A COMPARISON OF SELECTION AND BREEDING STRATEGIES FOR INCORPORATING WOOD PROPERTIES INTO A LOBLOLLY PINE (*Pinus taeda* L.) ELITE POPULATION BREEDING PROGRAM

A Dissertation

by

JENNIFER HELEN MYSZEWSKI

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2003

Major Subject: Forestry

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ABSTRACT

A Comparison of Selection and Breeding Strategies for Incorporating Wood Properties
into a Loblolly Pine (*Pinus taeda* L.) Elite Population Breeding Program.
(December 2003)
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The heritability of microfibril angle (MFA) in loblolly pine, *Pinus taeda* L., and its genetic relationships with height, diameter, volume and specific gravity were examined in two progeny tests with known pedigrees. Significant general combining ability (GCA), specific combining ability (SCA), and SCA x block effects indicated that there are both additive and non-additive genetic influences on MFA. Individual-tree narrow-sense heritability estimates were variable, ranging from 0.17 for earlywood (ring) 4 MFA to 0.51 for earlywood (ring) 20 MFA. Genetic correlations between MFA, specific gravity and the growth traits were non-significant due to large estimated standard errors.

Multiple-trait selection and breeding in a mainline and elite population tree improvement program were simulated using Excel and Simetar (Richardson 2001). The effects of four selection indices were examined in the mainline population and the effects of seven selection indices and four breeding strategies were examined in the elite population. In the mainline population, selection for increased growth caused decreased wood quality over time. However, it was possible to maintain the overall population mean MFA and mean specific gravity at levels present in the base population by implementing restricted selection indices. Likewise, selection for improved wood quality in the elite population resulted in decreased growth unless restricted selection indices or pulp indices derived from those of Lowe et al. (1999) were used. Correlated phenotypic responses to selection on indices using economic weights and heritabilities were dependent on breeding strategy. When a circular mating system (with parents randomly assigned to controlled-crosses) was used, the index trait with a higher economic weight was more influential in determining correlated responses in non-index traits than the index trait with a lower economic weight. However, when positive assortative mating was used, the index trait with a greater variance was more influential in determining correlated responses in non-index traits than the index trait with a lower variance regardless of economic weight.

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Finally, special thanks to my parents, Tom and Helen, and to my family and friends, especially Chris, Craig, Gayden, Richard, Pam and Jim. Without their constant love and support, I would not be where I am today.

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OVERVIEW

Problem

Improving wood quality through tree improvement has become more important than ever. The average rotation length for a southern pine plantation has decreased significantly in recent years. Because of the shorter rotations, core wood now accounts for a higher proportion of harvested wood than it has in the past. Studies have shown that core wood has both lower strength and lower density than outer wood (Pearson and Gilmore 1980; Schniewind and Gammon 1986; Megraw et al. 1999). Studies have also shown that core wood has greater longitudinal shrinkage than outer wood, making it more prone to defect (Meylan 1968; Megraw et al. 1998).

Traditional tree breeding programs in the southern United States have emphasized the maximization of volume production over the maintenance or improvement of wood properties like specific gravity. Though attempts have been made to hold wood properties constant during breeding efforts (Lowe and van Buijtenen 1991), negative genetic correlations between growth and specific gravity suggest that

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selecting for improved growth rate may cause a decrease in wood quality over time (e.g. Bridgwater et al. 1983; Rozenberg et al. 1997; Gwaze et al. 2001). The implications of such a decrease led several organizations to express interest in developing specialty breeding programs that focus on improving wood quality (Lowe et al. 1999).

Justification

Three main things must occur in order for wood properties to be incorporated into a breeding program. First, the genetics of wood properties and the relationship between wood properties and growth traits must be understood. Specific gravity and microfibril angle (MFA) are two wood properties of particular interest for breeding programs because of their influences on the quality of pulp and solid wood products. Specific gravity is highly heritable and studies by Talbert et al. (1983) suggest that large gains in specific gravity can be made through selection. The genetics of MFA is not well understood. However, Sewell et al. (2000) found there are both additive and non-additive genetic influences on MFA. Second, since wood properties can have unfavorable genetic correlations with growth traits, selection indices that weight each trait appropriately and allow the breeder to select for a desired aggregate genotype must be developed and tested. Stochastic simulation offers a viable alternative to the use of actual breeding and testing to evaluate different indices. However, to date, only one parameter-based, multiple-trait computer program has been published and it was written to simulate a nucleus breeding program in sheep (del Bosque Gonzalez 1989), not a tree improvement program. Last, an economic analysis should be done to incorporate appropriate relative economic weights for each trait in the selection indices. This study examined the inheritance and genetic correlations between specific gravity and MFA, and simulated multiple-trait and multiple-generation tree improvement alternatives using an original computer program. Alternative selection strategies were compared in both a mainline and elite population breeding program and the implications of each strategy on different forest end products was examined.

LITERATURE REVIEW

Specific Gravity

Wood specific gravity or wood density has long been considered the single most important wood property (Zobel and van Buijtenen 1989, p. 15; Zobel and Jett 1995, p. 78). Published studies on specific gravity and wood properties date back to the mid-1800s (Kollmann and Cote 1968, p. 160). Relationships between specific gravity and tensile strength appear in the literature as early as the 1920s (Kollmann and Cote 1968, p. 327) and correlations between specific gravity and latewood percentage appear as early as the 1930s (Kollmann and Cote 1968, p. 175-177).

Specific gravity has a dramatic impact on both pulp and solid wood products. A change of 0.02 in the specific gravity of a pulpwood cord translates into a 100 pound difference in the dry weight of the cord and a 50 pound difference in the amount of dry processed pulp obtainable from the cord (Mitchell 1964). A similar change in the specific gravity of clear southern pine wood corresponds to a 1000 pound per square inch change in the modulus of rupture (Mitchell 1964). Specific gravity explains up to 90% of the variation in clear wood strength (Bendtsen and Youngs 1981). It also affects the thermal, acoustical, and electrical properties of wood (Tsoumis 1991, p. 123) as well as tear strength in paper (Elliott 1970; Zobel and Jett 1995, pp. 78-79).

Specific gravity is highly variable in many conifer species. Geographically, specific gravity tends to increase from northeast to southwest (Mitchell 1964) and is higher around southern coastal regions than farther inland (Zobel and van Buijtenen 1989, pp. 39-42). Stands within a provenance tend to have similar specific gravity values on average but individual trees within a given stand have a significant amount of variation in their specific gravity (Zobel and van Buijtenen 1989, pp. 257-261). Specific gravity also varies within a tree, though the pattern of the variation depends on the species. Species with a low percentage of latewood tend to have an increase in specific gravity with height, while those species with a high percentage of latewood tend to have a decrease in specific gravity with height (Okkonen et al. 1972). In the southern pines, specific gravity tends to decrease with height (Mitchell 1964; Megraw 1985, pp. 7-13). However, at heights greater than 5 m, specific gravity in the innermost rings remains fairly constant (Megraw 1985, p. 9). Radial variation in specific gravity is also species-dependent. In the southern pines, specific gravity tends to increase from the pith outward until ring 15 after which it remains fairly constant (Megraw 1985, pp. 13-17). The gradient at which specific gravity increases in the radial direction is steeper at the base of the tree than it is farther up the bole. Within a given growth ring, specific gravity is much greater in the latewood portion of the ring than in the earlywood portion

(Megraw 1985, pp. 14-17). Latewood values increase for approximately the first 5 rings before leveling off, while earlywood specific gravity values remain consistent from pith to bark (Megraw 1985, pp. 14-17).

A large amount of the variation in specific gravity is genetic in nature (e.g. Talbert et al. 1983; Megraw 1985, pp. 18-20; Zobel and Jett 1995, pp. 98-125). Individual-tree heritability estimates exceeding 0.5 are not uncommon. Genetic correlations between core and outer wood specific gravity also tend to be high. This suggests that early selection on core wood specific gravity would have a favorable impact on outer wood and overall specific gravity (Talbert et al. 1983; Williams and Megraw 1994; Gwaze et al. 2002). Indeed, Gwaze et al. (2002) determined that the optimal selection age for total specific gravity (at age 25) in a loblolly pine (*Pinus taeda* L.) population was age 5.

Studies have indicated that selection for specific gravity could result in large economic gains. Borralho et al. (1993) showed that profits in a chemical kraft mill in Portugal could be increased by $475,000 per year if selection efforts in Eucalypts included wood density, pulp yield and volume. Similarly, Lowe et al. (1999) found that selection on wood density could increase profits in loblolly pulp mills by more than 3%. Despite these potential benefits, specific gravity is not widely used as a selection criterion in existing loblolly pine breeding programs because programs are generally not designed to target pulp production. Instead, tree improvement programs must remain flexible enough to address several product objectives, some of which may require wood with higher or lower specific gravity. Also, studies like Gwaze et al. (2001) have found genetic correlations between growth traits and specific gravity to be predominantly negative, which means selection for increased specific gravity would cause a corresponding loss in volume production. Several studies have concluded, however, that no genetic relationship exists between specific gravity and growth rate (Zobel 1970; Megraw 1985, p. 23) so selection on both traits may be possible.

Microfibril Angle

Microfibril angle (MFA) has been studied for decades and is considered by some to be the most important sub-microscopic wood property (Meylan and Probine 1969). With the decrease in rotation age in recent years, there has been renewed interest in MFA because differences in the MFA of core and outer wood partially explains differences in the properties of the two wood types. Megraw et al. (1999) found that the MFA in core wood can be 10-20° higher than the MFA in outer wood. Higher angles have been associated with lowered strength characteristics (Ifju and Kennedy 1962; Cave and Walker 1994; Evans and Ilic 2001).

MFA has a significant influence on paper and solid wood properties. For example, stretch is greater in pulp sheets containing fibers with higher MFAs than in pulp sheets containing fibers with lower MFAs (Watson and Dadswell 1964; Horn and Setterholm 1988). Stretch is also greater in paper made from core wood pulp than in paper made from outer wood pulp (Watson and Dadswell 1964). This is important because sheets with greater stretch require additional adjustments during conversion to avoid distortion (Watson and Dadswell 1964). When MFA is large (>30°-35°), longitudinal shrinkage increases dramatically in lumber (Meylan 1968, 1972). This is important because lumber with high longitudinal shrinkage is prone to defects such as crook (Megraw et al. 1998). Furthermore, breaking strength (Cave 1969), tensile strength and stiffness all decrease as the MFA increases (Ifju and Kennedy 1962; Cave and Walker 1994; Evans and Ilic 2001). Along with specific gravity, MFA accounts for 93% of the variation in the modulus of elasticity (MOE) of loblolly pine (Megraw et al. 1999). This is important because MOE indicates the amount of stress and strain a beam can withstand before internal damage occurs.

Though little is known about the geographic variability of MFA, it is well established that MFA varies significantly within a single tree (Megraw 1985, pp. 50-53). MFA tends to decrease with height (Pillow et al. 1953; Donaldson 1992, 1993; Megraw et al. 1998). It also tends to decrease from pith to bark (Pillow et al. 1953; Bendtsen and Senft 1986; Donaldson 1993). The radial change in MFA is greatest at upper heights and lowest at the base of the tree (Donaldson 1992; Megraw 1985, pp. 51-52). Within a given ring, latewood MFA tends to be greater than earlywood MFA in the core wood (Megraw et al. 1998). However, in the outer wood, the reverse is true. Latewood MFA tends to be lower than earlywood MFA. The point at which the earlywood/ latewood MFA relationship changes is dependent on height. Closer to the base of the tree, the relationship between early- and latewood MFA reverses at a greater number of rings from the pith than it does farther up the bole.

Studies have shown there are both additive and non-additive influences on MFA

(Sewell et al. 2000) and significant parent-offspring correlations for MFA (Jackson 1964). This suggests that MFA is heritable and thus could be used as a selection criterion in a tree improvement program.

Western Gulf Forest Tree Improvement Program Model

The first tree improvement program in the southern United States was established in the 1950s to investigate applied forest genetics in Texas, Arkansas and Louisiana (Zobel and Talbert 1991, pp. 2-6; van Buijtenen 2002). The Texas Forest Service Tree Improvement Program (TFSTIP) was originally comprised of the Texas Forest Service and 14 members of the private/corporate forest industry. Over the years, the TFSTIP gained additional members and expanded to include Oklahoma and Mississippi. In the late 1960s, the TFSTIP established several programs to target specific tree improvement interests. One of those programs was the Western Gulf Forest Tree Improvement Program (WGFTIP), a regional cooperative effort whose main focus is pine tree improvement. Its efforts include breeding programs for loblolly pine, slash pine (*P. elliotii* Engelm.), and several hardwood species. This study focuses on the loblolly pine breeding program.

Each WGFTIP member contributes selections to a region-wide mainline loblolly pine breeding population which is divided into eight breeding zones based on the seed transfer guidelines of Wells (1969) (Lowe and van Buijtenen 1986). Each breeding zone is sub-divided into multiple breeding groups or sublines and all breeding and testing is conducted within sublines to manage inbreeding in the production population.

Advanced generation breeding depends on complementary breeding and testing where polymix tests (controlled pollinations with a mixture of several male pollens) are used to estimate the general combining ability of all parent trees and to identify potential selections for seed orchards which provide seeds for plantation establishment. Modified, disconnected, partial diallel mating designs are used to cross parent trees and generate selection populations (Byram 2000, pp. 3-5). The best individuals within the best full-sibling families (based on progeny test performance) are then selected for generation advancement. Selections are based primarily on superior breeding values for volume but form, disease resistance, and specific gravity are also taken into consideration (Lowe and van Buijtenen 1991).

In addition to its mainline program, the WGFTIP is currently initiating a loblolly pine elite-population breeding program, which will focus on improved wood quality (Byram et al. 2001, 2002). In each breeding zone, approximately 30 trees will be selected from the first-generation breeding population and established as an elite population. Selections will be based on economic index values for pulpwood production and will not be restricted to members of those families carried forward into second-generation mainline breeding populations. Breeding and testing of the elite populations will be conducted separately from mainline breeding and testing. However, if families with superior wood properties are identified in the mainline population, they may be selected for infusion into the elite population in future generations. After each cycle of selection, polymix tests will be established to compare the elite and mainline breeding populations and to evaluate the separate selection strategies. Polymix data will also be used to design seed orchards, which may contain selections from more than one breeding group.

This approach allows the WGFTIP to maintain flexibility in their long-term improvement objectives and avoid sacrificing volume gains in the mainline breeding population. However, it may not be the most effective strategy for maintaining and/or improving wood quality throughout the program.

Simulation

Tree improvement programs around the world have realized the value of using computer simulation to study alternative strategies for selection, breeding, and testing schemes (e.g. McKeand and Bridgwater 1998; Andersson 1999; Byram 2000; Ruotsalainen 2002).

Several marker- and allele-based simulation models have already been generated to study different aspects of applied genetics. For example, Verrier et al. (1989) simulated a 200- and 1000-locus system to study the effects of mass selection and inbreeding on within-family genetic variances over 15 generations and de Boer and van Arendonk (1992) used 64 and 1600 unlinked, biallelic loci to compare simulated versus predicted additive and dominance effects in a small population over 5 generations. Verrier et al. (1989) assumed a completely additive model, while de Boer and van Arendonk (1992) compared a completely additive model and a model with complete dominance.

The first allele-based model that included not only additive gene effects but also effects due to partial dominance and that was designed specifically in a tree improvement context was written by Mahalovich (1990). She simulated a 50 unlinked, biallelic locus system to study the effects of positive assortative mating on gains in both mainline and elite breeding populations. Mahalovich's model was later tailored to study the effects of different selection schemes on expected gains and the effects of different methods of subline partitioning on genetic variances (Bridgwater et al. 1993); to compare advanced generation breeding strategies for maximizing short-term gain while maintaining diversity in the long-term (McKeand and Bridgwater 1998); and to compare breeding strategies that incorporate marker assisted selection with more traditional breeding strategies (Byram 2000).

Since little is known about the genetics of MFA, a parameter-based model is more appropriate for examining ways in which to incorporate wood properties into a tree improvement program. The first interactive, parameter-based simulation model designed specifically for tree improvement, POPSIM was produced by Mullin and Park (1995). POPSIM allowed the user to specify the additive, dominance, epistatic and environmental variances of a single trait in a base population and then tailor the selection, breeding and testing schemes of a theoretical improvement program to fit their objectives. It also allowed the user to pick different seed orchard designs and deployment populations. POPSIM has been used to study the effects of positive assortative mating on gains and genetic diversity when group coancestry is restricted (Rosvall and Mullin 1999); to compare the effects of phenotypic selection and combined index selection on gains (Andersson et al. 1998); and to compare the effects of group merit selection and restricted selection on gains and the control of coancestry (Rosvall and Andersson 1999).

Additional parameter-based models have also been written to focus on specific questions. For example, Loo-Dinkins et al. (1990) combined actual environmental data from loblolly pine progeny tests in Oklahoma and Arkansas with simulated height data to test the effects of different field designs on selection efficiencies; King and Johnson (1993) used Monte Carlo simulations to compare the effects of different mating schemes on within-family selection and effective population size; and Borralho and Dutkowski (1998) used simulation to compare discrete generation breeding strategies with rolling front breeding strategies.

Most of the parameter-based models available, including POPSIM, are limited to the consideration of a single trait. However, incorporating wood properties into a tree improvement program will require the simulation of multiple traits. The only available multiple-trait simulation model was written by del Bosque Gonzalez (1989) to simulate wool production in a nucleus breeding scheme. His model examined the effects of multiple genetic and environmental factors on four phenotypic traits but included assumptions not relevant to tree improvement scenario (e.g. proportion of dams lambing multiple progeny, sale of individuals in the flock).

OBJECTIVES

The overall objective of this study was to examine different strategies for incorporating wood properties into an existing breeding program like that of the WGFTIP. Chapters II-IV address the steps required to accomplish this objective.

The objective of Chapter II was to determine the degree of genetic control over wood properties, in particular specific gravity and microfibril angle, in the WGFTIP loblolly pine population. A sub-sample of families grown in two South Arkansas progeny tests were used to estimate the heritabilities of both traits. Then, genetic correlations were estimated to examine the relationship between wood properties and growth traits (height, diameter, and volume).

The objective of Chapter III was to compare the effects of using different selection indices to select genotypes for future generations of both the mainline and elite breeding populations in terms of the gains achieved in the traits of interest. To do this, computer programs were written to simulate five generations of selection, breeding and testing in a traditional tree improvement program. Then, up to seven different selection indices were compared in the programs, including indirect selection for mature traits via early selection on their juvenile equivalents, restricted index selection on one trait while holding a second trait constant, modified base index selection, and pulp index selection. Four different breeding strategies were also compared in the elite breeding population.

The objective of Chapter IV was to examine the impact of gains in specific traits on different forest end products. The cost of implementing the different selection and breeding strategies was weighed against the gains each achieved in the traits of interest. Then, the significance of improvements in each of the traits was discussed in terms of sawlog, pulp/paper, chip/composite, and veneer production.

CHAPTER II

GENETIC VARIATION IN MICROFIBRIL ANGLE

INTRODUCTION

Microfibril angle (MFA) influences the quality of several forest end products and could be used as a selection criterion for breeding efforts to improve wood quality. Before it can be incorporated into any selection scheme, however, an understanding of the genetics of MFA is required and few such studies exist. Jackson (1964) discovered a significant correlation in loblolly (*P. taeda* L.) and slash pines (*P. elliottii* Engelm.) between the MFA of female parent trees and that of their open- and control-pollinated progeny. Decades later, Donaldson (1993) found significant variation in MFA among progeny groups of radiata pine (*P. radiata* D. Don) and Donaldson and Burdon (1995) found high clonal repeatability for MFA. Through QTL analysis, Sewell et al. (2000) have shown that both additive and non-additive genes influence MFA in loblolly pine. Yet, the degree to which MFA is heritable and its genetic relationship with other traits in loblolly pine have not been reported.

The first objective of this study was to determine the level of genetic control over MFA in loblolly pine. Second, since selecting for one trait often has an effect on others, an additional objective was to examine the genetic relationship between MFA and different commercially important traits, in particular height, diameter, volume, and specific gravity.

MATERIALS AND METHODS

Study Locations

Two loblolly pine progeny tests, GP065 and GP258, established by Georgia Pacific Corporation (now managed by Plum Creek Timber Company) were sampled in this study. These tests were chosen because they had good survival and because long-term data were available from each test. GP065 and GP258 were established in 1974 and 1968, respectively, to evaluate the combining abilities of Western Gulf Forest Tree Improvement Program (WGFTIP) select trees. Both were planted in Ashley County, Arkansas on fine, silty loam soils with good internal drainage. Breeding was conducted using a modified half-diallel mating design (no selfs or reciprocals). GP065 contained 11 open-pollinated (op) families and 36 control-pollinated (cp) crosses and GP258 contained 6 op families and 22 cp crosses. Progeny were distributed among 10 blocks at GP065 and 5 blocks at GP258 using a randomized complete block design. Ten-tree row-plots (10 progenies per cross) were used at GP065 and 6 x 6-tree block-plots (36 progenies per cross) were used at GP258. Initial spacing was 2.4 m x 2.4 m at both sites. At the time of sampling, GP065 was 20 years old and had been mechanically thinned after age 15 to remove trees in positions 1, 4, 6, and 9. GP258 was 25 years old and had been silviculturally thinned twice from below (once after age 15 and once after age 20).

Wood Core Samples

Increment cores were collected from both test sites. Cores were taken bark-to-bark at breast height (1.37 m) and were approximately 9 mm in diameter. Progeny from 17 cp crosses (7 parents) were sampled in GP065 and progeny from 12 cp crosses (6 parents) were sampled in GP258. No crosses were common to both sites, but half-sibling progeny from 2 of the 11 parents were located at both sites. Approximately 20 trees per cross (2 trees per block) were sampled at GP065 and approximately 25 trees per cross (5 trees per block) were sampled at GP258. In all, 335 trees were sampled in GP065 and 297 trees were sampled in GP258. All of the parent trees used in the crosses sampled were selected in southern Arkansas, except for one parent used in GP065, which was selected in southern Mississippi. At GP258, cores were also collected from an unimproved checklot (comprised of a bulk collection of open-pollinated seed).

Each core was divided into three pieces: a single center piece containing growth rings 1 through 5 from the pith (5-0-5), and two radial pieces containing growth rings 6 through 20 from the pith. Specific gravity was measured on each core section individually using the maximum moisture content method of Smith (1954). Measurements from the two radial pieces were weighted based on the length of each piece and then averaged to obtain a single specific gravity value for rings 6 through 20. Similarly, measurements from the center and two radial pieces were weighted based on their lengths and then averaged to obtain a total specific gravity value. Rings 1-5 will be referred to as core wood and rings 6 through 20 as outer wood.

Rings 4 and 5 and rings 19 and 20 were chosen to estimate core and outer wood MFA, respectively. Each ring was separated using a razor blade. Then, to measure the variation in MFA that exists within individual growth rings (Megraw et al. 1998, p. 42), pieces of the earlywood and latewood portions of each ring were also separated. All ring separations were conducted based on ocular evaluation of the rings. No exclusions were made based on the presence of compression wood. MFA measurements were taken by Dr. Robert Megraw (Weyerhaeuser Company (retired), Department of Forest Science, Texas A&M University, College Station, TX 77843-2585) on the earlywood and latewood 4, 5, 19, and 20 samples using the X-ray diffraction technique described in Megraw et al. (1998, pp. 32-37). MFA measurements were identified by their corresponding within-ring position (earlywood, latewood) and ring number (4, 5, 19, 20) and were reported in degree deviations from vertical.

Growth Measurements

Height and diameter at breast height (DBH) measurements were taken at several ages in each test prior to core sample collection. In GP065, growth data were collected from all trees at ages 5, 10, 15, and 20. In GP258, growth data were collected from all trees at ages 15 and 20 while only the interior 16 trees of each plot were measured at age 10. Then, volume at ages 10, 15, and 20 were calculated in terms of mean annual increment (cubic meters per hectare per year). Only data from trees with MFA and specific gravity measurements were used in subsequent analyses.

Statistical Analyses

Exploratory data analysis was conducted using SAS (SAS Institute, Cary NC). The PROC MEANS procedure was used to calculate cross summary statistics and pair-wise t-tests (SAS Institute 1990, pp. 365-388). Analyses of variance were conducted using a modification of DIALL (Schaffer and Usanis 1969), and the Simple Interactive Statistical Analysis (SISA) (Uitenbroek 1997). A statistical model containing block, general combining ability (GCA), specific combining ability (SCA) and the SCA x block interaction was used to estimate genetic and environmental effects on microfibril angle. Variation due to the GCA x block interaction was pooled with the error because it was not significant for any of the traits examined. The model used in the analyses was:

$$Y_{ijkl} = \mu + B_i + G_j + G_k + S_{jk} + SB_{ijk} + e_{(ijk)l} \quad [1]$$

where Y_{ijkl} is the observation on the lth tree, μ is the population mean, B_i is the effect due to the ith block, G_j and G_k are the effects due to the general combining ability of the jth and kth parent, respectively, S_{jk} is the effect due to the specific combining ability of the jth by kth cross, SB_{ijk} is the effect due to the SCA x block interaction, and $e_{(ijk)l}$ is the within-plot residual error term. All variables were treated as random effects. Sums of squares and F-test statistics were calculated using DIALL and significance levels were calculated using SISA. DIALL was also used to generate variance and covariance components and coefficients for estimating individual-tree narrow-sense heritabilities, heritabilities of GCA effects, and genetic correlations. Individual-tree narrow-sense heritability and heritability of GCA effects were calculated using equations for the WGFTIP partial diallel as reported in van Buijtenen and Yeiser (1989):

$$h^2_{(individualtree)} = \frac{4\sigma_g^2}{2\sigma_g^2 + \sigma_s^2 + \sigma_{sb}^2 + \sigma_e^2} \quad [2]$$

$$h^2_{(GCAeffects)} = \frac{\sigma_g^2}{\sigma_g^2 + \frac{b}{a}\sigma_s^2 + \frac{c}{a}\sigma_{sb}^2 + \frac{1}{a}\sigma_e^2} \quad [3]$$

where σ^2_g is the variance component for GCA, σ^2_s is the variance component for SCA, σ^2_{sb} is the variance component for SCA x block and σ^2_e is the variance component for the within plot residual error; a is the coefficient representing the effective number of trees from a single cross sampled per site multiplied by (the number of parents minus 2), b is the coefficient representing the effective number of trees from a single cross sampled per site, and c is the coefficient representing the effective number of trees from a single cross sampled per block. Expected mean squares (EMS) coefficients for earlywood 4, latewood 4, earlywood 5, and latewood 5 MFA were a = 79.13, b = 19.70, and c = 1.99 at GP065 and a = 77.47, b = 24.74, and c = 4.95 at GP258. EMS coefficients for earlywood 19 MFA at GP065 were a = 58.68, b = 14.80, and c = 1.74 due to the exclusion of multiple samples. For latewood 20, they were a = 78.87, b = 19.63, and c = 1.99 due to one missing observation. At GP258, EMS coefficients for earlywood 19, latewood 19, and earlywood 20 MFA were a = 77.47, b = 24.74, and c = 4.95. For latewood 20 MFA, they were a = 77.22, b = 24.66, and c = 4.94 due to one missing observation. Standard errors for the heritability estimates were approximated according to the methods of Gordon et al. (1972). Additive genetic correlations were estimated as follows:

$$r_{A_{xy}} = \frac{\sigma_{A_{xy}}}{\sqrt{\sigma^2_{A_x} * \sigma^2_{A_y}}} \qquad [4]$$

where $\sigma_{A_{xy}}$ is the additive genetic covariance of traits x and y, $\sigma^2_{A_x}$ is the additive genetic variance of trait x, and $\sigma^2_{A_y}$ is the additive genetic variance of trait y. Standard errors were approximated according to the methods of Scheinberg (1966) and used to determine the significance of the genetic correlations. Correlations greater than two standard errors from zero were deemed significant.

RESULTS

Exploratory data analysis of GP065 revealed that latewood 19 and earlywood 20 MFA measurements were intermediate to earlywood 19 and latewood 20 MFA measurements. Pair-wise t-tests based on individual tree measurements showed that latewood 19 and earlywood 20 MFA values were significantly different from earlywood 19 and latewood 20 MFA values but not from each other at the α=0.05 level (Table 1). It appeared that some of the latewood 19 samples were contaminated with earlywood fibers and some of the earlywood 20 samples were contaminated with latewood fibers. Several of the sampled trees from GP065 had very narrow growth rings and clean separation of the earlywood and latewood within rings 19 and 20 proved to be

Table 1. Pair-wise t-tests of individual-tree MFA measurements.

	GP065			GP258		
Means Compared[a]	Differences Between Means[b]	t	Prob>|t|	Differences Between Means	t	Prob>|t|
Ew 4 - Ew 5	0.2°	1.33	0.1836	0.2°	1.03	0.3027
Lw 4 – Lw 5	1.5°	7.96	0.0001	0.5°	2.78	0.0057
Ew 19 – Ew 20	3.3°	11.47	0.0001	-0.3°	-0.60	0.5491
Lw 19 – Lw 20	5.5°	16.84	0.0001	1.0°	2.55	0.0112
Ew 4 – Lw 4	-1.7°	-8.72	0.0001	-2.2°	-12.29	0.0001
Ew 5 – Lw 5	-0.4°	-2.32	0.0208	-2.0°	-10.51	0.0001
Ew 19 – Lw 19	3.9°	13.17	0.0001	4.5°	11.23	0.0001
Ew 20 – Lw 20	6.1°	16.38	0.0001	5.7°	14.14	0.0001
Lw 4 – Ew 5	1.9°	10.68	0.0001	2.4°	13.53	0.0001
Lw 19 – Ew 20	-0.6°	-1.67	0.0967	-4.8°	-10.59	0.0001

[a] Ew = earlywood, Lw = latewood

[b] Positive means indicate the first angle listed is greater (less vertical) than the second; negative means indicate the angle is smaller (more vertical).

impossible with our methods. Thus, the latewood 19 and earlywood 20 measurements from GP065 were excluded from further analyses. To minimize the risk of contamination among additional samples, earlywood 19 measurements from 82 trees with narrow growth rings were also excluded.

Contamination was not a problem at GP258 where latewood 19 MFA was significantly different from earlywood 19, earlywood 20, and latewood 20 MFAs. On average, the difference between latewood 19 and latewood 20 MFAs was less than a degree. However, average differences between the outer wood early- and latewood MFAs ranged from 4.5° to 5.7°. Earlywood 19 and earlywood 20 MFAs were not significantly different from each other (average difference of less than 0.3°).

Latewood MFAs in the core wood were significantly different between rings 4 and 5 at both sites (average differences of 1.5° and 0.5° at GP065 and GP258, respectively). They were also significantly different from core earlywood MFAs at both sites (average differences of 0.4° to 1.7° and 2.0° to 2.2°, respectively). Earlywood 4 and 5 MFAs, however, were not significantly different from each other at either site (average differences of 0.2° at both sites).

A wide range of MFA values was observed among full-sib families at both progeny tests (Table 2). At both sites, latewood MFAs in the core wood were greater than earlywood MFAs and tended to be more variable than earlywood MFAs. The converse was true in the outer wood where earlywood MFAs were greater than latewood MFAs. MFAs in general were greater at GP065 than MFAs at GP258.

Core wood and total specific gravity measurements were slightly higher at

Table 2. Range of full-sib family means (with standard deviations) for wood quality and growth traits in loblolly pine.

	GP065	GP258
Earlywood 4 MFA[a]	38.8 ± 3.2 to 43.7 ± 3.3	37.0 ± 3.9 to 41.8 ± 4.7
Latewood 4 MFA	39.6 ± 3.7 to 45.8 ± 2.9	38.9 ± 4.4 to 44.9 ± 3.5
Earlywood 5 MFA	38.2 ± 3.1 to 44.0 ± 3.6	36.7 ± 3.7 to 40.9 ± 3.3
Latewood 5 MFA	37.0 ± 5.8 to 45.4 ± 3.5	37.9 ± 3.1 to 44.2 ± 4.1
Earlywood 19 MFA	28.1 ± 3.8 to 33.7 ± 3.0	20.2 ± 8.2 to 32.0 ± 5.6
Latewood 19 MFA[b]		13.3 ± 6.7 to 26.6 ± 5.7
Earlywood 20 MFA[b]		18.3 ± 8.5 to 31.2 ± 6.6
Latewood 20 MFA	16.1 ± 7.1 to 26.8 ± 6.5	12.4 ± 5.4 to 25.7 ± 7.7
Core Wood Sp. Gr.[c]	0.37 ± 0.02 to 0.42 ± 0.03	0.41 ± 0.03 to 0.46 ± 0.05
Outer Wood Sp. Gr.[c]	0.46 ± 0.03 to 0.55 ± 0.04	0.48 ± 0.02 to 0.54 ± 0.03
Total Sp. Gr.[c]	0.42 ± 0.02 to 0.49 ± 0.03	0.46 ± 0.02 to 0.50 ± 0.02
Height 5 (m)[d]	2.1 ± 0.5 to 3.0 ± 0.5	
Diameter 5 (cm)[d]	2.2 ± 1.0 to 3.9 ± 1.7	
Height 10 (m)	7.4 ± 1.2 to 9.0 ± 0.6	7.7 ± 0.6 to 10.1 ± 0.7
Diameter 10 (cm)	11.5 ± 2.1 to 15.9 ± 1.2	12.6 ± 1.4 to 16.0 ± 2.1
Volume 10 (m^3/ha/yr)	4.7 ± 2.0 to 10.0 ± 1.7	5.6 ± 1.5 to 11.3 ± 3.9

Table 2. Continued.

	GP065	GP258
Height 15 (m)	13.0 ± 1.5 to 14.7 ± 0.6	12.9 ± 0.8 to 14.9 ± 0.7
Diameter 15 (cm)	16.3 ± 3.0 to 22.0 ± 1.3	18.9 ± 1.5 to 22.0 ± 2.1
Volume 15 (m^3/ha/yr)	13.8 ± 5.3 to 27.0 ± 3.7	17.7 ± 3.5 to 27.3 ± 5.5
Height 20 (m)	16.8 ± 1.7 to 18.9 ± 1.1	16.7 ± 1.0 to 19.4 ± 0.8
Diameter 20 (cm)	19.4 ± 3.9 to 26.9 ± 1.8	22.8 ± 2.7 to 27.0 ± 2.2
Volume 20 (m^3/ha/yr)	19.2 ± 8.1 to 38.6 ± 6.1	25.3 ± 5.7 to 40.4 ± 7.5

[a] All microfibril angle measurements are reported in degrees from vertical

[b] Latewood 19 and earlywood 20 MFA measurements from GP065 were excluded due to corrupt samples (see Results)

[c] Core wood specific gravity is the specific gravity of the center piece of the core containing rings 1 through 5 (5-0-5); outer wood specific gravity is the weighted average of the two radial pieces containing rings 6 through 20; total specific gravity is the weighted average of the center and two radial pieces; weights based on the length of each piece

[d] Height 5 and diameter 5 were not measured in GP258

GP258 than at GP065. However, outer wood specific gravity measurements were similar at the two sites. Age-10 height measurements were greater at GP258 than at GP065 due to a severe tip moth infestation at GP065 but age-15 and age-20 height measurements were similar at the two sites. On average, diameter measurements were almost identical at both sites at all ages. However, the range of family means and the variances about those means were greater at GP065 than at GP258. As a result, trees with small diameters were present in all of the families in GP065.

Analyses of variance identified significant genetic and environmental effects (α=0.1; Table 3) for almost all of the MFA measurements taken. An α level of 0.1 was used for these analyses because of the unbalanced sample size and small number of degrees of freedom for GCA and SCA effects and because the presence of compression wood adds error variation (Megraw et al. 1998, p. 33). At GP065, GCA effects were statistically significant for earlywood 4 and 5 MFAs and for latewood 4, 5, and 20 MFAs. SCA effects were only significant for latewood 5 MFAs but SCA x block effects were statistically significant for earlywood 4 and 5 MFAs and for latewood 4, 5, and 20 MFAs. At GP258, GCA effects were statistically significant for earlywood 4, 19, and 20 MFAs and for all of the latewood MFAs and SCA effects were significant for latewood 5 and latewood 20 MFAs. SCA x block effects were significant for earlywood and latewood 4 MFAs where mean squares were similar in magnitude to those for SCA.

Individual-tree narrow-sense heritability estimates were low to moderate for all MFA measurements (Table 4). At GP065, they ranged from 0.21 for latewood 20 MFA to 0.41 for earlywood 4 MFA. At GP258, they ranged from 0.17 for earlywood 4 MFA

Table 3. Analyses of variance for earlywood and latewood 4, 5, 19 and 20 microfibril angle.

		GP065				GP258			
		df	MS	F	Prob>F	df	MS	F	Prob>F
Ew 4[a]	Block	9	37.99	3.21	0.0014	4	6.59	0.30	0.8764
	GCA[b]	6	113.77	9.66	0.0011	5	90.31	3.13	0.0987
	SCA[b]	10	11.77	1.00	0.4464	6	28.89	1.31	0.2729
	S x B[b]	143	11.82	1.41	0.0164	44	22.12	1.41	0.0562
	Error	166	8.39			237	15.68		
Lw 4[a]	Block	9	19.85	1.13	0.3455	4	26.79	1.11	0.3639
	GCA	6	145.87	7.23	0.0035	5	182.12	9.07	0.0091
	SCA	10	20.16	1.14	0.3368	6	20.07	0.83	0.5532
	S x B	143	17.62	1.32	0.0423	44	24.22	1.63	0.0116
	Error	166	13.31			237	14.83		
Ew 5	Block	9	35.43	2.50	0.0110	4	24.07	1.47	0.2276
	GCA	6	113.62	6.40	0.0054	5	57.76	2.72	0.1276
	SCA	10	17.75	1.25	0.2646	6	21.24	1.29	0.2817
	S x B	143	14.15	1.42	0.0147	44	16.42	1.14	0.2661
	Error	166	9.95			237	14.34		

Table 3. Continued.

		GP065				GP258			
		df	MS	F	Prob>F	df	MS	F	Prob>F
Lw 5	Block	9	40.91	2.03	0.0400	4	68.28	3.88	0.0087
	GCA	6	167.73	4.44	0.0190	5	165.44	4.37	0.0504
	SCA	10	37.82	1.88	0.0525	6	37.82	2.15	0.0664
	S x B	143	20.16	1.28	0.0625	44	17.60	1.10	0.3202
	Error	166	15.75			237	16.03		
Ew 19	Block	9	29.61	1.16	0.3260	4	174.51	3.41	0.0163
	GCA	6	70.43	2.03	0.1540	5	564.42	6.45	0.0210
	SCA	10	34.72	1.36	0.2059	6	87.52	1.71	0.1412
	S x B	131	25.50	1.08	0.3476	44	51.14	1.05	0.3959
	Error	95	23.66			237	48.89		
Lw 19^c	Block					4	47.25	1.08	0.3780
	GCA					5	661.70	8.06	0.0122
	SCA					6	82.11	1.87	0.1076
	S x B					44	43.81	0.72	0.9042
	Error					237	60.56		

Table 3. Continued.

		GP065				GP258			
		df	MS	F	Prob>F	df	MS	F	Prob>F
Ew 20[c]	Block					4	20.82	0.46	0.7646
	GCA					5	732.81	12.09	0.0043
	SCA					6	60.63	1.33	0.2643
	S x B					44	45.54	0.90	0.6532
	Error					237	50.58		
Lw 20	Block	9	55.50	0.69	0.7171	4	61.95	0.90	0.4722
	GCA	6	367.49	6.09	0.0065	5	601.93	4.15	0.0562
	SCA	10	60.39	0.75	0.6764	6	145.21	2.10	0.0724
	S x B	143	80.98	1.54	0.0037	44	69.08	1.19	0.2075
	Error	165	52.43			236	58.11		

[a] Ew = earlywood MFA, Lw = latewood MFA

[b] GCA = general combining ability, SCA = specific combining ability, G x B = GCA x Block, S x B = SCA x Block

[c] Lw 19 and Ew 20 MFA measurements from GP065 were excluded due to corrupt samples (see Results)

Table 4. Individual-tree narrow-sense heritability and heritability of GCA effects estimates (with standard errors) for microfibril angle, specific gravity, height, diameter and volume in loblolly pine.

	GP065		GP258	
	Indiv. Tree	GCA effects	Indiv. Tree	GCA effects
Earlywood 4 MFA	0.41 ± 0.18	0.90 ± 0.05	0.17 ± 0.13	0.68 ± 0.23
Latewood 4 MFA	0.34 ± 0.16	0.86 ± 0.09	0.40 ± 0.19	0.87 ± 0.05
Earlywood 5 MFA[a]	0.33 ± 0.16	0.84 ± 0.10		
Latewood 5 MFA	0.30 ± 0.17	0.77 ± 0.14	0.32 ± 0.19	0.77 ± 0.17
Earlywood 19 MFA[b]			0.39 ± 0.20	0.84 ± 0.11
Latewood 19 MFA[c]			0.39 ± 0.19	0.85 ± 0.10
Earlywood 20 MFA[c]			0.51 ± 0.21	0.91 ± 0.06
Latewood 20 MFA	0.21 ± 0.11	0.79 ± 0.09	0.31 ± 0.19	0.76 ± 0.17
Csg[d]	0.33 ± 0.20	0.71 ± 0.19	0.35 ± 0.18	0.86 ± 0.10
Oasg[d]	0.72 ± 0.24	0.88 ± 0.08	0.72 ± 0.22	0.95 ± 0.02
Tsg[d]	0.60 ± 0.25	0.82 ± 0.12	0.58 ± 0.22	0.92 ± 0.03
Height 5[e]	0.24 ± 0.12	0.79 ± 0.09		
Height 10	0.26 ± 0.14	0.79 ± 0.09	0.90 ± 0.25	0.83 ± 0.12
Diameter 10	0.47 ± 0.20	0.88 ± 0.07	0.73 ± 0.24	0.86 ± 0.05
Volume 10	0.42 ± 0.19	0.87 ± 0.08	0.77 ± 0.26	0.85 ± 0.10

Table 4. Continued.

	GP065		GP258	
	Indiv. Tree	GCA effects	Indiv. Tree	GCA effects
Height 15	0.41 ± 0.17	0.88 ± 0.05	0.62 ± 0.31	0.74 ± 0.19
Diameter 15	0.54 ± 0.20	0.92 ± 0.04	0.51 ± 0.24	0.83 ± 0.12
Volume 15	0.56 ± 0.21	0.92 ± 0.04	0.56 ± 0.27	0.79 ± 0.15
Height 20	0.25 ± 0.15	0.76 ± 0.16	0.58 ± 0.29	0.75 ± 0.18
Diameter 20	0.59 ± 0.21	0.92 ± 0.05	0.58 ± 0.24	0.88 ± 0.08
Volume 20	0.57 ± 0.21	0.92 ± 0.05	0.60 ± 0.26	0.83 ± 0.13

[a] No significant genetic effects detected at GP258 for earlywood 5 MFA

[b] No significant genetic effects detected at GP065 for earlywood 19 MFA or diameter 5

[c] Latewood 19 and earlywood 20 MFA measurements from GP065 were excluded due to corrupt samples (see Results)

[d] Csg = core wood specific gravity, Oasg = outer wood average specific gravity, Tsg = total specific gravity

[e] Height 5 was not measured in GP258

to 0.51 for earlywood 20 MFA. Estimates of the heritability of GCA effects were much higher than individual-tree estimates at both sites, ranging from 0.77 to 0.90 at GP065 and from 0.68 to 0.91 at GP258.

Additive genetic correlations between MFA, specific gravity, height, diameter and volume are presented in Tables 5 and 6. Core wood MFAs were positively correlated with outer wood MFAs at both sites but the correlations were mostly non-significant. The only significant correlations were at GP258 between core latewood and outer earlywood (Table 5b). The majority of genetic correlations between MFA and specific gravity were not significant at either site (Table 5) nor were the majority of correlations between the wood quality traits and the growth traits (Table 6).

DISCUSSION

The range of MFA values observed in this study was slightly greater than those reported by Donaldson (1992, 1993, 1997) and Megraw et al. (1998, pp. 42-45). Donaldson (1997) found MFAs ranging from 30° to 50° in core wood and from 15° to 25° in outer wood of *P. radiata*. Megraw et al. (1998) observed mean MFA values above 35° in growth rings 1 through 5 and MFAs from 20° to 35° in rings 6 through 20 in loblolly pine (at 1.22 m). In this study, core wood MFA values (estimated using rings 4 and 5) ranged from 21° to 54° at GP065 and from 22° to 54° at GP258. Outer wood MFA values (estimated using rings 19 and 20) ranged from 7° to 43° at GP065 and from 5° to 46° at GP258. The differences between these values and those reported in other

Table 5. Estimates of the genetic correlations (with standard errors) between microfibril angle and specific gravity. (Significant correlations marked with *)
a. at GP065

	Ew 4	Lw 4	Ew 5	Lw 5	Lw 20	Csg	Oasg
Lw 4[a]	0.94* (0.12)						
Ew 5[a]	1.02* (0.01)	0.86* (0.34)					
Lw 5	1.00* (0.07)	0.95* (0.10)	0.94* (0.11)				
Lw 20	0.56 (1.88)	0.25 (3.26)	0.67 (1.43)	0.75 (1.22)			
Csg[b]	0.44 (3.45)	0.14 (4.42)	0.49 (3.97)	0.59 (4.11)	0.78 (2.10)		
Oasg[b]	0.03 (3.45)	-0.27 (3.03)	0.04 (3.72)	0.10 (4.16)	0.34 (3.03)	0.88* (0.26)	
Tsg[b]	0.13 (3.68)	-0.17 (3.63)	0.12 (4.03)	0.22 (4.41)	0.45 (2.91)	0.94* (0.07)	0.98* (0.01)

[a] Lw = latewood, Ew = earlywood

[b] Csg = core wood specific gravity, Oasg = outer wood average specific gravity, Tsg = total specific gravity

Table 5. Continued.
b. at GP258

	Ew 4	Lw 4	Lw 5	Ew 19	Lw 19	Ew 20	Lw 20	Csg	Oasg
Lw 4	1.01*								
	(0.18)								
Lw 5	1.01*	1.08*							
	(0.16)	(0.11)							
Ew 19	0.68	0.93*	0.90*						
	(2.09)	(0.45)	(0.32)						
Lw 19	0.77	0.83	0.89	1.02*					
	(1.71)	(0.71)	(0.59)	(0.19)					
Ew 20	0.70	0.89	0.97*	1.08*	0.92*				
	(2.17)	(0.53)	(0.45)	(0.12)	(0.12)				
Lw 20	0.95	1.01	1.02	1.19	1.06*	1.00*			
	(3.27)	(1.06)	(0.85)	(0.81)	(0.09)	(0.10)			
Csg	-0.39	-0.64	-0.59	-0.63	-0.52	-0.55	-0.60		
	(4.47)	(1.61)	(2.53)	(2.13)	(2.67)	(2.16)	(2.77)		
Oasg	-0.32	-0.55	-0.56	-0.89*	-0.75	-0.76	-0.88*	0.69	
	(4.23)	(1.95)	(2.19)	(0.33)	(0.83)	(0.69)	(0.37)	(1.17)	
Tsg	-0.36	-0.60	-0.58	-0.82	-0.68	-0.69	-0.81	0.90*	0.94*
	(4.09)	(1.63)	(2.10)	(0.70)	(1.26)	(1.09)	(0.85)	(0.17)	(0.06)

Table 6. Estimates of the genetic correlations (with standard errors) between the wood quality and growth traits. (Significant correlations marked with *)
a. at GP065

	MFA					Specific Gravity		
	Ew 4[a]	Lw 4[a]	Ew5	Lw 5	Lw 20	Csg[b]	Oasg[b]	Tsg[b]
Ht 5[c]	0.09	0.51	-0.00	0.27	-0.20	-0.43	-0.70	-0.57
	(3.46)	(1.91)	(3.80)	(3.41)	(3.71)	(3.19)	(1.01)	(1.90)
Ht 10	-0.01	0.44	-0.12	0.15	-0.26	-0.55	-0.77	-0.66
	(3.65)	(2.36)	(3.97)	(3.99)	(3.60)	(2.54)	(0.68)	(1.39)
D 10[c]	0.54	0.85*	0.48	0.65	-0.03	-0.38	-0.69	-0.60
	(1.65)	(0.29)	(2.07)	(1.29)	(3.71)	(3.14)	(0.94)	(1.55)
Vol 10[c]	0.39	0.76	0.32	0.50	-0.14	-0.46	-0.75	-0.65
	(2.42)	(0.66)	(2.90)	(2.11)	(3.76)	(2.81)	(0.69)	(1.34)
Ht 15	0.02	0.46	-0.09	0.15	-0.50	-0.70	-0.81	-0.75
	(3.23)	(2.06)	(3.43)	(3.55)	(2.40)	(1.56)	(0.53)	(0.93)
D 15	0.35	0.73	0.28	0.47	-0.23	-0.58	-0.80	-0.73
	(2.46)	(0.75)	(2.88)	(2.22)	(3.38)	(2.09)	(0.50)	(0.96)
Vol 15	0.24	0.65	0.16	0.36	-0.35	-0.62	-0.82	-0.74
	(2.82)	(1.09)	(3.22)	(2.75)	(3.04)	(1.85)	(0.46)	(0.90)
Ht 20	0.12	0.53	-0.11	0.20	-0.48	-0.66	-0.76	-0.72
	(3.85)	(2.30)	(4.50)	(4.18)	(3.74)	(1.63)	(0.86)	(1.19)
D 20	0.22	0.66	0.12	0.35	-0.37	-0.59	-0.78	-0.70
	(2.89)	(1.13)	(3.33)	(2.83)	(3.02)	(2.00)	(0.60)	(1.12)
Vol 20	0.15	0.60	0.04	0.28	-0.43	-0.61	-0.77	-0.69
	(3.06)	(1.40)	(3.46)	(3.13)	(2.78)	(1.83)	(0.62)	(1.11)

[a] Ew = earlywood, Lw = latewood

[b] Csg = core wood specific gravity, Oasg = outer wood average specific gravity, Tsg = total specific gravity

[c] Ht = height, D = diameter, Vol = volume

Table 6. Continued.
b. at GP258

	MFA							Specific Gravity		
	Ew 4	Lw 4	Lw 5	Ew 19	Lw 19	Ew 20	Lw 20	Csg	Oasg	Tsg
Ht 10	0.00	0.03	-0.16	-0.14	0.14	-0.11	0.02	-0.68	-0.10	-0.43
	(5.13)	(4.82)	(4.08)	(4.67)	(4.37)	(6.35)	(7.60)	(1.40)	(4.30)	(2.97)
D 10	0.47	0.50	0.30	0.27	0.45	0.34	0.46	-0.74	-0.20	-0.50
	(3.16)	(2.61)	(3.38)	(3.92)	(2.69)	(3.91)	(4.04)	(0.94)	(3.77)	(2.39)
Vol 10	0.38	0.38	0.18	0.15	0.36	0.20	0.33	-0.73	-0.14	-0.46
	(4.02)	(3.49)	(3.97)	(4.50)	(3.32)	(4.94)	(5.38)	(1.12)	(4.09)	(2.72)
Ht 15	0.02	-0.17	-0.18	-0.18	0.35	-0.15	0.27	-0.24	-0.18	-0.29
	(7.23)	(4.75)	(5.40)	(4.97)	(4.82)	(4.69)	(5.98)	(4.55)	(4.27)	(3.88)
D 15	0.64	0.46	0.44	0.34	0.72	0.38	0.75	-0.55	-0.34	-0.48
	(3.03)	(2.63)	(3.38)	(3.73)	(1.60)	(3.44)	(2.85)	(2.32)	(3.18)	(2.42)
Vol 15	0.56	0.33	0.33	0.25	0.69	0.29	0.69	-0.49	-0.32	-0.45
	(4.57)	(3.64)	(4.52)	(4.46)	(2.23)	(4.14)	(3.72)	(2.88)	(3.49)	(2.77)
Ht 20	0.06	-0.13	-0.09	-0.13	0.42	-0.06	0.37	-0.27	-0.14	-0.26
	(7.04)	(4.76)	(5.58)	(4.96)	(4.42)	(4.77)	(6.01)	(4.45)	(4.33)	(4.00)
D 20	0.74	0.57	0.58	0.46	0.81	0.49	0.84	-0.53	-0.37	-0.48
	(2.09)	(1.88)	(2.36)	(2.90)	(0.93)	(2.63)	(1.96)	(2.32)	(2.88)	(2.30)
Vol 20	0.68	0.45	0.49	0.37	0.80	0.42	0.81	-0.48	-0.33	-0.45
	(3.34)	(2.81)	(3.46)	(3.71)	(1.40)	(3.36)	(2.83)	(2.83)	(3.28)	(2.70)

studies do not appear to be a result of selection on the parents or thinning in the progeny tests since the mean MFAs of the unimproved checklot were intermediate to those of the families in GP258, the site that was silviculturally thinned. Instead, the wider range of MFA values reported in this study is probably due to a much larger sample size and the presence of compression wood in the cores. Over 650 trees were sampled in this study while only 5 to 15 trees were sampled by Donaldson (1992, 1993, 1997) and approximately 100 trees were sampled by Megraw et al. (1998). Both Donaldson (1992, 1993, 1997) and Megraw et al. (1998) excluded samples with compression wood because it can have a higher MFA. However, no exclusions were made based on the presence of compression wood in this study.

At both sites, MFA was greatest in ring 4 and lowest in ring 20. Similar pith-to-bark decreases in MFA were noted in previous studies of *P. taeda* and *P. radiata* (Bendtsen and Senft 1986; Donaldson 1992, 1993; Megraw et al. 1998, pp. 42-45). In both species, the relationship between MFA and ring position has been shown to be a curvilinear decline. In the core wood, MFA was greater in the latewood than in the earlywood. The converse was true in the outer wood. That is, outer earlywood MFAs were greater than outer latewood MFAs. This same pattern was noted by Megraw et al. (1998, p. 42). In that study, latewood MFAs were greater than earlywood MFAs until ring 7 (at 1.22 m). After ring 7, earlywood MFAs exceeded latewood MFAs.

Results of the analyses of variance were fairly consistent at both sites. GCA was significant for most of the MFA measurements, indicating that there are additive genetic effects influencing MFA. The only MFA measurement for which GCA was not significant at GP065 was earlywood 19. Though attempts were made to minimize the contamination of earlywood 19 measurements by excluding trees with narrow growth rings, the presence of latewood fibers in the remaining earlywood 19 samples may have biased the results of the analysis of variance. Loss of degrees of freedom due to unequal sample sizes and to the exclusion of samples could also have biased the results. The 82 earlywood 19 measurements excluded were not distributed equally among families. Parents lost between 16 and 31 observations each and crosses lost between 2 and 8 observations each.

In addition to additive genetic effects, it appears that non-additive genetic effects also influence MFA. This is consistent with the QTL work of Sewell et al. (2000). At both test sites, SCA was a highly significant effect for some latewood measurements and SCA x block effects were a significant effect for some core wood measurements. The significance of the SCA x block interaction suggests that non-additive genes coding for MFA may be sensitive to changes in the environment. However, this result may simply be a product of within-plot variation or the fact that there were a large number of degrees of freedom for the SCA x Block effect, especially at GP065.

Individual-tree narrow-sense heritability and heritability of GCA effects estimates for the MFA measurements were low to moderate. The true heritability of MFA in loblolly pine may be lower than reported in this study. Since there were no full-sibling families common to both sites, the significance of genetic x environment interactions could not be tested. Should a significant genetic x environment interaction exist, the heritabilities reported in this study would overestimate the true heritability of

MFA. On the other hand, the true heritability of MFA may be much higher than reported here but the limited sample size available, small number of degrees of freedom involved, and added error variation from compression wood may have caused an underestimate. This may be the case for specific gravity, which is generally considered to be highly heritable. Megraw (1985, p. 20) reported that it is not uncommon to see narrow-sense heritability estimates for specific gravity exceeding 0.5. In our study, narrow-sense heritability estimates for core wood specific gravity reached only 0.33 to 0.35. However, it should be noted that specific gravity measurements were taken on un-extracted increment cores that were collected at maturity. The presence of resins and other extractives in the core portion could have lowered the estimates of core wood heritability.

Genetic correlations between MFA measurements were moderate to high even though most were non-significant (Tables 5a and 5b). The fact that all correlations were positive has important implications for tree improvement. If the direction of the true correlations is in fact positive, measurement and selection on a subset of core wood MFAs could indirectly improve/decrease the MFA throughout the core wood and improve core wood quality. This is especially important now that core wood accounts for a greater proportion of the wood harvested from southern pine plantations. Should the positive correlations between core and outer wood MFAs also represent the true direction of the correlations, early selection on core wood MFA could have a beneficial effect on outer wood MFAs as well and result in improvements in the wood quality of the whole tree. On the other hand, should correlations between core and outer wood

MFAs prove to be non-significant, early selection on core wood MFAs would not affect outer wood MFAs. This could also be beneficial because improvements could be made in core wood MFAs without causing a corresponding change in outer wood MFAs and a more uniform distribution of MFAs could be achieved from pith to bark. This would mean boards cut across multiple rings would have more uniform shrinkage properties and would be less prone to crook.

A genetic correlation between MFA and growth rate would also have important implications. Studies have shown that tracheid length decreases with increased diameter growth rate because the length of the cambial initials decreases (Megraw 1985, p. 38). Studies have also shown that MFA increases with decreased tracheid length (Megraw 1985, p. 49). While these studies were based on phenotypic data, this implies that trees with a greater diameter may have a greater MFA than smaller trees of the same age. The significant, positive genetic correlation between latewood 4 MFA and diameter growth at age 10 in GP065 supports this deduction (Table 6a). However, because the majority of correlations between MFA and diameter were not precisely estimated, caution should be used in interpreting the results of this research as proof of a positive genetic relationship between MFA and diameter growth.

Positive genetic correlations between MFA and growth traits are unfavorable because they mean that selection for increased volume growth may result in increased MFA. Negative relationships between height, diameter, volume and MFA would be more favorable for a tree improvement program since they indicate that simultaneous improvement in all of the traits would be possible. Negative correlations were observed at both sites but all had large standard errors, indicating that they may not be reliable estimates. Further research is required to more precisely estimate the genetic correlations between MFA and growth traits.

Negative genetic correlations between MFA and total core specific gravity would also be favorable for a tree improvement program. They imply that progenies with high specific gravity will also have low MFA and breeding for improvements in specific gravity, which is less expensive to measure and has a higher heritability than MFA, may indirectly produce desirable changes in the MFA. The genetic correlations between MFA and total specific gravity were imprecisely estimated and not significantly different from zero. Estimates from the two sites were almost always opposite in sign, either because the genetic samples were different or simply by chance (Tables 5a and 5b). Therefore, it is not possible to draw inferences from the trends.

Specific gravity is highly heritable and studies by Talbert et al. (1983) propose that large gains in specific gravity can be made through selection. However, specific gravity is not widely used as a selection criterion in existing loblolly pine breeding programs because of the overwhelming importance of growth characteristics. Likewise, MFA is not used because there is a lack of genetic data and there is a high cost associated with its measurement. If new breeding programs were designed to focus on wood quality rather than solely on faster growth, the results of this study suggest that both traits could be incorporated into selection strategies. However, the lack of significant correlations makes indirect selection and simultaneous gains in both infeasible. Therefore, the development of selection indices with proper weights for each trait will be necessary before specific gravity and MFA can be incorporated into a breeding program. Better estimates of genetic correlations between MFA and specific gravity would be required, however, before proper selection weights can be assigned to each trait.

CHAPTER III

SIMULATION OF MULTIPLE-TRAIT SELECTION AND BREEDING

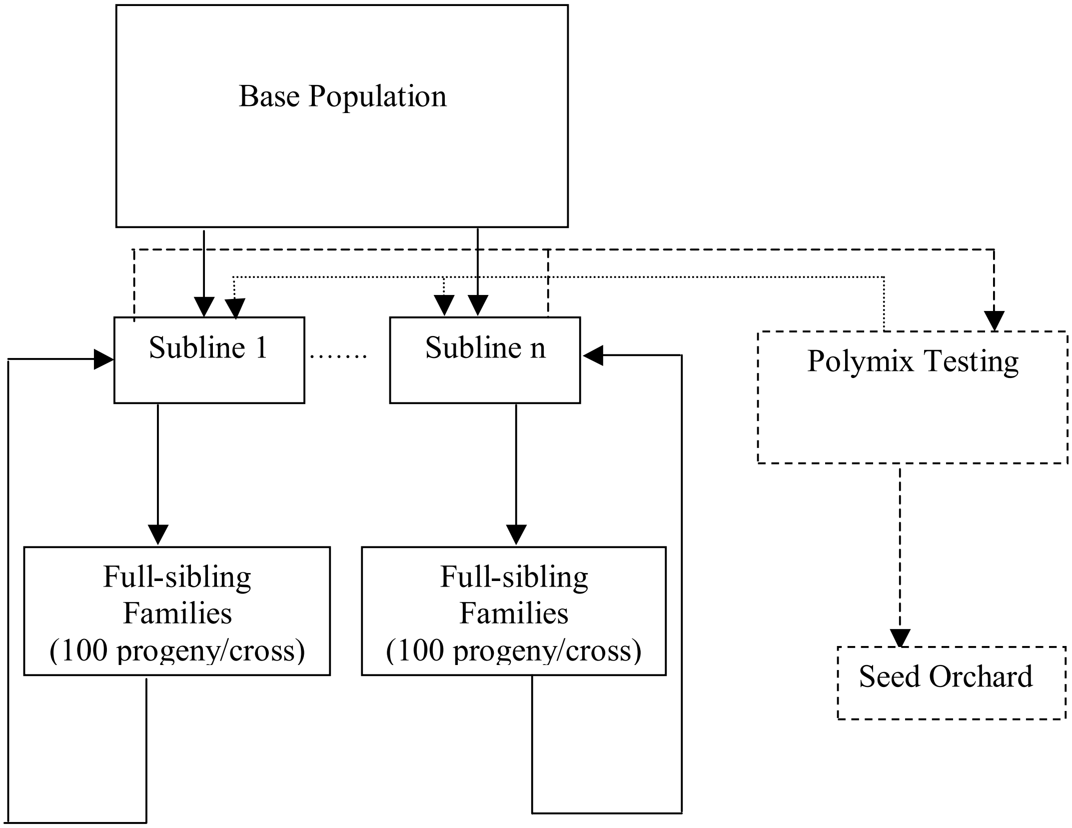
The long generation time of loblolly pine (*P. taeda* L.) makes empirical tests of breeding and selection alternatives impractical. Therefore, stochastic simulation was used to model five generations of elite and mainline population tree improvement. The objective of the simulations was to compare the effect of different selection indices and in the case of the elite population, different breeding strategies on simultaneous gains in growth and wood properties since improvement in both were desired.

METHODS

Simulation Programs

Five Excel-based computer programs were written to simulate elite and mainline population tree improvement for multiple traits. The Excel Add-In, Simetar (Richardson 2001), was used to generate random deviations and conduct the simulations. Each program incorporated a different mating design but all had the same general flow diagram (Figure 1). A variance/covariance structure was specified for a base population of undefined size, which served as the initial source of genetic material for the program. Then, either an elite breeding population was generated by selecting 30 trees at random from the base population or a mainline breeding population was generated by selecting 360 trees at random from the base population. All trees in the initial elite and mainline

Figure 1. Schematic representation of a tree breeding and testing program including polymix testing for seed orchard establishment. Solid lines and arrows represent breeding and testing for generation advancement; dashed lines represent polymix testing for seed orchard establishment; dotted lines represent polymix testing for parental ranking in the positive assortative mating scheme. The boxes labeled sublines 1 through n represent the select population for a given generation; the boxes labeled full-sibling families represent the overall population for a given generation.



populations were assumed to be unrelated and non-inbred. Selections were crossed according to the designated mating designs to produce full- and half-sibling families for evaluation. Full-sibling families were ranked based on the progeny mean and the top individuals from the top families were selected for generation advancement. Where sublines were used, initial selections were first randomly assigned to different sublines and then all crosses and subsequent selections for generation advancement were made within sublines. This process was repeated for 5 generations.

Breeding Strategies

Four breeding strategies were tested in the elite population. The first strategy, referred to as Elite-1L, employed a single subline of 30 individuals for breeding. Each generation, parental selections were randomly assigned to crosses and mated according to a circular mating scheme (partial-diallel with 4 crosses per parent – Byram 2000, p. 22; Figure 2). Then, phenotypes were generated for 100 progeny per cross. Full-sibling families were ranked based on their mean index value and the top individual from each of the top 30 families was selected and crossed to produce the next generation. No restrictions were placed on the number of half-siblings selected each generation or on matings between half-siblings.

The second and third strategies, Elite-PAM and Elite-PAM-P, were similar to Elite-1L but with one important difference. Rather than randomly assigning selected individuals to crosses, positive assortative mating (PAM) was used. In Elite-PAM, the top individual from each of the top 30 families was polymix tested first and then ranked

Figure 2. Circular mating design applied in the elite population.

	2	3	4	5	6	7	8	9	10	11	12	…	29	30	1	2
1	X	X														
2		X	X													
3			X	X												
4				X	X											
5					X	X										
6						X	X									
7							X	X								
8								X	X							
9									X	X						
10										X	X					
…											…	…				
27												…	X			
28													X	X		
29														X	X	
30															X	X

based on its breeding value. The highest-ranking individual was mated to the second and third highest-ranking individuals, the second highest-ranking to the third and fourth highest-ranking, etc. In Elite-PAM-P, the top individual from each of the top 30 families was ranked based on its phenotypic value rather than its polymix performance and then mated as described for Elite-PAM.

The last strategy (Elite-6L) tested in the elite population used 6 sublines of 5 trees each with all selection and breeding conducted within sublines. Parents selected for the initial breeding population were randomly assigned to one of the 6 sublines and mated using a 5-parent modified half-diallel design (no selfs or reciprocals). Then, phenotypes were simulated for 100 progeny per cross. Individual values and full-sibling family means were used to select the top individual from each of the top 5 families in each subline. These selections were then used to produce the next generation. Again, no restrictions were placed on the number of half-siblings selected each generation and half-siblings were not prevented from mating.

In the Mainline program, only one breeding strategy was used. Selections in the base generation were randomly assigned to one of 20 sublines (18 trees per subline). Within sublines, parents were randomly assigned to crosses and mated according to a circular mating design. Then, phenotypes were generated for 100 full-sibling progeny per cross and the 3 top individuals from each of the 6 top families in each subline were selected to produce the next generation.

Simulated Phenotypes

The phenotypic effects of each tree were estimated from the sum of its additive, dominance and environmental effects. For simplicity, epistatic effects were ignored, as were interactions between effects (e.g. additive x dominance effects).

The additive effects of each tree were estimated from a normal distribution with a mean equal to its mid-parent value and a variance equal to the Mendelian sampling contribution, reduced by the inbreeding coefficient of its parents (Dempfel 1990; Mullin and Park 1995):

$$A_p = \frac{(A_m + A_f)}{2} + r\sqrt{\frac{[1-0.5*(F_m+F_f)]*\hat{\sigma}_A^2}{2}} \qquad [5]$$

where A_p, A_m, and A_f are the individual additive effects of the progeny, male parent, and female parent, respectively; r is the correlated standard normal deviate (Appendix I); F_m and F_f are the inbreeding coefficients of the male and female parents, respectively; and σ^2_A is the additive genetic variance in the base population[1]. In the initial breeding populations, A_m, A_f, F_m, and F_f were assumed to be zero.

The dominance effects of each tree were estimated from a normal distribution with a mean reduced due to inbreeding depression and the inbreeding coefficient of the

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[1] As recommended in Readme.txt - Program Notes and Fixes for Popsim (Mullin and Park 1995), variances from the base population are used in calculating the genetic effects rather than variances from the parental population.

full-siblings and a variance comparable to that specified in the base population (Borralho 1994; Mullin and Park 1995)[2]:

$$D_p = 0 + r_{fm}\sqrt{\frac{1}{4}\hat{\sigma}_D^2} + r_i\sqrt{\frac{3}{4}\hat{\sigma}_D^2} + bF_{fm}\,\hat{\sigma}_P \qquad [6]$$

where D_p is the individual dominance effect of the progeny, r_{fm} is the correlated standard normal deviate for the full-sibling family, r_i is the correlated standard normal deviate for each individual, b is the regression coefficient correcting for inbreeding depression, F_{fm} is the inbreeding coefficient of the full-sibling progeny of cross f x m, σ^2_D is the dominance variance in the base population, and σ_P is the phenotypic standard deviation in the base population.

The environmental effects were sampled from a normal distribution with means and variances equivalent to those in the base population (Mullin and Park 1995):

$$E_P = \overline{E} + r\sqrt{\hat{\sigma}_E^2}\ . \qquad [7]$$

The environment itself was assumed to be common to all members of a given generation and across generations.

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[2] As recommended in Readme.txt - Program Notes and Fixes for Popsim (Mullin and Park 1995), the mean dominance effect was reset to zero each generation rather than using the mean in the parental population.

Inbreeding Coefficient

The inbreeding coefficient for each tree was calculated from (Falconer and Mackay 1996, pp. 82-84):

$$F_x = \sum \left(\frac{1}{2}\right)^n (1 + F_A) \qquad [8]$$

where n is the number of ancestors in the path of relationship (loop in the pedigree), and F_A is the inbreeding coefficient of the common ancestor. This equation predicts the expected average inbreeding coefficient among full-sibling family members. In reality, individual values would vary about this mean. However, for simplicity, all full-sibling progeny were assumed to have the same level of inbreeding and suffer the same amount of inbreeding depression.

Index Selection

In all, seven indices were compared in the elite population and four were compared in the mainline population (Table 7). The simplest type of index examined was direct selection on juvenile traits to improve the core wood portion of the tree. Direct selection to decrease earlywood 4 microfibril angle (MFA) and to increase core wood specific gravity (Csg) was used in the elite population while direct selection to increase volume at age 10 was used in the mainline population. These indices are referred to as *MFA*, *Csg*, and *Vol10*, respectively. *MFA*, *Csg*, and *Vol10* were used as

Table 7. General description of each index and its selection goal.

Pop.	Index	General Equation[1]	Goal[2]
Elite	*Base$_e$*	$1(h^2)$(Ew 4) + $1(h^2)$(Csg)	↓ Ew 4, ↑ Csg
	MFA	1(Ew 4) + 0(Csg) + 0(Vol 10)	↓ Ew 4
	Pulp-WG	0.078*BV(Vol 20) + 0.634*BV(Tsg)	↑ Vol 10, ↑ Csg
	Pulp-h^2	$0.078(h^2)$(Vol 10) + $0.634(h^2)$(Csg)	↑ Vol 10, ↑ Csg
	RSI(*MFA/Vol*)$_e$	b_1 (Ew 4) + 0(Csg) + b_2 (Vol 10)	↓ Ew 4, ~ Vol 10
	RSI(*Csg/Vol*)$_e$	0(Ew 4) + b_1 (Csg) + b_2 (Vol 10)	↑ Csg, ~ Vol 10
	Csg	0(Ew 4) + 1(Csg) + 0(Vol 10)	↑ Csg
Mainline	*Vol10*	0(Ew 4) + 0(Csg) + 1(Vol 10)	↑ Vol 10
	Base$_m$	$3(h^2)$(Vol 10) + $1(h^2)$(Csg)	↑ Vol 10, ↑ Csg
	RSI(*Vol/MFA*)$_m$	b_2(Ew 4) + 0(Csg) + b_1(Vol 10)	↑ Vol 10, ~ Ew 4
	RSI(*Vol/Csg*)$_m$	0(Ew 4) + b_2(Csg) + b_1(Vol 10)	↑ Vol 10, ~ Csg

[1] Ew 4 = earlywood 4 MFA, Csg = core wood specific gravity (measured at age 5), Vol = volume at the specified age (10 or 20), h^2 = heritability, BV = breeding value, Tsg = total specific gravity, b_n = index weight (changes depending on the variance structure of the population)

[2] ↑ = increase, ↓ = decrease, ~ = maintain at same level as in base population

the baseline for comparing the other indices.

Another type of index examined in the mainline and elite populations was a restricted selection index where gain in one trait is maximized while a second trait is held constant. In the elite population, the indices, $RSI(MFA/Vol)_e$ and $RSI(Csg/Vol)_e$, were used to decrease earlywood 4 MFA and increase core wood specific gravity, respectively, while holding volume at age 10 constant. In the mainline population, the indices, $RSI(Vol/MFA)_m$ and $RSI(Vol/Csg)_m$, were used to increase volume at age 10 while respectively holding earlywood 4 MFA and core wood specific gravity constant. Index weights for the restricted selection indices were calculated each generation using the general equation developed by Cunningham et al. (1970):

$$\mathbf{P}^{*}\mathbf{b} = \mathbf{G}^{*}\mathbf{v} \qquad [9]$$

or

$$\begin{pmatrix} V_{p1} & C_{p12} & C_{a12} \\ C_{p21} & V_{p2} & V_{a2} \\ C_{a21} & V_{a2} & 0 \end{pmatrix} \begin{bmatrix} b_1 \\ b_2 \\ b_d \end{bmatrix} = \begin{pmatrix} V_{a1} & C_{a12} \\ C_{a21} & V_{a2} \\ 0 & 0 \end{pmatrix} \begin{bmatrix} 1 \\ 0 \end{bmatrix}$$

where $\mathbf{P}^{*}$ is a 3x3 matrix containing phenotypic variances and covariances, additive genetic covariances, additive genetic variances for the trait held constant, and a zero (additive variances, covariances and zero from the second column of the $\mathbf{G}^*$ matrix); **b** is a 3x1 vector containing index weights; $\mathbf{G}^*$ is a 3x2 matrix containing additive genetic variances and covariances, and zeros; **v** is a 2x1 vector containing economic weights; V_{pi} is the phenotypic variance of the ith trait; C_{pij} is the phenotypic covariance of the ith and jth traits; V_{ai} is the additive genetic variance of the ith trait; C_{aij} is the additive genetic covariance of the ith and jth traits; b_i is the index weight of the ith trait; and b_d is the index weight of the dummy variable. When earlywood 4 MFA and core wood specific gravity were not used as a selection criterion or index trait, changes in the traits were still examined.

In addition to direct, indirect and restricted selection, modified base indices were also examined in the elite and mainline populations. The general model used was:

$$I = \sum a_i h_i^2 P_i \quad [10]$$

where a_i is the economic weight of the ith trait, h^2_i is the heritability of the ith trait, and P_i is the phenotypic value of the ith trait, standardized to the base population mean. The goal of the elite population index ($Base_e$) was to decrease earlywood 4 MFA and increase core wood specific gravity. Both were given equal economic weights since Cown et al. (1999) found both were significant influences on juvenile clearwood performance in Radiata pine (*P. radiata* D. Don). The goal of the mainline modified base index ($Base_m$) was to increase both volume at age 10 and core wood specific gravity simultaneously. Volume was given an economic weight 3 times that of core wood specific gravity because Greaves (1999) showed that in Radiata pine, growth traits have 3 times the influence of wood quality traits on the profitability of sawn timber ventures.

Two pulp indices were tested in the elite population alone. The first, *Pulp-WG*, was developed by Lowe et al. (1999) for minimizing the cost of Kraft pulp production:

$$I = 0.078BV_{Vol20} + 0.634BV_{Tsg} \qquad [11]$$

where I is the individual index value and BV_{Vol20} and BV_{Tsg} are the breeding values for volume and specific gravity, respectively. BV_{Vol20} and BV_{Tsg} were calculated from volume at age 10 and core wood specific gravity according to the methods of the WGFTIP as described by Lowe and van Buijtenen (1991). The second pulp index, *Pulp-h2*, used the same economic weights but estimated the breeding values as the product of the standardized progeny phenotypic value and the heritability of the trait.

Seed Orchards

Individuals selected for generation advancement were polymix tested each generation to identify the best genotypes for use as seed orchard parents. In the mainline population, 10 orchard parents were chosen since 10 is the minimum number of parents that would be used in a real-world orchard. In the elite population, 6 seed orchard parents were chosen because 6 was the greatest number of unrelated parents that could be identified in the fifth generation under the sublined breeding strategy. Polymix tests were assumed to be perfect and thus, to result in the correct ranking of breeding values among selections. In Elite-1L, Elite-PAM and Elite-PAM-P, the top polymix-ranked individual was selected for the seed orchard. Then, to minimize coancestry among orchard parents, the next highest ranked but least related individual was also selected. Selection of the highest-ranked, least-related individual was repeated until 6 orchard parents had been selected. In Elite-6L, the top polymix-ranked individual from each subline was selected to be an orchard parent. In Mainline, the top individual from each of the sublines was considered a candidate for selection and was ranked against the other candidates. The top ten candidates were then chosen as orchard parents

Expected mean phenotypes for seed orchard progeny were calculated by assuming a potentially infinite number of progeny could be produced with equal contributions from each seed orchard selection (i.e. all correlated standard normal deviates would average to zero):

$$\overline{P} = \overline{A} + \left(b\overline{F}\sigma_p^2\right) + \overline{E} \qquad [12]$$

where $\overline{A}$ is the average additive effect of the seed orchard selections, $\overline{F}$ is the average inbreeding coefficient of the seed orchard progeny.

Expected gains from the seed orchards were calculated as a percent improvement over the base population mean:

$$Gain = \frac{\overline{A}_{sel}}{\overline{P}_0} * 100 \quad . \qquad [13]$$

Simulations

A population with the characteristics listed in Table 8 was used as the initial base for each of the mating design/index combinations. Earlywood 4 MFA, core wood specific gravity, and volume at age 10 were used in the simulations because all were the earliest traits expressed for which there were data on heritabilities and genetic correlations. Their means in the base population were based on the results of Chapter II and on checklot data from similar tests in the WGFTIP program. The variances and heritability of earlywood MFA were based on the results of Chapter II. Variances for core wood specific gravity were based on checklot data while the heritability was based on those reported in Zobel and Talbert (1991, p. 130) and Megraw (1985, pp.19-20). The variances and heritability for volume at age 10 were based on the results Chapter II and on Gwaze et al. (2001), which reported heritabilities and correlations in several of the WGFTIP progeny tests. Covariances were estimated to calculate specific additive genetic and phenotypic correlations and represent a "worst-case-scenario" in which volume at age 10 was unfavorably correlated with both earlywood 4 MFA and core wood specific gravity. For volume at age 10 and earlywood 4 MFA, a genetic correlation of 0.4 and a phenotypic correlation of 0.2 were based on data reported in Chapter II. For volume at age 10 and core wood specific gravity, a genetic correlation of -0.3 and a phenotypic correlation slightly below zero were based on those reported in Gwaze et al. (2001) and based on the fact that according to Megraw (1985, p. 23), the environmental covariance could be positive, negative, or zero. Earlywood 4 MFA and core wood specific gravity were assumed to be uncorrelated based on data from this

Table 8. Phenotypic characteristics and covariance structure of the base population.

Trait	Ew 4 MFA	Core Wood Sp. Gr.	Volume 10
Mean	40.00[a]	0.4100	6.728[b]
Var (a)	4.25	0.0004	2.00
Var (d)	0.00	0.0000	0.50
Var (e)	8.00	0.0006	7.50
h^2	0.35	0.40	0.20
	MFA x Csg	MFA x Vol	Csg x Vol
Cov (a)	0	1.1662	-0.0085
Cov (d)	0	0	0
Cov (e)	0	1.0474	+0.008
Cov (p)	0	2.2136	-0.0005

[a] in degrees from vertical

[b] in cubic meters per hectare per year

study and on Megraw et al. (1999).

Inbreeding depression of growth is well studied in conifers (e.g. Sorensen and Miles 1982; Sniezko and Zobel 1988). Therefore, volume at age 10 was assumed to decrease one phenotypic standard deviation for every 0.5 increase in the inbreeding coefficient. The effect of inbreeding depression on specific gravity has rarely been studied but it appears to be non-significant (Williams and Savolainen 1996). It has not been studied in MFA. Therefore, earlywood 4 MFA and core wood specific gravity were assumed to suffer no inbreeding depression and for simplicity, have no dominance variance.

In the elite population simulations, all sublines were run concurrently and statistics based on individual subline and overall population performance were generated. In the mainline simulations, each subline was run individually due to computer limitations. As a result, only statistics on individual sublines were generated. Seed orchards from the elite line were generated as part of the simulation programs but seed orchards from the mainline were generated after the simulations were completed by selecting the top tree from ten sublines (based on index breeding value). The random number, 44485, was used as a seed for each of the elite population scenarios and for the first subline of the mainline population. Nineteen other random numbers were used to seed the remaining sublines of the mainline population[3]. Each simulation was run for 75 iterations, the means and variances of which are reported herein.

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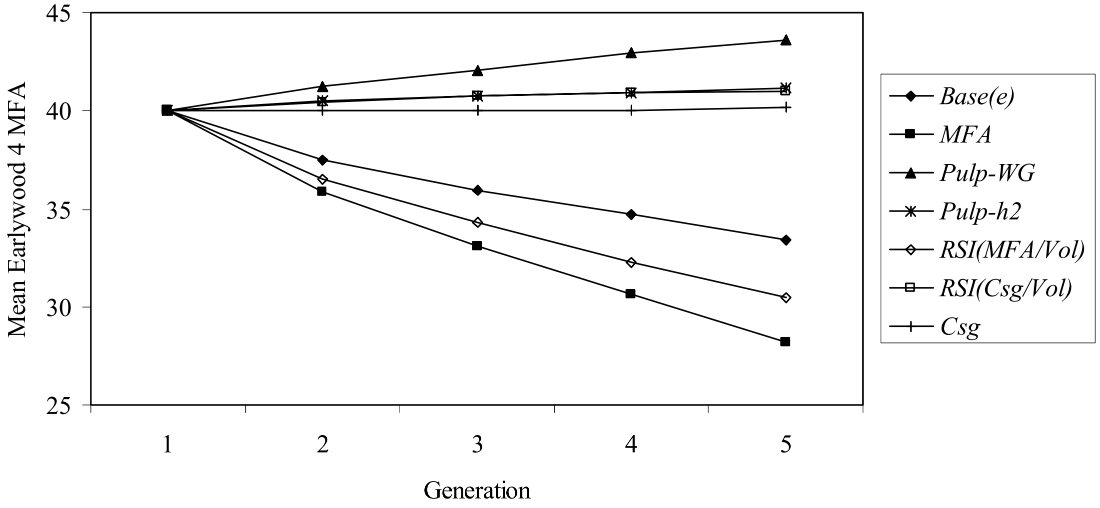
[3] Additional seed numbers: 17277, 37963, 44657, 44135, 47495, 27329, 70843, 88631, 28997, 98041, 97421, 21095, 67575, 54763, 24013, 61657, 15459, 59335, and 14805.

RESULTS AND DISCUSSION

Each of the selection indices caused significant responses in the overall elite and mainline population trait means (Appendix II). For example, in the elite population simulations, selection on *MFA, RSI*(*MFA/Vol*)$_e$ and *Base*$_e$ resulted in large decreases in mean earlywood 4 MFA values over time while selection on *Pulp-WG* resulted in increases in mean earlywood 4 MFA values (Figure 3). Selection on *RSI*(*Csg/Vol*)$_e$ caused small increases in mean earlywood MFA over time while selection on *Csg* caused very little change in mean earlywood MFA values. Differences in the breeding strategies enhanced these changes, with PAM causing slightly greater responses and Elite-6L causing slightly smaller responses. Interestingly, phenotypic responses to selection on *Pulp-h2* were different under PAM than under controlled random mating (Figure 4). When Elite-PAM or Elite-PAM-P was used, *Pulp-h2* produced results similar to *Pulp-WG* but when Elite-1L or Elite-6L was used, the *Pulp-h2* index produced results similar to *RSI*(*Csg/Vol*)$_e$ (Figure 3). This pattern was found in the responses of all three traits (earlywood 4 MFA, core wood specific gravity and volume at age 10). One possible explanation for this is that when controlled random mating is used, the reaction is driven by the economic/selection weights but when PAM is used, the reaction is driven by the genetic variances in the traits. With *Pulp-h2*, core wood specific gravity had a much higher selection weight than volume at age 10 so under controlled random mating, while trait means responded to both the genetic correlations with core wood specific gravity and with volume at age 10, the responses more closely resembled those

Figure 3. The effect of different selection indices on the overall elite population mean earlywood 4 MFA (in degrees from vertical) when different breeding strategies are used.

a. When the Elite-1L breeding strategy is used (trends were similar for Elite-6L).



b. When the Elite-PAM breeding strategy is used (trends were similar for Elite-PAM-P).

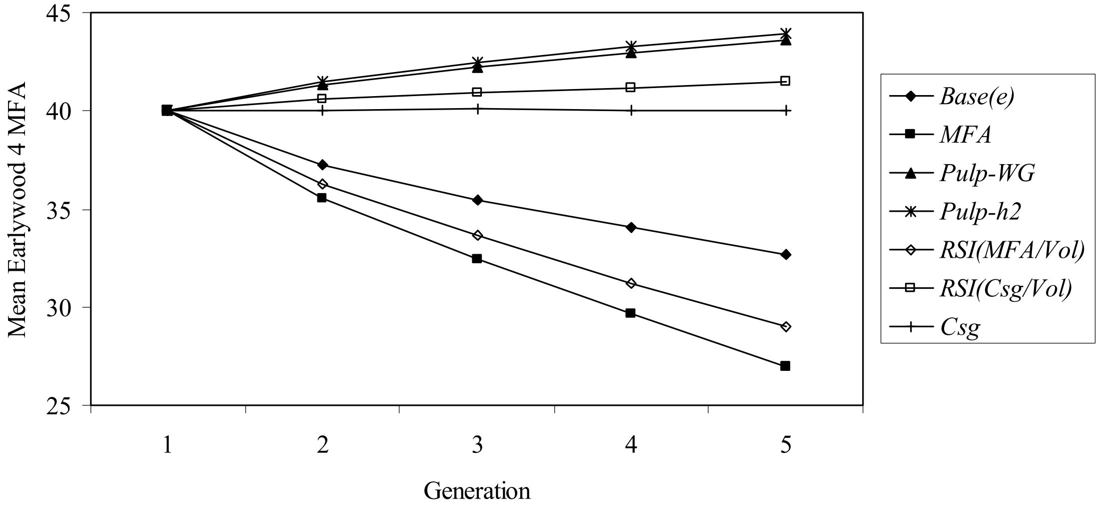
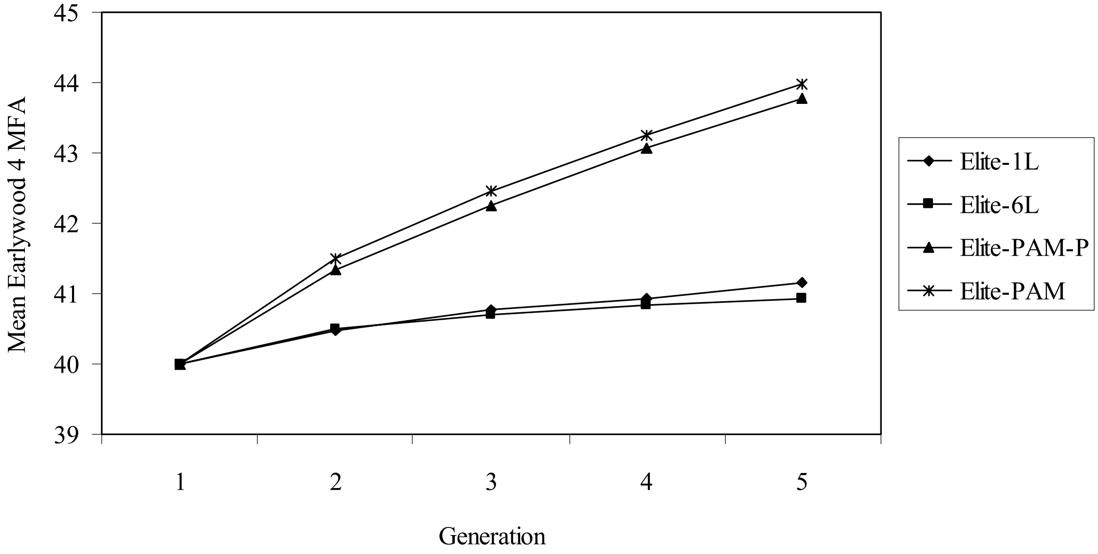


Figure 4. The effect of *Pulp-h2* on the overall elite population mean earlywood 4 MFA (in degrees from vertical) when different breeding strategies are used.



from the genetic correlation with core wood specific gravity. Under PAM, however, responses more closely resembled those from the genetic correlation with volume at age 10 because volume at age 10 has a much greater variance than core wood specific gravity. For example, when both core wood specific gravity and volume were selected on using *Pulp-h2* and controlled random mating was used, the observed increase in mean earlywood 4 MFA was small because the correlation with core wood specific gravity was minimizing the response to the correlation with volume (Figure 3). Under PAM, mean earlywood 4 MFA showed a greater increase due to its positive correlation with volume and despite the lack of a correlation with specific gravity. Similar trends were observed under controlled random mating in the mainline population when $Base_m$ was used.

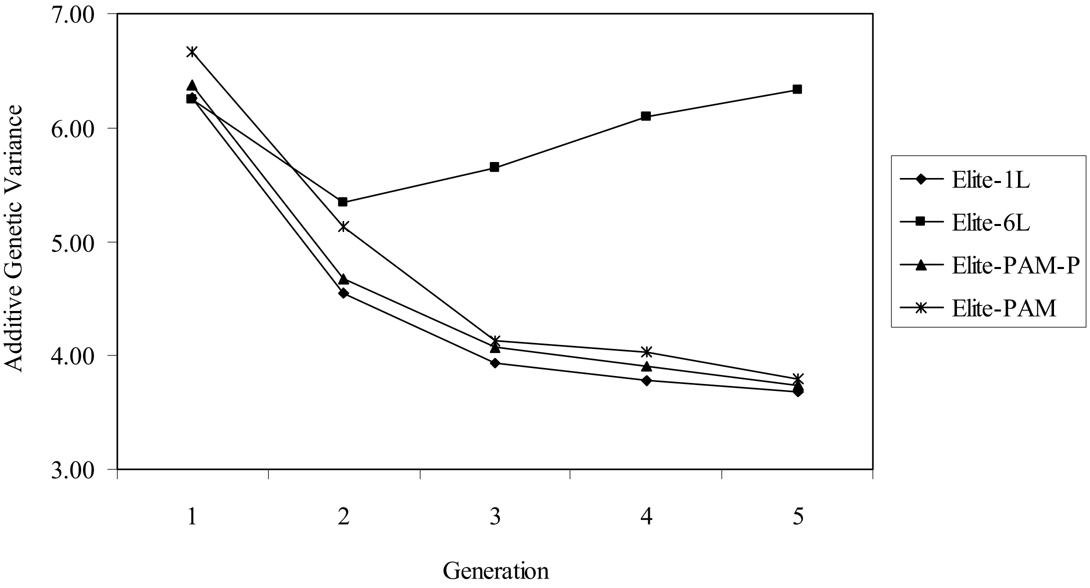
As expected, the variances about the means increased with generation number, indicating increased uncertainty/risk with time. In general, variances were lower when either traits were directly selected on or were included in the index than when traits were not included in the index. For example, the variance about the estimated overall mean earlywood 4 MFA was 10 to 20 times greater in generation 5 than in generation 1 and was more than four times greater under *Csg* and *Pulp-h2* than under *MFA*. However, with the *Pulp-h2* index, variances again appear to be primarily influenced by the economic weights under the circular mating scheme and by the genetic and phenotypic variances under PAM. The variance about the estimated overall mean core wood specific gravity was significantly lower when the circular mating design was used than when PAM was used and the variance about the estimated mean volume at age 10 was significantly lower when PAM was used than when the circular mating design was used.

Changes in the additive genetic variances over time were highly influenced by departures from Hardy-Weinberg equilibrium and differences in the breeding strategies. When the Elite-1L, Elite-PAM, or Elite-PAM-P breeding strategy was used, additive genetic variances increased over base population levels in the first generation then decreased through generation 5 (Figure 5). The initial increase was due to non-random mating of the initial select population and the generation of progeny phenotypes at the extremes. The subsequent decrease was due to selection, inbreeding and limited population size. Similar patterns were observed within sublines when Elite-6L was used but the total additive genetic variance across sublines showed an increase in generation 1, a decrease in generation 2, then either an increase or leveling off after generation 2. This pattern was due to subline divergence as predicted by Falconer and Mackay (1996, pp. 264-266). In the select population, additive variances for traits under direct selection showed less of an increase in generation 1 than in the overall population and then a dramatic reduction by generation 2 (Figure 6). Index traits under indirect selection showed a similar pattern but were less extreme. Variances in the select population were lower than in the overall population due to the effects of selection, except when Elite-6L was used. This is probably also the result of subline divergence.

Dominance variances increased in generation 2 when inbreeding occurred (Figure 7). This was counter to the expected decrease with inbreeding. One possible explanation is that the range of inbreeding coefficients within the population caused an

Figure 5. Changes in the total additive genetic variance of earlywood 4 MFA with selection on *Base*$_e$. Similar trends were noted in each of the variables.

a. Total additive genetic variance of earlywood 4 MFA in the overall elite population.



b. Total additive genetic variance of earlywood 4 MFA in the overall elite population and in each subline when the Elite-6L breeding strategy is used.

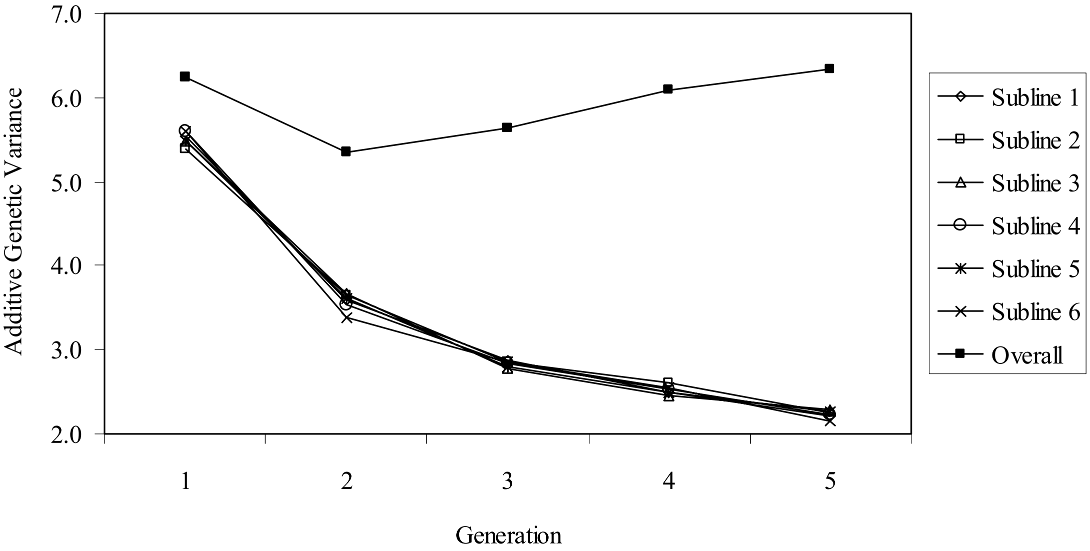
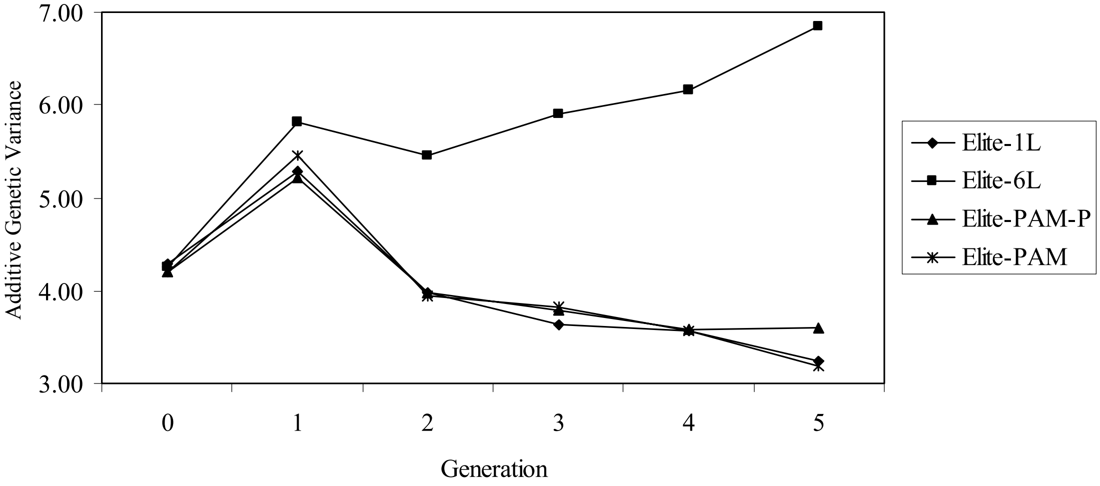


Figure 6. Changes in the additive genetic variance of earlywood 4 MFA in the select population with selection on $Base_e$. Similar trends were noted in each of the variables.
a. Additive genetic variance of earlywood 4 MFA in the elite select population.



b. Additive genetic variance of earlywood 4 MFA in the elite select population and in each subline when the Elite-6L breeding strategy is used.

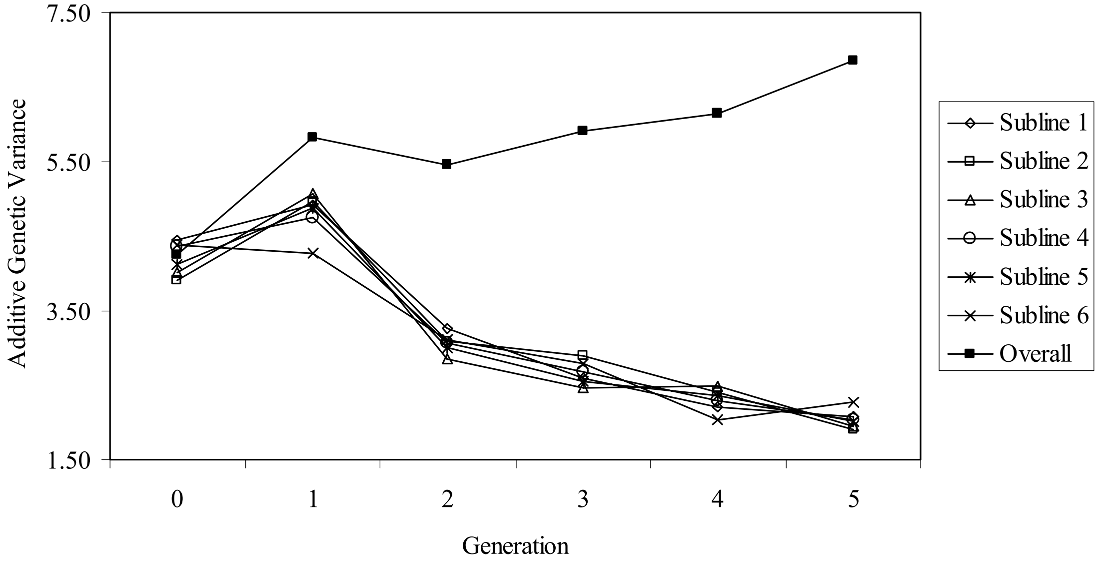
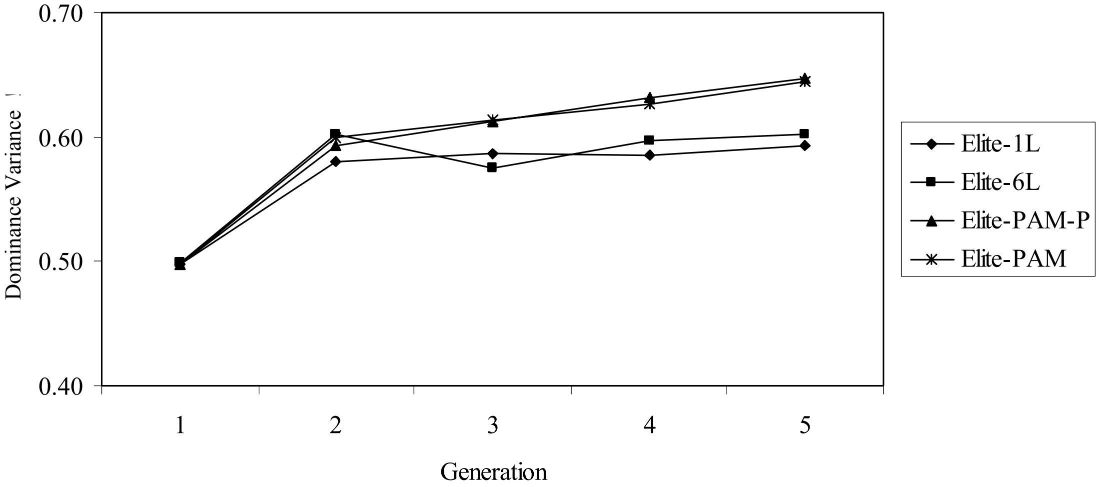
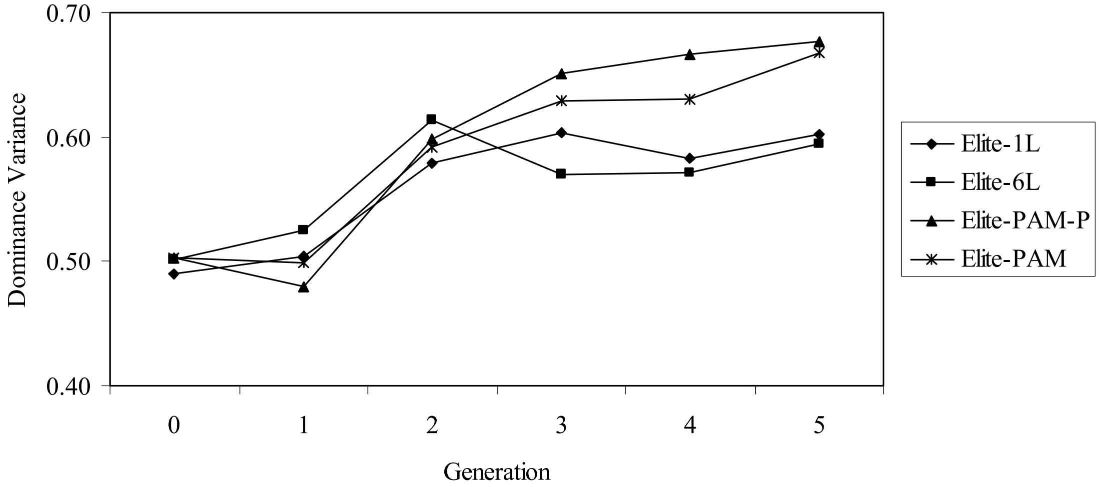


Figure 7. Changes in the dominance variance of volume at age 10 with selection on Base_e.

a. Dominance variance of volume at age 10 in the overall elite population.



b. Dominance variance of volume at age 10 in the elite select population.

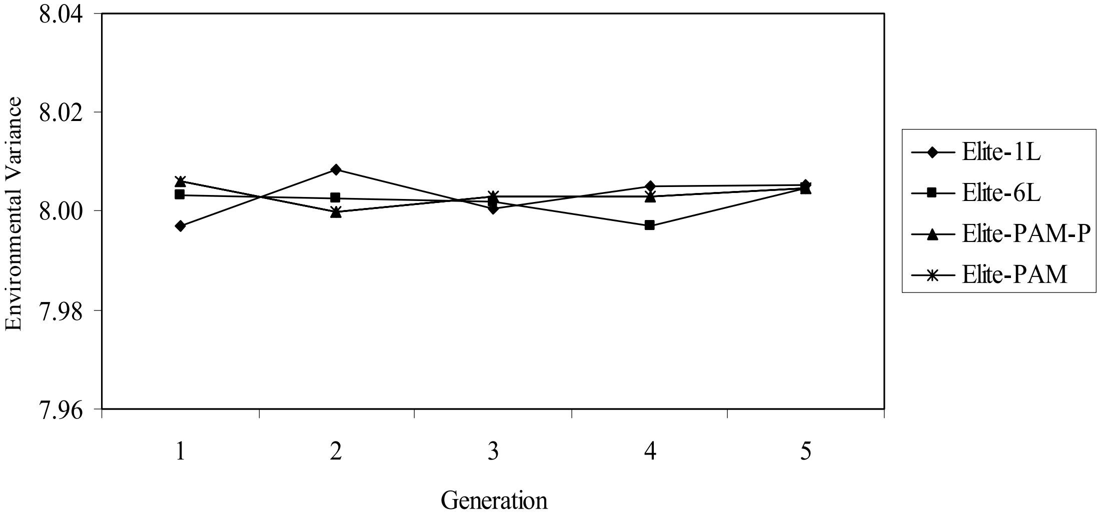


increase in the dominance variance. Inbreeding coefficients were calculated separately for each full-sibling family so each generation the overall and select populations contained individuals with a range of different inbreeding coefficients. Theoretically, the different inbreeding coefficients would have different influences on the dominance effect and thus could have caused an increase in the dominance variance. Another possible explanation is that non-random mating of the select population created a wider range of dominance effects than would have occurred under random mating. This deduction is supported by the fact that the breeding strategies that incorporate PAM cause a greater increase in the dominance variance than those that randomly assigned parents to crosses.

Environmental variances responded differently in the overall and select populations. In the overall population, environmental variances fluctuated about the base population mean (Figure 8). This was as expected since environmental variances should not be affected by selection or inbreeding (Mullin and Park 1995). In the select population, however, the environmental variances of index traits decreased dramatically following selection while those for non-index traits showed greater fluctuations about the base population mean (Figure 9). It appears that by selecting the best individuals from the best families, individuals with similar environmental responses were chosen. This trend in the environmental variance was observed with every selection index except *Pulp-h2*. As with the phenotypic effects, responses were different when PAM was used than when controlled random mating was used. The environmental variance of core wood specific gravity decreased sharply in the first generation when either Elite-1L or

Figure 8. Changes in the environmental variances of index and non-index traits in the overall elite population with selection on Base$_e$.

a. Environmental variance of earlywood 4 MFA in the overall elite population. Similar trends were observed in the environmental variance of core wood specific gravity.



b. Environmental variance of volume at age 10 in the overall elite population.

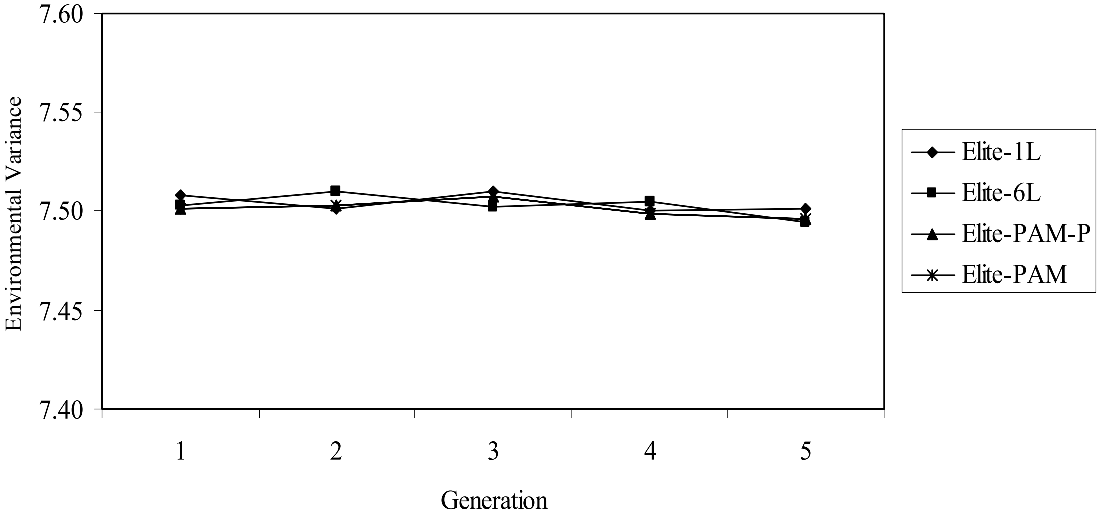
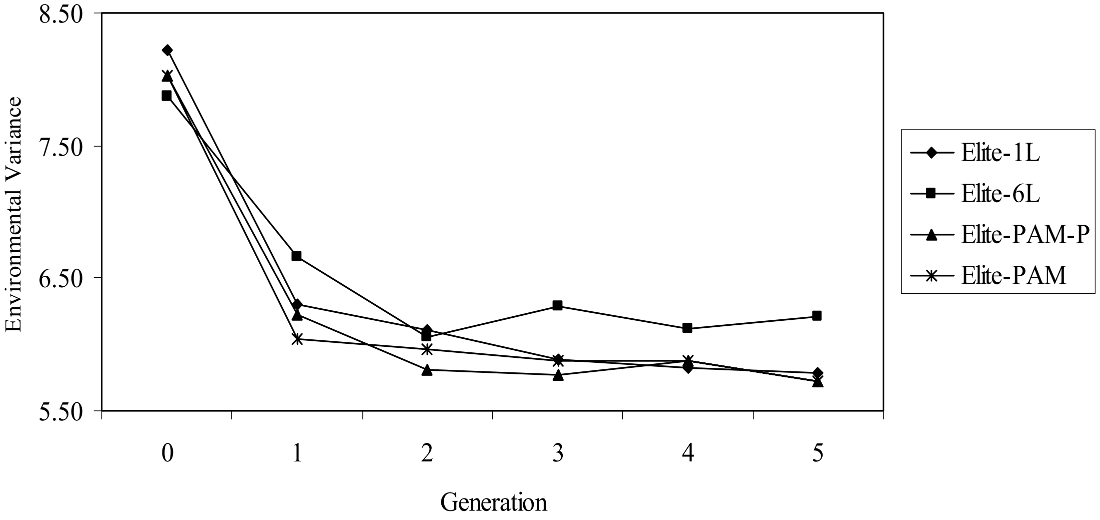


Figure 9. Changes in the environmental variances of index and non-index traits in the elite select population with selection on $Base_e$.

a. Environmental variance of earlywood 4 MFA in the elite select population. Similar trends were observed in the environmental variance of core wood specific gravity.



b. Environmental variance of volume at age 10 in the elite select population.

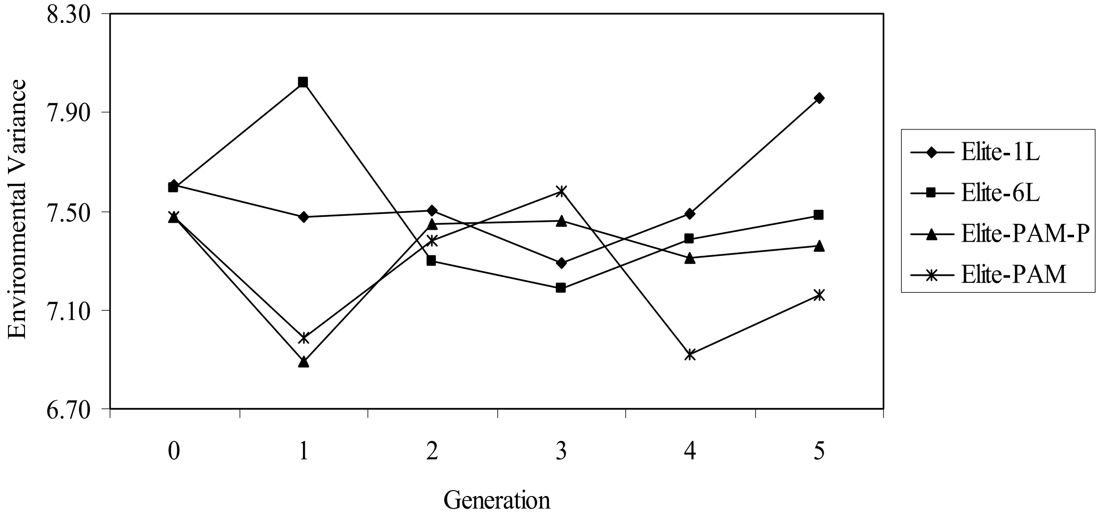
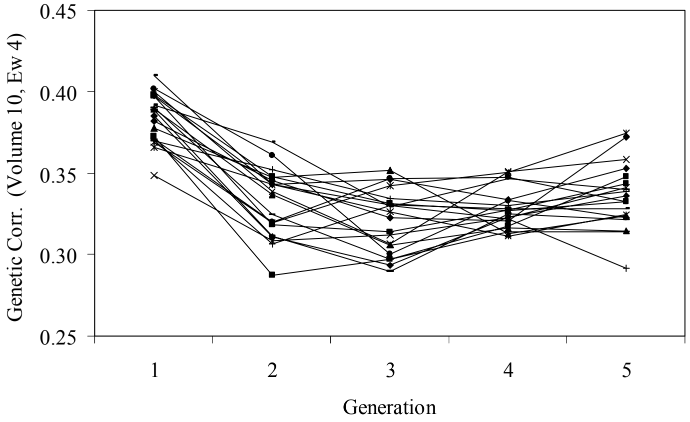
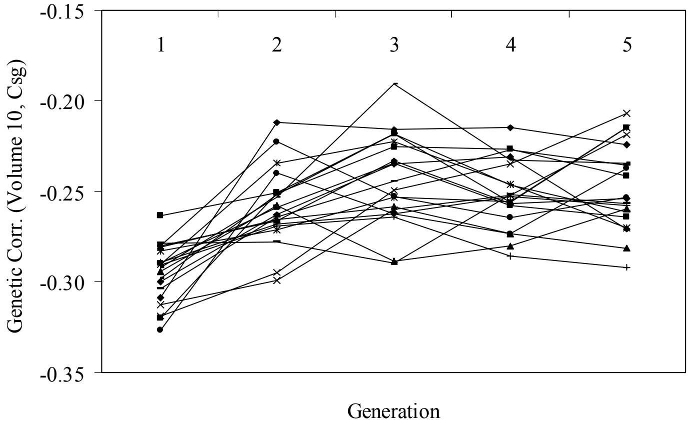


Figure 10. Changes in the genetic correlations as a result of direct selection on volume at age 10 in the overall mainline population. Each line represents a subline.

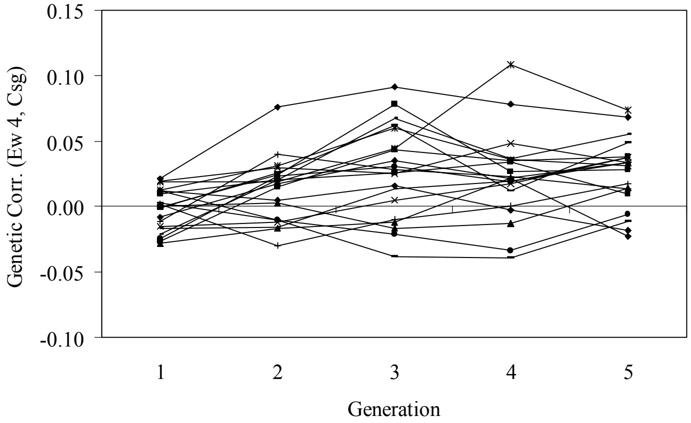
a. Genetic correlation between volume at age 10 and earlywood 4 MFA



b. Genetic correlation between volume at age 10 and core wood specific gravity



c. Genetic correlation between earlywood 4 MFA and core wood specific gravity



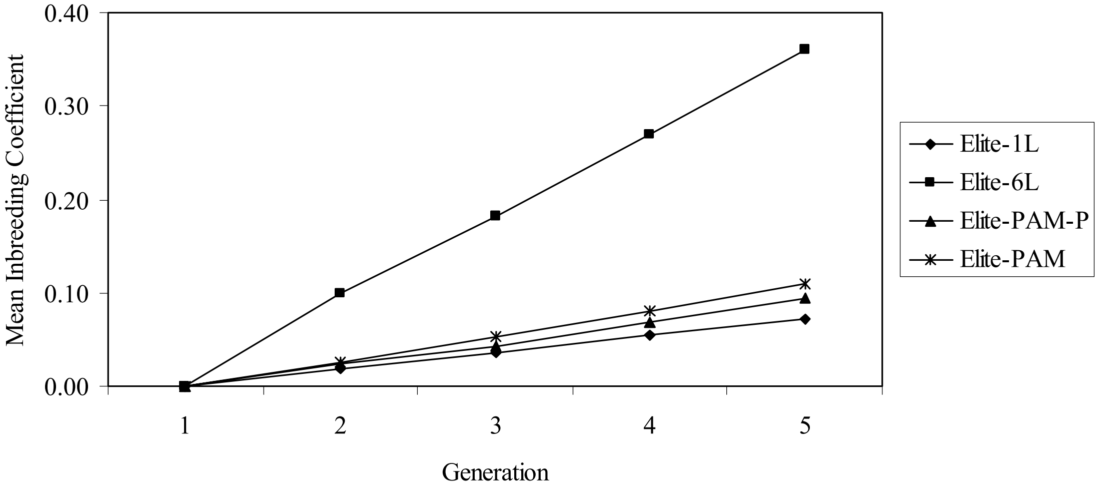
Elite-6L were used but fluctuated about the base population mean when either Elite-PAM or Elite-PAM-P were used. The environmental variance of volume 10 showed only a slight decrease when either Elite-1L or Elite-6L were used but decreased significantly when either Elite-PAM or Elite-PAM-P were used. This further supports the idea that when controlled random mating is used, the reaction is driven by the economic/selection weights but when PAM is used, the reaction is driven by the genetic variances in the traits.

Genetic correlations responded in different manners depending on the selection and breeding strategy. Villanueva and Kennedy (1990) predicted that the absolute value of correlations between traits under direct selection and traits not under direct selection should decrease. This was observed in the mainline when *Vol10* was used (Figure 10) and in the elite population when *MFA* and *Csg* were used. Correlations between traits not directly selected on can increase, decrease or stay the same (Villanueva and Kennedy 1990). Pray (1997) observed that some correlations will switch sign as the amount of inbreeding in the population increases. This occurred with the correlation between earlywood 4 MFA and core wood specific gravity in some sublines of the mainline population and in the elite population. This correlation was small, however, and the observed change in sign may simply have been a fluctuation around the base mean of zero. Correlations between earlywood 4 MFA and volume at age 10 and between core wood specific gravity and volume at age 10 tended to follow expected paths though some minor increases and decreases were observed.

The inbreeding coefficient increased in both the overall and select populations after generation 2. Values in the two populations were similar if the index traits did not suffer from inbreeding depression but inbreeding coefficients were lower in the select population than in the overall population if index traits did suffer from inbreeding depression (Figures 11 and 12). Likewise, inbreeding coefficients were lower in orchard selections than in the select population when index traits suffered inbreeding depression but similar when they did not. Average inbreeding coefficients resulting from Elite-1L, Elite-PAM, and Elite-PAM-P were similar in magnitude but those resulting from Elite-6L were four times greater by the fifth generation due to the small size of the sublines. In a mainline population tree improvement program, increased volume growth had the highest priority because it results in an increase in the amount of wood reaching the mill and the market. Use of $Base_m$, which selected on both volume at age 10 and core wood specific gravity, resulted in lower gains in volume at age 10 than selection on *Vol10* while use of restricted selection indices resulted in the lowest volume gains (Figure 13). Differences in volume gains were a direct result of the genetic correlations between the wood quality traits and volume at age 10. Should the correlation between volume and specific gravity or volume and MFA prove to be lower than the estimates used here, gains from $Base_m$, $RSI(Vol/Csg)_m$, and $RSI(Vol/MFA)_m$ would resemble those produced by *Vol10*.

On the other hand, should the correlations between volume and specific gravity and between volume and MFA prove to be similar to or greater than those used here, the incorporation of wood quality traits into a mainline population will only occur if the resulting losses in volume gains can be justified by a difference in the quality of the

Figure 11. Changes in the mean inbreeding coefficient with selection on Base$_e$.
a. Mean inbreeding coefficient in the overall elite population.



b. Mean inbreeding coefficient in the elite select population.

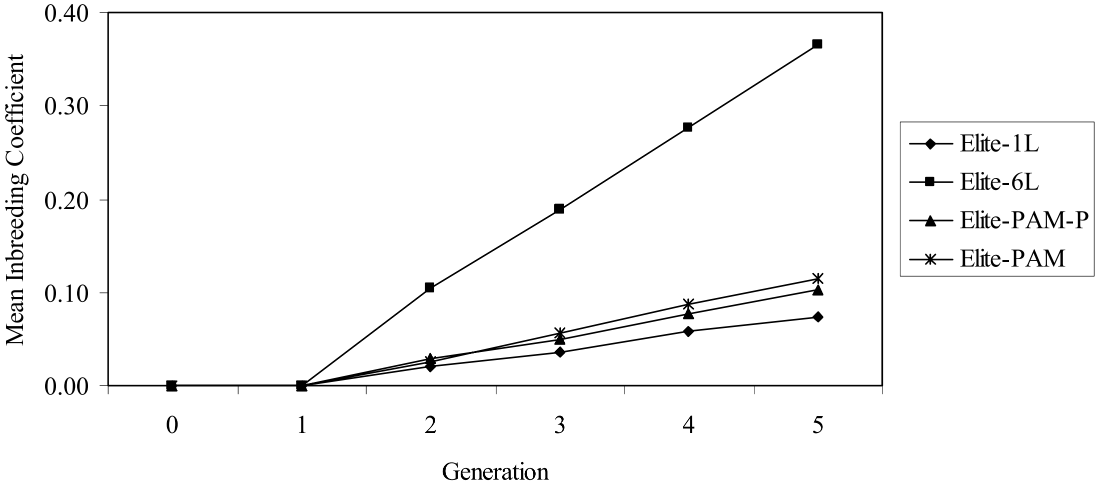
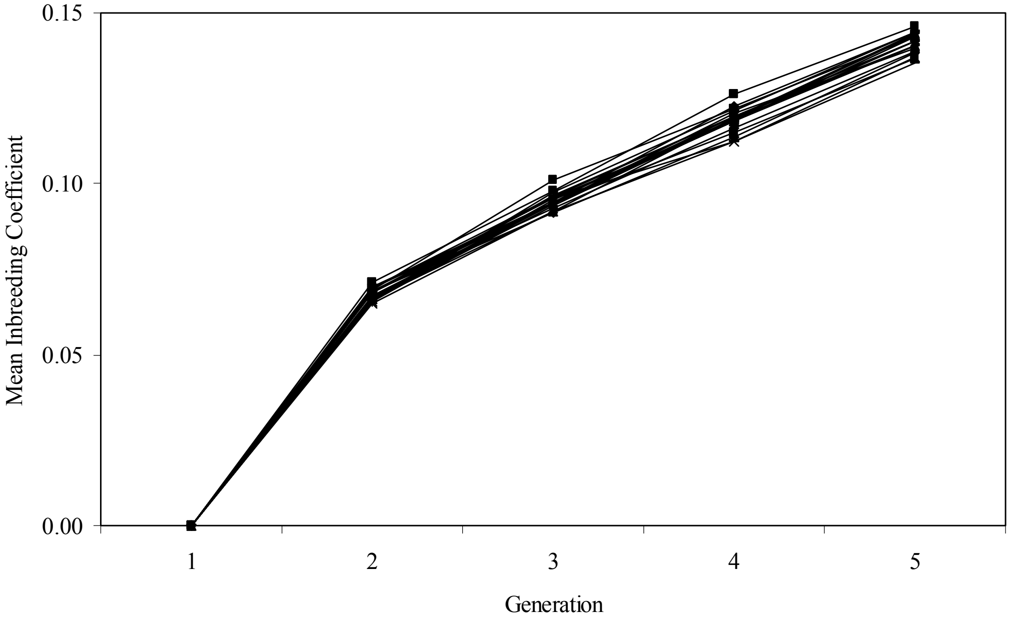


Figure 12. Changes in the mean inbreeding coefficient with selection on *Vol10* over 20 sublines.

a. Mean inbreeding coefficient in the overall mainline population.



b. Mean inbreeding coefficient in the mainline select population.

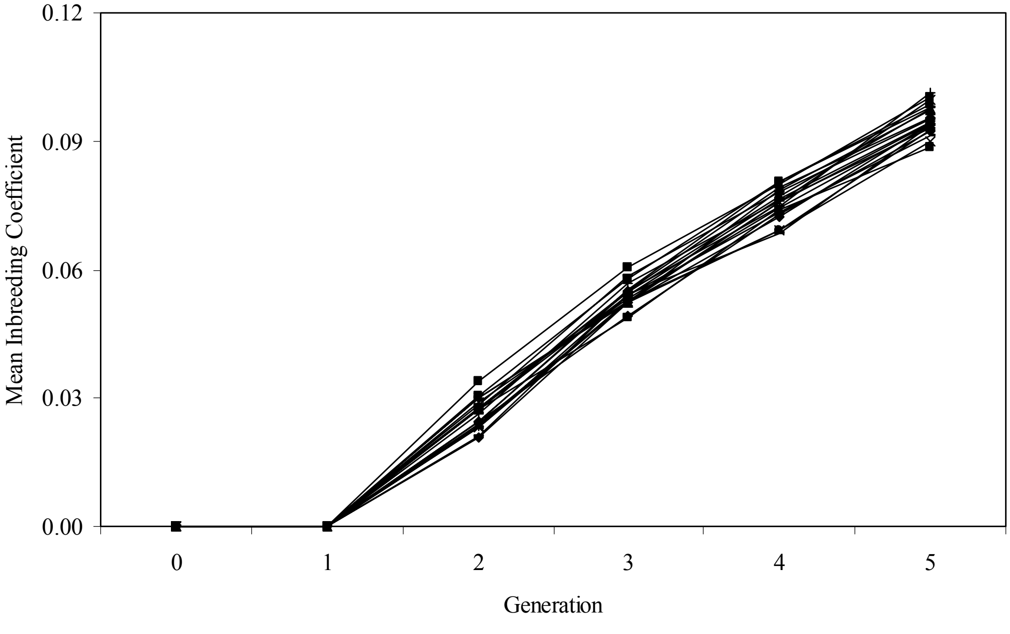
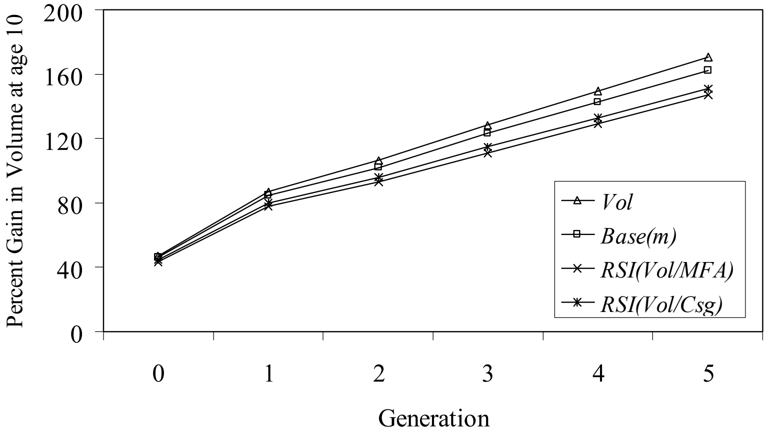
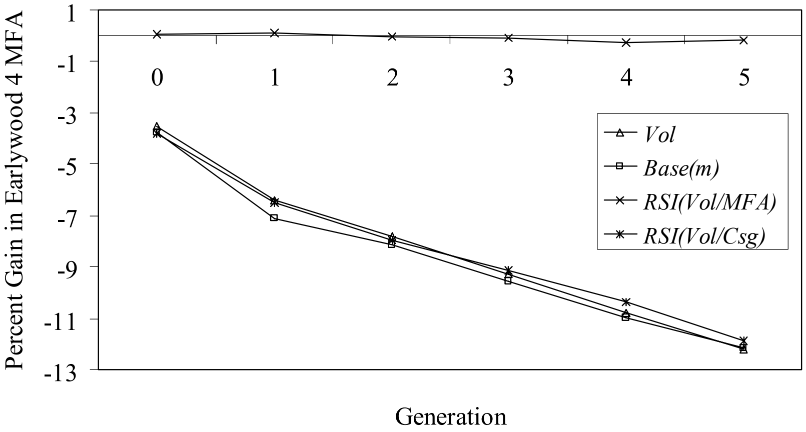


Figure 13. The effect of different selection indices on percent gains in the mainline seed orchards over 5 generations.

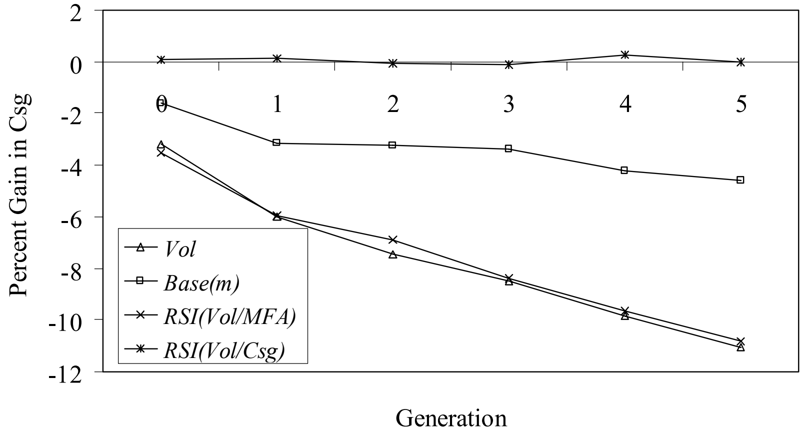
a. Gains in volume at age 10



b. Gains in earlywood 4 MFA



c. Gains in core wood specific gravity

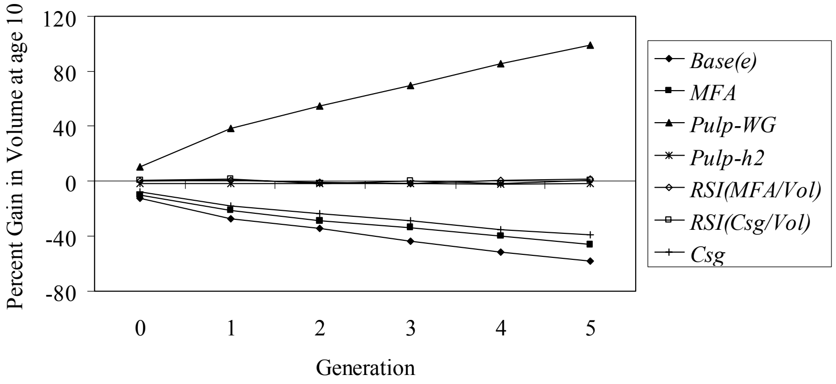


wood produced. *Vol10* resulted in losses in core wood specific gravity more than twice those produced by $Base_m$ though both produced similar increases in earlywood 4 MFA. $RSI(Vol/Csg)_m$ and $RSI(Vol/MFA)_m$ maintained their targeted wood quality trait (i.e. core wood specific gravity was maintain under $RSI(Vol/Csg)_m$ and earlywood 4 MFA was maintained under $RSI(Vol/MFA)_m$) but core wood specific gravity decreased in a similar manner when either *Vol10* or $RSI(Vol/MFA)_m$ was used and earlywood 4 MFA increased in a similar manner when either *Vol10* or $RSI(Vol/Csg)_m$ was used. Since the modulus of rupture (MOR) of wood is correlated with specific gravity (Mitchell 1964), these results suggest that the strength of the wood produced using *Vol10*, $Base_m$, and $RSI(Vol/MFA)_m$ will be lowered each generation while the strength of wood produced using $RSI(Vol/Csg)_m$ will be maintained at the same level as observed in the base population. Likewise, since longitudinal shrinkage increases almost linearly with increasing MFAs over 35° (Meylan 1968, 1972), the longitudinal shrinkage of wood produced using *Vol10*, $Base_m$, and $RSI(Vol/Csg)_m$ will be increased each generation while it will be maintained at the same level as observed in the base population when $RSI(Vol/MFA)_{m.}$ is used. If such losses in strength and/or increases in shrinkage are deemed important, a selection strategy other than selection on volume alone should be implemented.

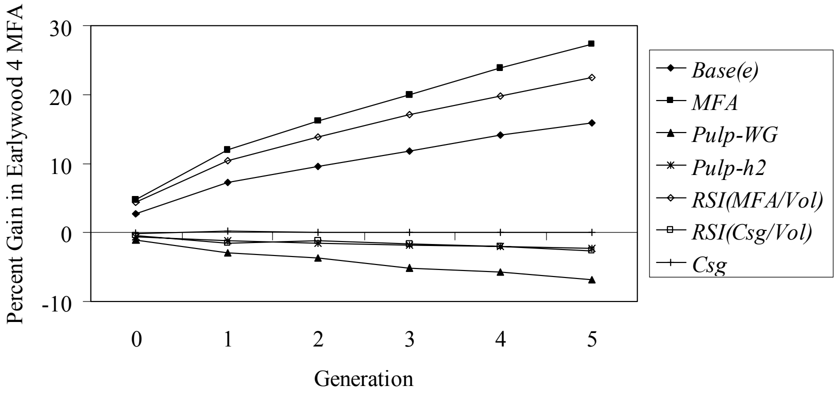
In the elite population, improving wood quality had the highest priority but the effects of each index on volume growth were still important. Selection on *MFA*, $RSI(MFA/Vol)_e$, and $Base_e$ resulted in favorable improvements (decreases) in earlywood 4 MFA while *Pulp-WG* and $RSI(Csg/Vol)_e$ produced unfavorable increases in earlywood 4 MFA each generation (Figure 14). Selection on *Csg*, $RSI(Csg/Vol)_e$, and $Base_e$

Figure 14. The effect of different selection indices on percent gains in the elite population seed orchards over 5 generations when Elite-6L is used.

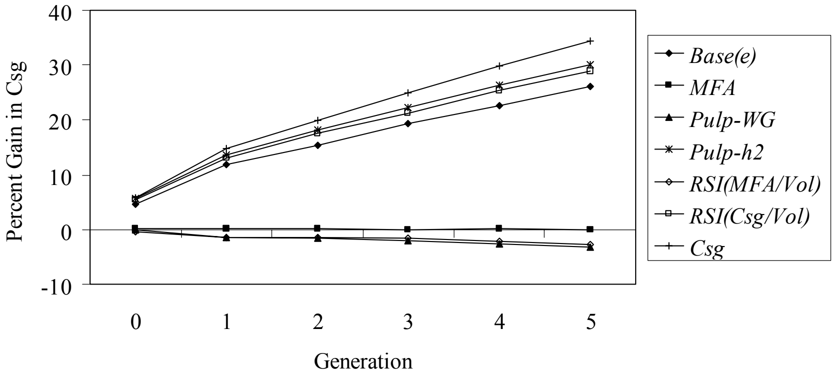
a. Gains in volume at age 10



b. Gains in earlywood 4 MFA



c. Gains in core wood specific gravity

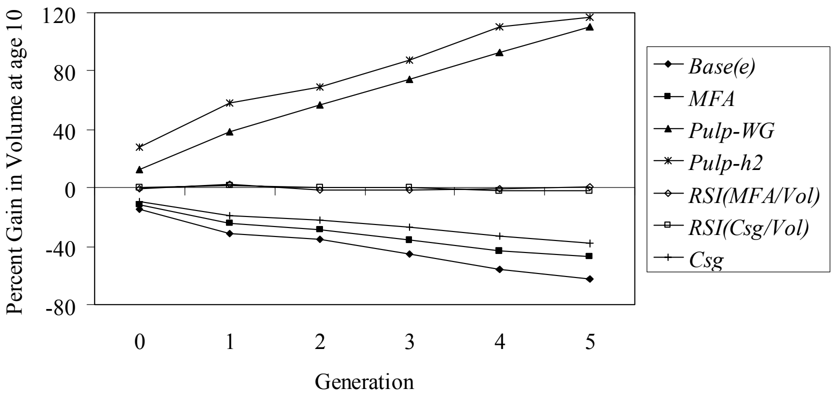


resulted in favorable improvements in core specific gravity while *RSI*(*MFA/Vol*)$_e$ and *Pulp-WG* resulted in small losses in core specific gravity each generation. Positive gains in volume at age 10 were possible with selection on *Pulp-WG* but losses occurred with selection on *Csg*, *MFA*, and *Base*$_e$. Again, these responses in volume gains were dependent on the genetic correlations with earlywood 4 MFA and with core wood specific gravity. Gains resulting from selection on *Pulp-h2* were influenced by the economic/selection weights when controlled random mating was used but were influenced by the genetic variances in the traits when PAM was used. Gains in each of the traits resulting from selection on *Pulp-h2* resembled those resulting from selection on *RSI*(*Csg/Vol*)$_e$ under controlled random mating but resembled those from selection on *Pulp-WG* under PAM (Figure 15).

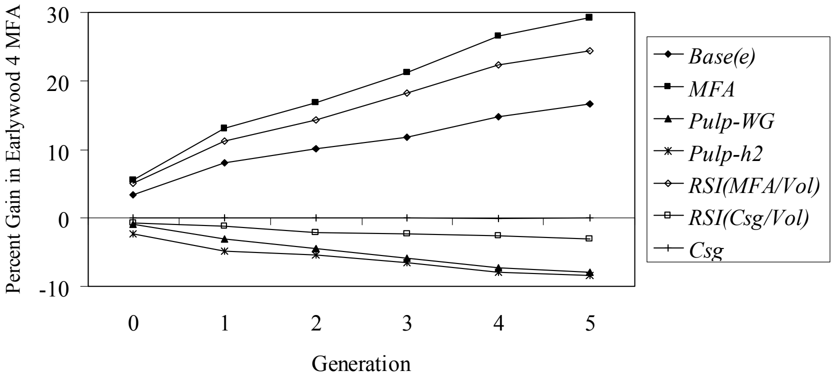
Which selection index produces the most favorable aggregate phenotypes in the seed orchard progeny depends on the economic importance of the three traits and the desired forest end products. *Pulp-WG* and, depending on breeding strategy, *Pulp-h2* did increase the volume production in seed orchard progeny at age 10 but it decreased the quality of possible end-products. The resulting solid wood produced would have less strength and greater longitudinal shrinkage due to slightly lower core wood specific gravity and greater core MFAs. Also, there would be a lower amount of dry processed pulp obtainable per unit volume (Mitchell 1964). This appears to defeat the purpose of having a specialty program to improve wood quality. However, if the aggregate phenotype is examined, the reduction in wood quality is less severe than was observed in any of the mainline simulations. Therefore, the pulp indices could serve to maintain in

Figure 15. The effect of different selection indices on percent gains in the elite population seed orchards over 5 generations when Elite-PAM is used.

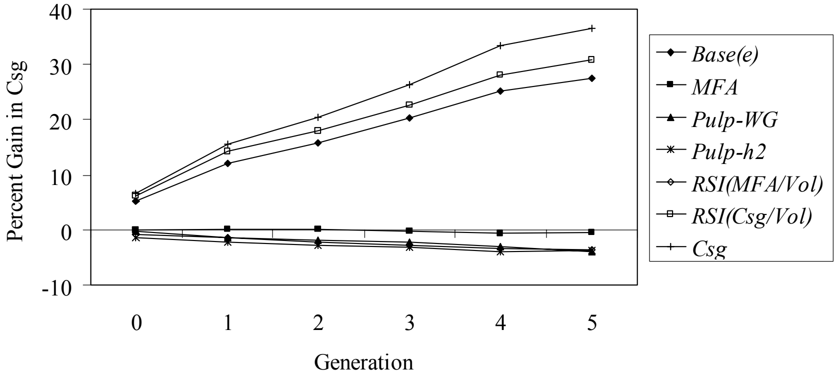
a. Gains in volume at age 10



b. Gains in earlywood 4 MFA



c. Gains in core wood specific gravity

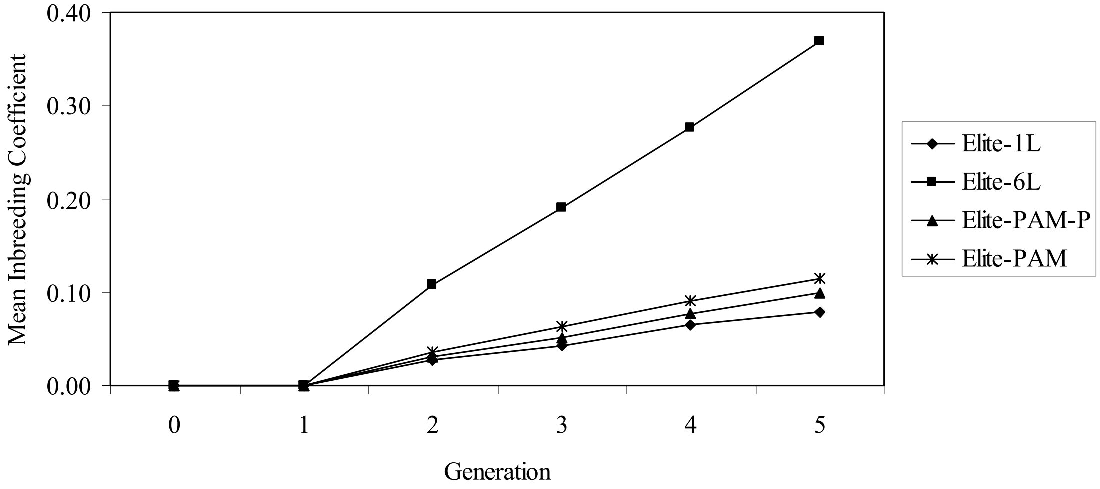


the elite population the level of wood quality existing in the mainline base population. The restricted selection indices maintained volume production at levels found in the base population while increasing wood quality by either decreasing the MFA or increasing the specific gravity. These options may be viable for a specialty breeding program because the resulting wood would exhibit less longitudinal shrinkage so less wood would be lost to defect, it would be stronger so a greater proportion may meet the specifications for structural and MSR lumber, and a greater amount of pulp would be obtained per unit volume.

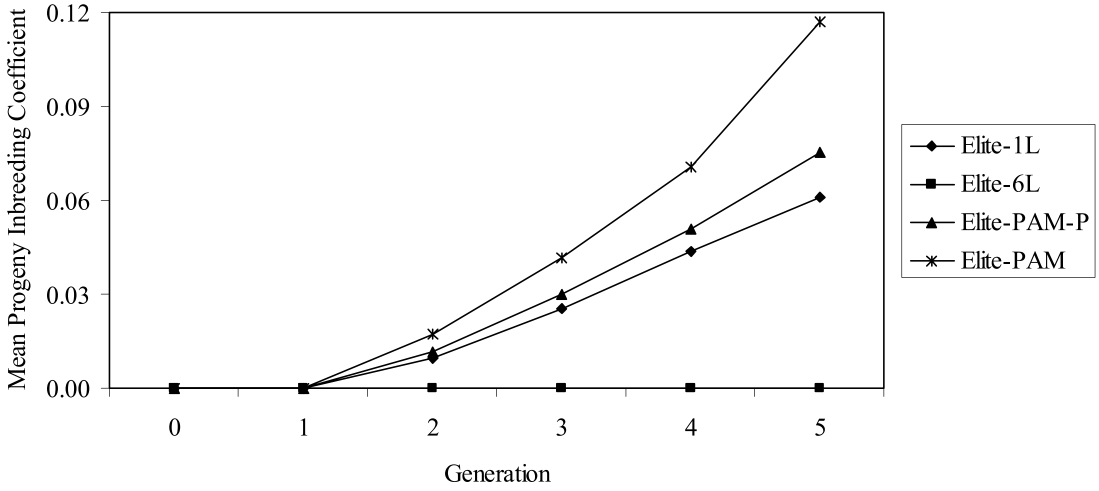
One additional factor that should be taken into consideration is the magnitude of the inbreeding coefficients in the orchard populations and orchard progeny. For example, orchard selections in Elite-6L had much greater inbreeding coefficients than those in Elite-PAM, Elite-PAM-P, or Elite-1L. However, seed orchard progeny in Elite-PAM, Elite-PAM-P and Elite-1L were inbred while those in Elite-6L were not (Figure 16). This is important because seed set in inbred conifers is lower than in outcrossed conifers (Williams and Savolainen 1996; Kuang et al. 1999). Survival of inbred progeny is also lower (Sorensen and Miles 1982; Williams and Savolainen 1996; Kuang et al. 1999).

Figure 16. Changes in the mean inbreeding coefficient of orchard selections and orchard progeny with selection on *Base*$_e$.

a. Mean inbreeding coefficient of the elite orchard selections.



b. Mean inbreeding coefficient of the elite orchard progeny.



CHAPTER IV

IMPLICATIONS FOR DIFFERENT FOREST END PRODUCTS

The benefits of any selection and breeding strategy must be weighed against the impact it has on associated costs, including not only the costs of managing traits in the tree improvement program but also the costs of milling and production operations. This is difficult in a tree improvement setting for several reasons including the length of time involved in each cycle of breeding and testing, the lack of economic data on the value of improved wood quality, the lack of coordination between field, mill, and sales objectives, and the fluctuation in price and demand for different forest end-products. Therefore, this chapter will contain only a general discussion of the costs associated with each of the selection and breeding strategies from Chapter III. The significance of changes in each of the traits in terms of value added to or lost from different forest end-products as a result of implementing each index will also be discussed. It must be emphasized that this discussion is based on results that are purely theoretical and influenced by assumptions made in previous chapters, the most important of which are that the genetic correlation between volume at age 10 and earlywood 4 MFA is positive, the genetic correlation between volume at age 10 and core wood specific gravity is negative and the genetic correlation between earlywood 4 MFA and core wood specific gravity is zero.

MAINLINE PROGRAM

There are several costs associated with the management of a mainline tree improvement program. Most are dependent on the size of the breeding and testing program (the number of individuals in each population), the number of control and polymix crosses made, and the timing of different operations (Byram 2000). Since the same breeding strategy and population sizes were used in all of the mainline simulations, these costs would be similar for each of the selection strategies compared. The one management cost that would differ between the strategies is the cost associated with the measurement of index traits. *Vol10* requires only the measurement of volume at age 10 for each tree in the program. This cost is shared by the other selection strategies as well. $Base_m$ and $RSI(Vol/CSG)_m$ require additional management costs for collecting increment cores from individuals in the breeding and testing populations and measuring their specific gravity. $RSI(Vol/MFA)_m$ also requires additional costs for collecting increment cores and for measuring their MFA. MFA costs can be significant if X-ray diffraction is used. However, near-infra-red and marker-assisted selection technology is currently in development and could make MFA measurement much less expensive.

On the production end, there are significant costs associated with establishing and managing plantations, harvesting, transportation, and mill efficiency/production (Borralho et al. 1993; Lowe et al. 1999) and benefits associated with supply quality and end-product value (Bridgwater and Smith 1997; Clark and McAlister 1998). Changes in volume, MFA and specific gravity will impact these costs and benefits differently depending on the resulting forest end-product(s).

One of the most valuable forest products is sawtimber. Increasing individual tree volume through tree improvement efforts would lead to an increase in the amount of sawtimber available for harvest and the amount of lumber recoverable from individual logs. This would decrease the costs of plantation establishment and management because it would take fewer hectares to produce the same volume of wood. However, Clark and McAlister (1998) found that the proportion of grade 1 or better lumber recovered from younger trees was lower and the proportion of grades 2 and 3 lumber was higher than that recovered from mature trees. This suggests that by improving volume and allowing trees to reach a given volume more quickly, the end-product value may decrease. Corresponding changes in MFA and/or specific gravity would also affect the quality and value of lumber from the sawtimber. Megraw et al. (1998) showed that wood with MFAs greater than 35° was linearly correlated with longitudinal shrinkage and that increased shrinkage was associated with increased average board crook. This is important because increased crook can lead to the downgrading of boards (Megraw et al. 1998) and may make some boards unsuitable for structural uses (Bendtsen and Senft 1986). In addition, Mitchell (1964) showed that small changes in specific gravity have a dramatic impact on the modulus of rupture (MOR) of southern pine clearwood and Megraw et al. (1999) showed that specific gravity and MFA together have a significant influence on the modulus of elasticity (MOE) of loblolly pine wood. MOE and MOR are important for grading lumber used in structural applications and for determining the value of machine stress-rated (MSR) lumber. The higher the stress rating of MSR lumber, the higher the retail price (International Paper, pers. comm. – all quoted prices were confidential). Based on the results of the simulations, crook may become an increasing problem if *Vol10*, $Base_m$ or $RSI(Vol/CSG)_m$ were implemented because they caused an increase in earlywood 4 MFA each generation (Table 9). As a result of increased crook, mill productivity and end-product value may decrease as a greater proportion of boards are considered unsuitable and/or lower grade. End-product value may also decrease if either *Vol10* or $RSI(Vol/MFA)_m$ were implemented because they caused a decrease in specific gravity and this could result in the production of boards with lower strength that are unsuitable for structural applications.

Another valuable forest product is veneer. In recent years, veneer ply logs have been as valuable as, if not more valuable than, sawtimber (Timber Mart-South 2001, 2002, 2003). Ply logs are used to produce plywood and laminated veneer lumber (LVL) for structural applications. Increases in volume mean a greater number of veneers can be cut per ply log. Groom et al. (2002) showed that fast-grown trees can produce twice as many veneers as conventionally-grown trees due to their increased diameter. *Vol10* produced the greatest gains in volume but this does not necessarily mean implementing *Vol10* would result in the greatest increase in veneer production or in the greatest decrease in costs. When ply logs of the same size are compared, MacPeak et al. (1987) showed that recovery of veneers was 12% lower from fast-grown trees than from conventionally-grown trees and that a lower proportion of veneers harvested from fast-grown trees were full-sheet veneers. This could translate into decreased mill efficiency and increased milling costs. Also, the quality of veneers and the quality of plywood and

Table 9. Mean (with standard deviation) volume at age 10, earlywood 4 MFA, and core wood specific gravity in the seed orchard progeny each generation.

Index	Generation	Earlywood 4 MFA[a]	Volume at age 10[b]	Core Wood Specific Gravity
Vol10	0	42 (3.5)	9.87 (2.81)	0.40 (0.03)
	1	43 (3.8)	12.56 (1.83)	0.39 (0.03)
	2	44 (3.8)	13.89 (1.77)	0.38 (0.03)
	3	45 (3.9)	15.35 (1.79)	0.38 (0.03)
	4	45 (3.9)	16.78 (1.77)	0.37 (0.04)
	5	46 (4.0)	18.19 (1.77)	0.36 (0.04)
$Base_m$	0	42 (3.5)	9.83 (2.98)	0.40 (0.03)
	1	44 (3.7)	12.43 (1.95)	0.40 (0.04)
	2	44 (3.7)	13.58 (1.92)	0.40 (0.04)
	3	45 (3.8)	14.99 (1.87)	0.40 (0.04)
	4	45 (3.8)	16.30 (1.89)	0.39 (0.04)
	5	46 (3.8)	17.62 (1.96)	0.39 (0.04)
$RSI(Vol/MFA)_m$	0	40 (3.5)	9.60 (3.02)	0.40 (0.03)
	1	40 (3.7)	11.93 (1.91)	0.39 (0.04)
	2	40 (3.5)	12.98 (1.96)	0.38 (0.03)
	3	40 (3.4)	14.18 (1.95)	0.38 (0.03)
	4	40 (3.5)	15.40 (2.03)	0.37 (0.03)
	5	40 (3.5)	16.62 (2.03)	0.37 (0.04)

Table 9. Continued.

Index	Generation	Earlywood 4 MFA	Volume at age 10	Core Wood Specific Gravity
$RSI(Vol/Csg)_m$	0	42 (3.5)	9.72 (2.96)	0.41 (0.03)
	1	43 (3.8)	12.12 (1.85)	0.41 (0.03)
	2	44 (3.8)	13.19 (1.94)	0.41 (0.03)
	3	45 (3.8)	14.44 (1.90)	0.41 (0.03)
	4	45 (3.8)	15.69 (1.99)	0.41 (0.03)
	5	46 (3.9)	16.89 (1.95)	0.41 (0.03)

[a] in degrees from vertical

[b] in cubic meters per hectare per year

LVL from fast-grown trees is lower than that of plywood and LVL from conventionally-grown trees. MacPeak et al. (1987) and Groom et al. (2002) both found that a lower proportion of the veneers produced from fast-grown trees than from conventionally-grown trees were grades A or B and a greater proportion were grade C or lower. Furthermore, several studies (e.g. MacPeak et al. 1987; Shupe et al. 1997; Groom et al. 2002) have shown that plywood and LVL produced from fast-grown trees have a lower modulus of elasticity and lower modulus of rupture than plywood and LVL from conventionally-grown trees. Economically this is important because the reduction in strength and stiffness could mean that these products would fail to meet the specifications for structural uses and therefore, would have less retail value. Shupe et al. (1997) attributes the difference in strength and stiffness to the lower specific gravity of veneers from fast-grown trees. However, it should be noted that age-related differences were not accounted for in the studies by MacPeak et al. (1987), Shupe et al. (1997), and Groom et al. (2002) and that the differences observed between fast-grown trees and conventionally grown trees could be a result of differences in the proportion of core wood in the samples. Core wood has both lower specific gravity and greater MFAs than outer wood. Use of $Vol10$ and $RSI(Vol/MFA)_m$ caused decreases in core wood specific gravity over time and therefore could result in decreased veneer product value. Increases in MFA as a result of implementing $Vol10$, $Base_m$ or $RSI(Vol/CSG)_m$ could further decrease veneer quality and value by increasing crook in the bolts and by decreasing dimensional stability in the final product. Schroeder and Phillips (1984) showed that the total volume of recoverable veneer and the average value of the veneer decreased with increasing crook and Heebink et al. (1964) reported that increased MFA was related to dimensional instability in plywood and flakeboard.

Flakeboard is one example of another type of forest-end product, composites. Trees used to produce composites usually meet some minimum diameter requirement but are too small for sawtimber or veneer production. Increases in individual tree volume may increase the proportion of trees available for use in composites, especially among trees harvested during mid-rotation thinnings. Indeed, Clark and McAlister (1998) found that chip volume and value increased with increasing tree volume.

However, this increased volume may not translate directly into increased composite production because a larger volume of fast-grown wood is required to produce boards with the same panel density as boards produced from conventionally-grown trees (Pugel et al. 1990). Unlike with other forest end-products though, increases in specific gravity are not favorable for chips and composites because the MOR of particleboards with a given board density decreases as the specific gravity of the chips increases (Kelley 1977). Pugel et al. (1990) showed that the MOR of flakeboards, particleboards and fiberboards from fast-grown trees was higher than that of boards from either mature wood or the juvenile core of mature trees. In addition to improved board strength, mats with lower specific gravity chips require less compression than mats with higher specific gravity chips to achieve the same board strength (Kelley 1977). This suggests that implementing an index like *Vol10* or $RSI(Vol/MFA)_m$, which caused an increase in volume and decrease in core wood specific gravity, may be more favorable for composite production than indices that maintain or improve specific gravity.

The last forest end product that will be discussed is pulp for paper. The effects of changes in volume, specific gravity, and MFA depend on the desired paper product. For example, core wood has opacity properties favorable for some printing grades so increasing core wood volume would be beneficial for this type of paper (Hatton and Johal 1995). However, more energy is required to refine core wood and energy requirements increase with decreasing specific gravity (Hatton and Johal 1995). Therefore, implementing *Vol10* or $RSI(Vol/MFA)_m$ may be desirable for printing grade papers but energy costs will increase each generation as a result. There will also be decreased mill efficiency because the amount of obtainable pulp from a given volume of wood decreases with decreasing specific gravity (Mitchell 1964). Mill efficiencies may further decrease if the MFA is increased as occurs with *Vol10*, *RSI*(*Vol/Csg*)$_m$ and *Base*$_m$. Increases in MFA are correlated with increased stretch in pulp sheets from unbeaten and beaten fibers (Horn and Setterholm 1988) and sheets with higher stretch are more apt to distort (Watson and Dadswell 1964). On the other hand, high MFA may be related to break strength in paper so increasing MFA may be favorable for other types of papers (Meylan and Probine 1969).

Given that mainline programs must remain flexible and address multiple end-product objectives, the results of this study suggest that the use of an index like *RSI*(*Vol/Csg*)$_m$ may be warranted in a mainline program. Slightly lower volume gains would be realized using a restriction index rather than selection for volume production alone but specific gravity would be maintained at existing levels and this means strength and stiffness characteristics would be maintained in sawtimber and the amount of pulp fiber obtainable per unit volume would not decrease.

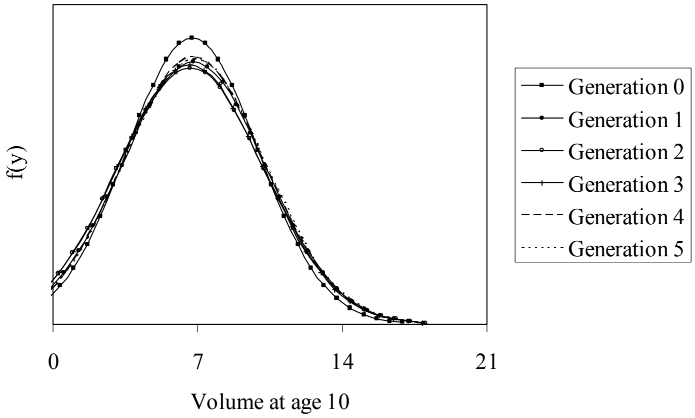
ELITE PROGRAM

In the elite population, costs dependent on the size of the elite breeding and testing program and the number of control and polymix crosses made would be similar for all of the selection strategies compared but other management costs would differ between the different selection and breeding strategies. Costs associated with the timing of operations would differ depending on breeding strategy. Elite-PAM used polymix tests to rank select individuals and assign them to crosses. This would delay generation advancement until polymix tests reach evaluation age. Elite-PAM-P used the select tree phenotypes to rank individuals rather than polymix data, which would only delay generation advancement until all of the selections were made. Elite-1L and Elite-6L, on the other hand, randomly assigned select individuals to crosses so theoretically controlled crossing for generation advancement could begin before all selections were made. Differences in timing are important because they affect the amount of time between the start of a cycle of breeding and testing and when gains are realized. As with the mainline simulations, the costs associated with measuring index traits would differ between selection strategies.

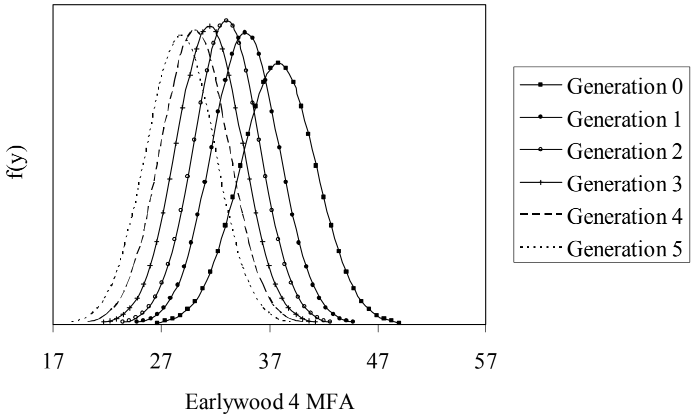
On the production end, costs and benefits would be dramatically impacted by selection and breeding for wood quality. Plantation establishment and management costs would be similar from generation to generation if $RSI(MFA/Vol)_e$ was implemented because volume and specific gravity were maintained at the levels present in the base population. The supply quality and the end-product value, on the other hand, would increase each generation as would mill efficiency. Selection for $RSI(MFA/Vol)_e$ shifted the distribution of earlywood 4 MFA values in seed orchard progeny (Figure 17). As a result, an increasing proportion of seed orchard progeny had earlywood 4 MFAs below 35° each generation. This suggests longitudinal shrinkage would become significantly less of a problem and as a result, less lumber would be downgraded due to crook. This also suggests there would be an increase in the value of recoverable veneer, increased

Figure 17. The effect of selection for the $RSI(MFA/Vol)_e$ index on the distribution of trait values in seed orchard progeny when Elite-6L is used.

a. Volume at age 10 (in cubic meters per hectare per year)



b. Earlywood 4 MFA (in degrees from vertical)



c. Core Wood Specific Gravity

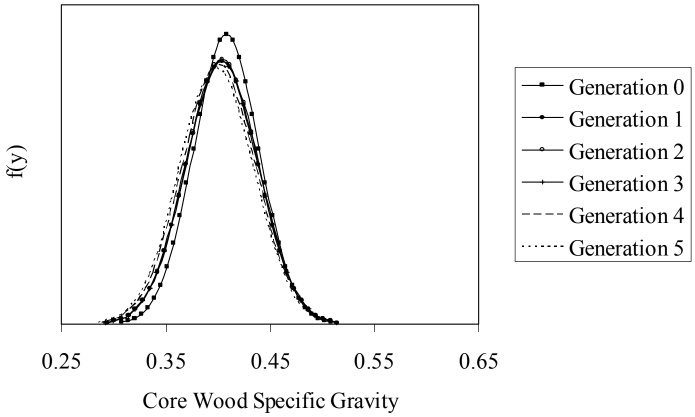
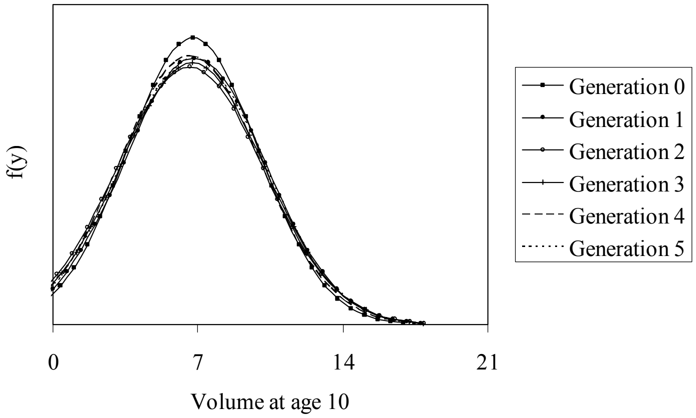
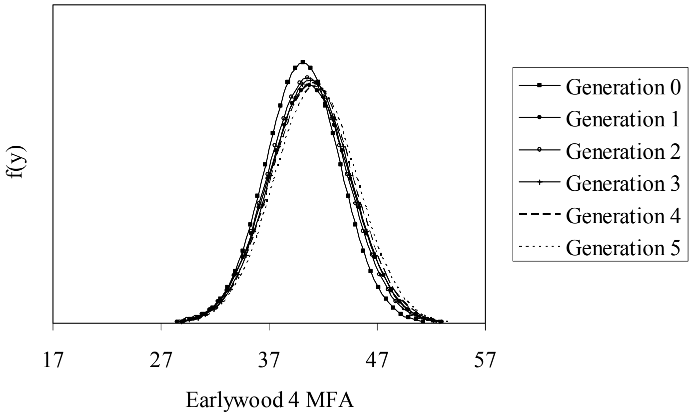


Figure 18. The effect of selection for the *RSI*(*Csg/Vol*)$_e$ index on the distribution of trait values in seed orchard progeny when Elite-6L is used.

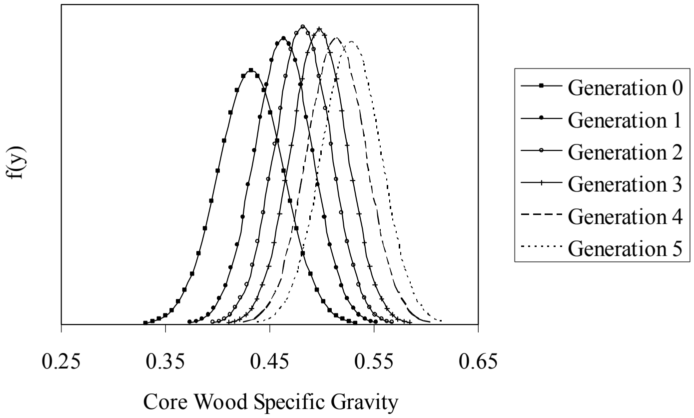
a. Volume at age 10 (in cubic meters per hectare per year)



b. Earlywood 4 MFA (in degrees from vertical)



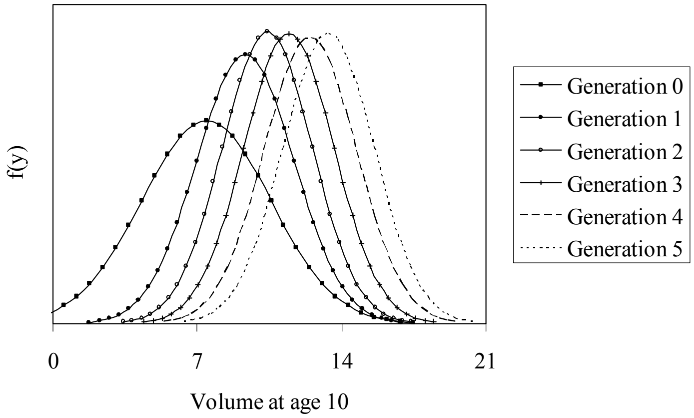
c. Core Wood Specific Gravity



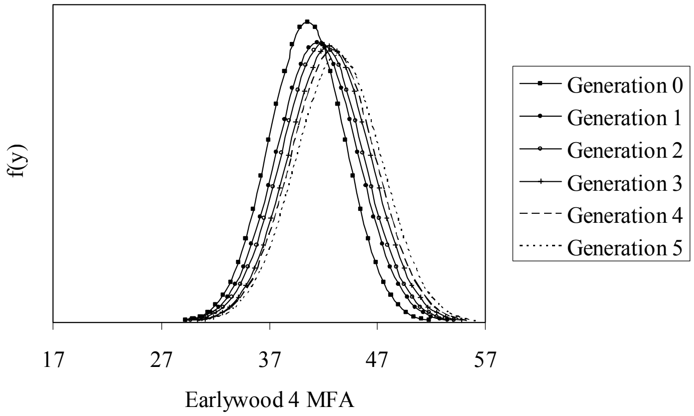
dimensional stability in plywood and flakeboard and decreased stretch in pulp sheets. If *RSI*(*Csg/Vol*)$_e$ was implemented, plantation establishment and management costs would decrease from generation to generation, even though volume did not change much, because a greater amount of pulp wood fiber would be obtainable per unit volume (Figure 18). Mill costs would also decrease due to increased pulp mill efficiency. Supply quality and end-product quality would increase because the distribution of core wood specific gravity values in seed orchard progeny would eventually resemble the outer wood specific gravity values reported in Chapter II. This means end-products would have significantly increased strength properties, which would be important for both the quality of lumber and veneers. Additional value may be realized if the increases in strength mean a greater proportion of lumber meets MSR and structural lumber standards. The one downside would be in composites where increased specific gravity would increase the amount of compression energy required to reach a given board density and would decrease the board strength. If the *Pulp-WG* index was implemented, plantation establishment and management costs would decrease because of the predicted increase in volume but there would be slight decreases in wood quality (Figure 19). This appears to defeat the purpose of having a specialty breeding program for improved wood quality but it does serve to maintain existing wood quality. If the aggregate phenotype is examined, the combined changes in both earlywood 4 MFA and core wood specific gravity are much smaller than those observed in any of the mainline population simulations. If *MFA*, *Csg*, or *Base*$_e$ were implemented, wood quality would increase but plantation establishment and management costs would be extremely high

Figure 19. The effect of selection for the *Pulp-WG* index on the distribution of trait values in seed orchard progeny when Elite-6L is used.

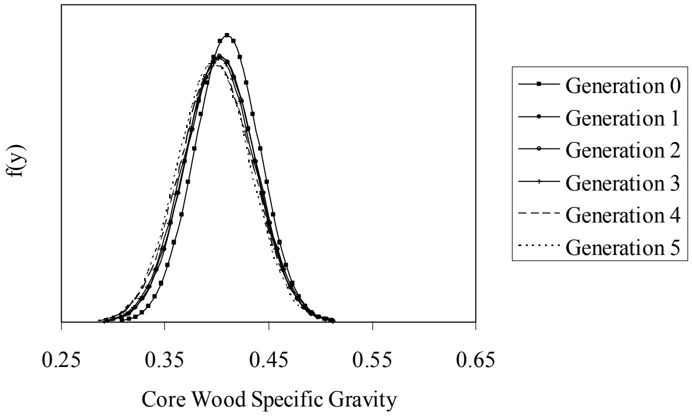
a. Volume at age 10 (in cubic meters per hectare per year)



b. Earlywood 4 MFA (in degrees from vertical)



c. Core Wood Specific Gravity



due to reduced volume growth. Selection for the *MFA*, *Csg*, and $Base_e$ indices caused such significant decreases in volume at age 10 that a proportion of the distribution of predicted volume values in seed orchard progeny was below zero. Obviously, negative volume phenotypes are not possible but this illustrates that the implementation of *MFA*, *Csg*, and $Base_e$ cannot be justified, even in an elite program where volume is not the primary focus.

Given that the goal of the elite population is to improve or maintain wood quality, the use of an index like $RSI(Csg/Vol)_e$ may be the most beneficial. Should the genetic correlations between MFA and specific gravity prove to be negative as they were at GP258, selection on Csg would indirectly improve MFA. As cost-effective methods of MFA measurement are developed, a three-way restricted index where improvements in both MFA and Csg are attempted while holding volume constant may also be worth investigating.

CHAPTER V

SUMMARY AND CONCLUSIONS

This study examined the genetic influences on microfibril angle (MFA) and its relationship with specific gravity, height, diameter and volume. It was found that significant additive genetic and dominance factors do influence MFA in loblolly pine and that MFA has a low to moderate heritability. This suggests that MFA could be used as a selection criterion in a tree improvement program. However, additional work is still necessary to understand the implications of incorporating MFA in a selection strategy. For example, more families need to be examined to increase the reliability of the results. Many of the genetic correlations were low and had extremely large estimated standard errors, which caused them to be non-significant. Sewell et al. (2000) identified QTLs for specific gravity and for MFA that mapped less than 10-20 cM apart, suggesting a genetic relationship between the two traits may exist. With additional sampling, correlations, such as those between MFA and specific gravity, may prove to be significant. Also, the heritability of MFA and its relationship with specific gravity and growth needs to be examined throughout the tree, not just at DBH. Megraw (1985, p. 52) noted that the core wood MFA in a given ring can be 15% greater at the base of the tree than in the same ring position further up the bole and that as a result, the relationship between specific gravity and MFA is different in the base than in the rest of the bole (p. 60). Furthermore, the experiment needs to be replicated across sites so that environmental influences and genetic by environmental interactions can be identified. Specific gravity has been shown to vary by site (Byram and Lowe 1988) and express a genotype x environment interaction (Jett et al. 1991). The presence of statistically significant block and SCA x block effects within locations suggests that there may also be significant environmental and genetic x environmental effects on MFA as well.

Additional research is also needed to determine the proper economic weights for wood quality traits. Assumptions were made regarding the economic importance of traits in several indices. With *Pulp-h2*, the economic weights determined which variables were most influential in determining correlated responses under controlled random mating. Determining accurate economic weights will require a better understanding of how changes in wood quality traits affect end-product quality and the profitability of any selection strategy. For example, Megraw et al. (1998) showed that MFAs greater than 35° were linearly correlated with the longitudinal shrinkage of small wood strips one ring in width and that the amount of crook and the lumber grade was related to the longitudinal shrinkage of the board. Is it safe to generalize that improving the MFA in one location (i.e. within a portion of a ring or in several rings at DBH) in the bole will improve MFAs throughout the tree and thus boards cut from a tree with improved MFAs will have less shrinkage, crook and/or degrade? The strength of the genetic correlations between values within the core section suggest that selection for improvement in one ring will cause favorable responses throughout the core wood but the large standard errors associated with genetic correlations between core and outer wood measurements make it unclear whether outer wood MFAs would respond to early selection. Again, these correlations are only applicable at DBH. The genetic correlations between measurements at DBH and measurements at different heights in the tree are unknown.

Additional assumptions should be tested as well. For example, it was assumed in the simulations that neither specific gravity nor earlywood 4 MFA suffered inbreeding depression. Very little work has been reported on the effect inbreeding has on wood quality in conifers (Williams and Savolainen 1996). Inbreeding depression for specific gravity has been studied in radiata pine and Norway spruce (*Picea abies* L.) but not in loblolly. The effect of inbreeding on MFA has not been studied in any species.

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APPENDIX I

PREDICTION OF CORRELATIONS

Stochastic simulation uses random normal deviates to generate variances about the mean. When more than one trait is involved, correlated standard normal deviates must be used to account for correlations between traits. This is not a problem if a population is in Hardy-Weinberg equilibrium because the correlations are the same from generation to generation. However, if a population is limited in size, is under selection, and/or is suffering from inbreeding depression as occurs in a tree breeding program, the correlations between traits will not be the same from one generation to the next. In order to predict how the correlations change, it was necessary to examine how the additive genetic (co)variances and the dominance (co)variances were affected by departures from Hardy-Weinberg equilibrium.

Villanueva and Kennedy (1990) showed that the additive genetic variances and covariances of progeny produced following the first generation of selection could be estimated from:

$$\hat{\sigma}_{A_iA_j(1)} = \hat{\sigma}_{A_iA_j(0)} - \frac{1}{2}\hat{h}^2_{1(0)}\,\hat{r}_{1i(0)}\,\hat{r}_{1j(0)}\,k\,\hat{\sigma}_{A_i(0)}\,\hat{\sigma}_{A_j(0)} \qquad [A1]$$

where $\sigma_{A_iA_j(1)}$ and $\sigma_{A_iA_j(0)}$ are the additive genetic (co)variances between the ith and jth trait in the progeny and base population (prior to selection), respectively; $h^2_{1(0)}$ is the heritability of the index (or the trait selected on) in the base population; $r_{1n(0)}$ is the additive genetic correlation between the index and the nth trait; k equals i(i-x) where i is the mean deviation of the selected group in terms of standard deviations from the population mean, and x is the truncation point in terms of standard deviations from the population mean; and $\sigma_{A_n(0)}$ is the standard deviation of the nth trait in the base generation. This translates to:

$$\hat{\sigma}_{A_iA_j(1)} = \hat{\sigma}_{A_iA_j(0)} + \frac{1}{2}(\hat{\sigma}_{A_iA_j(0)_{sel}} - \hat{\sigma}_{A_iA_j(0)}) \qquad [A2]$$

where $\sigma_{A_iA_j(0)_{sel}}$ is the additive genetic (co)variance in the select population.

Bulmer (1980, pp. 126-128) and Gianola (1982) showed that the additive genetic variances and covariances following the first generation of positive assortative mating (PAM) with no selection could be estimated from:

$$\hat{\sigma}_{A_iA_j(1)} = \hat{\sigma}_{A_iA_j(0)}(1 + \frac{1}{2}\hat{r}_m \hat{h}^2_{1(0)} \hat{r}_{1i(0)} \hat{r}_{1j(0)}) \qquad [A3]$$

where r_m is the correlation between mates.

By combining [A2] and [A3], the additive genetic (co)variances in the first generation following selection and PAM can be estimated as:

$$\hat{\sigma}_{A_iA_j(1)} = \hat{\sigma}_{A_iA_j(0)}[1+\frac{1}{2}(\hat{\sigma}_{A_iA_j(0)_{sel}} - \hat{\sigma}_{A_iA_j(0)}) + \frac{1}{2}\hat{r}_m \hat{h}^2_{1(0)} \hat{r}_{1i(0)} \hat{r}_{1j(0)}]\,. \quad [A4]$$

In generations two and higher, a portion of the variance lost due to selection and mating is recaptured due to recombination. Therefore, the additive genetic (co)variances after selection and mating in generation (t+1) become (Villanueva and Kennedy 1990):

$$\hat{\sigma}_{A_iA_j(t+1)} = \hat{\sigma}_{A_iA_j(t)} - \frac{1}{2}\hat{h}^2_{1(t)} \hat{r}_{1i(t)} \hat{r}_{1j(t)} k \hat{\sigma}_{A_i(t)} \hat{\sigma}_{A_j(t)} + \frac{1}{2}(\hat{\sigma}_{A_iA_j(0)} - \hat{\sigma}_{A_iA_j(t)})\,. \quad [A5]$$

The additive genetic (co)variances following PAM in generation (t+1) become (Bulmer 1980, pp. 126-128; Gianola 1982):

$$\hat{\sigma}_{A_iA_j(t+1)} = \frac{1}{2}\hat{\sigma}_{A_iA_j(t)}(1+\hat{r}_m \hat{h}^2_{1(t)} \hat{r}_{1i(t)} \hat{r}_{1j(t)}) + \frac{1}{2}\hat{\sigma}_{A_iA_j(0)}\,. \quad [A6]$$

Combining [A5] and [A6] yields the following equation for the additive genetic (co)variances in generation (t+1):

$$\hat{\sigma}_{A_iA_j(t+1)} = \hat{\sigma}_{A_iA_j(t)}[1+\frac{1}{2}(\hat{\sigma}_{A_iA_j(t-1)_{sel}} - \hat{\sigma}_{A_iA_j(t)}) + \frac{1}{2}\hat{r}_m \hat{h}^2_{1(t)} \hat{r}_{1i(t)} \hat{r}_{1j(t)}] + \frac{1}{2}(\hat{\sigma}_{A_iA_j(0)} - \hat{\sigma}_{A_iA_j(t)})\,.$$

[A7]

In populations with a limited size, inbreeding causes a decrease in the amount of total genetic variation within a subline. For traits with a large amount of dominance variance, the effect inbreeding has on the components of genetic variance is dependant on allele frequencies in the base population and cannot be predicted for a parameter based model (Falconer and Mackay 1996, pp. 266-267). However, for traits expressing little to no dominance variance, using one minus the average inbreeding coefficient of the progeny population as a correction factor will give a general approximation of the effect of inbreeding on the genetic variance. Therefore, for simplicity, it was assumed that there would be little dominance variance in any of the traits input and that the additive genetic and dominance variances could be adjusted accordingly to account for inbreeding in the progeny:

$$\hat{\sigma}_{A_iA_j(t+1)} = (1-F)\{\hat{\sigma}_{A_iA_j(t)}[1+\frac{1}{2}(\hat{\sigma}_{A_iA_j(t-1)_{sel}} - \hat{\sigma}_{A_iA_j(t)}) + \frac{1}{2}\hat{r}_m \hat{h}^2_{1(t)} \hat{r}_{1i(t)} \hat{r}_{1j(t)}]$$

$$+\frac{1}{2}(\hat{\sigma}_{A_iA_j(0)} - \hat{\sigma}_{A_iA_j(t)})\} \qquad [A8]$$

$$\hat{\sigma}_{D_iD_j(t+1)} = (1-F)\hat{\sigma}_{D_iD_j(t)}. \qquad [A9]$$

where F is the average inbreeding coefficient in the progeny population. For traits with a large amount of dominance variance, this model will be less reliable.

Correlations in the progeny population were estimated from the following equation:

$$r = \frac{\hat{\sigma}_{ij}}{\sqrt{\hat{\sigma}_i^2 \hat{\sigma}_j^2}} \quad [A10]$$

where σ_{ij} is the predicted covariance of the ith and jth trait in the progeny population, and σ^2_i and σ^2_j are the predicted variances of the ith and jth traits, respectively. Then, the correlations were used to calculate correlated standard normal deviates for the different effects.

APPENDIX II

SELECT SIMULATION RESULTS

Table 10. Results from the elite population simulations.

Elite Population Index	Population	Gen.	Var.	Breeding Strategy	Ew 4 MFA Mean(SD)[1]	Vol 10 Mean(SD)[1]	Csg Mean(SD)[1]
Base(e)	Overall	1	Phen.	1L	40.00(0.35)	6.73(0.26)	0.41(0.00)
				6L	40.00(0.34)	6.73(0.27)	0.41(0.00)
				PAM-P	40.00(0.44)	6.73(0.27)	0.41(0.00)
				PAM	40.00(0.44)	6.73(0.27)	0.41(0.00)
	Overall	2	Phen.	1L	37.46(0.70)	5.24(0.48)	0.44(0.01)
				6L	37.62(0.52)	4.87(0.45)	0.44(0.01)
				PAM-P	37.33(0.73)	5.16(0.49)	0.44(0.01)
				PAM	37.24(0.74)	5.09(0.48)	0.45(0.01)
	Overall	3	Phen.	1L	35.96(0.86)	4.30(0.58)	0.46(0.01)
				6L	36.16(0.64)	3.69(0.58)	0.46(0.01)
				PAM-P	35.73(0.95)	4.27(0.68)	0.46(0.01)
				PAM	35.44(1.00)	4.07(0.71)	0.47(0.01)
	Overall	4	Phen.	1L	34.68(0.99)	3.44(0.74)	0.48(0.01)
				6L	34.94(0.69)	2.57(0.67)	0.48(0.01)
				PAM-P	34.40(1.13)	3.43(0.82)	0.48(0.01)
				PAM	34.10(1.17)	3.17(0.85)	0.49(0.01)
	Overall	5	Phen.	1L	33.43(1.08)	2.68(0.85)	0.50(0.01)
				6L	33.82(0.72)	1.41(0.73)	0.49(0.01)
				PAM-P	33.07(1.33)	2.63(0.92)	0.50(0.01)
				PAM	32.66(1.38)	2.31(1.02)	0.51(0.01)
	Orchard	0	% Gain	1L	3.44(1.68)	-14.94(7.32)	5.21(1.70)
				6L	2.74(1.41)	-12.90(7.99)	4.59(1.62)
				PAM-P	3.27(1.49)	-14.39(7.70)	5.23(1.69)
				PAM	3.27(1.49)	-14.39(7.70)	5.23(1.69)
	Orchard	1	% Gain	1L	7.39(2.05)	-29.75(9.92)	12.12(2.05)
				6L	7.21(1.61)	-27.28(10.14)	11.84(2.21)
				PAM-P	7.94(2.37)	-30.26(12.19)	11.86(2.51)
				PAM	8.01(2.08)	-31.20(11.35)	12.09(2.53)
	Orchard	2	% Gain	1L	9.20(2.06)	-38.32(11.12)	14.88(2.03)
				6L	9.65(1.76)	-34.46(10.77)	15.35(2.27)
				PAM-P	9.65(2.20)	-35.60(11.50)	15.06(2.50)
				PAM	10.08(2.13)	-35.28(11.43)	15.74(2.62)
	Orchard	3	% Gain	1L	11.27(2.11)	-45.97(12.32)	18.23(2.43)
				6L	11.87(1.80)	-44.24(11.67)	19.20(2.34)
				PAM-P	11.71(2.44)	-44.19(12.36)	18.72(2.63)
				PAM	11.86(2.41)	-45.14(13.82)	20.24(2.68)
	Orchard	4	% Gain	1L	13.43(2.44)	-53.27(13.46)	22.60(2.63)
				6L	14.18(1.58)	-51.78(13.46)	22.62(2.40)
				PAM-P	14.00(2.72)	-52.53(13.14)	22.76(2.86)
				PAM	14.85(2.86)	-55.95(15.32)	25.10(3.11)
	Orchard	5	% Gain	1L	16.15(2.52)	-63.92(14.57)	26.37(2.98)
				6L	15.94(1.82)	-58.24(13.49)	26.15(2.53)
				PAM-P	16.64(3.23)	-62.58(14.90)	27.05(2.93)
				PAM	16.60(3.32)	-61.99(16.54)	27.56(3.26)

Table 10. Continued.

Elite Population Index	Population	Gen.	Var.	Breeding Strategy	Ew 4 MFA Mean(SD)	Vol 10 Mean(SD)	Csg Mean(SD)
MFA	Overall	1	Phen.	1L	40.00(0.35)	6.73(0.26)	0.41(0.00)
				6L	40.00(0.34)	6.73(0.27)	0.41(0.00)
				PAM-P	40.00(0.44)	6.73(0.27)	0.41(0.00)
				PAM	40.00(0.44)	6.73(0.27)	0.41(0.00)
	Overall	2	Phen.	1L	35.85(0.48)	5.49(0.51)	0.41(0.01)
				6L	36.16(0.46)	5.19(0.43)	0.41(0.01)
				PAM-P	35.71(0.56)	5.45(0.43)	0.41(0.01)
				PAM	35.50(0.56)	5.40(0.43)	0.41(0.01)
	Overall	3	Phen.	1L	33.11(0.64)	4.76(0.68)	0.41(0.01)
				6L	33.69(0.53)	4.09(0.51)	0.41(0.01)
				PAM-P	32.95(0.65)	4.65(0.65)	0.41(0.01)
				PAM	32.43(0.65)	4.61(0.66)	0.41(0.01)
	Overall	4	Phen.	1L	30.61(0.67)	4.10(0.81)	0.41(0.01)
				6L	31.57(0.58)	3.08(0.56)	0.41(0.01)
				PAM-P	30.39(0.69)	3.97(0.86)	0.41(0.01)
				PAM	29.64(0.71)	3.92(0.87)	0.41(0.01)
	Overall	5	Phen.	1L	28.18(0.72)	3.45(0.90)	0.41(0.01)
				6L	29.60(0.60)	2.09(0.61)	0.41(0.01)
				PAM-P	27.90(0.80)	3.28(1.02)	0.41(0.01)
				PAM	26.92(0.80)	3.16(1.07)	0.41(0.01)
	Orchard	0	% Gain	1L	5.57(1.27)	-11.62(7.65)	0.14(2.12)
				6L	4.77(1.13)	-10.12(7.74)	0.08(1.59)
				PAM-P	5.49(1.23)	-11.39(8.27)	-0.13(2.11)
				PAM	5.49(1.23)	-11.39(8.27)	-0.13(2.11)
	Orchard	1	% Gain	1L	12.68(1.23)	-24.99(10.64)	0.03(2.71)
				6L	12.02(1.32)	-21.25(11.50)	0.19(2.50)
				PAM-P	12.92(1.35)	-24.95(10.35)	0.25(2.87)
				PAM	13.09(1.38)	-24.18(9.66)	0.21(2.84)
	Orchard	2	% Gain	1L	15.62(1.64)	-30.31(11.76)	-0.19(2.91)
				6L	16.15(1.36)	-28.76(10.57)	0.16(2.49)
				PAM-P	15.92(1.56)	-29.79(11.36)	-0.19(2.99)
				PAM	16.75(1.59)	-28.54(11.18)	0.11(3.31)
	Orchard	3	% Gain	1L	19.69(1.53)	-35.66(13.85)	0.12(2.89)
				6L	19.99(1.25)	-33.49(10.62)	-0.13(3.09)
				PAM-P	19.96(1.69)	-35.05(14.04)	0.03(3.22)
				PAM	21.18(1.66)	-35.66(14.35)	-0.19(2.92)
	Orchard	4	% Gain	1L	24.09(1.61)	-43.79(13.78)	0.03(3.24)
				6L	23.89(1.23)	-39.92(10.68)	0.13(3.30)
				PAM-P	24.48(1.82)	-42.83(15.19)	0.04(3.33)
				PAM	26.52(1.75)	-43.55(16.39)	-0.57(3.57)
	Orchard	5	% Gain	1L	29.12(1.80)	-52.32(16.31)	-0.08(4.07)
				6L	27.29(1.35)	-46.32(11.73)	0.04(2.98)
				PAM-P	29.45(1.92)	-51.13(18.19)	0.05(3.69)
				PAM	29.25(1.92)	-46.64(16.91)	-0.52(3.98)
Pulp-WG	Overall	1	Phen.	1L	40.00(0.35)	6.73(0.26)	0.41(0.00)
				6L	39.97(0.42)	6.72(0.29)	0.41(0.00)
				PAM-P	40.00(0.44)	6.73(0.27)	0.41(0.00)
				PAM	40.00(0.44)	6.73(0.27)	0.41(0.00)

Table 10. Continued.

Elite Population Index	Population	Gen.	Var.	Breeding Strategy	Ew 4 MFA Mean(SD)	Vol 10 Mean(SD)	Csg Mean(SD)
Pulp-WG	Overall	2	Phen.	1L	41.24(0.67)	8.83(0.41)	0.41(0.01)
				6L	41.13(0.70)	8.20(0.36)	0.41(0.01)
				PAM-P	41.31(0.57)	8.83(0.41)	0.41(0.01)
				PAM	41.31(0.60)	8.86(0.40)	0.41(0.01)
	Overall	3	Phen.	1L	42.10(0.87)	10.22(0.47)	0.41(0.01)
				6L	41.76(0.80)	9.02(0.45)	0.41(0.01)
				PAM-P	42.26(0.94)	10.25(0.49)	0.41(0.01)
				PAM	42.20(0.90)	10.24(0.50)	0.41(0.01)
	Overall	4	Phen.	1L	42.92(1.13)	11.45(0.54)	0.41(0.01)
				6L	42.31(0.91)	9.61(0.44)	0.41(0.01)
				PAM-P	43.11(1.15)	11.48(0.54)	0.41(0.01)
				PAM	42.99(1.06)	11.50(0.53)	0.41(0.01)
	Overall	5	Phen.	1L	43.63(1.22)	12.62(0.54)	0.41(0.01)
				6L	42.83(0.94)	10.13(0.47)	0.41(0.01)
				PAM-P	43.74(1.28)	12.68(0.55)	0.41(0.01)
				PAM	43.65(1.11)	12.67(0.55)	0.41(0.01)
	Orchard	0	% Gain	1L	-1.08(1.59)	11.65(7.67)	-0.41(1.90)
				6L	-1.03(1.67)	10.58(7.90)	0.03(2.12)
				PAM-P	-0.95(1.71)	12.94(7.82)	-0.26(2.35)
				PAM	-0.95(1.71)	12.94(7.82)	-0.26(2.35)
	Orchard	1	% Gain	1L	-3.18(2.11)	38.96(10.44)	-1.58(2.39)
				6L	-2.86(2.49)	38.60(9.01)	-1.48(2.46)
				PAM-P	3.30(2.06)	38.36(9.13)	-1.04(2.25)
				PAM	-3.10(2.02)	38.50(9.28)	-1.40(2.53)
	Orchard	2	% Gain	1L	-4.33(2.22)	57.47(9.71)	-2.30(2.48)
				6L	-3.80(2.19)	54.68(9.19)	-1.68(2.53)
				PAM-P	-4.47(2.27)	56.60(9.71)	-1.74(2.64)
				PAM	-4.50(2.21)	56.52(9.60)	-1.72(2.81)
	Orchard	3	% Gain	1L	-5.76(2.24)	74.31(9.69)	-2.93(2.57)
				6L	-5.09(2.39)	70.17(8.29)	-2.03(2.48)
				PAM-P	-5.80(2.50)	72.21(9.95)	-2.42(2.92)
				PAM	-5.96(2.27)	74.13(9.71)	-2.28(3.09)
	Orchard	4	% Gain	1L	-7.10(2.77)	92.36(9.88)	-3.43(3.01)
				6L	-5.81(2.30)	85.67(9.32)	-2.56(2.87)
				PAM-P	-7.30(2.62)	93.53(8.97)	-3.29(3.13)
				PAM	-7.30(2.45)	93.08(9.99)	-3.05(3.27)
	Orchard	5	% Gain	1L	-8.83(2.80)	112.73(9.66)	-4.44(3.09)
				6L	-6.81(2.02)	98.76(9.39)	-3.12(2.54)
				PAM-P	-8.58(3.02)	111.84(10.21)	-3.51(3.19)
				PAM	-8.02(2.81)	110.39(11.47)	-3.95(4.11)
Pulp-h2	Overall	1	Phen.	1L	40.00(0.35)	6.73(0.26)	0.41(0.00)
				6L	40.00(0.34)	6.73(0.27)	0.41(0.00)
				PAM-P	40.00(0.44)	6.73(0.27)	0.41(0.00)
				PAM	40.00(0.44)	6.73(0.27)	0.41(0.00)
	Overall	2	Phen.	1L	40.49(0.75)	6.57(0.55)	0.45(0.01)
				6L	40.49(0.51)	6.10(0.49)	0.44(0.01)
				PAM-P	41.34(0.58)	8.79(0.42)	0.41(0.01)
				PAM	41.50(0.67)	9.00(0.41)	0.40(0.01)

Table 10. Continued.

Elite Population Index	Population	Gen.	Var.	Breeding Strategy	Ew 4 MFA Mean(SD)	Vol 10 Mean(SD)	Csg Mean(SD)
Pulp-h2	Overall	3	Phen.	1L	40.77(1.12)	6.46(0.72)	0.47(0.01)
				6L	40.72(0.72)	5.52(0.63)	0.47(0.01)
				PAM-P	42.26(0.91)	10.14(0.50)	0.41(0.01)
				PAM	42.46(1.01)	10.58(0.46)	0.40(0.01)
	Overall	4	Phen.	1L	40.94(1.36)	6.23(0.84)	0.49(0.01)
				6L	40.85(0.85)	4.97(0.70)	0.49(0.01)
				PAM-P	43.07(1.14)	11.34(0.54)	0.41(0.01)
				PAM	43.25(1.26)	12.03(0.56)	0.40(0.01)
	Overall	5	Phen.	1L	41.16(1.58)	6.08(0.98)	0.51(0.01)
				6L	40.94(0.95)	4.37(0.75)	0.50(0.01)
				PAM-P	43.78(1.22)	12.49(0.62)	0.41(0.01)
				PAM	43.98(1.48)	13.38(0.60)	0.40(0.02)
	Orchard	0	% Gain	1L	-0.66(1.72)	-2.45(8.00)	6.35(1.48)
				6L	-0.62(1.44)	-1.71(8.96)	5.57(1.34)
				PAM-P	-2.39(1.72)	27.40(6.12)	-0.55(2.13)
				PAM	-2.33(1.71)	28.02(5.91)	-1.35(2.25)
	Orchard	1	% Gain	1L	-1.33(2.60)	-2.39(11.53)	14.07(1.75)
				6L	-1.14(2.27)	-1.75(13.36)	13.68(1.94)
				PAM-P	-4.69(1.94)	55.83(7.77)	-0.76(3.02)
				PAM	-4.85(2.11)	58.17(7.64)	-2.12(2.96)
	Orchard	2	% Gain	1L	-1.49(2.41)	-3.32(11.61)	17.29(1.89)
				6L	-1.50(2.16)	-1.74(13.11)	18.03(1.80)
				PAM-P	-5.25(1.92)	63.48(8.95)	-0.99(2.76)
				PAM	-5.51(2.42)	69.07(9.29)	-2.73(2.77)
	Orchard	3	% Gain	1L	-1.76(3.00)	-4.08(12.49)	21.22(1.76)
				6L	-1.89(2.23)	-1.80(13.29)	22.20(1.92)
				PAM-P	-6.36(2.59)	77.84(9.15)	-1.08(2.85)
				PAM	-6.59(2.56)	87.40(9.63)	-3.18(3.36)
	Orchard	4	% Gain	1L	-2.30(3.50)	-4.89(16.27)	26.09(2.18)
				6L	-2.00(2.23)	-2.29(12.49)	26.31(1.80)
				PAM-P	-7.53(2.36)	95.35(9.98)	-1.39(3.31)
				PAM	-7.95(2.92)	110.53(10.59)	-3.94(3.81)
	Orchard	5	% Gain	1L	-2.96(3.61)	-2.32(15.77)	30.96(2.31)
				6L	-2.39(2.53)	-1.96(13.65)	30.02(1.95)
				PAM-P	-8.94(2.90)	112.16(11.28)	-1.28(4.29)
				PAM	-8.48(3.50)	116.99(10.50)	-3.82(4.29)
RSI(MFA/Vol)	Overall	1	Phen.	1L	40.00(0.35)	6.73(0.26)	0.41(0.00)
				6L	40.00(0.34)	6.73(0.27)	0.41(0.00)
				PAM-P	40.00(0.44)	6.73(0.27)	0.41(0.00)
				PAM	40.00(0.44)	6.73(0.27)	0.41(0.00)
	Overall	2	Phen.	1L	36.49(0.59)	6.59(0.31)	0.41(0.01)
				6L	36.80(0.53)	6.13(0.40)	0.41(0.01)
				PAM-P	36.46(0.64)	6.60(0.34)	0.40(0.01)
				PAM	36.27(0.68)	6.58(0.37)	0.40(0.01)
	Overall	3	Phen.	1L	34.27(0.82)	6.49(0.36)	0.40(0.01)
				6L	34.82(0.63)	5.66(0.48)	0.40(0.01)
				PAM-P	34.13(0.85)	6.49(0.36)	0.40(0.01)
				PAM	33.63(0.84)	6.42(0.39)	0.40(0.01)

Table 10. Continued.

Elite Population Index	Population	Gen.	Var.	Breeding Strategy	Ew 4 MFA Mean(SD)	Vol 10 Mean(SD)	Csg Mean(SD)
RSI(MFA/Vol)	Overall	4	Phen.	1L	32.29(0.98)	6.35(0.40)	0.40(0.01)
				6L	33.11(0.73)	5.16(0.52)	0.40(0.01)
				PAM-P	32.04(0.99)	6.34(0.41)	0.40(0.01)
				PAM	31.21(0.92)	6.22(0.48)	0.40(0.01)
	Overall	5	Phen.	1L	30.45(1.15)	6.25(0.48)	0.40(0.01)
				6L	31.58(0.75)	4.65(0.52)	0.40(0.01)
				PAM-P	30.11(1.20)	6.24(0.45)	0.40(0.01)
				PAM	28.97(1.08)	6.10(0.50)	0.40(0.01)
	Orchard	0	% Gain	1L	5.08(1.43)	0.61(9.18)	-1.12(2.08)
				6L	4.37(1.17)	0.26(7.82)	-0.47(1.92)
				PAM-P	5.08(1.30)	-0.38(8.39)	-0.89(2.24)
				PAM	5.08(1.30)	-0.38(8.39)	-0.89(2.24)
	Orchard	1	% Gain	1L	11.21(1.79)	-1.25(10.19)	-1.70(2.46)
				6L	10.43(1.63)	0.95(12.71)	-1.47(2.58)
				PAM-P	11.32(1.62)	-0.03(10.45)	-1.88(2.79)
				PAM	11.12(1.70)	2.22(10.58)	-1.49(3.15)
	Orchard	2	% Gain	1L	13.39(1.88)	-1.76(8.84)	-1.82(2.72)
				6L	13.90(1.52)	-1.16(10.80)	-1.47(2.37)
				PAM-P	13.69(2.06)	-2.13(9.87)	-1.95(2.88)
				PAM	14.24(1.85)	-1.21(7.31)	-2.20(2.77)
	Orchard	3	% Gain	1L	16.32(2.05)	-0.97(9.10)	-2.50(3.18)
				6L	17.08(1.49)	-1.57(10.26)	-1.60(2.54)
				PAM-P	16.77(2.18)	-1.61(8.48)	-2.95(3.04)
				PAM	18.24(2.12)	-1.04(9.49)	-2.71(3.35)
	Orchard	4	% Gain	1L	19.62(2.45)	-1.81(10.57)	-2.87(2.96)
				6L	19.78(1.66)	1.06(9.88)	-2.26(2.51)
				PAM-P	20.16(2.63)	0.04(10.34)	-3.51(3.50)
				PAM	22.32(2.32)	-0.74(10.34)	-3.45(3.38)
	Orchard	5	% Gain	1L	23.45(2.64)	-0.89(9.52)	-3.46(3.36)
				6L	22.40(1.72)	1.95(11.07)	-2.81(2.83)
				PAM-P	23.82(2.86)	0.52(11.30)	-4.16(4.08)
				PAM	24.36(2.73)	0.86(11.25)	-3.54(4.18)
RSI(Csg/Vol)	Overall	1	Phen.	1L	40.00(0.40)	6.73(0.25)	0.41(0.00)
				6L	40.00(0.34)	6.73(0.27)	0.41(0.00)
				PAM-P	40.00(0.42)	6.73(0.28)	0.41(0.00)
				PAM	40.00(0.42)	6.73(0.28)	0.41(0.00)
	Overall	2	Phen.	1L	40.43(0.71)	6.60(0.34)	0.45(0.01)
				6L	40.36(0.56)	6.09(0.41)	0.44(0.01)
				PAM-P	40.48(0.73)	6.62(0.42)	0.45(0.01)
				PAM	40.57(0.78)	6.57(0.39)	0.45(0.01)
	Overall	3	Phen.	1L	40.78(0.98)	6.50(0.38)	0.47(0.01)
				6L	40.59(0.66)	5.59(0.49)	0.46(0.01)
				PAM-P	40.83(1.03)	6.47(0.44)	0.47(0.01)
				PAM	40.89(1.11)	6.40(0.44)	0.48(0.01)
	Overall	4	Phen.	1L	40.93(1.20)	6.39(0.46)	0.49(0.01)
				6L	40.75(0.75)	5.04(0.55)	0.48(0.01)
				PAM-P	41.08(1.20)	6.33(0.51)	0.49(0.01)
				PAM	41.19(1.36)	6.21(0.48)	0.50(0.01)

Table 10. Continued.

Elite Population Index	Population	Gen.	Var.	Breeding Strategy	Ew 4 MFA Mean(SD)	Vol 10 Mean(SD)	Csg Mean(SD)
RSI(Csg/Vol)	Overall	5	Phen.	1L	41.03(1.30)	6.27(0.53)	0.51(0.01)
				6L	40.94(0.83)	4.53(0.56)	0.50(0.01)
				PAM-P	41.25(1.37)	6.17(0.52)	0.51(0.01)
				PAM	41.45(1.66)	6.04(0.54)	0.52(0.01)
	Orchard	0	% Gain	1L	-0.92(1.77)	0.93(9.25)	6.25(1.62)
				6L	-0.40(1.62)	0.41(7.94)	5.38(1.36)
				PAM-P	-0.76(1.91)	-0.17(8.36)	6.23(1.48)
				PAM	-0.76(1.91)	-0.17(8.36)	6.23(1.48)
	Orchard	1	% Gain	1L	-1.44(2.13)	-1.49(9.94)	14.19(1.96)
				6L	-1.48(2.17)	1.72(11.86)	12.99(1.72)
				PAM-P	-1.26(2.30)	-0.53(10.08)	14.09(1.95)
				PAM	-1.20(2.53)	1.30(11.28)	14.24(2.09)
	Orchard	2	% Gain	1L	-1.76(2.57)	-1.34(9.79)	16.72(2.29)
				6L	-1.20(2.04)	-1.84(11.30)	17.47(1.83)
				PAM-P	-1.27(2.72)	-2.09(11.19)	17.07(2.16)
				PAM	-2.18(2.44)	-0.14(9.21)	17.93(2.37)
	Orchard	3	% Gain	1L	-1.79(2.54)	-1.19(9.61)	20.42(2.73)
				6L	-1.70(1.90)	-0.14(10.10)	21.27(1.97)
				PAM-P	-2.09(2.72)	-1.03(9.57)	21.16(2.60)
				PAM	-2.25(2.87)	0.04(9.45)	22.64(2.89)
	Orchard	4	% Gain	1L	-2.19(2.99)	0.13(10.80)	24.92(2.94)
				6L	-2.03(1.87)	-1.70(10.88)	25.31(2.16)
				PAM-P	-2.52(3.02)	-0.81(10.18)	25.79(2.89)
				PAM	-2.59(3.53)	-2.20(9.18)	28.17(2.88)
	Orchard	5	% Gain	1L	-2.51(3.02)	0.00(9.86)	29.84(3.29)
				6L	-2.66(2.25)	0.57(10.89)	28.84(2.24)
				PAM-P	-2.82(3.54)	-1.96(10.99)	30.85(3.32)
				PAM	-3.12(3.76)	-1.98(10.13)	30.80(3.23)
Csg	Overall	1	Phen.	1L	40.00(0.35)	6.73(0.26)	0.41(0.00)
				6L	40.00(0.34)	6.73(0.27)	0.41(0.00)
				PAM-P	40.00(0.44)	6.73(0.27)	0.41(0.00)
				PAM	40.00(0.44)	6.73(0.27)	0.41(0.00)
	Overall	2	Phen.	1L	40.00(0.74)	5.67(0.53)	0.45(0.01)
				6L	40.08(0.58)	5.31(0.53)	0.45(0.01)
				PAM-P	40.06(0.74)	5.57(0.51)	0.45(0.01)
				PAM	40.02(0.74)	5.69(0.51)	0.46(0.01)
	Overall	3	Phen.	1L	40.03(1.04)	5.07(0.67)	0.48(0.01)
				6L	40.06(0.74)	4.32(0.67)	0.48(0.01)
				PAM-P	40.03(0.98)	5.15(0.68)	0.48(0.01)
				PAM	40.07(0.98)	5.00(0.76)	0.49(0.01)
	Overall	4	Phen.	1L	40.06(1.33)	4.43(0.90)	0.51(0.01)
				6L	40.05(0.80)	3.38(0.77)	0.50(0.01)
				PAM-P	40.12(1.26)	4.57(0.90)	0.51(0.01)
				PAM	40.04(1.17)	4.37(1.00)	0.52(0.01)
	Overall	5	Phen.	1L	40.15(1.53)	3.86(1.00)	0.53(0.01)
				6L	40.00(0.91)	2.41(0.84)	0.52(0.01)
				PAM-P	40.14(1.47)	3.97(1.10)	0.53(0.01)
				PAM	40.06(1.39)	3.75(1.21)	0.54(0.01)

Table 10. Continued.

Elite Population Index	Population	Gen.	Var.	Breeding Strategy	Ew 4 MFA Mean(SD)	Vol 10 Mean(SD)	Csg Mean(SD)
Csg	Orchard	0	% Gain	1L	0.14(1.74)	-9.73(7.44)	6.59(1.43)
				6L	-0.16(1.27)	-7.65(9.74)	5.73(1.37)
				PAM-P	0.02(1.80)	-9.38(8.55)	6.54(1.33)
				PAM	0.02(1.80)	9.38(8.55)	6.54(1.33)
	Orchard	1	% Gain	1L	0.14(2.60)	-21.24(10.88)	15.35(1.57)
				6L	0.22(2.03)	-17.80(12.96)	14.87(1.59)
				PAM-P	0.03(2.19)	-18.49(11.75)	15.53(1.62)
				PAM	0.03(2.20)	-18.62(12.53)	15.64(1.61)
	Orchard	2	% Gain	1L	-0.24(2.51)	-22.47(12.53)	19.32(1.83)
				6L	-0.01(2.10)	-23.37(13.28)	19.98(1.55)
				PAM-P	-0.25(2.46)	-20.53(12.72)	19.80(1.91)
				PAM	0.08(2.31)	-21.76(11.95)	20.50(1.98)
	Orchard	3	% Gain	1L	-0.09(2.85)	-29.49(14.16)	24.03(1.77)
				6L	0.11(2.24)	-29.24(14.55)	25.03(1.79)
				PAM-P	-0.10(2.50)	-27.14(13.46)	24.94(1.86)
				PAM	0.07(2.39)	-27.40(14.21)	26.33(2.15)
	Orchard	4	% Gain	1L	-0.34(3.24)	-36.16(15.26)	29.75(1.76)
				6L	0.09(2.23)	-35.66(14.08)	29.88(1.78)
				PAM-P	-0.10(3.43)	-30.65(16.28)	30.89(2.16)
				PAM	-0.08(2.92)	-32.78(19.33)	33.28(2.32)
	Orchard	5	% Gain	1L	-0.47(3.56)	-42.40(17.10)	35.72(2.07)
				6L	0.12(2.15)	-39.52(14.62)	34.27(1.90)
				PAM-P	-0.16(3.49)	-37.97(18.32)	36.62(2.53)
				PAM	0.06(3.39)	-37.75(20.04)	36.42(2.45)

[1] Refers to the mean and standard deviation of the estimates of mean phenotype and percent gain following 75 iterations

Table 11. Results of the t-tests to determine whether the overall elite population mean phenotype in generation t is significantly different from the base population mean (t-tests significant at α=0.05 marked with an x).

Breeding		Trait	Ew 4 MFA					Vol 10					Csg				
Strategy	Index	Gen.	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
1L	*Base*			x	x	x	x		x	x	x	x		x	x	x	x
	MFA			x	x	x	x		x	x	x	x					
	Pulp-WG			x	x	x	x		x	x	x	x		x	x	x	x
	Pulp-h2			x	x	x	x		x	x	x	x		x	x	x	x
	RSI(MFA/Vol)			x	x	x	x		x	x	x	x		x	x	x	x
	RSI(Csg/Vol)			x	x	x	x		x	x	x	x		x	x	x	x
	Csg								x	x	x	x		x	x	x	x
6L	*Base*			x	x	x	x		x	x	x	x		x	x	x	x
	MFA			x	x	x	x		x	x	x	x					
	Pulp-WG			x	x	x	x		x	x	x	x		x	x	x	x
	Pulp-h2			x	x	x	x		x	x	x	x		x	x	x	x
	RSI(MFA/Vol)			x	x	x	x		x	x	x	x		x	x	x	x
	RSI(Csg/Vol)			x	x	x	x		x	x	x	x		x	x	x	x
	Csg								x	x	x	x		x	x	x	x
PAM-P	*Base*			x	x	x	x		x	x	x	x		x	x	x	x
	MFA			x	x	x	x		x	x	x	x					
	Pulp-WG			x	x	x	x		x	x	x	x		x	x	x	x
	Pulp-h2			x	x	x	x		x	x	x	x		x	x	x	x
	RSI(MFA/Vol)			x	x	x	x		x	x	x	x		x	x	x	x
	RSI(Csg/Vol)			x	x	x	x		x	x	x	x		x	x	x	x
	Csg								x	x	x	x		x	x	x	x
PAM	*Base*			x	x	x	x		x	x	x	x		x	x	x	x
	MFA			x	x	x	x		x	x	x	x					
	Pulp-WG			x	x	x	x		x	x	x	x		x	x	x	x
	Pulp-h2			x	x	x	x		x	x	x	x		x	x	x	x
	RSI(MFA/Vol)			x	x	x	x		x	x	x	x		x	x	x	x
	RSI(Csg/Vol)			x	x	x	x		x	x	x	x		x	x	x	x
	Csg								x	x	x	x		x	x	x	x

Table 12. Results of the t-tests to determine whether the percent gain in the elite population seed orchard in generation t is significantly different from zero (t-tests significant at α=0.05 marked with an x).

Breeding		Trait	Ew 4 MFA						Vol 10						Csg					
Strategy	Index	Gen.	0	1	2	3	4	5	0	1	2	3	4	5	0	1	2	3	4	5
1L	*Base*		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	MFA		x	x	x	x	x	x	x	x	x	x	x	x						
	Pulp-WG		x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x
	Pulp-h2		x	x	x	x	x	x		x	x	x	x		x	x	x	x	x	x
	RSI(MFA/Vol)		x	x	x	x	x	x							x	x	x	x	x	x
	RSI(Csg/Vol)		x	x	x	x	x	x							x	x	x	x	x	x
	Csg								x	x	x	x	x	x	x	x	x	x	x	x
6L	*Base*		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	MFA		x	x	x	x	x	x	x	x	x	x	x	x						
	Pulp-WG		x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x
	Pulp-h2		x	x	x	x	x	x							x	x	x	x	x	x
	RSI(MFA/Vol)		x	x	x	x	x	x							x	x	x	x	x	x
	RSI(Csg/Vol)		x	x	x	x	x	x							x	x	x	x	x	x
	Csg								x	x	x	x	x	x	x	x	x	x	x	x
PAM-P	*Base*		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	MFA		x	x	x	x	x	x	x	x	x	x	x	x						
	Pulp-WG		x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x
	Pulp-h2		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	RSI(MFA/Vol)		x	x	x	x	x	x							x	x	x	x	x	x
	RSI(Csg/Vol)		x	x	x	x	x	x							x	x	x	x	x	x
	Csg								x	x	x	x	x	x	x	x	x	x	x	x
PAM	*Base*		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	MFA		x	x	x	x	x	x	x	x	x	x	x	x						
	Pulp-WG		x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x
	Pulp-h2		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	RSI(MFA/Vol)		x	x	x	x	x	x							x	x	x	x	x	x
	RSI(Csg/Vol)		x	x	x	x	x	x					x		x	x	x	x	x	x
	Csg								x	x	x	x	x	x	x	x	x	x	x	x

Table 13. Results of the t-tests to determine whether the overall elite population mean phenotype differs significantly by generation (t-tests significant at α=0.05 marked with an x).

Breeding		Trait	Ew 4 MFA				Vol 10				Csg			
Strategy	Index	Gen.	1 - 2	2 - 3	3 - 4	4 - 5	1 - 2	2 - 3	3 - 4	4 - 5	1 - 2	2 - 3	3 - 4	4 - 5
1L	*Base*		x	x	x	x	x	x	x	x	x	x	x	x
	MFA		x	x	x	x	x	x	x	x				
	Pulp-WG		x	x	x	x	x	x	x	x	x	x	x	
	Pulp-h2		x				x				x	x	x	x
	RSI(MFA/Vol)		x	x	x	x	x		x		x	x		
	RSI(Csg/Vol)		x	x			x				x	x	x	x
	Csg						x	x	x	x	x	x	x	x
6L	*Base*		x	x	x	x	x	x	x	x	x	x	x	x
	MFA		x	x	x	x	x	x	x	x				
	Pulp-WG		x	x	x	x	x	x	x	x	x			
	Pulp-h2		x	x			x	x	x	x	x	x	x	x
	RSI(MFA/Vol)		x	x	x	x	x	x	x	x	x			
	RSI(Csg/Vol)		x	x			x	x	x	x	x	x	x	x
	Csg						x	x	x	x	x	x	x	x
PAM-P	*Base*		x	x	x	x	x	x	x	x	x	x	x	x
	MFA		x	x	x	x	x	x	x	x				
	Pulp-WG		x	x	x	x	x	x	x	x	x	x		
	Pulp-h2		x	x	x	x	x	x	x	x	x			
	RSI(MFA/Vol)		x	x	x	x	x		x		x	x		
	RSI(Csg/Vol)		x	x				x			x	x	x	x
	Csg						x	x	x	x	x	x	x	x
PAM	*Base*		x	x	x	x	x	x	x	x	x	x	x	x
	MFA		x	x	x	x	x	x	x	x				
	Pulp-WG		x	x	x	x	x	x	x	x	x	x	x	
	Pulp-h2		x	x	x	x	x	x	x	x	x	x		
	RSI(MFA/Vol)		x	x	x	x	x	x	x		x			
	RSI(Csg/Vol)		x	x			x	x	x	x	x	x	x	x
	Csg						x	x	x	x	x	x	x	x

Table 14. Results of the t-tests to determine whether the percent gain in the elite population seed orchard differs significantly by generation (t-tests significant at α=0.05 marked with an x).

Breeding		Trait	Ew 4 MFA					Vol 10					Csg				
Strategy	Index	Gen.	0-1	1-2	2-3	3-4	4-5	0-1	1-2	2-3	3-4	4-5	0-1	1-2	2-3	3-4	4-5
1L	*Base*		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	MFA		x	x	x	x	x	x	x	x	x	x					
	Pulp-WG		x	x	x	x	x	x	x	x	x	x	x				x
	Pulp-h2												x	x	x	x	x
	RSI(MFA/Vol)		x	x	x	x	x										
	RSI(Csg/Vol)												x	x	x	x	x
	Csg							x		x	x	x	x	x	x	x	x
6L	*Base*		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	MFA		x	x	x	x	x	x	x	x	x	x					
	Pulp-WG		x	x	x		x	x	x	x	x	x	x				
	Pulp-h2												x	x	x	x	x
	RSI(MFA/Vol)		x	x	x	x	x						x				
	RSI(Csg/Vol)		x										x	x	x	x	x
	Csg							x	x	x	x		x	x	x	x	x
PAM-P	*Base*		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	MFA		x	x	x	x	x	x	x	x	x	x					
	Pulp-WG		x	x	x	x	x	x	x	x	x	x	x				
	Pulp-h2		x		x	x	x	x	x	x	x	x					
	RSI(MFA/Vol)		x	x	x	x	x						x		x		
	RSI(Csg/Vol)												x	x	x	x	x
	Csg							x		x		x	x	x	x	x	x
PAM	*Base*		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	MFA		x	x	x	x	x	x	x	x	x	x					
	Pulp-WG		x	x	x	x	x	x	x	x	x	x	x				
	Pulp-h2		x		x	x		x	x	x	x	x					
	RSI(MFA/Vol)		x	x	x	x	x		x								
	RSI(Csg/Vol)			x									x	x	x	x	x
	Csg							x		x			x	x	x	x	x

Table 15. Results of the t-tests to determine whether selection on different indices resulted in significant differences in the overall elite population mean phenotypes (within breeding strategies and generations, indices with the same letter produced results that are not significantly different from each other at α=0.05).

Breeding		Trait	Ew 4 MFA					Vol 10					Csg				
Strategy	Index	Gen.	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
1L	*Base*		a	d	d	d	d	a	e	e	e	e	a	c	c	c	d
	MFA		a	f	f	f	f	a	d	d	d	d	a	d	d	d	e
	Pulp-WG		a	a	a	a	a	a	a	a	a	a	a	e	e	e	f
	Pulp-h2		a	b	b	b	b	a	b	b	b	b	a	b	b	b	b
	RSI(MFA/Vol)		a	e	e	e	e	a	b	b	b	b	a	e	e	e	f
	RSI(Csg/Vol)		a	b	b	b	b	a	b	b	b	b	a	b	b	b	c
	Csg		a	c	c	c	c	a	c	c	c	c	a	a	a	a	a
			--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
6L	*Base*		a	d	d	d	d	a	e	e	e	f	a	d	d	d	d
	MFA		a	f	f	f	f	a	d	d	d	e	a	e	e	e	e
	Pulp-WG		a	a	a	a	a	a	a	a	a	a	a	f	f	f	f
	Pulp-h2		a	b	b	b	b	a	b	b	b	c	a	b	b	b	b
	RSI(MFA/Vol)		a	e	e	e	e	a	b	b	b	b	a	f	f	f	f
	RSI(Csg/Vol)		a	b	b	b	b	a	b	b	b	bc	a	c	c	c	c
	Csg		a	c	c	c	c	a	c	c	c	d	a	a	a	a	a
			--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
PAM-P	*Base*		a	d	d	d	d	a	e	e	e	e	a	c	c	c	c
	MFA		a	f	f	f	f	a	d	d	d	d	a	d	d	d	d
	Pulp-WG		a	a	a	a	a	a	a	a	a	a	a	ef	e	e	f
	Pulp-h2		a	a	a	a	a	a	a	a	a	a	a	de	d	d	e
	RSI(MFA/Vol)		a	e	e	e	e	a	b	b	b	b	a	f	e	e	f
	RSI(Csg/Vol)		a	b	b	b	b	a	b	b	b	b	a	b	b	b	b
	Csg		a	c	c	c	c	a	c	c	c	c	a	a	a	a	a
			--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
PAM	*Base*		a	d	d	d	d	a	f	f	f	f	a	c	c	c	c
	MFA		a	f	f	f	f	a	e	e	e	e	a	d	d	d	d
	Pulp-WG		a	a	a	a	a	a	b	b	b	b	a	e	e	e	e
	Pulp-h2		a	a	a	a	a	a	a	a	a	a	a	e	e	e	e
	RSI(MFA/Vol)		a	e	e	e	e	a	c	c	c	c	a	e	e	e	e
	RSI(Csg/Vol)		a	b	b	b	b	a	c	c	c	c	a	b	b	b	b
	Csg		a	c	c	c	c	a	d	d	d	d	a	a	a	a	a

Table 16. Results of the t-tests to determine whether selection on different indices resulted in significant differences in the percent gain in the elite population seed orchard (within breeding strategies and generations, indices with the same letter produced results that are not significantly different from each other at α=0.05).

Breeding		Trait	Ew 4 MFA						Vol 10						Csg					
Strategy	Index	Gen.	0	1	2	3	4	5	0	1	2	3	4	5	0	1	2	3	4	5
1L	*Base*		c	c	c	c	c	c	e	e	e	e	f	f	b	c	c	d	d	c
	MFA		a	a	a	a	a	a	d	d	d	d	e	e	c	d	d	e	e	d
	Pulp-WG		e	f	f	f	f	f	a	a	a	a	a	a	c	e	e	f	f	e
	Pulp-h2		e	e	e	e	e	e	c	b	b	b	c	c	a	b	b	b	b	ab
	RSI(MFA/Vol)		b	b	b	b	b	b	b	b	b	b	cb	b	d	e	e	f	f	e
	RSI(Csg/Vol)		e	e	e	e	e	e	b	b	b	b	b	b	a	b	b	c	c	b
	Csg		d	d	d	d	d	d	d	c	c	c	d	d	a	a	a	a	a	a
			--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
6L	*Base*		c	c	c	c	c	c	d	d	e	e	e	e	b	d	c	d	d	c
	MFA		a	a	a	a	a	a	c	c	d	d	d	d	c	e	d	e	e	d
	Pulp-WG		f	f	f	f	f	f	a	a	a	a	a	a	c	f	e	f	f	e
	Pulp-h2		e	e	e	e	e	e	b	b	b	b	b	b	a	b	b	b	b	ab
	RSI(MFA/Vol)		b	b	b	b	b	b	b	b	b	b	b	b	c	f	e	f	f	e
	RSI(Csg/Vol)		de	e	e	e	e	e	b	b	b	b	b	b	a	c	b	c	c	b
	Csg		d	d	d	d	d	d	c	c	c	c	c	c	a	a	a	a	a	a
			--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
PAM-P	*Base*		c	c	c	c	c	c	e	f	f	f	e	e	b	c	c	c	c	c
	MFA		a	a	a	a	a	a	d	e	e	e	d	d	c	d	d	d	d	d
	Pulp-WG		e	f	f	f	f	f	b	b	b	b	a	a	cd	e	ef	f	f	f
	Pulp-h2		f	g	g	f	f	f	a	a	a	a	a	a	cd	e	de	e	e	e
	RSI(MFA/Vol)		b	b	b	b	b	b	c	c	c	c	b	b	d	f	f	f	f	ef
	RSI(Csg/Vol)		e	e	e	e	e	e	c	c	c	c	b	b	a	b	b	b	b	b
	Csg		d	d	d	d	d	d	d	d	d	d	c	c	a	a	a	a	a	a
			--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
PAM	*Base*		c	c	c	c	c	c	e	f	f	f	f	f	b	c	c	c	c	c
	MFA		a	a	a	a	a	a	d	e	e	e	e	e	c	d	d	d	d	d
	Pulp-WG		e	f	f	f	f	f	b	b	b	b	b	b	cd	e	e	e	e	e
	Pulp-h2		f	g	g	f	f	f	a	a	a	a	a	a	e	e	f	e	e	e
	RSI(MFA/Vol)		b	b	b	b	b	b	c	c	c	c	c	c	de	e	ef	e	e	e
	RSI(Csg/Vol)		e	e	e	e	e	e	c	c	c	c	c	c	a	b	b	b	b	b
	Csg		d	d	d	d	d	d	d	d	d	d	d	d	a	a	a	a	a	a

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