ABSTRACT

SIMS, ANDREW DWIGHT. Genetic Parameter Estimates from 3rd-Cycle Pollen Mix Progeny Tests in Loblolly Pine (*Pinus taeda* L.). (Under the direction of Dr. Steven E. McKeand and Dr. Fikret Isik)

Breeding programs make genetic gain by iterative cycles of selection, breeding, and testing. Design of experiments and subsequent analysis of data yield information to make comparisons to previous cycles, assess the nature of genetic control of traits, and predict performance of progeny both for future breeding and for deployment. The North Carolina State University Cooperative Tree Improvement Program (NCSUCTIP) is the largest breeding program for loblolly pine (*Pinus taeda* L.), the most important commercial tree species in the southeast region of the United States. The objectives of this study were to evaluate data from the Cooperative's third-cycle testing program and compare genetic parameter estimates to previous studies and to evaluate genotype by environment (GxE) interactions.

This study considers polymix (PMX) half-sib data from four test series from the Coastal breeding population and three test series in the Piedmont breeding population. These trials were established to estimate the heritability for height, volume, stem straightness, stem forking, and incidence of fusiform rust (caused by *Cronartium quercuum* f. sp. *fusiforme*) in the population, determine genetic correlation among these traits, and to estimate genetic values of maternal parents.

Heritability estimates for volume and height were higher in these trials compared to previous testing cycles, attributed to improved test design and analytical technique. The opposite result was found for straightness, where heritability was decreased, presumably related to intense selection in previous cycles. Family-mean heritability in rust and forking and ramicorn incidence was high, in agreement with previous studies. There was no evidence of a relationship between heritability and site means. Genetic correlations among traits were consistent with previous results, with height and volume being highly correlated with each other and not correlated with straightness. No genetic correlations were considered for binary traits.

Several variance structures were evaluated in linear mixed models to evaluate GxE. We used the Factor Analytic (FA) covariance structure for the compound genetic model term, which is genotype nested within environments, to model GxE. This structure approximates the unstructured (US) covariance structure. The FA structure is favored over US structure because it is parsimonious. The FA structure was found to be optimal for fitting the data.

For the cross-classified model, GxE was found to be statistically significant at $\alpha = 0.001$ based on Likelihood Ratio Tests. However, genetic correlations were found to be high for all series, indicating that GxE is principally associated with differences in scale effects in each test series. We conclude that ranking of genotypes is largely consistent among environments. Heritability estimates were dramatically higher than those based on estimates from the cross-classified model.

Genetic Parameter Estimates from 3rd-Cycle Pollen Mix Progeny Tests in Loblolly Pine (*Pinus taeda* L.).

by
Andrew Dwight Sims

A thesis submitted to the Graduate Faculty of
North Carolina State University in partial fulfillment of the
requirements for the degree of
Master of Science

Forestry and Environmental Resources

Raleigh, North Carolina

2017

APPROVED BY:

_____	_____
Dr. Fikret T. Isik Committee Co-Chair	Dr. Steven E. McKeand Committee Co-Chair
_____	_____
Dr. Ross W. Whetten Minor Member	Dr. W. Patrick Cumbie

DEDICATION

To my bride, Samara; to my family, a never-ending support; and to my grandpa, the person who taught me how to walk in the woods.

BIOGRAPHY

Andrew Sims was born on March 13, 1992 in Hickory, North Carolina to Joseph and Glennie Sims. He grew up in a rural community called Dudley Shoals and spent much of his childhood walking around in the woods with his brother, spending time with his cousins at the family BBQ restaurant, and travelling with his family. Andrew graduated from South Caldwell High School in Hudson, NC in June of 2010 and began undergraduate studies at NC State University the following fall. After graduating with a B.S. in Statistics in May of 2014, he enrolled to obtain a master's degree in Forestry. Andrew's foray into forestry began as an undergraduate assistant with the NC State Cooperative Tree Improvement Program, with whom he worked in his graduate studies.

ACKNOWLEDGMENTS

I would like to thank Drs. Steve McKeand, Fikret Isik, Ross Whetten, and Patrick Cumbie for their advice in all parts of this study: formation of concept, understanding and collating data, statistical analysis, writing, and troubleshooting. My experience as a graduate student was vastly improved by virtue of their advising. Thanks also go to all of the other faculty, staff, and students of the NC State Cooperative Tree Improvement Program for their help with data collection and analysis. Lastly, I would like to thank Cooperating members of the Tree Improvement Program. It is because of these members that the Tree Improvement Program has been a force in the advancement of forest science and forest genetics for many decades, and this study was made possible because of their work.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1: Estimates of Genetic Parameters in Loblolly Pine Progeny Tests in the Coastal and Piedmont Regions

Abstract

Breeding programs make genetic gain by iterative cycles of selection, breeding, and testing. Design of experiments and subsequent analysis of data yield information to make comparisons to previous cycles, assess the nature of genetic control of traits, and predict performance of progeny both for future breeding and for deployment. The North Carolina State University Cooperative Tree Improvement Program (NCSUCTIP) is the largest breeding program for loblolly pine (*Pinus taeda* L.), the most important commercial tree species on the southeast region of the United States.

The Cooperative's third-cycle testing program was designed as a group of multi-site test series with pollen mix (half-sibling) families. These trials were established to estimate the heritability in the population, determine genetic correlation of traits, and to estimate genetic values of maternal parents. This study uses data from four test series from the Coastal breeding population and three test series in the Piedmont breeding population.

Heritability estimates for volume and height were higher in these trials compared to previous testing cycles, attributed to improved test design and analytical technique. The opposite result was found for straightness, where heritability was decreased, presumably related to intense selection in previous cycles. Family-mean heritability in fusiform rust incidence (caused by *Cronartium quercuum* f. sp. *fusiforme*) and forking and ramicorn incidence was high, in agreement with previous studies. There was no evidence of a relationship between heritability and site means. Genetic correlation among traits was consistent with previous

results, with height and volume being highly correlated with each other and not correlated with straightness. No genetic correlations were considered for binary traits.

Introduction

Loblolly pine (*Pinus taeda* L.) is the most important plantation crop tree in the Southeastern US, with more than one billion seedlings planted in past years over twelve southern states (McKeand et al. 2003). These southern states represent a large proportion of the overall number of acres planted; in 1998 representing as much as 79% of the total planted acres in the US (Moulton and Hernandez, 2000). Of this massive land base, 11 million hectares are in southern pine plantations – approximately 80% loblolly and 20% slash pine (*Pinus elliottii* var. *elliottii* Engelm.) (Li et al., 1999). Essentially every deployed seedling is a descendant of some sort of genetically improved germplasm: open-pollinated (OP) families or half-siblings, control-pollinated or full-sibling families, rooted cuttings, or somatic embryogenic (SE) clones (McKeand et al. 2003). All of this genetically improved planting stock is the product of some 60 years of dedicated southern pine breeding regimes housed both in private companies and in university-based industry cooperatives such as the North Carolina State University Cooperative Tree Improvement Program (NCSUCTIP), the Cooperative Forest Genetics Research Program (CFGRP) at the University of Florida, and the Western Gulf Forest Tree Improvement Program (WGFTIP) directed by the Texas A&M Forest Service.

Producing estimates of genetic parameters is a vitally important step in the assessment of genetic gain in a breeding population. These statistics inform the breeder about the degree to which a trait might be inherited (heritability), and the degree to which any two traits are genetically correlated. Producing these statistics to characterize a breeding population is necessary for making decisions for a selection and testing regime and to make gain in

successive iterations of the breeding and testing process (Zobel and Talbert 1984; Falconer and Mackay 1996).

Previous assessments of genetic parameters in pine, especially loblolly, have described a large number of traits and relationships among them. In a mainline breeding program, traits like stem volume, fusiform rust (caused by *Cronartium quercuum* f. sp. *fusiforme*) resistance, and stem form are among the most important. Other traits like wood specific gravity, percent sugar yield for ethanol production, microfibril angle, and percent lignin content are considered secondary in importance, and are often more difficult to screen in progeny tests (Zobel and Talbert 1984; Atwood et al. 2002; Isik et al. 2011; Barker 2014).

Estimates of narrow-sense heritability of growth traits, most importantly height and volume, have varied widely over breeding designs and field experimental designs (Isik et al. 2005). In NCSUCTIP's 2nd-Cycle, with data from full-sib crosses from six-tree disconnected half-diallels, the average heritability estimate was 0.19 and 0.16 for height and volume, respectively. With more than 3,000 selections tested, this is likely one of the most comprehensive testing efforts analyzed for a forest tree species (McKeand et al. 2008). Other studies have given similar estimates for loblolly pine and other forest tree species. Across a large range of test ages, estimates have usually ranged from 0.05 to 0.30 (Svensson et al. 1999; Sierra-Lucero et al. 2002; Xiang et al. 2003). In general, these estimates are relatively consistent across ages, studies, and species. In an analysis of results of many studies of a variety of forest tree species, Cornelius (Cornelius 1994) reported median heritabilities of

0.25 for height and 0.18 for volume and noted a band of 0.10 to 0.30 as the general trend of growth trait heritability.

Heritability in straightness has not been studied as extensively in loblolly pine as height and volume, but it is considered to be the trait where the most gain has been made (Li et al. 1999). Shelbourne and Stonecypher (Shelbourne and Stonecypher 1971) and Cornelius (Cornelius 1994) give estimates of narrow-sense individual tree heritability for straightness between 0.25 and 0.55, suggesting that this trait is more heritable than height and volume.

Genetic control of binary traits is difficult to describe on an individual tree basis since there is no gradient for incidence across individual stems, but family mean incidences are repeatable for forking. Data from the previously mentioned diallel studies had half-sib family mean heritability of 0.74 – 0.81 across a wide range of sites for fork incidence (Xiong et al. 2010). In a study of material from the spectrum of the geographic distribution, a half-sibling family mean heritability of 0.92 was reported for forking incidence (Cumbie et al. 2012). Forking is a complex trait influenced by nutrition, stem damage, disease, and many number of other genetic and environmental factors (Xiong et al. 2010). Nonetheless, family means of forking are expected to be highly repeatable.

Resistance to fusiform rust is one of the most valuable traits in southern pine and is a primary factor influencing survival and stem quality (Schmidt 2003). Fortunately, family mean heritability estimates indicate a high degree of genetic control (McKeand et al. 1999).

(Cumbie et al. 2012) reported a half-sib family mean heritability of 0.96 in a wide-cross study, suggesting that this repeatability is likely consistent among seed sources. In a study in which several regional provenances of fusiform rust inocula were applied to a seedlings from a variety of families, half-sib family-mean heritabilities were estimated to be 0.97 (Isik et al. 2008).

By virtue of the imprecision and different methodologies for producing some of these estimates, a 0.05 difference in h^2 is considered to be incidental, especially on a site-to-site basis (Zobel and Talbert 1984). Ability to produce estimates largely depends on experimental field designs and mating designs. Issues like lack of replications of tests, disconnected treatment levels among sites, and varying degrees of relatedness are examples of complications of estimation and comparison. For example, in the 2nd-Cycle NCSUCTIP diallel tests, connection of genetic material was highly limited among test series (Isik et al. 2005a).

Estimates of genetic parameters, while dependent on the actual degree of additive allelic control on traits, are also dependent on the quality of the test site (environmental factors) and data collection (measurement errors). Poor site preparation techniques, lack of control of competing vegetation, and general lack of maintenance results in phenotypes that are mainly determined by the environment rather than genetic factors, meaning that differences among phenotypes have limited useful interpretation. Poor testing practices increase environmental noise and can cause low heritability estimates with large standard errors. This non-uniformity

of the experimental site can cause a high degree of variance associated with the experimental unit (single tree plot), thus inflating the overall variance estimate associated with environment (σ_e^2). An increase in σ_e^2 (also called 'error' variance) increases the denominator value in the heritability calculation, resulting in lower estimates. Heritability estimates are maximized with uniform sites, well replicated tests, and proper analysis of data to account for heterogeneity of data using linear mixed models.

This study summarizes the estimates of genetic parameters of loblolly pine poly-mixed progeny tests in the third cycle of the breeding program managed by the NCSUCTIP. The objectives of this study were to:

1. Report estimates of genetic parameters of loblolly pine in the third cycle breeding in the Coastal and Piedmont regions for the NCSUCTIP.
2. Compare estimates of genetic parameters, especially heritability, to previous estimates.

Materials and Methods

Data were collected from four test series in the Coastal breeding population and three test series in the Piedmont breeding population with varying number of test sites within each series. Each of these test sites was established and measured as part of the collective effort of the NCSUCTIP and its cooperating members in mainline 3rd-Cycle breeding.

Genetic Material

The 3rd-Cycle mainline effort was focused on three breeding regions as described in Appendix Figure A-1. These regions represented a grouping of the 2nd-Cycle breeding and testing regions: the Northern region (Virginia and Northern North Carolina), the Coastal region (Atlantic Coastal Plains of southern NC, SC, GA, and the Lower Gulf Coast of AL and MS), and the Piedmont region (inland zones of South Carolina and Georgia and the Upper Gulf Coast of AL, MS, and TN). The mating scheme in each series was identical: poly-mix crossing to produce half-sibling families from a number of selections. Poly-mix, also known as pollen mix or PMX (henceforth called PMX), refers to crossing a specified mix of pollen from known male parents to known female parents. This strategy allowed for a common pollen source to be the male parent across a multitude of female parents and sites, reducing variation of genetic input of male parents within each provenance. Thus, each member of a PMX family has one parent in common and an average male parental value. For each breeding region, twenty well-characterized parents were selected to represent region-wide average breeding values and were grafted into each member's breeding orchard. Pollen was collected from ramets of each parent and blended with weight given to pollen germination percentage to impute equal genetic representation. For further explanation of the motivation for this strategy, see (McKeand and Bridgwater 1998).

For comparisons among tests and series, a checklot was developed for each region to represent the average genetic performance. These checklots are henceforth noted as CCK, PCK, and NCK for the Coastal, Piedmont, and Northern regions, respectively. These

checklots were developed by crossing the pollen mix for each region onto a subset of ten of the twenty parents. That is, for the Coastal region, the parentage of CCK would be a subset of ten Coastal PMX (CPMX) parents crossed with a pollen blend of all 20 CPMX parents. Additionally, seven well-characterized parents were crossed with the pollen mix for each respective series and incorporated into the testing. Four of these families were PMX crosses with two high-performing and two poor-performing parents from 1st- and 2nd- Cycle testing.

Experimental Design

Each site was established as a randomized complete block design with 20 blocks at each site. Single tree plots were used as experimental units. This strategy was chosen to efficiently produce breeding values of parents. An additional advantage to this strategy was that a large number of families were tested - approximately 70 PMX families were included at each site, including the three 3rd-Cycle checklots appropriate for testing in that region (CCK, PCK, NCK) and the seven common family checks, totaling a number in the range of 1400 trees at each site at the time of establishment.

Measurement Traits

Tests were measured between ages four and seven years. Height and diameter at breast height (1.4 meters, henceforth DBH) were measured to the nearest 0.1 foot and 0.1 inch, respectively. These measurements were converted into meters and centimeters and used to calculate volume in cubic decimeters on the basis of the inside-bark total stem equation derived by Sherrill et al. (2011). Straightness was visually assessed on a 1-6 scale where ‘1’

is straight and '6' is the most crooked at each site, therefore straightness should be distributed normally ~(3.5, 1) at each site. Binary traits including survival, and incidence of fusiform rust galls, ramicorn branching, and stem forking were assessed. Fusiform rust galls are swelled stem tissue, often yellow from the fungal spores and seeping sap. Forks are exhibited by the emergence of two codominant apical meristems from the bole, especially in the lower portion of the crown. Forks are different from ramicorns in that ramicorns are branches of unexpectedly large size, enough to affect growth and form but not necessarily codominant. For further discussion on the nature of forking and ramicorns, see Xiong et al. (2010). A value of 1 is assigned to a tree in case of incidence (presence of forking, ramicorn branches, and stem gall). Because forking and ramicorns cause essentially the same stem defect, their incidence was analyzed together as a single trait, 'forkram' (e.g. a tree was assigned a value of 1 if it had a fork and/or a ramicorn branch).

Statistical Analysis

Data were analyzed on a site basis first and then for the entire series in each region. Summary statistics of sites and test series were generated (Table 1-1) using the MEANS procedure of SAS software and JMP (SAS Institute Inc. 2011). Summary statistics for individual sites can be found in Appendix Tables A-1 through A-7. Traits included in the summary statistics were height, volume, straightness, rust, and forkram. These summaries were produced with checklots (e.g. CCK, NCK, or PCK) removed, but common family checks are included. Pearson correlations for site means were produced using R (Venables and Smith 2014).

Using the mixed modeling software ASReml (Gilmour et al. 2014), linear mixed models were used to analyze height, volume, and straightness at each site using the following equation:

$$\boldsymbol{y_{ijk} = \mu + R_i + F_j + e_{ijk}} \quad (1\text{-}1)$$

where y_{ijk} is the response variable, μ is the overall mean response, R_i is the random blocking effect of replication within a site ~N(0, σ_r^2), F_j is the random effect of female parent ~N(0, σ_f^2), and e_{ijk} is the residual error ~N(0, σ_e^2). All random effects and errors are assumed identically independently distributed (iid).

The following linear mixed model was used to analyze the data across sites for each series.

$$\boldsymbol{y_{ijkl} = \mu + S_i + R(S)_{j(i)} + F_k + SF_{ik} + e_{ijkl}} \quad (1\text{-}2)$$

where y_{ijk} is the response variable, μ is the overall mean response, S_i is the fixed site effect, $R(S)_{j(i)}$ is the random blocking effect nested within site ~N(0, σ_{rb}^2), F_k is the random effect of female parent ~N(0, σ_f^2), SF_{ik} is the site-female interaction term (GxE) ~N(0, σ_{sf}^2), and e_{ijkl} is the residual error ~N(0, σ_e^2). All random effects and errors are assumed to be iid.

For binary traits, a generalized linear mixed model was used to partition observed variance into its environmental and genetic components for rust incidence and forkram for each site and for the test series. For individual test site analyses, sites with incidence less than 20% were not analyzed because of environmental noise. Sites with less than 0.20 average

incidence level or heterogeneous survival among families were excluded from this analysis as these factors prevented model convergence. The model fit to individual test site data is as follows:

$$\boldsymbol{y_{ijk} = \ln\left(\frac{\pi}{1-\pi}\right) = \mu + R_i + F_j} \quad (1\text{-}3)$$

where y_{ijk} is the response variable, π represents the odds of trait incidence, μ is the mean, R_i is the random blocking effect ~N(0, σ_r^2), and F_j is the random effect of female parent ~N(0, σ_f^2). All random errors are assumed identically independently distributed (iid). This is the exact same model as Equation (1), except the response variable of interest is the log-odds of trait incidence, and error is defined outside of model evaluation. Note that generalized linear models do not consider an overall residual variance term.

The model for evaluating data across sites for each series is defined as:

$$\boldsymbol{y_{ijk} = \ln\left(\frac{\pi}{1-\pi}\right) = \mu + S_i + R(S)_{j(i)} + F_k + SF_{ik}} \quad (1\text{-}4)$$

where y_{ijk} is the response variable, π represents the odds of trait incidence, μ is the overall mean response, S_i is the fixed site effect, $R(S)_{j(i)}$ is the random blocking effect nested within site ~N(0, σ_{rb}^2), F_k is the random effect of female parent ~N(0, σ_f^2), and SF_{ik} is the site-female interaction term (GxE) ~N(0, σ_{sf}^2). Again, random errors are assumed to be independent. This model was evaluated for each test series for both forkram and rust. Although overall trait incidence was not above 0.20 in each case, models converged with relatively few iterations.

Estimation of Genetic Parameters

Using estimates of variance components, narrow-sense individual-tree heritability (h^2) was estimated for height, volume, and straightness at each site using the following formula:

$$\boldsymbol{h^2 = \left(4\,\sigma_f^2\right) / \left(\sigma_f^2 + \sigma_e^2\right)} \quad (1\text{-}5)$$

where h^2 is the narrow-sense individual heritability, σ_f^2 is the variance associated with the female parent, and σ_e^2 is the residual variance associated with environment. The genetic variance is multiplied by 4 to account for the proportion of relatedness among half-sibs. Any pair of half-sib progeny are each assumed to obtain 1/2 the genetic material of a common parent, and each sexual recombination event is assumed to be independent. Therefore, the expected value of the relatedness of two individuals is 1/2 * 1/2 = 1/4. Additive and residual variance components for each site are reported in Appendix Tables A-8 and A-9 and narrow-sense heritabilities for sites are listed in Appendix Table A-10.

For continuous traits, h^2 was calculated on a series basis as:

$$\boldsymbol{h^2 = \left(4\,\sigma_f^2\right) / \left(\sigma_f^2 + \sigma_{sf}^2 + \sigma_e^2\right)} \quad (1\text{-}6)$$

where h^2 is the narrow-sense individual-tree heritability, σ_f^2 is the multi-environment family variance, σ_{sf}^2 is the GxE (site-by-family) interaction term and σ_e^2 is the residual variance due to environment. The rationale for multiplying the numerator family variance is the same as in the case of individual sites. Variance components from each series are reported in Appendix Table A-10 and heritability estimates are reported in Table 1-2.

A separate estimate of h^2 was constructed for each series based by calculating the unweighted mean of heritability for all sites in a series. The formula for this estimate is:

$$\boldsymbol{h^2 = \frac{1}{n} \sum_{i=1}^{n} h_i^2} \quad (1\text{-}7)$$

where n is the number of sites in a series and h_i^2 is the narrow-sense individual-tree heritability at site *i*. This estimate is biased because GxE is ignored in the phenotype variance component; this estimate is constructed to compare to the unbiased estimate described in equation (5). These estimates are listed in Appendix Table A-17.

For binary traits, family mean heritability estimates were produced for each site using variance component estimates from equation (3). These estimates were produced with the following equation:

$$\boldsymbol{h_{fm}^2 = \sigma_f^2 / (\sigma_f^2 + \frac{\sigma_e^2}{n})} \quad (1\text{-}8)$$

where h_{fm}^2 is the narrow-sense family heritability, σ_f^2 is the family variance, and n is the average number of individuals per family per site, and σ_e^2 is the residual variance due to environment. Because we are estimating repeatability of family means rather than individual tree heritability, the numerator is not multiplied. Residual variance is divided by n to account for the average number of data points associated with each family for a site. For binary traits the σ_e^2 is set as 3.29, or $\pi^2/3$, as suggested by Gilmour (Gilmour et al. 1985). Variance components for each site are reported in Appendix Table A-12, and the n for each site is reported in Appendix Table A-13. Estimates of family mean heritability for estimable sites are found in Appendix Table A-14.

Using variance components derived from results of equation (4), narrow sense family mean heritability was estimated for each series using the following equation:

$$\boldsymbol{h_{fm}^2 = \sigma_f^2 / (\sigma_f^2 + \sigma_{fs}^2 + \frac{\sigma_e^2}{n})} \quad (1\text{-}9)$$

where h_{fm}^2 is the narrow-sense family heritability, σ_f^2 is the family variance, σ_{fs}^2 is the GxE variance, and n is the average number of individuals per family per series, and σ_e^2 is the residual variance due to environment, again defined as 3.29. Variance components are reported in Appendix Table A-15, the n for each series is reported in Appendix Table A-16, and heritabilities are listed in Table 1-3.

Scatter plots and Pearson correlations were produced between site incidence and site heritability for volume, height, forkram and rust using R (Venables and Smith 2014). These plots are displayed in Figure 1-1 for continuous traits and Figure 1-2 for binary traits. This type of correlation is useful for informing the relationship between trait performance at a site and amount of genetic control over performance exhibited at that site.

Scatter plots and correlations were not produced for straightness. Straightness is assessed categorically on a site-by-site basis, and each site should have a symmetric distribution of scores with a mean of exactly 3.5. If straightness is measured correctly, there should be no variation among sites.

Genetic correlations of continuous traits were calculated for each series using the following formula:

$$r_g = \frac{var(X)var(Y)}{cov(X,Y)} \quad (1\text{-}10)$$

where r_g is the genetic correlation, X is a trait of interest, and Y is another trait of interest. This statistic describes the correlation of genetic performances. Each of the estimators described above is detailed by Falconer and MacKay (Falconer and Mackay 1996). Genetic correlation was not considered for the forkram-rust relationship.

Results and Discussion

Summary Statistics and Trait Performance

Height means ranged from 8.4 meters in Coastal Test Series 3 (CPMX3) to 4.9 meters in Piedmont Test Series 3 (PPMX3), both of which were the oldest and youngest series, respectively (Table 1-1). Volumes exhibited similar variation among test series ranging from 54.6 to 20.1 dm^3 in the same respective series. Performance of growth traits among sites was generally consistent within series except for occasional presence of a small number of poor-performing test sites. An example can be found in Coastal Test Series (CPMX1), where mean site height was 7.7 meters, but site 11 (CPMX1-11) had a mean height of 3.9 meters (Appendix Table A-1). These poor-performing sites could be explained by site preparation and maintenance issues, nutrient or water deficiency, or any number of environmental issues. Summary statistics for individual test sites can be found in Appendix Tables A-1 through A-7.

Straightness means were similarly consistent among series, with a range of 3.01 to 3.46 (Table 1-1). This trait, not being physically measured but instead being categorically assessed, has the same expected value for each site. Scores range from 1 to 6 where a score of 1 indicates “most straight” a score of 6 indicates “least straight.” Ideally, these scores should be distributed approximately normally where ~70% are 3 or 4, ~95% are scored 2, 3, 4,or 5, and 100% are scored between 1 and 6. For this reason, the expected straightness score mean at a site is 3.5. For the majority of test sites, mean straightness scores were close to this value; 38 out of 51 sites exhibited mean straightness scores between 3.30 and 3.70. Many sites had mean scores less than 2.00 and none were higher than 3.67, indicating that straightness was measured with bias toward lower, more favorable scores at these sites. Sites with aberrant means were retained in the analysis because a stratification of scores is expected in spite of skewness of the distribution of scored values; however, it would be inappropriate to consider differences in site means as informative. Some explanations for bias toward a lower, more favorable straightness value include error in measurement procedures or unrealistic assumptions about the distribution of stem straightness. Because of the high number of sites with values aligning with expectations, the former explanation seems more plausible.

Mean rust incidence was higher in the Coastal region, a result that broadly falls in line with expectations according to rust hazard zones and rust incidence in sample plots (Randolph et al. 2015). Rust incidence at sites was highly variable within series, indicating that some sites

were more rust-prone than others during the trial period. This stratification among sites can be considered advantageous for multi-site analysis because the same families were exposed to a variety of rust incidence levels. Mean incidence levels of forking were relatively consistent among series, but highly variable among sites. There was no obvious explanation for differences in forkram incidence among sites; there was no apparent trend related with region, series, or age at measurement.

Phenotypic correlations for pairs of traits across all sites were fairly predictable. Height and volume were correlated at $r = 0.91$, almost completely explained by the fact that height is a component of the equation used to calculate volume. Mean rust incidence was correlated with height mean and volume mean at $r = 0.40$ and 0.29, respectively. This is not a particularly strong correlation, and the degree to which it exists is likely explained by overall height site means and rust incidence levels being higher in Coastal test sites than in Piedmont test sites. Simply, Coastal test sites had both higher levels of height growth and rust incidence. Mean forkram incidence was correlated at $r = -0.21$ with height and -0.19 with volume. Because volume and height are strongly associated, the inversion of these correlations suggests that they are largely incidental. For reasons described above, straightness was not considered in any correlation-focused analysis.

Heritability in Continuous Traits

Narrow-sense heritability estimates for sites (Table A-10) ranged from 0.05 to 0.72 for height, from 0.10 to 0.70 for volume, and from 0.05 to 0.43 for straightness. Standard errors

were generally low for estimates of each trait, with a maximum of 0.140 for height, 0.130 for volume, and 0.114 for straightness. Overall means of trait heritability across sites were $\bar{h}^2_{site}$ = 0.35 for height, $\bar{h}^2_{site}$ = 0.34 for volume, and $\bar{h}^2_{site}$ = 0.22 for straightness. Estimates of multi-site (series) narrow sense heritability (Table 1-2) ranged from 0.16 to 0.38 ($\bar{h}^2_{series}$ = 0.25) for height, 0.11 to 0.29 ($\bar{h}^2_{series}$ = 0.19) for volume, and 0.12 to 0.20 ($\bar{h}^2_{series}$ = 0.15) for straightness. Heritability on a series basis was consistently less than mean site heritability for the corresponding test series (Table A-17).

The NCSUCTIP 2nd-Cycle testing effort summary reported average unbiased narrow-sense individual tree heritabilities of $\bar{h}^2_{series}$ = 0.19 for height and $\bar{h}^2_{series}$ = 0.16 for volume across seven geographic regions (McKeand et al. 2008). These estimates are averages of estimates of heritability for many disconnected series with a few sites in each series, so the most appropriate comparison is to the mean heritability of all of the series. In the 3rd-cycle PMX tests, mean series heritability for was higher for both height ($\bar{h}^2_{series}$ = 0.25) and volume ($\bar{h}^2_{series}$ = 0.19). Possible explanations for different results from 2nd-Cycle results and 3rd-Cycle results are differences in testing strategy, experiment design, and improvements in quality and maintenance of selected sites.

Implementation of a randomized complete block experiment design with single-tree-plot experimental units could have resulted in more powerful tests. Each 3rd-Cycle series contained between 68 and 91 genetic entries in Coastal series and between 64 and 75 entries in Piedmont series. This scheme stands in contrast to the strategy executed in NCSUCTIP

2nd-Cycle mating, where two sets of six parents were mated in diallels to produce 30 full-sib crosses for each series (McKeand and Bridgwater 1998). While significantly fewer parents were tested in this study (~400 vs ~3000), more parents were tested in each series and at each site. The principle impact of this design is a change in experimental units and blocking factors. The 3rd-Cycle tests had 20 replications (repeated treatments in blocks) of ~75 plots per site with one tree in each plot. The 2nd-Cycle tests had six replications of six-tree row plots for 30 genetic entries (two, 6-parent diallels plus checklot plots) plus two entries of four checklots at each site (38 total plots), resulting in rep sizes of 228 trees. Therefore, blocking factors in the 3rd-Cycle tests required approximately one-third of the geographic space required in 2nd-Cycle tests (228 planted trees vs. ~75 planted trees), and individual experimental units decreased in size from six trees to a single tree. This decrease in the size of the blocking factor and the experimental unit result in increased replication of treatments, increased number of genetic entries, and smaller geographic area required for one test replication. This decreased experimental area required for a replication resulted in a better opportunity to identify contiguous plots with environmental homogeneity, allowing for reducing the residual variance. A reduction in environmental variance by virtue of smaller block sizes and better site selection, an increase in the number of tested families, more extensive replication of the genetic entries, and general improvement in test site maintenance are the likely causes for an increase in heritability.

Unlike the heritability estimates for growth traits, the mean series straightness heritability ($\bar{h}^2_{series}$= 0.15) is much lower than estimates from many early studies (Shelbourne and

Stonecypher 1971; Cornelius 1994). Assuming that a reduction in environmental variance or test design is the most important factor in heritability increase for this study, estimates of heritability in straightness were expected to be higher. One possible explanation for these results would be to conclude that straightness has been improved enough that variation has been decreased in breeding populations after two iterations of intensive selection. That is, the difference between the most straight and the least straight genotype is much smaller than the difference between the most and least straight genotypes in previous cycles because only superior genotypes have been carried forward into new breeding populations. Straightness is generally heralded as one of the traits for pine for which the most improvement has been made (Li et al. 1999), so this interpretation seems to be the most plausible.

Heritability is most informative when describing a large number of sites; repeatability of genetic performance across environments is the underpinning of predictive modelling of family performance. This study examines two methods for producing narrow-sense heritability estimates for continuous traits over multiple environments: an arithmetic mean of site heritabilities, and a singular estimate based on pooled variance terms across multiple sites. These two estimates are principally different in that the second accounts for GxE in the phenotypic variance pool, instead of ignoring it and declaring all sites homogeneous with respect to genetic performance. The first, in contrast, is biased because GxE is completely ignored. Because GxE is included as a term used in the models used to describe multiple-site (series) data, estimates of heritability should account for it as a component of the overall phenotypic variance. The percentage of deviation of the site means estimate ($\bar{h}^2_{site}$) relative to

the pooled variances estimate (h^2_{series}) is a quantity that describes reduction in heritability associated with accounting for GxE. For the data presented in this study, reductions ranged from 11% to 82% for height, 43% to 182% in volume, and 8% to 76% in straightness.

These large deviation percentages suggest that GxE is an important source of variation, but also motivates further investigation into genotype-environment assumptions. GxE variance can be a large variance component for a number of reasons, but not all of the reasons for its significance are interpreted in the same way. For instance, large GxE associated with scale differences in family performances among sites supports a different conclusion than differences in ranks of family performance. Previous studies such as (Roth et al. 2007) have indicated that GxE could be principally tied to scale differences. Analyzing these data using simple pooled variance terms assumes an unrealistic set of assumptions about genetic correlations of traits among sites and heterogeneity of site performance and quality. In order to account for GxE effects with the most realistic assumptions, variance structures useful for describing the genetic and GxE variance on a component basis would have to be employed. If these factors can be accounted for meaningfully, heritability could be increased dramatically. In-depth discussion of GxE, its components, and alternative calculation methods are also outside the scope of this discussion (it will be thoroughly described in Chapter 2), but relevant discussion can be found in (Isik et al. 2005b; Zapata-Valenzuela 2012; Cullis et al. 2014; Ogut et al. 2014), and elsewhere.

Heritability in Binary Traits

For analysis of binary traits, ideal mean incidence of traits is between 0.30 and 0.70; extreme levels of incidence often make estimation of variance components difficult to reliably compute, even using maximally efficient REML-based methods, because variance is maximized where incidence is 0.50. Reasons for varying levels of trait incidence are many for both rust and forking; some possible factors include rust hazard differences across a geographic gradient, tipmoth damage induced forking, or randomly occurring environmental factors (Xiong et al. 2010; Randolph et al. 2015). For NCSUCTIP, it is standard protocol to analyze binary traits between incidence levels of 0.20 and 0.80. Using this criterion, attempts were made to produce estimates of heritability at all sites where incidence was appropriate. For many tests, differences in mortality among families also prevented model convergence. After removing sites from analysis where models were unable to produce results, 19 sites for forkram and 29 sites for rust remained. For rust, h^2_{fm} estimates were relatively consistent across the 29 sites, ranging from 0.74 to 0.95. Site level estimates of family for forkram were widely variable, with a range of 0.19 to 0.83 across the 19 sites. Estimates of h^2_{fm} in forkram had standard errors as high as 0.950, suggesting that many site estimates are unreliable for interpretation. Overall, family mean heritability estimates for rust were clustered at the high end of the spectrum ($\bar{h}^2_{fm}$ = 0.86), and family mean heritability estimates for forkram were spread widely with mean $\bar{h}^2_{fm}$ = 0.58.

Producing estimates of family mean heritability can be difficult for multi-site data because incidence levels are often extremely heterogeneous across sites, as is the case for many series

in this study. Further, incidence levels may be acceptable at several sites within a series but not acceptable for the pooled data. Although some series had incidence levels below this threshold, diagnostics of each model reported log likelihood convergence, indicating success in model evaluation. Estimates of multi-site (series) family-mean heritability were produced using equation (9); these estimates are reported in Appendix Table A-9. For rust, series h_{fm}^2 ranged from 0.13 to 0.90 ($\bar{h}_{fm}^2$ = 0.66). Piedmont Series 1 (PPMX1) exhibited very low incidence across all sites, with overall incidence at 0.12 (Tables A-5, 1-1), so we will not interpret its result. Piedmont Series 3 (PPMX3) consists of three sites with extremely heterogeneous site incidence levels, a low mean (0.23), and very large standard errors of variance components (Tables A-7, 1-1), so interpretation of this estimates is also likely less informative than for the other test series. For forkram, h_{fm}^2 ranged from 0.31 to 0.61 ($\bar{h}_{fm}^2$ = 0.50). Because series-wide incidence levels are acceptable, there is no reasons to discard results for forkram as was in the case of PPMX1 and PPMX3 for rust.

For the five series where interpretation is appropriate, rust h_{fm}^2 estimates ranged from 0.72 to 0.90. These estimates are lower than, but comparable to those reported in (Cumbie et al. 2012), a report of similar-type field data ($h_{fm}^2 = 0.96$). An explanation for discrepancy is found in the relationship of genetic material included in the study and testing strategy. Cumbie et al. (2012) describe progeny of parents from three geographically distinct zones (Florida, Western Gulf, and Atlantic Coastal Plain) tested at four sites close to one another in southern Georgia, southern Alabama, and northern Florida. The similarity of environments and assumed differences based on provenance would both explain high heritability. These

results compare similarly to one of the most comprehensive recent rust studies (Isik et al. 2008), where half-sibling family mean heritability was greater than 0.95. In that experiment, figures were reported for data describing controlled inoculation of seedlings where all stems were exposed to a wide variety of regional strains from different rust zones. Because of the elimination of a number of environmental factors, it is an expected result that the heritability reported by Isik et al. (2008) would be higher than that for the data considered in this study.

The data considered in this study represent a large number of families deployed at test sites ranging from the North Carolina Coastal Plain to the Alabama Piedmont. Differences among these environments could contribute to relatively large GxE, resulting in lower heritability. For example, exposure to different rust strains may affect different families unequally as endemic resistance to regional inocula may be expressed differently in different regions. However, it has been demonstrated that this is likely the case for a small number of families (McKeand et al. 1999). The conclusion from these trials is that while estimates from this study are lower than that of some previous ones, repeatability of family means for rust remains to be consistently high.

Estimates of family mean heritability for forkram were lower than estimates of family mean heritability for forking observed in recent literature (Xiong et al. 2010; Cumbie et al. 2012). This could be attributable to many factors including GxE, difficulty in constructing meaningful estimates due to heterogeneous incidence among sites, or a genetic improvement of forking akin to the case of straightness. This study is likely not the decisive word on the

nature of genetic control of forking in loblolly pine, but the estimates derived from this analysis would imply that forking is primarily controlled by environment on a tree-to-tree basis, but there is meaningful stratification of family performance.

Correlations of Heritability and Trait Performance

For height and volume, site means were not significantly correlated with heritabilities at each site at $r = 0.06$ for height and $r < 0.001$ for volume (Figure 1-1). The lack of evidence of a strong correlation between site heritability and site performance indicates that site productivity does not exhibit any patterns of association with heritability. Because such a large number of sites were tested, and estimates of heritability were spread widely, it would be expected that an association between heritability and growth would be demonstrated if a meaningful trend existed. Differences in heritability for continuous traits among individual sites are most likely attributable to environmental heterogeneity and testing quality (maintenance). For this reason, heritability at a single site is perhaps more meaningfully interpreted as a diagnostic of site homogeneity and quality of test establishment and maintenance. Identification of specific components associated with differences in heritability, especially in growth traits, requires an analysis that is outside the scope of this study.

For rust incidence, the scatter plot of family mean heritability versus site mean incidence appears to show that there is no meaningful correlation ($r = 0.05$, Figure 1-2). The most intuitive interpretation of this plot is that there is a high degree of genetic control across sites, independent of rust incidence or hazard at that site. Simply, the best families are the best

families in almost any environment. This is a direct complement to the above discussion of multi-site estimates of family mean heritability. For forkram (r = -0.22, Figure 1-2), it is unclear if these data are valid for interpretation. Only 19 of 51 total sites were considered appropriate for estimating variance components on a site basis. Since this is a small subset, limited by incidence level and not a random sample, it may not capture an adequate sample to describe the true relationship of family mean heritability and stem fork and ramicorn incidence. There is no apparent association between the two parameters, so it seems most appropriate to conclude that there is no evidence of a meaningful correlation based on these data.

Genetic Correlation of Traits

Genetic correlations were strongly positive between height and volume, ranging from 0.76 to 0.82 across series (Table 1-4). Strong genetic correlations of height and volume is an expected result since height is a principal component in the volume equation; taller trees intuitively would have more volume. Genetic correlations between growth traits and straightness generally trended weakly negative; because straighter trees receive lower straightness scores, a negative relationship is favorable. One explanation for the correlation is that taller trees may grow straighter in the service of competition for light against neighboring stems. Discussion of stem and crown form and relationship to light competition can be found in (Staudhammer et al. 2009) and elsewhere. Another possible explanation is related to the comments about a decrease in heritability for straightness: the spectrum of genetic values for straightness may be small in comparison to growth traits. There is no

definitive interpretation of these correlation estimates; however, any inference drawn would be favorable for breeding loblolly pine. Namely, selection of growth and stem form is independent, or selection for more straight genotypes also selects in a favorable direction for growth genotypes.

Comments on Analytical Technique

Additional improvements could be made in analysis by accounting for spatial and pedigree correlations. The analysis of these data were assumed no relatedness of genetic entries and independence of individual tree plots. Introduction of a spatial factor could result in different heritability estimates by explaining more residual variance, resulting in a smaller phenotypic variance term. Analysis including this type of information would require data to be associated with a row-column blocking factor at time of measurement. While the test layout at each site would accommodate introduction of these blocking factors in analysis, spatial information was not readily available for each test site, and was found to be implausible to interpolate. Pedigree information was not incorporated in this analysis, so genotypes were assumed to be unrelated. This is likely not the most realistic set of assumptions because some connections likely exist even though the selections from which they descend come from all over the Southeast.

Conclusions

The data presented in this study represent one of the most thorough and modern efforts of testing of family performance for advanced-generation loblolly pine. In comparison to previous testing cycles, narrow-sense heritabilities for height and volume are increased.

Heritability in straightness is lower than previous studies indicate, but this result could be the product of intense selection of this trait and reduction in genetic variation. Binary traits are under strong genetic control, agreeing with previous studies that repeatability of family means is high. This result is especially important for rust, where there is essentially no difference in heritability related to site incidence level or hazard. Correlation of site trait performance and site heritability did not indicate any relationship, and genetic correlations of growth traits with stem form also indicate no relationship.

References

Atwood, R. A., T. L. White, and D. A. Huber. 2002. Genetic parameters and gains for growth and wood properties in Florida source loblolly pine in the southeastern United States. *Can. J. For. Res.* 32(6):1025–1038.

Barker, D. K. 2014. Potential of Loblolly Pine *(Pinus taeda L.)* as a Biofuel Feedstock. North Carolina State University. Available online at: http://gradworks.umi.com/35/84/3584284.html; last accessed May 1, 2016.

Burdon, R. D. 1977. Burdon RD. Genetic correlation as a concept for studying genotype-environment interaction in forest tree breeding. Silvae Genet 26: 168-175. *Silvae Genet.* 26:168–175.

Cornelius, J. 1994. Heritabilities and additive genetic coefficients of variation in forest trees. *Can. J. For. Res.* 24(2):372–379.

Cullis, B., B. Gogel, A. Verbyla, and R. Thompson. 1998. Spatial Analysis of Multi-Environment Early Generation Variety Trials. *Biometrics*. 54(1):1–18.

Cullis, B. R., P. Jefferson, R. Thompson, and A. B. Smith. 2014. Factor analytic and reduced animal models for the investigation of additive genotype-by-environment interaction in outcrossing plant species with application to a Pinus radiata breeding programme. *Theor. Appl. Genet.* 127(10):2193–2210.

Cumbie, W. P., F. Isik, and S. E. McKeand. 2012. Genetic Improvement of Sawtimber Potential in Loblolly Pine. *For. Sci.* 58(2):168–177.

Falconer, D. S., and T. F. C. Mackay. 1996. *Introduction to quantitative genetics*. 4. ed., [16. print.]. Pearson, Prentice Hall, Harlow. 464 p.

Gilmour, A. R., R. D. Anderson, and A. L. Rae. 1985. The Analysis of Binomial Data by a Generalized Linear Mixed Model. *Biometrika*. 72(3):593–599.

Gilmour, A. R., B. J. Gogel, B. R. Cullis, S. J. Welham, R. Thompson, D. Butler, M. Cherry, et al. 2014. ASReml user guide. Release 4.1 structural specification. *VSN Int. Ltd Hemel Hempstead HP1 1ES UK Www Vsni Co Uk*. Available online at: http://www.vsni.co.uk/downloads/asreml/release4/UserGuideStructural.pdf; last accessed May 3, 2016.

Isik, F., H. V. Amerson, R. W. Whetten, S. A. Garcia, B. Li, and S. E. McKeand. 2008. Resistance of *Pinus taeda* families under artificial inoculations with diverse fusiform rust pathogen populations and comparison with field trials. *Can. J. For. Res.* 38(10):2687–2696.

Isik, F., D. D. Boos, and B. Li. 2005a. The distribution of genetic parameter estimates and confidence intervals from small disconnected diallels. *Theor. Appl. Genet.* 110(7):1236–1243.

Isik, F., B. Goldfarb, A. LeBude, B. Li, and S. McKeand. 2005b. Predicted genetic gains and testing efficiency from two loblolly pine clonal trials. *Can. J. For. Res.* 35(7):1754–1766.

Isik, F., C. Maltecca, and J. Holland. 2017. *Genetic Data Analysis for Plant and Animal Breeding*. Springer International Publishing. Available online at: http://www.springer.com/gp/book/9783319551753; last accessed March 15, 2017.

Isik, F., C. R. Mora, and L. R. Schimleck. 2011. Genetic variation in Pinus taeda wood properties predicted using non-destructive techniques. *Ann. For. Sci.* 68(2):283–293.

Li, B., S. McKeand, and R. Weir. 1999. Impact of Forest Genetics on Sustainable Forestry—Results from Two Cycles of Loblolly Pine Breeding in the U.S. *J. Sustain. For.* 10(1–2):79–85.

Li, B. (North C. S. U., and S. E. McKeand. 1989. Stability of loblolly pine families in the Southeastern US. *Silvae Genet. Ger. FR*. Available online at: http://agris.fao.org/agris-search/search.do?recordID=DE90T0832; last accessed June 6, 2016.

McKeand, S. E., and F. E. ; Bridgwater. 1998. *A Strategy for the Third Breeding Cycle of Loblolly Pine in the Southeastern U.S.* Available online at: http://www.treesearch.fs.fed.us/pubs/1451; last accessed February 9, 2016.

McKeand, S. E., B. Li, J. E. Grissom, F. Isik, and K. J. S. Jayawickrama. 2008. Genetic parameter estimates for growth traits from diallel tests of loblolly pine throughout the southeastern United States. *Silvae Genet.* 57(3):101.

McKeand, S., B. Li, and H. V. Amerson. 1999. Genetic Variation in Fusiform Rust Resistance in Loblolly Pine Across a Wide Geographic Range. *Silvae Genet.* 48:255–260.

McKeand, S., T. Mullin, T. Byram, and T. White. 2003. Deployment of Genetically Improved Loblolly and Slash Pines in the South. *J. For.* 101(3):32–37.

Meyer, K. 2009. Factor-analytic models for genotype × environment type problems and structured covariance matrices. *Genet. Sel. Evol.* 41:21.

Moulton, R. J., and G. Hernandez. 2000. Tree planting in the United States-1998. Available online at: http://www.treesearch.fs.fed.us/pubs/5320; last accessed February 8, 2016.

Ogut, F., C. Maltecca, R. Whetten, S. McKeand, and F. Isik. 2014. Genetic Analysis of Diallel Progeny Test Data Using Factor Analytic Linear Mixed Models. *For. Sci.* 60(1):119–127.

Piepho, H. P., J. Möhring, A. E. Melchinger, and A. Büchse. 2007. BLUP for phenotypic selection in plant breeding and variety testing. *Euphytica*. 161(1–2):209–228.

Piepho, H.-P. 1998. Empirical best linear unbiased prediction in cultivar trials using factor-analytic variance-covariance structures. *Theor. Appl. Genet.* 97(1–2):195–201.

Randolph, K. C., E. B. Cowling, and D. A. Starkey. 2015. Long-Term Changes in Fusiform Rust Incidence in the Southeastern United States. *J. For.* 113(4):381–392.

Roth, B. E., E. J. Jokela, T. A. Martin, D. A. Huber, and T. L. White. 2007. Genotype×environment interactions in selected loblolly and slash pine plantations in the Southeastern United States. *For. Ecol. Manag.* 238(1–3):175–188.

SAS Institute Inc. 2011. *SAS/STAT® 9.3 User's Guide*. SAS Institute Inc., Cary, NC.

Schmidt, R. A. 2003. Fusiform rust of southern pines: A major success for forest disease management. *Phytopathology*. 93(8):1048.

Self, S. G., and K.-Y. Liang. 1987. Asymptotic Properties of Maximum Likelihood Estimators and Likelihood Ratio Tests Under Nonstandard Conditions. *J. Am. Stat. Assoc.* 82(398):605–610.

Shelbourne, C. J. A., and R. W. Stonecypher. 1971. The inheritance of bole straightness in young loblolly pine. *Silvae Genet.* 20:151–156.

Sherrill, J. R., B. P. Bullock, T. J. Mullin, S. E. McKeand, and R. C. Purnell. 2011. Total and merchantable stem volume equations for midrotation loblolly pine (Pinus taeda L.). *South. J. Appl. For.* 35(3):105–108.

Sierra-Lucero, V., S. E. McKeand, D. A. Huber, D. L. Rockwood, and T. L. White. 2002. Performance differences and genetic parameters for four coastal provenances of loblolly pine in the southeastern United States. *For. Sci.* 48(4):732–742.

Smith, A. B., B. R. Cullis, and R. Thompson. 2005. The analysis of crop cultivar breeding and evaluation trials: an overview of current mixed model approaches. *J. Agric. Sci.* 143(6):449–462.

Staudhammer, C. L., E. J. Jokela, and T. A. Martin. 2009. Competition dynamics in pure- versus mixed-family stands of loblolly and slash pine in the southeastern United States. *Can. J. For. Res.* 39(2):396–409.

Svensson, J. C., S. E. McKeand, H. L. Allen, and R. G. Campbell. 1999. Genetic variation in height and volume of loblolly pine open-pollinated families during canopy closure. *Silvae Genet.* 48:204–208.

Venables, W. N., and D. M. Smith. 2014. the R Core Team. *Introd. R Notes R Program. Environ. Data Anal. Graph. URL Ran R-Proj. Orgdocmanualsr-ReleaseR-Intro Pdf*.

Wickham, H., W. Chang, and M. H. Wickham. 2013. Package "ggplot2." Available online at: http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.449.8078&rep=rep1&type=pdf; last accessed October 14, 2016.

Xiang, B., B. Li, and F. Isik. 2003. Time trend of genetic parameters in growth traits of Pinus taeda L. *Silvae Genet.* 52(3–4):114–120.

Xiong, J. S., F. Isik, S. E. McKeand, and R. W. Whetten. 2010. Genetic variation of stem forking in loblolly pine. *For. Sci.* 56(5):429–436.

Zapata-Valenzuela, J. 2012. USE OF ANALYTIC FACTOR STRUCTURE TO INCREASE HERITABILITY OF CLONAL PROGENY TESTS OF Pinus taeda L. *Chil. J. Agric. Res.* 72(3):309–315.

Zobel, B., and J. Talbert. 1984. Applied forest tree improvement. :xv + 505 pp.

Table 1-1: Means with standard errors in parentheses of traits for each test series. Straightness is assessed on a 1 to 6 scale where 1 is the straightest. Rust and forkram are binary traits where incidence is recorded as 1 and absence is 0. The number of trees for each test series is n.

Series	Height (m)	Volume (dm^3)	Straightness	Rust	Forkram	N
CPMX1	7.7 (0.013)	51.3 (0.205)	3.01 (0.010)	0.31 (0.004)	0.18 (0.003)	15807
CPMX2	6.6 (0.019)	38.8 (0.287)	3.23 (0.015)	0.33 (0.005)	0.31 (0.005)	8870
CPMX3	8.4 (0.020)	54.6 (0.320)	3.25 (0.012)	0.37 (0.005)	0.28 (0.004)	10190
CPMX4	6.7 (0.021)	41.5 (0.266)	3.27 (0.016)	0.39 (0.005)	0.17 (0.005)	7520
PPMX1	6.7 (0.013)	39.3 (0.193)	3.46 (0.013)	0.12 (0.004)	0.20 (0.005)	7100
PPMX2	7.0 (0.017)	44.9 (0.235)	3.37 (0.011)	0.31 (0.005)	0.35 (0.005)	9286
PPMX3	4.9 (0.019)	20.2 (0.154)	3.44 (0.023)	0.23 (0.008)	0.31 (0.009)	2851

Table 1-2: Narrow-sense individual-tree heritabilities for quantitative traits for each test series; standard errors of the estimates are in parentheses.

Series	Height	Volume	Straightness
CPMX1	0.23 (0.041)	0.15 (0.029)	0.12 (0.024)
CPMX2	0.20 (0.039)	0.11 (0.027)	0.20 (0.038)
CPMX3	0.23 (0.041)	0.17 (0.033)	0.15 (0.029)
CPMX4	0.20 (0.042)	0.22 (0.046)	0.17 (0.034)
PPMX1	0.16 (0.037)	0.21 (0.046)	0.15 (0.035)
PPMX2	0.36 (0.062)	0.29 (0.055)	0.15 (0.033)
PPMX3	0.38 (0.093)	0.20 (0.065)	0.13 (0.042)

Table 1-3: Family-mean heritabilities on a series basis for binary traits; standard errors of the estimates are in parentheses. It is standard practice for analysis to be performed with trait incidence between 0.20 and 0.80 for binary traits, but models converged for evaluations of each series and trait even when this was not the case (forkram: CPMX1 and CPMX4; rust: PPMX1).

Series	Forkram	Rust
CPMX1	0.51 (0.129)	0.74 (0.054)
CPMX2	0.50 (0.166)	0.72 (0.068)
CPMX3	0.50 (0.132)	0.90 (0.041)
CPMX4	0.61 (0.221)	0.80 (0.064)
PPMX1	0.49 (0.255)	0.54 (0.137)
PPMX2	0.60 (0.127)	0.84 (0.056)
PPMX3	0.31 (0.172)	0.13 (0.137)

Table 1-4: Genetic correlations between pairs of traits for each test series.

Series	(Height, Volume)	(Height, Straightness*)	(Volume, Straightness*)
CPMX1	0.82	-0.13	-0.08
CPMX2	0.78	-0.13	-0.09
CPMX3	0.76	-0.19	-0.12
CPMX4	0.82	-0.13	-0.07
PPMX1	0.78	-0.09	-0.04
PPMX2	0.78	-0.04	0.03
PPMX3	0.84	-0.12	-0.06

* A negative correlation with straightness is favorable since straighter trees have lower values.

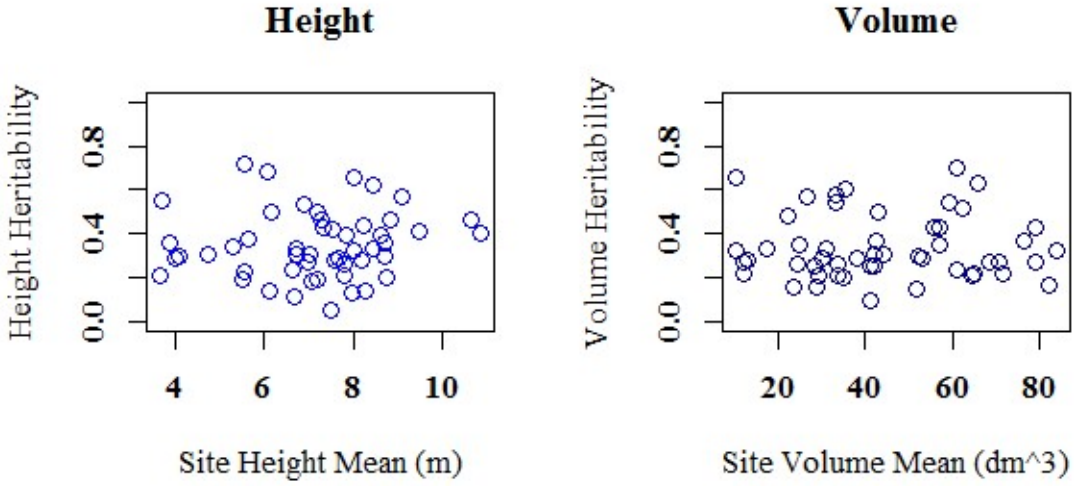

Figure 1-1: Scatter plots of site means versus site narrow-sense individual-tree heritability for height and volume. No obvious trend exists for either trait ($r = 0.06^{NS}$ for height and $r < 0.001^{NS}$ for volume). For 51 total sites, the lowest significant correlation would be $r \approx 0.28$.

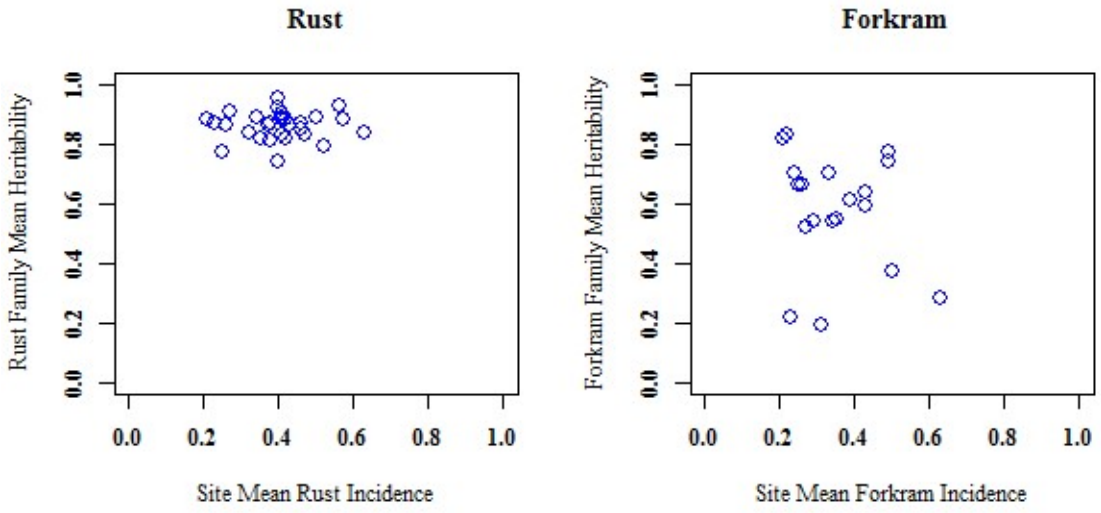

Figure 1-2: Scatter plots for family mean heritabilities for binary traits, rust incidence and forkram incidence. No obvious trend exists for either trait ($r = 0.05^{NS}$ for rust and $r = -0.22^{NS}$ for forkram).

Chapter 2: Estimates of Heritability and Genotype by Environment Interaction in Multi-Environmental Data Analysis in Loblolly Pine Progeny Tests

Abstract

Loblolly pine is the most important and widely planted forest tree in the Southeast US, and essentially all the planting stock is progeny of genetically improved selections. These selections have progeny that are tested in a large number of environments in order to produce predictions that apply across the entire deployment range. These multi-environmental trials can help to understand genotype by environment (GxE) interaction. The primary causes of statistical significance of GxE are commonly the scale differences in the performance of selections rather than rank changes of selections in different environments. Multi-environmental trials also provide insight on the degree of additive and environmental variance for the traits important for breeding.

In this study, a large number of polymix progeny tests in the Coastal and Piedmont breeding zones of loblolly pine (*Pinus taeda* L.) were analyzed to estimate variance components and to understand GxE interactions. We used the Factor Analytic (FA) covariance structure for the compound term, which is genotype nested within environments, to model GxE. This structure approximates the unstructured (US) covariance structure. The FA structure is favored over US structure because it is parsimonious. The FA structure model was compared to the scaled identity and uniform correlation structures using model fit statistics; model likelihood, AIC, and the average standard error of differences between pairs of predictions.

From the standpoint of model fit, the FA structure was found to be optimal for fitting the data. For the cross-classified model, GxE was found to be statistically significant at $\alpha = 0.001$

based on Likelihood Ratio Tests; however, genetic correlations were found to be high for all series, indicating that GxE is principally associated with differences in scale effect in each test series. For this reason, we conclude that ranking of genotypes is largely consistent among environments. Heritability estimates were obtained from the final model assuming complete balanced data. These estimates were dramatically higher than those based on estimates from the cross-classified model.

Introduction

Loblolly pine (*Pinus taeda* L.) is the most important forest tree in the Southeast, representing the vast majority (80%) of regeneration in the southern US (Li et al. 1999). There are about 11 million hectares of pine plantations in the south, 79% of which is established with loblolly pine (Moulton and Hernandez 2000). Today, all planted loblolly pine is genetically improved material (McKeand et al. 2003). This advanced genetic material is the product of many decades of breeding, testing, and selection efforts carried out by private companies and university-based industry cooperatives; North Carolina State University Cooperative Tree Improvement Program (NCSUCTIP), the Cooperative Forest Genetics Research Program (CFGRP) at the University of Florida, and the Western Gulf Forest Tree Improvement Program (WGFTIP) directed by the Texas A&M Forest Service.

Estimation of genetic parameters is an important step in prediction of genetic gain in a breeding population. Genetic parameters inform the breeder about the degree to which a trait might be inherited (heritability), and the degree to which trait performances are correlated due to genetic effects. Producing these statistics to characterize a breeding population is necessary for making decisions for selection and defining breeding and deployment zones (Zobel and Talbert 1984; Falconer and Mackay 1996). In forest tree progeny testing, selections are usually tested in a range of environments to draw general conclusions for a deployment zone. Multi-environmental trials (METs) are useful for understanding the repeatability of genetic performances across sites in order to rank genotypes.

Because METs are intended to provide information about the performance of genotypes across many environments, it is of interest to test for the interaction of genetic effects across different environments. Statistical significance of the GxE term can occur because of rank changes of family performances among sites or because of scale differences among families. GxE has been found to be statistically significant in numerous studies of loblolly pine. (Li and McKeand 1989) and (Roth et al. 2007) both reported significant ($\alpha < 0.01$) GxE interactions. Li and McKeand concluded that GxE was principally caused by the scale effect and concluded that the highest performing genotypes tend to rank highly across all environments (Li and McKeand 1989). Roth et al. reported rank changes of genotypes, but only for eight genetic entries (Roth et al. 2007). These outcomes and others motivate further investigation into analytical methods available for assessment of genotype performance across multiple environments and its interpretation.

Traditionally, this genotype by environment (GxE) interaction is evaluated in cross-classified models, where selections tested in different trials are assumed to have uniform correlation and that genetic variances among environments are homogeneous. It is also assumed that sites have the same residual variance. These residual errors are assumed to be independently and identically distributed (IID) at a given site (Cullis et al. 1998). Because forest tree progeny tests require large tracts of land and are replicated in multiple environments, data from METs in forest tree progeny testing is inherently noisy. Issues often arise in analysis of METs with unrealistic assumptions about heterogeneity of test environments, unbalanced data, and potential of differing performance of genetic material at different sites (Piepho et al.

2007). Test sites vary widely in environmental factors, site quality, and test maintenance, and different genotypes may exhibit a non-homogeneous response to differences in environments.

For the cross-classified model, the null hypothesis for GxE in these models is that variances are identically and independently distributed (IID) and imply an assumption of homogeneity of residual variances at sites and independence of genotype performance among sites. While this type of analysis was common for many years in plant and tree breeding, more complex variance structures are necessary to account for heterogeneity in the data (Smith et al. 2005). The cross-classified model does not exploit the observed heterogeneity among sites, resulting in under-fit models in analysis of MET trials (Ogut et al. 2014). Appropriate analysis of MET data requires choosing appropriate variance structures that account for heterogeneity among sites.

The Factor Analytic (FA*k*) variance structure has been suggested to fully describe GxE, because it uses a smaller number of parameters than an unstructured (US) variance structure specification (Smith et al. 2005; Ogut et al. 2014) while accounting for genetic variances and covariances among sites (Piepho 1998). The FA*k* structure approximates the US structure, using the multivariate factor analysis approach to reduce the dimensions of the covariance matrix. It makes the model more parsimonious and thus more likely to converge the parameter estimates. By accounting for GxE, the FA*k* structure also allows for more accurate estimates of heritability compared to cross-classified models. Factor analytic variance

structures have been demonstrated to improve goodness-of-fit for linear models and produce increased estimates of heritability (Zapata-Valenzuela 2012; Cullis et al. 2014; Ogut et al. 2014) for METs.

The FA*k* variance structure estimates MET-wide "intercepts" for genetic families and "slopes" for individual sites based on the loading associated with that site. These components are used to produce Best Linear Unbiased Predictions (BLUPs), a linear combination that describes the genetic value of a selection at any given site. In this way, GxE can be accounted for and explained for each level of each factor (genotype and site) instead of being absorbed into a grouped variance component. More rigorous statistical justification and explanation of the FA*k* variance structure can be found in Meyer (Meyer 2009) and Cullis et al. (Cullis et al. 2014).

In this study, we investigate the FA*k* variance structure in generalized form, specifically the Extended Factor Analytic (XFA*k*) variance structure, compared to the traditional cross classified model. The XFA*k* structure is a different parameterization of the FA model that helps with model convergence by adding an additional (dummy variable) to the design matrix and fixing it to zero. The XFA model is also compared to the CORUV and the CORUH structures. The CORUV assumes constant genetic correlation among sites and homogeneity of genetic variances among sites, while CORUH assumes constant genetic correlation between sites with heterogeneous variances at sites.

Interpretation of GxE using the relaxed assumptions not only explains the heterogeneity in the data, but also aids interpretation of heritability for multiple sites. If GxE is important because of scale effect differences among genotypes, it can be assumed that heritability for a certain set of genotypes is a random variable from a sampling distribution, because GxE is caused by different additive variances among sites ((Isik et al. 2005a). In this way, heritability can be estimated by interpreting site additive and phenotypic variances as random samples.

The data examined in this study represent one of the most geographically diverse testing efforts in the third cycle of the NCSUCTIP loblolly pine breeding program. The objectives of this study are: (1) Compare linear mixed models with different variance-covariance structures in multi-environmental models to explain GxE, and (2) Estimate genetic parameters (heritability and pair-site genetic correlations) based on the models.

Materials and Methods

Material

Data were collected from four Coastal breeding population test series and three Piedmont breeding population test series with a variety of number of sites within each series. Each of these test sites was established and measured as part of the collective effort of NCSUCTIP and its cooperating members in mainline 3rd-Cycle breeding.

The 3rd-Cycle mainline effort was focused on three breeding regions as described in Appendix Figure A-1. These regions represented a grouping of the 2nd-Cycle breeding and testing regions: the Northern region (Virginia and Northern North Carolina), the Coastal region (Atlantic Coastal Plains of southern NC, SC, GA, and the Lower Gulf Coast of AL and MS), and the Piedmont region (inland zones of South Carolina and Georgia and the Upper Gulf Coast of AL, MS, and TN).

The mating scheme in each series was identical: polymix crossing to produce half-sibling families to predict general combining ability of parents. Polymix, also known as pollen mix or PMX (henceforth called PMX), refers to crossing a specified mix of pollen from known male parents to known female parents. This mating strategy uses a common bulked pollen source to mate large number of female parents, reducing variation of genetic input of male parents within each provenance. Thus, each progeny of a PMX cross has one female parent in common and theoretically different male parents. For each breeding region, twenty well-characterized parents with average breeding values were selected to represent the pollen donor in a region. Pollen was collected from ramets of each male parent and blended using the pollen germination percentage as the weight factor. Details of the mating design are reported by (McKeand and Bridgwater 1998).

To connect tests series, a checklot system was developed for each region. Checklots are bulked seeds from average performing families. These checklots are CCK, PCK, NCK for

the Coastal, Piedmont, and Northern regions, respectively. These checklots were developed by crossing the pollen mix for each region onto a subset of ten of the twenty parents. That is, for the Coastal region, the parentage of CCK would be a subset of ten Coastal female parents crossed with a pollen blend of all 20 male parents. Additionally, seven well-characterized parents were crossed with the pollen mix for each respective series and incorporated into the testing. Four of these families were PMX crosses with two high-performing and two poor-performing parents from 1st- and 2nd- Cycle testing.

Experimental Design

Half-sib families of a given PMX test series were tested using a randomized complete block design with 20 blocks at each site. Single-tree-plots were used as experimental units. Approximately 70 half-sib families were included at each site, including three checklots (CCK, PCK, NCK) and seven common family checks that were used for connection. About 1400 trees were planted at each site at the time of establishment. The experiment was replicated at different environments, ranging from three to 13 sites for a given test series (see Appendix Table A-13 for details).

Measurement Traits

Tests were measured between ages four and seven years. Height and diameter at breast height (DBH) were measured to the nearest 0.1 foot and 0.1 inch, respectively. These measurements were converted into meters and centimeters. Inside-bark volume (in cubic

decimeters) was calculated according to Sherrill et al. (2011). Because volume is the only trait considered in this study, commentary on other measured traits is excluded.

Statistical analysis

Cross classified mixed model

The following linear mixed model was used to analyze the data on a series basis.

$$\boldsymbol{y_{ijkl} = \mu + S_i + R(S)_{j(i)} + F_k + SF_{ik} + e_{ijkl}} \quad (2\text{-}1)$$

where y_{ijk} is the response variable, μ is the overall mean response, S_i is the fixed site effect, $R(S)_{j(i)}$ is the random blocking effect nested within site ~N(0, σ^2_{rb}), F_k is the random effect of female parent ~N(0, σ^2_f), SF_{ik} is the site-female interaction term (GxE) ~N(0, σ^2_{sf}), and e_{ijkl} is the residual error ~N(0, σ^2_e). All random effects and errors are assumed to be IID. This is a typical cross-classified model with usual ANOVA assumptions.

Female variance component was divided by the sum of the female variance component and female by site interaction variance components to estimate type B genetic correlation as suggested by (Burdon (Burdon 1977):

$$\boldsymbol{r_B = \frac{\sigma^2_f}{\sigma^2_f + \sigma^2_{fs}}} \quad (2\text{-}2)$$

Where σ^2_f is the family genetic variance and σ^2_{fs} is the GxE effect. This statistic has a range of 0 and 1, with higher values suggesting lack of significant GxE interactions.

Statistical significance of the GxE term was assessed using the residual maximum likelihood ratio test (LRT) from two nested models with the same fixed effects (Self and Liang (Self and Liang 1987). The model in equation (2-1) would be the full model. The same model without the GxE term would be the reduced model.

$$\boldsymbol{\chi^2 = -2[LogL(full\ model) - LogL(reduced\ model)]} \quad (2\text{-}3)$$

Here, χ^2 is a Chi-square distributed random variable representing the difference in LogL. This statistic has 1 degree of freedom since the full model has one additional random effect (GxE). Significance of the Chi-square variable suggests that the GxE term is significant.

Relaxing assumptions of the mixed models

The cross-classified model assumptions (uniform correlation between pairs of sites and homogenous genetic and residual variance structures) are not realistic in forest trees progeny tests. We first relaxed the homogenous residual structure by fitting a block diagonal residual variance structure. That is, each environment has different residual error variance, and the residual errors are identical and independent within an environment. The model fit statistics improved substantially. In order to explain the heterogeneity in family and family by environment interaction effects, a genetic variance structure assuming uniform correlations among sites with homogenous genetic variance (CORUV) was fit. The generalized equation is shown below:

$$\boldsymbol{y_{ijkl} = \mu + S_i + R(S)_{j(i)} + u_{ik} + e_{ijkl}} \quad (2\text{-}4)$$

Where y_{ijkl} is the response variable (volume), μ is the mean, S_i is the fixed site effect, $R(S)_{j(i)}$ is the random blocking effect nested within site ~N(0, σ^2_{rs}), u_{ik} is the random covariance of genotype at a pair of sites, (*i,k*), where the number of sites *t* = *i* = *k*. In this compound term the genotypes are nested within sites. e_{ijkl} is the residual error ~N(0, $\sigma^2_{e_i}$). This model has the same number of parameters, but parameterization is different as the genetic and GxE terms are combined in one term. The variance components from CORUV structure produced one genetic variance (family effect) and one correlation (equal to type B genetic correlation from the cross-classified model). The assumptions of homogeneous genetic correlations in the CORUV structure were further relaxed by fitting a heterogeneous genetic covariance structure with uniform correlation between pairs of sites (CORUH) and Factor Analytic covariance structure (XFA) for u_{ik} term.

Results of implementing XFA structure

Genetic correlations between all pairs of sites as well as unique site loadings and site specific variances are estimated by specifying the factor analytic variance structure. Pair-site covariances are calculated as a linear combination of site loadings and estimated multiplicative factors. Using the "heatmap.2" function in the ggplot2 package in R (Wickham et al. 2013), symmetric heatmap images of these site-site genetic correlations were produced to visualize the correlations between sites. Percent genetic variance explained by the multiplicative terms in the factor analytic structure were reported as direct model output. This term describes the amount of genetic variance retained in the *k*-factor estimation of the covariance matrix. Explicitly, it is the amount of genetic variance explained as a linear

combination by the first *k* factors and the site loadings. Ideally, 100% of all of the variance would be captured, but this is not always the case in a dimension reduction exercise. This figure can be explained as the "cost" of a more parsimonious model.

Estimation of heritability

Narrow-sense individual-tree and family-mean heritability estimates were obtained from models to compare their efficiency for selection and gain prediction. Estimates were obtained for each test series. For the cross-classified model, narrow-sense individual-tree (h_i^2) and family-mean heritability (h_f^2) were estimated from linear combinations of variance components for each test series:

$$\boldsymbol{h_i^2} = \frac{\boldsymbol{4\sigma_f^2}}{\boldsymbol{\sigma_f^2 + \sigma_{sf}^2 + \overline{\sigma_e^2}}} \tag{2-5}$$

$$\boldsymbol{h_f^2} = \frac{\boldsymbol{\sigma_f^2}}{\boldsymbol{\sigma_f^2 + \frac{\sigma_{sf}^2}{s} + \frac{\overline{\sigma_e^2}}{sn}}} \tag{2-6}$$

where $4\sigma_f^2$ is the additive variance assuming families consist of half-sibs, σ_f^2 is the family variance, σ_{sf}^2 is the site-family interaction (i.e. GxE), and $\overline{\sigma_e^2}$ is the pooled residual variance across sites, s is the number of sites, and n is the harmonic mean number of trees per family per site. For this calculation, the phenotypic variance pool includes additive family variance, non-additive GxE variance, and residual variance across all sites.

For the factor analytic structure, heritability estimates were calculated using linear combinations of variance components. Family variance components were averaged across

site assuming completely balance data. Similarly, residual variance components were averaged across sites. Narrow-sense individual tree heritability is calculated as described in (Isik et al. 2017):

$$\boldsymbol{h_i^2 = \frac{4 * \overline{\sigma_{fi}^2} * \overline{\rho_{fi}}}{\overline{\sigma_{fi}^2} + \overline{\sigma_e^2}}} \quad (2\text{-}7)$$

and family mean heritability was calculated as

$$\boldsymbol{h_f^2 = \frac{\overline{\sigma_{fi}}}{\frac{\overline{\sigma_{fi}^2}}{s} + (s-1)\frac{\overline{\sigma_{fi}}}{s} + \frac{1}{s^2}\frac{\overline{\sigma_e^2}}{n}}} \quad (2\text{-}8)$$

where $\overline{\sigma_{fi}}$ is the mean genetic covariance between pairs of sites sites, $\overline{\rho_{fi}}$ is the average pari-site genetic correlation, $\overline{\sigma_{fi}^2}$ is the average within-site family variance, and $\overline{\sigma_e^2}$ is the mean residual variance for all sites. Here, we assume that the site variances also implicitly describe GxE, and the average genetic correlation multiplied by the average site variance approximates the mean additive variance at each site. For family mean heritability, *s* is the number of sites, and *n* is the number of trees per family per site. In this way, we treat each site of the MET as a random variable from a sampling distribution. Justification and formal explanation of the motivation for these methods is found in Isik et al. (2005).

Results

Model fit statistics for the ANOVA-type IID model and models with XFA1, XFA2, CORUH, and CORUV variance structure specifications suggest that a more complex variance structure that accommodates both site-specific genotype variances and genetic covariances among sites is a better fit for describing these data than the cross-classified model, which explicitly

defines a unique GxE term (Table 2-2). We observed consistent decrease in AIC and BIC model fit statistics, demonstrating an improvement in goodness-of-fit. From a model selection standpoint, the XFA1, XFA2, and CORUH variance structures were the best models.

For the ANOVA-type IID model, evaluation of GxE did not yield clear results. Depending on the test series, Type-B genetic correlations for this model ranged from 0.41 to 0.61. The GxE interaction effect was significant at an $\alpha = 0.001$ level for each series based on the likelihood ratio tests previously described (Table 2-1). Because statistically significant GxE could be due to family rank changes between sites and scale differences of families at different environments, type B genetic correlations are not particularly informative. Performance of genotypes across multiple sites is never expected to be independent in practice, since resemblance of relatives is expected to have some sort of continuity across environments. The major drawback of cross-classified models and compound symmetry models is that they assume a uniform genetic correlation between sites.

The factor analytic variance structure explicitly described the heterogeneous structure of GxE (Table B-2 to B-8). The mean correlation for test series is shown in Table 2-3. Mean correlations for series ranged from 0.66 for CPMX1 to 0.86 for PPMX3. Overall, genetic correlations were high across sites. This result is more intuitively understood by examining heatmaps for each series (Figure 2-1 and Appendix Figures B-1 to B-6), where strong

correlations are demonstrated for most sites, with a small number of errant sites seeming to show poor relationship with one another.

The mean percent variance explained by genetic covariance effects for each site in a series ranged from 0.61% to 93.3% (Table 2-4). Here, higher percentages suggest that definable, additive effects are primarily responsible for genetic variance. Further, the loading associated with the *k* multiplicative factors for sites within a series were informative in the way of describing the relationship between sites. For example, in CPMX1, loadings for factor 1 were all essentially the same magnitude, suggesting that each site contributed to the variance at different levels, but in the same "direction." The second factor was weighted heavily toward site 5, suggesting that this site in particular had something different about it than the other sites. This paradigm held true in view of the correlations among sites, where site 5 had weaker correlations with most of the other sites in the series.

Individual-tree narrow-sense and family-mean heritability estimates are presented in Tables 2-5 and 2-6. Heritability estimates from more complex models were significantly greater for each test series. Narrow-sense heritability estimates based on variance components derived from the ANOVA-type IID model ranged from 0.11 in CPMX2 to 0.29 in PPMX2. For factor-analytic models, these estimates ranged from 0.17 in CPMX1 to 0.40 in PPMX2. The per-series increase was even more dramatic for family-mean heritability. For the ANOVA-type IID model, family-mean heritability estimates ranged from 0.30 in CPMX2 to 0.55 in PPMX2. In contrast, these estimates ranged from 0.69 in PPMX3 to 0.94 in CPMX1 for the

FA model. It is important to note that these heritability estimates are based on roughly the same site-specific variances, but the methods for calculating these estimates can be quite complex when data are not balanced.

Discussion

Strictly from the perspective of models fitting data, statistics for the models considered in this study suggest that implementation of the one- and two-factor XFA structures represented an improvement in goodness of fit relative to the IID models in each testing series. We conclude that the FA approach is superior in comparison to the standard cross-classified IID model, likely due to its ability to describe GxE and accommodate heterogeneous variances. This is an expected result and has been widely reported in the literature (Zapata-Valenzuela 2012; Cullis et al. 2014; Ogut et al. 2014). From a statistical standpoint, the advantage of the XFA*k* variance structure is that it approximates unstructured (US) genetic covariances with much smaller number of parameters (Piepho 1998). The US structure assumes that sites have different variances, and pairs of sites have different genetic covariances. Namely, all pairs of sites have different genetic correlations and a unique genetic and residual variance. This assumption of complete heterogeneity requires the estimation of an unwieldy number of parameters, losing degrees of freedom, and requiring more computation resources. Because the XFA*k* model accommodates heterogeneity more with more parsimoniously than the US model while accommodating flexible covariance assumptions, it has lower AIC and BIC.

The XFA2 variance structure was overall the best according to model fit statistics. However, it is noteworthy that the CORUH structure, specifying heterogeneous variances across sites with a common genetic correlation for all pairs of sites, was often close in model fit and was occasionally better. The most intuitive explanation for this result is that if genetic correlations are high for all pairs of sites, the correlations would likely be close to homogeneous. If indeed correlations among sites are homogeneous, the CORUH model would be preferred for fit statistics because it would be more parsimonious than the XFA2 model. Simply, instead of estimating the covariance matrix with two factors, *p* site loadings for each factor, and *p* site-specific variances, it would be estimated with *p* site specific variances and a single correlation term. For this reason, instances where the CORUH model is superior with respect to AIC or BIC, it is likely because genetic correlations are similar. Therefore, because the homogeneous correlation model is not as informative, the XFA2 model is preferred for evaluation of these data.

Employing a variance structure that accommodates non-specific correlations of genotypes among sites is also more intuitive for describing data for multiple environments. Incorporating a set of variance assumptions that are not restricted to strictly identical residual variances represents a much more realistic approach for attempting to describe this type of data. An example demonstrating the importance of this result is the CPMX1 series, where site 5 exhibits poor correlation, but other sites are highly correlated to one another. This result is an important one because while the IID model would require accounting for this information by an increase in GxE, the FA structure, while not explicitly defining a cause for

the aberration, explains it incidentally. While it is not based on formal statistical testing, it can be intuitively seen that it would be misleading to ascribe a low heritability for an entire group of genotypes based on what ultimately is the aberration of one particular site. This can be understood visually with a heatmap of genetic correlations, where the disparity of site 5 is obvious in view of the others (Figure 2-1). Heatmaps for other series are found in Appendix Figures B-1 through B-6.

The statistical significance of GxE in the ANOVA-type IID model serves as confirmation that selecting a model with assumptions of homogeneous error variances and genetic variances is not appropriate for describing these data. Genetic correlations between pairs of sites were very high when heterogeneity was accounted with more complex variance-covariance structures. The cross-classified model does not allow for describing meaningful sets of environmental delineations. For example, yearly precipitation, and minimum, and mean temperatures, have been conjectured by (Roth et al. 2007) to be important factors to account for differences in genotype performances among sites. Any of these variables could cause genotypes to rank differently among sites. The advantage of using the FA covariance structure is that GxE can be better explained. The results showed that GxE for volume growth in loblolly pine was negligible for a given test series.

Because FA structures result in better-fitting models, they produced heritability estimates substantially higher than those of cross classified models (Tables 2-5 and 2-6). GxE is described with a series of pair-site genetic covariances, so it is no longer considered a ‘black

box' term as in the case of the cross-classified IID model and thus is not part of the phenotypic variance. Therefore, the 'penalty' of high GxE associated with differences in scale of family rank is overcome, and heritability is increased in magnitude and theoretical accuracy. FA-based estimates of both narrow-sense and family-mean heritability imply that volume is more heritable and that repeatability of family means is much higher than estimates with the cross-classified model would suggest. The method used to calculate estimates of heritability in this study assume completely balanced data. If the data were imbalanced across sites, the heritability estimates would be adjusted according to the harmonic means of families per site. Although the assumption of completely balanced data is flawed, relative balance across sites and consistency of method motivated exclusion of the harmonic mean term. The clear outcome of this study shows that the FA structure is preferable to analyzing MET data using the traditional cross-classified model.

Conclusions

The factor analytic variance structure was found to be the optimal structure to fit the data for each series according to model fit statistics. Although GxE was found to be statistically significant based on the cross classified model, we found that it was not important with respect to prediction of ranks across multiple environments. Genetic correlations among sites were high for each test series, so GxE was principally associated with scale differences among genotype ranks rather than switches in rank change among sites; these are the two possible explanations for high GxE. Although there is some unexplained GxE because genetic correlations are not perfect, the overwhelming trend is consistency of family rank

among sites. Because GxE is accounted for with genetic correlation, it is ignored in estimates of heritability. Therefore, heritability estimates were dramatically increased over those from the cross-classified model.

References

Atwood, R. A., T. L. White, and D. A. Huber. 2002. Genetic parameters and gains for growth and wood properties in Florida source loblolly pine in the southeastern United States. *Can. J. For. Res.* 32(6):1025–1038.

Barker, D. K. 2014. *Potential of Loblolly Pine (Pinus taeda L.) as a Biofuel Feedstock*. North Carolina State University. Available online at: http://gradworks.umi.com/35/84/3584284.html; last accessed May 1, 2016.

Burdon, R. D. 1977. Burdon RD. Genetic correlation as a concept for studying genotype-environment interaction in forest tree breeding. Silvae Genet 26: 168-175. *Silvae Genet.* 26:168–175.

Cornelius, J. 1994. Heritabilities and additive genetic coefficients of variation in forest trees. *Can. J. For. Res.* 24(2):372–379.

Cullis, B., B. Gogel, A. Verbyla, and R. Thompson. 1998. Spatial Analysis of Multi-Environment Early Generation Variety Trials. *Biometrics*. 54(1):1–18.

Cullis, B. R., P. Jefferson, R. Thompson, and A. B. Smith. 2014. Factor analytic and reduced animal models for the investigation of additive genotype-by-environment interaction in outcrossing plant species with application to a Pinus radiata breeding programme. *Theor. Appl. Genet.* 127(10):2193–2210.

Cumbie, W. P., F. Isik, and S. E. McKeand. 2012. Genetic Improvement of Sawtimber Potential in Loblolly Pine. *For. Sci.* 58(2):168–177.

Falconer, D. S., and T. F. C. Mackay. 1996. *Introduction to quantitative genetics*. 4. ed., [16. print.]. Pearson, Prentice Hall, Harlow. 464 p.

Gilmour, A. R., R. D. Anderson, and A. L. Rae. 1985. The Analysis of Binomial Data by a Generalized Linear Mixed Model. *Biometrika*. 72(3):593–599.

Gilmour, A. R., B. J. Gogel, B. R. Cullis, S. J. Welham, R. Thompson, D. Butler, M. Cherry, et al. 2014. ASReml user guide. Release 4.1 structural specification. *VSN Int. Ltd Hemel Hempstead HP1 1ES UK Www Vsni Co Uk*. Available online at: http://www.vsni.co.uk/downloads/asreml/release4/UserGuideStructural.pdf; last accessed May 3, 2016.

Isik, F., H. V. Amerson, R. W. Whetten, S. A. Garcia, B. Li, and S. E. McKeand. 2008. Resistance of *Pinus taeda* families under artificial inoculations with diverse fusiform rust pathogen populations and comparison with field trials. *Can. J. For. Res.* 38(10):2687–2696.

Isik, F., D. D. Boos, and B. Li. 2005a. The distribution of genetic parameter estimates and confidence intervals from small disconnected diallels. *Theor. Appl. Genet.* 110(7):1236–1243.

Isik, F., B. Goldfarb, A. LeBude, B. Li, and S. McKeand. 2005b. Predicted genetic gains and testing efficiency from two loblolly pine clonal trials. *Can. J. For. Res.* 35(7):1754–1766.

Isik, F., C. Maltecca, and J. Holland. 2017. *Genetic Data Analysis for Plant and Animal Breeding*. Springer International Publishing. Available online at: http://www.springer.com/gp/book/9783319551753; last accessed March 15, 2017.

Isik, F., C. R. Mora, and L. R. Schimleck. 2011. Genetic variation in Pinus taeda wood properties predicted using non-destructive techniques. *Ann. For. Sci.* 68(2):283–293.

Li, B., S. McKeand, and R. Weir. 1999. Impact of Forest Genetics on Sustainable Forestry—Results from Two Cycles of Loblolly Pine Breeding in the U.S. *J. Sustain. For.* 10(1–2):79–85.

Li, B. (North C. S. U., and S. E. McKeand. 1989. Stability of loblolly pine families in the Southeastern US. *Silvae Genet. Ger. FR*. Available online at: http://agris.fao.org/agris-search/search.do?recordID=DE90T0832; last accessed June 6, 2016.

McKeand, S. E., and F. E. ; Bridgwater. 1998. *A Strategy for the Third Breeding Cycle of Loblolly Pine in the Southeastern U.S.* Available online at: http://www.treesearch.fs.fed.us/pubs/1451; last accessed February 9, 2016.

McKeand, S. E., B. Li, J. E. Grissom, F. Isik, and K. J. S. Jayawickrama. 2008. Genetic parameter estimates for growth traits from diallel tests of loblolly pine throughout the southeastern United States. *Silvae Genet.* 57(3):101.

McKeand, S., B. Li, and H. V. Amerson. 1999. Genetic Variation in Fusiform Rust Resistance in Loblolly Pine Across a Wide Geographic Range. *Silvae Genet.* 48:255–260.

McKeand, S., T. Mullin, T. Byram, and T. White. 2003. Deployment of Genetically Improved Loblolly and Slash Pines in the South. *J. For.* 101(3):32–37.

Meyer, K. 2009. Factor-analytic models for genotype × environment type problems and structured covariance matrices. *Genet. Sel. Evol.* 41:21.

Moulton, R. J., and G. Hernandez. 2000. Tree planting in the United States-1998. Available online at: http://www.treesearch.fs.fed.us/pubs/5320; last accessed February 8, 2016.

Ogut, F., C. Maltecca, R. Whetten, S. McKeand, and F. Isik. 2014. Genetic Analysis of Diallel Progeny Test Data Using Factor Analytic Linear Mixed Models. *For. Sci.* 60(1):119–127.

Piepho, H. P., J. Möhring, A. E. Melchinger, and A. Büchse. 2007. BLUP for phenotypic selection in plant breeding and variety testing. *Euphytica*. 161(1–2):209–228.

Piepho, H.-P. 1998. Empirical best linear unbiased prediction in cultivar trials using factor-analytic variance-covariance structures. *Theor. Appl. Genet.* 97(1–2):195–201.

Randolph, K. C., E. B. Cowling, and D. A. Starkey. 2015. Long-Term Changes in Fusiform Rust Incidence in the Southeastern United States. *J. For.* 113(4):381–392.

Roth, B. E., E. J. Jokela, T. A. Martin, D. A. Huber, and T. L. White. 2007. Genotype×environment interactions in selected loblolly and slash pine plantations in the Southeastern United States. *For. Ecol. Manag.* 238(1–3):175–188.

SAS Institute Inc. 2011. *SAS/STAT® 9.3 User's Guide*. SAS Institute Inc., Cary, NC.

Schmidt, R. A. 2003. Fusiform rust of southern pines: A major success for forest disease management. *Phytopathology*. 93(8):1048.

Self, S. G., and K.-Y. Liang. 1987. Asymptotic Properties of Maximum Likelihood Estimators and Likelihood Ratio Tests Under Nonstandard Conditions. *J. Am. Stat. Assoc.* 82(398):605–610.

Shelbourne, C. J. A., and R. W. Stonecypher. 1971. The inheritance of bole straightness in young loblolly pine. *Silvae Genet.* 20:151–156.

Sherrill, J. R., B. P. Bullock, T. J. Mullin, S. E. McKeand, and R. C. Purnell. 2011. Total and merchantable stem volume equations for midrotation loblolly pine (Pinus taeda L.). *South. J. Appl. For.* 35(3):105–108.

Sierra-Lucero, V., S. E. McKeand, D. A. Huber, D. L. Rockwood, and T. L. White. 2002. Performance differences and genetic parameters for four coastal provenances of loblolly pine in the southeastern United States. *For. Sci.* 48(4):732–742.

Smith, A. B., B. R. Cullis, and R. Thompson. 2005. The analysis of crop cultivar breeding and evaluation trials: an overview of current mixed model approaches. *J. Agric. Sci.* 143(6):449–462.

Staudhammer, C. L., E. J. Jokela, and T. A. Martin. 2009. Competition dynamics in pure- versus mixed-family stands of loblolly and slash pine in the southeastern United States. *Can. J. For. Res.* 39(2):396–409.

Svensson, J. C., S. E. McKeand, H. L. Allen, and R. G. Campbell. 1999. Genetic variation in height and volume of loblolly pine open-pollinated families during canopy closure. *Silvae Genet.* 48:204–208.

Venables, W. N., and D. M. Smith. 2014. the R Core Team. *Introd. R Notes R Program. Environ. Data Anal. Graph. URL Ran R-Proj. Orgdocmanualsr-ReleaseR-Intro Pdf*.

Wickham, H., W. Chang, and M. H. Wickham. 2013. Package "ggplot2." Available online at: http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.449.8078&rep=rep1&type=pdf; last accessed October 14, 2016.

Xiang, B., B. Li, and F. Isik. 2003. Time trend of genetic parameters in growth traits of Pinus taeda L. *Silvae Genet.* 52(3–4):114–120.

Xiong, J. S., F. Isik, S. E. McKeand, and R. W. Whetten. 2010. Genetic variation of stem forking in loblolly pine. *For. Sci.* 56(5):429–436.

Zapata-Valenzuela, J. 2012. USE OF ANALYTIC FACTOR STRUCTURE TO INCREASE HERITABILITY OF CLONAL PROGENY TESTS OF Pinus taeda L. *Chil. J. Agric. Res.* 72(3):309–315.

Zobel, B., and J. Talbert. 1984. Applied forest tree improvement. :xv + 505 pp.

Table 2-1: Likelihood ratio tests results to determine significance of the GxE term for volume in cross-classified model. The "Full Model" is given in equation (2-1), and the reduced model is a linear model with no GxE effect.

Series	Full Model	Reduced model	Difference[1]	P-value
CPMX1	-1975.98	-2013.71	75.46	<0.001
CPMX2	-7593.33	-7632.39	78.12	<0.001
CPMX3	5406.17	5373.80	64.74	<0.001
CPMX4	-3900.38	-3951.42	102.08	<0.001
PPMX1	-355.33	-399.52	88.36	<0.001
PPMX2	-6247.94	-6293.07	90.26	<0.001
PPMX3	-6527.10	-6536.61	19.02	<0.001

[1] Chi-square critical value for 1 DF is 3.88.

Table 2-2: Model fit statistics (Akaike Information Criterion, Bayesian Information Criterion, log likelihood, and number of parameters) for volume in the PMX data. For each statistic, a smaller number indicates better model fit.

CPMX1	AIC	BIC	LL	Parameters
IID	103960	103991	-51976	4
CORUH	99033	99248	-49489	28
CORUV	99185	99308	-49577	16
XFA1	99029	99320	-49477	38
XFA2	99030	99398	-49467	48

CPMX2	AIC	BIC	LL	Parameters
IID	55195	55223	-27593	4
CORUH	48445	48558	-24206	16
CORUV	48563	48634	-24271	10
XFA1	48451	48607	-24203	22
XFA2	48441	48611	-24197	24

CPMX3[2]	AIC	BIC	LL	Parameters
IID	-70804	-70775	5406	4
CORUH	-74031	-73901	7033	18
CORUV	-73958	-73879	6990	11
XFA1	-74025	-73844	7037	25
XFA2	NA	NA	NA	NA

[2] Model diagnostics for CPMX3 are inverted positive because LogL is reported as positive because of small variance component estimates in ASReml. Nonetheless, the XFA1 structure is preferred. A model incorporating the XFA2 structure did not converge.

Table 2-2 (con't): Model fit statistics (Akaike Information Criterion, Bayesian Information Criterion, log likelihood, and number of parameters) for volume in the polymix data. For each statistic, a smaller number indicates better model fit.

CPMX4	AIC	BIC	LL	Parameters
IID	47809	47836	-23900	4
CORUH	44008	44105	-21990	14
CORUV	44185	44247	-22083	9
XFA1	44008	44139	-21985	19
XFA2	44012	44164	-21984	22

PPMX1	AIC	BIC	LL	Parameters
IID	40719	40746	-20355	4
CORUH	39701	39811	-19834	16
CORUV	39758	39827	-19869	10
XFA1	39707	39858	-19831	22
XFA2	39708	39880	-19829	25

PPMX2	AIC	BIC	LL	Parameters
IID	49875	50037	-24914	4
CORUH	49899	50012	-24934	16
CORUV	50089	50160	-25035	10
XFA1	49899	50040	-24929	20
XFA2	49875	50037	-24914	23

Table 2-2 (con't): Model fit statistics (Akaike Information Criterion, Bayesian Information Criterion, log likelihood, and number of parameters) for volume in the polymix data. For each statistic, a smaller number indicates better model fit.

PPMX3	AIC	BIC	LL	Parameters
IID	13062	13086	-6527	4
CORUH	11964	12012	-5974	8
CORUV	12000	12036	-5994	6
XFA1	11964	12018	-5973	9
XFA2	11964	12017	-5973	9

Table 2-3: The mean genetic correlation between all pairs of sites for each PMX test series. Correlations were obtained from XFA structures.

Test series	Average correlation
CPMX1	0.66
CPMX2	0.73
CPMX3	0.80
CPMX4	0.77
PPMX1	0.78
PPMX2	0.85
PPMX3	0.86

Table 2-4: Percent genetic variance explained by XFA2 model terms. Sites are indexed by test series name along the top row and site number along the first column.

Site	CPMX1	CPMX2	CPMX3[3]	CPMX4	PPMX1	PPMX2	PPMX3
1	61.6	34.9	95.6	66.5	53.1	100.0	100.0
2	94.5	81.1	66.1	100.0	79.8	100.0	100.0
3	59.6	100.0	.	80.8	77.9	87.1	72.7
4	100.0	.	68.0	81.5	100.0	86.3	.
5	100.0	.	61.4	86.7	100.0	100.0	.
6	84.4	72.9	37.6	.	83.1	100.0	.
7	89.9	.	39.5	.	43.1	79.5	.
8	97.8	32.7	50.1	37.6	.	.	.
9	54.3	100.0	.	.	.	.	.
10	70.3	100.0	69.9	.	.	.	.
11	60.0	.	.	.	.	.	.
12	72.8	.	.	.	.	.	.
13	100.0	.	.	.	.	.	.
Mean	80.4	74.5	61	75.5	76.7	93.3	90.9

[3] This series did not have global loglikelihood convergence with the XFA2 structure, so XFA1 results are shown.

Table 2-5: Series-wide narrow-sense heritability estimates (with standard errors in parentheses) for the scaled identity and the XFA2 covariance structures. Heritability estimates were always higher when variance components from the XFA2 structure are used.

Series ID	Scaled identity (IID)	XFA2 Structure[4]
CPMX1	0.15 (0.029)	0.17[5]
CPMX2	0.11 (0.027)	0.19
CPMX3	0.17 (0.033)	0.24
CPMX4	0.22 (0.046)	0.32
PPMX1	0.21 (0.046)	0.31
PPMX2	0.29 (0.055)	0.40
PPMX3	0.20 (0.065)	0.33

[4] CPMX3 was calculated based off of XFA1-derived variance components.
[5] Standard errors were not calculated in these estimates of heritability.

Table 2-6: Series-wide family-mean heritability estimates for the scaled identity and the XFA2 covariance structures. Heritability estimates were dramatically higher than those estimated with the cross-classified model, and expected result given the high repeatability of family performance observed across sites with genetic correlations.

Series ID	Scaled identity (IID)	XFA2 Structure[6]
CPMX1	0.41[7]	0.94
CPMX2	0.30	0.80
CPMX3	0.38	0.88
CPMX4	0.47	0.85
PPMX1	0.42	0.87
PPMX2	0.55	0.90
PPMX3	0.39	0.69

[6] CPMX3 was calculated based off of XFA1-derived variance components.
[7] Standard errors for these estimates were not calculated.

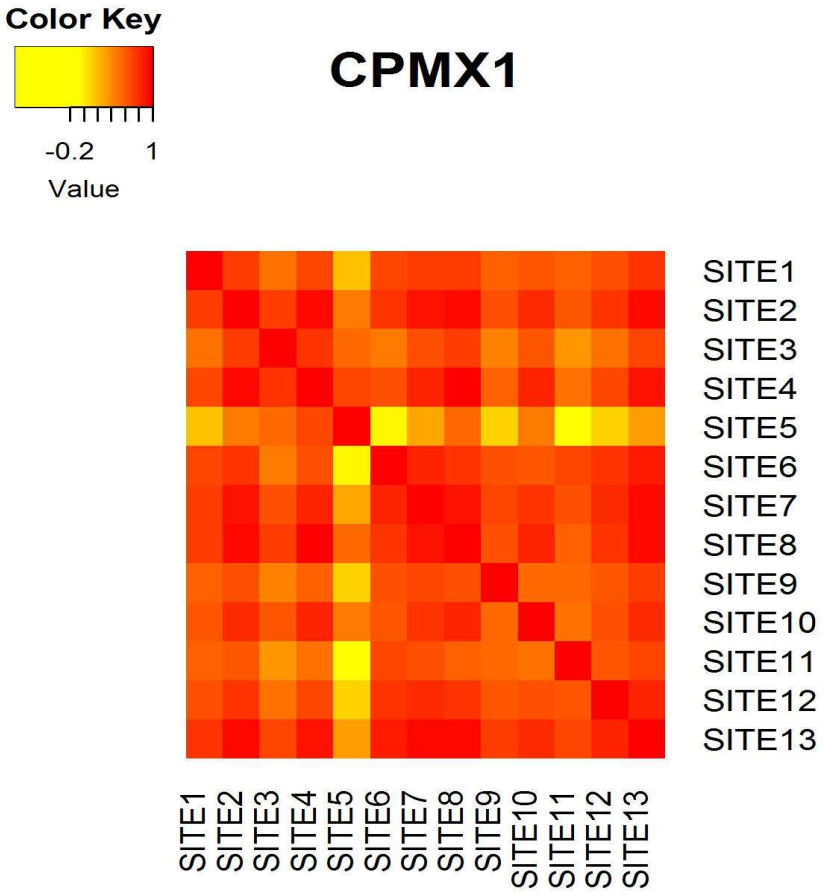

Figure 2-1: A heatmap of genetic correlation among sites for Coastal series 1 (CPMX1) based on XFA2 structure. Dark colors show high correlations. Site 5 had weak correlations with the rest of the sites. Overall GxE seems not important in the test series.

Appendixes

Appendix A: Supplementary Tables and Figures for Chapter 1.

Table A-1: Means and standard errors of traits measured in the CPMX1 series. Straightness is visually assessed on a 1-6 scale where 1 is the straightest. Rust and forkram are binary (0, 1) where 1 indicates incidence. Number of measured trees for height is represented by n.

Test	Height (m)	Volume (dm^3)	Straightness Score	Rust Incidence	Forkram[8] Incidence	n
1	7.27 (0.028)	43.04 (0.431)	3.56 (0.034)	0.02 (0.004)	0.34 (0.013)	1284
2	9.09 (0.018)	76.30 (0.444)	3.53 (0.019)	0.20 (0.011)	0.49 (0.014)	1256
3	8.46 (0.029)	52.06 (0.529)	3.41 (0.024)	0.37 (0.013)	0.10 (0.008)	1269
4	7.80 (0.024)	51.73 (0.453)	1.90 (0.022)	0.27 (0.012)	0.22 (0.011)	1306
5	8.74 (0.030)	82.32 (0.762)	1.80 (0.042)	0.46 (0.014)	0.21 (0.012)	1175
6	6.64 (0.032)	31.24 (0.332)	1.36 (0.016)	0.34 (0.014)	0.06 (0.007)	1198
7	8.85 (0.027)	68.57 (0.658)	3.48 (0.038)	0.63 (0.013)	0.15 (0.010)	1164
8	8.70 (0.020)	71.50 (0.509)	3.53 (0.037)	0.26 (0.012)	0.27 (0.013)	1238
9	7.85 (0.025)	38.35 (0.346)	3.55 (0.023)	0.41 (0.013)	0.05 (0.006)	1295
10	8.02 (0.026)	53.00 (0.508)	3.56 (0.022)	0.40 (0.014)	0.17 (0.012)	1064
11	3.87 (0.020)	10.46 (0.089)	3.40 (0.024)	0.10 (0.009)	0.02 (0.004)	1197
12	8.60 (0.031)	57.09 (0.646)	3.53 (0.037)	0.50 (0.014)	0.07 (0.007)	1092
13	6.67 (0.022)	33.81 (0.301)	2.30 (0.021)	0.02 (0.004)	0.13 (0.010)	1269

[8] Forkram is the incidence of forking or ramicorn branching.

Table A-2: Means and standard errors of traits measured in the CPMX2 series. Straightness is visually assessed on a 1-6 scale where 1 is the straightest. Rust and forkram are binary (0, 1) where 1 indicates incidence. Number of measured trees for height is represented by n.

Test	Height (m)	Volume (dm^3)	Straightness Score	Rust Incidence	Forkram[9] Incidence	n
1	8.27 (0.033)	79.01 (0.676)	1.74 (0.040)	0.18 (0.011)	0.08 (0.008)	1258
2	6.07 (0.022)	26.69 (0.237)	3.55 (0.036)	0.38 (0.013)	0.63 (0.013)	1282
3	8.69 (0.027)	64.89 (0.614)	3.54 (0.036)	0.46 (0.014)	0.50 (0.014)	1240
6	7.52 (0.020)	44.36 (0.341)	3.67 (0.025)	0.42 (0.013)	0.18 (0.011)	1297
8	6.70 (0.023)	28.29 (0.263)	2.99 (0.031)	0.46 (0.014)	0.18 (0.010)	1348
9	4.07 (0.015)	12.09 (0.088)	3.58 (0.034)	0.18 (0.010)	0.29 (0.012)	1397
10	4.74 (0.018)	17.27 (0.138)	3.50 (0.042)	0.23 (0.013)	0.32 (0.014)	1048

[9] Forkram is the incidence of forking or ramicorn branching.

Table A-3: Means and standard errors of traits measured in the CPMX3 series. Straightness is visually assessed on a 1-6 scale where 1 is the straightest. Rust and forkram are binary (0, 1) where 1 indicates incidence. Number of measured trees for height is represented by n.

Test	Height (m)	Volume (dm^3)	Straightness Score	Rust Incidence	Forkram[10] Incidence	n
1	10.89 (0.025)	84.17 (0.873)	3.65 (0.021)	0.43 (0.013)	0.26 (0.012)	1404
2	10.65 (0.027)	70.66 (0.676)	3.60 (0.023)	0.41 (0.013)	0.15 (0.010)	1427
4	9.50 (0.025)	79.13 (0.971)	3.64 (0.033)	0.41 (0.013)	0.20 (0.011)	1326
5	7.97 (0.029)	64.54 (0.600)	1.68 (0.040)	0.32 (0.012)	0.20 (0.010)	1445
6	7.19 (0.025)	29.18 (0.331)	3.60 (0.023)	0.38 (0.014)	0.10 (0.009)	1199
7	5.62 (0.023)	24.69 (0.296)	3.13 (0.023)	0.40 (0.014)	0.92 (0.008)	1203
8	7.08 (0.018)	41.42 (0.372)	3.45 (0.022)	0.19 (0.011)	0.17 (0.011)	1223
10	6.98 (0.027)	29.05 (0.586)	3.27 (0.033)	0.39 (0.015)	0.32 (0.015)	963

[10] Forkram is the incidence of forking or ramicorn branching.

Table A-4: Means and standard errors of traits measured in the CPMX4 series. Straightness is visually assessed on a 1-6 scale where 1 is the straightest. Rust and forkram are binary (0, 1) where 1 indicates incidence. Number of measured trees for height is represented by n.

Test	Height (m)	Volume (dm^3)	Straightness Score	Rust Incidence	Forkram[11] Incidence	n
1	5.56 (0.027)	30.06 (0.347)	3.29 (0.034)	0.25 (0.012)	0.13 (0.010)	1214
2	8.17 (0.025)	42.02 (0.378)	3.58 (0.022)	0.40 (0.013)	0.07 (0.007)	1371
3	7.17 (0.025)	41.40 (0.450)	3.57 (0.031)	0.35 (0.013)	0.35 (0.014)	1209
4	8.21 (0.026)	59.48 (0.622)	3.59 (0.040)	0.52 (0.013)	0.20 (0.012)	1083
5	7.34 (0.026)	62.18 (0.495)	1.99 (0.041)	0.57 (0.013)	0.15 (0.009)	1474
8	3.68 (0.016)	10.39 (0.068)	3.79 (0.031)	0.18 (0.011)	NA	1169

[11] Forkram is the incidence of forking or ramicorn branching.

Table A-5: Means and standard errors of traits measured in the PPMX1 series. Straightness is visually assessed on a 1-6 scale where 1 is the straightest. Rust and forkram are binary (0, 1) where 1 indicates incidence. Number of measured trees for height is represented by n.

Test	Height (m)	Volume (dm^3)	Straightness Score	Rust Incidence	Forkram[12] Incidence	n
1	7.04 (0.021)	33.81 (0.273)	3.51 (0.034)	0.16 (0.011)	0.14 (0.010)	1163
2	6.89 (0.023)	35.40 (0.300)	3.50 (0.037)	0.14 (0.011)	0.24 (0.013)	1096
3	7.48 (0.035)	57.08 (0.488)	3.51 (0.045)	0.10 (0.010)	0.29 (0.015)	956
4	7.66 (0.022)	55.57 (0.469)	3.46 (0.025)	0.13 (0.010)	0.11 (0.010)	1056
5	6.13 (0.034)	41.99 (0.589)	2.99 (0.057)	0.01 (0.005)	0.23 (0.019)	491
6	5.52 (0.017)	23.85 (0.189)	3.50 (0.020)	0.12 (0.010)	0.16 (0.011)	1135
7	6.15 (0.022)	33.40 (0.300)	3.48 (0.036)	0.10 (0.009)	0.28 (0.013)	1203

[12] Forkram is the incidence of forking or ramicorn branching.

Table A-6: Means and standard errors of traits measured in the PPMX2 series. Straightness is visually assessed on a 1-6 scale where 1 is the straightest. Rust and forkram are binary (0, 1) where 1 indicates incidence. Number of measured trees for height is represented by n.

Test	Height (m)	Volume (dm^3)	Straightness Score	Rust Incidence	Forkram[13] Incidence	n
1	7.58 (0.020)	42.75 (0.311)	3.45 (0.023)	0.56 (0.013)	0.17 (0.010)	1443
2	6.70 (0.030)	35.30 (0.428)	3.64 (0.036)	0.42 (0.013)	0.25 (0.012)	1422
3	3.98 (0.018)	12.85 (0.103)	3.29 (0.034)	0.23 (0.012)	0.39 (0.014)	1212
4	6.16 (0.024)	33.17 (0.299)	3.44 (0.025)	0.41 (0.014)	0.49 (0.014)	1243
5	8.00 (0.021)	65.91 (0.491)	3.12 (0.024)	0.21 (0.011)	0.43 (0.014)	1302
6	7.78 (0.023)	60.99 (0.511)	3.16 (0.029)	0.18 (0.011)	0.43 (0.015)	1124
7	8.45 (0.020)	60.86 (0.443)	3.42 (0.031)	0.11 (0.008)	0.33 (0.012)	1540

[13] Forkram is the incidence of forking or ramicorn branching.

Table A-7: Means and standard errors of traits measured in the PPMX3 series. Straightness is visually assessed on a 1-6 scale where 1 is the straightest. Rust and forkram are binary (0, 1) where 1 indicates incidence. Number of measured trees for height is represented by n.

Test	Height (m)	Volume (dm3)	Straightness Score	Rust Incidence	Forkram14 Incidence	n
1	5.29 (0.025)	24.74 (0.291)	3.46 (0.042)	0.47 (0.016)	0.31 (0.015)	955
2	5.54 (0.017)	22.20 (0.166)	3.52 (0.038)	0.10 (0.009)	0.15 (0.011)	1082
3	3.64 (0.015)	12.02 (0.088)	3.32 (0.037)	0.13 (0.012)	0.54 (0.017)	814

[14] Forkram is the incidence of forking or ramicorn branching.

Table A-8: Additive genetic variances with standard errors in parentheses for height, volume, and straightness. Additive variance σ_a^2 is four times the family variance σ_f^2 since progeny for half-sib families are expected to share 1/4 of their genetic material from the known parent.

Site	Height	Volume	Straightness
cpmx1_1	0.46 (0.114)	119.7 (29.2)	0.40 (0.121)
cpmx1_2	0.20 (0.046)	85.5 (22.9)	0.09 (0.032)
cpmx1_3	0.23 (0.063)	68.6 (22.0)	0.25 (0.070)
cpmx1_4	0.15 (0.051)	38.9 (15.6)	0.05 (0.030)
cpmx1_5	0.21 (0.075)	117.2 (46.7)	0.42 (0.154)
cpmx1_6	0.28 (0.092)	40.5 (11.7)	0.03 (0.017)
cpmx1_7	0.32 (0.081)	125.3 (39.7)	0.24 (0.108)
cpmx1_8	0.14 (0.042)	70.9 (23.9)	0.29 (0.112)
cpmx1_9	0.27 (0.069)	38.9 (11.4)	0.16 (0.050)
cpmx1_10	0.19 (0.058)	69.6 (22.2)	0.19 (0.054)
cpmx1_11	0.16 (0.045)	2.9 (0.8)	0.17 (0.056)
cpmx1_12	0.37 (0.102)	153.9 (45.3)	0.30 (0.112)
cpmx1_13	0.07 (0.033)	23.6 (8.1)	0.06 (0.029)
cpmx2_1	0.18 (0.081)	154.8 (46.9)	0.43 (0.144)
cpmx2_2	0.34 (0.075)	36.7 (8.4)	0.36 (0.115)
cpmx2_3	0.26 (0.071)	91.2 (31.0)	0.56 (0.153)
cpmx2_6	0.21 (0.053)	46.2 (12.9)	0.23 (0.066)
cpmx2_8	0.22 (0.060)	22.6 (7.0)	0.28 (0.091)
cpmx2_9	0.09 (0.026)	2.8 (0.8)	0.56 (0.145)
cpmx2_10	0.09 (0.027)	6.2 (1.9)	0.62 (0.175)

Table A-8 (con't): Additive genetic variances with standard errors in parentheses for height, volume, and straightness. Additive variance σ_a^2 is four times the family variance σ_f^2 since progeny for half-sib families are expected to share 1/4 of their genetic material from the known parent.

Site	Height	Volume	Straightness
cpmx3_1	0.34 (0.082)	369.3 (97.2)	0.13 (0.044)
cpmx3_2	0.44 (0.103)	180.7 (51.1)	0.31 (0.074)
cpmx3_4	0.35 (0.084)	505.8 (132.0)	0.39 (0.113)
cpmx3_5	0.16 (0.065)	113.8 (36.6)	0.18 (0.105)
cpmx3_6	0.28 (0.068)	26.5 (9.0)	0.17 (0.053)
cpmx3_7	0.24 (0.065)	29.1 (8.9)	0.06 (0.035)
cpmx3_8	0.07 (0.026)	16.6 (9.1)	0.15 (0.048)
cpmx3_10	0.18 (0.062)	67.7 (27.3)	0.09 (0.065)
cpmx4_1	0.18 (0.060)	39.6 (12.0)	0.24 (0.096)
cpmx4_2	0.21 (0.059)	55.4 (15.1)	0.30 (0.071)
cpmx4_3	0.14 (0.051)	58.0 (18.8)	0.20 (0.077)
cpmx4_4	0.30 (0.078)	221.7 (53.3)	0.28 (0.118)
cpmx4_5	0.41 (0.096)	182.4 (40.7)	0.37 (0.144)
cpmx4_8	0.15 (0.037)	3.4 (0.8)	0.18 (0.074)
ppmx1_1	0.11 (0.033)	17.6 (5.7)	0.17 (0.079)
ppmx1_2	0.27 (0.067)	58.2 (14.3)	0.22 (0.093)
ppmx1_3	0.04 (0.044)	90.2 (25.7)	0.35 (0.151)
ppmx1_4	0.11 (0.035)	84.8 (23.0)	0.18 (0.058)
ppmx1_5	0.06 (0.051)	33.3 (17.9)	0.24 (0.186)
ppmx1_6	0.06 (0.023)	6.1 (2.6)	0.03 (0.023)
ppmx1_7	0.27 (0.068)	59.0 (13.9)	0.58 (0.156)

Table A-8 (con't): Additive genetic variances with standard errors in parentheses for height, volume, and straightness. Additive variance σ_a^2 is four times the family variance σ_f^2 since progeny for half-sib families are expected to share 1/4 of their genetic material from the known parent.

Site	Height	Volume	Straightness
ppmx2_1	0.16 (0.046)	48.9 (12.7)	0.22 (0.065)
ppmx2_2	0.20 (0.056)	28.9 (10.1)	0.57 (0.165)
ppmx2_3	0.10 (0.032)	3.3 (1.0)	0.20 (0.093)
ppmx2_4	0.27 (0.066)	54.8 (13.4)	0.08 (0.042)
ppmx2_5	0.36 (0.082)	196.3 (44.5)	0.11 (0.050)
ppmx2_6	0.13 (0.044)	65.3 (23.2)	0.16 (0.072)
ppmx2_7	0.32 (0.070)	191.6 (40.6)	0.41 (0.115)
ppmx3_1	0.18 (0.056)	25.8 (8.0)	0.08 (0.090)
ppmx3_2	0.21 (0.049)	12.2 (3.2)	0.33 (0.123)
ppmx3_3	0.04 (0.017)	1.3 (0.6)	0.14 (0.078)

Table A-9: Residual (environmental) variances with standard errors in parentheses for height, volume, and straightness.

Site	Height	Volume	Straightness
cpmx1_1	0.89 (0.036)	209.5 (8.6)	1.43 (0.058)
cpmx1_2	0.29 (0.012)	210.9 (8.7)	0.45 (0.019)
cpmx1_3	0.63 (0.026)	269.2 (11.1)	0.67 (0.028)
cpmx1_4	0.67 (0.027)	243.4 (9.9)	0.56 (0.023)
cpmx1_5	0.97 (0.041)	656.4 (28.1)	1.73 (0.080)
cpmx1_6	1.09 (0.046)	114.1 (4.9)	0.27 (0.012)
cpmx1_7	0.62 (0.027)	438.1 (18.9)	1.64 (0.070)
cpmx1_8	0.45 (0.019)	298.6 (12.4)	1.62 (0.067)
cpmx1_9	0.62 (0.025)	126.7 (5.2)	0.63 (0.025)
cpmx1_10	0.55 (0.025)	226.2 (10.2)	0.46 (0.021)
cpmx1_11	0.41 (0.017)	8.3 (0.4)	0.64 (0.027)
cpmx1_12	0.86 (0.038)	403.2 (17.9)	1.38 (0.061)
cpmx1_13	0.57 (0.023)	106.5 (4.4)	0.48 (0.020)
cpmx2_1	1.28 (0.053)	531.5 (22.0)	1.73 (0.073)
cpmx2_2	0.42 (0.017)	55.4 (2.3)	1.45 (0.059)
cpmx2_3	0.66 (0.027)	396.1 (16.5)	1.46 (0.061)
cpmx2_6	0.45 (0.018)	135.4 (5.5)	0.73 (0.030)
cpmx2_8	0.62 (0.025)	84.8 (3.4)	1.15 (0.046)
cpmx2_9	0.29 (0.011)	9.7 (0.4)	1.41 (0.055)
cpmx2_10	0.26 (0.012)	17.3 (0.8)	1.50 (0.068)

Table A-9 (con't): Residual (environmental) variances with standard errors in parentheses for height, volume, and straightness.

Site	Height	Volume	Straightness
cpmx3_1	0.76 (0.030)	1052.3 (39.7)	0.60 (0.023)
cpmx3_2	0.85 (0.033)	622.6 (23.5)	0.67 (0.026)
cpmx3_4	0.72 (0.029)	1300.3 (49.0)	1.29 (0.052)
cpmx3_5	1.12 (0.043)	503.1 (19.1)	2.07 (0.083)
cpmx3_6	0.48 (0.020)	116.9 (4.8)	0.57 (0.024)
cpmx3_7	0.56 (0.024)	102.7 (4.2)	0.61 (0.026)
cpmx3_8	0.36 (0.015)	165.5 (6.8)	0.55 (0.023)
cpmx3_10	0.62 (0.030)	411.9 (16.9)	0.99 (0.047)
cpmx4_1	0.73 (0.031)	129.2 (5.5)	1.35 (0.057)
cpmx4_2	0.68 (0.027)	164.3 (6.5)	0.61 (0.024)
cpmx4_3	0.68 (0.029)	222.0 (9.4)	1.10 (0.046)
cpmx4_4	0.61 (0.027)	352.4 (15.8)	1.55 (0.070)
cpmx4_5	0.85 (0.032)	304.3 (11.6)	2.26 (0.089)
cpmx4_8	0.24 (0.010)	4.3 (0.2)	1.00 (0.043)
ppmx1_1	0.33 (0.014)	63.5 (2.7)	1.24 (0.053)
ppmx1_2	0.44 (0.019)	82.2 (3.6)	1.30 (0.058)
ppmx1_3	0.81 (0.038)	187.7 (9.0)	1.87 (0.088)
ppmx1_4	0.35 (0.016)	174.8 (7.9)	0.61 (0.027)
ppmx1_5	0.44 (0.030)	127.2 (8.7)	1.56 (0.106)
ppmx1_6	0.30 (0.013)	36.3 (1.6)	0.44 (0.019)
ppmx1_7	0.48 (0.020)	87.3 (3.7)	1.40 (0.059)

Table A-9 (con't): Residual (environmental) variances with standard errors in parentheses for height, volume, and straightness.

Site	Height	Volume	Straightness
ppmx2_1	0.52 (0.021)	121.1 (4.9)	0.73 (0.029)
ppmx2_2	0.60 (0.024)	140.5 (5.7)	1.67 (0.068)
ppmx2_3	0.33 (0.015)	10.9 (0.5)	1.33 (0.059)
ppmx2_4	0.47 (0.020)	88.2 (3.9)	0.67 (0.029)
ppmx2_5	0.46 (0.019)	263.9 (11.2)	0.74 (0.031)
ppmx2_6	0.47 (0.021)	253.3 (11.6)	0.91 (0.041)
ppmx2_7	0.44 (0.017)	227.4 (8.8)	1.38 (0.054)
ppmx3_1	0.49 (0.023)	66.5 (3.2)	1.58 (0.075)
ppmx3_2	0.24 (0.011)	22.6 (1.0)	1.50 (0.067)
ppmx3_3	0.17 (0.009)	5.8 (0.3)	0.93 (0.048)

Table A-10: Narrow-sense heritabilities by site on an individual-tree basis for continuous traits with standard errors in parentheses.

Site	Height	Volume	Straightness
CPMX1_1	0.46 (0.103)	0.50 (0.109)	0.26 (0.076)
CPMX1_2	0.57 (0.117)	0.37 (0.092)	0.18 (0.066)
CPMX1_3	0.33 (0.086)	0.30 (0.091)	0.35 (0.089)
CPMX1_4	0.21 (0.069)	0.15 (0.060)	0.09 (0.052)
CPMX1_5	0.20 (0.072)	0.17 (0.067)	0.23 (0.081)
CPMX1_6	0.24 (0.076)	0.33 (0.089)	0.12 (0.061)
CPMX1_7	0.46 (0.105)	0.27 (0.081)	0.14 (0.062)
CPMX1_8	0.30 (0.083)	0.22 (0.073)	0.17 (0.064)
CPMX1_9	0.39 (0.093)	0.29 (0.080)	0.23 (0.072)
CPMX1_10	0.32 (0.092)	0.29 (0.087)	0.38 (0.099)
CPMX1_11	0.36 (0.092)	0.32 (0.087)	0.25 (0.079)
CPMX1_12	0.39 (0.099)	0.35 (0.096)	0.20 (0.075)
CPMX1_13	0.11 (0.056)	0.21 (0.070)	0.13 (0.058)
CPMX2_1	0.14 (0.060)	0.27 (0.078)	0.24 (0.076)
CPMX2_2	0.68 (0.127)	0.57 (0.114)	0.23 (0.072)
CPMX2_3	0.36 (0.091)	0.22 (0.072)	0.35 (0.089)
CPMX2_6	0.42 (0.096)	0.31 (0.083)	0.29 (0.080)
CPMX2_8	0.33 (0.085)	0.25 (0.074)	0.23 (0.072)
CPMX2_9	0.30 (0.078)	0.27 (0.075)	0.36 (0.087)
CPMX2_10	0.31 (0.092)	0.33 (0.094)	0.37 (0.099)

Table A-10 (con't): Narrow-sense heritabilities by site on an individual-tree basis for continuous traits with standard errors in parentheses.

Site	Height	Volume	Straightness
CPMX3_1	0.40 (0.091)	0.32 (0.080)	0.21 (0.067)
CPMX3_2	0.46 (0.097)	0.27 (0.073)	0.42 (0.091)
CPMX3_4	0.41 (0.091)	0.43 (0.101)	0.28 (0.078)
CPMX3_5	0.13 (0.053)	0.21 (0.068)	0.08 (0.049)
CPMX3_6	0.50 (0.110)	0.21 (0.070)	0.28 (0.082)
CPMX3_7	0.38 (0.096)	0.26 (0.077)	0.10 (0.056)
CPMX3_8	0.18 (0.066)	0.10 (0.053)	0.25 (0.078)
CPMX3_10	0.27 (0.089)	0.16 (0.062)	0.08 (0.063)
CPMX4_1	0.23 (0.074)	0.29 (0.082)	0.17 (0.067)
CPMX4_2	0.28 (0.076)	0.31 (0.080)	0.43 (0.095)
CPMX4_3	0.19 (0.070)	0.25 (0.076)	0.17 (0.066)
CPMX4_4	0.44 (0.105)	0.54 (0.116)	0.17 (0.071)
CPMX4_5	0.43 (0.092)	0.52 (0.104)	0.16 (0.060)
CPMX4_8	0.55 (0.117)	0.66 (0.130)	0.17 (0.069)
PPMX1_1	0.31 (0.088)	0.26 (0.080)	0.13 (0.060)
PPMX1_2	0.53 (0.120)	0.60 (0.129)	0.16 (0.067)
PPMX1_3	0.05 (0.054)	0.43 (0.112)	0.18 (0.075)
PPMX1_4	0.29 (0.089)	0.43 (0.108)	0.27 (0.085)
PPMX1_5	0.14 (0.111)	0.25 (0.128)	0.15 (0.114)
PPMX1_6	0.19 (0.070)	0.16 (0.067)	0.07 (0.052)
PPMX1_7	0.50 (0.110)	0.58 (0.119)	0.37 (0.094)

Table A-10 (con't): Narrow-sense heritabilities by site on an individual-tree basis for continuous traits with standard errors in parentheses.

Site	Height	Volume	Straightness
PPMX2_1	0.28 (0.078)	0.37 (0.088)	0.28 (0.078)
PPMX2_2	0.31 (0.082)	0.20 (0.067)	0.32 (0.086)
PPMX2_3	0.29 (0.085)	0.28 (0.084)	0.15 (0.066)
PPMX2_4	0.50 (0.112)	0.54 (0.117)	0.11 (0.061)
PPMX2_5	0.66 (0.129)	0.63 (0.123)	0.14 (0.064)
PPMX2_6	0.26 (0.084)	0.24 (0.083)	0.17 (0.074)
PPMX2_7	0.62 (0.116)	0.70 (0.125)	0.28 (0.074)
PPMX3_1	0.34 (0.100)	0.35 (0.103)	0.05 (0.056)
PPMX3_2	0.72 (0.140)	0.48 (0.112)	0.21 (0.075)
PPMX3_3	0.21 (0.089)	0.22 (0.091)	0.15 (0.079)

Table A-11: Additive genetic variance, GxE interaction variance, and residual variance for traits in each test series with standard errors in parentheses. Additive genetic variance σ_a^2 is four times the family variance σ_f^2.

Additive Genetic Variance			
Series	Height	Volume	Straightness
CPMX1	0.16 (0.031)	40.64 (8.168)	0.12 (0.024)
CPMX2	0.12 (0.025)	21.03 (5.205)	0.29 (0.058)
CPMX3	0.18 (0.033)	0.00 (0.123)	0.15 (0.029)
CPMX4	0.14 (0.031)	48.43 (10.698)	0.24 (0.049)
PPMX1	0.08 (0.018)	24.69 (5.615)	0.19 (0.045)
PPMX2	0.19 (0.036)	52.94 (10.701)	0.17 (0.385)
PPMX3	0.13 (0.035)	7.07 (2.418)	0.18 (0.061)
GxE Variance			
Series	Height	Volume	Straightness
CPMX1	0.02 (0.003)	7.33 (1.084)	0.02 (0.004)
CPMX2	0.02 (0.004)	7.42 (1.206)	0.03 (0.008)
CPMX3	0.02 (0.004)	0.00 (0.000)	0.01 (0.004)
CPMX4	0.02 (0.004)	11.35 (1.726)	0.01 (0.006)
PPMX1	0.01 (0.003)	5.94 (0.944)	0.02 (0.007)
PPMX2	0.01 (0.003)	7.88 (1.212)	0.02 (0.006)
PPMX3	0.01 (0.004)	1.58 (0.499)	0.01 (0.012)
Residual Variance			
Series	Height	Volume	Straightness
CPMX1	0.66 (0.008)	251.35 (2.935)	0.91 (0.011)
CPMX2	0.57 (0.009)	174.66 (2.719)	1.34 (0.021)
CPMX3	0.70 (0.010)	0.00 (0.000)	0.92 (0.013)
CPMX4	0.64 (0.011)	197.39 (3.342)	1.32 (0.022)
PPMX1	0.44 (0.008)	103.59 (1.809)	1.16 (0.020)
PPMX2	0.47 (0.008)	159.31 (2.533)	1.08 (0.017)
PPMX3	0.30 (0.008)	32.61 (0.901)	1.37 (0.038)

Table A-12: Family variances for binary traits with standard errors in parentheses. Blank cells indicate that incidence levels were not in acceptable range for estimation of genetic parameters.

Site	Forkram[15]	Rust
cpmx1_1	0.06 (0.055)	.
cpmx1_2	0.18 (0.071)	.
cpmx1_3	.	0.32 (0.098)
cpmx1_4	0.26 (0.106)	0.52 (0.150)
cpmx1_5	0.25 (0.111)	0.30 (0.096)
cpmx1_6	.	0.45 (0.132)
cpmx1_7	.	0.28 (0.091)
cpmx1_8	0.06 (0.061)	0.34 (0.118)
cpmx1_9	.	0.50 (0.130)
cpmx1_10	.	0.61 (0.157)
cpmx1_11	.	.
cpmx1_12	.	0.41 (0.113)
cpmx1_13	.	.
cpmx2_1	.	.
cpmx2_2	0.03 (0.047)	0.27 (0.085)
cpmx2_3	0.04 (0.047)	0.39 (0.110)
cpmx2_6	.	0.28 (0.110)
cpmx2_8	.	.
cpmx2_9	.	.
cpmx2_10	.	.

[15] Forkram is the incidence of forking or ramicorn branching.

Table A-12 (con't): Family variances for binary traits with standard errors in parentheses. Blank cells indicate that incidence levels were not in acceptable range for estimation of genetic parameters.

Site	Forkram[16]	Rust
cpmx3_1	0.13 (0.066)	0.41 (0.106)
cpmx3_2	.	0.51 (0.125)
cpmx3_4	.	0.33 (0.099)
cpmx3_5	.	0.34 (0.104)
cpmx3_6	.	0.45 (0.125)
cpmx3_7	.	0.19 (0.093)
cpmx3_8	.	.
cpmx3_10	.	.
cpmx4_1	.	0.18 (0.083)
cpmx4_2	.	1.03 (0.220)
cpmx4_3	0.07 (0.060)	0.25 (0.089)
cpmx4_4	.	0.21 (0.072)
cpmx4_5	.	0.39 (0.103)
cpmx4_8	.	.
ppmx1_1	.	.
ppmx1_2	0.21 (0.097)	.
ppmx1_3	0.10 (0.080)	.
ppmx1_4	.	.
ppmx1_5	0.02 (0.136)	.
ppmx1_6	.	.
ppmx1_7	.	.

[16] Forkram is the incidence of forking or ramicorn branching.

Table A-12 (con't): Family variances for binary traits with standard errors in parentheses. Blank cells indicate that incidence levels were not in acceptable range for estimation of genetic parameters.

Site	Forkram[17]	Rust
ppmx2_1	.	0.67 (0.160)
ppmx2_2	0.11 (0.067)	0.39 (0.112)
ppmx2_3	0.09 (0.065)	0.35 (0.124)
ppmx2_4	0.16 (0.075)	0.42 (0.122)
ppmx2_5	0.10 (0.059)	0.41 (0.132)
ppmx2_6	0.08 (0.063)	.
ppmx2_7	0.14 (0.065)	.
ppmx3_1	0.02 (0.054)	0.32 (0.111)
ppmx3_2	.	.
ppmx3_3	.	.

[17] Forkram is the incidence of forking or ramicorn branching.

Table A-13: Number of individuals per site per family in each test series. It is assumed that each site in a series has the same number of families and each site has the same number of replications. Here, n indicates the average number of measured trees per family per site.

Series	Trait	# Tests	# Families	Data Points	n
CPMX1	Forkram[18]	5	68	6258	18.41
	Rust	9	68	11524	18.83
CPMX2	Forkram	2	82	2522	15.38
	Rust	3	82	4033	16.39
CPMX3	Forkram	1	91	1404	15.43
	Rust	6	91	8296	15.19
CPMX4	Forkram	1	74	1212	16.38
	Rust	5	74	6816	18.42
PPMX1	Forkram	3	75	2543	11.30
	Rust[19]	NA	NA	NA	NA
PPMX2	Forkram	6	75	7838	17.42
	Rust	5	75	6920	18.45
PPMX3	Forkram	1	64	985	15.39
	Rust	1	64	985	15.39

[18] Forkram is the incidence of forking or ramicorn branching.
[19] No sites in this test series had rust incidence levels appropriate for analysis.

Table A-14: Family mean narrow sense heritabilities (with their standard errors) of binary response traits. This estimate was only possible on sites with mean trait incidence between 0.20 and 0.80. Blank cells indicate that incidence levels at the site for the trait pair were not in an acceptable range for estimation of genetic parameters.

Site	Forkram[20]	Rust
cpmx1_1	0.54 (0.213)	.
cpmx1_2	0.77 (0.070)	.
cpmx1_3	.	0.86 (0.038)
cpmx1_4	0.83 (0.059)	0.91 (0.024)
cpmx1_5	0.82 (0.063)	0.85 (0.041)
cpmx1_6	.	0.89 (0.028)
cpmx1_7	.	0.84 (0.043)
cpmx1_8	0.52 (0.255)	0.86 (0.041)
cpmx1_9	.	0.90 (0.023)
cpmx1_10	.	0.92 (0.019)
cpmx1_11	.	.
cpmx1_12	.	0.89 (0.028)
cpmx1_13	.	.
cpmx2_1	.	.
cpmx2_2	0.28 (0.372)	0.81 (0.049)
cpmx2_3	0.37 (0.291)	0.87 (0.033)
cpmx2_6	.	0.82 (0.056)
cpmx2_8	.	.
cpmx2_9	.	.
cpmx2_10	.	.

Table A-14 (con't): Family mean narrow sense heritabilities (with their standard errors) of binary response traits. This estimate was only possible on sites with mean trait incidence between 0.20 and 0.80. Blank cells indicate that incidence levels at the

[20] Forkram is the incidence of forking or ramicorn branching.

site for the trait pair were not in an acceptable range for estimation of genetic parameters.

Site	Forkram[21]	Rust
cpmx3_1	0.66 (0.117)	0.86 (0.031)
cpmx3_2	.	0.88 (0.025)
cpmx3_4	.	0.83 (0.042)
cpmx3_5	.	0.84 (0.041)
cpmx3_6	.	0.87 (0.031)
cpmx3_7	.	0.74 (0.096)
cpmx3_8	.	.
cpmx3_10	.	.
cpmx4_1	.	0.77 (0.084)
cpmx4_2	.	0.95 (0.010)
cpmx4_3	0.55 (0.197)	0.82 (0.053)
cpmx4_4	.	0.79 (0.057)
cpmx4_5	.	0.88 (0.029)
cpmx4_8	.	.
ppmx1_1	.	.
ppmx1_2	0.70 (0.097)	.
ppmx1_3	0.54 (0.191)	.
ppmx1_4	.	.
ppmx1_5	0.22 (0.950)	.
ppmx1_6	.	.
ppmx1_7	.	.

[21] Forkram is the incidence of forking or ramicorn branching.

Table A-14 (con't): Family mean narrow sense heritabilities (with their standard errors) of binary response traits. This estimate was only possible on sites with mean trait incidence between 0.20 and 0.80. Blank cells indicate that incidence levels at the site for the trait pair were not in an acceptable range for estimation of genetic parameters.

Site	Forkram[22]	Rust
ppmx2_1	.	0.93 (0.017)
ppmx2_2	0.66 (0.139)	0.88 (0.031)
ppmx2_3	0.61 (0.173)	0.87 (0.041)
ppmx2_4	0.74 (0.090)	0.89 (0.029)
ppmx2_5	0.64 (0.138)	0.88 (0.033)
ppmx2_6	0.59 (0.184)	.
ppmx2_7	0.70 (0.100)	.
ppmx3_1	0.19 (0.541)	0.83 (0.047)
ppmx3_2	.	.
ppmx3_3	.	.

[22] Forkram is the incidence of forking or ramicorn branching.

Table A-15: Additive and GxE variance for series analysis of binary traits.

Additive Variance		
Series	Forkram[23]	Rust
CPMX1	0.06 (0.017)	0.29 (0.056)
CPMX2	0.05 (0.017)	0.24 (0.048)
CPMX3	0.07 (0.023)	0.36 (0.062)
CPMX4	0.08 (0.028)	0.27 (0.053)
PPMX1	0.03 (0.017)	0.00 (0.028)
PPMX2	0.07 (0.020)	0.36 (0.071)
PPMX3	0.03 (0.026)	0.03 (0.029)
GxE Variance		
Series	Forkram	Rust
CPMX1	0.04 (0.022)	0.09 (0.019)
CPMX2	0.02 (0.023)	0.06 (0.023)
CPMX3	0.04 (0.027)	0.01 (0.016)
CPMX4	0.01 (0.036)	0.04 (0.022)
PPMX1	0.14 (0.047)	0.09 (0.047)
PPMX2	0.02 (0.020)	0.04 (0.024)
PPMX3	0.00 (0.000)	0.10 (0.072)

[23] Forkram is the incidence of forking or ramicorn branching.

Table A-16: Number of individuals per family series in each test series. It is assumed that each site in a series has the same number of families and each site has the same number of replications. Here, n represents the mean number of individuals in a half-sib family for each series.

Series	Trait	# Tests	# Families	Data Points	n
CPMX1	Forkram	13	68	15915	234.04
	Rust	13	68	16587	243.93
CPMX2	Forkram	7	82	8727	106.43
	Rust	7	82	9107	111.06
CPMX3	Forkram	8	91	10211	112.21
	Rust	8	91	10581	116.27
CPMX4	Forkram	6	74	6354	85.86
	Rust	6	74	8011	108.26
PPMX1	Forkram	7	75	7126	95.01
	Rust	7	75	7153	95.37
PPMX2	Forkram	7	75	8517	113.56
	Rust	7	75	8856	118.08
PPMX3	Forkram	3	64	2879	44.98
	Rust	3	64	2912	45.50

Table A-17: Means of the site heritability estimates for each test series (denoted $\bar{h}_s^2$), an overall heritability term based on pooled variance for each series (denoted h^2), and percent difference between the two figures. The $\bar{h}_s^2$ term is biased because GxE is ignored across sites. Note that bias is consistently higher than 50% due to the presence of GxE.

		CPMX1	CPMX2	CPMX3	CPMX4	PPMX1	PPMX2	PPMX3
Height	$\bar{h}_s^2$	0.33	0.36	0.34	0.35	0.29	0.41	0.42
	h^2	0.23	0.20	0.23	0.20	0.16	0.36	0.38
	% bias	49%	82%	47%	74%	78%	16%	11%
Volume	$\bar{h}_s^2$	0.29	0.32	0.25	0.43	0.39	0.42	0.35
	h^2	0.15	0.11	0.17	0.22	0.21	0.29	0.20
	% bias	91%	182%	43%	95%	81%	43%	78%
Straightness	$\bar{h}_s^2$	0.21	0.30	0.21	0.21	0.19	0.21	0.14
	h^2	0.12	0.20	0.15	0.17	0.15	0.15	0.13
	% bias	76%	48%	43%	24%	23%	35%	8%

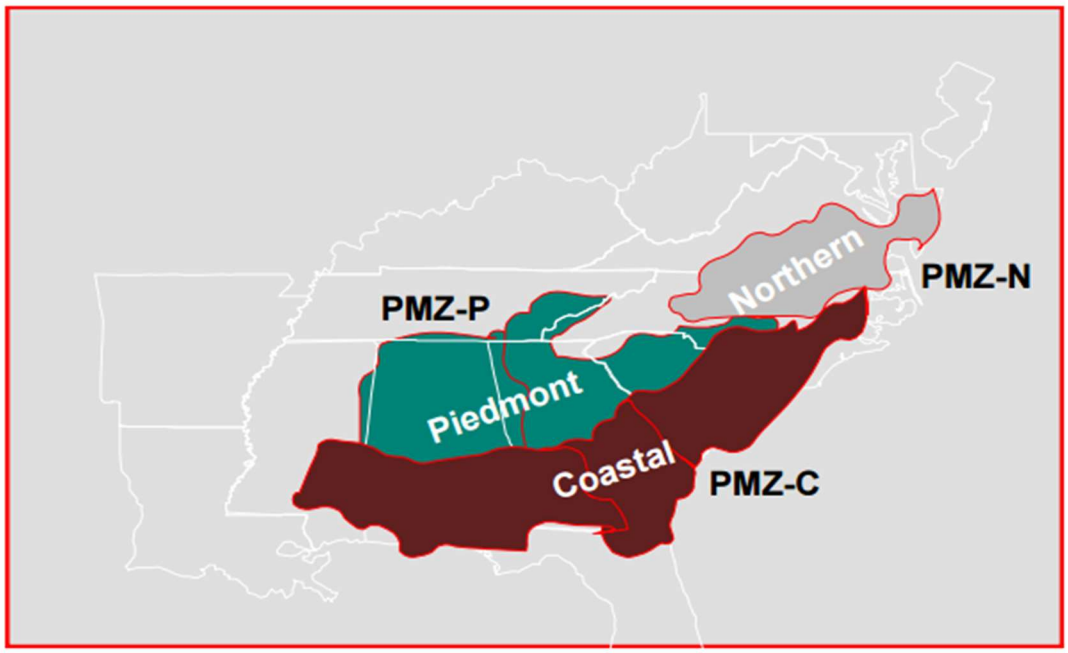

Figure A-1: 3rd-cycle breeding zones: Coastal, Piedmont, and Northern. The overlays show that the regions are delineated by weather and temperature patterns.

Appendix B: Supplementary Tables and Figures for Chapter 2.

Table B-1: Type-B genetic correlations of volume in respective test series with standard errors in parentheses. Type-B genetic correlations are the proportion of genetic variance that is additive.

Series	Volume
CPMX1	0.58 (0.062)
CPMX2	0.41 (0.076)
CPMX3	0.57 (0.068)
CPMX4	0.52 (0.070)
PPMX1	0.51 (0.073)
PPMX2	0.63 (0.062)
PPMX3	0.53 (0.135)

Table B-2: Genetic correlations of volume among sites for Coastal Series 1.

Site	2	3	4	5	6	7	8	9	10	11	12	13
1	0.73	0.52	0.68	0.18	0.70	0.74	0.73	0.58	0.62	0.57	0.67	0.78
2		0.73	0.94	0.49	0.76	0.90	0.96	0.67	0.81	0.61	0.77	0.95
3			0.77	0.55	0.49	0.65	0.75	0.46	0.63	0.37	0.53	0.69
4				0.70	0.65	0.85	0.97	0.60	0.82	0.49	0.70	0.90
5					<0.01	0.28	0.53	0.11	0.47	<0.01	0.13	0.32
6						0.83	0.76	0.67	0.63	0.71	0.77	0.87
7							0.90	0.69	0.76	0.67	0.80	0.95
8								0.66	0.83	0.60	0.77	0.96
9									0.56	0.55	0.63	0.73
10										0.50	0.65	0.81
11											0.64	0.70
12												0.84

Table B-3: Genetic correlations of volume among sites for Coastal Series 2.

Site	2	3	6	8	9	10
1	0.59	0.71	0.70	0.53	0.73	0.73
2		0.97	0.91	0.69	0.66	0.66
3			0.96	0.74	0.78	0.78
6				0.68	0.75	0.75
8					0.53	0.53
9						1.00

Table B-4: Genetic correlations of volume among sites for Coastal Series 3.

Site	2	4	5	6	7	8	10
1	0.79	0.81	0.77	0.60	0.61	0.69	0.82
2		0.67	0.64	0.50	0.51	0.57	0.68
4			0.65	0.51	0.52	0.58	0.69
5				0.48	0.49	0.55	0.66
6					0.38	0.43	0.51
7						0.44	0.53
8							0.59

Table B-5: Genetic correlations of volume among sites for Coastal Series 4.

Site	2	3	4	5	8
1	0.68	0.91	0.88	0.91	0.61
2		0.67	0.75	0.64	0.68
3			0.94	0.96	0.64
4				0.93	0.72
5					0.62

Table B-6: Genetic correlations of volume among sites for Piedmont Series 1.

Site	2	3	4	5	6	7
1	0.85	0.80	0.84	0.66	0.85	0.66
2		0.90	0.91	0.69	0.95	0.73
3			0.80	0.50	0.90	0.72
4				0.91	0.96	0.74
5					0.78	0.55
6						0.78

Table B-7: Genetic correlations of volume among sites for Piedmont Series 2.

Site	2	3	4	5	6	7
1	0.77	0.99	0.98	0.67	0.73	0.66
2		0.83	0.83	0.99	1.00	0.96
3			0.97	0.75	0.80	0.73
4				0.75	0.80	0.74
5					1.00	0.96
6						0.96

Table B-8: Genetic correlations of volume among sites for Piedmont Series 3.

Site	2	3
1	0.89	0.74
2		0.95

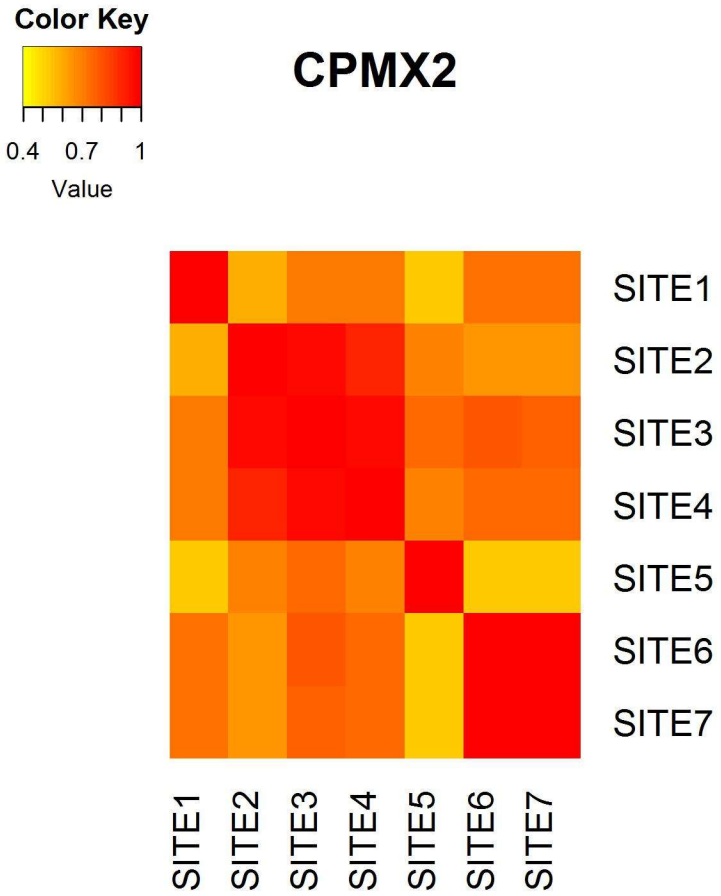

Figure B-1: A heatmap of genetic correlation among sites for Coastal series 2 (CPMX2) based on XFA2 assumptions. This image represents the correlation matrix form of the variance/covariance structure for this test series.

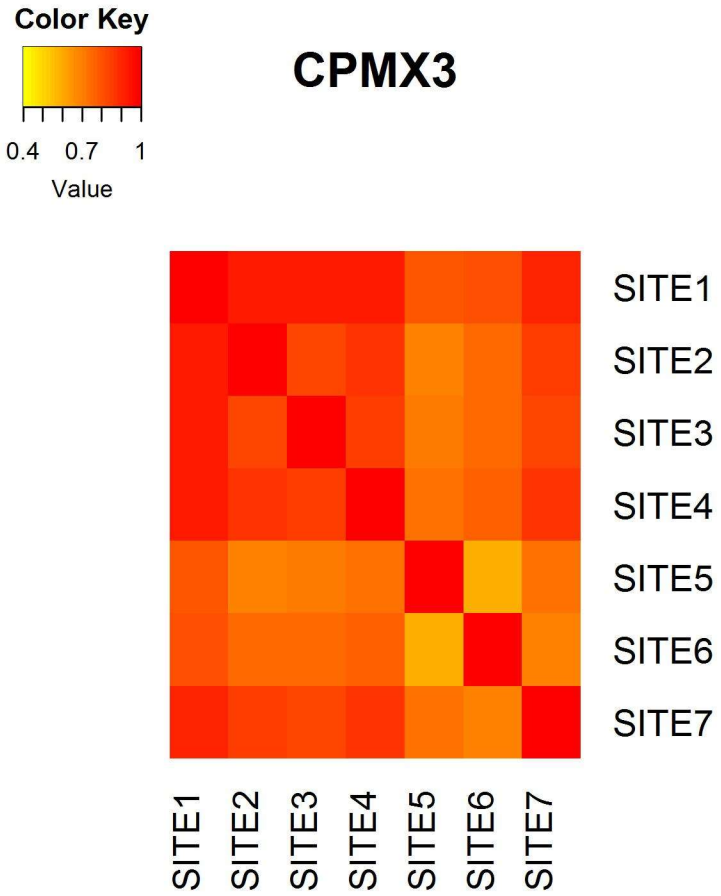

Figure B-2: A heatmap of genetic correlation among sites for Coastal series 3 (CPMX3) based on XFA1 assumptions. This image represents the correlation matrix form of the variance/covariance structure for this test series.

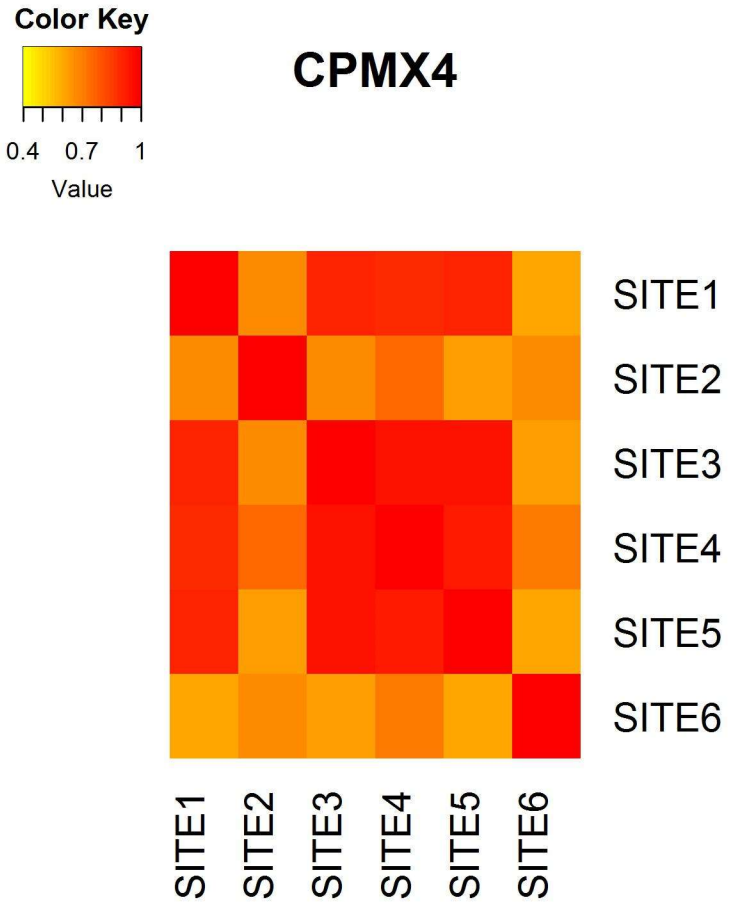

Figure B-3 A heatmap of genetic correlation among sites for Coastal series 4 (CPMX4) based on XFA2 assumptions. This image represents the correlation matrix form of the variance/covariance structure for this test series.

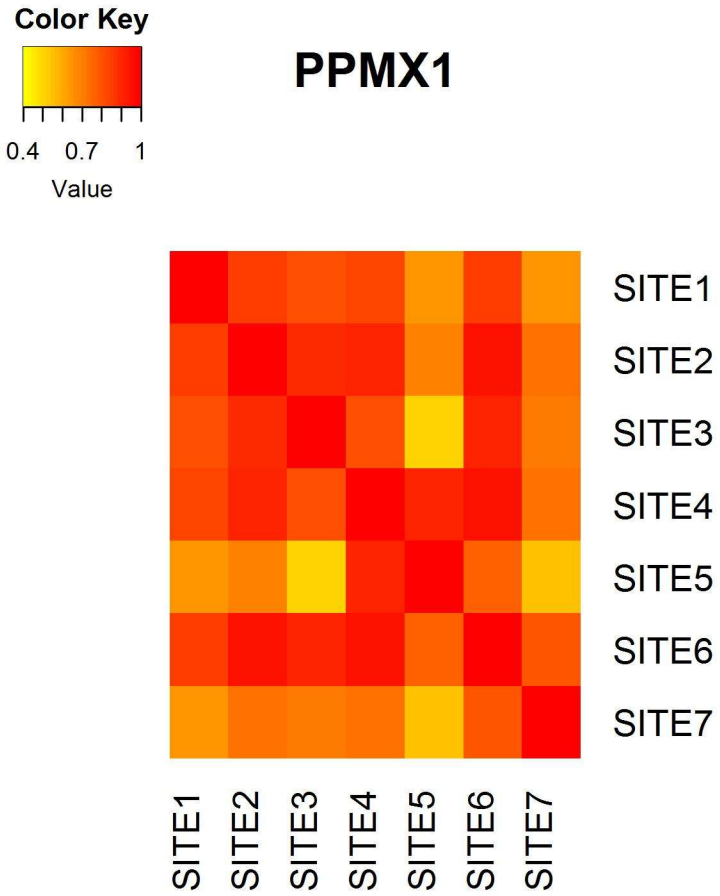

Figure B-4: A heatmap of genetic correlation among sites for Piedmont series 1 (PPMX1) based on XFA2 assumptions. This image represents the correlation matrix form of the variance/covariance structure for this test series.

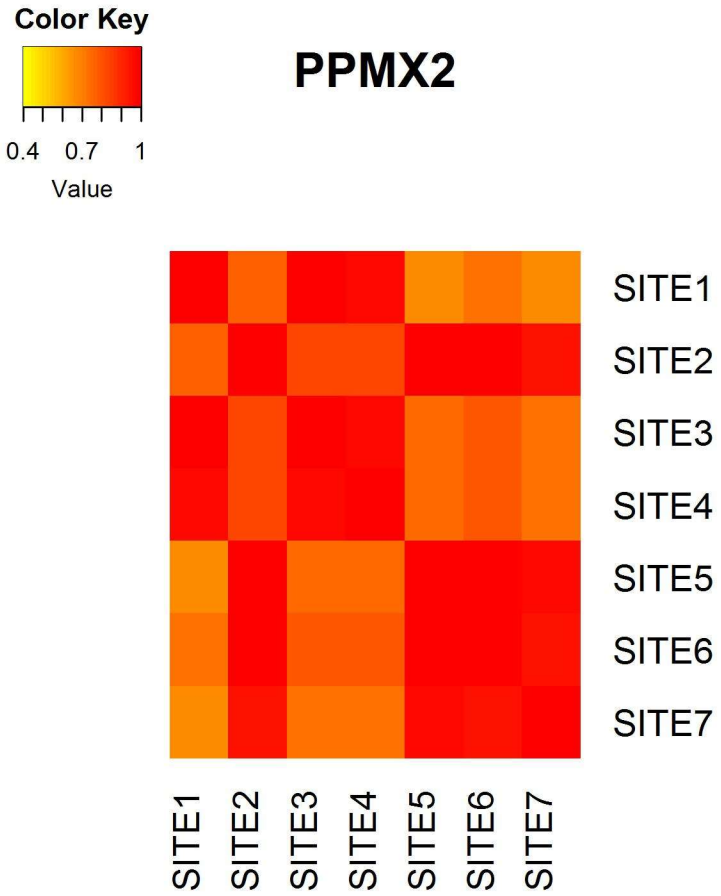

Figure B-5: A heatmap of genetic correlation among sites for Piedmont series 2 (PPMX2) based on XFA2 assumptions. This image represents the correlation matrix form of the variance/covariance structure for this test series.

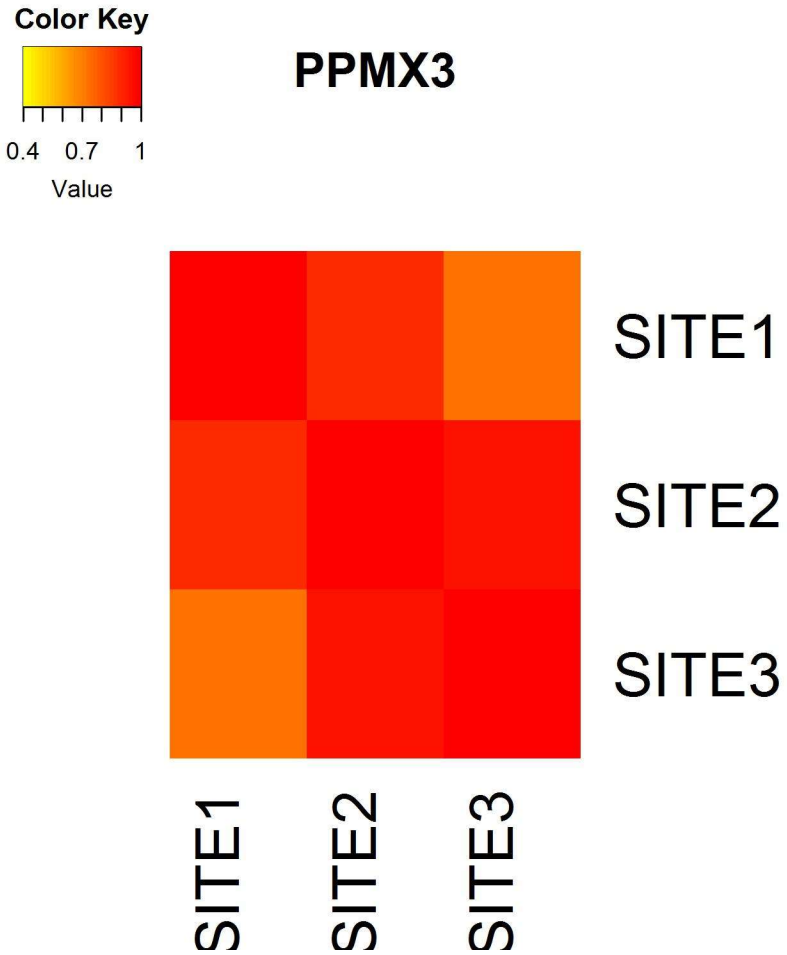

Figure B-6: A heatmap of genetic correlation among sites for Piedmont series 3 (PPMX3) based on XFA2 assumptions. This image represents the correlation matrix form of the variance/covariance structure for this test series.

Appendix C: Sample code for data analysis using ASReml.

Script C-1: ASReml4 code describing an unstructured iid model for each site in Coastal Series 1.

```
!ARGS ht vol strt  !RENAME 1 !OUTFOLDER
C:\Users\ADS\Dropbox\AndrewThesis\data\CPMX1\outputfiles
#for ht, dbh, vol, sweep, strt measurements
Title: CPMX1_nochecks.
#ser,Test,Rep,female,Male,status,rust,strt,fork,ram,sweep,HT(m),DBH(cm),VOL(dm),check,
forkram
#CPMX1,1,1,PCK,PPMX,1,0,5,1,0,2.5,7.16,10.92,34.99,2,1
#CPMX1,1,1,PCK,PPMX,4,,,,,,,,2,
 ser  !A      # CPMX1
 test  !A
 rep  *
 female  !A
 male  !A
 status  *
 rust    strt    fork    ram    sweep   ht    dbh   vol
 check  *
 forkram

#!Folder  W:\AndrewThesis\data\CPMX1
!Folder  C:\Users\ADS\Dropbox\AndrewThesis\data\CPMX1
CPMX1_nochecks.csv  !SKIP 1  !FILTER check !EXCLUDE 2  !WORKSPACE 1000
!CONTINUE  !NODISPLAY

# define model terms
# variance structure: US
$1  ~ mu  !r   diag(test).id(rep)  diag(test).id(female)        # Specify model
            residual sat(test).id(units)
VPREDICT !DEFINE
# site1
F evar1  Residual_1
F fvar1  diag(test).id(female)[1]
F phen1  evar1 + fvar1
F avar1  fvar1*4
```

Script C-1 (con't): ASReml4 code describing an unstructured iid model for each site in Coastal Series 1.

```
# site2
F evar2  Residual_2
F fvar2  diag(test).id(female)[2]
F phen2  evar2 + fvar2
F avar2  fvar2*4
# site3
F evar3  Residual_3
F fvar3  diag(test).id(female)[3]
F phen3  evar3 + fvar3
F avar3  fvar3*4
# site4
F evar4  Residual_4
F fvar4  diag(test).id(female)[4]
F phen4  evar4 + fvar4
F avar4  fvar4*4
# site5
F evar5  Residual_5
F fvar5  diag(test).id(female)[5]
F phen5  evar5 + fvar5
F avar5  fvar5*4
# site6
F evar6  Residual_6
F fvar6  diag(test).id(female)[6]
F phen6  evar6 + fvar6
F avar6  fvar6*4
# site7
F evar7  Residual_7
F fvar7  diag(test).id(female)[7]
F phen7  evar7 + fvar7
F avar7  fvar7*4
# site8
F evar8  Residual_8
F fvar8  diag(test).id(female)[8]
F phen8  evar8 + fvar8
F avar8  fvar8*4
```

Script C-1 (con't): ASReml4 code describing an unstructured iid model for each site in Coastal Series 1.

```
# site9
F evar9  Residual_9
F fvar9  diag(test).id(female)[9]
F phen9  evar9 + fvar9
F avar9  fvar9*4
# site10
F evar10  Residual_10
F fvar10  diag(test).id(female)[10]
F phen10  evar10 + fvar10
F avar10  fvar10*4
# site11
F evar11  Residual_11
F fvar11  diag(test).id(female)[11]
F phen11  evar11 + fvar11
F avar11  fvar11*4
# site12
F evar12  Residual_12
F fvar12  diag(test).id(female)[12]
F phen12  evar12 + fvar12
F avar12  fvar12*4
# site13
F evar13  Residual_13
F fvar13  diag(test).id(female)[13]
F phen13  evar13 + fvar13
F avar13  fvar13*4
# heritability
H h2i_1  avar1 phen1
H h2i_2  avar2 phen2
H h2i_3  avar3 phen3
H h2i_4  avar4 phen4
H h2i_5  avar5 phen5
H h2i_6  avar6 phen6
H h2i_7  avar7 phen7
H h2i_8  avar8 phen8
H h2i_9  avar9 phen9
H h2i_10  avar10 phen10
H h2i_11  avar11 phen11
H h2i_12  avar12 phen12
H h2i_13  avar13 phen13
```

Script C-2: ASReml4 code describing a linear mixed model for all sites in Coastal Series 1 with iid variance assumptions.

```
!ARGS ht vol strt !RENAME 1 !OUTFOLDER
C:\Users\ADS\Dropbox\AndrewThesis\data\CPMX1\outputfiles
#for ht, dbh, vol measurements
Title: CPMX1_nochecks.
#ser,Test,Rep,female,Male,status,rust,strt,fork,ram,sweep,HT(m),DBH(cm),VOL(dm),check,
forkram
#CPMX1,1,1,PCK,PPMX,1,0,5,1,0,2.5,7.16,10.92,34.99,2,1
#CPMX1,1,1,PCK,PPMX,4,,,,,,,,2,
 ser  !A      # CPMX1
 test  !A
 rep  *
 female  !A
 male  !A
 status  *
 rust    strt    fork    ram    sweep   ht    dbh   vol
 check  *
 forkram

#!Folder  W:\AndrewThesis\data\CPMX1
!Folder  C:\Users\ADS\Dropbox\AndrewThesis\data\CPMX1
CPMX1_nochecks.csv  !DOPART 1 !SKIP 1  !FILTER check !EXCLUDE 2
!WORKSPACE 1000  !CONTINUE  !NODISPLAY

  # reduced model
# $1  ~ mu  test !r  female  test.rep          # Specify model
#               residual units

tabulate vol ~ test
```

Script C-2 (con't): ASReml4 code describing a linear mixed model for all sites in Coastal Series 1 with iid variance assumptions.

```
 # full model
$1  ~ mu  test !r  female  test.rep   test.female          # Specify model
            residual units
VPREDICT !DEFINE
# overall
F evar  Residual
F fvar  female
F phen  evar + fvar + test.female
F avar  fvar*4
H h2i  avar phen
F GxE test.female
F gvar fvar + GxE
H typeBcorr fvar gvar
```

Script C-3: ASReml4 code used to generate genetic correlations of traits for Coastal Series 1 with iid assumptions.

```
!RENAME !OUTFOLDER C:\Users\ADS\Dropbox\AndrewThesis\data\CPMX1\outputfiles
#for ht, dbh, vol, sweep, strt measurements
Title: CPMX1_nochecks.
#ser,Test,Rep,female,Male,status,rust,strt,fork,ram,sweep,HT(m),DBH(cm),VOL(dm),check,
forkram
#CPMX1,1,1,PCK,PPMX,1,0,5,1,0,2.5,7.16,10.92,34.99,2,1
#CPMX1,1,1,PCK,PPMX,4,,,,,,,,2,
 ser  !A      # CPMX1
 test  !A
 rep  *
 female  !A
 male  !A
 status  *
 rust    strt    fork    ram    sweep   ht    dbh   vol
 check  *
 forkram

#!Folder  W:\AndrewThesis\data\CPMX1
!Folder  C:\Users\ADS\Dropbox\AndrewThesis\data\CPMX1
CPMX1_nochecks.csv  !SKIP 1  !FILTER check !EXCLUDE 2  !WORKSPACE 1000
!CONTINUE  !NODISPLAY

ht vol strt  ~ Trait  !r   Trait.diag(test).id(rep)  Trait.diag(test).id(female)        # Specify
model
            residual units.us(Trait)
1 2 2
0 0 ID
Trait 0 US
4*0

Trait.female 4
Trait 0 CORR
5
0.4   5
0.4   0.4    5
0.4   0.4    0.4    5 !GP
female 0 ID
```

Script C-4: ASReml4 code describing a linear mixed model for all Coastal Series 1 data with an Extended Factor Analytic variance structure. This code was used to generate a solution for both XFA1 and XFA2 models.

```
!ARGS ht vol strt !RENAME 1 !OUTFOLDER
C:\Users\ADS\Dropbox\AndrewThesis\data\CPMX1\output_FA
#for ht, dbh, vol measurements
Title: CPMX1_FA.
#ser,Test,Rep,female,Male,status,rust,strt,fork,ram,sweep,HT(m),DBH(cm),VOL(dm),check,
forkram
#CPMX1,1,1,PCK,PPMX,1,0,5,1,0,2.5,7.16,10.92,34.99,2,1
#CPMX1,1,1,PCK,PPMX,4,,,,,,,,2,
 ser  !A      # CPMX1
 test  !A
 rep  *
 female  !A
 male  !A
 status  *
 rust     strt     fork     ram     sweep   ht     dbh   vol
 check  *
 forkram

#!Folder  W:\AndrewThesis\data\CPMX1
!Folder  C:\Users\ADS\Dropbox\AndrewThesis\data\CPMX1
CPMX1_nochecks.csv  !DOPART 1 !SKIP 1  !FILTER check !EXCLUDE 2
!WORKSPACE 1000  !CONTINUE  !NODISPLAY



$1 ~ mu test  !r  xfa1(test).id(female) test.rep
            residual sat(test).id(units)

predict female !present female test
```

Script C-4 (con't): ASReml4 code describing a linear mixed model for all Coastal Series 1 data with an Extended Factor Analytic variance structure. This code was used to generate a solution for both XFA1 and XFA2 models.

```
VPREDICT !DEFINE
V female xfa1(test)
#
# phenotypic variances
F phen1 at(test,01).id(units) + 41
F phen2 at(test,02).id(units) + 43
F phen3 at(test,03).id(units) + 46
F phen4 at(test,04).id(units) + 50
F phen5 at(test,05).id(units) + 55
F phen6 at(test,06).id(units) + 61
F phen7 at(test,07).id(units) + 68
F phen8 at(test,08).id(units) + 76
F phen9 at(test,09).id(units) + 85
F phen10 at(test,10).id(units) + 95
F phen11 at(test,11).id(units) + 106
F phen12 at(test,12).id(units) + 118
F phen13 at(test,13).id(units) + 131
#
# additive variances
F add1 41 * 4
F add2 43 * 4
F add3 46 * 4
F add4 50 * 4
F add5 55 * 4
F add6 61 * 4
F add7 68 * 4
F add8 76 * 4
F add9 85 * 4
F add10 95 * 4
F add11 106 * 4
F add12 118 * 4
F add13 131 * 4
#
```

Script C-4 (con't): ASReml4 code describing a linear mixed model for all Coastal Series 1 data with an Extended Factor Analytic variance structure. This code was used to generate a solution for both XFA1 and XFA2 models.

```
# heritabilities
H h2i_1 add1 phen1
H h2i_2 add2 phen2
H h2i_3 add3 phen3
H h2i_4 add4 phen4
H h2i_5 add5 phen5
H h2i_6 add6 phen6
H h2i_7 add7 phen7
H h2i_8 add8 phen8
H h2i_9 add9 phen9
H h2i_10 add10 phen10
H h2i_11 add11 phen11
H h2i_12 add12 phen12
H h2i_13 add13 phen13
#
# total e variance and mean
F evar 2 + 3 + 4 + 5 + 6 + 7 + 8 + 9 + 10 + 11 + 12 + 13 + 14
# multiply by 1/13
F avg_evar evar * 0.0769
# familiy var avg
F fvar 41 + 43 + 46 + 50 + 55 + 61 + 68 + 76 + 85 + 95 + 106 + 118 + 131
# multiply by 1/13, multiply by 4
F avg_fvar   fvar * 0.0769
#additive variance
F avar avg_fvar * 4
# total p var
F pvar avg_fvar + avg_evar
H h2i_avg avar pvar
```