} \qquad (72)$$

(3) Correlated selection response on Y of selection f - X

$$E_x(G_y)(1) = i_x(1)\, h_x(1)\, h_y(1)\, r\,)\, \sigma_y(1)$$

$$= E_x(G_y)(0)\frac{1-\frac{1}{2}h_x^2(0)\,k}{\sqrt{1-\frac{1}{2}h_x^4(0)\,k}} \qquad (73)$$

It is apparent that $E_x(G_y)(1) < E_x(G_y)(0)$ for $h_x^2 \leq 1$. This suggests that the correlated response of a mature trait due to selection of a early trait will decline after each consecutive generation of selection.

For n generations of early selection, the correlated genetic variance and phenotypic variance of Y and the genetic correlation between X and Y can be derived in the same manner if it is assumed that selection does not change the regression relationship of the mature genetic value on the early genetic value. This assumption is justified if the number of loci controlling the early and mature traits is effectively infinite. Genetic variance of the correlated trait after n generations of selection is deduced as (see Appendix 2.4)

$$\sigma^2_{G_y}(n) = \sigma^2_{G_y}(0) - D_y(n) \quad , \tag{74}$$

where $D_y(n)$ is the reduction of genetic variance on the correlated mature trait Y with

$$\begin{aligned} D_y(n) = {} & r^2(n-1)\,\frac{k}{2}h_x^2(n-1)\,\sigma^2_{G_y}(n-1) + r^2(n-2)\,\frac{k}{4}h_x^2(n-2)\,\sigma^2_{G_y}(n-2) \\ & + \cdots + r^2(0)\,\frac{k}{2^n}h_x^2(0)\,\sigma^2_{G_y}(0) \\ & - \sum_{i=0}^{n-1} r^2(i)\,\frac{k}{2^{n-i}}h_x^2(i)\,\sigma^2_{G_y}(i) \quad . \end{aligned}$$

Similarly, the genetic correlation after n generations of early selection is

$$r(n) = r(0)\sqrt{\frac{1-\dfrac{D_x(n)}{\sigma^2_{G_x}(0)}}{1-\dfrac{D_y(n)}{\sigma^2_{G_y}(0)}}} \tag{76}$$

and the phenotypic variance is

$$\sigma^2_y(n) = \sigma^2_y(0) - D_y(n) \quad . \tag{77}$$

Thus, the correlated gain in the mature trait after n generations of early selection is

$$E_x(G_y)\ (n) = E_x(G_y)\ (0)\ \frac{1-\frac{D_x(n)}{\sigma^2_{G_x}(0)}}{\sqrt{1-\frac{D_x(n)}{\sigma^2_x(0)}}} \quad . \qquad (78)$$

It is noted that the correlated selection response in Y after n-generations of early selection is a function of the reduced genetic variance ($D_x(n)$) in the directly selected trait, X, but also a function of the reduced genetic variance ($D_y(n)$) in the correlated trait, Y (as showed in equation 79). The correlated response to selection declines as the quantity in the denominator of equation 78 is always greater than the numerator. This is similar to the response to direct selection. After several generations of early selection, response to correlated selection will reach a limiting value. Using the full ancestral covariance structure from Tallis (1987), the reduction in the genetic variance of the mature trait after n-generations of early selection is derived here as

$$D_y(n) = \frac{cov^2(G_x(0)\ G_y(0))}{\sigma^4_{G_x}(0)} D_x(n) \quad . \qquad (79)$$

This equation also shows the relationship between reductions in genetic variances of directly selected and correlated traits. By this result, the limiting value of the genetic variance reduction in the correlated trait, Y is derived here as

$$D_y(\infty) = \frac{r^2(0)\, h^2_x(0)\, \sigma^2_y(0)}{h^2_y(0)\, \sigma^2_x(0)} D_x(\infty) \qquad (80)$$

and correspondingly, the limiting value of selection response of Y can be estimated by

$$E_x(G_y)\ (\infty) - E_x(G_y)\ (0)\ \frac{1-\frac{D_x(\infty)}{\sigma^2_{G_x}(0)}}{\sqrt{1-\frac{D_x(\infty)}{\sigma^2_x(0)}}} \quad . \qquad (81)$$

Several conclusions can be drawn from the above derivation of multi-generation theory of indirect selection:

(1) The genetic correlation will decline after each generation of selection, but will never change sign. Under this infinite locus model, when generation n approaches infinity, the genetic correlation (r) approaches a limiting value.

(2) Genetic variances of the directly selected and correlated traits decline after each generation of selection. Comparing $D_x(n)$ with $D_y(n)$, it is apparent that reduction in genetic variance of a correlated trait will be slower than the reduction of genetic variance of a selected trait, because $r^2 \leq 1$.

(3) Selection responses of directly selected and correlated traits decline after each consecutive generation of selection and soon approach a limiting value. The decline of selection response in the correlated trait will be slower than the decline in selection response for trait X.

(4) In reality, the effective number of loci for direct and correlated traits is limited. Thus, the reduction of genetic variances and selection responses in the direct trait and correlated trait will be larger than predicted under effective infinite loci model because gene frequency will change under the finite locus model. However, one can still regard the theoretical prediction of selection response over several generations of selection as an upper limit of the actual selection response.

3.2 Numerical example

Bulmer's numerical example of the effect of direct selection (1976) can be extended to correlated genetic gain. Assume 20% of the population is selected through early selection each generation. Thus, the intensity of selection is f(a)/p, where p=20%, a is the standard normal deviate corresponding to p, and f(a) is the standard normal density function at a. Thus, a=0.8416, f(a)=0.2800, and i_x=1.400 with k=0.7818. We further assume in the base population $h_x^2(0)=h_y^2(0)=0.5$, $\sigma_{G_x}^2(0)=\sigma_{G_y}^2(0)=50$, $\sigma_x^2(0)=\sigma_y^2(0)=100$, and r(0)=0.5. Reduction of genetic variance ($D_y(n)$) of the correlated trait Y, phenotypic variance and heritability of the correlated trait, genetic correlation, and correlated selection response in the first four generations are shown in Table 2.4. The response to correlated selection declines in each consecutive generation of selection, but soon reaches a limiting value at 2.004.

The above theory and numerical example of indirect selection are derived under assumptions of infinite population size and infinite number of gene loci. However, selection programs in practice have finite population sizes and numbers of gene loci. Therefore, random drift due to finite population size and gene frequency change due to finite number of gene loci will play important roles in genetic response under continuing selection. The limit theory of direct selection with finite number of gene loci has been developed by Robertson (1960) and Hill (1969). Long-term experiments in maize (Dudley 1977), *Drosophila* (Yoo 1980) and *Tribolium* (Enfield 1980), showed genetic responses after 75, 76 and 120 generations of selection,

respectively. Hill (1982a, 1982b, 1987) regarded these continuing responses as the result of new mutations. The limiting theory for indirect selection has not been adequately addressed. Experimental studies over several generations of indirect selection showed correlated responses were irregular in *Drosophila* (Sheridan and Barker 1974a, 1974b), primarily due to the effects of random drift and small numbers of gene loci. The infinite model presented here is only the first approximation for predicting expected genetic gain under several generations of indirect selection. As stated earlier, this response can only be regarded as the upper limit of indirect selection. Decrease in the response after each generation of indirect selection would be greater under finite population size and numbers of gene loci due to random drift and gene frequency change.

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Table 2.1 Genetic correlations necessary for relative efficiency of early selection (ratio of genetic gain in mature trait due to selection on early trait to genetic gain when mature trait is directly selected) to be unity, from different values of the ratio of selection intensities of two traits and ratios of their heritabilities

	i_x/i_y [a]										
h_y^2/h_x^2 [b]	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0
0.25	0.500	0.455	0.417	0.385	0.357	0.333	0.313	0.294	0.278	0.263	0.25
0.36	0.600	0.545	0.500	0.462	0.429	0.400	0.375	0.353	0.333	0.316	0.30
0.49	0.700	0.636	0.583	0.538	0.500	0.467	0.438	0.412	0.389	0.368	0.35
0.64	0.800	0.727	0.667	0.615	0.571	0.533	0.500	0.471	0.444	0.421	0.40
0.81	0.900	0.818	0.750	0.692	0.643	0.600	0.563	0.529	0.500	0.474	0.45
1.00	1.000	0.909	0.833	0.769	0.714	0.657	0.652	0.588	0.556	0.526	0.50

[a] i_x/i_y is ratio of juvenile selection to mature selection intensities.
[b] h_y^2/h_x^2 is ratio of heritability of mature trait to juvenile trait.

Table 2.2 The value of $Q=\sqrt{(1-\rho^2 k)}$ when phenotypic correlation $\rho=0.5$, for different proportions selected at early stage (P%) *

P%	10	20	30	40	50	60	70	80	90
a	1.282	0.842	0.524	0.253	0.000	-0.253	-0.524	-0.842	-1.282
i_x	1.755	1.400	1.159	0.966	0.798	0.644	0.497	0.350	0.195
k	0.830	0.78	0.736	0.689	0.637	0.578	0.507	0.417	0.288
Q	0.89	0.90	0.90	0.91	0.917	0.925	0.934	0.947	0.963

* a is the truncation point of the normal curve when selection proportion is P%. i_x is selection intensity of early trait.
$k=i_x(i_x - a)$.

Table 2.3 Genetic gain ratio of two stage selection (early selection plus mature selection with selection intensities i_x and i_y, respectively) to one stage mature selection only (with selection intensity i_y) when phenotypic correlation $\rho = r \cdot h_x = 0.5$ and $i_x = i_y$, $h_x \cdot r = h_y$ *

P%	10	20	30	40	50	60	70	80	90
i_x	1.755	1.400	1.159	0.966	0.798	0.644	0.497	0.350	0.195
$R_{xy.y}$	1.89	1.90	1.90	1.91	1.92	1.93	1.93	1.95	1.96

* P% is selection proportion at early stage in two stage selection.
r is genetic correlation between early and mature traits.
h_x and h_y are heritabilities of early and mature traits.
$R_{xy.y}$ is gain ratio of two stage selection to one stage mature selection.

Table 2.4 Effect of selection of early trait X on genetic parameters and genetic gain of correlated mature trait Y in different generations [a]

	Generation (n)					
	0	1	2	3	4	∞
$D_x(n)$[b]	0	9.8	11.9	12.4	12.5	12.5
$\sigma_{G_x}^2(n)$	50	40.2	38.1	37.6	37.5	37.5
$\sigma_x^2(n)$	100	90.2	88.1	87.6	87.5	87.5
$h_x^2(n)$	0.5	0.446	0.432	0.429	0.428	0.428
$E_x(G_x)(n)$	7.00	5.93	5.68	5.63	5.61	5.61
$D_y(n)$	0	2.443	2.975	3.096	3.125	3.125
$\sigma_{G_y}^2(n)$	50	47.557	47.025	46.904	46.875	46.875
$\sigma_y^2(n)$	100	97.557	97.025	96.904	96.875	96.875
$h_y^2(n)$	0.5	0.4875	0.4847	0.4840	0.4839	0.4839
r(n)	0.5	0.4599	0.4501	0.4477	0.4399	0.4399
$E_x(G_y)(n)$	2.50	2.116	2.030	2.009	2.004	2.004

[a] assume 20% is selected each generation.

[b] $D_x(n)$ and $D_y(n)$ are reductions of genetic variances of early trait X and mature trait Y at nth-generation.

$E_x(G_y)(n)$ is genetic gain of mature trait Y after nth generation of early selection on trait X.

CHAPTER THREE

EARLY EVALUATION OF LODGEPOLE PINE (*PINUS CONTORTA* SPP. *LATIFOLIA* Englm.) IN GREENHOUSE TEST

1. INTRODUCTION

Within the last several decades, lodgepole pine (*Pinus contorta* spp. *latifolia*) has achieved significant status as a commercial forest species, not only in North America but throughout much of Northern Europe (Lines 1976, Critchfield 1980). Because of the species' commercial importance, many tree improvement programs (provenance testing and progeny testing of plus trees) have been established in the last thirty years (Illingworth 1975, Wheeler 1981, Dhir 1983, Ying et al. 1985, Rehfeldt 1987). It has been shown that lodgepole pine has large amounts of genetic variation for morphology and growth traits, as well as biochemical markers (Critchfield 1957, Critchfield 1980, Hager 1970, 1980, Perry and Lotan 1978, Wheeler and Guries 1982, Wheeler and Critchfield 1985, Yeh et al. 1985, Ying and Illingworth 1986, Ying 1991).

Lodgepole pine is the second most important reforestation species in Alberta. It occupies about 15 percent of the forested area and accounts for approximately 35 percent of the merchantable timber inventory (Dhir 1983). Thus, yield and quality improvement of lodgepole pine is particularly important in Alberta in order to

increase tree productivity in the future reforestation regions of the species. The genetic improvement of lodgepole pine was started in Alberta by the Alberta Forest Service in the late 1970s. The objective of this program is to develop genetically superior strains through selection and breeding, and to produce improved seed for production of nursery planting stock for reforestation in selected regions. The breeding work has been confined to west central Alberta, which has been subdivided into four breeding regions. Plus trees were selected and field tests of open-pollinated progenies from these trees were established during the late 1970s and early 1980s in all four breeding regions. These testing programs are the most expensive component of tree improvement programs in lodgepole pine.

The lower limit of rotation age of lodgepole pine in Alberta is about 70 years (Smithers 1961). Waiting for such long rotation age or even half rotation age for final evaluation and selection is extremely inefficiency for lodgepole pine breeding. Thus, early testing and selection for shortening breeding cycle and reducing field testing size in this species is necessary to increase genetic gain per unit time and reduce cost of field testing. To reduce length of the breeding cycle in lodgepole pine, the genetic evaluation and preliminary selection of superior trees from these progeny tests are carried out recently by the Alberta Forest Service. To further investigate the possibility of very early selection (early selection at one or two years old), a retrospective study of lodgepole pine has been implemented utilizing stored seedlots of a large sample of families (120) in order to estimate genetic parameters at the seedling stage and to evaluate the relationships between seedling and field tree

performance.

This chapter summarizes the results of the genetic evaluation of seedling traits in the greenhouse which addressed three specific questions: (1) what seedling traits of lodgepole pine in Alberta populations exhibit genetic differentiation under greenhouse conditions? (2) can early testing under artificial greenhouse conditions enhance heritability estimation? (3) what are the relationships among lodgepole pine traits reflecting growth, biomass and tree form at an early age. Significant genetic differentiation in early traits is a prerequisite for early selection since only early traits which show genetic variation have potential value for early selection. Early selection efficiency depends on genetic parameters at the seedling stage, especially on heritabilities of seedling traits since early selection efficiency is directly proportional to the square root of heritability of seedling traits. Thus, precise and high estimates of heritability could increase early selection efficiency. Selection for some early traits may result in unfavourable correlated responses in other traits. For example, selection for increased partitioning of biomass to stem may lead to reduced root biomass, which may lead to a reduction in drought tolerance (St. Clair 1989). Thus, the genetic relationships among early traits must be understood in order to evaluate the impact of selection for one early trait on the other traits. In addition to these three questions, the effects of seed weight and seedling emergency rate on early seedling traits were also studied.

2. MATERIALS AND METHODS

2.1 The material

Wind-pollinated seeds were collected from 1977 to 1980 by the Alberta Forest Service and in 1981 by Blue Ridge Lumber Ltd. from one of four central Alberta lodgepole pine breeding region located at north latitude 53°58'-55°12', west longitude 115°11'-116°50', and at elevations from 855 to 1160m. This breeding region covers the Swan Hills plateau general area and some of the surrounding benchlands and is a lodgepole pine dominated extension of the foothills forest. A total of 224 open-pollinated seedlots were collected from 56 stands located throughout the region with four parent trees selected per stand. A subset of this material consisting of 120 families was used in the present study. Location and origin of the stands is shown in Appendix 3.1. The selection intensity of the field selected parent trees has been estimated to be at least 1:500 (Dhir 1983). Qualifying criteria required for selected trees were: (1) very good to excellent stem form; (2) relatively low taper and superior natural pruning characteristics; (3) desirable crown and branching characteristics; (4) height superior to any dominant tree growing within 300-m radius; and (5) freedom from any apparent disease, defect, or spiral grain. After seeds were extracted from cones, weight of 1,000 seeds was estimated for every tree by weighing eight samples of 100 seeds (Anon. 1976). Seeds used in this study were stored by family in the freezer at -4°C.

2.2 The experiment

One hundred and twenty families studied here were already in field tests and their seeds had been stored for 8 to 12 years. Seeds imbibed in tap water for one day before sowing. Thirty seeds per family were sown into individual plastic cells filled with peat moss during the fourth week of February, 1989. The thirty cells from each family were grouped together on a bench in a greenhouse at the University of Alberta. The numbers of seedlings emerged in each family were recorded every two days until 46 days after sowing. Average germination rate per family was 59.6%. This is 28.8% less than the average germination rate of these families shortly after seed collection. The seedlings were transplanted in the middle of June into 5.6 litre plastic pots in the same greenhouse. The plastic pots were filled with a mixture of peat moss and sand to allow for accelerated free growth through artificial photoperiod extension. Only 116 families were transplanted due to the low germination rate of four families (less than ten seedlings). The transplanted seedlings were studied for two growing seasons (periods) with daylength shortened to induce dormancy of seedlings between the growing seasons. The greenhouse regime was selected based on optimal growth conditions of lodgepole pine recommended by Carlson (1983) and Dymock (1986). The total growth period of seedlings was nine months from transplanting to harvesting, and is divided into five stages (Table 3.1).

In the first and second growth periods, high pressure sodium vapour lights (with PPFD intensity of 300-340 $\mu mol.m^{-2}.s^{-1}$) were utilized when natural daylight was shorter than 16 hours. Watering and fertilizing took place twice and once a week,

respectively, during the two growth stages (fertilizer formula: N-P-K 28-14-14 and 20-0-15 plus iron chelate). After the first growth period, day/night length was shifted to 12/12 hours for three weeks to induce dormancy, followed by an eight week dormancy period (8/16 day/night lighting). After the second growth period, day/night regime was shifted to 8/16 hours to induce pre-harvest dormancy. During the dormancy period, watering and fertilizing was applied once a week (fertilizer formula N-P-K 10-52-10 and 0-0-62 plus iron chelate). Day/night temperatures were set at 25°C/20°C during the growth and periods.

The original design called for one seedling of each family randomized as to position in each of 20 replications on benches in the greenhouse after transplanting (Cochran and Cox 1957). However, 73 families did not have 20 seedlings, mainly due to low germination rate (10 to 20 seedlings with average 16.8 after transplanting, for families with more than 20 seedlings emerged, only 20 seedlings were randomly selected). Therefore, the data were unbalanced. The fact that the seeds were not stratified likely contributed to the low germination rate in this sample of lodgepole pine.

2.3 Measurements

The choice of early traits selected for measurement were primarily based on other early selection studies. Seedling growth and biomass traits chosen for greenhouse measurements exhibited significant family correlations with field performance in black spruce and radiata pine (Pharis et al. 1990), in loblolly pine

(Cannell et al. 1978, Williams 1989) or in an earlier study with lodgepole pine (Jiang 1988). Additional bud and branch characteristics were also assessed.

Seedling height two weeks after transplanting (H1) and at the end of the first growth period (H2) were evaluated. Stem height (H3), basal diameter (D3), bud number on main stem (BUDN), total number of branches (BRN1), bud size (BUDS), and branch strength (BRS) were assessed at the end of the dormancy period. Basal diameter was measured just above the root collar. Bud size was classified as either small (<2.5mm), medium, or large (>5mm) by diameter. Branch strength was classified as weak (the length of branch was less than main shoot), average (the length of branch was about same as main shoot), or strong (the length of branch was longer than main shoot); this trait may reflect crown form in older trees. In the second growth period, the height of seedlings at three weeks (H4), six weeks (H5) and nine weeks (H6) were recorded. At the end of second growth period, seedling height (H7) and basal diameter (D7) were measured. At the end of the pre-harvest period, basal diameter (D8) and branch number (BRN2) were recorded. Seedlings were individually harvested, separated into parts and oven dried at 80°C for 48 hours; weights of the stem (SB), branches (BB), needles (NB) and roots (RB) were recorded. Six derived traits: HG1, growth increment of height from two weeks after transplanting to end of first growth period (i.e. H2-H1); HG2, growth increment of height from the beginning of dormancy induction to the start of second growth period (i.e., H3-H2); HG3, growth increment of height in second growth period (i.e., H7-H3); DG, growth increment of diameter in second growth period (i.e., D7-D3); TLB,

total biomass (i.e. SB+BB+NB+RB); and, GB, above ground biomass (i.e. SB+BB+NB), were also computed. In addition, three ratio traits: HI, harvest index (i.e. SB/GB)(Karki and Tigerstedt 1985); SR, ratio of above-ground biomass to root biomass (i.e. GB/RB)(Thompson 1985); RHD, ratio of height to basal diameter at the end of second growth period (i.e. H7/D7) were studied. These ratio traits are important for early seedling assessment, and also for mature selection. Harvest index reflects allocation of biomass to bole versus other above-ground parts of the tree. Higher harvest index suggests greater photosynthetic products are being allocated into the tree bole. SR and RHD are important nursery traits which have commonly been referred to as the shoot-root ratio and sturdiness quotient, respectively. SR reflects allocation of above-ground and below-ground biomass and may be related to adaptation such as tolerance to water stress (Cannell et al. 1978). The RHD is related to tree taper and reflects tree bole quality. RHD also is a good indicator of the ability to withstand physical damage due to wind, drought, and frost (Thompson 1985). The abbreviation and description of these seedling traits are separately listed in Appendix 3.2 for later reference.

2.4 Statistical and genetic analyses

Analyses of variance and covariance were conducted for all traits using the following linear model:

$$Y_{ijk} = \mu + S_i + F_{j(i)} + R_k + SR_{ik} + E_{ijk} \ , \qquad (1)$$

where

μ - grand mean

S_i - i^{th} stand effect

$F_{j(i)}$ - j^{th} family effect within the i^{th} stand

R_k - k^{th} replication effect

SR_{ik} - replication by stand interaction

E_{ijk} - residual error.

Analyses of variance and covariance were made by the fitting constant method (Searle 1971, 1987). Expected mean squares (EMS) and expected mean cross products (EMCP) were calculated by the Hartley synthesis method (Milliken and Johnson 1984, SAS 1985). The effects for families within stands and replication-by-stand interaction could be tested directly by F-tests, but Satterthwaite's approximate test procedure (1946) was required to test for other effects in the model.

Preliminary analyses of the categorical data (bud size, bud number, branch number and branch strength) indicated nonnormal distributions. Two transformations were used to remove the nonnormal bias that would have occurred in the F-tests from original data (Steel and Torrie 1980): (1) square root of bud size and branch strength, and (2) square root of bud number and branch number after adding one-half to the measured observations.

Assuming open pollinated families estimate one-quarter of the additive genetic variance (Cotterill 1987, Namkoong 1979), heritability estimates for individual, family and stand were computed as

$$\textit{individual heritability,}\quad h_i^2 = \frac{4\times\sigma^2_{f(s)}}{\sigma^2_e+\sigma^2_{f(s)}} \qquad (2)$$

$$\textit{Family heritability,}\quad h_f^2 = \frac{\sigma^2_{f(s)}}{\sigma^2_e/k_7+\sigma^2_{f(s)}} \qquad (3)$$

$$\textit{Stand heritability,}\quad h_s^2 = \frac{\sigma^2_s}{\sigma^2_e/k_6+k_4\sigma^2_{rs}/k_6+k_5\sigma^2_{f(s)}/k_6+\sigma^2_s} \qquad (4)$$

where all terms are described in Table 3.2. Exact confidence intervals could not be estimated for individual and family heritability estimates due to imbalance in the data (Knapp and Bridge 1987). Therefore, standard errors of the heritabilities were estimated through the Taylor expansion method (Kendall et al. 1987) (see Appendix 3.3). Estimates of genetic correlations were calculated as

$$r = \frac{cov(f_x\ f_y)}{\sqrt{\sigma^2_{f_x}\ \sigma^2_{f_y}}} \qquad (5)$$

where cov(f_x f_y) is the family covariance between traits X and Y, and σ_{fx}^2 and σ_{fy}^2 are their corresponding family (i.e. family within stand) variances. Standard errors of genetic correlations were approximated as Tallis (1959) and Scheinberg (1966) (see Appendix 3.4).

3. RESULTS

The shift from longer to shorter day had the expected result of inducing dormancy after both growth periods. In the dormancy period, seedlings ceased

growth, seedling colour changed from green to brownish green and bud set occurred in most seedlings. Results of data analyses are presented in two groups; first for the fourteen height and basal diameter traits, and second, for the fourteen bud, branch, biomass, and ratio traits.

3.1 Height and basal diameter

Grand means of these traits and their coefficients of variation are listed in Table 3.3. Coefficients of variation increased gradually with height and diameter increase, and coefficients of variation in height increments were more than twice that of absolute height and diameter. Analyses of variance showed that family effects of all height and basal diameter traits were highly significant (1% probability level)(Table 3.4). Stand effects were significant only at the ten percent probability level for height measurements after the first growth period (from H3). During the growth process, percentages of total variance due to replication increased while those for family(stand) and residual decreased. The percentage of the total variance due to stand effects was relatively stable at 3 to 4% for most traits except for height and diameter increments (0-2%). The residual effects explained the greatest proportion of the total variance, ranging from 63% to 78%. No traits had significant replication by stand interaction effect.

Estimates of individual and family heritabilities for absolute height measurements were highest among growth traits (from 0.543 to 0.949 for individual; from 0.721 to 0.837 for family)(Table 3.5). The estimates of individual and family

heritabilities for seedling height declined from the first height measurement to last height measurement. This is in agreement with the decline in family variance. On the other hand, stand heritability increased as seedlings grew. The estimates of individual and family heritabilities for absolute diameter measurements were lower than that for absolute height (from 0.427 to 0.491 for individual; from 0.663 to 0.697 for family). The estimates of individual and family heritabilities for height and diameter increments were the lowest (from 0.212 to 0.277 for individual; from 0.480 to 0.551 for family). When comparing heritabilities for height and diameter traits at the three hierarchical levels, family heritability (averaged h^2=0.736) was highest followed by individual (average h^2=0.602) and stand (average h^2=0.417). The only exception is H1, in which individual heritability was the highest.

Genetic correlations among the height and basal diameter traits (Table 3.6) can be viewed in three broad classes. The first class contains correlations among absolute height and basal diameters traits. Among the height traits, genetic correlations were greater than 0.725 and the majority were in the range 0.7-0.9. Correlations between absolute height and basal diameter were greater than 0.64 and the majority were in the range 0.7-0.8. Correlations declined as the interval between two height measurements i ed. The second class contains correlations between growth increment traits, which were moderate and ranged from 0.5 to 0.75. The one exception was the relatively low correlation (r=0.37) between height increments in the first growth period (HG1) and in the dormancy induction period (HG2). The third class contains correlations between growth increments and absolute

measurements for either height or basal diameter. Here, the genetic correlations were also moderate, mostly in the range of 0.5 to 0.7. Exceptions involved height two weeks after transplanting (H1), which was weakly correlated with HG1 (0.142), HG2 (0.074), and HG3 (0.224), and basal diameter at the end of second growth period (D7), which was strongly correlated with basal diameter increment in second growth period (DG, 0.924). Genetic correlations between D7 and height over time increased with the age of height measurement; however, the maximum genetic correlation was not with height at the end of second growth period (H7), but with height at six weeks (H5) and nine-weeks (H6) in the second growth period. Both HG1 and HG2 had high genetic correlations with HG3 (0.64 and 0.758, respectively). As expected, HG3 and DG also had a high genetic correlation (0.719).

Genetic correlations between height and height increment were lower than genetic correlations among absolute heights in the same growth period (Table 3.6). In the first growth period, the correlation between H1 and HG1 was 0.142 and between H1 and H2 was 0.918. In the second growth period, they were 0.570 for H3 with HG3 and 0.948 for H3 with H7, respectively. The correlation of basal diameter (D3) with its increment (DG) at 0.78 is also less than the correlation of the two absolute measurements (r=0.96 for D3 with D7).

3.2 Bud, branch, biomass, and ratio traits

Grand means of bud and branch characteristics, biomass measurements, and three ratio traits together with their coefficients of variation are listed in Table 3.7.

Most of the biomass was due to needles and roots. In the analyses of variance, family effects were highly significant (1% probability level) for all bud, branch, biomass, and ratio traits (Table 3.8). Stand effects were significant (5% probability level) only for branch number after the second growth period (BRN2), needle biomass (NB), above-ground biomass (GB), and shoot to root biomass ratio (SR). Stands were also significant for branch biomass and total biomass at the 10% probability level. There was no significant interaction between stand and replication for any traits. The percentage of total variance due to family effects was greater for biomass traits than that for growth increment traits, but was less than that for absolute height and basal diameter traits (Tables 3.4, 3.8). The percentage of the total variance due to residual effects for bud and branch characters, biomass and ratio traits ranged from 71% to 92%.

Estimates of individual and family heritabilities for bud, branch, biomass, and ratio traits were lower than the estimates for absolute height and basal diameter. Estimates of individual heritabilities for biomass, harvest index (HI), and sturdiness quotient (RHD) were moderate (between 0.308 and 0.433), while estimates for bud, branch characteristics and shoot-root ratio (SR) were among the lowest among any traits, similar in magnitude to those for height and diameter increments (between 0.145 and 0.325). The relative ranking of the magnitudes of heritability for biomass traits at the individual, family and stand levels were not the same as for height and basal diameter traits. Here, family heritabilities were largest on average (mean 0.627), stand heritabilities second (0.460) and individual heritabilities the least (0.374).

Genetic correlations between bud size (BUDS) and bud number (BUDN) after the first growth period, and between branch numbers after the first and second growth periods (BRN1 with BRN2), were strong (0.853 and 0.725, respectively) (Table 3.10). BRN1 was moderately correlated with BUDN and BUDS (0.535 and 0.684, respectively). Among the biomass traits, genetic correlations were greater (average 0.829). Stem, needle and root biomass were strongly intercorrelated (0.711 to 0.993). Branch biomass (BB) had moderate or strong genetic relationships with other biomass traits (from 0.576 to 0.749). BRN2 had a strong genetic correlation with BB (0.876), but was only moderately correlated with other biomass traits. BUDN was strongly correlated with stem biomass (SB, 0.710) but moderately correlated with needle biomass (NB, 0.654). Branch strength (BRS) was weakly correlated with the most other traits. Harvest index (HI), shoot-root ratio (SR), and sturdiness quotient (RHD) were also weakly correlated with bud, branch, and biomass traits. Exceptions were moderate correlation of SB with harvest index (0.453) and the high correlation between BUDN and SR.

Genetic correlations between height or basal diameter traits and bud, branch, biomass or ratio traits were also analyzed (Table 3.11). Their general trends are summarized as follows:

(1) BUDN, BUDS, BRN1 and BRN2 were moderately correlated with height (from 0.30 to 0.75), but BRS had weak or negative genetic correlation with height.

(2) Correlations between SB, NB, and RB biomass and height increased as height measurements approached harvest age.

(3) Basal diameters had better genetic correlations with biomass than heights.

(4) Height increments in the two growth periods (HG1 and HG3) generally had weak or negative genetic correlations with bud and branch traits. The exception is height increment during the dormancy induction period (HG2) which had a strong genetic correlation with BUDN (0.749). Diameter increment (DG) had moderate correlations with BUDN and BRN2.

(5) Height increment during the second growth period (HG3) had a better correlation with biomass than either height increment at the first growth period (HG1) or HG2. Biomass traits were more strongly correlated with DG than with height increments (HG1, HG2 and HG3).

(6) Harvest index (HI) was moderately correlated with height traits (0.418 to 0.522), but weakly correlated with basal diameter traits (0.280 to 0.349).

(7) Sturdiness quotient (RHD) was moderately correlated with height traits (0.370 to 0.598), but was not correlated with basal diameter traits (-0.021 to 0.022).

(8) There were no significant correlations between shoot-root ratio (SR) and height and basal diameter traits.

4. DISCUSSION: IMPLICATIONS FOR EARLY SELECTION

In this study, genetic differentiation of seedling quantitative traits in lodgepole pine was well developed during the first and second seasons of seedling growth under uniform greenhouse growth conditions. Family differences were not only expressed

for total height, diameter and biomass traits, but also for growth increments, bud and branch characteristics and three ratio traits. This shows an inherent ability to grow rapidly could be detected at quite early ages in lodgepole pine. This data supports the point stated by Bongarten and Hanover (1985) that under optimal growth conditions, trees express their inherent genetic variation earlier. The early genetic differentiation of lodgepole pine gives us an opportunity for early selection.

Family differences at early ages may be affected by maternal or preconditioning effects such as seed size, nutrition and germination rate. For example, early seedling growth was significantly influenced by seed weight in loblolly pine (Waxler and van Buijtenen 1980, Cannell et al. 1978). If maternal or preconditioning effects were important, they would influence levels of family differentiation detected at the seedling stage, heritability estimates and early-mature genetic correlations. Thus, the presence of maternal or preconditioning effects can reduce the accuracy of genetic differentiation studies, leading to poor estimates of variance components and inaccurate ranking of parents. With regard to the high heritability estimates of this study, especially, the first height measurement (h_i^2=0.949 and h_f^2=0.837)(Table 3.5), relative to other studies in lodgepole pine (h_i^2 ranged from 0.11 to 0.57, Illingworth 1976, Rehfeldt 1985, Fries 1986) it is particularly important to examine maternal or preconditioning effects. The low estimated genetic correlations between height growth increments in the both periods (HG1, HG3) and initial growth (H1) before transplanting (0.142 and 0.224, respectively (Table 3.6)) suggests maternal or preconditioning effects may not have had much influence on

seedling growth after transplanting even if these effects are important before transplanting. If maternal or preconditioning effects significantly influenced H1 and measurements afterwards, H1 should have had higher correlations with both growth increments. However, H1 is highly correlated with H2-H7. Thus, maternal or preconditioning effects may have been large initially and some of them may carried over to absolute height all along, but height increment was little influenced by initial height.

Effects of seed size and seedling emergency rate have been proposed as two major maternal or preconditioning factors to be related to seedling performance in some conifer species (Bonner 1988, St. Clair 1989). To understand whether seed size and seedling emergency rate have contributed the high estimates of heritabilities in this study, two analyses were done. In the first analysis, Pearson's correlations between average seed weight per family and seedling growth traits were computed (Table 3.12). This analysis indicated only marginal correlations between seed weight and H1 ($r=0.149$), GB ($r=0.170$) and TLB ($r=0.179$). In addition, family seed weight was not significantly correlated with D3, D7, HG1, HG2, HG3, DG, and NB. Although correlations with the rest of the height measurements were significant (5% probability level), the relationships were weak (under 0.235). In the second analysis, parameter of seedling emergency rate was calculated from probit analysis described by Campbell and Sorenson (1979), and correlations between seedling emergency rate and seedling traits were computed (Table 3.12). In general, correlations between seedling emergency rate and seedling traits were smaller than the correlations

between seed weight and seedling traits. Therefore, there is little or no evidence that seedling growth is related to seed size and seedling emergency rate.

The most possible reasons for high heritability of initial height (H1) was due to preconditioning family block effect. Since families were grown as blocks in the first three and half months after sowing, genetic and environmental effects were confounded initially. After transplanting, the proportion of the confounding environmental effect diminished due to growth of seedlings in the replicated experiment design. For example, percentage of family variance dropped from 23% in H1 to 16% in H2 (Table 3.4). The greatest drop of heritability also occurred from H1 to H2 (Table 3.5). Although heritability of absolute height declined with time from H2, the differences of heritabilities after H2 may not be very significant if one considers the standard errors (Table 3.5). Thus, the heritabilities of height after H2 are relative reliable and probably reflect inherent family differentiation. The high heritabilities in height traits after H2 may also be due to following reasons. First, it was probably due to the homogenous greenhouse environment and growth conditions. Second, it may be due to efficient single seedling plot design. One of the advantages of single-seedling plot design is that it exposes the family to the environment more evenly over the whole test and makes replication more compact. Thus, a single tree plot design would be more powerful in differentiating families before the onset of inter-family competition.

One advantage of early selection for mature performance is higher heritability estimates of juvenile traits in early genetic tests (Lambeth 1980, Kang 1985). The

indirect response of mature traits due to selection of early traits can be greater than that direct response when $r>h_m/h_j$, where h_m and h_j are the heritabilities of mature and early traits, respectively, r is the genetic correlation and selection intensities for both types of selection are identical. Thus, higher heritability of early traits means higher early selection efficiency. In this early genetic test of lodgepole pine, the estimates of height heritability are relatively higher compared to other estimates reported for single populations of lodgepole pine. For example, individual heritability of height from ten British Columbia populations ranged from 0.23 to 0.57 (Illingworth 1976) at age three in a nursery; individual heritabilities of height estimated by Fries (1986) were from 0.11 to 0.34 at age ten; individual heritability estimates of six-year-old tree height varied from 0.12 to 0.36 (Rehfeldt 1985). But in this study, individual heritabilities for height, diameter and biomass were above 0.3 (Tables 3.5, 3.9). Height had higher heritabilities than the other traits with its range from 0.543 to 0.949 (Table 3.5). Estimates of family heritabilities for height were mostly above 0.6. High heritability in this study answers our second question that higher genetic differentiation and heritability estimates can be obtained under artificial growth conditions. Using heritability estimates in this study, the levels of genetic correlations between early and mature performance required to achieve the same level of mature genetic gain when selection is practised at early ages can be computed. Results for heritability of mature trait at 0.1, 0.2, 0.3, and 0.4 are illustrated in Figure 3.1. Genetic correlations of 0.325 to 0.429, corresponding to heritabilities of H1 to H7, are required for early selection of height traits to be as efficient as direct mature

selection when heritability of a mature trait is 0.1. When heritability of a mature trait is 0.2, genetic correlations of 0.459 to 0.607 are required for indirect selection based on seedling height traits to be as efficient. Since early selection will shorten the breeding cycle, indirect early selection benefits will be much greater if we consider genetic gain per unit time and potentially higher selection intensities at the juvenile stage.

Selection for one early trait would affect another trait if there is a genetic correlation between them. From genetic correlations estimated among the 28 seedling traits, the following relationships are particularly important to early selection in Alberta lodgepole pine: (1) Selection for higher harvest index (HI=SB/GB) would increase root biomass (RB) since the genetic correlation between these traits was positive (0.370)(Table 3.10). Selection and breeding for higher harvest index in forest trees has been proposed by many authors as a method to increase timber productivity per unit area (Cannell 1978, Karki and Tigerstedt 1985, St. Clair 1989), but concerns have been expressed whether increasing harvest index would adversely affect drought tolerance of trees. In this study, the positive correlation between HI and RB indicates selection for increased biomass partitioning to the tree bole would lead to a increase in root biomass, and presumably greater drought tolerance. Selection for higher harvest index would also result in increases in height and basal diameter, increase in bud number and bud size, increase or no change in branch number, and a decrease in branch strength (Tables 3.10, 3.11). Thus, selection for harvest index in lodgepole pine may be promising for increasing forest productivity, increasing

tolerance to drought, and reducing branch strength (resulting in narrow crowns and compact trees). (2) Selection for a higher sturdiness quotient (RHD=height/diameter) would increase tree height but would neither increase nor decrease diameter since there was no genetic correlation between RHD and basal diameter. Selection and breeding for low tree taper in lodgepole pine has been proposed as a method to increase lodgepole pine timber quality in Alberta and probably increase the efficiency of space and light use. In this study, genetic correlations existed only between RHD and height indicating that selection for increased RHD should result in increased timber volume and more uniform lower and upper logs (less taper). Selection for RHD should also result in an increase in stem biomass and harvest index, no change in branch number, and a decrease in branch strength (Table 3.10). (3) Selection for higher shoot to root ratio (SR=GB/RB) would increase needle biomass as expected since NB was more than 80% of total above-ground biomass. Selection for higher SR also has moderately negative effects on root biomass and corresponding harvest index (Table 3.10). Selection for SR would not have much impact on height and diameter since there were no significant correlations between SR and H7 and D7 (Table 3.11). Similarly, selection for SR would have little effect on branch number, branch strength, and RHD, but would increase the number of buds (Table 3.10).

One seedling trait, HG2 (growth increment at the dormancy induction period) should be emphasized here. HG2 has a relative low genetic correlation with all other seedling traits, but its correlation with BUDN is high (0.749)(Table 3.11). This may

indicate a close biological link between bud number and strong growth in the dormancy induction period. HG2 may be related to growth cessation characteristics and may reflect growth potential, since families with high HG2 either had high growth potential before the dormancy condition was imposed or had a longer growing season due to a slow response to the dormancy induction condition. The potential value of HG2 for early selection will be examined in Chapter Six.

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Table 3.1 Seedling growth stage, light regime and duration

Stage	Day/Night Length	Duration
First Growth Period	16 / 8 hours	June 14 to Aug. 31 (11 weeks)
Dormancy Induction	12 / 12 hours	Aug. 31 to Sept. 20 (3 weeks)
Dormancy Period	8 / 16 hours	Sept. 20 to Nov. 15 (8 weeks)
Second Growth Period	16 / 8 hours	Nov. 15 to Feb. 21 (14 weeks)
Pre-Harvest	8 / 16 hours	Feb. 21 to March 14 (3 weeks)

Table 3.2 Structure of analyses of variance and covariance of seedling traits

Source of Variation	D.F.	EMS or EMCP [a]
Replication	19	$\sigma_e^2+k_1\sigma_{rs}^2+k_2\sigma_s^2+k_3\sigma_r^2$
Stand	32	$\sigma_e^2+k_4\sigma_{rs}^2+k_5\sigma_{f(s)}^2+k_6\sigma_s^2$
Family(stand)	83	$\sigma_e^2+k_7\sigma_{f(s)}^2$
Replication * stand	588	$\sigma_e^2+k_8\sigma_{rs}^2$
Residual	1213	σ_e^2
Total	1935	

[a] EMS and EMCP are expected mean squares and expected mean cross-products, respectively. σ_r^2, σ_s^2, $\sigma_{f(s)}^2$, σ_{rs}^2 and σ_e^2 are variances or covariances of replication, stand, family-within-stand, replication-by-stand interaction and residual.

k_1=3.257, k_2=0.145, k_3=96.592, k_4=3.168, k_5=17.232, k_6=58.548, k_7=16.471, k_8=3.009.

Table 3.3 Means and coefficients of variation (C.V.)[a] for fourteen seedling height and basal diameter traits [b]

Traits	H1 (mm)	H2 (mm)	H3 (mm)	H4 (mm)	H5 (mm)	H6 (mm)	H7 (mm)
Mean	79	109	119	129	142	148	159
C.V.	22.4	23.4	23.7	25.1	26.9	26.6	27.0

Traits	D3 (mm)	D7 (mm)	D8 (mm)	HG1 (mm)	HG2 (mm)	HG3 (mm)	DG (mm)
Mean	4.60	7.56	7.74	31	10	39	2.97
C.V.	20.2	22.8	23.5	56.7	101.9	61.7	37.9

[a] C.V. - coefficient of variation for individual observations.

[b] see Appendix 3.2 for description of traits.

Table 3.4 Analyses of variance presented as intraclass correlation coefficients (percentage of total variance) for height and basal diameter traits [a]

Source of variation	H1	H2	H3	H4	H5	H6	H7
Replication	1 **	5 **	10**	17**	18**	18**	21**
Stand	3	4	4 °	4 °	4 °	4 °	4 °
Family(stand)	23**	16**	14**	12**	11**	11**	10**
Replication*Stand	1	3	2	2	2	2	1
Residual	72	72	71	66	65	65	63
Source of variation	D3	D7	D8	HG1	HG2	HG3	DG
Replication	9**	13**	15**	15**	16**	24**	16**
Stand	3	3	3	1	0	2	1
Family(stand)	11**	9**	10**	5**	4**	5**	4**
Replication*Stand	1	1	1	2	2	1	1
Residual	77	75	71	76	78	68	78

[a] see Appendix 3.2 for description of traits.

°, *, and ** represent 10%, 5%, and 1% significance levels.

Table 3.5 Estimates of individual (h_i^2), family (h_f^2), and stand (h_s^2) heritabilities and their standard errors (s.e.) for fourteen height and basal diameter traits [a]

Traits	H1	H2	H3	H4	H5	H6	H7
h_i^2	0.949	0.711	0.650	0.601	0.572	0.589	0.543
s.e.	0.137	0.118	0.113	0.109	0.106	0.108	0.103
h_f^2	0.837	0.781	0.762	0.745	0.733	0.740	0.721
s.e.	0.026	0.035	0.038	0.041	0.043	0.042	0.044
h_s^2	0.271	0.399	0.435	0.470	0.464	0.470	0.488
s.e.	0.209	0.172	0.162	0.152	0.154	0.152	0.147
Traits	D3	D7	D8	HG1	HG2	HG3	DG
h_i^2	0.491	0.427	0.486	0.265	0.212	0.277	0.207
s.e.	0.098	0.091	0.096	0.073	0.066	0.074	0.066
h_f^2	0.697	0.663	0.681	0.539	0.480	0.551	0.473
s.e.	0.049	0.054	0.052	0.074	0.084	0.072	0.084
h_s^2	0.365	0.398	0.413	0.268	0	0.389	0.364
s.e.	0.183	0.174	0.167	0.211	0	0.177	0.185

[a] see Appendix 3.2 for description of traits.

Table 3.6 Matrix of genetic correlation estimates (r, upper diagonal) and their standard errors (lower diagonal) among fourteen height and basal diameter traits [a]

r	H1	H2	H3	H4	H5	H6	H7	D3	D7	D8	HG1	HG2	HG3	DG
H1		0.918	0.878	0.831	0.785	0.772	0.725	0.688	0.640	0.642	0.142	0.074	0.224	0.487
H2	0.027		0.982	0.953	0.921	0.912	0.888	0.729	0.728	0.731	0.522	0.213	0.449	0.632
H3	0.037	0.007		0.989	0.965	0.958	0.948	0.766	0.777	0.769	0.563	0.394	0.570	0.690
H4	0.049	0.016	0.005		0.988	0.984	0.980	0.768	0.814	0.807	0.592	0.479	0.672	0.771
H5	0.060	0.026	0.012	0.005		1.000	0.988	0.798	0.827	0.818	0.611	0.508	0.740	0.758
H6	0.062	0.028	0.015	0.006	0.001		0.990	0.795	0.820	0.822	0.617	0.517	0.756	0.747
H7	0.072	0.036	0.019	0.009	0.005	0.004		0.760	0.814	0.809	0.658	0.581	0.802	0.781
D3	0.085	0.076	0.069	0.070	0.064	0.065	0.074		0.960	0.925	0.340	0.417	0.524	0.780
D7	0.096	0.079	0.068	0.061	0.057	0.058	0.061	0.024		0.979	0.446	0.476	0.642	0.924
D8	0.093	0.082	0.071	0.066	0.060	0.063	0.067	0.021	0.018		0.474	0.481	0.675	0.918
HG1	.160	0.119	0.114	0.111	0.111	0.110	0.106	0.156	0.147	0.139		0.374	0.640	0.533
HG2	.171	0.172	0.152	0.143	0.140	0.138	0.129	0.164	0.157	0.173	0.198		0.758	0.495
HG3	.154	0.139	0.123	0.102	0.084	0.079	0.064	0.137	0.115	0.120	0.150	0.131		0.719
DG	0.145	0.127	0.116	0.100	0.101	0.102	0.095	0.114	0.041	0.124	0.172	0.186	0.126	

[a] see Appendix 3.2 for description of traits.

Table 3.7 Means and coefficients of variation (C.V.)[a] for fourteen bud, branch, biomass, and ratio traits [b]

Traits[c]	BUDN	BUDS	BRN1	BRS	BRN2	SB (cg)	NB (cg)
Mean	1.56	1.35	1.78	1.64	3.92	277	1626
C.V.	19.6	31.1	19.9	17.5	24.2	59.6	46.1
Traits	BB (cg)	RB (cg)	TLB (cg)	GB (cg)	HI	SR	RHD
Mean	91	673	2671	1997	0.138	3.10	21.3
C.V.	84.4	54.9	47.2	47.0	25.3	38.6	24.7

[a] C.V. - coefficient of variation for individual observations.

[b] see Appendix 3.2 for description of traits.

[c] The means of BUDS and BRS are means of three categories represented by numbers 1, 2, and 3; cg=1/100g.

Table 3.8 Analyses of variance presented as intraclass correlation coefficients (percentage of total variance) for fourteen bud, branch, biomass, and ratio traits [a]

Source of variation	BUDN	BUDS	BRN1	BRS	BRN2	SB	NB
Replication	1**	0	3**	1	3**	14**	15**
Stand	0	2	1	1	4*	3	4*
Family(stand)	3**	7**	6**	6**	7**	8**	9**
Replication*Stand	3	0	0	0	0	2	1
Residual	92	91	90	92	85	73	72

Source of variation	BB	RB	TLB	GB	HI	SR	RHD
Replication	6**	9**	14**	15**	1**	3**	19**
Stand	4°	2	4°	4*	1	2*	0
Family(stand)	7**	7**	8**	9**	9**	4**	6**
Replication*Stand	0	2	2	1	0	2	0
Residual	83	80	71	71	89	89	75

[a] see Appendix 3.2 for description of traits.

°, *, and ** represent 10%, 5%, 1% significance levels.

Table 3.9 Estimates of individual (h_i^2), family (h_f^2), and stand (h_s^2) heritabilities and their standard errors (s.e.) for fourteen bud, branch, biomass, and ratio traits [a]

Traits	BUDN	BUDS	BRN1	BRS	BRN2	SB	NB
h_i^2	0.145	0.293	0.248	0.235	0.325	0.401	0.424
s.e.	0.060	0.070	0.073	0.064	0.080	0.088	0.091
h_f^2	0.366	0.584	0.501	0.549	0.594	0.647	0.661
s.e.	0.100	0.066	0.079	0.066	0.083	0.056	0.054
h_s^2	0.000	0.353	0.215	0.147	0.557	0.417	0.515
s.e.	0.000	0.138	0.186	0.175	0.109	0.137	0.118
Traits	BB	RB	TLB	GB	HI	SR	RHD
h_i^2	0.308	0.317	0.422	0.433	0.369	0.183	0.315
s.e.	0.078	0.079	0.091	0.092	0.093	0.064	0.095
h_f^2	0.579	0.586	0.660	0.667	0.574	0.396	0.550
s.e.	0.067	0.066	0.054	0.052	0.085	0.053	0.071
h_s^2	0.537	0.344	0.493	0.522	0.283	0.588	0
s.e.	0.115	0.153	0.123	0.116	0.124	0.176	0

[a] see Appendix 3.2 for description of traits.

Table 3.10 Matrix of genetic correlation estimates (r, upper diagonal) and their standard errors (lower diagonal) among bud, branch, biomass, and ratio traits *

r	BUDN	BUDS	BRN1	BRS	BRN2	SB	BB	NB	RB	TLB	GB	HI	SR	RHD
BUDN		.853	.535	.321	.452	.710	.254	.654	.379	.600	.645	.354	.784	.166
BUDS	.061		.684	.522	.129	.304	.034	.158	.120	.180	.170	.401	-.08	.248
BRN1	.176	.100		.655	.725	.440	.555	.389	.306	.402	.421	.170	.157	.092
BRS	.213	.131	.114		.246	.034	.342	.164	.101	.149	.160	-.26	.056	-.23
BRN2	.180	.169	.090	.172		.650	.876	.605	.565	.643	.650	.058	.237	-.02
SB	.106	.147	.145	.173	.095		.687	.912	.936	.959	.939	.453	.134	.293
BB	.214	.174	.134	.164	.041	.088		.711	.576	.722	.749	-.04	.192	-.17
NB	.120	.156	.151	.166	.103	.26	.082		.867	.985	.996	.076	.329	.161
RB	.195	.170	.174	.183	.119	.021	.119	.041		.934	.885	.370	-.23	.185
TLB	.135	.155	.149	.167	.095	.012	.079	.005	.021		.993	.196	.171	.173
GB	.119	.154	.145	.166	.093	.018	.072	.001	.035	.003		.133	.297	.165
HI	.148	.137	.165	.171	.104	.122	.161	.169	.143	.159	.156		-.34	.389
SR	.094	.117	.134	.108	.201	.140	.182	.155	.181	.167	.152	.162		-.02
RHD	.164	.170	.182	.183	.211	.151	.162	.159	.153	.162	.165	.141	.105	

* see Appendix 3.2 for description of traits.

Table 3.11 Matrix of genetic correlation estimates (r) and their standard errors (s.e.) between height, basal diameter traits and bud, branch, biomass, and ratio traits *

r	H1	H2	H3	H7	D3	D7	D8	HG1	HG2	HG3	DG
BUDN	.469	.499	.615	.603	.644	.622	.626	.238	.749	.404	.511
s.e.	.135	.131	.118	.126	.123	.129	.125	.269	.129	.197	.181
BUDS	.525	.545	.519	.361	.374	.288	.293	.232	.033	-.04	.134
s.e.	.095	.072	.106	.131	.132	.147	.141	.204	.222	.178	.191
BRN1	.737	.699	.628	.492	.627	.532	.521	.159	-.15	.091	.331
s.e.	.067	.080	.097	.127	.129	.127	.123	.234	.242	.197	.193
BRS	.114	.134	.081	-.08	.249	.119	.122	.089	-.23	-.36	-.07
s.e.	.139	.148	.154	.160	151	.169	.158	.229	.225	.167	.207
BRN2	.574	.565	.531	.553	.714	.734	.741	.176	-.02	.432	.667
s.e.	.090	.098	.105	.106	.078	.075	.073	.213	.226	.147	.110
SB	.645	.792	.861	.940	.849	.941	.949	.592	.595	.811	.945
s.e.	.074	.051	.036	.017	.040	.018	.012	.135	.082	.059	.020
BB	.493	.522	.499	.475	.689	.704	.701	.244	.040	.290	.633
s.e.	.103	.106	.190	.120	.120	.083	.091	.210	.229	.169	.121
NB	.538	.671	.741	.804	.853	.898	.903	.518	.569	.683	.842
s.e.	.089	.074	.062	.050	.037	.029	.021	.150	.143	.090	.054
RB	.457	.651	.721	.833	.850	.890	.905	.643	.562	.796	.828
s.e.	.106	.083	.071	.047	.038	.034	.028	.130	.156	.067	.063
TLB	.554	.704	.772	.848	.882	.932	.941	.568	.567	.738	.879
s.e.	.087	.068	.055	.040	.035	.020	.018	.139	.143	.077	.060
GB	.570	.702	.767	.828	.867	.919	.923	.527	.552	.698	.871
s.e.	.084	.068	.056	.045	.036	.023	.019	.149	.146	.086	.063
HI	.418	.457	.480	.522	.280	.336	.349	.220	.298	.446	.372
s.e.	.186	.142	.122	.109	.163	.188	.143	.201	.173	.152	.131
SR	.271	.106	.113	.032	.131	.113	.165	-.32	.064	-.13	.074
s.e.	.162	.187	.175	.208	.147	.181	.163	.154	.202	.182	.195
RHD	.370	.503	.529	.598	-.02	.022	.011	.458	.329	.545	.079
s.e.	.124	.105	.104	.090	.205	.221	.249	.111	.149	.097	.194

* see Appendix 3.2 for description of traits.

Table 3.12 Family mean correlations between seed weight (r_w), seedling emergency rate (r_s) and seedling traits of height, basal diameter, and biomass [a]

Traits	H1	H2	H3	H4	H5	H6	H7	D3	D7
r_w	0.149	0.210	0.211	0.235	0.222	0.225	0.211	0.090	0.101
Pr.[b]	0.112	0.024	0.013	0.011	0.017	0.015	0.023	0.336	0.279
r_s	0.163	0.162	0.185	0.199	0.209	0.203	0.182	0.196	0.168
Pr.	0.081	0.082	0.047	0.032	0.024	0.029	0.051	0.035	0.0168
Traits	HG1	HG2	HG3	DG	SB	NB	RB	GB	TLB
r_w	0.189	0.166	0.112	0.084	0.215	0.165	0.188	0.170	0.179
Pr.	0.062	0.074	0.230	0.373	0.021	0.078	0.043	0.069	0.054
r_s	0.074	0.141	0.109	0.113	0.108	0.145	0.126	0.137	0.138
Pr	0.432	0.132	0.245	0.094	0.250	0.121	0.179	0.135	0.141

[a] see Appendix 3.2 for description of traits.
[b] Pr. is probability under null hypothesis that r_w is equal to zero.

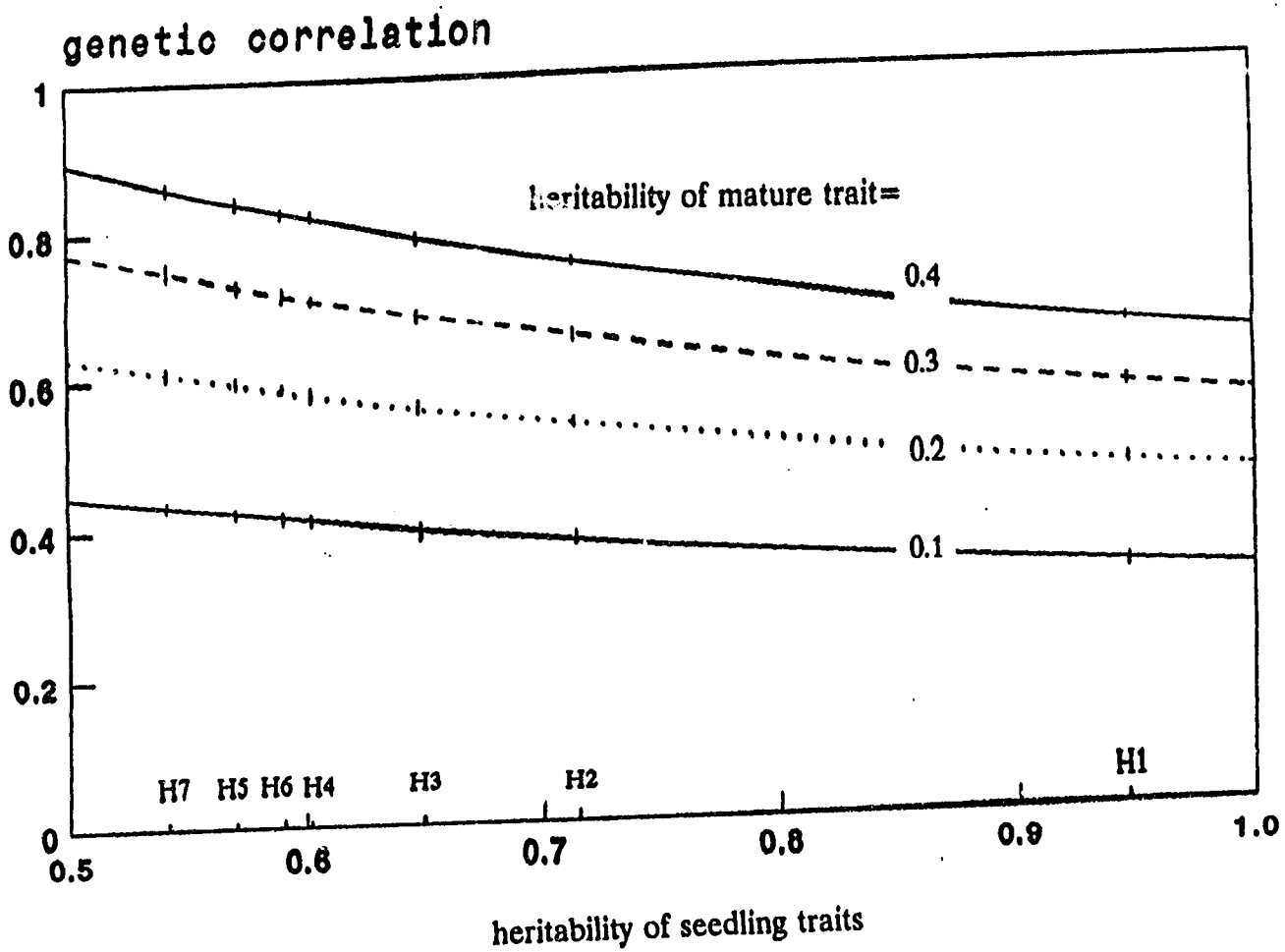

Figure 3.1 Genetic correlations required between an early and mature trait, for different heritabilities of seedling traits, in order for early (indirect) selection to achieve the same genetic gain in the mature trait as direct selection

CHAPTER FOUR

GENETIC ANALYSIS OF LODGEPOLE PINE IN THE FIELD TESTS

1. INTRODUCTION

Pinus contorta spp. *latifolia* is one of the most widely distributed tree species in Western Canada, and a commercially important conifer native to Alberta. It is valued for its growth potential, good form characteristics and relative freedom from major pests. This species is one of the most genetically diverse of forest trees (Critchfield 1980). Variability in economic traits such as growth, form and wood quality is expressed both within and among populations (see Yanchuk 1988). *P. contorta* spp. *latifolia* is, therefore, a prime candidate for improvement through selective breeding.

Tree improvement programs in *P. contorta* spp. *latifolia* in Western Canada have generally followed phenotypic selection in wild stands and use of this material for seed production in clonal or seedling seed orchards. Selection criteria have emphasized height growth and form traits, and additive genetic effects have been assumed (Wheeler 1979; Carlson 1990). In Alberta, Dr. Narinder Dhir of the Alberta Forest Service initiated phenotypic selection among stands and families within stand for growth and form traits in the late 70's. The Alberta improvement program is organized into four breeding regions based on geographic-ecological evaluation of the

area. Each breeding region has a separate genetic-improvement project and serves as a target area within which plus tree were selected and tested to develop genetically superior strain(s) of seed for reforestation only within that region. By 1980, more than 200 parent trees had been selected from each of the four breeding populations across west central Alberta (Dhir et al. 1983). Open-pollinated seeds of these select trees have been propagated in breeding arboreta and in seedling seed orchards designed to meet the immediate seed requirements.

Field progeny tests were established in all regions. In this paper, only nine-year results of testing in one of four regions were analyzed. In this region, open-pollinated progenies were planted on four sites distributed across the major biogeoclimatic units. The field tests in the region will be used to reconstruct pedigreed populations to provide both the material and the source of information for advanced generation breeding. Nine-year height data in a sample of 120 families from total 224 families collected from this region were provided by the Alberta Forest Service and were the sources for analyses. The purpose of this study is to partition the total phenotypic variation of height of *P. contorta* spp. *latifolia* into portions of family effect, interaction of sites with family, residual effect and random error, particularly to estimate height heritability of field trials and extent of family by test site interaction.

2. MATERIALS AND METHODS

Open-pollinated seeds used in this study were collected from select trees from the central Albertan *P. contorta* spp. *latifolia* breeding region (north latitude 53°58' - 55°12', west longitude 115°11' - 116°50' and elevation 885-1160m) (Figure 4.1). This breeding region covers the Swan Hills plateau general area and some of the surrounding benchlands. It is a *P. contorta* spp. *latifolia* dominated extension of the foothills forest. A total of 224 parent trees were selected in this region. In selection, emphasis was placed on the above average and excellent phenotypes in the dominant/codominant crown classes within mature, well-stocked stands with closed canopies. The selection intensity of the field trees has been estimated to be at least 1:500 (Dhir 1983)(Chapter Three, this thesis). Identity of seedlots were maintained by individual parent tree through cone collection, storage, and all subsequent handling.

Seedlings from each parent tree (open-pollinated family) were raised at the Smoky Lake Nursery as long-season styro-8 plugs. Seeds were sown in February 1981 using a randomized block design. The seedlings were planted in the fall of 1982 (without cold storage) at four locations referred to as sites A, B, C, and D (Figure 4.1), where *P. contorta* spp. *latifolia* would be a good choice for reforestation. Each site required an adequate uniform area of freshly logged land, and care was taken to distribute the test sites across the major biogeoclimatic units. Site preparation consisted of windrowing and subsequent burning of slash, brushing and fencing.

A randomized complete block design with 4-tree row plots and subblocking by sets, with twelve families per set, was used. Spacing between trees was 2.5 m. All entries were replicated five times on each of four sites. These 120 families are part of the field plantation since the original field design was for 224 families. Family number within set ranges from three to twelve families and 7% of trees were missing in these particular 120 families. Height and survival were assessed after nine growing seasons from planting (Table 4.1) and indvidual family means for the four sites are listed in Appendix 4.1.

Analyses of variance and calculation of variance components for nine year tree height were conducted by combining data over all sites, and also for each site separately. Preliminary analysis indicated stand effects were not significant. Thus, the appropriate models for analysis without stand structure were:

Combined over sites:

$$Y_{ijkl} = \mu + S_i + R_{j(i)} + T_k + S*T_{ik} + R*T_{kj(i)} + F_{l(k)} + S*F_{il(k)} + E_{ijkl} \qquad (1)$$

where μ - grand mean

S_i - i^{th} site effect

$R_{j(i)}$ - j^{th} replication effect within i^{th} site

T_k - k^{th} set effect

$S*T_{ik}$ - site by set interaction

$R*T_{jk(i)}$ - replication by set interaction

$F_{l(k)}$ - l^{th} family effect within k^{th} set

$S*F_{il(k)}$ - site by family within set interaction

E_{ijkl} - residual error;

Single site:

$$Y_{jkl} = \mu + R_j + T_k + R*T_{kj} + F_{l(k)} + R*F_{jl(k)} + E_{jkl} \quad , \qquad (2)$$

where μ - grand mean

R_j - j^{th} replication effect

T_k - k^{th} set effect

$R*T_{jk}$ - replication by set interaction

$F_{l(k)}$ - l^{th} family effect within set

$R*F_{jl(k)}$ - replication by family within set interaction

E_{jkl} - residual error.

All effects except the overall mean were considered random. Direct F-tests could not be made for sources of variation except for site-by-family interaction in the analysis across sites, and replication-by-family interaction in single site analyses, because the data were unbalanced due to differing numbers of families within sets, missing plots, and missing trees within plot. Satterthwaite's (1946) approximate test procedure, therefore, was used to synthesize approximate error terms for each source.

The variance component for open-pollinated families was assumed to estimate one-quarter of the additive genetic variance (Wright 1976, Yanchuk et al. 1988). Heritability estimates for nine-year tree height were computed by substituting the appropriate values in the equations. For example, in the estimates for individual sites, individual tree (h_i^2) and family mean heritabilities (h_f^2) were estimated by:

$$h_i^2 = \frac{4 \times \sigma^2_{f(t)}}{\sigma^2_e + \sigma^2_{r*f(t)} + \sigma^2_{f(t)}} \qquad (3)$$

and

$$h_f^2 = \frac{\sigma^2_{f(t)}}{\sigma^2_e / k_{14} + k_{13} * \sigma^2_{r*f(t)} / k_{14} + \sigma^2_{f(t)}} \qquad (4)$$

with the notation defined in Table 4.3. The k_{13} and k_{14} are coefficients of variance of replication-by-family-within-set and variance of family-within-set in the expected mean square of family-within-set variation. These k_i values, which are coefficients of the expected mean squares, and mean squares, were obtained from a complete least squares solution for all effects in the analyses (Searle 1971, Milliken and Johnson 1986). Standard errors of heritabilities were derived using Taylor's expansion (Kendall et al. 1987).

3. RESULTS

Survival of the 120 families following nine growing seasons after planting averaged 83%, and varied from a low of 79% at site A to a high of 85% at sites B and C (Table 4.1). Mortality was primarily the result of browsing and poor choice of the planting spots within the sites. Differential survival of the seedlings attributable to family effect was not apparent.

In the combined analysis across sites, significant differences at the 5% probability level in nine-year tree height were observed for sites, replications, sets,

family within sets, set-by-replication interaction and family-within-sets-by-site interaction (Table 4.2). Estimates of individual and family heritabilities across all four sites were 0.125±0.027 and 0.6603±0.038, respectively.

In the analyses of nine-year tree height on individual sites, all effects except that for sets on sites A, B, and D, were significant at the 5% probability level (Table 4.3). The estimates of individual heritability varied from 0.1203±0.030 for site C to 0.1773±0.041 for site D (Table 4.4). Estimates of family heritability were more than twice those for individual heritabilities, ranging from 0.2779±0.021 to 0.3924±0.031.

4. DISCUSSION

Family differences in nine-year tree height were significant within and across sites. Thus, there is potential for the genetic improvement of nine-year tree height in lodgepole pine in Alberta from individual and family selection. Sites were significant at the 1% probability level and had major influence on the growth of lodgepole pine in this study. Mean heights after nine-years in the worst site (site A) and the best site (site B) were 89.8% and 120.3% of the grand mean, respectively (Table 4.1). The effect of sites for nine-year height is not surprising because of the broad spectrum of physiography and soil in this breeding region. The causes of the observed site effect, however, cannot be specifically identified, since elements important to tree growth such as soil nutrient level and moisture, temperature, and length of the growing season, have not been well defined for these sites. Highly

significant differences for family effects in the combined analysis across sites probably indicate planting by sets helped precision of family variance estimation as evident by the statistically significant set effect.

The distribution of variance in this study seems to correspond to patterns found in tests of young trees of most conifers (Rink and Thor 1976; Falkenhagen 1977; Khalil 1978; Yeh and Rasmussen 1985; Yeh and Heaman 1987). Although replications, set-by-replication, family-within-set, and plot error (replication-by-family-within-set interaction), were significant sources of variation in four of the sites, the largest percentage of the variation within individual sites was due to the within-plot effect (i.e. differences among trees within families)(from 62.4% for site B to 80.9% for site D). Variability among trees within open-pollinated families may be indicative of the large number of effective pollen parents and the maintenance of considerable genetic variability for outcrossing species. Differential responses of family members to within-site heterogeneity and variable degrees of inbreeding among the progenies from each seed tree could also contribute to the large within-plot variance.

The estimates of individual tree heritability for nine-year tree height on individual sites (from 0.120 to 0.177)(Table 4.4) were significantly lower than estimates of heritability of seedling height for the same families in the greenhouse (from 0.543 to 0.949)(Table 3.5). This difference is likely the result of either different efficiency of the designs between greenhouse and field tests or higher heterogeneity in field sites than greenhouse, or both. The non-contiguous single seedling plot design in the greenhouse is more efficient due to an increase in degrees of freedoms

for the residual variance, because the plot error was combined with the within-plot error. For example, the percentage of residual variance in the greenhouse for traits of height varied from 63 to 72% of the total variance, but in the four field sites the sum of percentage variances for plot and within-plot varied from 75% to 88% of the total variances. Controlled culture regimes and significantly smaller size of blocks in the greenhouse are probable causes of homogenous environment.

Family by test environment (GE) interaction was highly significant across sites and, could potentially have a major impact on breeding of lodgepole pine in this region. Thus, GE interaction should be analyzed to fully understand its causes and its impact on selection of nine-year tree height.

It is well known that performance of genotypes relative to each other can vary according to the testing environment. Genotypes which are superior in one environment may not be correspondingly superior elsewhere, or the degree of difference among genotypes may vary according to the test environment. These phenomena are defined as genotype-by-environment interactions (Haldane 1947, Burdon 1977). Genotype-by-environment interaction is important in many aspects of a breeding program. When such interaction is strong, tree breeders must decide whether to select for stability of performance and accept a slower rate of population improvement, or to develop populations specifically adapted to each environment and to maximize gain, but with greater program costs (Bridgwater and Stonecypher 1978, Gregorius and Namkoong 1986).

Genotype-by-environment interaction (GE) in field sites is important not only

for mature selection but also for early selection. Early selection appropriate for one site may not be appropriate for another site when there is strong GE interaction across sites. When evaluating the effectiveness of selection, it is imperative to determine whether the GE interaction on field sites is large enough to have a meaningful impact. There are two types of GE interaction, qualitative crossover and quantitative noncrossover. Crossover interaction involves change in the genotypic ranking from one environment to another. Thus, it reflects the lack of perfect correlation in the ranking of genotypes between the environments. Noncrossover interaction reflects heterogeneity of genotypic variance across environments (Baker 1988). In mature and early selection, only qualitative interaction is important because it alone will affect prediction of mature performance in different environments.

In theory, these two types of GE interaction may arise for two reasons (Cockerham 1963 and Yang 1990), one being the difference in response of the same set of genes to different environments, and the other being the expression of a different set of genes in different environments (Falconer 1952, Robertson 1959). When the same set of genes is expressed, response difference may be viewed as heterogeneity of genetic variance across environments. When different sets of genes are expressed, genetic correlations between pairs of environments for a trait are expected to be less than unity (Falconer 1981). Thus, GE interaction either reflects heterogeneity of genetic variance or lack of perfect genetic correlation between environments or both, as indicated by its components (Cockerham 1963 and Yamada 1962)

$$\sigma^2_{G*E} = \frac{1}{2}(\sigma_1 - \sigma_2)^2 + \sigma_1\sigma_2(1-r) \quad , \qquad (5)$$

where σ_1^2 and σ_2^2 are genetic variances in environments 1 and 2 and r is the genetic correlation between environments. Thus, based on equation 5, we can determine the causes of GE interaction by examining if $r_G \leq 1$ and if $\sigma_1^2 \neq \sigma_2^2$.

Since additive genetic variance is directly proportional to the family variance, a test of homogeneity of the family variances among sites is equivalent to a test of homogeneity of the genetic variances. Family variance for each site was estimated by equating mean squares to expected mean squares and solving appropriately (Table 4.3). Tests for homogeneity of genetic variances between pairs of sites were performed by a synthetic F-test. This F test was calculated as a ratio of the greater family variance to the smaller family variance. Degrees of freedom for the synthetic F test were calculated using Satterthwaite's approximation formula (Satterthwaite 1946). Results of six pair-wise F tests indicated a lack of significant heterogeneity of the genetic variances between these four sites (Table 4.5).

Since the between-site family and error variances were found to be homogeneous (Tables 4.5, 4.6), between-site genetic correlations (r) can be estimated using the linear model 1 following Yamada's method (1962) (see Chapter 5 and Appendices 5.1 and 5.2 for detailed description for this method). The appropriate formula for estimating the between-site genetic correlation (r) is:

$$r = \frac{\sigma^2_{f(t)}}{\sigma^2_{f(t)} + \sigma^2_{s*f(t)} - \theta(\sigma_i)} \qquad (6)$$

$$\text{where } \theta(\sigma_i) = \frac{(\sigma_{f(t)1} - \sigma_{f(t)2})^2}{2}$$

and where $\sigma_{f(t)}^2$ and $\sigma_{s*f(t)}^2$ are, respectively, the estimated variances for family-within-set and family-by-site from the combined site analysis, and $\sigma_{f(t)1}^2$ and $\sigma_{f(t)2}^2$ are the estimated family-within-set variances for the two sites being considered in the correlation.

Estimates of pair-wise genetic correlations between the four sites are given in Table 4.7 along with the family mean correlations. The 95% confidence interval of genetic correlation was computed (Table 4.7) by Fisher' transformation method (Steel and Torrie 1985, Kendall et al. 1987). This 95% confidence interval can be used to approximately test the null hypothesis that the genetic correlation is unity. The results indicated that pair-wise genetic correlations between sites differed significantly from unity. This suggests that family ranks changed across sites.

GE interaction due to family rank changes across sites is important in practical breeding and progeny testing. Because the GE interaction accounted for 78% of the family variance (computed from Table 4.2), breeders must decide whether to select stable families for overall sites and accept a slower rate of population improvement, or to develop breeding populations specifically adapted to different environments within this region and to maximize gain, but with greater program costs. It is unlikely that breeders in Alberta will develop different site-specific breeding populations for this region due to its small reforestation size, and financial and administrative

constraints. Certainly, this might involve some sacrifice of local growth potential because families that grew well only on one or some sites would be rejected.

The second question concerning the existence of GE interaction is what environmental differences may have contributed to the apparent interaction in this study. Environmental variation has been divided into predictable and unpredictable categories by Allard and Bradshaw (1964). Predictable and unpredictable variation can further be subdivided into cultural and natural environmental variation (Shelbourne 1972). Predictable cultural variation in the environment includes silviculture practices associated with intensive forestry; for example, thinning regimes, site preparation, and fertilization. Unpredictable cultural variation occurs when any of these practices is poorly implemented or their influence on forest stands is imperfectly understood. Predictable variation in the natural environment is usually associated with climate, physiography or soil, while unpredictable natural environmental variation is associated with the irregularity of weather. In cultural variation of the environment, many authors reported different fertilization and water stress treatments caused G x E interactions (Roberds et al. 1976, Doddard et al. 1976, Jiang 1988). The climatic differences among the four sites in this study are probably not major contributors to GE interaction because the four sites are located within less than half degree of latitude, one degree of longitude, and within 61m of elevation. Most likely, the broad spectrum of physiographic and soil variation among the sites contributed to the apparent GE interaction in this study. However, the specific physiographic and soil variation cannot be identified because factors

important to growth of lodgepole pine, such as soil nutrient level, moisture, temperature, and length of the growing season, have not been well defined for these four sites. Thus, further assessment of physical conditions such as soil nutrients and moisture on these sites are neccessary.

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Table 4.1 Location of four sites, height, and survival rate among 120 open-pollinated families after nine years from planting

Site	Latitude	Longitude	Elevation	Survival	Height (cm)
A	54°26'N	116°34'W	1033m	79%	194.47
B	54°28'N	115°37'W	1064m	85%	260.65
C	54°42'N	116°30'W	1003m	85%	204.52
D	54°43'N	116°34'W	1064m	84%	207.04

Table 4.2 Joint analyses of nine year tree height across four sites

Source of variation	D.F.	MS	EMS [a]	F	Pr.>F [b]
Site (s)	3	1779821	$\sigma_e^2+16.96\sigma_{s*f(t)}^2+0.18\sigma_{f(t)}^2+28.96\sigma_{t*r(s)}^2$ $+143.91\sigma_{t*s}^2+0.32\sigma_t^2+398.48\sigma_{r(s)}^2$ $+1991.5\sigma_s^2$	40.95	0.0001
Replication(site)	16	45728	$\sigma_e^2+0.18\sigma_{s*f(t)}^2+0.18\sigma_{f(t)}^2+28.95\sigma_{t*r(s)}^2$ $+0.20\sigma_{t*s}^2+0.20\sigma_t^2+398.35\sigma_{r(s)}^2$	6.24	0.0001
Set (t)	16	17999	$\sigma_e^2+16.83\sigma_{s*f(t)}^2+66.71\sigma_{f(t)}^2+23.33\sigma_{t*r(s)}^2$ $+115.76\sigma_{t*s}^2+461.81\sigma_t^2$	2.35	0.0125
Site*Set	48	4469	$\sigma_e^2+16.77\sigma_{s*f(t)}^2+0.15\sigma_{f(t)}^2+23.25\sigma_{t*r(s)}^2$ $+115.35\sigma_{t*s}^2$	0.66	0.9574
Set*Replication(Site)	256	6124	$\sigma_e^2+0.16\sigma_{s*f(t)}^2+0.16\sigma_{f(t)}^2+23.05\sigma_{t*r(s)}^2$	4.33	0.0001
Family(Set)	103	5058	$\sigma_e^2+16.612\sigma_{s*f(t)}^2+65.84\sigma_{f(t)}^2$	2.52	0.0001
Site*family(Set)	309	1998	$\sigma_e^2+16.41\sigma_{s*f(t)}^2$	1.43	0.0001
Residual	7216	1401	σ_e^2		
Total	7967				

[a] MS and EMS are mean squares and expected mean squares.
σ_e^2 - residual variance, $\sigma_{s*f(t)}^2$ - variance of site-by-family-within-set interaction,
$\sigma_{f(t)}^2$ - family variance within set, $\sigma_{t*r(s)}^2$ - variance of set-by-replication interaction,
σ_{t*s}^2 - variance of set-by-site interaction, σ_t^2 - set variance
$\sigma_{r(s)}^2$ -variance of replication within site, σ_s^2 - site variance.
[b] Pr.>F is probability of a larger F value.

Table 4.3 Analyses of variance of nine-year tree height at each of four individual sites

Site A

Source of variation	D.F.	MS	EMS [a]	F	Pr.>F [b]
Replication	4	72537	$\sigma_e^2+3.42\sigma_{r*f(t)}^2+0.22\sigma_{f(t)}^2+27.28\sigma_{r*t}^2$ $+0.26\sigma_t^2+379.12\sigma_r^2$	10.88	0.0001
Set	16	7622	$\sigma_e^2+3.41\sigma_{r*f(t)}^2+16.15\sigma_{f(t)}^2+22.21\sigma_{r*t}^2$ $+109.97\sigma_t^2$	1.148	0.3279
Set*Replication	64	5714	$\sigma_e^2+3.37\sigma_{r*f(t)}^2+0.19\sigma_{f(t)}^2+21.94\sigma_{r*t}^2$	3.106	0.0001
Family(Set)	103	2675	$\sigma_e^2+3.31\sigma_{r*f(t)}^2+15.62\sigma_{f(t)}^2$	1.471	0.0057
Replication*family(Set)	408	1783	$\sigma_e^2+3.11\sigma_{r*f(t)}^2$	1.426	0.0001
Residual	1300	1251	σ_e^2		
Total	1895				

Site B

Source of variation	D.F.	MS	EMS	F	Pr.>F
Replication	4	44173	$\sigma_e^2+3.59\sigma_{r*f(t)}^2+0.18\sigma_{f(t)}^2+29.77\sigma_{r*t}^2$ $+0.19\sigma_t^2+405.18\sigma_r^2$	3.688	0.0104
Set	16	6164	$\sigma_e^2+3.55\sigma_{r*f(t)}^2+16.99\sigma_{f(t)}^2+23.63\sigma_{r*t}^2$ $+117.32\sigma_t^2$	0.577	0.8923
Set*Replication	64	9849	$\sigma_e^2+3.53\sigma_{r*f(t)}^2+0.17\sigma_{f(t)}^2+23.42\sigma_{r*t}^2$	4.907	0.0001
Family(Set)	103	2762	$\sigma_e^2+3.50\sigma_{r*f(t)}^2+16.75\sigma_{f(t)}^2$	1.387	0.0141
Replication*family(Set)	406	1958	$\sigma_e^2+3.36\sigma_{r*f(t)}^2$	1.693	0.0001
Residual	1432	1156	σ_e^2		
Total	2025				

Site C

Source of variation	D.F.	MS	EMS	F	Pr.>F
Replication	4	27486	$\sigma_e^2+3.57\sigma_{r*f(t)}^2+0.16\sigma_{f(t)}^2+29.01\sigma_{r*t}^2+0.17\sigma_t^2+406.13\sigma_r^2$	7.657	0.0001
Set	16	9821	$\sigma_e^2+3.57\sigma_{r*f(t)}^2+17.21\sigma_{f(t)}^2+23.73\sigma_{r*t}^2+117.87\sigma_t^2$	2.486	0.0040
Set*Replication	64	3228	$\sigma_e^2+3.54\sigma_{r*f(t)}^2+0.13\sigma_{f(t)}^2+23.54\sigma_{r*t}^2$	1.874	0.0039
Family(Set)	103	2406	$\sigma_e^2+3.49\sigma_{r*f(t)}^2+16.79\sigma_{f(t)}^2$	1.407	0.0110
Replication*family(Set)	409	1689	$\sigma_e^2+3.35\sigma_{r*f(t)}^2$	1.424	0.0001
Residual	1434	1186	σ_e^2		
Total	2030				

Site D

Source of variation	D.F.	MS	EMS	F	Pr.>F
Replication	4	38715	$\sigma_e^2+3.57\sigma_{r*f(t)}^2+0.16\sigma_{f(t)}^2+29.75\sigma_{r*t}^2+0.20\sigma_t^2+402.99\sigma_r^2$	5.730	0.0007
Set	16	7797	$\sigma_e^2+3.52\sigma_{r*f(t)}^2+16.80\sigma_{f(t)}^2+23.52\sigma_{r*t}^2+116.64\sigma_t^2$	1.114	0.3570
Set*Replication	64	5704	$\sigma_e^2+3.48\sigma_{r*f(t)}^2+0.16\sigma_{f(t)}^2+23.28\sigma_{r*t}^2$	2.910	0.0001
Family(Set)	103	3210	$\sigma_e^2+3.48\sigma_{r*f(t)}^2+16.68\sigma_{f(t)}^2$	1.640	0.0004
Replication*family(Set)	407	1931	$\sigma_e^2+3.34\sigma_{r*f(t)}^2$	1.477	0.0001
Residual	1420	1307	σ_e^2		
Total	2014				

[a] MS and EMS are mean squares and expected mean squares.
σ_e^2 - residual variance, $\sigma_{r*f(t)}^2$ - variance of replication-by-family-within-set interaction, $\sigma_{f(t)}^2$ - family variance within set, σ_{r*t}^2 - variance of replication-by-set interaction, σ_t^2 - set variance, and σ_r^2 -variance of replication.
[b] Pr.>F is probability of a larger F value.

Table 4.4 Estimates of individual (h_i^2), family (h_f^2) heritabilities, and their standard error (s.e.) of nine-year tree height among 120 open-pollinated families on four sites

Site	A	B	C	D
Individual h_i^2	0.148	0.127	0.120	0.177
s.e.	0.039	0.032	0.030	0.041
Family h_f^2	0.320	0.278	0.289	0.392
s.e.	0.025	0.021	0.023	0.031

Table 4.5 Pairwise test of homogeneity of family variances of nine-year tree height among four sites

Site pair	AB	AC	AD	BC	BD	CD
F-value	1.195	1.323	1.378	1.107	1.647	1.823
f_1[a]	9.44	9.44	14.53	7.02	14.53	14.53
f_2	7.02	7.65	9.44	9.65	7.02	7.65
Pr>F[b]	0.4172	0.3563	0.3150	0.4429	0.2583	0.2035

[a] f_1 and f_2 are degrees of freedom of numerator and denominator in the F-test.
[b] Pr>F is probability under null hypothesis that two variances are equal (if Pr>F is less than 0.025, then there is significant difference between two variances at 5% probability level since the null hypothesis test is a two-tail hypothesis test (Steel and Torrie 1985)).

Table 4.6 Pairwise test of homogeneity of error variances of nine-year tree height among four sites

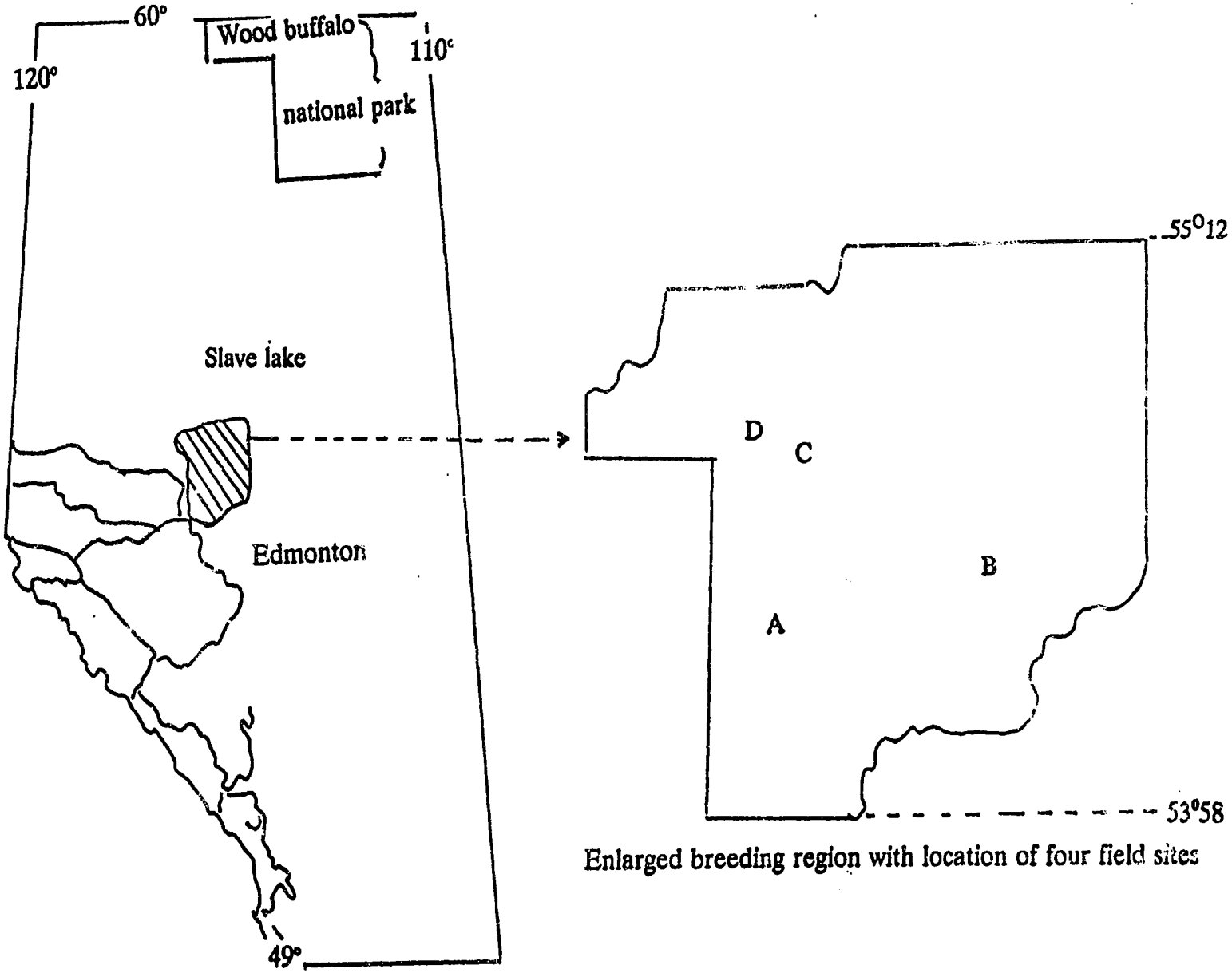
Site pair	AB	AC	AD	BC	BD	CD
F-value	1.081	1.054	1.045	1.026	1.120	1.101
f_1	1300	1300	1300	1432	1432	1434
f_2	1432	1434	1420	1434	1420	1420
Pr>F	0.075	0.165	0.170	0.314	0.026	0.035

[a] f_1 and f_2 are degrees of freedom of numerator and denominator in the F-test.
[b] Pr>F is probability under null hypothesis that two variances are equal (if Pr>F is less than 0.025, then there is significant difference between two variances at 5% probability level since the null hypothesis test is a two-tail hypothesis test (Steel and Torrie 1985)).

Table 4.7 Estimates of family-mean correlations (r_f) and genetic correlations (r_g) for nine-year tree height for pairs of four sites and 95% confidence interval of genetic correlations

Site pair	AB	AC	AD	BC	BD	CD
r_f	0.364	0.338	0.199	0.326	0.192	0.367
Pr.[a]	0.0001	0.0002	0.0296	0.0003	0.0362	0.0001
r_g	0.7308	0.6807	0.4862	0.6320	0.3234	0.6013
low limit [b]	0.640	0.575	0.345	0.514	0.244	0.473
upper limit	0.805	0.768	0.610	0.735	0.568	0.702

[a] Pr. is probability of a larger F value.
[b] low and upper limit represent the limits of 95 % confidence interval.



Enlarged breeding region with location of four field sites

Figure 4.1 Geographic location of breeding region for 224 open-pollinated families

CHAPTER FIVE

ESTIMATION OF EARLY-MATURE GENETIC CORRELATIONS

1. INTRODUCTION

Genetic correlations among traits are usually estimated when the traits have been measured on the same individuals. In this case, the genetic covariance component among traits can be estimated by the same linear model used to estimate the components of genetic variance. Correlations obtained in this manner have been designated as type A genetic correlations. When the traits are measured on different individuals within the same genetic groups, genetic correlations between traits have been designated as type B genetic correlations (Burdon 1977). Examples of type B genetic correlations are correlations between siblings tested at the same age but on different sites, or the special case when siblings are measured at different ages and on different sites as in retrospective early testing studies. The methods of estimating type B genetic correlations are different from those of estimating type A genetic correlations, since the linear model used to estimate components of genetic variance cannot be used to estimate genetic covariance. This chapter describes estimation of type B genetic correlations in general and its application to lodgepole pine.

2. METHODS FOR ESTIMATING TYPE B GENETIC CORRELATIONS

Two methods can be used to estimate the genetic correlation between "traits" (the same or different traits) in two environments. The first is the covariance method (or combined ANOVA with ANOCOVA method, Yamada et al.1988), in which the covariance between the traits and the variances of each of the component traits are estimated separately. The genetic correlation is then estimated from the ratio of between-traits family covariance to the square root of the product of family variances on each environment. The second method handles the same or different traits in two environments as a main effect in a linear model. Regardless of the experimental designs in the two environments, the genetic correlation is then derived from the genetic group variance and the interaction variance between this main effect and the genetic group effect (it is often referred as genotype-environment (GE) interaction) in a framework of two-way analyses of variance as in equation 3 of Appendix 5.2. This method will be designated as the linear model method in this thesis. Robertson (1959) first derived the theoretical relationship between the parameters of the t methods, under the restriction of homogeneous genetic and error variances between the traits in two environments in balanced data. Yamada (1962) extended the linear model method to the situation of heterogenous genetic variances between the traits in two environments in the balanced data. When data are balanced, an adjustment can be made for differences in genetic variances between two environments in order to obtain an unbiased estimate of genetic correlation (Yamada 1962). Fernando et

al. (1984) suggested that the direct application of Yamada's (1962) method would give a biased estimate of the genetic covariance for unbalanced data unless the traits have identical genetic and error variances in the two environments. However, Yamada et al. (1988) and Itoh et al. (1990) have shown that application of Yamada's (1962) method would still give an unbiased estimate of genetic correlation if the following two conditions are assumed. These conditions are: (1) covariances between genetic group effects and interaction effects exist; (2) covariances among interaction effects exist. However, conditions (1) and (2) outlined by Yamada et al. (1988) and Itoh et al. (1990) are not assumed in a usual ANOVA linear model because one must assume the covariances between genetic group effects and interaction effects, and the covariances between the interaction effects are zero in the linear model in order to estimate variance components. Thus, when conditions (1) and (2) are not assumed in the usual linear model, such as in the fitting constant method (Searle 1987), it is necessary to assume that genetic and error variances are homogenous for the linear model method. The detailed reason is illustrated in Appendix 5.1.

The assumption of homogenous genetic and error variances needed to obtain unbiased estimates of genetic correlation from the linear model method with unbalanced data may not be met for two traits in two environments. But there are possible ways to make the genetic variances or error variances or both homogeneous. Data standardization or data transformation are two examples. If data standardization or an appropriate data transformation could make both genetic and error variances homogenous, the linear model could still be used to estimate unbiased

genetic correlation.

The major utility of the linear model method results from the fact that in many complex experiment designs, unbiased estimates of genetic correlation can be directly estimated by the linear model method. In the covariance method, regardless of the experimental design, family mean covariance is used to estimate genetic covariance. Estimates of genetic covariance from family mean covariance in some experimental designs, such as family nested within sets, or family nested within provenances, will be biased. For example, family mean covariance in Chapter Four of this thesis was not appropriate for estimating genetic covariance due to the inclusion of set covariance between two sites and covariances between set effects in one site and family effects in the other. However, the linear model method can be used directly to attain unbiased estimates of genetic correlation in this situation if genetic and error variances are homogeneous. Since set effects could be adjusted before family and family-by-environment variances are estimated in the linear model (see Searle 1971), the estimated family and family-by-environment variances would be free from set effects. Thus, genetic correlation estimated from the estimates of family variance and family-by-environment variance in the linear model method are unbiased. Similarly, one can adjust original observations for set or provenance effect and use adjusted values or use least square estimates of family effects to calculate family covariance.

3. ESTIMATION OF GREENHOUSE-FIELD CORRELATIONS IN LODGEPOLE PINE

Seeds from 120 open-pollinated families of lodgepole pine from a breeding region in central Alberta (see Chapter Three of this thesis for details) were provided by the Alberta Forest Service. Four of the 120 families were excluded from the greenhouse study due to low germination. In the remaining 116 families, six families were not outplanted in the particular four field sites studied in Chapter Four of this thesis. Thus, the common 110 families were the sources for greenhouse and field correlation studies.

3.1 Family mean correlations

Due to significant family-by-site interaction for nine-year tree height, both family-means for nine-year height across all field sites and for individual sites, were correlated with different greenhouse traits. Two correlation coefficients of family means were computed:

(1) Pearson product-moment correlation (Steel and Torrie 1985), and

(2) Spearmann rank correlation (Steel and Torrie 1985).

The Pearson product-moment correlation is a parametric measure of linear association between two variables and a test of significant of the correlation is only valid if the association between the variables has a bivariate normal distribution. The Spearmann rank correlation is a nonparametric measure of association between ranks

of two variables and can be used to test significance of association between two variables without distribution assumptions. Estimates of these two correlations between greenhouse traits and nine-year tree height, and the probability under the null hypothesis that the correlation is zero, are given in Tables 5.1, 5.2, 5.3, 5.4, and 5.5. It is evident that greenhouse traits did not significantly correlate with the average of nine-year tree height across sites, or with nine-year tree height on sites A, C and D. However, on site B, nine-year tree height correlated significantly at the 5% probability level with basal diameter at harvest (D8) and height increment during the dormancy induction period (HG2). In addition, seven correlations between greenhouse traits (H4, H5, H7, D7, DG, BRN1, BRN2) and nine-year tree height on site B were significant at the 10% probability level. Ten Spearmann rank correlations between greenhouse traits (H3, H4, H5, H6, H7, D7, DG, BUDS, BRN1, BRN2) and nine-year tree height on site B were significant at the 10% probability level.

3.2 Genetic correlations

Genetic correlation (r) between a greenhouse trait (x) and nine-year tree height (y) can be estimated with the covariance method by the following equation:

$$r = \frac{cov(f_x\ f_y)}{\sqrt{\sigma^2_{f_x}\ \sigma^2_{f_y}}} \qquad (1)$$

where $cov(f_x\ f_y)$ is family covariance between x and y, and $\sigma_{f_x}^2$ and $\sigma_{f_y}^2$ are family variances of x and y, respectively. The family covariance between a greenhouse trait and nine-year tree height was estimated from the family-mean covariance, and family

variance was estimated based on the following equation:

$$Y_{ij} = \mu + F_i + E_{ij} \quad (2)$$

where F_i is family effects

E_{ij} is residual error.

Equation (2) was used because the greenhouse and field test designs and their corresponding linear models to estimate variance components were different. When family variances were estimated from differing linear models, the corresponding family-mean covariance cannot be used to estimate family covariance and genetic correlation since family-mean covariance not only include family covariance but also several confounding components as described below. The statistical model for analysis in the greenhouse was

$$Y_{ijk} = \mu + S_i + F_{j(i)} + R_k + SR_{ik} + E_{ijk}\ , \quad (3)$$

where μ - grand mean

S_i - i^{th} stand effect

$F_{j(i)}$ - j^{th} family effect within the i^{th} stand

R_k - k^{th} replication effect

SR_{ik} - replication by stand interaction

E_{ijk} - residual error.

The corresponding family mean is

$$\overline{Y_{ij.}} = \mu + S_i + F_{j(i)} + \overline{SR_{i.}}, \quad (4)$$

The statistical model for analysis of nine-year tree height within individual site was

$$X_{lmno} = \mu + R_l + T_m + R*T_{lm} + F_{n(m)} + R*F_{ln}(m) + E_{lmno}, \quad (5)$$

where μ - grand mean

R_l - l^{th} replication effect

T_m - m^{th} set effect

$R*T_{lm}$ - replication-by-set interaction

$F_{n(m)}$ - n^{th} family effect within set

$R*F_{ln(m)}$ - replication-by-family-within-set interaction

E_{lmno} - residual error.

The corresponding family mean is

$$\overline{X_{.mn.}} = \mu + T_m + \overline{R*T_{.m}} + F_{n(m)} + \overline{R*F_{.n(m)}}, \quad (6)$$

Therefore, family mean covariance between a greenhouse trait and nine-year tree height within individual sites is

$$\begin{aligned} cov(\overline{Y_{ij.}}\ \overline{X_{.mn.}}) = {} & cov(S_i\ T_m) + cov(S_i\ \overline{RT_{.m}}) + cov(S_i\ \overline{F_{n(m)}}) \\ & + cov(S_i\ \overline{RF_{.n(m)}}) + cov(\overline{RS_{.i}}\ T_m) + cov(\overline{RS_{.i}}\ \overline{RT_{.m}}) \\ & + cov(\overline{RS_{.i}}\ \overline{F_{n(m)}}) + cov(\overline{RS_{.i}}\ \overline{RF_{.n(m)}}) + cov(F_{j(i)}\ T_m) \\ & + cov(F_{j(i)}\ \overline{RT_{.m}}) + cov(F_{j(i)}\ F_{n(m)}) + cov(F_{j(i)}\ \overline{RT_{.n(m)}}). \end{aligned} \quad (7)$$

Thus, when equations 3 and 5 are used to estimate family variances, the family covariance estimated from family-mean covariance would be biased upward unless

all components except cov($F_{j(i)}$ $F_{n(m)}$) in equation 7 were zero. This is unlikely for the lodgepole pine greenhouse and field studies. For example, the component, cov(S_i T_m), could not be zero as sets and stands had families in common. Only the families were common between the greenhouse and field test designs. Therefore, only equation 2 can be used to estimate the genetic correlation between a greenhouse trait and nine-year tree height in this lodgepole pine study using the covariance method.

The genetic correlation between a greenhouse trait and nine-year tree height on site B was also estimated using the linear model method (Yamada et al. 1988). The procedure and results are in Appendix 5.2. They were computed for comparison purposes with the genetic correlation estimates derived from the covariance method.

Estimates of genetic correlations (r) between greenhouse traits and nine-year tree height across all sites, and between greenhouse traits and nine-year tree height at each site individually are given in Tables 5.1 and 5.6, respectively. Five of 28 greenhouse traits (HG2, HG3, SR, BUDS, and BRN1) correlated at the 5% or 1% levels of probability with nine-year tree height across sites. Estimates of genetic correlations between greenhouse traits and nine-year tree height varied considerably among the four sites. On site C, none of the 28 estimates of r were significant, even at the 10% level of probability. Only four of 28 estimates of r on site A (HG3, SR, BUDN and BRN1) and site D (HG1, BUDN, BUDS and BRS) were significant at the 5% or 1 % levels of probability. This contrasts sharply with site B, where only four greenhouse traits (HG1, BB, RHD and BRS) did not significantly correlate with nine-year tree height. The greenhouse traits most highly correlated with nine-year

tree height on site B were HG2 (0.5027), D8 (0.3624), DG (0.3675), BRN1 (0.3411) and SR (0.3286). Estimates of genetic correlations between greenhouse traits and nine-year tree height on site B by the linear model method after the data were standardized, were similar to the estimates from the covariance method (see Appendix 5.2, Tables 5.7, 5.8, and 5.9). Estimates of genetic correlations between greenhouse traits and nine-year tree height across sites and individual site B were greater than estimates of their corresponding family-mean correlations (see for example, Table 5.1 for across sites, and Tables 5.3, 5.6 for site B).

4. DISCUSSION

In general, seedling traits were correlated genetically with nine-year tree height only on site B. This is not surprising since significant genotype-by-environment interaction in nine-year tree height was observed. The reasons why there were many significant genetic correlations between nine-year tree height on site B and greenhouse traits, but essentially few in the other sites may be due to different site conditions. However, as detailed physical and climatic conditions for the four sites are not well defined, one can only speculate about the observed patterns of the genetic correlation estimates from the analysis of nine-year tree height on individual sites. Site B is the most productive of the four sites; nine-year tree height after planting averaged 260.65 cm. This is significantly greater than the nine-year tree height in sites A (194.47 cm), C (204.52 cm) and D (207.04 cm). This suggests that

growth conditions for nine-year lodgepole pine were probably more optimal in site B, relative to growth conditions on the other sites. Growth conditions for lodgepole pine in greenhouse were optimized by regular watering, fertilization, temperature and lighting control. Therefore, the existence of correlations for site B may indicate that growth conditions for lodgepole pine on site B were closer to the greenhouse conditions than the other sites. This supports the suggestion based on results of earlier studies, that early tests should be conducted under simulated field conditions (Lambeth 1983, Cannell et al. 1978).

The observation that genetic correlations existed between most greenhouse traits and nine-year tree height on site B and few genetic correlation existed between greenhouse traits and nine-year tree height on the other three sites has major implications for implementing early selection in tree improvement of lodgepole pine. Breeders can either implement early selection for broadly adapted families across sites or for families that are adapted only to site B. However, it may not be safe to select for families adapted only to site B to supply the seed requirements of this breeding region. From a practical consideration of lodgepole pine breeding in Alberta, early testing for performance in site B only may not be adequate. Thus, the breeder may sacrifice the specific genetic correlations between greenhouse traits and nine-year tree height on site B and select best families for all sites using the five greenhouse traits (HG2, HG3, BUDS, BUN1 and SR), which exhibited significant genetic correlations with the average of nine-year tree height across sites.

In this study, family-mean correlations may be poor indicator of genetic

correlations between greenhouse traits and nine-year tree height. This may indicate family-mean correlations should not be used to assess the effectiveness of early selection in lodgepole pine in Alberta. The finding that genetic correlation estimates are greater than family-mean correlations has been observed in many other early-mature correlation studies (Lambeth 1983, Loo et al. 1984, Cotterill and Dean 1988, Riemenschneider 1988). The early trait which best correlated with nine-year tree height across all sites was SR (Table 5.1), while early traits HG2 was best correlated with nine-year tree height on site B (Table 5.6). These may suggest that traits of adaptive value (such as SR) and traits of early growth potential (such as HG2) may be more promising for early selection of growth in lodgepole pine in Alberta.

In the lodgepole pine in this study, height growth in the second growth period (HG3) was significantly correlated with nine-year tree height across sites, and at sites A and B. However, height growth in the first growth period (HG1) had actually zero correlation with nine-year tree height across sites, and for sites A and B. This corroborates the observation in an early selection study of loblolly pine conducted by Williams (1987) that height increment in the second growth period was well correlated with field height, but height increment in the first growth period was negatively correlated with field height. This may be, in part, due to effects of germination and transplanting shock. Thus, height growth in the first growth period does not appear to be useful for early selection. Shoot to root weight ratio of seedlings was found to be the best predictor of field growth in loblolly pine (Waxler and van Buijtenen 1981). However, in another loblolly pine study, Cannell et

al.(1978) found that this ratio in a mild-stressed seedling test environment was negatively correlated with field performance under well-drained field condition. They argued that a superior bole volume-producer on better-drained sites avoids water stress by producing an extensive root system. In this study of lodgepole pine, the shoot to root ratio (SR) had a significant positive genetic correlation with nine-year tree height across sites, and on sites A and B. This may suggest that SR under free growing conditions is a useful early trait for selection in lodgepole pine.

In loblolly pine (Lambeth 1983) and in an earlier retrospective study with lodgepole pine (Jiang 1988), dry weight of seedlings was correlated better with field performance than seedling height or diameter. But in this study, seedling height and diameter were correlated better with nine-year tree height than biomass traits. These results suggest that population parameters such as genetic correlations should always be interpreted with caution because they are applicable only to the defined base population and reference test environments.

Early-mature genetic correlations are only one aspect of early selection. To fully understand the potential of early selection, it is necessary to study the efficiency of early selection, which is the content of the next chapter.

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Table 5.1 Estimated family mean and genetic correlations between greenhouse traits and nine-year tree height across four sites [a]

Trait	H1	H2	H3	H4	H5	H6	H7	D3	D7	D8
Pearson [b]	0.014	0.001	0.041	0.051	0.063	0.053	0.077	0.092	0.064	0.050
Pr.[c]	0.893	0.981	0.678	0.598	0.523	0.582	0.437	0.303	0.519	0.606
Spearmann	0.009	0.008	0.033	0.041	0.044	0.023	0.065	0.085	0.052	0.056
Pr.	0.998	0.979	0.705	0.612	0.696	0.775	0.503	0.372	0.614	0.564
Genetic	0.018	0.001	0.056	0.072	0.090	0.079	0.112	0.135	0.094	0.075
Pr.	0.425	0.496	0.279	0.226	0.174	0.204	0.123	0.081	0.165	0.219

Trait	HG1	HG2	HG3	DG	BUDN	BUDS	BRN1	BRS	BRN2
Pearson	-0.02	0.130	0.119	0.032	0.024	0.130	0.108	0.020	0.074
Pr.	0.832	0.223	0.237	0.738	0.874	0.198	0.243	0.834	0.457
Spearmann	-0.03	0.113	0.107	0.034	0.024	0.112	0.097	0.033	0.069
Pr.	0.784	0.260	0.280	0.727	0.812	0.231	0.204	0.793	0.503
Genetic	-0.05	0.252	0.206	0.059	0.052	0.211	0.177	0.035	0.107
Pr.	0.684	0.004**	0.015*	0.271	0.297	0.014*	0.032*	0.359	0.133

Trait	SB	BB	NB	RB	TLB	GB	HI	SR	RHD
Pearson	0.044	0.008	0.050	0.036	0.040	0.050	0.041	0.159	0.046
Pr.	0.634	0.412	0.602	0.734	0.682	0.602	0.681	0.093	0.643
Spearmann	0.018	0.013	0.046	0.019	0.032	0.040	0.032	0.134	0.045
Pr.	0.843	0.872	0.646	0.833	0.714	0.621	0.719	0.112	0.663
Genetic	0.067	0.013	0.070	0.057	0.066	0.067	0.065	0.270	0.083
Pr.	0.244	0.448	0.235	0.276	0.248	0.245	0.249	0.002**	0.195

[a] see Appendix 3.2 for description of traits.
[b] Pearson - Pearson product-moment correlation; Spearmann - Spearmann rank correlation; Genetic - genetic correlation.
[c] Pr. is probability under null hypothesis that correlation is equal to zero.
*, ** represent significant levels at 5% and 1%.

Table 5.2 Estimated family mean correlations between greenhouse traits and nine-year tree height of site A [a]

Trait	H1	H2	H3	H4	H5	H6	H7	D3	D7	D8
Pearson [b]	-0.02	0.011	0.027	0.023	0.024	0.033	0.058	0.062	0.025	0.039
Pr.[c]	0.842	0.912	0.774	0.813	0.800	0.732	0.547	0.520	0.795	0.683
Spearmann	-0.05	-0.01	0.006	-0.01	-0.14	-0.02	0.025	-0.02	-0.01	0.009
Pr.	0.602	0.948	0.952	0.922	0.881	0.833	0.795	0.860	0.881	0.925

Trait	HG1	HG2	HG3	DG	BUDN	BUDS	BRN1	BRS	BRN2
Pearson	0.054	0.029	0.087	-0.02	0.079	0.070	0.095	-0.01	0.086
Pr.	0.572	0.756	0.361	0.877	0.411	0.467	0.320	0.938	0.304
Spearmann	0.030	0.018	0.039	-0.03	0.013	0.025	0.081	-0.06	0.076
Pr.	0.753	0.850	0.680	0.777	0.892	0.795	0.395	0.540	0.423

Trait	SB	BB	NB	RB	TLB	GB	HI	SR	RHD
Pearson	0.014	-0.03	0.034	0.003	0.219	0.027	0.048	0.172	0.057
Pr.	0.884	0.746	0.719	0.974	0.819	0.776	0.617	0.072	0.552
Spearmann	-0.02	-0.01	-0.01	-0.02	-0.01	-0.01	0.003	0.082	0.029
Pr.	0.850	0.972	0.949	0.843	0.909	0.920	0.979	0.394	0.765

[a] see Appendix 3.2 for description of traits.
[b] Pearson - Pearson product-moment correlation; Spearmann - Spearmann rank correlation.
[c] Pr. is probability under null hypothesis that correlation is equal to zero.
*, ** represent significant levels at 5% and 1%.

Table 5.3 Estimated family mean correlation between greenhouse traits and nine-year tree height of site B [a]

Trait	H1	H2	H3	H4	H5	H6	H7	D3	D7	D8
Pearson [b]	0.138	0.106	0.155	0.173	0.166	0.155	0.172	0.151	0.174	0.194
Pr.[c]	0.150	0.266	0.104	0.069	0.081	0.105	0.071	0.114	0.068	0.042*
Spearman	0.112	0.137	0.176	0.178	0.174	0.163	0.178	0.117	0.178	0.189
Pr.	0.243	0.153	0.064	0.062	0.068	0.087	0.062	0.222	0.062	0.048*
Trait	HG1	HG2	HG3	DG	BUDN	BUDS	BRN1	BRS	BRN2	
Pearson	-0.02	0.209	0.145	0.159	0.085	0.116	0.167	-0.01	0.117	
Pr.	0.880	0.030*	0.130	0.095	0.374	0.226	0.081	0.979	0.076	
Spearman	-0.01	0.229	0.147	0.173	0.056	0.172	0.181	0.028	0.192	
Pr.	0.997	0.016*	0.123	0.070	0.558	0.071	0.057	0.766	0.051	
Trait	SB	BB	NB	RB	TLB	GB	HI	SR	RHD	
Pearson	0.132	0.036	0.124	0.094	0.119	0.123	0.089	0.156	0.061	
Pr.	0.168	0.703	0.195	0.326	0.213	0.199	0.352	0.102	0.525	
Spearman	0.147	0.045	0.124	0.141	0.130	0.136	0.105	0.049	0.045	
Pr.	0.125	0.635	0.194	0.139	0.175	0.154	0.272	0.607	0.639	

[a] see Appendix 3.2 for description of traits.
[b] Pearson - Pearson product-moment correlation; Spearmann - Spearmann rank correlation.
[c] Pr. is probability under null hypothesis that correlation is equal to zero.
*, ** represent significant levels at 5% and 1%.

Table 5.4 Estimated family mean correlations between greenhouse traits and nine-year tree height of site C [a]

Trait	H1	H2	H3	H4	H5	H6	H7	D3	D7	D8
Pearson [b]	-0.06	-0.07	-0.05	-0.05	-0.04	-0.04	-0.02	0.020	-0.02	-0.06
Pr.[c]	0.549	0.489	0.638	0.630	0.696	0.697	0.835	0.834	0.831	0.528
Spearman	-0.05	-0.03	-0.02	-0.31	-0.03	-0.05	-0.01	0.005	-0.05	-0.08
Pr.	0.627	0.748	0.818	0.746	0.765	0.642	0.892	0.958	0.620	0.391

Trait	HG1	HG2	HG3	DG	BUDN	BUDS	BRN1	BRS	BRN2
Pearson	-0.05	0.044	0.028	-0.05	-0.01	0.044	-0.01	-0.04	-0.02
Pr.	0.639	0.648	0.768	0.641	0.880	0.644	0.880	0.644	0.881
Spearman	-0.05	0.049	0.021	-0.05	-0.04	0.091	-0.01	-0.07	-0.02
Pr.	0.605	0.607	0.823	0.608	0.657	0.339	0.907	0.478	0.891

Trait	SB	BB	NB	RB	TLB	GB	HI	SR	RHD
Pearson	-0.03	-0.03	-0.01	-0.01	-0.01	-0.01	-0.05	0.046	-0.02
Pr.	0.728	0.749	0.934	0.918	0.888	0.882	0.618	0.631	0.845
Spearman	-0.04	-0.03	-0.04	-0.06	-0.04	-0.04	-0.01	-0.02	0.020
Pr.	0.706	0.748	0.675	0.537	0.671	0.655	0.999	0.809	0.833

[a] see Appendix 3.2 for description of traits.
[b] Pearson - Pearson product-moment correlation; Spearmann - Spearmann rank correlation.
[c] Pr. is probability under null hypothesis that correlation is equal to zero.
*, ** represent significant levels at 5% and 1%.

Table 5.5 Estimated family mean correlations between greenhouse traits and nine-year tree height of site D [a]

Trait	H1	H2	H3	H4	H5	H6	H7	D3	D7	D8
Pearson	-0.04	-0.07	-0.05	-0.04	-0.03	-0.04	-0.02	0.024	0.029	-0.01
Pr.	0.665	0.444	0.574	0.669	0.794	0.664	0.802	0.799	0.759	0.966
Spearman	-0.01	-0.05	-0.03	-0.02	0.003	-0.02	0.006	0.035	0.058	0.014
Pr.	0.921	0.640	0.764	0.812	0.975	0.863	0.951	0.719	0.548	0.883
Trait	HG1	HG2	HG3	DG	BUDN	BUDS	BRN1	BRS	BRN2	
Pearson	-0.08	0.046	0.029	0.034	-0.11	0.081	0.016	0.090	0.017	
Pr.	0.353	0.627	0.763	0.725	0.249	0.395	0.860	0.344	0.834	
Spearman	-0.09	0.036	0.039	0.076	-0.09	0.116	0.033	0.095	0.045	
Pr.	0.344	0.707	0.680	0.424	0.327	0.226	0.728	0.318	0.705	
Trait	SB	BB	NB	RB	TLB	GB	HI	SR	RHD	
Pearson	-0.01	0.064	-0.01	0.034	0.003	-0.01	-0.01	0.056	-0.06	
Pr.	0.930	0.504	0.888	0.723	0.973	0.941	0.971	0.555	0.511	
Spearman	0.031	0.077	-0.02	0.021	0.012	-0.01	0.017	-0.01	-0.03	
Pr.	0.748	0.423	0.879	0.821	0.893	0.975	0.854	0.916	0.767	

[a] see Appendix 3.2 for description of traits.
[b] Pearson - Pearson product-moment correlation; Spearmann - Spearmann rank correlation.
[c] Pr. is probability under null hypothesis that correlation is equal to zero.
*, ** represent significant levels at 5% and 1%.

Table 5.6 Estimated genetic correlations (r) between greenhouse traits and nine-year tree height of each individual site and probability level [a]

Site	A		B		C		D	
	r	Pr>r[b]		Pr>r	r	Pr>r	r	Pr>r
H1	-0.029	0.6191	0.2226	0.0097**	-0.0780	0.7911	-0.0618	0.7393
H2	0.0167	0.4310	0.1795	0.0303*	-0.0938	0.8352	-0.1137	0.8816
H3	0.0447	0.3213	0.2663	0.0025**	-0.0650	0.7502	-0.0852	0.8119
H4	0.0377	0.3478	0.3053	0.0006**	-0.0682	0.7607	-0.0664	0.7549
H5	0.0409	0.3356	0.2959	0.0009**	-0.0559	0.7193	-0.0408	0.6642
H6	0.0548	0.2848	0.2727	0.0020**	-0.0553	0.7169	-0.0675	0.7583
H7	0.0942	0.1639	0.3118	0.0005**	-0.0376	0.6517	-0.0498	0.6973
D3	0.1065	0.1339	0.2753	0.0018**	0.0308	0.3746	0.0409	0.3354
D7	0.0417	0.3326	0.3177	0.0004**	-0.0336	0.6362	0.0466	0.3143
D8	0.0695	0.2352	0.3624	0.0001**	-0.0952	0.8387	-0.0069	0.5286
HG1	0.1125	0.1208	-0.032	0.6286	-0.0830	0.8055	-0.1800	0.9701*
HG2	0.0681	0.2399	0.5027	0.0000**	0.0889	0.1777	0.1037	0.1405
HG3	0.1783	0.0312*	0.3116	0.0005**	0.0511	0.2982	0.0572	0.2764
DG	-0.032	0.6311	0.3675	0.0001**	-0.0867	0.8162	0.0716	0.2286
SB	0.0251	0.3973	0.2505	0.0042**	-0.0531	0.7093	-0.0146	0.5602
BB	-0.054	0.7141	0.0679	0.2403	-0.0478	0.6900	0.1094	0.1274
NB	0.0600	0.2666	0.2281	0.0083**	-0.0123	0.5506	-0.0228	0.5934
RB	0.0058	0.4759	0.1887	0.0242*	-0.0165	0.5681	0.0626	0.2579
TLB	0.0383	0.3454	0.2207	0.0102**	-0.0209	0.5861	0.0054	0.4776
GB	0.0471	0.3124	0.2249	0.0091**	-0.0218	0.5894	-0.0118	0.5489
HI	0.0908	0.1729	0.1783	0.0312*	-0.0802	0.7976	-0.0063	0.5261
SR	0.3417	0.0001**	0.3286	0.0002**	0.0815	0.1987	0.1098	0.1266
RHD	0.1205	0.1049	0.1364	0.0776	-0.0351	0.6420	-0.1295	0.9112
BUDN	0.1960	0.0201*	0.2242	0.0093**	-0.0318	0.6291	-0.2669	0.9976**
BUDS	0.1332	0.0827	0.2341	0.0069**	0.0752	0.2174	0.1518	0.0507*
BRN1	0.1845	0.0268*	0.3411	0.0001**	-0.0248	0.6014	0.0318	0.3708
BRS	-0.015	0.5629	-0.006	0.5228	-0.0809	0.7996	0.1814	0.0289*
BRN2	0.0919	0.1697	0.2435	0.0052**	0.02913	0.3812	0.0344	0.3606

[a] see Appendix 3.2 for description of traits.

[b] Pr>r is probability under null hypothesis that correlation is equal to zero.

*, ** represent significant levels at 5% and 1% (A t-test for null hypothesis that genetic correlation was zero was used (Steel and Torrie 1985)).

Table 5.7 Homogeneity test of error variances between greenhouse traits and nine-year tree height of site B [a]

	Before data standardized				After data standardized			
Trait	F-value	FN [b]	FD	Pr>F [c]	F-value	FN	FD	Pr>F
H1	5.41	1754.0	1777.0	0.0000	1.26	1754.0	1777.0	0.0000
H2	2.60	1754.0	1776.0	0.0000	1.17	1754.0	1776.0	0.0006
H3	1.95	1754.0	1771.0	0.0000	1.14	1754.0	1771.0	0.0032
H4	1.35	1754.0	1761.0	0.0000	1.11	1754.0	1761.0	0.0147
H5	1.02	1757.0	1754.0	0.3037	1.10	1754.0	1757.0	0.0265
H6	1.09	1750.0	1754.0	0.0391	1.11	1754.0	1750.0	0.0178
H7	1.38	1740.0	1754.0	0.0000	1.09	1754.0	1740.0	0.0430
D3	6.11	1771.0	1754.0	0.0000	1.07	1754.0	1771.0	0.0649
D7	20.01	1740.0	1754.0	0.0000	1.06	1754.0	1740.0	0.1280
D8	21.88	1735.0	1754.0	0.0000	1.06	1754.0	1735.0	0.1282
HG1	4.84	1754.0	1776.0	0.0000	1.00	1754.0	1776.0	0.4894
HG2	14.21	1754.0	1771.0	0.0000	1.01	1771.0	1754.0	0.4021
HG3	2.28	1754.0	1740.0	0.0000	1.01	1754.0	1740.0	0.3979
DG	3.98	1740.0	1754.0	0.0000	1.00	1740.0	1754.0	0.4694
SB	17.97	1735.0	1754.0	0.0000	1.05	1754.0	1735.0	0.1459
BB	3.79	1735.0	1754.0	0.0000	1.06	1754.0	1735.0	0.0980
NB	388.18	1735.0	1754.0	0.0000	1.07	1754.0	1735.0	0.0905
RB	86.23	1735.0	1754.0	0.0000	1.03	1754.0	1735.0	0.2983
TLB	1054.55	1735.0	1754.0	0.0000	1.06	1754.0	1735.0	0.1054
GB	605.25	1735.0	1754.0	0.0000	1.07	1754.0	1735.0	0.0797
HI	1395082	1754.0	1735.0	0.0000	1.04	1754.0	1735.0	0.2181
SR	1194.39	1754.0	1735.0	0.0000	1.01	1754.0	1735.0	0.4565
RHD	616666	1754.0	1740.0	0.0000	1.00	1754.0	1740.0	0.4588
BUDN	31938.4	1754.0	1776.0	0.0000	1.02	1776.0	1754.0	0.3614
BUDS	12964.6	1754.0	1776.0	0.0000	1.03	1754.0	1776.0	0.2558
BRN1	16460.3	1754.0	1776.0	0.0000	1.03	1754.0	1776.0	0.2886
BRS	36074.6	1754.0	1776.0	0.0000	1.01	1754.0	1776.0	0.4130
BRN2	6743.26	1754.0	1735.0	0.0000	1.08	1754.0	1735.0	0.0534

[a] see Appendix 3.2 for description of traits.
[b] FN FD are degrees of freedom of numerator and denominator in the F-test.
[c] Pr>F is probability under null hypothesis that two variances are equal (if Pr>F is less than 0.025, then there is significant difference between two variances at 5% probability level since the null hypothesis test is a two-tail hypothesis test (Steel and Torrie 1985)).

Table 5.8 Homogeneity test of family variances between greenhouse traits and nine-year tree height of site B [a]

	Before data standardized				After data standardized			
Trait	F-value	FN [b]	FD	Pr>F [c]	F-value	FN	FD	Pr>F
H1	1.24	78.74	25.69	0.2713	5.03	78.75	27.87	0.0000
H2	1.79	69.13	25.69	0.0502	3.77	69.11	27.87	0.0001
H3	2.08	65.02	25.69	0.0211	3.36	65.01	27.87	0.0004
H4	2.53	59.65	25.69	0.0057	2.91	59.64	27.87	0.0014
H5	3.22	56.95	25.69	0.0009	2.71	56.89	27.87	0.0027
H6	3.63	58.68	25.69	0.0003	2.85	58.71	27.87	0.0017
H7	4.02	54.11	25.69	0.0001	2.53	54.12	27.87	0.0048
D3	16.34	51.97	25.69	0.0000	2.35	51.94	27.87	0.0085
D7	45.30	46.01	25.69	0.0000	2.02	46.01	27.87	0.0250
D8	49.56	45.93	25.69	0.0000	2.03	45.94	27.87	0.0249
HG1	4.44	25.69	24.61	0.0002	1.03	24.55	27.87	0.4706
HG2	17.60	25.69	17.48	0.0000	1.30	27.87	17.49	0.2898
HG3	1.74	25.69	29.22	0.0754	1.23	29.23	27.87	0.2948
DG	8.82	21.53	25.69	0.0000	1.07	27.87	21.53	0.4380
SB	39.13	44.66	25.69	0.0000	1.96	44.68	27.87	0.0315
BB	9.24	48.31	25.69	0.0000	2.16	48.24	27.87	0.0159
NB	965.26	48.97	25.69	0.0000	2.20	48.93	27.87	0.0139
RB	139.14	35.17	25.69	0.0000	1.49	35.19	27.87	0.1423
TLB	2523.42	47.72	25.69	0.0000	2.13	47.72	27.87	0.0177
GB	1551.67	49.97	25.69	0.0000	2.26	49.97	27.87	0.0113
HI	742123	25.69	40.06	0.0000	1.71	39.91	27.87	0.0705
SR	1016.48	25.69	26.01	0.0000	1.10	26.03	27.87	0.3979
RHD	528418	25.69	25.92	0.0000	1.10	25.91	27.87	0.4048
BUDN	45477.2	25.69	14.75	0.0000	1.48	27.87	14.76	0.2153
BUDS	7423.87	25.69	38.32	0.0000	1.60	38.34	27.87	0.0998
BRN1	10031.1	25.69	36.35	0.0000	1.51	36.34	27.87	0.1324
BRS	27971.9	25.69	29.19	0.0000	1.21	29.21	27.87	0.3117
BRN2	2409.08	25.69	52.81	0.0000	2.45	52.81	27.87	0.0062

[a] see Appendix 3.2 for description of traits.
[b] FN FD are degrees of freedom of numerator and denominator in the F-test.
[c] Pr>F is probability under null hypothesis that two variances are equal (if Pr>F is less than 0.025, then there is significant difference between two variances at 5% probability level since the null hypothesis test is a two-tail hypothesis test (Steel and Torrie 1985)).

Table 5.9 Comparison of estimated genetic correlations (r) of greenhouse traits with nine-year tree height at site B, by covariance and by linear model methods [a]

Trait	Linear model method [b]		Covariance method [c]	
	r		r	Pr>r
H1	0.2697	b	0.2226	0.0097**
H2	0.1898	b	0.1795	0.0303*
H3	0.2457	b	0.2663	0.0025**
H4	0.2659	b	0.3053	0.0006**
H5	0.2567	b	0.2959	0.0009**
H6	0.2360	b	0.2727	0.0020**
H7	0.2548	b	0.3118	0.0005**
D3	0.2552	b	0.2753	0.0018**
D7	0.2836		0.3177	0.0004**
D8	0.3070		0.3624	0.0001**
HG1	-0.116		-0.032	0.6286
HG2	0.4456		0.5027	0.0000**
HG3	0.3025		0.3116	0.0005**
DG	0.3027		0.3675	0.0001**
SB	0.1998		0.2505	0.0042**
BB	0.0149	b	0.0679	0.2403
NB	0.1036	b	0.2281	0.0083**
RB	0.1558		0.1887	0.0242*
TLB	0.1434	b	0.2207	0.0102**
GB	0.1483	b	0.2249	0.0091**
HI	0.1474		0.1783	0.0312*
SR	0.3458		0.3286	0.0002**
RHD	0.0818		0.1364	0.0776
BUDN	0.1925		0.2242	0.0093**
BUDS	0.2210		0.2341	0.0069**
BRN1	0.3383		0.3411	0.0001**
BRS	0.0748		-0.006	0.5228
BRN2	0.2128	b	0.2435	0.0052**

[a] see Appendix 3.2 for description of traits.

[b] genetic correlations were estimated by equation 1 in Appendix 5.2 using standardized data; symbol b indicates that genetic correlation is biased due to either heterogenous family variances or heterogenous family and error variances between greenhouse traits and nine-year tree height of site B even after data were standardized.

[c] genetic correlations were estimated by equation 1 in Chapter five;
*, ** represent significant levels at 5% and 1% for covariance method.

CHAPTER SIX

EARLY SELECTION STRATEGY IN LODGEPOLE PINE

1. INTRODUCTION

The genetic correlations between seedling traits in the greenhouse and nine-year tree height for the common 110 families were presented in Chapter Five (Tables 5.1 and 5.6). This chapter applies the theory described in Chapter Two to evaluate the effectiveness of early selection in lodgepole pine. The application of early selection is based on the premise of an effective genetic correlation between early and mature traits. Five seedling traits were significantly correlated with nine-year tree height across sites. Of the four sites, only nine-year tree height at site B was significantly correlated with the majority of seedling traits. Thus, nine-year tree heights of the families at site B and across all sites will be utilized further to investigate early selection efficiency in this species. Five aspects of early selection efficiency will be addressed:

(1). Selection for a single early trait.

(2). Index selection based on multiple early traits.

(3). Index selection based on mature and early traits.

(4). Two-stage selection based on early and mature traits.

(5). Multi-generation selection based on early traits.

2. SELECTION FOR A SINGLE EARLY TRAIT

Genetic correlation and heritability are needed to estimate early selection efficiency from a single early trait. The genetic correlations between twenty-eight direct and derived seedling traits and nine-year tree height across sites and on site B are listed in Tables 5.1 and 5.6. Estimates of individual heritabilities based on 110 families and individual heritabilities are given in Table 6.1. The efficiencies $R_{x,y}$ of indirect early mass and family selection based on individual seedling traits relative to direct field selection across all sites or for site B only, are given in Table 6.2.

None of the seedling traits had $R_{x,y}$ greater than unity, indicating indirect selection of seedling traits would result in smaller expected genetic gains than direct mass and family selection for height at age nine. Indirect early selection for nine-year tree height on site B is more efficient than for nine-year tree height across sites, (for example, in mass selection, the average $R_{x,y}$ is 0.317 for across sites, but for site B is 0.397 for 24 seedling traits, and 0.379 when the same five seedling traits are utilized). In the five seedling traits, which were significantly correlated with nine-year height across sites, SR was the most efficient greenhouse trait for both early mass and family selection of performance across all sites. On average, early mass selection based on absolute hight and diameter measurements are most efficient for performance on site B ($R_{x,y}$ = 0.482), while early mass selection on growth increments are more efficient than on biomass measurements ($R_{x,y}$ = 0.392, and 0.326, respectively). When early family selection is for tree height performance on site B, selection efficiencies of

absolute height and diameter are similar to that of growth increments, but selection efficiencies of height and diameter are greater than that of biomass measurements.

A comparison of selection efficiencies and genetic correlations from site B indicates that seedling traits having the best genetic correlations with nine-year tree height are not necessarily the most effective traits for early selection. For example, height growth (HG2) is best correlated with nine-year tree height, yet the most efficient traits for early selection are absolute height and diameter measurements. The reason why growth increments are not the most efficient seedling traits for early mass selection is that these traits have low individual heritabilities. Thus, the information on genetic correlations alone is not sufficient for choosing traits for early selection. Genetic variances and heritabilities of early traits must also be examined.

3. INDEX SELECTION BASED ON MULTIPLE EARLY TRAITS

As indicated in Table 6.2, the most efficient seedling traits for indirect mass and family selection of nine-year tree height on site B are height and diameter in early selection based on individual traits. Selection based on several seedling traits simultaneously may increase selection efficiency substantially. Here, the efficiencies of combinations of multiple seedling traits for indirect selection of nine-year tree height on site B are presented. Indirect early selection with several seedling traits can be implemented by constructing an early selection index. This index can be

generated for early mass selection, family selection, and combined family and individual selection. However, only details of selection indices for early mass selection will be presented since the efficiencies of early selection based on families or combined information of families and individuals were similar. The index for early mass selection has the form (Falconer 1981 and White and Hodge 1990)

$$I = b_1x_1 + b_2x_2 + \ldots + b_px_p \ , \qquad (1)$$

where x_1, x_2, ... x_p are phenotypic values of early traits 1, 2, ... p, and b_1, b_2, ... b_p are index coefficients. To estimate the index coefficients, the following two matrices (phenotypic variance-covariance matrix (P) and genetic variance-covariance matrix (G)) must be first estimated:

$$P = \begin{bmatrix} \sigma^2_{x_1} & cov(x_1\ x_2) & \ldots & cov(x_1\ x_p) \\ cov(x_2\ x_1) & \sigma^2_{x_2} & \ldots & cov(x_2\ x_p) \\ \ldots & & & \\ cov(x_p\ x_1) & cov(x_p\ x_2) & \ldots & \sigma^2_{x_p} \end{bmatrix} \qquad (2)$$

and

$$G' = [cov(G_y\ G_{x_1})\ \ cov(G_y\ G_{x_2})\ \ \ldots\ \ cov(G_y\ G_{x_p})] \ , \qquad (3)$$

where $\sigma_{x_i}^2$, i=1, 2, ... p, are the phenotypic variances of the seedling traits,

$cov(x_i\ x_j)$ i, j=1, 2, ... p, ($i \neq j$) are the covariances between seedling traits,

$cov(G_y\ G_{x_i})$ are the genetic covariances of nine-year tree height and seedling traits i, which is four times the family covariances among open-pollinated families of lodgepole pine.

The estimated phenotypic, genetic variances and covariances can be found in Appendices 6.1, 6.2, and 6.3. Combinations of two and three seedling traits were investigated.

With two seedling traits, the index form is

$$I = b_1 x_1 + b_2 x_2 \qquad with \quad b' = [b_1 \;\; b_2] = P^{-1}G \; . \tag{4}$$

When seedling traits H7 (growth trait) and SR (biomass ratio) were used as an example, matrix P and vector G' were estimated (Henderson 1984 and Lin 1978) as

$$P = \begin{bmatrix} 2145.253 & 1.164 \\ 1.164 & 1.482 \end{bmatrix} \tag{5}$$

$$G' = [210.120 \;\; 0.864] \; . \tag{6}$$

Thus, the vector of index coefficients is

$$b' = [0.097 \;\; 2.262] \tag{7}$$

with the selection index (I) being

$$I = 0.097 \; X_{H1} + 2.262 \; X_{D7} \; . \tag{8}$$

The relative efficiency of this early selection index compared to direct selection of nine-year tree height is 0.670. Thus, selection using this index is expected to be more efficient than selection based on either of the seedling traits taken individually (R_{xy}=0.510 for H7 and R_{xy}=0.356 for SR). Using the same approach, the vectors of index coefficients for any two of twenty-four seedling traits that correlated with nine-year tree height on site B can be calculated; a total of 276 combinations is

possible. The average selection efficiency from these 276 early indices is 0.531, which is greater than the average selection efficiency (0.397) based on twenty-four effective individual seedling traits; the increase is 0.134 (34%). Twelve of the 276 pairs of seedling traits have expected selection efficiencies greater than 0.65 (Table 6.3). The best combination is D8 with SR ($R_{I,y}$=0.690). If one compares index selection based on two seedling traits with indirect selection based on individual seedling traits, the efficiencies (R_{I,x_i}) are always larger than unity (see R_{I,x_1} and R_{I,x_2} columns in Table 6.3). This indicates index selection using two seedling traits always has greater expected genetic gain than selection based on an individual seedling trait.

With three seedling traits, there are 2,021 possible combinations of indices. Only indices with selection efficiencies greater than 0.76 are listed (Table 6.4). The average selection efficiency for indices with three seedling traits is 0.584. This is an average increase of 10% in selection efficiency over selection indices based on two seedling traits. The combination of seedling traits which produced the index with the greatest selection efficiency was D8, GB and SR.

Early selection indices for family selection were also computed. In the early family indices, the increases of efficiency with selection indices over single seedling traits were lower than the mass selection. For example, average selection efficiency of family indices for two seedling traits was 0.386. This is an average increase of 19% from family selection based on individual seedling traits (average 0.324). With three seedling traits, the average selection efficiency of family indices was 0.411, which is a 6% increase in selection efficiency over selection indices based on two seedling

traits.

4. INDEX SELECTION BASED ON MATURE AND EARLY TRAITS

Information about early traits can be used to enhance the accuracy of mature trait selection and increase expected genetic gain. This can be done by including information about early traits, along with information on the mature trait, into selection indices designed for improvement of the mature trait. This aspect of early evaluation is particularly useful when the efficiency of mature evaluation is low due to heterogeneity of test environments. Therefore, in situations when there is low reliability in predicting the breeding value of mature traits, combining early and mature traits into a selection index can increase selection precision (Burdon 1988, White and Hodge 1990).

In retrospective studies, only the value of employing family information on early traits to enhance efficiency of mature trait selection can be evaluated. Family information on early traits can enhance efficiency of mass, family, and combined family with individual selection for mature traits. Here, only details of selection index for mature mass selection on site B will be presented. Thus, the selection index for combined mature and early traits has the form

$$I = ay + b_1\bar{x}_1 + b_2\bar{x}_2 + \ldots + b_p\bar{x}_p \quad , \qquad (9)$$

where $b' = [a\ b_1 \ldots b_p]$ is the vector of index coefficients and $\bar{x}_1$, $\bar{x}_2$,...$\bar{x}_p$ are family means of seedling traits and y is an individual observation on the mature trait. To

estimate the index coefficients, the phenotypic variance-covariance matrix (P) and the genetic variance-covariance matrix (G) must be first estimated. The matrix P and G have the form

$$P=\begin{bmatrix} \sigma_y^2 & cov(y\ \bar{x}_1) & \dots & cov(y\ \bar{x}_p) \\ cov(y\ \bar{x}_1) & \sigma_{\bar{x}_1}^2 & \dots & cov(\bar{x}_1\ \bar{x}_p) \\ \dots & & & \\ cov(y\ \bar{x}_p) & cov(\bar{x}_1\ \bar{x}_p) & \dots & \sigma_{\bar{x}_p}^2 \end{bmatrix} \qquad (10)$$

and

$$G=\left[\sigma_{G_y}^2\ cov(G_y\ G_{x_1})\ cov(G_y\ G_{x_2})\ \dots\ cov(G_y\ G_{x_p})\right], \qquad (11)$$

where σ_y^2 is the phenotypic variance of nine-year tree height on site B,

$\sigma_{\bar{x}_i}^2$, i=1, 2, 3,...,p, are the phenotypic variances of family means of the seedling traits,

cov(y $\bar{x}_i$), i=1, 2, 3,...,p, are the phenotypic covariances between nine-year tree height and corresponding family means of seedling traits,

cov($\bar{x}_i$ $\bar{x}_j$), i, j=1, 2, 3,...,p, (i≠j) are family mean covariances between seedling traits,

$\sigma_{G_y}^2$ is the genetic variance of nine-year tree height at site B, and

cov(G_y G_{x_i}) are the genetic covariances between nine-year tree height and seedling traits.

The estimated variances and covariances are given Appendices 6.1, 6.2, and 6.3.

In this selection approach, several schemes will be considered. The first scheme is mature selection with the aid of one early trait. In this case, information

on a single early trait and mature trait are incorporated into the selection index:

$$I = a\,y + b_i\,\bar{x}_i \qquad with\ b' = [a \quad b] = P^{-1}G \quad . \tag{12}$$

Using seedling trait H7 as an example, matrix P and G' were estimated as

$$P = \begin{bmatrix} 1785.86 & 52.53 \\ 52.53 & 471.19 \end{bmatrix} \tag{13}$$

$$G' = [191.36 \quad 83.28] \tag{14}$$

so that the vector of index coefficients is

$$b' = [0.175 \quad 0.426] \quad . \tag{15}$$

Thus, we have the selection index

$$I = 0.175\ Y + 0.426\ \bar{X}_{H7} \ , \tag{16}$$

where $\bar{x}_{H7}$ is the family mean of seedling trait H7. The relative efficiency of this selection index computed by equation 36 in Chapter Two is 1.538. This suggests that selection based on this index is 54% more efficient than selection based on nine-year tree height only. By the same procedure, index coefficients for indices involving each of the twenty-four seedling traits that were significantly correlated with nine-year tree height on site B were calculated, as were their relative selection efficiencies (Table 6.5). Efficiency of selection for nine-year tree height based on the combination of this trait with any single seedling trait is expected to be larger than selection based on nine-year tree height alone (average increase is 39.7%). The magnitude of

efficiency increase is dependent on the seedling trait used. HG2 is the best seedling trait to enhance selection of nine-year tree height on site B ($R_{I,y}$=1.760). The other prominent traits are D8 ($R_{I,y}$=1.632), H7 ($R_{I,y}$=1.538) and H4 ($R_{I,y}$=1.535). These four seedling traits were among the individual traits that were most efficient for indirect early selection of nine-year height.

The second scheme is mature selection with the aid of two early traits. When family means of H7 and SR are used, the selection index is

$$I = 0.162\ Y + 0.113\ \bar{X}_{H7} + 16.21\ \bar{X}_{RGR}\ . \qquad (17)$$

The relative efficiency of selection by this index is 1.834, which indicates this index is more efficient than selection based on nine-year tree height alone or on either combination of nine-year tree height with one of the component seedling traits (i.e., for H7, $R_{I,y}$=1.538, and for SR, $R_{I,y}$=1.428). In the same manner, the index vectors including family means for all pairwise combinations of the twenty-four seedling traits with nine-year height were calculated. There are a total of 378 indices possible, but only selection indices with relative selection efficiencies greater than 1.850 are listed in Table 6.6. The average increase of selection efficiency with two seedling traits is 55.2% compared with selection based on nine-year tree height alone. This is 12% greater than the average selection efficiency when a single seedling trait was used in the index.

For family selection using combined nine-year tree height on site B and seedling traits, the increases in efficiency over direct selection of nine-year tree height was relative small compared to mass selection. For example, average increase of

selection efficiency of family indices combining nine-year tree height with one seedling trait was only 2% over nine-year tree direct selection. When nine-year tree height was combined with two seedling traits, the average increase was only 1% over selection efficiencies of indices combining nine-year tree height with one seedling trait.

5. TWO-STAGE SELECTION BASED ON EARLY AND MATURE TRAITS

Two-stage selection having two different objectives will be addressed:
(1) to reduce test size without reducing overall gain, by culling inherently poor families at the seedling stage prior to outplanting.
(2) to increase overall selection intensity and genetic gain without increasing test size.
Regarding the first objective, the specific question is how many families can be culled after early testing without reducing or substantially reducing total genetic gain in the mature traits.

Since SR had the best genetic correlation with nine-year tree height across all sites and D8 had the best correlation for site B, the effects of early selection as first stage culling in two-stage selection, based on seedling traits SR and D8, were assessed using the quantitative genetic theory developed in Chapter Two. For example, when nine-year tree height across all sites is considered, families would be selected at the first stage on the basis of mean SR values in the greenhouse, with subsequent selection of the remaining families based on average nine-year height in all field tests.

Assuming 10% of the families are to remain after both stages of family selection, overall genetic gains in nine-year tree height for different populations of families selected at the greenhouse stage (from 90% to 10% with a 10% interval), were computed utilizing equation 15 in Chapter Two (Tables 6.7 and 6.8). Expected genetic gain is 12.01cm when family selection for nine-year height is based only on mean performance across all test sites (i.e., no early selection). It is evident from Table 6.7 that any early selection based on SR would result in less genetic gain in nine-year tree height, even if 90% of families remained after the greenhouse stage (gain is 11.90cm). Nevertheless, Table 6.7 also indicates that as much as 40% of the families could be culled at greenhouse stage, while still retaining more than 90% of the gain expected if all families were selected based on field performance. With more than 40% of the families culled at the greenhouse stage, the expected reduction in total genetic gain increases rather rapidly.

For performance on site B only, expected genetic gain was 10.84cm when all family selection was postponed to the field stage. Under two stage selection scenario based on seedling trait D8 and nine-year tree height on site B, more than 50% of families could be culled at seedling stage, with expected gain after both stages greater than 95% of gain expected if all selection is based on performance in field only (Table 6.8). If 30% families be culled in the first stage, one can still get 99% of gain expected if all selection was postponed to age nine. If more than 60% of families were culled at the greenhouse stage, the expected reduction in total genetic gain increases rather quickly.

With regards to the second objective, the question is how much genetic gain in mature trait can be increased when the field testing population remains the same size, but early testing is used to cull an initially larger population down to that size. Assuming field test size is 110 families, total 220 families will be greenhouse tested, and after nine-years in the field, 10% of families will be selected. The increased gain from this two-stage selection scenario over one-stage selection of 110 families can be computed by equation 24 in Chapter Two. Genetic gain in nine-year tree height from two-stage selection across all sites is expected to be 10% greater than expected if all selection is only from field testing. When selection is only for site B, genetic gain in nine-year tree height from two-stage selection is expected to be 16% greater than expected from field selection only.

6. MULTIPLE GENERATION EARLY SELECTION

In section 2, it was observed that one generation of early selection based on seedling traits is never as efficient as direct selection for nine-year tree height ($R_{x,y}<1$, see Table 6.2). However, one of the main advantages of early selection is shortening the breeding cycle. If the time factor was considered, genetic gain per unit time from early selection might be greater than selection at maturity since early testing takes less time than mature testing. Precise comparison between the effectiveness of early selection and conventional selection can be made by considering the expected genetic gain for several generations of early selection within a cycle of conventional breeding.

Using conventional field testing, the duration of one breeding cycle of lodgepole pine in Alberta is about thirty years (Dr. Yeh, Personal Communication). An alternative breeding scheme would be to reduce the breeding cycle to ten years, based on results of early selection of seedling traits (lodgepole pine can reproduce at age 5, Critchfield 1980). Hence, there can be three breeding cycles from early selection within the thirty year conventional breeding period. Assuming 20% of the population is selected each generation and that genetic parameters for tree height at age nine are applicable at age thirty, expected genetic gains in tree height at age thirty across sites were computed for three generations of early mass selection, based on each of two seedling traits, HG3 and SR (Table 6.9). The correlated genetic gains in thirty-year height after three generations of early selection based on HG3 and SR were 6.72cm and 8.36cm, respectively. Thus, three generations of early selection based on SR would produce more genetic gain than direct selection for thirty-year tree height across sites (8.01cm).

Same selection scheme was applied to site B, for three generations of early mass selection based on each of three seedling traits, H7 (representing height), GB (representing biomass) and BRN2 (representing branch, bud characteristics)(Table 6.10). Expected correlated genetic gains in thirty-year height after three generations of early selection were 17.09cm, 11.51cm and 11.10cm for selection based on H7, GB, and BRN2, respectively. Thus, in all three cases, genetic gains from three generations of early selection exceeded one generation of selection for height at age thirty (11.06cm). In case of H7, expected genetic gain is 50% greater.

7. DISCUSSION AND CONCLUSIONS

The evaluation of different early selection schemes in this study demonstrated the potential of varied uses of early testing, and in particular the potential use of early greenhouse testing for Alberta lodgepole pine, even when early-mature genetic correlation is not high. This study indicates the major utilities of greenhouse testing in Alberta lodgepole pine are culling of poor families in the seedling stage prior to outplanting, increasing overall selection intensity, and generating genetic information to aid field selection.

Seedling selection as a first-stage culling in this lodgepole pine population would reduce field test size without reduction of overall genetic gain. For example, when two-stage selection was practised on trait D8 and nine-year height on site B, a 20% reduction in the size of the field test would result in a genetic gain of nine-year tree height identical to that based on field selection alone. The findings in this study are similar to the two-stage selection results in coastal Douglas-fir that 20-30% of the families could have been culled on the basis of one-year height in the nursery with little or no loss of genetic gain in tree height at age 15 (Adams et al. 1992). A two-stage selection in lodgepole pine can also increase the total selection intensity and genetic gain without increasing the size of the field test. For example, if the number of families tested in the greenhouse were doubled (to 220) and half of them were culled in the greenhouse based on D8, the number of families on site B would remain at 110. Under this two-stage selection scheme, the genetic gain of nine-year height

on site B would increase by 16% relative to that based on field testing with base population of 110 families alone.

In the lodgepole pine population investigated in this study, indices which include information on seedling traits substantially increased selection efficiencies of nine-year height. For example, increase in selection efficiency with the addition of individual seedling traits averaged 39.7% in mass selection. This large increase is due to the high individual heritabilities of most seedling traits and low individual heritability of nine-year tree height on site B. Thus information from early traits can substantially increase precision of predicting individual breeding values. Usefulness of genetic information generated from early testing to predict mature breeding value may be one of major utilities of early testing in this study. The best seedling trait to increase selection efficiency of nine-year tree height was HG2, the early trait with the highest genetic correlation with nine-year tree height on site B. The possibility that HG2 reflects seedling growth potential and a longer seedling growth season may explain the high contribution of HG2 to prediction of nine-year tree height. If HG2 is closely associated with growth potential at later ages, HG2 may be valuable to either early prediction of nine-year tree height (see selection efficiencies of HG2 in Table 6.2) or aiding selection of nine-year height when included in an index with this trait. If selection for HG2 results in longer growing seasons, HG2 should be used with caution since selection for HG2 might lengthen growing season and make trees more susceptible to early fall frost in Alberta. Therefore, the traits reflecting growth potential are more safe to use for early selection in lodgepole pine than traits

reflecting longer growing season in Alberta. The other seedling traits that substantially enhanced selection of nine-year tree height were absolute height and diameter measurements because they often had higher heritability estimates and were better correlated with nine-year tree height on site B than the other traits. Seedling traits D8 and SR were also very efficient in enhancing nine-year tree height selection (Tables 6.5 and 6.6).

One generation of early selection based on individual seedling traits was less efficient than direct selection for nine-year tree height across sites and on site B in this study, even estimates of heritability in seedling traits are very high. This is mainly due to low genetic correlations between seedling traits and nine-year height ($r<0.3$ in most cases). Among 28 seedling traits, early selection on height and diameter traits were most efficient. Height and diameter traits probably demonstrate more growth potential than biomass, branch, and bud traits. In other species, results on early selection efficiencies for individual traits are mixed. For example, relative efficiencies of early individual tree selection based on height from age two to four in Douglas-fir were 69 to 78% for volume at age fifteen (Bastien and Roman-Amat 1990). This parallels the finding in this study of lodgepole pine that efficiency of indirect selection is less than that of direct selection. However, relative efficiencies of correlated responses for volume index (DBH^2*HT) at age ten when early selection was for height at age one to seven, were from 84 to 108% in Norway spruce (Bentzer et al. 1989). In sycamore (Nebgen and Lowe 1985), selection for three and five year height was almost as efficient as direct selection for seven-year-old volume, but the

relative efficiencies of indirect selection of height and diameter for wood specific gravity at age seven or earlier were extremely low (from 7 to 13%). In radiata pine, Cotterill and Dean (1988) found that the relative efficiencies of early selection on height increments for volume at age sixteen were often better than on absolute height measurements.

Results from analyses of multi-trait indices of early traits indicated that index selection in the greenhouse can substantially increase efficiency of early selection. For example, early index selection with two seedling traits was estimated to be 34% more efficient than early selection based on an individual trait. Nevertheless, the percentage gain in efficiency of the early selection index declined with each additional seedling trait. For example, selection indices based on three seedling traits were only 10% more efficient, on average, than indices based on two seedling traits. In all cases of early index selection with one, two, and three early traits, none of the indices had unit or larger selection efficiencies. Thus, selection based on early indices with up to three seedling traits, were still less efficient than direct nine-year tree height selection. For early index selection based on two seedling traits, the best combination was D8 with SR; the best combination of three traits was D8 with SR and GB. D8, basal diameter at harvest after two growing seasons, probably reflect seedling growth potential. SR is shoot-root biomass ratio, a trait which often reflects adaptedness of seedlings to soil moisture conditions (Cannell et al. 1981). The combinations of seedling traits D8 and SR in an index of two seedling traits and the combination of seedling traits D8, SR, and GB in an index of three seedling traits might optimize

seedling growth potential on site B. Early index selection was also investigated in some conifers. For example, in loblolly pine Foster (1986) found selection based on early indices from age 1 to age 10 had relative efficiencies ranging from 71% to 92% compared to direct selection for total volume at age 15. The study of Bastien and Roman-Amat in Douglas-fir (1990) showed that the index of square girth with total height at age 8 could produce 89% the selection gain of direct selection of volume at age 15. However, in radiata pine Cotterill and Dean (1988) found that index selection based on height and basal area at age 10.5 was more efficient than direct selection for volume at age 16. This is one example where selection based on early multi-trait index would be more efficient than direct selection.

Theoretically, the efficiency of selection indices would increase with increasing numbers of seedling traits as long as there are genetic correlations. In reality, the increase in selection efficiency after three or more seedling traits would be offset by the increase in standard error. This is because selection indices are a function of several heritabilities, genetic correlations, and phenotypic and genetic variances. These parameters alone are subject to large estimation error. In theory, addition of each trait would substantially increase the standard error of predicted genetic gain (Harris 1963, 1964). Often, large standard errors will make the increase of genetic gain unreliable. Unless the precision of genetic gain prediction through index selection is thoroughly investigated, the extent to which additional information on early traits can be reliably used is still a question.

The analyses of different early selection schemes in this study indicate early

selection has several potential applications for lodgepole pine in Alberta: (1) Early selection on similar conditions to the field environment may be more efficient. (2) Early traits reflecting growth (or growth potential) such as height and diameter, and adaptive value such as SR have great potential value for early selection of tree growth. (3) When heritabilities are low in the mature traits such as nine-year tree height, use of early traits with high heritabilities and genetic correlation with the mature trait can substantially increase the prediction of the breeding value of the mature trait and, consequently, can increase the expected genetic gain. (4) If more than one early trait is available, an index of early traits might be more efficient than selection based on a single early trait. In particular, indices based on traits reflecting growth potential and adaptation may substantially increase the efficiency of early selection. (5) Early selection as the first of a two-stage selection to cull poor families prior to field testing can reduce the size of field test and its associated cost without compromising the expected genetic gain.

In this study, only early selection for tree height was examined. But early selection for height or bole volume to reduce the length of the breeding cycle would have a negative effect on improvement of lodgepole pine if trees selected at early age are more susceptible to attacks by insect and disease, maladapted to planting sites, and have low wood quality, high stem sinuosity or bad branching habits. Therefore, to implement early selection in a practical tree improvement program, the relationship between early traits and those reflecting tree quality and adaptive value must be fully understood. Fortunately, some quality and adaptive traits can be tested

and selected at an early age. For example, De Souza et al.(1992) reported that the indices of seedling traits after inoculation of fusiform rust fungus on slash pine seedlings could partially predict the breeding value of trees for disease resistance in the field. Gonzalez and Richards (1988) indicated selection for wood density at age 50 could be efficiently accomplished between ages ten and fifteen. Vargas-Hernandez and Adams (1992) found that early selection of core density at age seven improved the overall wood density at age fifteen.

Some studies showed that early selection for height might produce low quality trees. For example, Adams et al. (1989) found a moderate correlation (0.44) between stem sinuosity and height in nursery seedlings, which indicated trees with faster growth appeared to produce crooked stems. In such a case, early selection based on a single growth trait may have limited value. One possibility is to use restricted early indices (Kempthorne and Norskorg 1959, Cotterill and Dean 1988) that increase genetic gain in traits of height or bole volume while maintaining stem quality.

In this study of lodgepole pine, the trait measured in the field was only at nine-year old. Therefore, there was little advantage from early selection to reduce the breeding cycle. But if the pattern of growth and inheritance for field trees is maintained, say to age 30, the advantage of early selection would be obvious for lodgepole pine. In Alberta, one breeding cycle of lodgepole pine conventionally takes 30 years. However, this can be reduced to ten years based on early selection at age two and flower induction and breeding between ages six and eight. Under this

scheme of one breeding cycle per ten years, the conventional 30-year breeding cycle would allow three cycles of breeding from early traits. However, the expected genetic gains from three generations of early selection would depend on the seedling traits under study and the selection targets (across sites or site B). Three cycles of breeding based on early selection of H7 in the greenhouse could produce 1.54 times the genetic gain expected from direct selection of 30-year tree height on site B. Two breeding cycles (twenty years) based on early selection of H7 would result in genetic gain similar to direct selection of 30-year tree height in a conventional breeding cycle.

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Table 6.1 Estimates of individual heritabilities (h_i^2) and their standard errors (s.e.) for greenhouse traits, nine-year tree height across sites (HT) and on site B (HTB) in the common 110 family population *

Traits	H1	H2	H3	H4	H5	H6	H7	D3	D7	D8
h_i^2	0.965	0.747	0.666	0.577	0.537	0.565	0.501	0.466	0.401	0.401
s.e.	0.157	0.148	0.143	0.132	0.139	0.133	0.131	0.110	0.102	0.089
Traits	HG1	HG2	HG3	DG	SB	BB	NB	RB	TLB	GB
h_i^2	0.204	0.153	0.244	0.185	0.388	0.429	0.437	0.295	0.422	0.449
s.e.	0.085	0.074	0.087	0.074	0.096	0.107	0.115	0.081	0.092	0.108
Traits	HI	SR	RHD	BUDN	BUDS	BRN1	BRS	BRN2	HT	HTB
h_i^2	0.339	0.219	0.217	0.134	0.318	0.287	0.239	0.485	0.116	0.187
s.e.	0.104	0.083	0.092	0.095	0.103	0.109	0.097	0.116	0.021	0.044

* see Appendix 3.2 for description of traits.

Table 6.2 Estimates of relative efficiency ($R_{x,y}$) of early mass selection and family selection based on individual greenhouse traits for overall sites and site B [a]

Site	Overall sites		Site B			Overall sites		Site B	
	Mass	Family	Mass	Family		Mass	Family	Mass	Family
Traits	$R_{x,y}$ [b]	$R_{x,y}$	$R_{x,y}$	$R_{x,y}$	Traits	$R_{x,y}$	$R_{x,y}$	$R_{x,y}$	$R_{x,y}$
H1			0.506	0.304	DG			0.366	0.365
H2			0.359	0.238	SB			0.361	0.298
H3			0.503	0.347	NB			0.349	0.277
H4			0.536	0.390	RB			0.237	0.211
H5			0.501	0.374	TLB			0.332	0.267
H6			0.474	0.347	GB			0.349	0.175
H7			0.510	0.388	HI			0.246	0.206
D3			0.435	0.340	SR	0.371	0.232	0.356	0.342
D7			0.465	0.398	BUDN			0.190	0.202
D8			0.531	0.460	BUDS	0.349	0.208	0.305	0.279
HG2	0.289	0.197	0.455	0.458	BRN1	0.278	0.165	0.423	0.384
HG3	0.298	0.183	0.356	0.334	BRN2			0.393	0.302

[a] see Appendix 3.2 for description of traits.

[b] $R_{x,y}$ - Efficiency of indirect selection for nine-year tree height based on individual traits compared to direct selection. Only traits which were significantly (5%) correlated with performace in the field are presented.

Table 6.3 Index coefficients (b_1, b_2) of selection indices for improving the mature trait in individual trees (nine-year tree height) when two greenhouse traits (x_1, x_2) are included in the index. The relative efficiencies of these indices to mature selection ($R_{I,y}$) and to indirect selection based on individual greenhouse trait for mature trait ($R_{I,x1}$, $R_{I,x2}$) are also given (only combinations of traits where $R_{I,y}$ >0.65 are listed out of the 276 possible pairs)[a]

Greenhouse traits x_1	x_2	b_1	b_2	$R_{I,y}$	$R_{I,x1}$	$R_{I,x2}$
H1	D8	0.141	0.018	0.658	1.301	1.239
H1	HG2	0.190	0.347	0.688	1.362	1.514
H2	H3	-0.336	0.420	0.657	1.830	1.307
H2	H4	-0.222	0.288	0.680	1.896	1.256
H4	SR	0.130	2.222	0.677	1.351	1.905
H4	BRN1	0.119	8.333	0.679	1.266	1.608
H5	BRN1	0.096	8.568	0.656	1.308	1.552
H7	SR	0.097	2.262	0.670	1.312	1.883
H7	BRN1	0.089	8.611	0.675	1.323	1.597
D8	SR	0.025	2.573	0.690	1.299	1.940
D8	HG2	0.028	0.235	0.671	1.432	1.674
HG2	SR	0.187	2.124	0.664	1.532	1.347

[a] see Appendix 3.2 for description of traits.

Table 6.4 Index coefficients (b_1, b_2, and b_3) of selection indices for improving the mature trait in individual trees (nine-year tree height) when three greenhouse traits (x_1, x_2, and x_3) are included in the index. The relative efficiencies of these indices to mature selection ($R_{I,y}$) and to indirect selection based on individual greenhouse trait for mature trait ($R_{I,x1}$, $R_{I,x2}$, and $R_{I,x3}$) are also given (only combinations of traits where $R_{I,y}$ >0.76 are listed out of 2,021 possible pairs) [a]

Greenhouse traits			b_1	b_2	b_3	$R_{I,y}$	$R_{I,x1}$	$R_{I,x2}$	$R_{I,x3}$
x_1	x_2	x_3							
H1	H2	H3	0.236	-0.479	0.431	0.764	1.510	2.128	1.519
H1	H2	H4	0.263	-0.393	0.310	0.779	1.592	2.244	1.501
H1	SR	HG2	0.183	2.226	0.351	0.769	1.520	2.161	1.690
H1	HG2	BRN1	0.168	0.341	8.424	0.772	1.526	1.697	1.827
H2	H4	BRN1	-0.244	0.289	9.178	0.778	2.169	1.451	1.841
H4	D8	TLB	0.132	0.044	-0.006	0.769	1.434	1.449	2.320
H4	SR	BRN1	0.116	2.333	8.742	0.768	1.431	2.159	1.817
H7	D8	TLB	0.102	0.045	-0.006	0.764	1.498	1.440	2.307
H7	SR	BRN1	0.087	2.371	9.006	0.767	1.502	2.156	1.814
D8	NB	SR	0.048	-0.007	3.126	0.765	1.441	2.193	2.151
D8	TLB	SR	0.051	-0.004	2.739	0.771	1.452	2.323	2.166
D8	GB	SR	0.052	-0.006	3.128	0.782	1.463	2.224	2.179

[a] see Appendix 3.2 for description of traits.

Table 6.5 Index coefficients (a, b_1) of selection indices for improving the mature trait (nine-year tree height) when the individual value for the mature trait and the family mean for a single greenhouse trait are included in the index. The relative efficiencies ($R_{I,y}$) of these indices are also given [a]

Greenhouse traits	a	b_1	$R_{I,y}$ [b]	Greenhouse traits	a	b_1	$R_{I,y}$
H1	0.180	0.636	1.344	DG	0.177	0.214	1.482
H2	0.183	0.401	1.223	SB	0.181	0.099	1.339
H3	0.178	0.543	1.438	NB	0.182	0.019	1.296
H4	0.175	0.547	1.535	RB	0.184	0.035	1.183
H5	0.176	0.462	1.502	TLB	0.182	0.011	1.277
H6	0.178	0.408	1.443	GB	0.182	0.015	1.291
H7	0.175	0.426	1.538	HI	0.185	344.6	1.166
D3	0.179	0.173	1.409	SR	0.178	19.70	1.428
D7	0.176	0.119	1.528	BUDN	0.185	63.9	1.160
D8	0.173	0.128	1.632	BUDS	0.182	44.5	1.273
HG2	0.169	3.424	1.760	BRN1	0.176	74.15	1.514
HG3	0.178	0.859	1.429	BRN2	0.180	32.18	1.348

[a] see Appendix 3.2 for description of traits.
[b] $R_{I,y}$ is efficiency of index selection relative to nine-year tree height selection alone.

Table 6.6 Index coefficients (a, b_1, and b_2) of selection indices for improving the mature trait (nine-year tree height) when the individual value for the mature trait and family means for two greenhouse traits are included in the index. The relative efficiencies (R_{Ly}) of these indices are also given (only combinations of traits where $R_{Ly} > 1.85$ are listed out of possible 276 pairs) [a]

Greenhouse traits		a	b_1	b_2	R_{Ly} [b]	Greenhouse traits		a	b_1	b_2	R_{Ly}
H1	HG2	0.164	0.516	3.211	1.902	H2	H3	0.159	-3.77	3.939	2.011
H2	H4	0.161	-2.24	2.291	1.980	H4	HG2	0.163	0.282	2.742	1.823
D8	RB	0.165	0.270	-0.09	1.856	D8	TLB	0.161	0.403	-0.04	1.967
D8	GB	0.164	0.351	-0.04	1.389	D8	HG2	0.164	0.076	2.550	1.881
HG2	SR	0.160	19.17	3.385	2.016	HG2	BUDS	0.165	3.256	34.91	1.861
HG2	BRN1	0.159	3.280	68.67	2.046	HG2	BRN2	0.146	3.224	26.30	1.987

[a] see Appendix 3.2 for description of traits.
[b] R_{Ly} is efficiency of index selection relative to nine-year tree height selection alone.

Table 6.7 Estimated genetic gain in nine-year tree height after two-stages of family selection, when selection in the first stage is based on SR (shoot to root biomass ratio) of seedlings in the greenhouse, selection in the second stage is on mean nine-year height across all test sites, and the final selection proportion is 10% *

	Selection proportion at the first stage									
	100%	90%	80%	70%	60%	50%	40%	30%	20%	10%
i_x		0.195	0.350	0.497	0.644	0.798	0.966	1.159	1.40	1.755
a		-1.282	-0.842	-0.524	-0.253	0	0.253	0.524	0.842	1.282
k		0.288	0.417	0.507	0.578	0.637	0.689	0.736	0.780	0.830
$\sqrt{(1-\rho^2 k)}$		0.9963	0.9947	0.9936	0.9927	0.9919	0.9913	0.9907	0.9900	0.9893
i_y'	1.755	1.705	1.647	1.580	1.497	1.400	1.271	1.091	0.798	
$1-r^2 h_x^2 k$		0.9897	0.9850	0.9818	0.9793	0.9772	0.9753	0.9736	0.9720	
Gain	12.01	11.90	11.72	11.47	11.13	10.61	10.09	9.18	7.59	2.79

* i_x is selection intensity at the first stage.
a is truncation point corresponding i_x.
$k=i_x(1-i_x)$.
i_y' is selection intensity at the second stage.
ρ is family mean correlation between greenhouse trait SR and nine-year tree height across sites.
r is genetic correlation between greenhouse trait SR and nine-year tree height across sites.
h_x^2 is family heritability of greenhouse trait SR.

Table 6.8 Estimated genetic gain in nine-year tree height after two-stages of family selection, when selection in the first stage is based on D8 (basal diameter at harvest) of seedlings in the greenhouse, selection in the second stage is on mean nine-year height at site B, and the final selection proportion is 10% *

	Selection proportion at the first stage									
	100%	90%	80%	70%	60%	50%	40%	30%	20%	10%
i_x		0.195	0.350	0.497	0.644	0.798	0.966	1.159	1.40	1.755
a		-1.282	-0.842	-0.524	-0.253	0	0.253	0.524	0.842	1.282
k		0.288	0.417	0.507	0.578	0.637	0.689	0.736	0.780	0.830
$\sqrt{(1-\rho^2 k)}$		0.9946	0.9921	0.9904	0.9891	0.9879	0.9869	0.9861	0.9852	0.9843
i_y'	1.755	1.705	1.647	1.580	1.497	1.400	1.271	1.091	0.798	
$1-r^2h_x^2k$		0.9753	0.9643	0.9566	0.9505	0.9454	0.9410	0.9370	0.9332	
Gain	10.84	10.85	10.83	10.76	10.61	10.41	10.07	9.51	6.20	2.79

* i_x is selection intensity at the first stage.
a is truncation point corresponding i_x.
$k=i_x(1-i_x)$.
i_y' is selection intensity at the second stage.
ρ is family mean correlation between greenhouse trait D8 and nine-year tree height across sites.
r is genetic correlation between greenhouse trait D8 and nine-year tree height across sites.
h_x^2 is family heritability of greenhouse trait D8.

Table 6.9 Estimated correlated response in tree height across sites from three generations of selection based on greenhouse traits HG3 and SR, and changes in genetic paramaters over breeding generations [a]

	Greenhouse traits					
	HG3			SR		
Generation	0	1	2	0	1	2
D_x	0	18.427	24.618	0	0.0283	0.0382
$\sigma_{G_x}^2$	193.20	174.77	168.58	0.330	0.3017	0.2918
σ_x^2	793.50	775.07	768.88	1.5080	1.4801	1.4720
h_x^2	0.2441	0.2252	0.2193	0.2192	0.2039	0.1991
D_y	0	1.152	1.537	0	1.759	2.377
$\sigma_{G_y}^2$	281.8	280.6	280.3	281.8	280.0	279.4
σ_y^2	2434.6	2433.4	2433.1	2434.6	2432.8	2430.4
h_y^2	0.116	0.115	0.115	0.116	0.115	0.114
r	0.207	0.197	0.194	0.270	0.259	0.255
$E_x(G_y)$	2.406	2.188	2.127	2.972	2.739	2.651
$\Sigma E_x(G_y)$	2.406	4.594	6.721	2.972	5.711	8.362

[a] D_x - cumulative reduction of genetic variance in greenhouse trait.
$\sigma_{G_x}^2$ - genetic variance in greenhouse trait.
σ_x^2 - phenotypic variance in greenhouse trait.
h_x^2 - heritability of greenhouse trait.
D_y - cumulative reduction of genetic variance in tree height across sites.
$\sigma_{G_y}^2$ - genetic variance of tree height across sites.
σ_y^2 - phenotypic variance of tree height across sites.
h_y^2 - heritability of tree height across sites.
r - genetic correlation between greenhouse trait and tree height across sites.
$E_{H7}(G_y)$ - genetic gain in tree height across sites.
$\Sigma E_{H7}(G_y)$ - cumulative genetic gain in tree height across sites.

Table 6.10 Estimated correlated response in tree height on site B from three generations of selection based on greenhouse traits H7, GB and BRN2, and changes in genetic paramaters over breeding generations [a]

	Greenhouse traits								
	H7			GB			BRN2		
Generation	0	1	2	0	1	2	0	1	2
D_x	0	387.90	449.16	0	128861	153263	0	0.0263	0.0322
$\sigma_{G_x}^2$	1458	1070.1	1008.8	570726	441865	417463	0.139	0.1127	0.1068
σ_x^2	2142	1754.1	1692.8	988059	859198	834796	0.287	0.2607	0.2548
h_x^2	0.6806	0.6101	0.5959	0.5776	0.5143	0.5001	0.484	0.432	0.4192
D_y	0	8.68	10.04	0	3.83	4.56	0	3.78	4.62
$\sigma_{G_y}^2$	335.4	326.7	325.4	335.4	331.6	330.8	335.4	331.6	330.8
σ_y^2	1785.9	1777.2	1775.9	1785.9	1782.1	1781.3	1785.9	1782.1	1781.3
h_y^2	0.188	0.184	0.183	0.188	0.186	0.185	0.188	0.186	0.185
r	0.312	0.271	0.263	0.225	0.199	0.194	0.244	0.221	0.215
$E_x(G_y)$	6.605	5.358	5.124	4.387	3.637	3.486	4.355	3.702	3.04
$\Sigma E_x(G_y)$	6.605	11.963	17.087	4.387	8.024	11.510	4.355	8.057	11.097

[a] D_x - cumulative reduction of genetic variance in greenhouse trait.
$\sigma_{G_x}^2$ - genetic variance in greenhouse trait.
σ_x^2 - phenotypic variance in greenhouse trait.
h_x^2 - heritability of greenhouse trait.
D_y - cumulative reduction of genetic variance in tree height across sites.
$\sigma_{G_y}^2$ - genetic variance of tree height across sites.
σ_y^2 - phenotypic variance of tree height across sites.
h_y^2 - heritability of tree height across sites.
r - genetic correlation between greenhouse trait and tree height across sites.
$E_{H7}(G_y)$ - genetic gain in tree height across sites.
$\Sigma E_{H7}(G_y)$ - cumulative genetic gain in tree height across sites.

CHAPTER SEVEN

GENERAL DISCUSSION AND CONCLUSIONS

The longevity of most tree species has at least two constraints for forest tree improvement. First, tree breeders have to wait a long time for results from selection and testing. Second, long-term field testing makes tree breeding more expensive. Thus, forest tree breeders are particularly interested in developing techniques that enable them to predict mature tree performance on the basis of performance of young trees, i.e., early selection.

The first part of this thesis extensively reviewed the literature on early selection and studied the theoretical results of early selection on expected genetic gain of a mature trait under different early selection schemes for one generation and from multi-generations of early selection. The second part of this thesis investigated height growth of lodgepole pine at age nine in four field tests and the performance of the same families at the seedling stage in a greenhouse trial. The data permitted an assessment of the correlations between greenhouse and field performance in this species and the evaluation of a variety of early selection schemes (selection based on a single seedling trait, and on multiple seedling traits, index selection based on seedling traits and nine-year tree-height, two-stage selection based on seedling traits and nine-year tree height, and multi-generation selection based on seedling traits).

1. THEORETICAL DEVELOPMENT OF EARLY SELECTION

Early selection has two major advantages for tree breeding: (1) shortening the breeding cycle and, (2) increasing the overall selection intensity or reducing size of the long-term testing. The theoretical bases of these two advantages were developed in this thesis.

Methods of evaluating expected genetic gain from multi-generations of indirect early selection for the purpose of shortening the breeding cycle were derived using regression models. These methods can be used to study expected genetic gains from several generations of early selection within the period of one conventional breeding cycle. The results of this theoretical investigation indicated that: (1) Genetic correlations between early and mature traits will decline after each generation of early selection and will approach a fixed value as the number of generations approaches infinity. (2) Genetic and phenotypic variances, and heritabilities of both the early and mature traits, will decline after each generation of early selection. The reduction of genetic variance in the mature trait will be slower than the that of the early trait. (3) Selection response in both early and mature traits will decline after each generation of early selection and soon will approach a limiting value. The decline of selection response in the mature trait will be slower than that of the early trait.

The theoretical results of multi-generations of indirect selection were derived assuming an additive gene action model and effectively infinite number of gene loci.

These assumptions seem appropriate for economic traits in forest trees that are generally polygenic in nature and exhibit predominantly additive genetic variance. However, if one considers the effects of nonadditive gene action and finite number of gene loci, greater decreases of genetic variance and correlated selection response over generations would be expected. Therefore, the genetic variances and selection responses for correlated traits predicted from the model used in this study, must be considered as upper limit values for multi-generations of indirect selection. The effect of random drift due to small population size on genetic parameters and expected gains was not considered in the models. Hence, theoretical investigations incorporating random drift and limited number of gene loci into multi-generation indirect selection models are needed.

New equations for predicting genetic gain from two-stage selection for increasing overall selection intensity or reducing the size of long-term testing were derived. They are particularly useful to study the efficiency of early selection as first-stage culling in two-stage selection scheme relative to selection based on long-term tests alone. These equations can also evaluate the relationship of genetic parameters under conditions such as when the size of long-term testing can be reduced without any loss in ultimate genetic gain of the mature trait, and when any selection at an early stage will result in less gain than if all selection is at the mature stage. The parameter relationships under these conditions are functions of heritabilities, genetic correlation and selection intensities and would thus have large errors of estimation.

2. EXPERIMENTAL RESULTS IN LODGEPOLE PINE

The results of this study have major implications for developing breeding strategies for lodgepole pine in Alberta. The greenhouse results suggested that growing seedlings in the greenhouse will reduce experimental error, increase the possibility of detecting family differences and thus, enhance estimates of heritability. Since relative efficiency of early selection is directly proportional to the square root of ratio of heritability of early trait to heritability of mature trait, regardless of genetic correlation between early and mature traits (equation 7 in Chapter Two), higher estimates of heritability in the early traits will increase early selection efficiency. The fact that seed weight and seedling emergency rate were only weakly correlated with seedling characters indicates seed weight and seedling emergency speed have little influence on the efficiency of very early selection in lodgepole pine.

In general, genetic correlation between HG1 and nine-year tree height was near zero, while that for HG2 and HG3 were significantly positive with performances across all sites, single sites A and B. Perhaps, the correlation was poor for HG1 because of transplanting shock.

The observation that nine-year tree height correlated genetically with 24 of 28 seedling traits only on the best growing site (site B) and few or none on the other three sites may indicate that indirect selection of field tree height in lodgepole pine in Alberta on the basis of early traits might be most effective for selection of mature performance on better sites. It is not clear whether greenhouse environment was

more similar to site B than any other sites. However, tree growth on dry field sites correlated better with seedling growth in the drought early test environment than in other environments in loblolly pine (Cannell et al. 1978). The choice of seedling traits is also important for early evaluation of lodgepole pine in Alberta. In general, growth traits such as height and diameter, and adaptive traits such as shoot-root biomass ratio are most effective for early selection of field tree height in lodgepole pine in Alberta. Similar observations were reported for other conifers. Seedling growth rate of loblolly pine in the greenhouse correlated positively with volume at age eight (Cannell et al. 1978), and shoot-root ratio of seedlings correlated positively with long-term field performance of families (Waxler and van Buijtenen 1981). Growth and phenology of Douglas-fir seedlings in the greenhouse were significantly correlated with field heights at ages nine, twelve and fifteen (Riiter and Perry 1987). In jack pine, seedling height of sixteen to 21 months in two different greenhouses were positively correlated with seven-year field height (Carter et al. 1990) and nursery height of half-sib families at age four was correlated with twelve-year field height at each of two sites (Magnussen and Yeatman 1986).

Estimates of heritability for nine-year tree height in lodgepole pine were low, ranging from 0.1203±0.030 to 0.1773±0.041. In contrast, estimates of heritability for seedling height in the greenhouse were more than three times greater and suggest the use of early traits can substantially increase genetic gain in nine-year tree height. For example, selection indices based on individual greenhouse traits and nine-year tree height on site B, increased selection efficiencies by 39.7%, on average, compared to

selection on nine-year tree height only.

Genotype-by-environment interaction (GE) in field sites can have a huge effect on expected efficiencies of early selection. If there are family rank change in the field, early traits which are effective for selection on one or more field sites may not be effective on other sites. If breeders want to select families from early tests when GE in field sites is significant, they may choose an early trait or a combination of early traits having the best selection efficiency across sites. In lodgepole pine from Alberta, shoot to root biomass ratio (SR) should be selected in early tests since SR had the best selection efficiency across all sites. While doing so, families which exhibited superior performance only on one or few sites would be culled. If it is desirable to select families in early tests to maximize the genetic gain only on the most productive sites, such as site B, seedling trait D8 should be selected since it had the best selection efficiency for site B.

Nine-year tree height was the only field measurement jointly studied with the seedling traits in this study of lodgepole pine. To implement early selection in lodgepole pine, further studies on early-mature relationships involving timber quality, wood density, insect and disease resistance, and adaptedness traits are required. In the literature of early selection, most reports on early-mature correlations and efficiencies of early selection are confined to growth traits (Lambeth 1980, 1983, Foster 1986, Jiang 1985, Bastien and Roman-Amat 1990). There are few reports on early-mature correlations in other important traits (Gonzalez and Richards 1988, Vargas-Hernandez and Adams 1992, and De Souza et al. 1992). Unless these basic

relationships are fully understood in lodgepole pine, application of early selection for mature height or volume, in order to shorten breeding cycle could result in trees more susceptible to insect and disease, with undesirable timber quality, low wood density etc.

Early selection as it stands now, is best for reducing progeny test size or increasing selection intensity by culling the poorest families at an early stage (Adams et al. 1989, 1992). In a breeding population, two-stage selection could have the following form: individual or family selection in the nursery or other controlled environment, field testing of selected material, and finally, mature selection of individual or family, based on field performance. If this applies to a seed orchard, the sequence might be to establish orchards on the basis of results from early selection, then waiting until mature testing results for final rouging. The total genetic gain by this approach can be estimated from formulas for two-stage gain developed by Young and Weiler (1960), Namkoong (1970), or by Cotterill and James (1984), but could be more readily estimated by equation 11 or 15 in Chapter Two. If genetic parameters of early and mature stages are known, then the theory of two-stage selection could be applied to estimate the optimal allocation of two-stage selection intensities. In this study of lodgepole pine, the two-stage selection approach has shown early selection as first stage culling can either reduce the size of the field test without reducing genetic gain or increase the total selection intensity and genetic gain without increasing the size of the field test.

The study of seedling quantitative and qualitative traits should be extended to

physiological and biochemical traits such as photosynthetic rate or hormonal level, to further explore inherent links between early and mature performance. Generation interval and long-term tests are major component of an indepth cost-benefit analysis of tree improvement strategies. Only when genetic and economic benefits could be realised through early tests from selection on growth and the other traits such as timber quality, wood density, insect and disease resistance, adaptedness, would early selection become a standard tree breeding approach.

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Appendix 1.1 Age-age correlation studies in tree species [a]

Type	Correlation Matrix	Sample size	Reference
Family mean	H2 H3 H4 H5 H3 0.787 H4 0.577 0.810 H5 0.425 0.668 0.830 H6 0.461 0.651 0.756 0.952	35-52 half-sib families White ash	Clausen K.E. 1982
Genetic	H2 to H15 with V15 all above 0.75 G8 to G15 with V15 from 0.9 to 1.	30 half-sib families Douglas-fir	Bastien J.CH. and Roman-Amat B. 1990
Family mean	H27 D27 V27 V27/plot H1 -0.25 -0.34 -0.44 0.32 H3 0.39 0.15 -0.08 0.84 H6 0.28 0.30 0.06 0.86	9 half-sib families Sitka spruce	Gill J.G.S. 1987
Genetic	H0 H3 H6 H10 D10 H3 0.363 H6 0.407 0.948 H10 0.339 0.870 0.926 D10 0.492 0.810 0.903 0.828 D15 0.292 0.722 0.778 0.790 0.917		
Phenotypic Genetic	SG2 SG4 SG6 SG8 SG10 SGM 0.27 0.40 0.44 0.45 0.45 SGM 0.73 0.90 0.99 0.99 0.95	15 half-sib families Loblolly pine	Loo J.A. and Tauer C.G. 1984
Phenotypic	TL2 TL4 TL6 TL8 TL10 TLM 0.30 0.39 0.45 0.51 0.54		
Genetic	H11 with H22 are 0.62 and 0.60 H8 with H22 are 0.69 and 0.94	8-18 10-16 half-sib families White spruce	Ying C.C. and Morgenstern E.K. 1979
Family	H3 H5 H7 H8 H12 H20 H25 H5 0.67 H7 1.0 1.0 H8 0.77 0.93 0.88 H12 -0.47 0.52 0.05 0.14 H20 -0.38 0.58 0.0 0.13 1.0 H25 -0.19 0.28 -0.52 -0.61 0.63 0.82 H29 0.05 0.19 -0.47 -0.60 0.64 0.85 1.0	71 half-sib families Ponderosa pine	Namkoong G. and Conkle M.T. 1976

Type	Correlation Matrix	Sample size	Reference
Family mean	H9 with H15 are 0.943 and 0.930	55 half-sib families White spruce	Nienstaedt H. and Riemenschneider D.E. 1985
Family mean	H4 H8 H12 H12 0.74 0.89 H16 0.61 0.83 0.92	18-60 full-sib families Loblolly pine	McKeand S.E. 1988
Genetic (above diagonal) Phenotypic (below diagonal)	H2.5 H6.5 H10.5 H16 H2.5 0.26 0.24 -0.12 H6.5 0.34 0.98 0.79 H10.5 0.34 0.72 0.84 H16 0.34 0.63 0.76	28 half-sib families Radiata pine	Cotterill P.P and Dean C.A. 1988
	BA4.5 BA6.5 BA10.5 BA16 BA4.5 0.78 0.29 0.10 BA6.5 0.89 0.87 0.73 BA10.5 0.71 0.90 0.96 BA16 0.54 0.72 0.88		For base area increment, Genetic correlations are larger than phenotypic ones
Genetic (above diagonal) Phenotypic (below diagonal)	H1 H2 H3 H5 H7 H1 0.99 0.92 0.81 0.67 H2 0.54 0.99 0.94 0.84 H3 0.48 0.80 0.98 0.90 H5 0.40 0.67 0.84 0.94 H7 0.34 0.57 0.73 0.88	101 half-sib families Jack pine	Riemenschneider D.E. 1988
Genetic	H1 H2 H3 H4 H5 H6 H2 0.83 H3 0.92 0.96 H4 0.95 0.89 0.97 H5 0.82 0.83 0.96 0.97 H6 0.77 0.86 0.95 0.92 1.00 H7 0.55 0.72 0.84 0.82 0.96 0.96	11 half-sib families Loblolly pine	Foster G.S. 1986
	H8 H10 H15 TV10 TV15 H1 0.51 0.46 0.31 0.26 0.25 H2 0.57 0.48 0.25 0.57 0.41 H3 0.80 0.77 0.58 0.77 0.67 H4 0.92 0.84 0.66 0.65 0.57 H5 1.02 0.95 0.74 0.70 0.58 H6 0.99 0.99 0.71 0.71 0.53 H7 0.86 0.94 0.50 0.64 0.40 H8 1.00 1.15 0.85 0.53 0.37 H10 1.15 1.00 0.96 0.89 0.81 H15 0.85 0.96 1.00 0.59 0.70		

Type	Correlation Matrix	Sample	Reference
Genetic (above diagonal) Phenotypic (below diagonal)	H5 H10 H15 H20 H5 0.85 0.78 0.68 H10 0.74 0.99 0.84 H15 0.62 0.84 0.94 H20 0.52 0.76 0.83 genetic correlation > family mean correlation > phenotypic correlation for either height and volume traits	15-48 half-sib families Loblolly pine	Lambeth C.C. et al. 1983
Between family Within family Total	H3 H8 H14 H18 H25 0.00 0.80 0.96 0.98 half-sib H25 0.53 0.20 0.68 0.78 full-sib H25 0.14 0.60 0.81 0.87 half-sib H25 0.14 0.33 0.66 0.81 full-sib H25 0.10 0.53 0.81 0.88 half-sib H25 0.10 0.30 0.62 0.80 full-sib	8 half-sib and 8 full-sib families Slash pine	Squillace A.E. and Gansel C.R. 1974
Phenotypic	H17 H41 H11 0.955 0.794 H17 1.00 0.901	15 half-sib families Norway spruce	Nanson A. 1987
Phenotypic	H6 H11 H16 H11 0.88 H16 0.77 0.96 H50 -0.80 -0.96 -0.93		Giertych M. 1974 Scotch pine
Family	H10 H12 H15 H18 H23 H28 H33 H5 0.64 0.14 -0.07 -0.23 -0.20 -0.44 -0.57 H10 1.00 0.60 0.01 -0.01 -0.14 -0.58 -0.74 H12 0.60 1.00 -0.11 -0.21 -0.37 -0.91 -1 H15 0.01 -0.11 1.00 1.00 0.64 0.26 0.24 H18 -0.01 -0.21 1.00 1.00 0.85 0.77 0.93 H23 -0.14 -0.37 0.64 0.85 1.00 0.95 0.97 H28 -0.58 -0.91 0.26 0.77 0.95 1.00 0.96	116 half-sib families Douglas-fir	Namkoong G. et al. 1972

[a] H-height, V-volume, V/plot-volume per plot, G-girth length, D-diameter, SG-specific gravity of wood, SGM-specific gravity of mature wood, TL-tracheid length, and BA-tree basal area. Numerals next to the traits are measurement ages in years.

Appendix 2.1 Selection effect on genetic variance of a correlated trait and the genetic covariance between the selected and correlated traits

Assume breeding value of mature trait Y is G_y and breeding value of juvenile trait X is G_x, regresion relationship in the base population is

$$G_y = a G_x + E_y$$

and genetic correlation r is

$$r = \frac{cov(G_x\ G_y)}{\sigma_{G_x}\sigma_{G_y}} \quad .$$

Thus, $E_y = G_y$ - a G_x and it's variance is

$$\sigma^2_{E_y} = \sigma^2_{G_y} + a^2\sigma^2_{G_x} - 2\ a\ cov(G_x\ G_y) \quad .$$

The regression coefficient a is

$$a = \frac{cov(G_x\ G_y)}{\sigma^2_{G_x}}$$

and genetic variance of mature trait Y is

$$\sigma^2_{G_y} = a^2\ \sigma^2_{G_x} + \sigma^2_{E_y} \quad .$$

After selection, genetic variance $\sigma_{G_x}^2$ of direct selection trait X is changed into $\sigma_{G_x}^{2'}$ with

$$\sigma^{2'}_{G_x} = (1 - h^2_x k)\ \sigma^2_{G_x} \quad .$$

Similarly, genetic variance of $\sigma_{G_y}^2$ of correlated trait Y is changed into $\sigma_{G_y}^{2'}$ which is

derived as following

$$\sigma^{2'}_{G_y} = a^2 \sigma^{2'}_{G_x} + \sigma^2_{E_y}$$

$$= a^2 \sigma^2_{G_x}(1-h^2_x k) + \sigma^2_{G_y} + a^2 \sigma^2_{G_x} - 2a\,cov(G_x\ G_y)$$

$$= r^2(1-h^2_x k)\,\sigma^2_{G_y} + \sigma^2_{G_y} + r^2\sigma^2_{G_y} - 2r^2\sigma^2_{G_y}$$

$$= (1-r^2 h^2_x k)\,\sigma^2_{G_y}$$

The covariance between breeding value of juvenile trait and mature trait in the selected population is estimated as

$$cov(G_x\ G_y)' = a\ \sigma^{2'}_{G_x} = a\ (1-h^2_x k)\,\sigma^2_{G_x}$$

$$= cov(G_x\ G_y)\ (1-h^2_x k) \quad .$$

Appendix 2.2 Correlated genetic variance of mature trait Y in the progeny after a parental generation of selection on juvenile trait X

Assume breeding value of mature trait Y is $G_y(0)$ and breeding value of juvenile trait X is $G_x(0)$ in the base population, the regresion relationship in the base population is

$$G_y(0) = a\,G_x(0) + E_y(0) \quad .$$

Thus, an estimate of regression coefficient a is

$$a = \frac{cov(G_x(0)\ G_y(0))}{\sigma^2_{G_x}(0)} = r(0)\ \frac{\sigma_{G_y}(0)}{\sigma_{G_x}(0)}$$

and $E_y(0)=G_y(0)$ - a $G_x(0)$ with variance

$$\sigma^2_{E_y}(0) = [1-r^2(0)]\,\sigma^2_{G_y}(0) \quad .$$

Assuming same regression of breeding values in the progeny after random mating in the selected population, the genetic variance of mature trait Y in the progeny population is

$$\sigma^2_{G_y}(1) = a^2\,\sigma^2_{G_x}(1) + \sigma^2_{E_y}(1)$$

$$- r^2(0)\,\frac{\sigma^2_{G_y}(0)}{\sigma^2_{G_x}(0)}\left\{\frac{1}{2}\left[1 - h_x^2(0)\,k\right]\sigma^2_{G_x}(0) + \frac{1}{2}\sigma^2_{G_x}(0)\right\}$$

$$- r^2(0)\,\sigma^2_{G_y}(0)\left\{\frac{1}{2}\left[1 - h_x^2(0)\,k\right] + \frac{1}{2}\right\}$$

$$- r^2(0)\,\sigma^2_{G_y}(0)\,\frac{1}{2} - r^2(0)\,\sigma^2_{G_y}(0)\,\frac{1}{2}h_x^2(0)\,k + \frac{1}{2}r^2(0)\,\sigma^2_{G_y}(0)$$

$$- \frac{1}{2}r^2(0)\left[1 - h_x^2(0)\,k\right]\sigma^2_{G_y}(0) + \frac{1}{2}r^2(0)\,\sigma^2_{G_y}(0)$$

and with the same environment variance in both generation ($\sigma_{E_y}(1)=\sigma_{E_y}(0)$). Thus, genetic variance of mature trait in the progeny is

$$\sigma^2_{G_y}(1) = -\frac{1}{2}r^2(0)\,\sigma^2_{G_y}(0) - \frac{1}{2}r^2(0)\,\sigma^2_{G_y}(0)\,h_x^2(0)\,k + \frac{1}{2}r^2(0)\,\sigma^2_{G_y}(0) + [1 - r^2(0)$$

$$- \sigma^2_{G_y}(0) - \frac{1}{2}r^2(0)\,\sigma^2_{G_y}(0)\,h_x^2(0)\,k$$

$$- \frac{1}{2}\left[1 - h_x^2(0)\;k\,r^2(0)\right]\sigma^2_{G_y}(0) + \frac{1}{2}\sigma^2_{G_y}(0)$$

Appendix 2.3 Phenotypic variance of mature trait Y in the progeny after a parental generation of selection on juvenile trait X

Assume constant environment variance and reduction in the phenotypic variance in the progeny only due to reduction of genetic variance. Thus, phenotypic variance in the progeny is

$$\begin{aligned}
\sigma^2_{P_y}(1) &= \sigma^2_{P_y}(0) - \frac{1}{2} h^2_x(0)\, k r^2(0)\, \sigma^2_{G_y}(0) \\
&= \sigma^2_{P_y}(0) - \frac{1}{2} h^2_x(0)\, k r^2(0)\, \sigma^2_{P_y}(0)\, h^2_y(0) \\
&= \sigma^2_{P_y}(0) - \frac{1}{2} h^2_x(0)\, h^2_y(0)\, k r^2(0)\, \sigma^2_{P_y}(0) \\
&= [1 - \frac{1}{2} h^2_x(0)\, h^2_y(0)\, k r^2(0)]\, \sigma^2_{P_y}(0) \\
&= \frac{1}{2} [1 - h^2_x(0)\, h^2_y(0)\, k r^2(0)]\, \sigma^2_{P_y}(0) + \frac{1}{2} \sigma^2_{P_y}(0) \quad .
\end{aligned}$$

Appendix 2.4 Correlated genetic variance of mature trait Y in the progeny after n generations of selection on juvenile trait X

By random mating, the genetic variance of mature trait Y at generation t+1 [$\sigma_{G_y}^2(t+1)$] has the following relationship with genetic variance at generation t [$\sigma_{G_y}^2(t)$] and genetic variance at base population $\sigma_{G_y}(0)$ (see Bulmer 1980)

$$\sigma_{G_y}^2(t+1) = \frac{1}{2}\sigma_{G_y}^{2'}(t) + \frac{1}{2}\sigma_{G_y}^2(0)$$

where $\sigma_{G_y}^{2'}(t)$ is genetic variance in the selected population after t generations. Thus, genetic variance after one-generation of selection is

$$\sigma_{G_y}^2(1) = \frac{1}{2}[1-r^2(0)\,h_x^2(0)\,k]\,\sigma_{G_y}^2(0) + \frac{1}{2}\sigma_{G_y}^2(0)$$

$$= \sigma_{G_y}^2(0) - \frac{1}{2}r^2(0)\,k h_x^2(0)\,\sigma_{G_y}^2(0) \quad .$$

and genetic variance after two-generations of selection is

$$\sigma_{G_y}^2(2) = \frac{1}{2}\sigma_{G_y}^{2'}(1) + \frac{1}{2}\sigma_{G_y}^2(0)$$

where

$$\sigma_{G_y}^{2'}(1) = [1-r^2(1)\,h_x^2(1)\,k]\,\sigma_{G_y}^2(1)$$

$$= [1-r^2(1)\,h_x^2(1)\,k]\,\frac{1}{2}[1-r^2(0)\,k h_x^2(0)\,\sigma_{G_y}^2(0)] \quad .$$

Thus,

$$\sigma^2_{G_y}(2) = \frac{1}{2}\left[1 - r^2(1)\, h_x^2(1)\, k\right] \sigma^2_{G_x}(1) + \frac{1}{2}\sigma^2_{G_y}(0)$$

$$- \frac{1}{2}\sigma^2_{G_y}(1) - \frac{1}{2} r^2(1)\, h_x^2(1)\, k + \sigma^2_{G_y}(0)$$

$$- \frac{1}{2}\left[\sigma^2_{G_y}(0) - \frac{1}{2} r^2(0)\, h_x^2(0)\, k \sigma^2_{G_y}(0)\right] - \frac{1}{2} r^2(1)\, h_x^2(1)\, k\, \sigma^2_{G_y}(1) + \frac{1}{2}\sigma^2_{G_y}$$

$$- \sigma^2_{G_y}(0) - \frac{1}{2} r^2(1)\, h_x^2(1)\, k\, \sigma^2_{G_y}(1) - \frac{1}{4} r^2(0)\, h_x^2(0)\, k\, \sigma^2_{G_y}(0) \quad .$$

Similarly, the genetic variance after three-generations of selection is

$$\sigma^2_{G_y}(3) = \sigma^2_{G_y}(0) - \frac{1}{2} r^2(2)\, h_x^2(2)\, k \sigma^2_{G_y}(2) - \frac{1}{4} r^2(1)\, h_x^2(1)\, k\, \sigma^2_{G_y}(1)$$

$$- \frac{1}{8} r^2(0)\, h_x^2(0)\, k\, \sigma^2_{G_y}(0) \quad .$$

Thus, after n-generations of selection, the genetic variance is

$$\sigma^2_{G_y}(n) = \sigma^2_{G_y}(0) - D_y(n)$$

where $D_y(n)$ is

$$D_y(n) = \frac{k}{2} r^2(n-1)\, h_x^2(n-1)\, \sigma^2_{G_y}(n-1) + \frac{k}{4} r^2(n-2)\, h_x^2(n-2)\, \sigma^2_{G_y}(n-2) +$$

$$\ldots + \frac{k}{2^n} r^2(0)\, h_x^2(0)\, k\, \sigma^2_{G_y}(0) \quad .$$

Appendix 3.1 Location of the lodgepole pine parent trees used in the greenhouse experiment and field testing *

Stand	Parent tree codes				Latitude	Longitude	Elevation(m)
1	1780*	1781	1782	1783	54°28'	115°46'	1022
2	1788	1789	1790	1791	54°36'	115°55'	1110
3	1816	1817	1818	1819	54°53'	115°33'	1110
4	1836	1837	1838	1839	54°49'	115°16'	1080
5	1860	1861	1862	1863	54°46'	115°18'	1140
6	1864	1865	1866	1867	54°49'	115°28'	990
7	1868*	1869	1870	1871	54°57'	115°33'	1000
8	1872	1873	1874	1875	54°57'	115°11'	855
9	1884	1885	1886	1887	54°42'	115°29'	1110
10	1888	1889	1890	1891	54°43'	115°27'	1130
11	2252	2253	2254	2255	55°57'	116°32'	1033
12	2260	2261	2262	2263	54°28'	115°37'	1050
13	2272*	2273	2274	2275	54°26'	116°31'	975
14	2280	2281	2282	2283	54°34'	116°50'	1094
15	994*	995	996*	997	54°29'	115°26'	1030
16	1002	1003	1004	1005	54°29'	115°27'	1130
17	1010	1011	1012	1013	54°26'	115°34'	1070
18	1014	1015	1016	1017	54°26'	115°33'	1070
18	1018*	1019	1020*	1021	54°27'	115°33'	1160
20	1022	1023	1024	1025	54°28'	115°35'	1130
21	1026	1027	1028	1029	54°25'	115°34'	1030
22	1030	1031	1032	1033	54°26'	115°30'	1070
23	1034*	1035	1036	1037*	54°28'	115°36'	1100
24	1038*	1039*	1040	1041	54°25'	115°36'	1000
25	1046	1047	1048	1049	54°27'	115°39'	1000
26	1050	1051	1052	1053*	54°25'	115°38'	1070
27	1054	1055	1056	1057	54°27'	115°37'	1070
28	1058	1059	1060	1061	54°28'	115°38'	1030
29	1062*	1063	1064*	1065	54°28'	115°39'	1070
30	1070	1071	1072	1073	54°29'	115°41'	1130
31	1074	1075	1076*	1077	54°32'	115°46'	1130
32	1078	1079	1080	1081	54°23'	115°39'	1070
33	1082*	1083	1084	1085	54°25'	115°42'	970

* Total 33 stands and 132 families.
Only 116 Families were used in the greenhouse experiment; families with * were not included.

Appendix 3.2 Abbreviation and description of greenhouse traits

H1	Height at two weeks after transplant	
H2	Height at the end of the first growth period	
H3	Height	at the end of first dormancy period
D3	Basal diameter	
BUDN	Bud number	at the end of dormancy
BUDS	Bud size	
BRN1	Branch number	
BRS	Branch strengh	
H4	Height of seedlings at three weeks	in the second period
H5	Height of seedlings at six weeks	
H6	Height of seedlings at nine weeks	
H7	Height and	at the end of second growth period
D7	Basal diameter	
D8	Basal diameter	at the end of pre-harvesting
BRN2	Branch number	
SB	Stem biomass	at harvesting
BB	Branch biomass	
NB	Needle biomass	
RB	Root biomass	
HG1	Height growth in the first period (i.e. H2-H1)	
HG2	Height growth in the dormancy induction period (i.e., H3-H2)	
HG3	Height growth in the second growth period (i.e., H7-H3)	
DG	Diameter growth in the second growth period (i.e., D7-D3)	
TLB	Total biomass (i.e. SB+BB+NB+RB)	
GB	Above ground biomass (i.e. SB+BB+NB)	
HI	Harvest index (i.e., SB/GB)	
SR	Shoot-root ratio (i.e., GB/RB)	
RHD	Sturdiness quotient (i.e., H7/D7).	

Appendix 3.3 Estimation of the variances of individual, family, and stand heritability estimates

1. Variance of individual heritability

$$Var(\hat{h}_i^2) = 2*(\hat{h}_i^2)^2*\left[\frac{\frac{M_{f(s)}^2}{f_f+2}+\frac{M_e^2}{f_e+2}}{(M_{f(s)}-M_e)^2}+\frac{\frac{(k_7-1)^2*M_e^2}{f_e+2}+\frac{M_{f(s)}^2}{f_f+2}}{[(k_7-1)*M_e+M_{f(s)}]^2}\right.$$

$$\left.+2*\frac{\frac{M_{f(s)}^2}{f_f+2}-\frac{(k_7-1)*M_e^2}{f_e+2}}{(M_{f(s)}-M_e)*[(k_7-1)*M_e+M_{f(s)}]}\right] .$$

since $M_{f(s)}^2$ and M_e^2 are independent.

2. Variance of family heritability

$$var(\hat{h}_f^2) = \frac{2*M_e^2}{M_{f(s)}^2}*\left(\frac{f_e+f_f}{f_e*f_f}\right)$$

3. Variance of stand heritability:

$$Var(\hat{h}_s^2) = 2*(\hat{h}_s^2)^2*$$

$$\left[\frac{\frac{M_s^2}{f_s+2}+\left(\frac{k_5}{k_7}\right)^2*\frac{M_{f(s)}^2}{f_f+2}+\left(\frac{k_4}{k_8}\right)^2*\frac{M_{rs}^2}{f_{rs}+2}+\left(\frac{k_7*k_8-k_5*k_8-k_7*k_4}{k_7*k_8}\right)^2*\frac{M_e^2}{f_e+2}}{\left(M_s-\frac{k_5}{k_7}*M_{f(s)}-\frac{k_4}{k_8}*M_{rs}-\frac{k_7*k_8-k_5*k_8-k_7*k_4}{k_7*k_8}*M_e\right)^2}\right.$$

$$\left.+\frac{1}{f_s+2}-2*\frac{\frac{M_s^2}{f_s+2}}{M_s*\left(M_s-\frac{k_5}{k_7}*M_f-\frac{k_4}{k_8}*M_{rs}-\frac{k_7*k_8-k_5*k_8-k_7*k_4}{k_7*k_8}*M_e\right)}\right] .$$

where M_s--Mean square of stand;

$M_{f(s)}$--Mean square of family within stand;

M_{rs}--Mean square of interaction of replicate with stand;

M_e--mean square of residual;

f_s--degrees of freedom of stand;

f_f--degrees of freedom of family within stand;

f_{rs}--degrees of freedom of interaction of replicate with stand;

f_e--degrees of freedom of residual.

the k coefficient were derived by least square sulution. Although M_s, M_f, and M_{rs} are not independent under imbalance data, covariances among M_s, M_f, and M_{rs} are not considered.

Appendix 3.4 Estimation of the variance of genetic correlation estimates (r_g)

$$Var(\hat{r}_g) = \frac{2}{k_7^2} * \hat{r}_g^2 * \left[\frac{\frac{M_{f_{11}}^2}{f_f+2} + \frac{M_{e_{11}}^2}{f_e+2}}{4 * \left(\frac{1}{k_7} * (M_{f_{11}} - M_{e_{11}})\right)^2} + \frac{\frac{M_{f_{22}}^2}{f_f+2} + \frac{M_{e_{22}}^2}{f_e+2}}{4 * \left(\frac{1}{k_7} * (M_{f_{22}} - M_{e_{22}})\right)^2} \right.$$

$$+ \frac{\frac{(M_{f_{11}} * M_{f_{22}} + M_{f_{12}}^2)}{f_f+2} + \frac{(M_{e_{11}} * M_{e_{22}} + M_{e_{12}}^2)}{f_e+2}}{2 * \left[\frac{1}{k_7} (M_{f_{12}} - M_{e_{12}})\right]^2} - \frac{\frac{M_{f_{11}} * M_{f_{12}}}{f_f+2} + \frac{M_{e_{11}} * M_{e_{12}}}{f_e+2}}{\frac{1}{k_7} (M_{f_{11}} - M_{e_{11}}) * \frac{1}{k_7} (M_{f_{12}} - M_{e_{12}})}$$

$$\left. - \frac{\frac{M_{f_{22}} * M_{f_{12}}}{f_f+2} + \frac{M_{e_{22}} * M_{e_{12}}}{f_e+2}}{\frac{1}{k_7} (M_{f_{22}} - M_{e_{22}}) * \frac{1}{k_7} (M_{f_{12}} - M_{e_{12}})} + \frac{\frac{M_{f_{12}}^2}{f_f+2} + \frac{M_{e_{12}}^2}{f_e+2}}{2 * \frac{1}{k_7} (M_{f_{11}} - M_{e_{11}}) * \frac{1}{k_7} (M_{f_{22}} - M_{e_{22}})} \right]$$

where $M_{f_{ii}}$ - mean square of family within stand of ith trait;

$M_{f_{ij}}$ - mean crossproduct of family within stand in the ith and jth traits;

$M_{e_{ii}}$ - mean square of residual of ith trait;

$M_{e_{ij}}$ - mean crossproduct of residual in the ith and jth traits;

f_f - degrees of freedom of family within stand;

f_e - degrees of freedom of residual.

the k coefficients were derived by least square sulution.

Appendix 4.1 Family means for nine-year tree height in the four field sites (A, B, C, D) *

Family	A	B	C	D	Family	A	B	C	D
1002	189.82	272.71	197.39	208.39	1003	221.88	268.32	209.50	207.56
1004	172.25	249.22	204.68	207.21	1005	190.83	254.40	215.18	214.00
1010	202.92	262.69	222.33	220.06	1011	183.00	269.17	211.07	209.89
1012	172.88	251.42	213.84	218.89	1013	182.56	289.30	232.44	205.89
1014	205.78	261.32	197.29	222.84	1015	191.43	261.29	207.45	198.28
1016	182.75	259.94	185.07	183.72	1017	165.17	259.88	190.13	196.75
1018	207.56	254.45	186.11	200.25	1019	174.73	224.09	189.83	192.80
1020	207.81	269.26	209.94	201.82	1021	175.13	248.69	209.73	196.57
1022	185.63	247.06	218.33	208.35	1023	170.60	248.00	215.92	229.11
1024	202.13	254.50	217.29	219.44	1025	202.44	266.37	174.83	182.47
1026	188.33	260.50	210.61	205.24	1027	194.19	275.07	193.06	210.78
1028	181.06	272.50	187.20	187.94	1029	187.47	258.00	192.14	189.44
1030	184.00	246.24	195.35	204.16	1031	182.20	247.25	204.95	183.07
1032	201.50	254.13	207.53	222.84	1033	177.47	253.35	190.37	198.11
1046	197.38	256.47	187.95	192.68	1047	204.76	272.05	228.72	236.05
1048	213.41	278.00	205.39	230.28	1049	204.62	237.73	226.54	214.71
1050	218.84	300.78	217.83	204.32	1051	217.00	290.79	193.18	199.07
1052	212.53	265.00	204.43	201.69	1053	186.93	232.43	208.38	192.53
1054	185.31	246.13	211.29	209.13	1055	194.17	263.60	202.06	210.61
1056	188.67	256.35	210.30	207.00	1057	204.72	232.47	190.00	226.37
1058	182.33	253.82	182.20	189.33	1059	181.25	274.56	204.56	197.27
1060	190.50	256.31	205.06	230.20	1061	208.22	251.67	211.21	210.42
1062	175.50	248.84	209.11	208.53	1063	197.26	269.45	207.11	194.00
1064	221.08	292.78	219.00	216.07	1065	198.83	277.39	205.50	183.40
1070	225.76	266.63	234.84	225.18	1071	206.00	261.56	234.25	186.83
1072	207.19	290.07	234.78	250.74	1073	202.13	267.67	237.30	172.71
1074	184.60	239.88	186.44	189.57	1075	195.13	240.17	179.80	202.61
1076	191.19	241.82	197.00	190.82	1077	182.73	245.15	194.43	220.14
1078	193.38	280.21	183.40	209.35	1079	202.07	276.77	197.43	191.31
1080	199.08	264.60	167.33	186.69	1081	181.07	248.61	167.94	175.73
1082	213.60	259.63	201.33	229.89	1083	223.06	262.17	217.33	215.81
1084	214.53	284.26	223.30	225.70	1085	211.71	267.10	213.06	202.94
1780	200.00	256.44	190.44	189.36	1781	190.88	258.57	207.13	210.00
1782	202.81	269.89	205.11	187.11	1783	192.83	257.88	206.67	185.06
1788	179.35	270.71	205.78	202.40	1789	191.41	251.53	182.53	220.32
1790	202.07	265.53	212.79	216.10	1791	184.47	260.22	173.39	219.94
1816	194.25	246.13	193.79	204.53	1817	214.73	267.74	201.89	220.17
1818	201.00	288.87	207.69	216.29	1819	197.94	282.53	213.25	207.90

continued

Family	A	B	C	D	Family	A	B	C	D
1836	193.93	246.94	195.73	200.00	1837	219.16	272.89	210.50	196.19
1838	187.75	245.53	209.25	211.55	1839	217.86	275.88	211.35	219.18
1860	216.13	264.17	217.94	191.77	1861	177.43	270.93	208.65	202.27
1862	201.86	253.72	195.11	190.23	1863	192.68	260.63	218.75	194.06
1864	188.20	256.90	212.58	214.94	1865	190.79	243.45	191.89	197.44
1866	199.81	275.30	227.88	230.40	1867	150.53	236.44	193.54	209.25
1868	205.06	240.71	212.76	182.94	1869	183.39	256.93	194.17	207.69
1870	185.87	259.29	197.35	200.13	1871	173.68	256.71	181.31	181.63
1872	184.59	261.83	189.44	189.71	1873	193.94	265.89	208.37	202.00
1874	180.53	255.00	202.29	217.75	1875	182.75	259.41	190.31	214.89
1884	200.35	248.21	199.58	212.17	1885	201.38	248.38	212.16	222.68
1886	209.25	230.33	181.88	217.00	1887	173.64	250.53	211.38	212.13
1888	187.65	272.30	192.53	223.39	1889	176.31	251.22	204.00	198.35
1890	201.22	269.32	196.89	234.65	1891	217.41	285.21	226.82	237.94
2252	181.78	269.89	227.72	230.05	2253	211.80	277.18	218.39	222.28
2254	190.06	260.47	222.11	218.79	2255	203.56	254.00	211.83	217.30
2260	196.63	255.06	208.56	196.56	2261	195.06	266.69	207.94	184.17
2262	199.35	252.33	202.06	202.53	2263	211.70	243.77	200.69	198.00
2272	188.57	247.19	204.60	210.39	2273	221.56	250.94	225.42	212.88
2274	183.79	242.08	188.05	192.06	2275	183.88	255.00	198.71	191.95
2280	173.29	286.79	204.17	212.83	2281	175.53	268.44	210.56	214.60
2282	180.08	250.53	196.22	214.89	2283	165.44	248.63	181.35	210.28

* measurement unit: cm

Appendix 5.1 Illustration of the necessity conditions of homogeneous genetic and error variances in order to apply the linear model to estimating genetic correlation when data are unbalanced

By the notation of Itoh et al. (1990), if traits in two different environments (the same or different traits) are analyzed separately, the linear model (model A) is

$$y=\begin{bmatrix}y_1\\y_2\end{bmatrix}=\begin{bmatrix}1_1\mu_1\\1_2\mu_2\end{bmatrix}+\begin{bmatrix}Z_1 & 0\\0 & Z_2\end{bmatrix}\begin{bmatrix}u_1\\u_2\end{bmatrix}+\begin{bmatrix}e_1\\e_2\end{bmatrix} \quad (1)$$

where $\mathbf{y}_i$ (i=1 or 2) is a n_i x 1 vector of observation for the trait in environment 1 or 2; μ_i is the expected value of the trait in environment 1 or 2; $\mathbf{1}_i$ is an n_i x 1 vector of all ones; $\mathbf{u}_i$ is a p x 1 vector of random genetic-group effects for the trait in environment 1 or 2; $\mathbf{Z}_i$ is a n_i x p incidence matrix; $\mathbf{e}_i$ is a n_i x 1 vector of residuals for the trait in environments 1 or 2. The expectation and variance-covariance assumptions for this model are:

$E(\mathbf{y}_i)=\mathbf{1}_i\mu_i$, $E(\mathbf{u}_i)=\mathbf{0}$, $E(\mathbf{e}_i)=\mathbf{0}$ and

$$Var\begin{bmatrix}u_1\\u_2\end{bmatrix}=\begin{bmatrix}I\sigma_1^2 & I\sigma_{12}\\I\sigma_{21} & I\sigma_2^2\end{bmatrix} \quad (2)$$

$$Var\begin{bmatrix}e_1\\e_2\end{bmatrix}=\begin{bmatrix}I_1\sigma_{e_1}^2 & 0\\0 & I_2\sigma_{e_2}^2\end{bmatrix} \quad (3)$$

$\text{cov}(\mathbf{u}_1\ \mathbf{e}_2)=\text{cov}(\mathbf{u}_2\ \mathbf{e}_1)=\mathbf{0}$, where $\mathbf{I}$, $\mathbf{I}_1$ and $\mathbf{I}_2$ are identity matrices of appropriate order; σ_1^2 and σ_2^2 are genetic variances in environments 1 and 2, respectively; σ_{12} is the

genetic covariance between environment 1 and 2,; $\sigma_{e_1}^2$ and $\sigma_{e_2}^2$ are error variances in environment 1 and 2, respectively. Thus, the variance of the model A is

$$Var\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} Z_1 Z_1' \sigma_1^2 & Z_1 Z_2' \sigma_{12} \\ Z_2 Z_1' \sigma_{21} & Z_2 Z_1' \sigma_2^2 \end{bmatrix} + \begin{bmatrix} I_1 \sigma_{e_1}^2 & 0 \\ 0 & I_2 \sigma_{e_2}^2 \end{bmatrix} \quad (4)$$

with variance and covariance of y_i's as

$$Var(y_1) = Z_1 Z_1' \sigma_1^2 + I_1 \sigma_{e_1}^2 \quad (5)$$

$$Var(y_2) = Z_2 Z_2' \sigma_2^2 + I_2 \sigma_{e_2}^2 \quad (6)$$

$$cov(y_1\ y_2) = Z_1 Z_2' \sigma_{12} \quad (7)$$

If a combined analysis of same traits in two environments is assumed for the same observations (conventional two-way analysis of variance), three conditions are assumed for these parameters (Itoh et al. 1990): (1) the error variances may be heterogenous; (2) covariances between genetic group effects and interactions exist; and (3) covariance among interactions exists. Therefore, the combined linear model (model B) has the form

$$y = \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} 1_1 \mu_1 \\ 1_2 \mu_2 \end{bmatrix} + \begin{bmatrix} Z_1 \\ Z_2 \end{bmatrix} u_G + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} u_{I_1} \\ u_{I_2} \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix} \quad (8)$$

where y_i, μ_i, 1_i, and Z_i are defined earlier; u_G is a vector of genetic-group effects averaged over environments 1 and 2; u_{I_1} or u_{I_2} is a n_1 x 1 or n_2 x 1 vector of genetic-group by environment interaction in environment 1 or 2, respectively; and ϵ_1 or ϵ_2 is a n_1 x 1 or n_2 x 1 vector of residual in environment 1 or 2, respectively. From these

three conditions, the expectation and variance-covariance in the model B is $E(\mathbf{y}_i)=\mathbf{1}_i\mu_i$, $E(\mathbf{u}_G)=0$, $E(\mathbf{u}_{i_i})=0$, thus $\mathbf{u}_{i_1}=-\mathbf{u}_{i_2}$, $E(\epsilon_i)=0$ $var(\mathbf{u}_G)=I\sigma_G^2$ and

$$Var\begin{bmatrix}u_{I_1}\\ u_{I_2}\end{bmatrix}=\begin{bmatrix}I\sigma^2_{I_1} & I\sigma_{I_{12}}\\ I\sigma_{I_{21}} & I\sigma^2_{I_2}\end{bmatrix}=\begin{bmatrix}I\sigma^2_I & -I\sigma^2_I\\ -I\sigma^2_I & I\sigma^2_I\end{bmatrix} \tag{9}$$

since $\sigma_{i_1}^2=\sigma_{i_2}^2=-\sigma_{i_{12}}=-\sigma_{i_{21}}=\sigma_i^2$ in the two environment situation; and

$$Var\begin{bmatrix}e_1\\ e_2\end{bmatrix}=\begin{bmatrix}I_1\sigma^2_{e_1} & 0\\ 0 & I_2\sigma^2_{e_2}\end{bmatrix} \tag{10}$$

with $cov(\mathbf{u}_G\ \epsilon_2)=cov(\mathbf{u}_G\ \epsilon_1)=0$, $cov(\mathbf{u}_{i_1}\ \epsilon_2)=cov(\mathbf{u}_{i_2}\ \epsilon_1)=0$ and $\sigma_{G_i}=cov(\mathbf{u}_G\ \mathbf{u}_{i_1})=-cov(\mathbf{u}_G\ \mathbf{u}_{i_2})$; where σ_G^2 is the genetic-group variance component; $\sigma_{i_1}^2$ and $\sigma_{i_2}^2$ are interaction variance components in environment 1 and 2, respectively and $\sigma_{i_{12}}$ and $\sigma_{i_{21}}$ are the covariance components between interactions in environment 1 and 2, respectively; $cov(\mathbf{u}_G\ \mathbf{u}_{i_1})$ and $cov(\mathbf{u}_G\ \mathbf{u}_{i_2})$ are covariances between genetic-group and interaction in environment 1 and 2, respectively; $\sigma_{e_1}^2$ and $\sigma_{e_2}^2$ are error variance in the environment 1 and 2, respectively. Under these alternative assumption in model B, the combined model has the following variances

$$Var\begin{bmatrix}y_1\\ y_2\end{bmatrix}=\begin{bmatrix}Z_1Z_1' & Z_1Z_2'\\ Z_2Z_1' & Z_2Z_2'\end{bmatrix}\sigma^2_G+\begin{bmatrix}Z_1Z_1' & -Z_1Z_2'\\ -Z_2Z_1' & Z_2Z_2'\end{bmatrix}\sigma^2_I+\begin{bmatrix}2Z_1Z_1' & 0\\ 0 & -2Z_2Z_2'\end{bmatrix}\sigma_{GI}+\begin{bmatrix}I_1\sigma^2_{e_1} & 0\\ 0 & I_2\sigma^2_{e_2}\end{bmatrix} \tag{11}$$

with variance and covariance of y_i's as

$$Var(y_1)=Z_1Z_1'(\sigma^2_G+\sigma^2_I+2\sigma_{GI})+I\sigma^2_{e_1} \tag{12}$$

By this derivation, the genetic correlation in the random model(r) is

$$Var(y_2) = Z_2 Z_2' (\sigma_G^2 + \sigma_I^2 - 2\sigma_{GI}) + I\sigma_{e_2}^2 \qquad (13)$$

$$cov(y_1\ y_2) = Z_1 Z_2' (\sigma_G^2 - \sigma_I^2) \qquad (14)$$

$$r = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_I^2 - \theta(\sigma_i)} \qquad (15)$$

$$where\ \ \theta(\sigma_i) = \frac{(\sigma_1 - \sigma_2)^2}{2}$$

which is the special case of Itoh et al.'s average genetic correlation (1990) and consistent with Yamada's formula (1963).

It is important to note that when model B is used in the conventional two-way analysis of variance, for example in fitting constant method (Searle 1971), it is always assumed that the covariances between genetic-group and interaction ($cov(\mathbf{u}_G\ \mathbf{u}_{I_1})$ and $cov(\mathbf{u}_G\ \mathbf{u}_{I_2})$) are zero. The interaction variance $cov(\mathbf{u}_{I_1}\ \mathbf{u}_{I_2})$ between the interaction in the two environments is also assumed to be equal to zero with

$$Var\begin{bmatrix} u_{I_1} \\ u_{I_2} \end{bmatrix} = \begin{bmatrix} I\sigma_I^{2'} & 0 \\ 0 & I\sigma_I^{2'} \end{bmatrix} \qquad (16)$$

Thus, the estimator of the interaction term $\sigma_I^{2'}$ by conventional analysis of variance is not same as the interaction term of model B under its alternative assumption. Hence, the interaction from conventional analysis of variance is confounded with covariances between genetic group effects and interactions, and covariance among interactions. But when error variance and genetic-group variances are equal, we still can obtain same results without alternative assumptions. The difference is the

interaction from conventional analysis of variance not confounded with covariances between genetic group effects and interactions, and covariance among interactions since these interactions are zero under equal error and genetic variance.

Thus, from the above consideration we must consider the following three conditions for practical estimation of genetic correlation with unbalanced data:

(1) When error variances of the traits in the two environments are not homogeneous, conventional analysis of variance cannot be used to estimate the genetic correlation.

(2) When error variances from two environments are homogeneous, direct two-way conventional analysis of variance is still biased when estimating the genetic correlation. The statistical method to partition $\sigma_I^{2'}$ from the conventional analysis of variance into σ_I^2 under alternative assumption of model B and other covariances needs to be developed. Until then, the adjusted interaction term σ_I^2 in the conventional analysis of variance can be used to estimate the genetic correlation.

(3) When error variances and genetic variances are homogeneous in two environments, conventional analysis of variance can be used to estimate the genetic correlation (Fernando et al. 1984). Thus, when using conventional analysis of variance to estimate genetic correlation, the homogeneity of error variances and genetic variances must be examined.

Appendix 5.2 Estimation of genetic correlations between greenhouse traits and nine-year tree height on site B using linear model method

Since only families are common factors in the greenhouse and field tests, the model that can be used to estimate genetic correlation using the linear model method is of the form:

$$Y_{ijk} = \mu + F_i + S_j + F*S_{ij} + E_{ijk} \qquad (1)$$

where F_i is i^{th} family effect

S_j is either greenhouse effect or field site effect (environment effect)

$F*S_{ij}$ is family-by-environment interaction

E_{ijk} is residual error.

Corresponding to equation (1), the family variances and residual error variances were independently estimated by the model:

$$Y_{ik} = \mu + F_i + E_{ik}, \qquad (2)$$

where F_i is i^{th} family effects

E_{ik} is residual error.

The following equation was used to estimate genetic correlation (r) between greenhouse and site B (Yamada 1962):

$$r = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_{s*f}^2 - \theta(\sigma_i)} \qquad (3)$$

$$where \quad \theta(\sigma_i) = \frac{(\sigma_{f_1} - \sigma_{f_2})^2}{2}$$

and where, σ_f^2 is family variance and σ_{s*f}^2 is family-by-site interaction variance in equation 1, σ_{f1}^2 and σ_{f2}^2 are family variances in greenhouse and site B, respectively.

Since our data were unbalanced in the greenhouse and field site B, to obtain unbiased estimates of genetic correlations, the error and family variances must be homogenous. Thus, before estimating genetic correlations, homogeneity of error and family variance should be investigated. If they are homogeneous, we can directly use the linear model method. If they are heterogenous, data standardization or transformation may be used to make error and family variances homogenous in order to obtain unbiased estimates of genetic correlations.

1. Homogeneity test of error and family variances

Each pair of error variances between greenhouse traits and 9-year height on site B was tested using synthesized Satterthwaite's F-test (1946) as a ratio of the greater variance to the smaller variance. For the test of homogeneity of family variance, the same synthesized F-test was used. The degrees of freedom for the synthesized F-value were computed by Satterthwaite approximation (1946). The results of homogeneity test of error variances suggested that all variance pairs between greenhouse traits and nine-year tree height of site B were heterogeneous in the original scale except for one greenhouse trait H5 (Table 5.7). The results of homogeneity test of family variances indicated that all variance pairs between greenhouse traits and nine-year tree height were heterogenous in the original scale except for two greenhouse traits; H1 and HG3 (Table 5.8).

2. Data standardization and estimation of genetic correlations

Since error and family variances were not homogenous in the original data, data standardization was used to make error and family variances as homogeneous as possible. After the data were standardized, the pairs of error variances between most greenhouse traits (23 out of total 28 traits) and nine-year tree height at site B became homogeneous (Table 5.7); while the pairs of family variances between 15 greenhouse traits and nine-year tree height of site B also became homogeneous. Therefore, the standardized data were used to estimate genetic correlations between greenhouse traits and nine-year tree height at site B. The estimates of genetic correlation between 15 greenhouse traits and nine-year tree height on site B were unbiased from the standardized data, but the other 13 estimates of genetic correlation were still biased due to heterogenous genetic variances or heterogenous error variances or both. The estimates of genetic correlations from the linear model method were similar to estimates of genetic correlation from the covariance method (Table 5.9).

Appendix 6.1 Family variance and covariance of seedling traits in the greenhouse [a]

	H1	H2	H3	D3	H4	H5	H6	H7	D7	D8
H1	107.04	119.53	123.53	269.51	130.50	142.80	148.47	149.42	408.60	398.07
H2	119.53	155.66	165.61	370.93	180.46	199.77	209.42	217.35	605.30	592.69
H3	123.53	165.61	180.73	417.31	199.77	221.95	232.85	245.22	692.55	690.14
D3	269.51	370.93	417.31	1520.90	471.29	544.34	573.80	585.54	2396.97	2419.53
H4	130.50	180.46	199.77	471.29	224.75	251.60	265.01	280.20	810.55	814.77
H5	142.80	199.77	221.95	544.34	251.60	286.71	303.12	319.79	935.20	948.71
H6	148.47	209.42	232.85	573.80	265.01	303.12	320.82	338.42	987.46	1002.58
H7	149.42	217.35	245.22	585.54	280.20	319.79	338.42	364.86	1049.72	1071.10
D7	408.60	605.30	692.55	2396.97	810.55	935.20	987.46	1049.72	4156.67	4309.83
D8	398.07	592.69	690.14	2419.53	814.77	948.71	1002.58	1071.10	4309.83	4511.81
SB	430.90	637.44	725.84	2031.49	829.50	948.00	1003.87	1082.61	3635.69	3799.72
BB	151.51	234.37	250.92	860.39	290.05	343.45	359.22	362.60	1485.52	1511.16
NB	1680.38	2718.75	3150.62	10314.04	3720.71	4328.45	4544.86	4773.69	17806.51	18576.44
RB	593.06	995.35	1172.91	3700.64	1389.79	1610.11	1696.18	1853.73	6528.60	6819.32
TLB	2855.85	4585.91	4300.29	16906.76	6230.04	7230.01	7604.13	8072.63	29456.32	30706.65
GB	2262.79	3590.56	4127.38	13206.12	4840.26	5619.90	5907.95	6218.90	22927.72	23887.33
HI	0.05	0.06	0.06	0.08	0.06	0.06	0.07	0.08	0.13	0.13
SR	0.95	1.09	1.14	3.82	1.25	1.61	1.63	1.50	5.80	6.45
RHD	0.07	0.10	0.11	0.04	0.12	0.14	0.15	0.16	0.13	0.10
HG1	12.49	36.13	42.08	101.42	49.96	56.98	60.95	67.93	196.70	194.62
HG2	4.00	9.95	15.12	46.39	19.31	22.18	23.43	27.87	87.25	97.46
HG3	25.89	51.74	64.49	168.23	80.43	97.84	105.57	119.64	357.17	380.96
DG	139.09	234.37	275.24	876.08	339.25	390.86	413.66	464.18	1759.70	1890.30
BUDN	0.22	0.27	0.33	1.15	0.36	0.38	0.39	0.42	1.72	1.72
BUDS	0.49	0.63	0.68	1.98	0.69	0.70	0.71	0.72	2.56	2.59
BRN1	0.46	0.58	0.60	2.32	0.63	0.72	0.75	0.72	3.24	3.20
BRS	-0.04	0.01	0.01	0.59	-0.01	0.01	-0.01	-0.04	0.73	0.72
BRN2	0.99	1.41	1.50	5.60	1.67	2.03	2.13	2.22	9.32	9.44

Appendix 6.1 Family variance and covariance of seedling traits in the greenhouse

	SB	BB	NB	RB	TLB	GB	HI	SR	RHD	HG1
H1	430.90	151.51	1680.28	593.06	2855.85	2262.79	0.05	0.95	0.07	12.49
H2	637.44	234.37	2718.75	995.35	4585.91	3590.56	0.06	1.09	0.10	36.13
H3	725.84	250.92	3150.62	1172.91	5300.29	4127.38	0.06	1.14	0.11	42.08
D3	2031.49	860.59	10314.04	3700.64	16906.76	13206.1	0.08	3.82	0.04	101.42
H4	829.50	290.05	3720.71	1389.79	6230.04	4840.26	0.06	1.25	0.12	49.9(
H5	948.00	343.45	4328.45	1610.11	7230.01	5619.90	0.06	1.61	0.14	56.9(
H6	1003.87	359.22	4544.86	1696.18	7604.13	5907.95	0.07	1.63	0.15	60.95
H7	1082.61	362.60	4773.69	1853.73	8072.63	6218.90	0.08	1.50	0.16	67.93
D7	3635.69	1485.52	17806.51	6528.60	29456.32	22927.7	0.13	5.80	0.13	196.70
D8	3799.72	1511.16	18576.44	6819.32	30706.65	23887.3	0.13	6.45	0.10	94.62
SB	3540.86	1364.93	16217.97	6280.89	27404.64	21123.7	0.22	5.05	0.31	206.55
BB	1364.93	794.93	7059.82	2265.55	11485.23	9219.68	0.01	3.23	0.03	82.86
NB	16217.97	7059.82	89061.18	29554.09	141893.11	12339.0	0.12	43.46	0.97	1038.37
RB	6280.89	2265.55	29554.09	12580.09	50680.61	38100.5	0.29	0.92	0.45	402.29
TLB	27404.64	11485.23	141893.15	10680.61	231463.51	80782.9	0.38	52.65	1.76	1730.06
GB	21123.76	9219.68	112339.03	8100.52	180782.91	42682.4	0.09	51.74	1.31	1327.77
HI	0.22	-0.01	-0.12	0.29	0.38	0.09	0.00	0.00	0.00	0.00
SR	5.05	3.23	43.46	0.92	52.65	51.74	0.00	0.08	0.00	0.14
RHD	0.31	0.03	0.97	0.45	1.76	1.31	0.00	0.00	0.00	0.03
HG1	206.55	82.86	1038.37	402.29	1730.06	1327.77	0.00	0.14	0.03	23.65
HG2	88.39	16.55	431.87	177.56	714.38	536.82	0.01	0.05	0.01	5.95
HG3	356.77	111.68	1623.07	680.82	2772.34	2091.52	0.02	0.36	0.05	25.85
DG	1604.21	624.93	7492.47	2827.95	12549.55	9721.60	0.06	1.98	0.09	95.28
BUDN	1.57	0.36	7.81	1.78	11.52	9.75	0.00	0.01	0.00	0.05
BUDS	2.31	0.69	8.62	3.17	14.79	11.63	0.00	0.00	0.00	0.14
BRN1	2.48	1.46	12.28	3.86	20.08	16.22	0.00	0.00	0.00	0.12
BRS	0.25	0.52	3.21	1.27	5.25	3.98	0.00	0.00	0.00	0.05
BRN2	7.99	4.69	42.04	13.28	68.00	54.72	0.00	0.02	0.00	0.42

Appendix 6.1 Family variance and covariance of seedling traits in the greenhouse

	HG2	HG3	DG	BUDN	BUDS	BRN1	BRS	BRN2
H1	4.00	25.89	139.09	0.22	0.49	0.46	-0.04	0.99
H2	9.95	51.74	234.37	0.27	0.63	0.58	0.01	1.41
H3	15.12	64.49	275.24	0.33	0.68	0.60	0.01	1.50
D3	46.39	168.23	876.08	1.15	1.98	2.32	0.59	5.60
H4	19.31	80.43	339.25	0.36	0.69	0.63	-0.01	1.67
H5	22.18	97.84	390.86	0.38	0.70	0.72	0.01	2.03
H6	23.43	105.57	413.66	0.39	0.71	0.75	-0.01	2.13
H7	27.87	119.64	464.18	0.42	0.72	0.72	-0.04	2.22
D7	87.25	357.17	1759.70	1.72	2.56	3.24	0.73	9.32
D8	97.46	380.96	1890.30	1.72	2.19	3.20	0.72	9.44
SB	88.39	356.77	1604.21	1.57	2.31	2.48	0.25	7.99
BB	16.55	111.68	624.93	0.36	0.69	1.46	0.52	4.69
NB	431.87	1623.07	7492.47	7.81	8.62	12.28	3.21	42.04
RB	177.56	680.82	2827.95	1.78	3.17	3.86	1.27	13.28
TLB	714.38	2772.34	12549.55	11.52	14.79	20.08	5.25	68.00
GB	536.82	2091.52	9721.60	9.75	11.63	16.22	3.98	54.72
HI	0.01	0.02	0.06	0.00	0.00	0.00	0.00	0.00
SR	0.05	0.36	1.98	0.01	0.00	0.00	0.00	0.02
RHD	0.01	0.05	0.09	0.00	0.00	0.00	0.00	0.00
HG1	5.95	25.85	95.28	0.05	0.14	0.12	0.05	0.42
HG2	5.17	12.75	40.86	0.06	0.04	0.02	0.00	0.09
HG3	12.75	55.15	188.94	0.09	0.04	0.12	0.05	0.71
DG	40.86	188.94	883.62	0.57	0.58	0.92	0.14	3.73
BUDN	0.06	0.09	0.57	0.00	0.00	0.00	0.00	0.00
BUDS	0.04	0.04	0.58	0.00	0.01	0.01	0.00	0.00
BRN1	0.02	0.12	0.92	0.00	0.01	0.01	0.00	0.01
BRS	0.00	-0.05	0.14	0.00	0.00	0.00	0.00	0.00
BRN2	0.09	0.71	3.73	0.00	0.00	0.01	0.00	0.03

* see Appendix 3.2 for despription of seedling traits.

Appendix 6.2 Phenotypic variance and covariance of seedling traits in the greenhouse [a]

	H1	H2	H3	D3	H4	H5	H6	H7	D7	D8
H1	409.15	426.91	443.25	815.52	464.24	505.90	521.74	529.29	1338.48	1424.81
H2	426.91	763.83	801.77	1622.23	868.59	954.10	976.13	1009.54	2788.41	2938.81
H3	443.25	801.77	946.52	1898.50	1032.40	1141.68	1172.74	1241.45	3444.41	3622.53
D3	815.52	1622.23	1898.50	10610.32	2185.95	2580.83	2652.68	2755.23	15072.34	15566.59
H4	464.24	868.59	1032.40	2185.95	1235.52	1376.12	1409.77	1504.78	4186.96	4391.44
H5	505.90	954.10	1141.68	2580.83	1376.12	1663.03	1700.83	1811.14	5042.31	5300.29
H6	521.74	976.13	1172.74	2652.68	1409.77	1700.83	1789.62	1901.90	5216.37	5499.93
H7	529.29	1009.54	1241.45	2755.23	1504.78	1811.14	1901.90	2145.25	5698.53	5976.50
D7	1338.48	2788.41	3444.41	15072.34	4186.96	5042.31	5216.37	5698.53	32997.73	32586.60
D8	1424.81	2938.81	3622.53	15566.59	4391.44	5300.29	5499.93	5976.50	32586.60	36412.96
SB	1577.23	3094.50	3908.94	11929.70	4802.95	5850.96	6075.05	6663.07	25599.49	27022.04
BB	414.87	768.89	811.21	3991.69	930.94	1140.86	1190.41	1204.70	8079.46	8578.25
NB	5743.52	12360.46	15355.37	61075.94	18916.34	23224.13	24061.80	25909.41	124842.39	131023.95
RB	2269.23	5016.76	6246.63	24594.88	7633.60	9274.30	9671.79	10560.24	52361.29	55409.97
TLB	10004.85	21240.60	26322.16	101592.2	32283.82	39490.25	40999.05	44337.42	210882.63	222034.22
GB	7735.61	16223.84	20075.53	76997.33	24650.22	30215.95	31327.26	33777.18	158521.34	166624.25
HI	0.21	0.31	0.40	0.27	0.48	0.57	0.60	0.68	0.90	0.94
SR	1.15	1.04	0.91	-0.55	1.32	1.58	1.43	1.16	-11.91	-14.19
RHD	0.32	0.50	0.60	-0.80	0.71	0.85	0.91	1.08	-2.34	-1.72
HG1	17.76	336.92	358.52	806.71	404.35	448.20	454.40	480.24	1449.93	1514.00
HG2	16.34	37.93	144.76	276.27	163.81	187.58	196.61	231.91	656.00	683.72
HG3	86.04	207.77	294.92	856.73	472.38	669.46	729.16	903.80	2254.12	2353.97
DG	522.96	1166.18	1545.91	4462.02	2001.01	2461.47	2563.69	2943.30	17925.40	17020.01
BUDN	0.47	1.23	1.45	6.63	1.63	1.96	2.01	2.08	7.72	7.69
BUDS	1.08	2.44	2.75	13.43	2.97	3.24	3.40	3.62	17.44	17.40
BRN1	1.05	1.70	1.82	12.46	1.89	2.07	2.21	2.18	18.74	19.28
BRS	-0.23	0.14	0.11	6.31	0.13	0.22	0.22	0.12	9.30	9.79
BRN2	2.40	4.40	4.62	21.08	5.17	6.13	6.21	6.20	35.38	36.66

Appendix 6.2 Phenotypic variance and covariance of seedling traits in the greenhouse

	SB	BB	NB	RB	TLB	GB	HI	SR	RHD	HG1
H1	1577.23	414.87	5743	2269.23	10004	7735.61	0.21	1.15	0.32	17.76
H2	3094.50	768.89	12360	5016.76	21240	16223.84	0.31	1.04	0.50	336.92
H3	3908.94	811.21	15355	6246.63	26322	20075.53	0.40	0.91	0.60	358.52
D3	11929.70	3991.69	61075	24594.88	101592	6997.33	0.27	-0.55	-0.80	806.71
H4	4802.95	930.94	18916	7633.60	32283	24650.22	0.48	1.32	0.71	404.35
H5	5850.96	1140.86	23224	9274.30	39490	30215.95	0.57	1.58	0.85	448.20
H6	6075.05	1190.41	24068	9671.79	40999	31327.26	0.60	1.43	0.91	454.40
H7	6663.07	1204.70	25909	10560.24	44337	33777.18	0.68	1.16	1.08	480.24
D7	25599.49	8079.46	124842	2361.29	210882	58521.3	0.90	-11.91	-2.34	1449.93
D8	27022.04	8578.25	131023	5409.97	222034	66624.2	0.94	-14.19	-1.72	1514.00
SB	29378.48	5636.73	115435	7940.85	198391	50451.0	2.57	-2.45	0.94	1517.27
BB	5636.73	6816.89	38639	15138.01	66231	51093.34	-0.68	2.35	-0.72	354.02
NB	115435.83	8639.72	632440	31610.2	101812	6786515	-0.72	70.40	-2.72	6616.94
RB	47940.85	15138	231610	43372.44	38061	94689.0	1.56	-101.98	-1.78	2747.53
TLB	198391.86	6231.35	1018126	438061.4	1720811	1282749	2.74	-31.69	-4.28	11235.6
GB	150451.05	1093.34	786515	94689.0	1282749	988060	1.17	70.29	-2.50	8488.23
HI	2.57	-0.68	-0.72	1.56	2.74	1.17	0.00	-0.01	0.00	0.10
SR	-2.45	2.35	70.40	-101.98	-31.69	70.29	-0.01	1.48	0.01	-0.11
RHD	0.94	-0.72	-2.72	-1.78	-4.28	-2.50	0.00	0.01	0.00	0.18
HG1	1517.27	354.02	6616.94	2747.53	11235	8488.23	0.10	-0.11	0.18	319.16
HG2	814.44	42.33	2994.92	1229.87	5081	3851.69	0.09	-0.13	0.10	21.59
HG3	2754.13	393.49	10554.0	4313.61	18015	13701.65	0.29	0.25	0.48	121.72
DG	13669.79	4087.77	63766.4	27766.4	109290	1524.02	0.63	-11.36	-1.54	643.22
BUDN	7.66	1.43	36.44	12.73	58.25	45.52	0.00	0.01	0.00	0.76
BUDS	13.73	2.40	61.90	28.95	106.97	78.02	0.00	-0.02	-0.00	1.37
BRN1	10.01	7.36	66.53	27.99	111.89	83.90	-0.00	-0.02	-0.00	0.65
BRS	2.31	4.87	32.62	14.81	54.60	39.80	-0.00	-0.01	-0.00	0.38
BRN2	27.07	23.40	167.9	58.43	276.85	218.42	-0.00	0.04	-0.00	2.00

Appendix 6.2 Phenotypic variance and covariance of seedling traits in the greenhouse

	HG2	HG3	DG	BUDN	BUDS	BRN1	BRS	BRN2
H1	16.34	86.04	522.96	0.47	1.08	1.05	-0.23	2.40
H2	37.93	207.77	1166.18	1.23	2.44	1.70	0.14	4.40
H3	144.76	294.92	1545.91	1.45	2.75	1.82	0.11	4.62
D3	276.27	856.73	4462.02	6.63	13.43	12.46	6.31	21.08
H4	163.81	472.38	2001.01	1.63	2.97	1.89	0.12	5.17
H5	187.58	669.46	2461.47	1.96	3.24	2.07	0.22	6.13
H6	196.61	729.16	2563.69	2.01	3.40	2.21	0.22	6.21
H7	231.91	903.80	2943.30	2.08	3.62	2.18	0.12	6.20
D7	656.00	2254.12	17925.40	7.72	17.44	18.74	9.30	35.38
D8	683.72	2353.97	17020.01	7.69	17.40	19.28	9.79	36.66
SB	814.44	2754.13	13669.79	7.66	13.73	10.01	2.31	27.07
BB	42.33	393.49	4087.77	1.43	2.40	7.36	4.87	23.40
NB	2994.92	10554.04	63766.45	36.44	61.90	66.53	32.62	167.95
RB	1229.87	4313.61	27766.41	12.73	28.95	27.99	14.81	58.43
TLB	5081.56	18015.27	109290.4	58.25	106.97	111.89	54.60	276.85
GB	3851.69	13701.65	81524.02	45.52	78.02	83.90	39.80	218.42
HI	0.09	0.29	0.63	0.00	0.00	0.00	0.00	0.00
SR	-0.13	0.25	-11.36	0.01	-0.02	-0.02	-0.01	0.04
RHD	0.10	0.48	-1.54	0.00	0.00	0.00	0.00	0.00
HG1	21.59	121.72	643.22	0.76	1.37	0.65	0.38	2.00
HG2	106.82	87.15	379.73	0.22	0.31	0.11	0.04	0.21
HG2	87.15	608.88	1397.39	0.63	0.87	0.37	0.02	1.58
DG	379.73	1397.39	13463.38	1.09	4.01	6.28	2.99	14.30
BUDN	0.22	0.63	1.09	0.05	0.03	0.01	0.01	0.02
BUDS	0.31	0.87	4.01	0.03	0.14	0.05	0.03	0.01
BRN1	0.11	0.37	6.28	0.01	0.05	0.11	0.04	0.06
BRS	-0.04	0.02	2.99	0.01	0.03	0.04	0.05	0.02
BRN2	0.21	1.58	14.30	0.02	0.01	0.06	0.02	0.28

* see Appendix 3.2 for description of seedling traits.

Appendix 6.3 Estimated family mean variances of greenhouse traits ($\sigma_{\bar{x}_i}^2$), phenotypic covariances between family mean of greenhouse traits and nine-year tree height on site B ($cov(y\ \bar{x}_i)$), genetic covariances between greenhouse traits and nine-year tree height on site B ($cov(G_y\ G_{x_i})$) for 24 effective greenhouse traits, and individual phenotypic (σ_y^2) and genetic ($\sigma_{G_y}^2$) variances of nine-year tree height on site B [a]

Greenhouse traits	$\sigma_{\bar{x}_i}^2$	$cov(y\ \bar{x}_i)$	$cov(G_y\ G_{x_i})$	Greenhouse traits	$\sigma_{\bar{x}_i}^2$	$cov(y\ \bar{x}_i)$	$cov(G_y\ G_{x_i})$
H1	125.09	20.82	83.28	DG	1634.97	91.53	366.12
H2	191.98	20.16	80.64	SB	5084.05	131.42	525.68
H3	226.46	32.19	128.76	NB	121515.29	594.27	2377.08
H4	285.12	40.75	163.00	RB	20391.85	186.63	746.52
H5	368.91	44.56	178.24	TLB	320416.96	929.64	3718.56
H6	408.54	43.57	174.28	GB	193173.82	743.01	2972.04
H7	471.19	52.53	210.12	HI	0.0001882	0.017	0.068
D3	2063.78	93.31	373.24	SR	0.1677	0.864	3.456
D7	5879.25	183.55	7342	BUDN	0.00526	0.088	0.352
D8	6417.16	213.96	852.76	BUDS	0.0195	0.228	0.912
HG2	11.24	10.05	40.20	BRN1	0.0147	0.286	1.144
HG3	88.22	19.84	79.36	BRN2	0.0494	0.416	1.664

Field trait	σ_y^2	$\sigma_{G_y}^2$
HT [b]	1785.86	335.44

[a] see Appendix 3.2 for description of traits; only 24 effective greenhouse traits that are correlated significantly with nine-year tree height on site B are considered.
[b] HT - nine-year tree height at field site B.