

## ABSTRACT

GRÄNS, OLOF ANDERS DANIEL. Effects of Genetics and Silviculture and Their Interactions on Loblolly Pine and Norway Spruce Growth and Wood Properties. (Under the direction of Dr. Steven E. McKeand).

Effects of genetics on important growth and wood quality traits were investigated in a 26-year old Norway spruce (*Picea abies* L. Karst) clonal trial in southern Sweden, and effects of imposed silvicultural treatments and genetics were investigated in a loblolly pine (*Pinus taeda* L.) trial in southwestern Georgia, USA at age 15 and 16 years. The loblolly pine trial was designed with different fertilizer and herbicide treatment combinations applied to 25 open-pollinated first- and second-generation families.

In the Norway spruce trial, high broad-sense heritability values were found for wood density (0.48), microfibril angle (0.41), and wood stiffness (0.50). All investigated growth traits had similar heritability values as reported in earlier studies. The Norway spruce material also showed high age-age correlations between different sections of the wood cores sampled at breast height when moving from pith to bark. This indicated that early selection for wood quality traits would be possible. Unfavorable genetic correlations between volume growth and wood stiffness indicated that selection for volume only at age 10 would result in a 0.27% decrease in wood stiffness associated with every 1% increase for volume growth at age 26.

In the loblolly pine trial, the means for individual-tree stem volume were 185 dm<sup>3</sup> in the combined fertilization and herbicide treatments, while in the other extreme, the control plots (with no treatments), mean stem volume averaged 91 dm<sup>3</sup>. Significant differences among treatment combinations for height, volume, sweep, forking defect, squared acoustic velocity,

and wood density were also found. Squared acoustic velocity ranged from 14.5 km<sup>2</sup>/s<sup>2</sup> in the fertilization only plots to 16.4 km<sup>2</sup>/s<sup>2</sup> in the herbicides only plots, while the average core density varied from 465 kg/m<sup>3</sup> in the control plots to 450 kg/m<sup>3</sup> in the combined fertilization and herbicide plots. The loblolly pine trial had significant family effects for every trait.

Individual-tree heritability values were 0.26 for height, 0.33 for volume, 0.10 for sweep, 0.39 for branch angle, 0.29 for forking defect, 0.23 for fusiform rust incidence (caused by the fungus *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*), 0.41 for squared acoustic velocity, 0.32 for whole core weighted density, 0.28, for ring 2-6 core section density, and 0.78 for ring 7-16 core section density. Corresponding values for family-mean heritability values were 0.85 for height, 0.86 for volume, 0.60 for sweep, 0.90 for branch angle, 0.87 for forking defect, 0.84 for rust, 0.90 for squared velocity, 0.88 for whole core weighted density, 0.86 for ring 2-6 core section density, and 0.95 for ring 7-16 core section density. The genetic and phenotypic correlations between the growth and form traits were generally low and non-significant. Genetic and phenotypic correlations were significant for a number of combinations of wood quality traits while correlations were generally low and non-significant between growth and form traits and wood quality traits.

Interactions between silviculture and genetics were not significant for any of the measured traits, and the family rankings were stable across treatment combinations. Based on the results from this trial, the risk of losing value in terms of growth or wood quality due to unfavorable interactions between genetic material and silvicultural prescriptions is low when selected and improved half-sib coastal loblolly pine genetic material is used.

Effects of Genetics and Silviculture and Their Interactions on Loblolly Pine and  
Norway Spruce Growth and Wood Properties

by  
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## **DEDICATION**

This dissertation is dedicated to my parents.

## **BIOGRAPHY**

Olof Anders Daniel Gräns was born in 1977 and grew up on a farm outside of a small town called Kramfors in northern Sweden. After graduating from high school, he completed his military service in the neighboring town of Sollefteå. In the fall of 1997 he started studying forestry at the Swedish University of Agricultural Sciences (SLU) in Umeå. After finishing his degree in forest management at SLU he went to North Carolina State University to pursue a Doctoral degree in Forestry and Environmental Resources focusing on genetics, silviculture, and wood quality, supported by the Gunnar and Lilian Nicholson Graduate Fellowship.

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## CHAPTER 1

# GENETIC VARIATION AND RELATIONSHIPS TO GROWTH TRAITS FOR MICROFIBRIL ANGLE, WOOD DENSITY, AND MODULUS OF ELASTICITY IN A PICEA ABIES CLONAL TRIAL IN SOUTHERN SWEDEN

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## Abstract

Genetic variation in wood density, microfibril angle (MFA), wood stiffness (MOE), height, diameter, and volume was investigated in a 26-year old Norway spruce [*Picea abies* (L.) Karst.] clonal trial in southern Sweden. Wood quality measurements were performed on 10 mm increment cores using SilviScan. For MFA, mean values of annual rings showed the highest value (30°) at ring 2 counting from the pith, followed by a steep decrease and a gradual stabilization around ring 12 at approximately 14°. MOE showed a monotonic increase from 5 GPa to 14 GPa when moving from pith to bark. High broad-sense heritability values were found for wood density (0.48), MFA (0.41), and MOE (0.50). All growth traits displayed heritability values of similar magnitudes as reported in earlier studies. The generally high age-age correlations between different sections of the wood cores suggested that early selection for wood quality traits would be successful. Owing to unfavorable genetic correlations between volume and MOE, the correlated response indicated that selection for volume only at age 10 would result in a 0.27% decrease in weighted MOE at age 26 for every 1% increase in volume.

## **Introduction**

Over the recent decades, the forest industry in many parts of the world has started to move towards usage of more fast-growing plantation timber to keep up with their raw material needs and to reduce costs. From the point of view of the solid wood products industry, this has already and will probably lead to lower wood stiffness i.e. modulus of elasticity (MOE) and stability problems such as warping in larger portions of their products (e.g. Rozenberg & Cahalan, 1997). These changes in product properties are primarily due to the relative increase in the proportion of juvenile wood in the raw material from fast-grown plantations compared with wood from natural, older, slow-grown stands. Tree breeding for selected wood properties such as MOE has been suggested as a possible solution to these problems. Genetic selection provides a tool for modifying overall wood quality in plantations, as well as producing trees with juvenile wood that more resembles mature wood, thus increasing the overall uniformity from pith to bark within the tree (Lindström et al., 2005).

Wood density and microfibril angle (MFA) in the secondary cell wall are key properties determining clearwood (no knots present) MOE (e.g. Persson, 1997). Wood density has been well studied (e.g. Newlin & Wilson, 1919) and has shown to be a moderate predictor of MOE within species. The effect of MFA has relied heavily on theoretical models that have been difficult to verify practically owing to the lack of efficient measurement techniques. Recent development of the X-ray diffraction technique within the SilviScan instrument has enabled rapid characterization of wood with respect to MFA (Evans, 2006). With the

technique, the MFA of large numbers of tracheids are measured. This is important for material characterization, since it is shown that the MFA varies strongly also within annual rings (Brändström, 2002) and thus, that measurements on small numbers of fibers are not adequate. In several recent studies, SilviScan-estimated MOE has shown good agreement with direct measurements of dynamic and static MOE (Evans, 2006; Raymond et al., 2007). Development of the new measurement technique offers new opportunities to improve MOE through genetic selection.

Genetic parameters of wood density have been published for a wide range of species. The results across species generally show a high heritability, a low genotype by environment interaction, and strong positive age-age correlations (i.e. selection based on early measurements are efficient) (Zobel & Jett, 1995). In Norway spruce [*Picea abies* (L.) Karst.], strong negative genetic relationships have been found with growth traits (Hysten, 1997; Hannrup et al., 2004). This indicates that genotypes combining high wood density and growth are rare but have nevertheless been identified (Zubizarreta Gerindian et al., 2007).

The inheritance patterns of MFA and MOE have been explored in *Pinus radiata* D. Don in several recent studies based on SilviScan measurements, and the results show the traits to be moderately to highly heritable (Dungey et al., 2006; Kumar et al., 2006; Wu et al., 2007). In *Pinus taeda* L., Isik et al. (2008) reported high clone mean heritabilities for MFA. In Norway spruce, moderate narrow-sense heritabilities were reported for MFA measured in SilviScan (Steffenrem et al. 2009). Based on microscopic measurements of specific year rings in spruce



species (Ivkovich et al., 2002), and (Hannrup et al., 2004) found heritabilities of similar magnitude. In the latter study on Norway spruce, MFA had a weak non-significant relationship with growth traits, and as a result of the combined effect of MFA and wood density, MOE was moderately, negatively, genetically correlated with volume growth. This indicates that it is possible simultaneously to improve growth and MOE in Norway spruce by taking into account the combined effect of MFA and wood density. However, more knowledge is required about genetic parameters of MFA in general, and how MOE and its underlying traits are genetically correlated with growth traits. In Steffenrem et al. 2009, wood density, MFA, and MOE was found to be more adversely correlated with diameter growth than height growth.

In this study, estimates of genetic parameters for wood stiffness, MFA, and wood density from a Norway spruce clonal trial are provided. The combination of a clonal material and SilviScan measurements makes the study unique and enables high-precision estimates to be made for the wood quality traits. The specific objectives of the study were: (1) to evaluate the amount of variation as well as the magnitude of genetic control in the wood quality traits; (2) to examine age-age correlations of the wood quality traits and their patterns of transition from juvenile to mature wood; and (3) to study the degree of association between wood quality traits and important growth traits (height, diameter, and volume).

## **Materials and Methods**

### *Sampling and measurements*

Wood cores were collected from a 26-year-old clonal Norway spruce trial located in Gålarp, close to Svalöv in southern Sweden (56°06'N, 13°11'E; 165 m elevation). In total 98 clones were included in the trial. The material consisted of seven clones that originated from crosses between Swedish plus trees, 10 clones originating from a commercial seed lot of the Slovakian Zakammenne provenance, and the remaining 81 clones from a commercial seedlot of the Christinehof provenance. The latter provenance is a plantation in southern Sweden established with seeds of west continental origin. Seeds of the three sources were sown in a nursery and among 3-year-old seedlings, plants were selected for superior height and vegetatively propagated by cuttings. Previous studies have shown the effect of such a selection to be small (Högberg & Karlsson, 1998; Hannerz et al., 1999), and therefore the nursery selection effect was considered to be negligible in this study.

The field trial was planted in the spring of 1978 with 3-year-old cuttings at a spacing of 2 x 2 m. Each of the 98 clones tested in the trial was represented by six to 10 ramets. The cuttings were randomized in single-tree plots in 10 blocks with at the most one ramet per block and clone. For this study, a subset of 40 representative clones was used. All clones originated from the Christinehof provenance and in this study all the clones included in the sample were assumed to be unrelated. Increment cores (10 mm) were taken at breast height from 200 trees in 2003. The sampling was made across all 10 blocks in the trial and each of the 40 clones

was represented with five randomly sampled ramets. Diameter data, collected in 2000, were used to ensure that the sample of the clones reflected the distribution of mean clonal diameters. Wood cores were packed and stored in a freezer. About 30 trees had to be re-sampled because of problems with broken cores. These trees were sampled by taking wood discs. Diameter at breast height and total tree height were also measured for all trees included in the study.

#### *SilviScan measurements*

The wood samples were measured with the SilviScan instrument at STFI-Packforsk. SilviScan combines image analysis with X-ray absorption and X-ray diffraction in a way that makes it possible to determine wood and fiber properties efficiently and with high resolution (Evans, 2006). Before measuring, the samples were cut into 2 x 7 mm strips from pith to bark, and then extracted in acetone to remove resins. The top surface of each strip was polished to obtain a fine surface for imaging of the fiber cross-sections. The samples were conditioned in the laboratory to a moisture content of approximately 8%. The volume and mass of each sample were taken to calculate average density values for calibration purposes. Density was measured on air-dried samples which meant conditioned weight on conditioned volume. Measurement on air-dried samples results in higher density values compared with the widely used basic density, which is oven-dried weight on raw (green) volume.

The radial variation in the orientations of the annual rings (and fiber widths in radial and tangential direction) was determined by video microscopy. The radial variation in wood

density was determined by using X-ray absorption. The measured orientation of the annual rings was used to rotate the sample during densitometry to keep the X-ray beam constantly aligned with the latewood bands and thereby increase precision in the data for ring position, ring width, and earlywood and latewood boundaries, as well as for the density of each ring.

Wood stiffness, here expressed as acoustic MOE, is related to wood density and MFA, but to an even higher degree is related to wood density and the coefficient of variation of the azimuthal intensity profile,  $I_{CV}$  (Evans, 2006). In SilviScan, a focused X-ray beam is used to interact with the wood structure, and from the resulting X-ray diffraction pattern (diffractogram) the  $I_{CV}$  parameter can be determined and thereafter combined with wood density data to predict MOE according to the following equation:

$$MOE = A(I_{CV} * D)^B \quad (\text{Eq.1.1})$$

where  $A$  is a scaling factor,  $B$  is an exponent making curvature possible, and  $D$  is the density. In Evans (2006), values 0.165 for  $A$  and 0.85 for  $B$  were used for a former version of SilviScan. The current SilviScan system is set up to be more sensitive and  $A$  has been changed to 0.14, based on cross-calibration on the same samples (R. Evans, personal communication, March 24, 2009).

In total, SilviScan data were obtained from 186 cores that were visually inspected to confirm the year ring boundaries based on SilviScan measurements. Numbers were assigned to each

ring starting from the pith. The pith was included in 108 of the increment cores but for 78 increment cores the pith was missing. To estimate the number of missing rings, those samples were placed on a transparent, plastic film with concentric circles. Thereafter, the angle of the year rings was aligned with the circles so that the distance from the pith from the increment core to the actual center of the tree could be determined and the number of missing rings was estimated. Each ring in these samples was renumbered based on these measurements. The ring numbers were used for calculating weighted values on sections and age-age correlations between sections. Data for ring 1 were not used in this analysis owing to its proximity to the pith, containing wood very different from the rest of the sample. Each year ring was also assigned a chronological number based on the year of formation, starting from the latest formed outer ring and counting backwards towards the pith. These ring numbers were used when the relationship between wood traits and growth traits was investigated.

The variation in wood density, MFA and MOE was analyzed at whole core level and on sections of the increment cores. Area-weighted values were calculated and utilized in the study since these better reflect the average properties of the wood in one entire section. This is due to the fact that different year rings can represent different proportions of the total volume of wood in the sample. The area-weighted values of the cores and the segments were calculated as:

$$AB = \frac{\sum_{i=\min}^{\max} a_i * b_i}{\sum_{i=\min}^{\max} a_i} \quad (\text{Eq.1.2})$$

where  $a_i$  is the cross-sectional area represented by year ring  $i$ ,  $b_i$  is the wood density or MFA or MOE of year ring  $i$  and min and max represent the lowest and highest year ring number of the whole core/core section respectively.

Two different ways of grouping rings into sections were used depending on the kind of analysis and comparisons intended. First, rings were grouped according to their position outwards from the pith (at breast height). This meant that the rings number 2-5, 6-10 11-15, 16-20, and 2-20 were grouped and weighted together to represent different general stages in the development of wood density, MFA, and MOE. These sections were used to calculate genetic parameters, and genotypic age-age correlations. In the second approach, year rings were grouped together based on the chronological year which they were formed. The reason for this was to enable comparisons between growth traits measured at a certain point in time and the wood formed up to that point, regardless the variation in the number of rings at breast height that existed in the trial due to the fact that different trees reached breast height in different years.

Data on growth traits from earlier measurements were included in the analysis.

Measurements were available for diameter at ages 10, 22, and 25 years, and height at ages 7,

10, and 26 years in the field. Volume was calculated for each tree using a function by Brandel (1990). Growth data were available for all trees in the trial for ages 7, 10, and 22. Therefore, to increase precision, all 81 clones in the Christinehof provenance were included when genetic parameters were calculated. Growth data for years 25 and 26 were available only for the trees sampled for wood cores. Genetic correlations between growth and wood quality traits were calculated based on a completely balanced data set (40 clones).

### *Statistical analyses*

The following linear mixed model was fit to data to estimate variance components:

$$Y_{ij} = \mu + b_i + c_j + e_{ij} \quad (\text{Eq.1.3})$$

where  $Y_{ij}$  is the observation on the tree of the  $j$ th clone in the  $i$ th block,  $\mu$  is the overall mean,  $b_i$  is the fixed effect of the  $i$ th block,  $c_j$  is the random effect of the  $j$ th clone, and  $e_{ij}$  is the random residual effect. The random clonal and residual effects were assumed to be independent and normally distributed with an expected mean of zero and variances  $\sigma_c^2$  and  $\sigma_e^2$ , respectively. The model could also be expressed in matrix notation:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u} + \mathbf{e} \quad (\text{Eq.1.4})$$

where  $\mathbf{y}$  is the vector of individual phenotypic observations,  $\mathbf{X}$  is the design matrix of fixed effects (intercept, block),  $\boldsymbol{\beta}$  is the vector of fixed effects,  $\mathbf{Z}$  is the design matrix of random effects (clone),  $\mathbf{u}$  is the vector of random effects with a multivariate normal distribution and expected value zero,  $\mathbf{E}(\mathbf{u})=0$ ; and  $\mathbf{e}$  is the vector of randomly and independently distributed residuals  $\mathbf{E}(\mathbf{e})=0$ . The variance of  $\mathbf{y}$  vector is  $\text{Var}(\mathbf{y}) = \mathbf{Z}\mathbf{G}\mathbf{Z}^T + \mathbf{R}$ , where  $\mathbf{G}$  is the diagonal variance-covariance matrix of random effects (clone) and  $\mathbf{R}$  is the variance-covariance matrix of random errors ( $\mathbf{R} = \sigma^2\mathbf{I}_n$ , where  $\sigma^2$  is the variance and  $\mathbf{I}_n$  the identity matrix) and  $\mathbf{Z}^T$  is the transpose of the design matrix (Littell et al., 1996). Variance components from the mixed model were estimated with the Mixed procedure in the SAS software (SAS Institute, 2004). The variance observed for clonal differences is genetic ( $\sigma_C^2$ ). Within-clone variance is environmental ( $\sigma_E^2$ ) because all the copies of a clone are genetically identical. Using the observed variance components for clones and within-clones (error) phenotypic variance ( $\sigma_P^2$ ) can be estimated as  $\sigma_P^2 = \sigma_C^2 + \sigma_E^2$ . Broad-sense heritability ( $H^2$ ) was calculated on individual tree basis as:

$$H^2 = \sigma_C^2 / \sigma_P^2 \quad (\text{Eq.1.5})$$

The genotypic coefficient of variation ( $CV_G$ ) expressed as a percentage was calculated using the following equation:



$$CV_G = \frac{\sigma_c}{\mu} * 100 \quad (\text{Eq.1.6})$$

where  $\mu$  is the mean of the measured trait. Estimates of the standard errors of the genetic parameters were calculated according to the Delta method (Lynch & Walsh, 1998, Appendix 1) and calculated by a SAS IML code (Isik et al., 2008). Genotypic correlations ( $r_G$ ) between two traits  $X$  and  $Y$  or between two ages of the same trait (age-age) were estimated as follows (Falconer & Mackay, 1996):

$$r_G = \frac{\sigma_{c(XY)}}{\sqrt{\sigma_{c(X)}^2 \sigma_{c(Y)}^2}} \quad (\text{Eq.1.7})$$

where  $\sigma_{c(XY)}$  is the genotypic covariance between two traits  $X$  and  $Y$ , and  $\sigma_{c(X)}^2$  and  $\sigma_{c(Y)}^2$  are the genetic variances of the traits. Genotypic correlations between pairs of traits were calculated by fitting a bivariate linear mixed model and using a Mixed procedure code of SAS (Isik et al., 2008).

Expected relative correlated response was calculated as the ratio of the relative correlated response to the relative direct response as:

$$\frac{CR_Y}{R_X} = \frac{r_G * i * H_{\bar{c}_x} * CV_{G_y}}{i * H_{\bar{c}_x} * CV_{G_x}} = \frac{r_G * CV_{G_y}}{CV_{G_x}} \quad (\text{Eq.1.8})$$

where  $H_{\bar{c}}$  is the square root of the repeatability of clone means, which is the ratio between the square root of  $(\sigma_C^2)$  in the numerator and the square root of  $(\sigma_C^2)$  plus  $(\sigma_E^2)$  divided by the number trees per clone in the denominator,  $y$  and  $x$  are indices for the correlated and the selected trait, respectively.

## Results

There was a strong association between the radial MFA (Figure 1.1a) and the corresponding ring width (Figure 1.1d). MFA peaked around 30° at ring 2 from the pith followed by a steep decrease and a gradual stabilization around ring 12 at approximately 14°. Wood density showed an initial drop followed by a monotonic increase from ring 6 to the bark (Figure 1.1b). Wood density displayed an inverse relationship with ring width. As a combined effect of the radial increase in density and decrease in MFA, MOE showed a monotonic increase from around 5 GPa to approximately 14 GPa when moving from pith to bark (Figure 1.1c).

Estimates of heritabilities with standard errors, arithmetic means, and genotypic coefficients of variation for wood properties and growth traits are shown in Table 1.1.

The inner wood section (rings 2 to 5) had the highest MFA value compared with other ring groups. The means for MFA decreased for subsequent ring groups towards the outer wood. In contrast, as expected, the average MOE increased from the inner rings towards the outer rings. For example the mean for the section consisting of rings 2-5 went from 5.4 to 12.3 for the ring group 16-20. Genetic variation for MFA and wood density had similar trends from the inner wood to outer wood. For both traits, coefficient of genetic variance was smaller in the inner wood compared with ring groups towards the bark. There was no apparent trend for MOE. MFA and MOE, here expressed as weighted averages of sections of the wood cores, displayed high to moderate individual-tree broad-sense heritabilities in all four- and five-ring

sections as well as in the ring 2-20 sections. Wood density displayed lower values in the outermost sections in comparison to the values for MFA and MOE. Heritabilities for the growth traits were generally moderate or low and below 0.30. For volume at age 26, heritability values were slightly higher. All heritabilities had standard errors between approximately 0.04 and 0.09.

Genotypic correlations between whole-tree values (ring 2-20) and the four- and five-ring sections at various ages were high for all wood properties (Tables 1.2-1.4). For example, the genetic correlation between inner wood rings and the whole tree for MFA, density, and MOE was 0.88, 0.78 and 0.91, respectively (Tables 1.2 to 1.4). The genetic relationships were also strong between individual four- or five-ring sections, but there was a trend towards decreasing values of correlations with increasing distance between sections. This trend was most pronounced for wood density and MOE (Tables 1.3-1.4).

Estimates of genotypic correlations between wood quality traits and diameter, height, and volume at age 10 and 26 years in the field are presented in Table 1.5. MFA had weak to moderate (0.03 to 0.40) positive but adverse correlations with the growth traits, suggesting that fast growing trees tend to have higher MFAs in wood. MOE had negative correlations with the growth traits of about the same magnitude as MFA. For both MFA and MOE, similar levels of genetic association at both ages 10 and 26 with the growth traits were observed, although the genetic relationships of MFA and MOE observed at age 26 with the growth traits were somewhat higher.

Wood density and MOE showed negative correlations with the growth traits, generally of higher magnitudes than those for MFA. Volume at age 10 was adversely correlated with all wood quality traits measured at age 26, including wood density (Table 1.5). A majority of the correlation estimates had standard errors greater than half of the correlation value, suggesting that most correlations are probably not significantly different from zero.

Expected relative correlated responses for the wood quality traits with selection for volume at age 10 are presented in Table 1.6. The response for MFA was positive, whereas it was negative for wood density and MOE. When selection is made for volume at age 10, the expected relative response in MFA at age 26 is 0.16%, suggesting that wood produced by planting fast-growing clones may increase MFA. Similarly, selection on volume at age 10 is predicted to decrease density and MOE by 0.12%, and 0.27% respectively for every 1% increase in volume.

## Discussion

### *Mean values*

The radial development of MFA (Figure 1.1a) as well as the corresponding trend for ring width (Figure 1.1d) expressed a gradual decrease when moving from the pith towards the bark. The initial decrease in values of MFA was followed by a gradual stabilization as the distance from the pith increased further. In terms of peak value, as well as time and levels of stabilization, the radial MFA development showed a very similar pattern to previously reported radial profiles from studies of fast-grown Norway spruce in southern Sweden (Lundgren, 2004). Since the trial used in the present study was established on a fertile site, previously used for agriculture, it had extremely high growth rates and wide growth rings (Figure 1.1d). It appears as if Norway spruce grown on extremely fertile sites tend to display similar radial MFA patterns to *P. radiata* (Dungey et al., 2006) and *P. taeda* (Clark et al., 2006), two fast-growing pine species. It needs to be stressed, however, that under more normal growth conditions, Norway spruce seems to have lower peak values for MFA as well as a considerably earlier stabilization compared with the material in this study (Lindström et al., 1998; Steffenrem, 2008).

The wood density values from SilviScan used in this study were calibrated against gravimetrically determined density values on air-dried samples. The calibration against air-dried samples is estimated to give density values approximately 15% higher than the basic density (Lundgren, 2004). This should be taken into account when these values are compared

against results from other studies. In general, density increased with year ring number after an initial drop in the first few rings (Figure 1.1b), which is consistent with patterns generally found for planted Norway spruce (e.g. Pape, 1999; Lundgren, 2004).

One possible explanation for the continued increase in density in the last few year rings could be recent overstocking. There was an urgent need for thinning in the trial at the time of sample collection.

MOE showed a dramatic increase in absolute values from pith to bark in this material (Figure 1.1c). This emphasizes the large variation between juvenile and mature wood present in terms of properties important for solid wood products. The significant variation in the two component traits, MFA and wood density, results in a major variation in MOE.

#### *Genetic parameters*

Heritability values for MFA found in this study (Table 1.1) are generally somewhat higher than earlier published estimates from studies using microscopic techniques in spruce species (Ivkovich et al., 2002; Hannrup et al., 2004). Narrow-sense heritability estimates for SilviScan measured MFA reported for Norway spruce by Steffenrem et al., (2009) were slightly lower. In pines, heritabilities estimated based on SilviScan measured MFA in general show moderate to high values on the tree level (Donaldson & Burdon, 1995; Dungey et al., 2006; Wu et al., 2007), even though the variations among individual rings may be large. Isik

et al. (2008) reported high clone mean heritabilities from a *P. taeda* experiment in the southern USA.

The genetic control of wood density was generally strong (Table 1.1) which agrees with previous studies in *P. abies* (Hysten, 1999; Hannrup, et al., 2004; Steffenrem et al. 2009). However, wood density has a significantly lower coefficient of genotypic variation than MFA, MOE and the growth traits, which limits the selection progress that can be made for this trait. The highest heritability among the studied traits was observed for SilviScan-estimated MOE ( $H^2=0.50$ , Table 1.1) which is considerably higher than reported earlier for Norway spruce (Hannrup et al., 2004; Steffenrem et al., 2009). Wu et al. (2007) found high heritabilities for radiata pine, but the values were associated with large standard errors and also were lower in magnitude than corresponding values for wood density and MFA.

For the growth traits, estimates of broad-sense heritability ( $H^2$ ) and genotypic coefficients of variation ( $CV_G$ ) in this study were in accordance with earlier findings from a compilation of estimates in Norway spruce (Rosvall et al., 2001).

There were moderate to high heritabilities for sections along the core for all wood quality traits, with decreasing values observed in the outer sections for wood density (Table 1.1), possibly partly explained by competition effects due to the delay in thinning of the trial.



In an earlier study on Norway spruce (Hysten, 1999) estimated that cumulative wood density leveled off somewhat towards the bark. In the same study, estimates of individual tree heritability for wood density fluctuated considerably from ring to ring.

In a study on radiata pine, Dungey et al. (2006) reported high heritabilities in the corewood for SilviScan-estimated MFA, wood density, and MOE, while values decreased to moderate or low in the outerwood. Also, for the same species, Kumar et al. (2006) made similar observations regarding the variation in heritability from pith to bark for SilviScan based MOE.

#### *Age-age correlations*

The high genotypic correlations between the ring 2-20 values and the ring 2-5 values ( $r_G=0.88$  for MFA, 0.78 for wood density, and 0.91 for MOE) indicate that there were few ranking shifts among the clones for MFA, wood density, and MOE during the studied time interval (Tables 1.2-1.4). This generally confirms the results by Hysten (1999) who found consistently high genetic correlations from the pith towards the bark for wood density. Furthermore, the results suggest that early selection (based on the ring 2-5 section) for MFA as well as for wood density could be efficient for improving the target trait, juvenile wood stiffness. In addition, selection for improved juvenile wood MOE using non-destructive methods based on indirect associations with MOE such as acoustic techniques would be an option, even at later stages of growth where the measurements would largely reflect the properties in sections farther away from the core sections. A few changes in rank between clones, could still be expected with increasing age, however, since the correlation gradually

went down over time. The results agree with earlier studies in radiata pine in terms of generally high age-age correlations gradually decreasing with distance (Kumar et al., 2006; Wu et al., 2007). The possibility of carrying out early selection in radiata pine has been suggested as favorable even though variation in the magnitude of the age-age correlations could also occur between sites (Dungey et al., 2006).

#### *Relationships between wood properties and growth traits*

The correlations between the growth traits and the wood quality traits (Table 1.5) revealed a tendency for the latter traits to show weaker relationships with height than with diameter and volume. Furthermore, tree volume after 10 years in the field showed generally significant adverse genotypic correlations with the wood quality traits at the two ages studied. Similar results were reported by Hannrup et al. (2004) and Steffenrem et al. (2009). These correlations indicate that a selection for tree volume based on 10-year data, which is normal practice in the Swedish Norway spruce breeding (Karlsson & Rosvall, 1993), would increase MFA in the juvenile wood. The corresponding effect on wood density and MOE would be decreased values.

If the present results can be generalized for all Norway spruce, this is a clear warning sign of decreased wood quality in the future following from current selection practice. However, as the correlations do not indicate an extremely strong relationship ( $r_G \sim 0.5$ ), the adverse effects could be counteracted by active identification and vegetative propagation of clones that combine good growth with acceptable MOE. Such possibilities should be further explored. In

a clonal study (Zubizzareta Gerendiain et al., 2007), results based on phenotypic correlation estimates show that if selection were made only for wood density it would result in a large reduction in volume production. The study suggests a compromise between the two objectives and mentions the possibility of selecting specific clones that combine high volume production with reasonably high wood density.

### *Practical implications*

The expected relative correlated response in MOE when selecting for volume at age 10 was -0.27% (Table 1.6). Hence, for a 1% increase in volume there would be a 0.27% decrease in MOE if selection were based on volume at age 10 only. As the tree breeding program progresses with continued cycles of testing and selection, large gains in volume production are projected. In the first breeding generation of Norway spruce in Sweden expected gains are in the magnitude of 30-35% if selection is performed on one trait only (Rosvall et al., 2001). Even though several traits are usually combined into an index to facilitate the improvement of a number of traits simultaneously, it is necessary to consider and quantify the effects on additional important traits currently excluded from these indices.

The observed values of MOE in this material ranged from 5 GPa to 14 GPa. Normal strength requirements for structural timber are in the range of 7-14 GPa depending on the class. With a scenario based on selection of the 20 % best performing of the measured clones in terms of volume at age 10, a 38 % volume gain would be accompanied by approximately a 10% reduction in MOE at age 26. A decrease in wood stiffness of about 1 GPa could make the

solid wood products move from one class to another in the Swedish classification system for structural lumber (Anon, 1998).

The example above highlights the risk of negatively affecting MOE when selecting for early volume growth. In addition, in this material the values of wood density were not as adversely affected by selection for early volume growth as were the values of MOE. The majority of previously performed wood variation studies have focused mostly on wood density. These results suggest that by measuring MOE, the precision could be increased when attempting to quantify effects on wood quality.

It needs to be stressed that the material on which this study was based is limited in terms of what general conclusions that can be drawn from it. The study was performed on sample trees from just one site, which prevents any attempts at quantifying possible genotype by environment interactions. In addition, the trial was established on former agriculture land with a considerably higher site index than is normal for forest land in southern Sweden, and there is a risk that differences in the studied traits were expressed to a higher degree owing to fast growth. Therefore, it is of major importance to investigate and quantify further the genotypic variation in the studied wood quality traits on a number of different sites representing the conditions in operational forestry. Recent developments in measurement technology (e.g. SilviScan measurements on increment cores, acoustic technologies on standing trees) make this feasible at much lower costs than was previously possible.

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## TABLES

**Table 1.1.** Traits with units, field age, number of observations (n), arithmetic mean values, individual-tree broad-sense heritabilities ( $H^2$ ) with their standard errors in parentheses, and genotypic coefficients of variation ( $CV_G$ ) for the studied wood and growth traits.

Trait	Field age*	n	Aritmetic mean	$H^2$ (SE)	$CV_G$
Weighted MFA (degrees)					
	2-20	186	20.2	0.41 (0.08)	13.0
	2-5	185	27.1	0.37 (0.08)	9.8
	6-10	186	19.9	0.41 (0.08)	16.4
	11-15	184	15.2	0.35 (0.08)	16.7
	16-20	169	13.0	0.40 (0.09)	16.8
Weighted wood density (kg/m <sup>3</sup> )					
	2-20	186	396.3	0.48 (0.08)	7.3
	2-5	186	359.1	0.41 (0.08)	6.5
	6-10	186	348.9	0.46 (0.08)	7.7
	11-15	184	392.7	0.29 (0.08)	8.9
	16-20	168	439.3	0.32 (0.09)	10.6
Weighted MOE (GPa)					
	2-20	186	9.2	0.50 (0.08)	15.7
	2-5	185	5.4	0.43 (0.08)	15.9
	6-10	186	7.6	0.45 (0.08)	19.0
	11-15	184	10.3	0.40 (0.08)	17.4
	16-20	169	12.3	0.36 (0.09)	15.1
Growth traits					
Height (dm)	7	658	24.0	0.18 (0.04)	13.5
Height (dm)	10	658	43.5	0.19 (0.04)	11.8
Height (dm)	26	196	165.8	0.26 (0.08)	8.3
Diameter (mm)	10	636	67.2	0.23 (0.04)	16.5
Diameter (mm)	22	602	171.8	0.23 (0.04)	13.9
Diameter (mm)	25	200	177.5	0.28 (0.08)	15.9
Volume (dm <sup>3</sup> )	10	634	12.6	0.24 (0.04)	31.9
Volume (dm <sup>3</sup> )	26	196	240.8	0.39 (0.08)	35.6

Note: \*Field age 26 corresponds to approximately year ring number 1-20 from the pith in the samples taken at breast height. MFA=microfibril angle; MOE=modulus of elasticity.

**Table 1.2.** Genotypic correlations between area-weighted averages of MFA in different ring groups.

	Ring 2-5	Ring 6-10	Ring 11-15	Ring 16-20
Ring 2-20	0.88 (0.06)	0.95 (0.03)	0.98 (0.03)	0.92 (0.07)
Ring 2-5		0.89 (0.06)	0.88 (0.10)	0.79 (0.12)
Ring 6-10			1.00 (0.03)	0.95 (0.08)
Ring 11-15				0.95 (0.06)

Note: Standard errors are shown in parentheses.

**Table 1.3.** Genotypic correlations between area-weighted averages of wood density in different ring groups.

	Ring 2-5	Ring 6-10	Ring 11-15	Ring 16-20
Ring 2-20	0.78 (0.10)	0.98 (0.02)	0.96 (0.04)	0.86 (0.07)
Ring 2-5		0.79 (0.11)	0.66 (0.17)	0.47 (0.19)
Ring 6-10			0.86 (0.08)	0.73 (0.12)
Ring 11-15				0.85 (0.08)

Note: Standard errors are shown in parentheses

**Table 1.4.** Genotypic correlations between area-weighted averages of modulus of elasticity in different ring groups.

	Ring 2-5	Ring 6-10	Ring 11-15	Ring 16-20
Ring 2-20	0.91 (0.05)	1.00 (0.01)	0.97 (0.02)	0.88 (0.05)
Ring 2-5		0.93 (0.04)	0.83 (0.09)	0.70 (0.13)
Ring 6-10			0.95 (0.03)	0.87 (0.07)
Ring 11-15				0.95 (0.04)

Note: Standard errors are shown in parentheses



**Table 1.5.** Genotypic correlations between growth traits measured at age 10, 25 and 26, and area-weighted averages of microfibril angle (MFA), wood density (WD), and modulus of elasticity (MOE) at age 10 and 26.

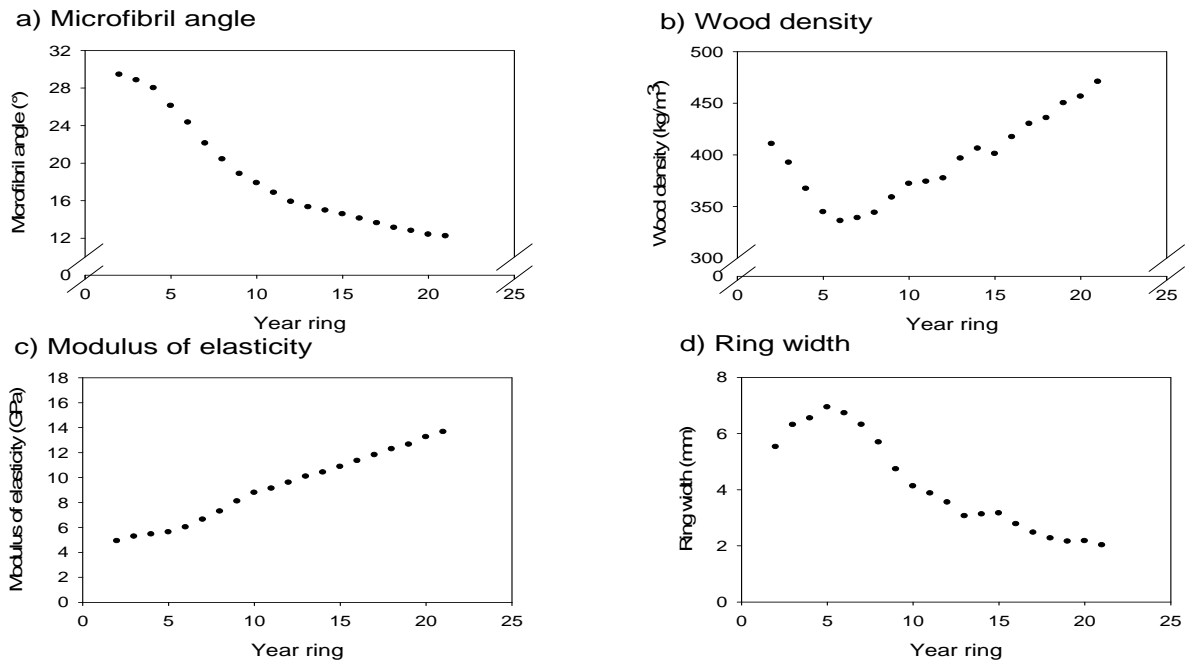
	DBH 10	Ht 10	Vol 10	DBH25	Ht 26	Vol 26
MFA 10	0.35 (0.26)	0.14 (0.26)	0.36 (0.26)	0.39 (0.22)	0.03 (0.23)	0.28 (0.22)
WD 10	-0.50 (0.24)	-0.21 (0.27)	-0.49 (0.24)	-0.24 (0.27)	-0.01 (0.26)	-0.14 (0.26)
MOE 10	-0.40 (0.24)	-0.15 (0.24)	-0.49 (0.23)	-0.47 (0.20)	0.03 (0.22)	-0.35 (0.20)
MFA 26	0.40 (0.21)	0.29 (0.22)	0.40 (0.21)	0.39 (0.20)	0.29 (0.22)	0.21 (0.20)
WD 26	-0.46 (0.18)	-0.35 (0.19)	-0.53 (0.17)	-0.54 (0.15)	-0.23 (0.20)	-0.45 (0.16)
MOE 26	-0.47 (0.18)	-0.44 (0.19)	-0.56 (0.17)	-0.59 (0.15)	-0.40 (0.19)	-0.46 (0.16)

Note: Standard errors are shown in parentheses

**Table 1.6.** Expected relative correlated response for weighted microfibril angle (MFA), wood density (WD), and modulus of elasticity (MOE) at age 26 with selection for volume at age 10.

Response trait	Relative response (%)
MFA 26	0.16
WD 26	-0.12
MOE 26	-0.27

## FIGURES



**Figure 1.1.** Year ring number (starting from the pith) plotted against mean ring values for (a) microfibril angle, (b) wood density, (c) modulus of elasticity, and (d) year ring width.

## CHAPTER 2

### FAMILY RESPONSE TO IMPOSED HERBICIDE AND FERTILIZATION TREATMENTS ON GROWTH AND FORM TRAITS IN LOBLOLLY PINE

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## Abstract

The effects of imposed silvicultural treatments and genetics were investigated in a 15-year-old loblolly pine (*Pinus taeda* L.) trial in southwestern Georgia, USA. The trial was designed with different fertilizer and herbicide treatment combinations applied to 25 open-pollinated first- and second-generation families. Focus in the study was directed towards analyzing growth and form traits having a large impact on volume production and the quality of solid wood products. In the combined fertilization and herbicide treatment plots, the mean for individual-tree stem volume was 185.2 dm<sup>3</sup>, while in the other extreme, the control plots, mean stem volume was 91.2 dm<sup>3</sup>. The variation in traits such as height, sweep, branch angle, percentage trees with forking defects, and fusiform rust infections (caused by the fungus *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*) was also studied, and there were large, significant differences among treatment combinations for height, volume, sweep, and forking defect.

Family effects were significant for all traits when pooled across all treatments. Individual-tree heritability values were 0.26 for height, 0.33 for volume, 0.10 for sweep, 0.39 for branch angle, 0.29 for forking defect, and 0.23 for rust incidence. Pooled family mean heritability values were 0.85 for height, 0.86 for volume, 0.60 for sweep, 0.90 for branch angle, 0.87 for forking defect, and 0.84 for rust. Genetic and phenotypic correlations between growth and form traits were generally rather low and non-significant except for a few combinations of traits.

Overall, no important culture by genetics interactions were found, and family rankings across treatment combinations were generally stable for most traits. Even though the study was limited to one site, the range of silvicultural treatment levels (4) and the number of families included (25) should make it possible to make broader inferences about GxE due to imposed cultural treatments. For these selected loblolly pine families, the occurrence of genetics by culture interactions is low for the important growth and form traits. The data suggest that the risk of losing value due to suboptimal matching between genetic material and silvicultural prescriptions is generally low if the treatments are applied in a similar way and at similar stages of stand development as they were in the current study.

## **Introduction**

There has been a long-term trend towards more intensive forestry in the South, and the total area of pine plantations as well as the silvicultural intensity is likely to continue to increase for decades (Prestemon & Abt 2002). In a global context, pine plantations are expected to become a larger part of the total worldwide industrial wood production (Carle & Holmgren 2008). Southern pine plantation forestry has had sharp increases in the number of hectares of plantations as well as greater management intensities (Fox et al. 2007). In many cases, however, the South is not living up to its potential when it comes to wood production per area unit (Borders & Bailey 2001; Allen et al. 2005). Several studies have suggested potential future growth levels of similar magnitudes in the U.S. South to those achieved in intensively managed pine plantations in parts of the Southern Hemisphere (Borders & Bailey 2001; Yin & Sedjo 2001; Allen et al. 2005; Fox et al. 2007). Additional studies need to focus on the interactions between site, climate, genetics, and eco-physiological relationships in plantations (Adegbedi et al. 2002; Jokela et al. 2004).

The total amount of wood harvested depends on factors that are difficult to predict, such as the national demand for forest products, and the development of the U.S. and the world economy (Prestemon & Abt 2002; Wear & Greis 2002) as well as political regulations (Carle & Holmgren 2008). The ongoing change in land ownership in the South is resulting in new categories of landowners, sometimes with different objectives compared to the former owners (Stanturf et al. 2003; Clutter 2005), but many landowners still want to optimize their



stand and property value (McKeand et al. 2006a; Fox et al. 2007). With more intensive management, more wood can be produced on a smaller land area (Yin & Sedjo 2001), and therefore it can also offer a way to offset the increasing demand for land to be used for other purposes, such as development, recreation, and conservation, as well as decreasing the pressure for harvesting in older forests with high levels of biodiversity (Gladstone & Ledig 1990; Carle & Holmgren 2008).

A forest stand can be manipulated in many ways to achieve different objectives. Intensive southern pine management programs often aim towards increased volume production. Different types of site preparation, planting of high-quality, genetically improved seedlings, chemical and mechanical weed control for herbaceous and woody competition, fertilization (predominantly with nitrogen and/or phosphorous, and maybe also with potassium, and micronutrients), alteration of stand density, and shorter rotations are all common practices (Allen 1987; Borders & Bailey 2001; Yin & Sedjo 2001; Martin & Shiver 2002; Jokela et al. 2004; Martin & Jokela 2004; Allen et al. 2005; Bridgwater et al. 2005; Fox et al. 2007). Major efforts have been made towards developing guidelines for optimizing the effects of intensive silviculture (Stanturf et al. 2003). A wide range of responses can be expected depending on when and where different methods are applied. Treatments such as applications of herbicides and fertilization can at least partly work as substitutes for each other, but can also when applied in combination result in further improvements in overall survival and growth compared to when only one of the treatments has been applied (Borders & Bailey 2001; Albaugh et al. 2003; Borders et al. 2004). The effects of most treatments depend very

much on the local site conditions (Albaugh et al. 2003; Jokela et al. 2004). Different management regimes can also be utilized to manipulate the proportions of different products such as sawtimber and pulpwood produced in a stand over a certain time period (Yin et al. 1998).

It is not only stand characteristics connected to bulk volume production such as height and diameter growth that can be manipulated using silvicultural methods. Overall nutrient supply as well as the proportions of available nutrients can have an impact on forking (Espinoza 2009), stem form (Espinoza et al. 2012), and possibly to some degree the occurrence of defects due to fusiform rust (caused by the fungus *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*) (Espinoza 2009). Stem form can be negatively affected when large amounts of nitrogen only are added to a site (Zobel & van Buijtenen 1989; Espinoza 2012), and other factors such as regeneration method can affect tree stability and stem straightness (Lindström & Rune 1999). Stem straightness affects the occurrence of reaction wood which has a large impact on wood quality (Zobel & Jett 1995) and recovery (Larson et al. 2001). Wood density is another important trait often determining the quality of wood as a raw material (Bowyer et al. 2003), and environmental effects on this trait are sometimes observed but with mixed kinds of responses, depending on many different factors (Megraw 1985). Chapter 3 will go further into the subject of loblolly pine wood quality.

Tree improvement is a crucial component of southern forestry (Schultz 1999), and stands consisting of improved seedlings generally produce more wood compared to stands of

unimproved material (Fox et al. 2007). Genetic gains can also be obtained for other important traits such as wood density (Zobel & Jett 1995). Stem form (Shelbourne 1969; Espinoza 2012), and decreased frequencies of forking defects (Xiong et al. 2010) also often display an important genetic component. Resistance against fusiform rust is another important trait, and it is included in the pine tree improvement programs in the South (Bridgewater et al. 2005). Simultaneous improvement of a combination of economically important traits is often preferred (White et al. 2007).

Loblolly pine grows naturally in a wide range of environments and has adapted to different site conditions (Schultz 1999). Foresters have usually had their focus directed towards producing seedlings that perform well over a number of different site conditions (McKeand et al. 2006b). As the knowledge advances regarding possible interactions between genotypes and different sites as well as the genotypes' interactions with imposed silvicultural treatments, forest managers will be able to move towards the use of a smaller number of genotypes when establishing new stands (McKeand et al. 2006a). This could offer additional possibilities to optimize overall value (Yin et al. 1998; Yin & Sedjo 2001; Borders & Bailey 2001; Allen et al. 2005; Fox et al. 2007) and grow wood for specific products (Allen et al. 2005). It is already common practice to establish family or clonal blocks to maximize gain in new plantations (McKeand et al. 2003b), but this requires knowledge about how to match families and sites (Duzan & Williams 1988). It is likely that less genetically diverse material will have lower overall tolerance towards stress factors in the environment, and these stands could be less stable for traits such as fusiform rust resistance (Bridgewater et al. 2005).

Most GxE studies in loblolly pine have assessed different families planted across diverse environments. Interactions between genetic entry and environmental factors are usually low or non-significant even for very different genetic material that has been subjected to a wide range of environmental conditions (McKeand et al. 2006b). GxE interaction across very broad geographic regions is more commonly observed (Lambeth et al. 2005), and negative effects of GxE interactions could also be expected if a seed source is moved too far outside of the zone for which it is adapted (Schmidting 2001). In a review of recently published results (McKeand et al. 2006b), GxE interactions at different sites within climatic regions were found to be rather low in most cases for half-sib families as well as for full-sib families and clones. However, the authors also pointed out that this was not observed for all of the material expected to be deployed. Some studies show exceptions to this general conclusion. Genetic material has usually been selected to perform well under a range of different conditions, but many previous studies have been limited to a rather small number of families or clones restricting inferences to larger populations. It is also common that only a few families in each test will show significant GxE interaction (Zobel & Jett 1995). In a study by Yeiser et al. (2001), open-pollinated loblolly pine families from four seed zones were planted at 15 locations in the Western Gulf Region to assess GxE interactions. There were interactions present for volume at age 5 and 10, but the amount of GxE differed considerably among families and seed zones. In another loblolly pine study looking at traits such as volume per hectare at age 14, significant interactions between fertilization and provenance were found due to higher mortality in the Atlantic Coastal provenance compared to the Drought-Hardy provenance in the fertilized treatment (Smith 2010). The provenance level

rank changes for volume increment started appearing in that trial already around age 10, but no important provenance or family by site interactions were found at younger ages (McKeand et al. 2004; Smith 2010). The study was conducted in a trial specially designed for detecting possible interactions between open-pollinated families from two very different loblolly pine provenances growing in non-fertilized plots and in plots with good nutrient supply created by repeated fertilization treatments. In another study, open-pollinated loblolly pine families from Florida displayed significant rank changes among sites across the southeastern Lower Coastal Plain (Sierra-Lucero et al. 2003). In a study consisting of first-generation genetically improved loblolly pine planted and managed with or without intensive control of competing vegetation, Martin & Shiver (2002) found no genetics by vegetation control interactions for standing volume at age 12. However in parts of the material, they found significant interaction effects between genetic material and vegetation control with regards to basal area and survival. In Roth et al. (2007), a combined genetics and silviculture study established at two locations was evaluated. A limited number of elite full-sib families, planted at different spacing and subjected to different levels of silvicultural input were included. Growth traits such as stem volume showed significant interactions for some combinations of factors as early as year 2 or 3, and the level of significance was gradually increasing with time. The interactions were mainly due to scale effects meaning that the absolute differences in production between families varied from one treatment to the other. Some families responded stronger than others, and some displayed more stability across treatments than others. Genetics by silviculture interactions were not as strong as they were for genetics by site.

It was reported by McKeand et al. (1997) that the relatively better performing families were most responsive to site changes. Also, family rank usually did not change in the studied material when it came to growth characteristics. Interactions for other traits than those directly connected to volume production have also been observed in some studies. McKeand et al., (2003a) reported that the most stable families regarding resistance to fusiform rust were the least predictable in terms of rust infection when tested at different sites. Also, McKeand et al. (1999) observed significant family by environment interactions for rust among open-pollinated loblolly pine families grown at 28 different sites. In a recent study by Chamblee (2011) significant interactions between seed source and test site for traits such as volume, straightness, and fusiform rust infection percentage were reported based on a relatively large number of investigated families, seed sources, and test sites.

Since few studies have been designed to specifically investigate interaction effects among different genetic entries subjected to imposed silvicultural treatments, there is a need for detailed studies of families and clones across treatments as well as across sites (McKeand et al. 2006b). More studies should include enough families to allow for inferences about populations. Higher levels of genetic gain could be achievable if specific families and clones were matched to specific treatments and sites (Roth et al. 2007, White et al. 2007).

The objectives of the study were to investigate:

- 1) the effect of silvicultural treatment combinations (based on fertilization and herbicide applications) on growth and form traits of loblolly pine
  
- 2) the possible interaction between treatment combination and genetic entry (half-sib family) in terms of growth and form traits

## **Materials and Methods**

### *Field trial*

The field trial was located in Decatur County, GA at latitude 30°48'42.16''N and longitude 84°46'41.13''W. The study was established by International Paper Company on their Southlands Experimental Forest located near Bainbridge, GA, USA. The soil at the site is classified as being Lakeland, Wagram, and Troup series. The parent material consists of sandy and/or loamy marine sediments or in the case of the Lakeland series, sandy marine or eolian (deposited by wind) sediments (USDA-NRCS Southeast Coastal Plain and Caribbean Soil Survey Region Web site 2010). To control competing vegetation, the site was chemically treated with 0.6 liters/hectare (0.5 pints/acre) of Arsenal and 1.2 liters/hectare (1 pint/acre) of Accord, and burned prior to stand establishment. The experimental design was a split-plot with herbicide and fertilization treatments as the main plots and loblolly pine families as the sub plots. The study was replicated in five blocks and was planted in December 1990 (See Figure 2.1 for layout). Each block was divided into four main plots of the same size and then subjected to different silvicultural management alternatives (treatment combinations). Each main-plot was further divided into sub-plots. All of the loblolly pine families were then planted on each sub-plot and arranged as six-tree noncontiguous sub-plots (e.g. individual trees from each family were randomly planted throughout the treatment plot). Two buffer rows were planted around each treatment plot. The spacing was 2.44 by 3.05 m. The experiment was not originally designed with the intention to keep it for 15 years, so the buffer size was increased before data collection and analysis. Extra buffer rows were added



to minimize competition effects. The original measurement plots were thereby decreased by up to 3 rows depending on the treatment in the neighboring plots (e.g. if a non-treated plot was adjacent to a fertilized and herbicide treated plot, 3 border rows were added. If two adjacent plots were the same treatment, then no border rows were added). Because of this, data became somewhat unbalanced due to differences in the sizes of additional buffer zones combined with smaller differences in survival.

The imposed herbicide treatment (H) consisted of the following major components: One application of sulfometuron-methyl and atrazine tank mix in the spring of 1991; later weed control treatments were applied as directed sprayings of 2% glyphosate. Sapling control was performed using a simple method for killing trees with herbicides called “hack and squirt” and included the use of triclopyr and diesel. A release treatment with an aerial application of imazapyr was performed in the winter of 1996/1997. The imposed fertilization treatment (F) included the following actions: Application of 85 grams (3 oz) per tree of 20-4-15 in April 1992, and in June 1992. In April 1993, 280 kg/ha (250 lbs/ac) of diammonium phosphate was added. Application of 1120 kg/ha (1000 lbs/ac) of 20-5-15 with micronutrients was done in March 1996 and a new application in January 2000. These imposed treatments together with the option of no treatment were combined into four unique silvicultural management alternatives assigned randomly to one of the plots in each block so that all four treatment combinations were represented once in each block. The different combinations were the following:

- A) No herbicides and no fertilization
- B) Herbicides and no fertilization
- C) Fertilization and no herbicides
- D) Herbicides and fertilization

There were 25 open-pollinated families from the North Carolina and South Carolina Coastal Plain; some of the families were related. There were a number of pedigree relationships among the different parents, and some of the OP parents were also grandparents of other OP families (See Appendix 2.1). Seed was collected in the late 1980's from seed orchards.

#### *Data collection*

In year 14 after establishment, the following traits were measured: Rust (Yes/No), Forking (Yes/No), Ramicorn branches (Yes/No), Sweep (by using an 2.44 meter (8-foot) straightedge, maximum deviation from a straight line along the stem in the bottom 3.66 meters (12 feet) of the stem was measured in cm), Branch angle at the base of the live crown (in degrees with five different classes where 90 degree was flat or perpendicular from the stem, class 1=flat and class 6=steep). In the analysis the trait “forking defect” was created as a combination of data on forking and data on ramicorn branching.

In year 15, diameter at breast height (in cm), and height (in m) were measured, and rust score (Yes/No) was observed. The number of missing trees surrounding a measurement tree were summed (adjacent trees=1, diagonal trees=0.5) to give a competition score that indicated if

there were missing trees allowing extra resources for the measured tree or not. Rust scores from year 14 and year 15 were combined into one trait for rust. If a tree had rust in either year, it was counted a yes for rust. Stem volume (total inside-bark) was calculated by using the following equation developed by Sherrill et al. (2011):

$$VOL = -0.06906 + 0.00178 * (DBH^2 * HT) \quad (\text{Eq. 2.1})$$

Where VOL is the total inside-bark individual stem volume in cubic feet, DBH is the diameter at breast height in inches, and HT is the height in feet. Thereafter VOL was converted into dm<sup>3</sup>/tree.

### *Statistical analysis*

The following general linear mixed model was used to test the effects of the fertilization and herbicide treatment combinations and interactions on growth and quality traits:

$$Y_{ijk} = \mu + B_i + T_j + BT_{ij} + e_{ijk} \quad (\text{Eq. 2.2})$$

Where  $Y_{ijk}$  is the dependent variable (the observation of the  $k$ th tree of the  $j$ th treatment level of the  $i$ th block),  $\mu$  is the overall mean,  $B_i$  is the fixed effect of the  $i$ th block ( $i = 1, 2, \dots, 5$ ),  $T_j$  is the fixed effect of the  $j$ th level of treatment ( $j = 1, 2, \dots, 4$ ),  $BT_{ij}$  is the fixed interaction effect between block and treatment, and  $e_{ijk}$  is the random error, assumed to be  $\sim \text{NID}(0, \sigma_e^2)$ .

The GLM procedure of SAS Software (SAS Institute Inc. 2008) was used to run the model,

the RANDOM statement and the TEST option were used to obtain correct F-tests.

Differences between the four treatment combination means were investigated using Tukey's studentized range test. Binary traits were analyzed by using a generalized linear mixed model with a logit link function as previously described by Isik et al. (2008). The following equation was used to model the probability of rust damage or the occurrence of a forking defect on an individual tree:

$$y_{ijk} = \log[\pi/(1-\pi)] = \mu + B_i + T_j + BT_{ij} + e_{ijk} \quad (\text{Eq. 2.3})$$

Where  $y_{ijk}$  is the  $k$ th observation of the  $j$ th treatment level of the  $i$ th block,  $\pi$  is the proportion of rust infected trees, alternatively the proportion of trees with forking defect,  $\mu$  is the conditional mean,  $B_i$  is the fixed effect of the  $i$ th block ( $i = 1, 2, \dots, 5$ ),  $T_j$  is the fixed effect of the  $j$ th level of treatment combination ( $j = 1, 2, \dots, 4$ ),  $BT_{ij}$  is the fixed interaction effect of the  $i$ th block by the  $j$ th treatment,  $e_{ijk}$  is the random error, assumed to be  $\sim \text{NID}(0, \mathbf{I}\sigma_e^2)$ , and  $\mathbf{I}$  is a  $n \times n$  identity matrix. The GLIMMIX procedure in SAS was used for the analysis of the two binary traits (SAS Institute Inc. 2008). The *pdiff* option in SAS Proc GLIMMIX was used to display differences between least square means of the binary traits.

In order to understand the effects of treatments on genetic variances and heritabilities, the following linear mixed model was used:

$$Y_{ijkl} = \mu + B_i + T_j + BT_{ij} + F_k + FB_{ik} + FT_{jk} + FBT_{ijk} + e_{ijkl} \quad (\text{Eq. 2.4})$$

Where  $Y_{ijkl}$  is the dependent variable (the observation of the  $l$ th tree of the  $k$ th family in the  $j$ th treatment combination in the  $i$ th block),  $\mu$  is the overall mean,  $B_i$  is the fixed block effect ( $i = 1, 2, \dots, 5$ ),  $T_j$  is the fixed treatment effect ( $j = 1, 2, \dots, 4$ ),  $F_k$  is the random family effect ( $k = 1, 2, \dots, 25$ ), with expectations  $\sim \text{NID}(0, \sigma^2_f)$ ,  $BT_{ij}$  is the fixed block by treatment interaction,  $FB_{ik}$  is the random family by block interaction, with expectations  $\sim \text{NID}(0, \sigma^2_{fb})$ ,  $(FT)_{jk}$  is the random family by treatment combination interaction, with expectations  $\sim \text{NID}(0, \sigma^2_{ft})$ ,  $(FBT)_{ijk}$  is the random family by block by treatment interaction, expected to be  $\sim \text{NID}(0, \sigma^2_{fbt})$ , and  $e_{ijk}$  the random error term with expectations  $\sim \text{NID}(0, \sigma^2_e)$ . The ASReml software was used to obtain variance components and to calculate functions of variance components (Gilmour et al. 2009). In fitting the model, the Log Likelihood ratio test was used to see if additional terms were significant.

Variance components for binary traits were estimated by using a generalized linear mixed model with a logit link function and the following equation was used to model the probability of rust damage or the occurrence of a forking defect on an individual tree:

$$y_{ijkl} = \log[\pi/(1-\pi)] = \mu + B_i + T_j + BT_{ij} + F_k + FB_{ik} + FT_{jk} + FBT_{ijk} + e_{ijkl} \quad (\text{Eq. 2.5})$$

Where  $y_{ijkl}$  is the  $l$ th observation of the  $k$ th family of the  $j$ th treatment combination in the  $i$ th block,  $\pi$  is the proportion of rust infected trees, alternatively the proportion of trees with forking defect,  $\mu$  is the conditional mean,  $B_i$  is the fixed effect of the  $i$ th block ( $i = 1, 2, \dots, 5$ ),  $T_j$  is the fixed effect of the  $j$ th level of treatment ( $j = 1, 2, \dots, 4$ ),  $BT_{ij}$  is the fixed interaction

effect between the  $i$ th block and the  $j$ th treatment,  $F_k$  is the random effects of the  $k$ th family ( $k= 1, 2, \dots, 25$ ), expected to be  $\sim \text{NID}(0, \mathbf{I}\sigma_f^2)$ ,  $(\text{FB})_{ik}$  is the random interaction effect of the  $i$ th block and the  $k$ th family, expected to be  $\sim \text{NID}(0, \mathbf{I}\sigma_{fb}^2)$ ,  $(\text{FT})_{jk}$  is the random family by treatment combination interaction effect, with expectations  $\sim \text{NID}(0, \mathbf{I}\sigma_{ft}^2)$ ,  $(\text{FBT})_{ijk}$  is the random interaction of the  $k$ th family by the  $i$ th block by the  $j$ th treatment, expected to be  $\sim \text{NID}(0, \mathbf{I}\sigma_{fbt}^2)$ , and  $e_{ijk}$  is the random error, also assumed to be independent and normally distributed with the expected mean zero and variance  $\mathbf{I}\sigma_e^2$ , where  $\mathbf{I}$  is a  $n \times n$  identity matrix. The ASReml software was used to obtain variance components and to calculate functions of variance components (Gilmour et al. 2009). The open-pollinated families were not independent since there was some relatedness among them. In order to account for relatedness in estimation of variance components, a pedigree file was used in the analysis. Competition score was initially included in the models but then excluded due to negligible effects. The Log Likelihood ratio test was used to look for significant terms.

### *Heritability estimates*

Individual tree narrow-sense heritability ( $h^2_i$ ) values were estimated as follows:

$$h^2_i = 4 \sigma_f^2 / (\sigma_f^2 + \sigma_{fb}^2 + \sigma_{ft}^2 + \sigma_{fbt}^2 + \sigma_e^2) \quad (\text{Eq. 2.6})$$

Where  $\sigma_f^2$  is the family variance component,  $\sigma_{fb}^2$  is the family by block interaction variance component,  $\sigma_{ft}^2$  is the family by treatment interaction variance component,  $\sigma_{fbt}^2$  is the family

by block by treatment interaction variance component, and  $\sigma_e^2$  is the error variance component. The error variance was fixed to 3.29 for the two binary traits.

Family mean heritability ( $h^2_F$ ) values were estimated as follows:

$$h^2_F = \sigma_f^2 / (\sigma_f^2 + \sigma_{fb}^2/b + \sigma_{ft}^2/t + \sigma_{fbt}^2/bt + \sigma_e^2/btn) \quad (\text{Eq. 2.7})$$

Where t is the number of treatments,  $\sigma_{fbt}^2$  is the family by block by treatment interaction variance component, n is the average number of trees of each family in each block and treatment combination (4.3), and  $\sigma_e^2$  is the error variance component. The error variance component was fixed to 3.29 for the two binary traits. The other terms were previously explained. Standard errors of heritabilities were estimated using the Delta method (Isik et al. 2008).

### *Correlations*

Phenotypic correlations (Pearson's product moment correlations) between pairs of traits were calculated based on family means using PROC CORR. Approximate genetic correlations were obtained by producing product-moment correlations using BLUP values.

## Results

Survival was generally high, ranging between 80 and 88 % in different treatment combinations and at 86% overall. Differences in survival were therefore not further analyzed. The data were still somewhat unbalanced in terms of total amount of sampled units for the 25 families, ranging from a total of 74 trees measured for height for one family to rust observations for 98 trees for one family. The number of observations per treatment combination also ranged from 430 trees for the trait forking defect in the control to 667 for the trait rust incidence in the fertilization only plots. There were generally lower numbers of sampled trees in the control plots compared to the other plots (See Appendix 2.2). The total sample size however, was well over 2000 sampled trees for all traits, and the large sample size was assumed to compensate for the slightly unbalanced data in the further analysis.

Overall means (with standard errors), and treatment combination means are presented in Table 2.1. In the combined fertilization and herbicide treatment plots, the arithmetic mean for stem volume was highest,  $185.2 \text{ dm}^3$ , while the control plots had the lowest average stem volume,  $91.2 \text{ dm}^3$ . Values for height, sweep, average branch angle, percentage trees with forking defects, and percentage trees with rust was 17.5 m, 2.4 cm,  $55.3^\circ$ , 34.2 %, and 24.7% respectively in the combined fertilization and herbicide plots, compared to 13.9 m, 1.9 cm,  $54.6^\circ$ , 18.6 %, and 28.5% in the control plots (Table 2.1).



Results from F-tests of treatment effects, block effects, and their interactions are given for growth and form traits in Table 2.2. Treatment effects were significant for height ( $p=.005$ ), volume ( $p<.0001$ ), sweep ( $p=.003$ ), but not for branch angle ( $p=.493$ ). Block effects were also significant for height, volume, and sweep but not for branch angle. Block by treatment interactions were significant for all four traits.

F-tests for significant effects for the binary traits are given in Table 2.3. Treatment effects were significant for forking defect ( $p<.0001$ ) but not for rust. Block and block by treatment interaction was significant for forking defect but not for rust.

Different letters following means in Table 2.1 indicate significant differences between treatment combination means. All treatment combinations were significantly different from each other for height and volume. For sweep the control and the fertilization only had similar means and were different from the herbicides only and the fertilization plus herbicides plots. The fertilization only plots were also significantly different from the herbicides and the fertilization plus herbicides plots for sweep. For branch angle the fertilization only plots were different from the control. Differences were also found for forking defect where the fertilization plus herbicides plots were significantly different from the three other plot types, and also had the highest forking defect percentages in the trial. There were no significant plot differences found for rust percentage. Main effects (fertilizer, herbicides) and their interactions were also analyzed separately (See Appendix 2.4-2.5), and significant herbicides effects were found for height, volume, sweep, and forking defect, while significant

fertilization effects were found for height, volume, and forking defect. The herbicides x fertilization interaction effects were generally insignificant except for height ( $p=0.032$ ), and forking defect ( $p=0.035$ ).

There were rather larger differences between family means for different traits when pooled across the different treatments. Variance components for family with standard errors, as well as components for family by treatment, family by block interactions, and error, based on pooled data from all treatment combinations are given in Table 2.4. The percent variance explained by family varied from 9.6% for branch angle to 2.5 % for sweep. Except for the family by block interaction for sweep, none of the family by block or family by treatment interactions was significant based on Log Likelihood ratio tests. Family rankings across treatment combinations were stable for most traits. A few families behaved somewhat different than others, changing rank at different treatment combination plots (Figures 2.2-2.7). Pooled arithmetic means across treatment combinations for all families and the number of observations on each family are given in Appendix 2.2. Heritability estimates with corresponding standard errors are presented in Table 2.4. Individual-tree ( $h^2_i$ ) heritability values were moderate for most growth, form, and stem quality traits (0.26 for height, 0.33 for volume, 0.39 for branch angle, 0.29 for forking, and 0.23 for rust), and low (0.10) for sweep. Family-mean heritability ranged from 0.60 for sweep to 0.90 for branch angle.

Phenotypic correlations between pairs of traits based on family means are presented above the diagonal in Table 2.5 and were found to be rather low based on the pooled data across

treatment combinations with very few exceptions (volume vs. height and forking defect vs. sweep). Genetic correlations pooled across treatments and based on family BLUP-values are presented below the diagonal in Table 2.5. The genetic correlations were generally low and insignificant. As expected, different growth traits such as volume and height were highly correlated but except for a weak negative correlation between height and branch angle (-0.28), none of the stem form or quality traits were significantly correlated with growth. Sweep vs. forking defect, and branch angle vs. forking defect were also somewhat correlated.

## Discussion

### *Cultural Treatment Effects*

Treatment differences were significant as expected (Table 2.2) for many traits due to the range in treatments (spanning from no treatment to combined intense fertilization and weed control). This outcome was expected despite the fact that the last treatments were applied at age 9, and the growth, form, and stem quality traits were measured at ages 14 or 15.

Significant differences ( $p \leq 0.05$ ) for height and volume were found between means for all four treatment combinations (Table 2.1). Repeated applications of fertilizer and usage of herbicides against competing vegetation resulted in a doubled average individual tree volume production, going from an average of  $91.2 \text{ dm}^3 / \text{tree}$  in the control plots to  $185.2 \text{ dm}^3 / \text{tree}$  measured at year 15 (Table 2.1). The results agree with many earlier studies suggesting large possible volume increases in southern pine plantations with the use of intensive silviculture (Allen et al. 2005), and confirmed the potential of intensive silviculture for increased volume production.

For stem sweep, herbicides only plots and herbicides plus fertilization plots were significantly different from the control and fertilization only plots. There was a large increase in mean forking defect in the most intensive treatment plots compared to the others (Table 2.1). Forking defect in the most intensive treatment was also significantly different from the other treatment levels. The highest values for sweep and forking defect percentage was 2.4 cm, and 34.2% respectively, and they were recorded in the most intensive treatment

combination (Fertilization + Herbicides). Recently, Espinoza (2009) reported a connection between nutrient supply and stem form as well as the occurrence of forking defects in loblolly pine, and this association was found in our study as well.

The fertilization only plots were different from the control plots for branch angle, while rust incidence displayed no significant differences between the four treatment levels. In a study by Shiver & Martin (2002) no obvious site preparation effects on the percentage of fusiform rust infected trees were found. It has also been shown however, that nutrient supply can have an effect on rust resistance in loblolly pine (Espinoza 2009). It needs to be stressed that effects from most treatments are very dependent on the local site conditions (Albaugh et al. 2003). It has been suggested that with binary data for such traits as rust incidence and forking percentage, an incidence level lower than 30% or higher than 70% could give less accurate variance components (Gilmour et al. 1985). In another recent study focusing on forking defect recorded as a binary trait, Xiong et al. (2010) instead used 20% incidence level as the lower boundary. In the present study, both of the binary traits (rust and forking defect) were just below 30%, but we considered the incidence level high enough to analyze.

Fertilization only resulted in larger responses in terms of volume production per tree than herbicides only. As in several earlier studies (Borders & Bailey 2001; Albaugh et al. 2003; Borders et al. 2004), herbicides and fertilizer applications partly worked as substitutes for each other, while gains in traits such as volume were highest when the treatments were combined. The percentage of trees with forking defect also showed a steep increase in the

plots with combined fertilization and herbicide application compared to the other plots (Table 2.1). Again, it is important to point out that effects vary with site conditions, and fertilization only treatments can often result in much larger amounts of competing vegetation, which in turn affects the mortality in the pine plantation in an unfavourable way and lowers timber production (Borders & Bailey 2001). There were no statistically significant interactions between fertilization and herbicide main effects for volume, even though for height, a weak FxH interaction effect ( $p=0.032$ ) was found (Appendix 2.4), and a FxH effect for forking defect ( $p=0.035$ ) was also registered (Appendix 2.5). For the remaining traits no significant FxH interactions were found.

Treatment combination effects were significant for height, volume, sweep, and forking defect based on the F-tests presented in Table 2.2 and Table 2.3. Results regarding treatment effects are in line with other long-term loblolly pine experiments such as one in south-central Florida (Martin & Jokela 2004) investigating the effects at year 18 of weed control and fertilization. In the Florida study, treatment means varied in a somewhat similar way compared to this study with the tallest trees on average in the combined fertilizer and weed control treatment.

#### *Genetic and Genetic x Culture Effects*

The main purpose of this study was to look at the results from different levels of intensive silviculture and search for possible interactions between treatments and families for a relatively large number of half-sib families and important growth, form, and stem quality traits. Family effects were significant for all the studied traits, and estimated individual-tree

heritability values were generally moderate, except for sweep where they were low (Table 2.4). The percent variance explained by family also varied considerably from 9.6% for branch angle to 2.5% for sweep. In general, the heritability values were of the same magnitudes as could be expected when comparisons are made with other studies of the same traits in conifers and broadleaved species (Cornelius 1994). Both individual-tree heritability values and family-mean heritability values were similar or in some instances somewhat higher compared to another recent study on growth and form traits in loblolly pine (Cumbie et al. 2012) who reported low individual-tree heritabilities for diameter, forking, sweep, branch angle, and volume, (ranging from 0.13 to 0.16), slightly higher values for height and rust (0.22 for both traits), and much higher for family-mean heritabilities (ranging between 0.73 to 0.96) for the same traits as above.

In a study of the inheritance of forking defects based on a large number of families and tests distributed over a number of geographic regions, Xiong et al. (2010) reported low individual-tree heritabilities for forking defect ( $h^2_i=0.06$ ) which is typical for binary traits. As in our study, at the family level, heritabilities were much higher ( $h^2_f=0.76$ ), indicating that family selection would be most effective to reduce forking.

Family means by treatment combination were plotted separately in Figures 2.2 to 2.7 for each trait. There was a considerable range in average family values for traits such as height and volume. As an example the lowest value in the control plot for individual-tree stem volume pooled across treatments ranged from 109 dm<sup>3</sup> / tree to 196 dm<sup>3</sup> / tree (Appendix 2.2).

Overall, there was very little family by treatment interaction in the study (Table 2.4). For example, the family with the highest average volume in the control treatment often also had the highest or among the highest volumes in the combined herbicides and fertilization plots. While there were no statistically significant genetic by silviculture interactions for any of the growth and form traits (Table 2.4), there are a few indications of individual families behaving differently in different silvicultural intensities when family means are plotted against treatment combination (Figures 2.2-2.7). The size of the difference in growth can also change somewhat between families in different treatment combinations (scale effects) without causing an actual family rank change as reported for a material consisting of a limited number of full-sib families in different silvicultural input (Roth et al. 2007). Overall, most previous studies have indicated high stability in the behavior of half-sib families when they have been subjected to different site conditions, climate, and/or level of silvicultural input (Sherrill 2005; McKeand et al. 2006b; McKeand et al. 2008), but there are exceptions such as the reported variation in family performance for fusiform rust resistance observed at different sites (McKeand et al. 2003b) sometimes also causing rank changes among families in terms of traits such as tree height (Lopez-Upton et al. 1999). Interactions between half-sib families and site conditions have also been reported for volume in some instances (Sierra-Lucero et al. 2003), indicating that half-sib families are not always stable in varying environments.

Low GxE for open-pollinated families does not mean that GxE will also be low for full-sib families or clones subjected to imposed silvicultural treatments. Most studies indicate that the risk of unfavorable effects on growth and form due to genetics by silviculture interactions are



generally low (McKeand et al. 2006b), but there are very few studies with imposed silvicultural treatments to compare results against. The present study is also based on measurements taken at one specific point in time. It was also performed several years after the last treatment application which could also affect the results. Therefore, it would be of interest to look at earlier measurements from the trial as well as data from later stages of stand development, and more field trials with imposed treatments applied to different genetic entries should be established to evaluate GxE further.

The phenotypic and genetic correlations (Table 2.5) between pairs of traits were rather low except for the correlation between volume and height which was expected to be high since volume was calculated using diameter and height. Forking defect was also moderately correlated with sweep, and branch angle somewhat negatively correlated with height. Genetic correlations were generally not significant, but numbers were of a similar magnitude or for some traits somewhat lower compared to results from Cumbie et al. (2012) (i.e. for volume vs. forking, and volume vs. branch angle). Cumbie et al. 2012 investigated a large loblolly pine genetic material based on progeny from 48 elite parents replicated over four different sites, calculating additive genetic correlations between continuously distributed traits, and correlations based on breeding values among binary traits. Based on a young loblolly pine field trial in South Carolina, Espinoza et al. (2012) reported non-significant phenotypic correlations between stem sinuosity and height. The absence of unfavorable genetic correlations between certain pairs of traits is advantageous since it simplifies selection efforts

to improve one trait of interest through direct selection without the risk of negatively affecting the other trait.

### *Conclusions*

No large culture by genetic interactions were found, and family rankings across treatment combinations were mostly stable indicating that families that performed well in one cultural regime also performed well in the other regimes. The risk of losing value due to suboptimal matching between genetic material and silvicultural prescriptions should be low if the treatments are applied in a similar way and at similar stages of stand development as they were in the current study.

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## TABLES

**Table 2.1.** Overall means and treatment combination means for growth, sweep, branch angle, forking defect and rust incidence. Different letters following treatment combination means for a given trait indicate significant differences between treatment combination means at the  $p \leq 0.05$  level.

Treatment combination	Height (m)	Volume (dm <sup>3</sup> )	Sweep (cm)	Branch angle (deg.)	Forking def.* (%)	Rust (%)
Control	13.9 <b>a</b>	91.2 <b>a</b>	1.9 <b>a</b>	54.6 <b>a</b>	18.6 <b>a</b>	28.5 <b>a</b>
Herbicides	16.0 <b>b</b>	129.6 <b>b</b>	2.3 <b>b</b>	55.7 <b>ab</b>	19.5 <b>a</b>	25.1 <b>a</b>
Fertilization	16.4 <b>c</b>	147.9 <b>c</b>	2.0 <b>a</b>	55.8 <b>b</b>	24.0 <b>a</b>	25.8 <b>a</b>
Fert.+Herb.	17.5 <b>d</b>	185.2 <b>d</b>	2.4 <b>b</b>	55.3 <b>ab</b>	34.2 <b>b</b>	24.7 <b>a</b>
Overall mean**	16.1 (2.8)	141.5 (81.8)	2.2 (1.2)	55.4 (7.3)	24.5 (43.0)	25.8 (43.8)

\*Forking defect is a combination of forking and ramicorn branching.

\*\*Standard errors (SE) for overall means are given within parenthesis.

**Table 2.2.** F-values and probabilities of F-tests for block, silvicultural treatment effects, and their interactions for growth, form, and stem quality traits. Probabilities of  $\leq 0.05$  were considered significant.

Source	Height		Volume		Sweep		Branch Angle	
	F	Pr>F	F	Pr>F	F	Pr>F	F	Pr>F
Block	11.9	<b>0.004</b>	7.9	<b>0.002</b>	3.7	<b>0.036</b>	1.0	0.443
Treatment	12.4	<b>0.005</b>	21.1	<b>&lt;.0001</b>	8.6	<b>0.003</b>	0.9	0.493
Block x Treatment	28.7	<b>&lt;.0001</b>	7.7	<b>&lt;.0001</b>	3.2	<b>0.0002</b>	3.2	<b>0.0002</b>

The degrees of freedom for Block, Treatment, and Block x Treatment were 4, 3, and 12

respectively. The degrees of freedom for Residual ranged from 2134 (height) to 2092 (branch angle).



**Table 2.3.** F-values and probabilities of F-tests for block, silvicultural treatment effects, and their interactions for binary growth, form, and stem quality traits\*.

Source	Forking defect**		Rust	
	F	Pr>F	F	Pr>F
Block	3.19	<b>0.013</b>	0.50	0.735
Treatment	13.95	<b>&lt;.0001</b>	0.83	0.476
Block x Treatment	2.54	<b>0.003</b>	1.42	0.150

\*Probabilities of  $\leq 0.05$  were considered significant. The degrees of freedom for Block, Treatment, and Block x Treatment were 4, 3, and 12 respectively. The degrees of freedom for Residual were 2255 for Forking defect and 2153 for Rust.

\*\*Forking defect was a combination of forking and ramicorn branching

**Table 2.4.** Variance components for family, family by treatment (FT), family by block (FB) and residual (Error), individual-tree ( $h^2_i$ ) and family mean ( $h^2_f$ ) heritability values for different growth, form, and stem quality traits. In the table, t value is the ratio of the family variance component and its standard error. Percent (%) variance explained by family effect in the total variance is also given. Standard errors (SE) associated with family variances and heritabilities are reported.

Trait	Family (SE)	t	%	FT***	FB***	Error	$h^2_i$ (SE)	$h^2_f$ (SE)
Height	0.24 (0.09)	2.79	6.6	0.3E-06	0.1E-01	3.40	0.26 (.09)	0.85 (.05)
Volume	3.96 (1.41)	2.82	8.2	0.39	0.28	43.63	0.33 (.11)	0.86 (.05)
Sweep	0.03 (0.02)	1.85	2.5	0.01	0.02	1.2	0.10 (.05)	0.60 (.15)
Branch angle	5.20 (1.72)	3.02	9.6	0.5E-05	0.5E-05	48.7	0.39 (.12)	0.90 (.03)
Forking def.*	0.26 (0.10)	2.56	7.3	0.2E-06	0.3E-06	3.29**	0.29 (.11)	0.87 (.04)
Rust	0.19 (0.08)	2.24	5.3	0.4E-01	0.7E-07	3.29**	0.23 (.09)	0.84 (.06)

\* Forking defect is a combination of forking and ramicorn branching.

\*\* Residual variance for binary traits forking and rust is fixed to 3.29.

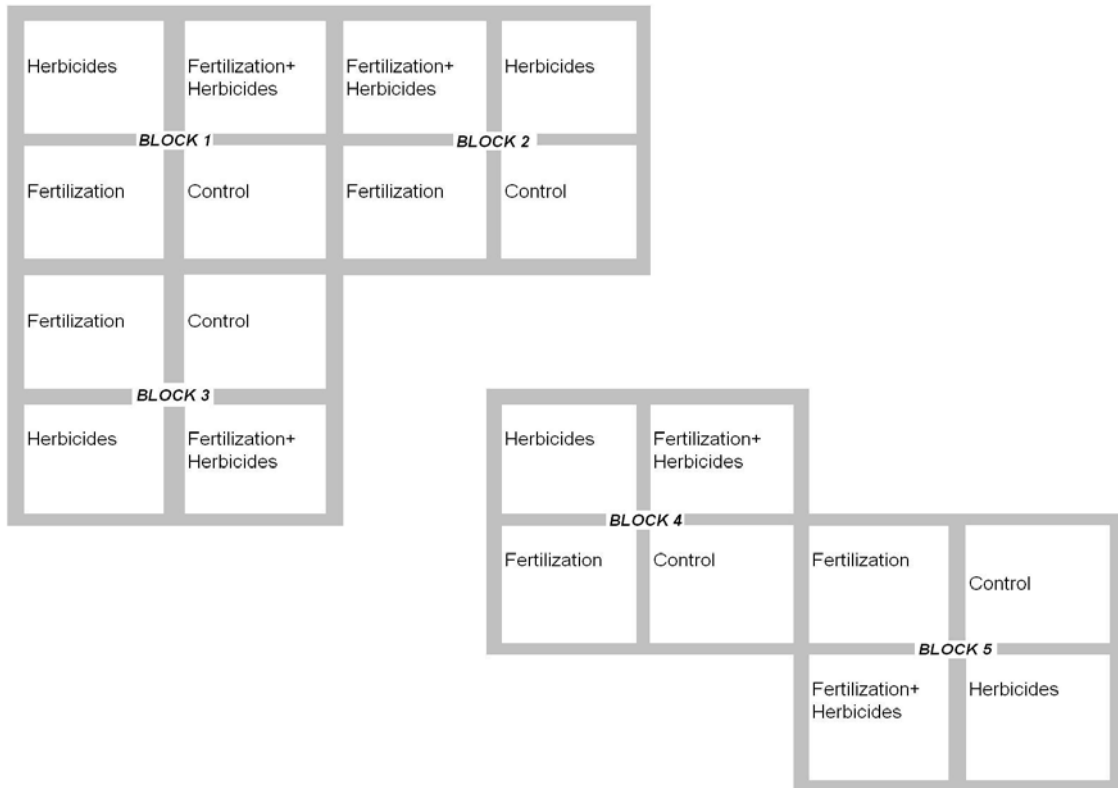
\*\*\* Except for a weakly significant family by block interaction for sweep, no family by treatment or family by replication interaction was significant based on Log Likelihood ratio tests.

**Table 2.5.** Pearson product-moment correlation coefficients based on family means (above diagonal) and genetic correlations based on BLUP values (below diagonal) pooled across treatments among growth, form, and stem quality traits\*. Probability values of correlation coefficients (H0:  $r=0$ ) were also reported. Probabilities of  $\leq 0.05$  were considered significant.

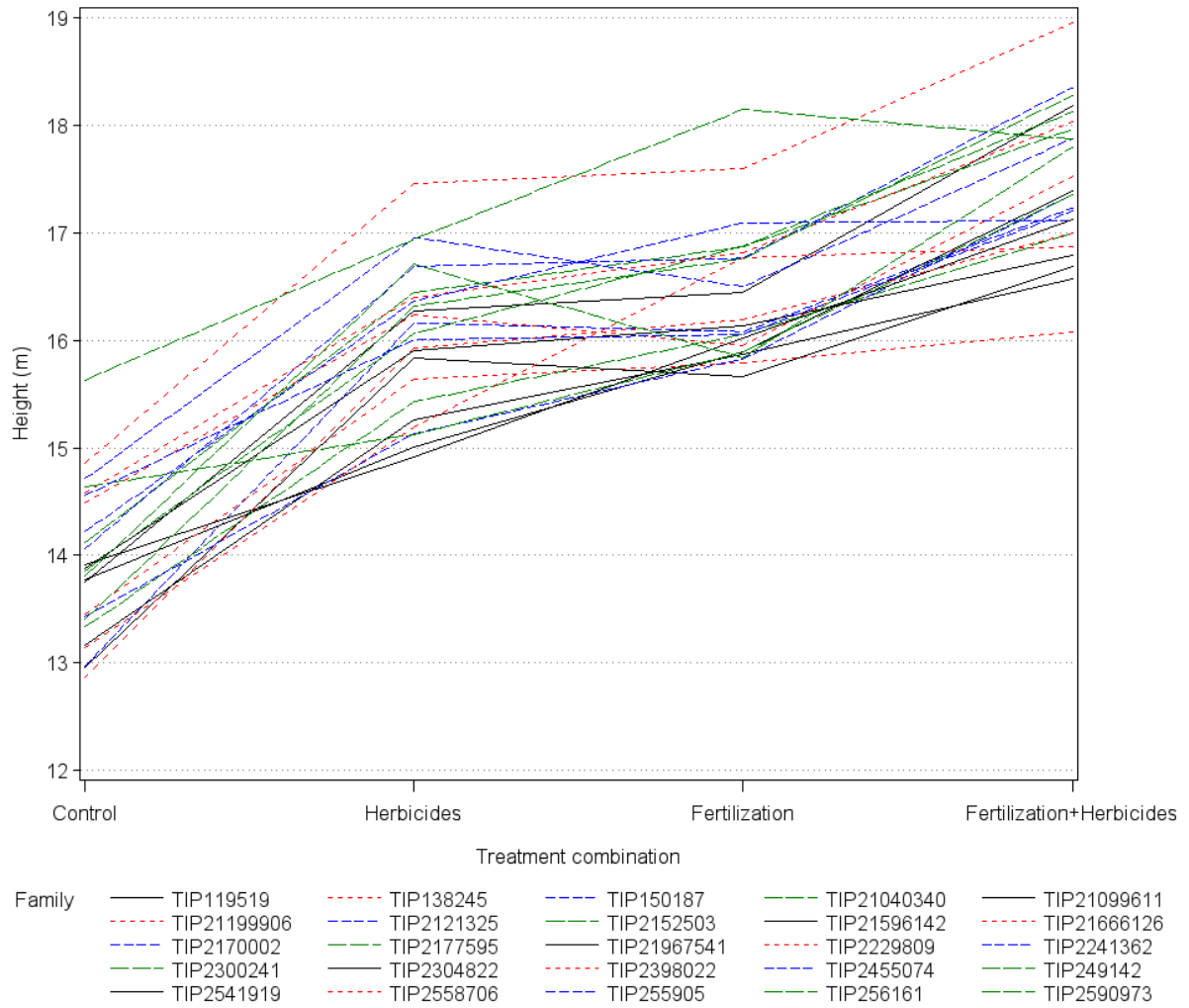
	Height	Volume	Sweep	Branch angle	Forking def**	Rust
Height	-	<b>0.88 (&lt;.001)</b>	-0.15 (.468)	-0.32 (.120)	0.27 (.185)	-0.09 (.671)
Volume	<b>0.90 (&lt;.001)</b>	-	-0.17 (.423)	-0.20 (.347)	0.20 (.361)	0.00 (.999)
Sweep	-0.19 (.172)	-0.24 (.077)	-	0.14 (.497)	<b>0.41 (.044)</b>	-0.10 (.607)
Branch angle	-0.28 (.042)	-0.15 (.274)	0.16 (.257)	-	-0.31 (.129)	0.20 (.343)
Forking def**	0.21 (.127)	0.14 (.312)	<b>0.40 (.003)</b>	<b>0.29 (.033)</b>	-	-0.19 (.352)
Rust	-0.00 (.983)	0.08 (.567)	-0.16 (.235)	0.15 (.279)	-0.23 (.092)	-

\*For the Pearson product-moment correlations based on family means the sample size was 25. Sample size (# of families) for genetic correlation coefficients was 54. \*\*Forking defect is a combination of forking and ramicorn branching.

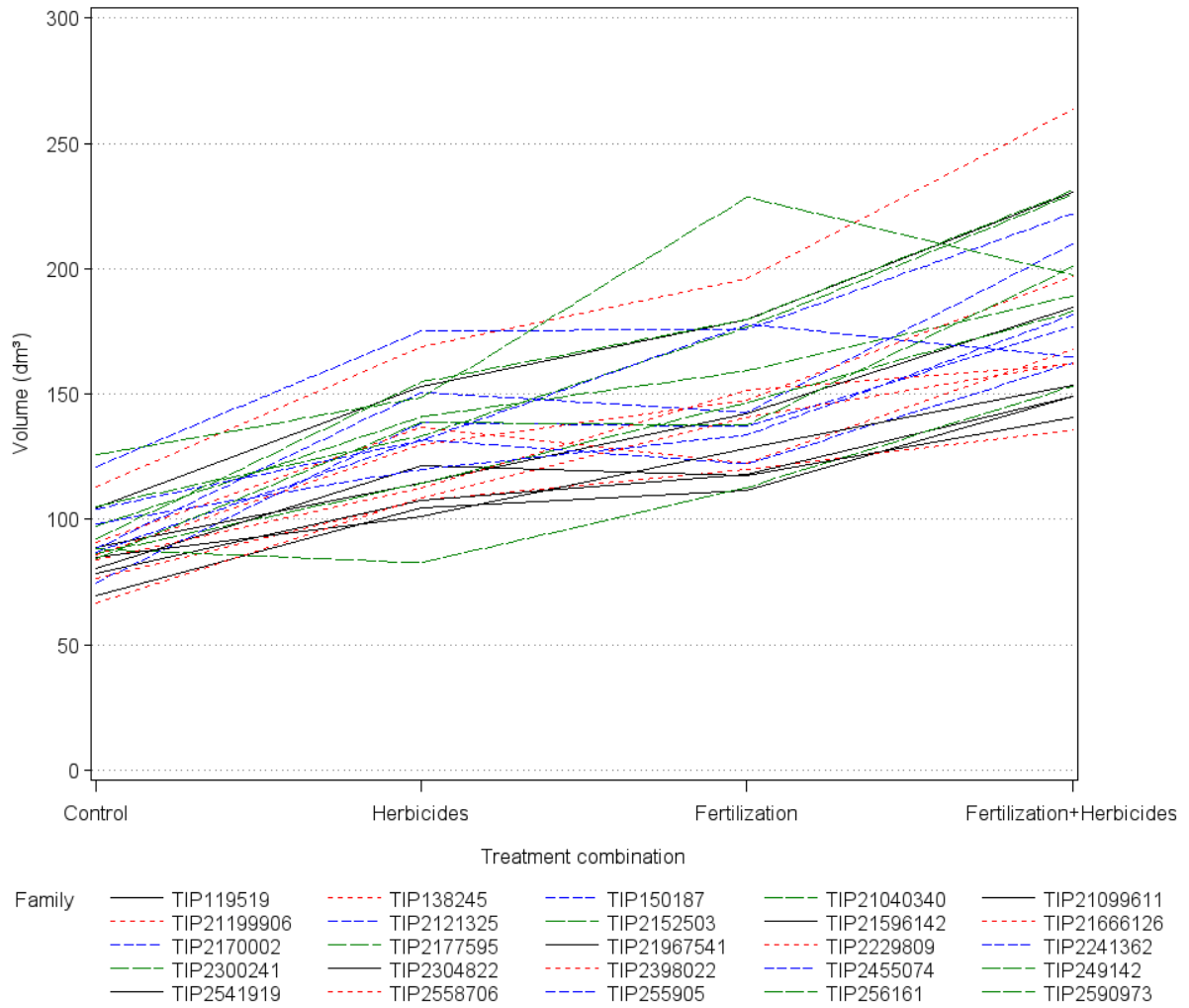
## FIGURES



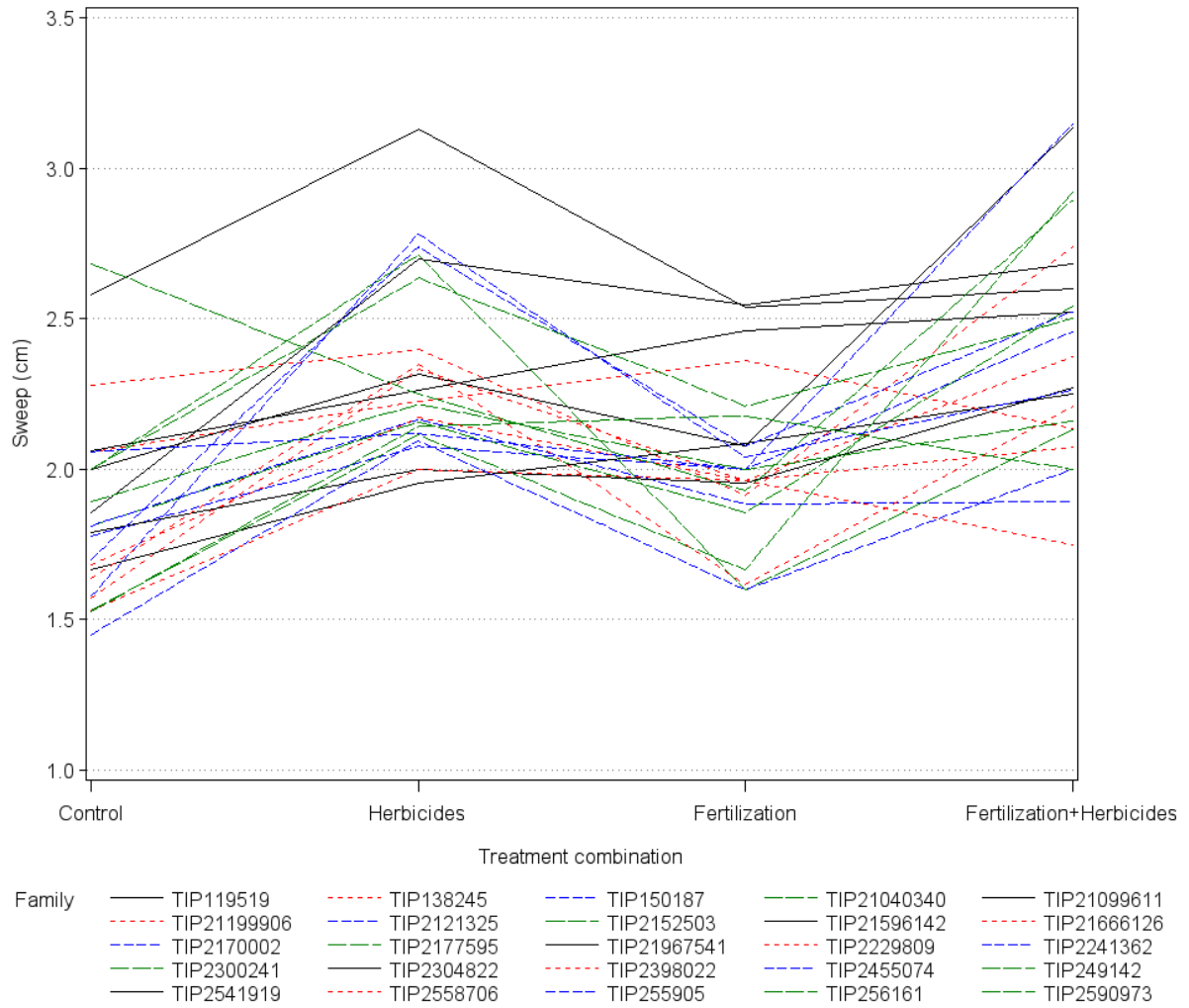
**Figure 2.1.** Trial layout for genetics and silvicultural treatment combinations. A split-plot design was used to study the interactions of family by treatments using 5 blocks in one location.



**Figure 2.2.** Family means for height (m) by treatment combination.

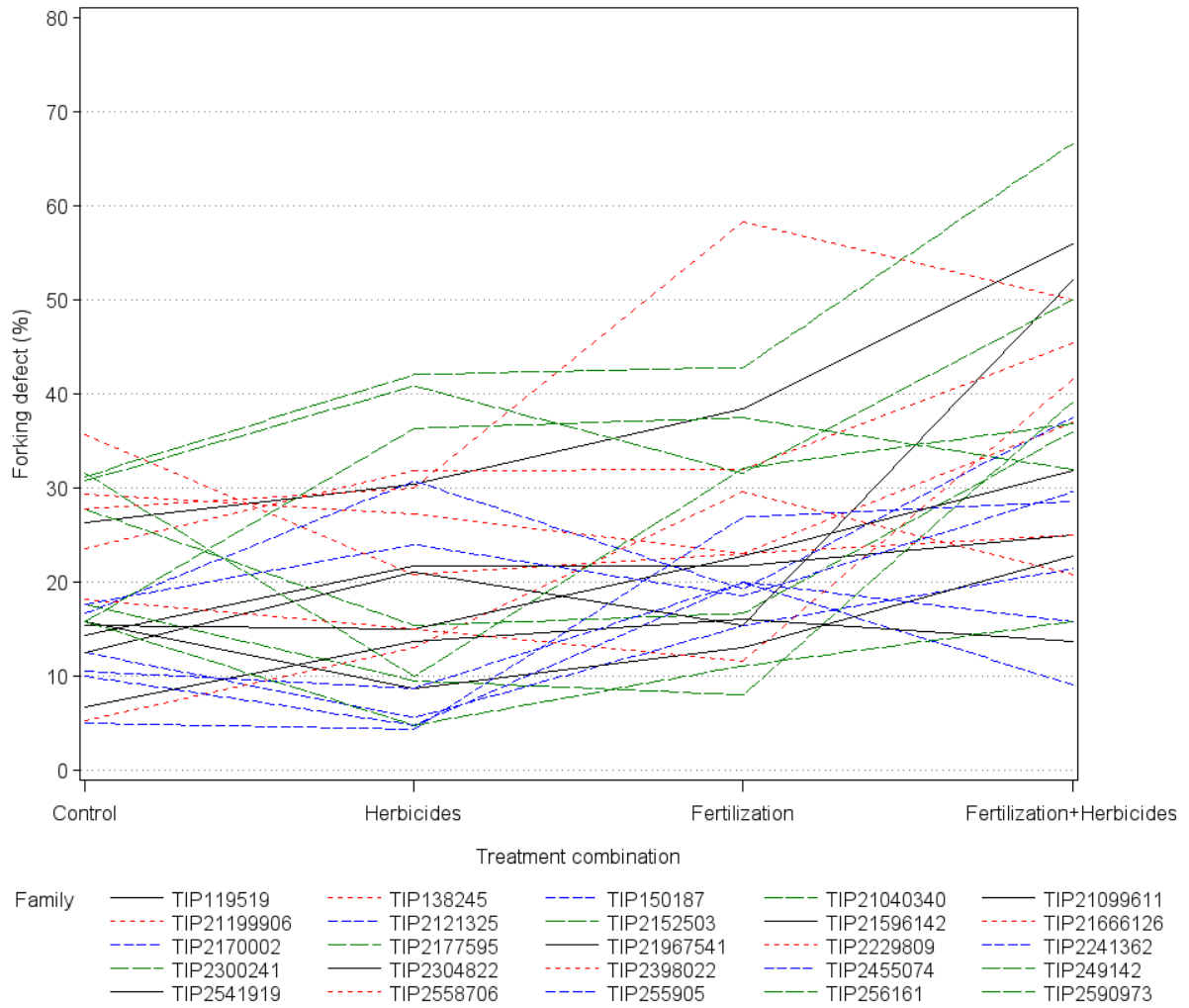


**Figure 2.3.** Family means for individual-tree volume (dm<sup>3</sup>) by treatment combination.

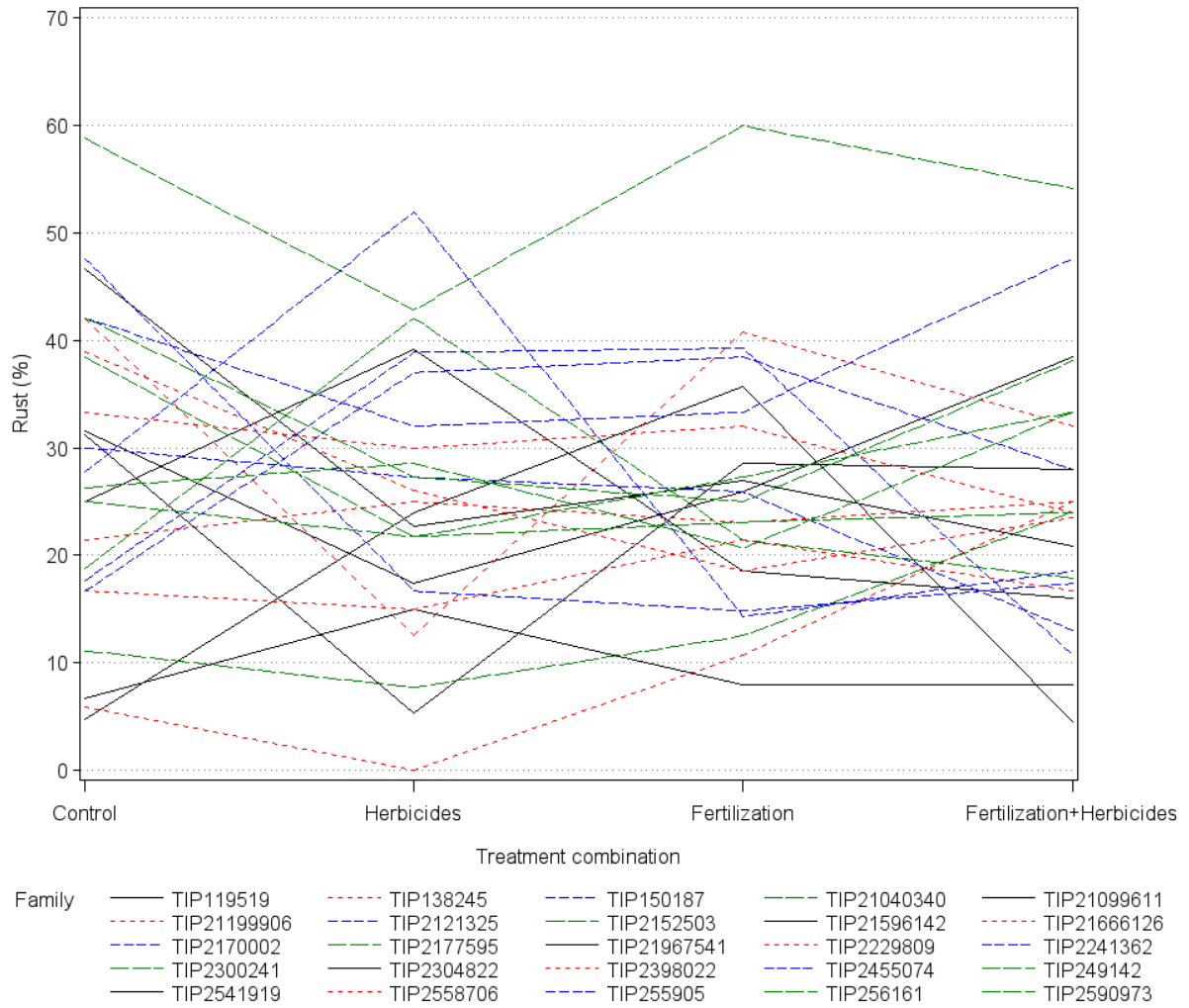


**Figure 2.4.** Family means for sweep (cm) by treatment combination.

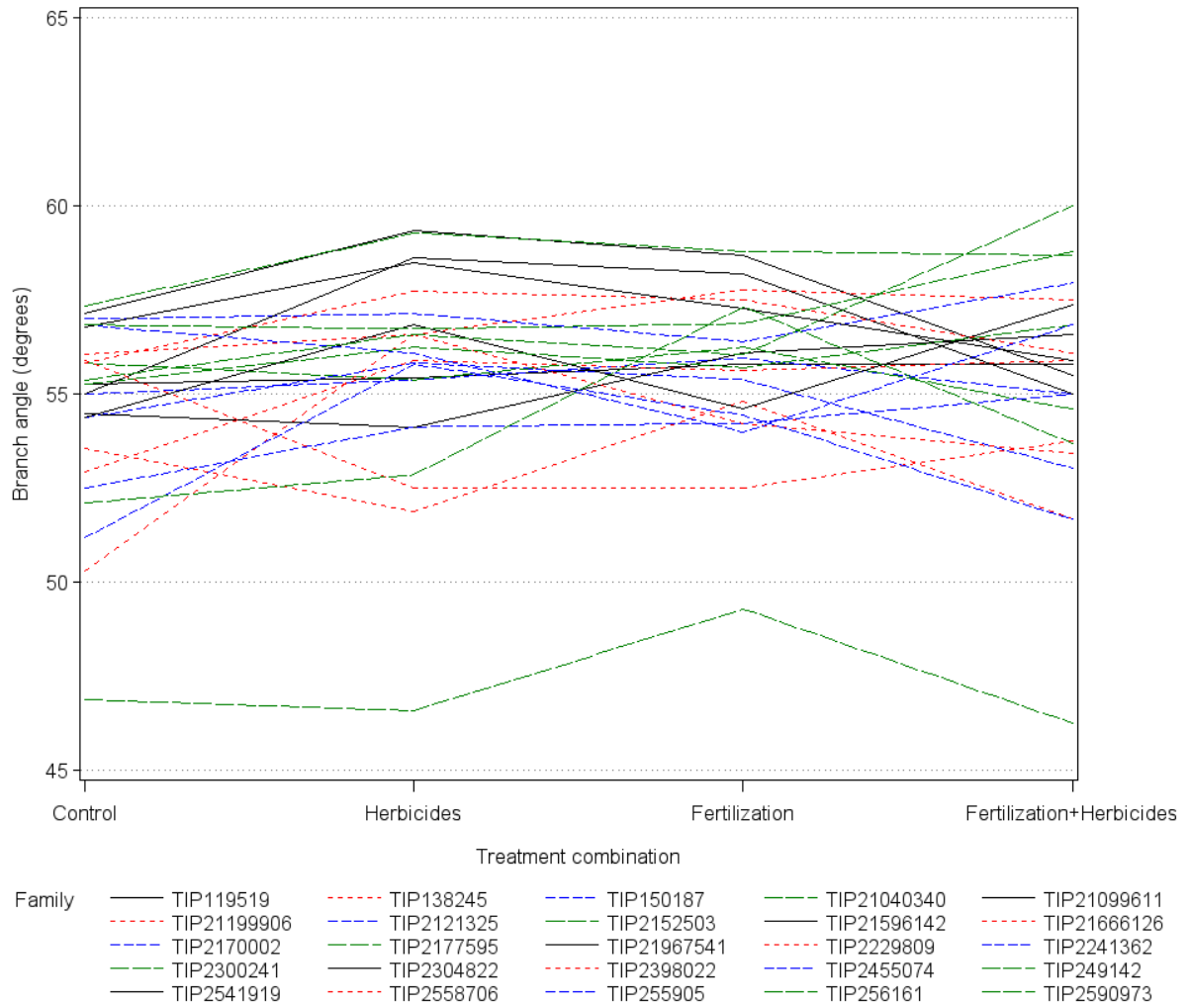




**Figure 2.5.** Family means for forking defect (%) by treatment combination (Forking defect is a combination of forking and ramicorn branching).



**Figure 2.6.** Family means for rust infection (%) by treatment combination.



**Figure 2.7.** Family means for branch angle (degrees) by treatment combination.

## APPENDICES

**Appendix 2.1.** Ancestry table with list of families included in the trial and relationships

between parents and grandparents. Families that appear more than once are marked with an\*.

OP Family (coded ID)	Selection Cycle	ID Parent 1 (coded ID)	ID Parent 2 (coded ID)
TIP2300241	Second	TIP1174558	TIP1159174
TIP119519*	First	Unknown	Unknown
TIP138245*	First	Unknown	Unknown
TIP150187*	First	Unknown	Unknown
TIP2170002	Second	TIP138245*	TIP1389204*
TIP2590973	Second	TIP1440382*	TIP1389204*
TIP2398022	Second	TIP1487936	TIP119519*
TIP21040340	Second	TIP11038493	TIP1857822
TIP21666126	Second	TIP1879215	TIP1440382*
TIP256161	Second	TIP150484	TIP1609597*
TIP255905	Second	TIP157854	TIP1440382*
TIP2121325	Second	TIP138245*	TIP1609597*
TIP2177595	Second	TIP150187*	TIP119519*
TIP249142	Second	TIP181745	TIP119519*
TIP2558706	Second	TIP143184	TIP1672933
TIP21199906	Second	TIP11563990*	TIP1218280*
TIP21967541	Second	TIP1685530	TIP1218280*
TIP21596142	Second	TIP166526	TIP1158645
TIP2152503	Second	TIP189053	TIP1218280*
TIP2304822	Second	TIP1321927	TIP11563990*
TIP2455074	Second	TIP170699	TIP176296
TIP2541919	Second	TIP1536913	TIP1213202
TIP21099611	Second	TIP1587442	TIP1136373
TIP2229809	Second	TIP138245*	TIP1243915*
TIP2241362	Second	TIP1243277	TIP1243915*

**Appendix 2.2.** Pooled means across treatment combinations for growth, form, and stem quality traits. Standard errors of means are given in the parentheses, N=number of observations.

Family	Survival (%)	Height (m)	Volume (dm <sup>3</sup> )	Sweep (cm)	Forking defect* (%)	Rust (%)	Branch Angle (deg)
TIP119519	89.69 (30.6) N=97	16.29 (3.3) N=94	170.79 (108.3) N=94	2.71 (1.1) N=93	38.71 (49.0) N=93	24.21 (43.1) N=95	55.60 (6.9) N=92
TIP138245	93.75 (24.3) N=96	17.54 (2.8) N=91	196.19 (97.2) N=91	2.03 (1.0) N=91	28.57 (45.4) N=91	23.91 (42.9) N=92	52.91 (7.5) N=91
TIP150187	89.22 (31.2) N=102	15.80 (3.0) N=93	135.72 (77.6) N=93	2.10 (0.9) N=94	26.60 (44.4) N=94	31.25 (46.6) N=96	55.37 (7.3) N=94
TIP21040340	77.32 (42.1) N=97	16.49 (2.5) N=76	150.26 (66.5) N=76	2.13 (1.0) N=80	47.50 (5.3) N=80	24.18 (43.1) N=91	47.25 (7.2) N=80
TIP21099611	84.47 (36.4) N=103	15.49 (2.7) N=86	131.63 (73.2) N=86	1.99 (0.9) N=87	20.69 (40.7) N=87	18.75 (39.2) N=96	57.76 (6.7) N=87
TIP21199906	83.33 (37.5) N=102	16.13 (2.6) N=83	131.39 (69.7) N=83	2.21 (0.9) N=86	33.72 (47.6) N=86	10.99 (31.4) N=91	55.24 (7.0) N=85
TIP2121325	87.63 (33.1) N=97	16.76 (2.9) N=87	155.88 (81.8) N=87	1.93 (0.8) N=88	14.77 (35.9) N=88	26.37 (44.3) N=91	54.55 (7.9) N=88
TIP2152503	85.87 (35.0) N=92	15.57 (2.6) N=83	134.90 (79.5) N=83	2.09 (1.2) N=86	18.60 (39.1) N=86	54.02 (50.1) N=87	58.60 (5.5) N=86
TIP21596142	80.81 (39.6) N=99	15.30 (2.8) N=87	110.03 (62.7) N=87	2.01 (1.0) N=87	14.94 (35.9) N=87	28.42 (45.3) N=95	55.34 (7.0) N=87
TIP21666126	85.58 (35.3) N=104	15.34 (3.0) N=92	112.06 (70.5) N=92	2.06 (0.8) N=93	18.28 (38.9) N=93	31.58 (46.7) N=95	57.07 (6.8) N=92
TIP2170002	83.50 (37.3) N=103	16.55 (2.5) N=87	174.80 (95.5) N=87	1.78 (1.3) N=88	11.36 (31.9) N=88	23.91 (42.9) N=92	57.10 (7.5) N=88
TIP2177595	87.62 (33.1) N=105	16.40 (2.7) N=93	165.03 (92.8) N=93	2.11 (1.5) N=92	23.66 (42.7) N=93	13.98 (34.9) N=93	55.48 (6.9) N=93
TIP21967541	86.96 (33.9) N=92	15.47 (3.0) N=81	116.99 (67.9) N=81	2.36 1.0 N=84	26.19 (44.2) N=84	23.86 (42.9) N=88	55.84 (6.8) N=83

\*Forking defect is a combination of forking and ramicorn branching.

**Appendix 2.2. (continued).** Pooled means across treatment combinations for growth, form, and stem quality traits. Standard errors of means are given in the parentheses, N=number of observations.

Family	Survival (%)	Height (m)	Volume (dm <sup>3</sup> )	Sweep (cm)	Forking defect* (%)	Rust (%)	Branch Angle (deg)
TIP2229809	77.67 (41.8) N=103	16.47 (2.5) N=81	139.58 (71.5) N=81	1.84 (0.8) N=81	25.93 (44.1) N=81	25.88 (44.1) N=85	53.89 (7.4) N=81
TIP2241362	83.65 (37.2) N=104	15.47 (2.9) N=88	126.34 (72.9) N=88	2.27 (1.2) N=90	16.67 (37.5) N=90	23.16 (42.4) N=95	54.00 (7.7) N=90
TIP2300241	83.00 (37.8) N=100	15.73 (2.6) N=81	108.55 (60.2) N=81	2.38 (1.44) N=86	27.91 (45.1) N=86	26.67 (44.5) N=90	55.99 (6.7) N=86
TIP2304822	88.17 (32.5) N=93	15.83 (2.7) N=82	117.83 (60.2) N=82	2.40 (1.6) N=84	13.10 (33.9) N=84	27.59 (45.0) N=87	56.93 (6.9) N=83
TIP2398022	86.81 (34.0) N=91	15.67 (3.2) N=84	131.16 (80.5) N=84	2.33 (0.9) N=84	43.02 (49.8) N=86	29.55 (45.9) N=88	56.82 (6.6) N=85
TIP2455074	81.82 (38.8) N=99	16.26 (2.5) N=85	145.94 (70.5) N=85	2.19 (1.4) N=86	13.95 (34.9) N=86	38.04 (48.8) N=92	55.81 (6.8) N=86
TIP249142	79.80 (40.4) N=99	17.30 (2.2) N=74	179.02 (85.6) N=78	2.39 (1.1) N=80	40.00 (49.3) N=80	29.41 (45.8) N=85	57.38 (6.7) N=80
TIP2541919	76.77 (42.4) N=99	15.67 (2.7) N=77	120.52 (71.7) N=77	2.50 (1.1) N=78	22.08 (41.7) N=77	9.41 (29.4) N=85	57.12 (6.4) N=78
TIP2558706	83.16 (37.6) N=95	15.91 (2.85) N=79	129.35 (71.7) N=79	1.98 (1.1) N=81	22.22 (41.8) N=81	17.86 (38.5) N=84	53.33 (7.5) N=81
TIP255905	88.46 (32.1) N=104	16.10 (2.74) N=95	137.39 (75.3) N=95	2.36 (1.6) N=96	22.92 (42.3) N=96	27.55 (44.9) N=98	53.44 (7.5) N=96
TIP256161	83.67 (37.2) N=98	16.22 (3.0) N=85	164.96 (95.8) N=85	1.99 (1.1) N=87	11.63 (32.2) N=86	32.22 (47.0) N=90	54.31 (8.0) N=87
TIP2590973	86.27 (34.6) N=102	16.16 (3.0) N=87	143.70 (80.6) N=87	2.08 (0.9) N=91	31.11 (46.6) N=90	23.40 (42.6) N=94	57.36 (6.6) N=91

\*Forking defect is a combination of forking and ramicorn branching.

### Appendix 2.3. Analysis of fertilization and herbicide main effects.

Main effects were broken out and separately analyzed for average height, volume, sweep, and branch angle, using the following linear model:

$$Y_{ijkl} = \mu + B_i + N_j + W_k + NW_{jk} + BN_{ij} + BW_{ik} + BNW_{ijk} + e_{ijkl} \quad (\text{Eq. 2.8})$$

Where  $Y_{ijkl}$  is the dependent variable (the observation of the  $l$ th tree of the  $k$ th herbicide treatment level of the  $j$ th fertilization level of the  $i$ th block),  $\mu$  is the overall mean,  $B_i$  is the fixed effect of the  $i$ th block ( $i = 1, 2, \dots, 5$ ),  $N_j$  is the fixed effect of the  $j$ th level of fertilization ( $j = 1, 2$ ),  $W_k$  is the fixed effect of the  $k$ th level of herbicide treatment ( $k = 1, 2$ ),  $NW_{jk}$  is the fixed interaction effect between the fertilizer and herbicide treatment,  $BN_{ij}$  is the fixed interaction effect between block and fertilization,  $BW_{ik}$  is the fixed interaction effect between block and herbicide treatment,  $BNW_{ijk}$  is the fixed three-way interaction between block, fertilization, and herbicide treatment, and  $e_{ijkl}$  is the random error, expected to be  $\sim \text{NID}(0, \sigma_e^2)$ . The GLM procedure of SAS Software (SAS Institute Inc. 2004-2008) was used to run the model. To get the correct F-tests, the RANDOM statement and the TEST option was used. The binary traits (forking defect and rust) were analyzed using a generalized model (Eq. 2.9) and SAS Proc GLIMMIX in a similar way as described earlier in the Materials and Methods section.

$$y_{ijkl} = \log[\pi/(1-\pi)] = \mu + B_i + N_j + W_k + NW_{jk} + BN_{ij} + BW_{ik} + BNW_{ijk} + e_{ijkl} \quad (\text{Eq. 2.9})$$



Where  $y_{ijkl}$  is the  $l$ th observation of the  $k$ th herbicide treatment level of the  $j$ th fertilization level of the  $i$ th block,  $\mu$  is the overall mean,  $B_i$  is the fixed effect of the  $i$ th block ( $i = 1, 2, \dots, 5$ ),  $N_j$  is the fixed effect of the  $j$ th level of fertilization ( $j = 1, 2$ ),  $W_k$  is the fixed effect of the  $k$ th level of herbicide treatment ( $k = 1, 2$ ),  $NW_{jk}$  is the fixed interaction effect between the fertilizer and herbicide treatment,  $BN_{ij}$  is the fixed interaction effect between block and fertilization,  $BW_{ik}$  is the fixed interaction effect between block and herbicide treatment,  $BNW_{ijk}$  is the fixed three-way interaction between block, fertilization, and herbicide treatment,  $e_{ijkl}$  is the random error, expected to be  $\sim \text{NID}(0, \mathbf{I}\sigma_e^2)$ , and  $\mathbf{I}$  is a  $n \times n$  identity matrix.

Results are shown in Appendix 2.4-2.5. There were few significant fertilization by herbicides treatment interactions in the plots, even though for height ( $p=0.032$ ), and forking defect ( $p=0.035$ ) significant interactions were found. In addition, fertilizer effects on height, volume, and forking defect were significant, as well as herbicide treatment effects on height, volume, sweep, and forking defect. The remaining traits had no significant main effects or important interactions.

**Appendix 2.4.** Probability of F-tests for the imposed silvicultural treatment main effects (herbicides and fertilization) and their interactions for important growth, form, and stem quality traits\*.

Source	Height	Volume	Sweep	Branch angle
Herbicides	<b>0.049</b>	<b>0.042</b>	<b>0.004</b>	0.703
Fertilization	<b>0.005</b>	<b>&gt;.001</b>	0.261	0.381
Fert x Herb	<b>0.032</b>	0.186	0.777	0.175

\*Fertilization, herbicides, and the interaction term had 1 DF. The denominator degrees of freedom were 4 for all the terms. Probabilities of  $\leq 0.05$  were considered significant.

**Appendix 2.5.** Probability of F-tests for the imposed silvicultural treatment main effects (herbicides and fertilization) and their interactions for important binary growth, form, and stem quality traits\*.

Source	Forking defect**	Rust
Herbicides	<b>0.007</b>	0.235
Fertilization	<b>&gt;.001</b>	0.406
Fert x Herb	<b>0.035</b>	0.565

\*Fertilization, herbicides, and the interaction term had 1 DF. The denominator degrees of freedom were 4 for all the terms. Probabilities of  $\leq 0.05$  were considered significant.

\*\*Forking defect is a combination of forking and ramicorn branching.

## CHAPTER 3

# FAMILY RESPONSE IN WOOD DENSITY AND ACOUSTIC VELOCITY TO IMPOSED HERBICIDE AND FERTILIZATION TREATMENTS IN LOBLOLLY PINE

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## Abstract

Silvicultural and genetic effects as well as silviculture by genetics interactions were investigated for wood quality traits in a 16-year-old loblolly pine (*Pinus taeda* L.) field trial in southwestern Georgia, USA. The trial was designed with different fertilizer and herbicide treatment combinations applied to 25 open-pollinated first- and second-generation families. The study concentrated on analyzing variation in wood density and squared acoustic velocity (considered as a surrogate trait for wood stiffness). Squared acoustic velocity ranged from 14.5 km<sup>2</sup>/s<sup>2</sup> in the fertilization only plots to 16.4 km<sup>2</sup>/s<sup>2</sup> in the herbicides only plots, and there were significant differences between several treatment combinations for this trait. Average core density varied from 465 kg/m<sup>3</sup> in the control plots to 450 kg/m<sup>3</sup> in the combined fertilization and herbicide plots. Ring 2-6 core section density varied from 445 kg/m<sup>3</sup> in the control plot to 435 kg/m<sup>3</sup> in the combined fertilization and herbicide plots, and ring 7-16 core section density varied from 590 kg/m<sup>3</sup> in the herbicides only plots to 538 kg/m<sup>3</sup> in the fertilization only plots.

Genetic effects were significant for all traits, and there was a range in family means for each trait. When pooled across treatments, individual-tree heritability values were 0.41 for squared velocity, 0.32 for whole core weighted density, 0.28, for ring 2-6 core section density, and 0.78 for ring 7-16 core section density. Pooled family mean heritability values were 0.90 for squared velocity, 0.88 for whole core weighted density, 0.86 for ring 2-6 core section density, and 0.95 for ring 7-16 core section density. Genetic and phenotypic correlations

were significant between several combinations of wood quality traits. In contrast, correlations were generally low and non-significant between growth and form traits (measured for another study in the same trial) and wood quality traits.

Silviculture by genetics interaction effects were non-significant for all traits, and family rankings across treatment combinations were generally stable. For improved open-pollinated Coastal loblolly pine families, the occurrence of genetics by culture interactions was low for wood density and squared acoustic velocity, and the data indicate that the risk of losing value in terms of wood quality due to suboptimal matching between genetic material and silvicultural prescriptions is generally low.

## **Introduction**

Forest plantations represent less than five percent of the world's forest covered area, but they produce 35% of the total harvested roundwood, and predictions point towards a significantly increased share by the year 2020 (Sands 2005; Anon 2007). In the southern United States, the 12.1 million hectares of pine plantations are about 16% of the 75.6 million hectares of commercial forest and about 14% of the 87 million hectares of total forests (Conner & Hartsell 2002). While pine plantations occupied only 16% of the South's timberland area, they provide 43% of all softwood growth and 35% of all softwood removals (Conner & Hartsell 2002). Management methods for southern pine plantations have been continuously improving total wood production as well as yield per hectare (McKeand & Allen 2005; Carter & Foster 2006), and much of the focus has been directed towards optimizing management activities to obtain increased growth levels and improved value for land owners (Allen et al. 2005; Dougherty et al. 2010). The gains have been achieved by focusing on tree improvement and by developing more site-specific operational silvicultural treatments and combinations of treatments (Fox et al. 2007).

Altered wood properties and changes in product performance have often been the consequences of the increased proportions of wood harvested from more intensively managed young plantations (Senft et al. 1985; Kretschmann & Bendtsen 1992; Larson et al. 2001; Gartner 2005). In many cases, these changes have not been favourable, even though they could be good for the manufacturing of some products such as newsprint (Zobel &

Sprague 1998). Since different traits are important for different kinds of products, it is difficult to generalize (Gartner 2005).

The juvenile wood core has features such as lower density and stiffness that negatively impact solid wood properties. Detailed descriptions of properties, within tree variation, classification, and potential for predicting or manipulating the extent and properties of the juvenile or core wood in trees are given by Zobel & Sprague (1998), Larson et al. (2001), and recently by Burdon et al. (2004).

The overall degree of uniformity of the wood within the tree is also an issue in young, intensively managed, early-harvested stands (Zobel & Sprague 1998; Gartner et al. 2005).

The demand for knowledge about wood quality in fast-grown plantations has therefore increased over the last decades (Stanturf et al. 2003), and increased focus towards producing wood that is suitable as raw material for certain industries has often been suggested (Zobel 1984; Allen et al. 2005).

Methods to better predict and influence certain raw material properties in plantations could still be quite advantageous for the forest sector. For example wood stiffness or modulus of elasticity (MOE) is an important trait for the solid wood products industry and is a good quality indicator for manufacturers of material intended for structural use (Bowyer et al. 2003). In a study on radiata pine, Ivkovic et al. (2006) found that wood stiffness, when genetically improved, was one of the traits that contributed most to the increased value for an



integrated forest company producing solid wood products. There are different methods for measuring MOE, such as laboratory bending tests (Bowyer et al. 2003), near infra red spectroscopy (Schimleck et al. 2005), micro-drill resistance (Eckard et al. 2010), and X-ray diffractometry (Evans 2006). A short description of X-ray diffractometry using SilviScan is available in the materials and methods section of Chapter 1.

Measuring acoustic velocity is a less labour-intensive method that does not require collection of wood samples, laboratory work, or drilling through stems, and the acoustic method can be used to obtain indirect estimations of wood stiffness (Andrews 2002a; Huang et al. 2003). By using acoustic velocity measurements as a substitute for MOE data, it is possible to measure stiffness on standing trees with a time of flight (TOF) tool such as TreeSonic (Fakopp Enterprise website 2011). In 8-year-old loblolly pine, Eckard et al. (2010) found significant phenotypic correlations between acoustic velocity and MOE measured in the laboratory. Based on a study in 25 year-old Douglas-fir (*Pseudotsuga menziesii*), Cherry et al. (2008) found that acoustic velocity was moderately correlated with bending stiffness measured in the laboratory. Other studies show mixed results. Matheson et al. (2002), studying *Pinus radiata*, found correlations between acoustic velocity and board stiffness to vary from no to rather low correlations. Nevertheless, acoustic velocity was reported to be useful in clonal testing programs for loblolly pine (Eckard et al. 2010) and radiata pine (Lindström et al. 2002; Lindström et al. 2004). Based on a study of slash pine (*Pinus elliottii*) families at a number of different sites, Li et al. (2007) concluded that acoustic velocity could be utilized when ranking families for wood stiffness in the bottom log and there are also indications that

it could be better to select for velocity than density when trying to improve MOE (Li et al. 2007).

The stress wave velocity method mainly measures the outermost rings in the tree (Wang et al. 2002; Gorman et al. 2003) limiting the amount of information it yields compared to methods that produce a measurement profile from pith to bark. In *Pinus radiata* however, Grabianowski et al. (2006) found correlations between acoustic measurements in wood from sections close to the bark and the sections close to the pith. Results from studies such as the one on *Pinus radiata* by Toulmin & Raymond (2007) indicate a potential for improved precision if measurements are taken on more than just one side of the tree. Mahon et al. (2009) recently recommended applying the TOF transmitter and receiver probes at opposite sides of the stem instead of the on the same side to decrease variability in the velocity measurements. A recent study on loblolly pine suggest that when making estimations of MOE using acoustic velocity on standing trees, measurements of wood green density combined with moisture content taken from a sub sample of trees should be included (Mora et al. 2009).

Microfibril angle (MFA) is one of the major factors determining MOE and dimensional stability in wood from intensively grown conifers (Megraw 1985; Dinwoodie 2000; Burdon et al. 2004) and especially in the juvenile wood (Cave & Walker 1994). MFA usually refers to the angle of the microfibrils in the relatively thick secondary (S<sub>2</sub>) layer of the cell wall. Lindström et al. (2004), when looking at 3-year old radiata pine, reported low correlations

between acoustic MOE and density, and found that the clonal variation in MOE at this stage was mainly due to differences in MFA. MFA changes when moving from pith to bark, and the pattern of change also varies somewhat at different height levels in the tree (Megraw 1985; Burdon et al. 2004). Further away from the pith, MFA levels gradually stabilize, and rings become more similar (Bendtsen & Senft 1986; Clark et al. 2006). There are indications that outerwood variations in MOE are not as closely associated with MFA as it is in corewood, and for outerwood stiffness, density becomes more important (Cown et al. 1999). MFA is still a rather time consuming and expensive trait to measure, even though recent developments in technology based on x-ray diffraction have changed that in some respects (Evans 2006).

Wood density or specific gravity is the most widely studied wood quality trait (Newlin & Wilson 1919; Megraw 1985; Simpson 1993; Zobel & Jett 1995; Bowyer et al. 2003) and is commonly measured by using X-ray technology (Megraw 1985) or the more recently developed near infrared spectroscopy methods (Schimleck et al. 2005) on samples prepared from increment cores. Wood density generally varies considerably within a tree from pith to bark and at different heights along the stem (Megraw 1985; Jayawickrama et al. 2009). Density follows a pattern where it increases rapidly in the initial year rings moving from the pith. The rate of increase eventually levels off and values stabilize in the outer wood (Megraw 1985; Jordan et al. 2008).

Density is associated with wood stiffness in many species (Dinwoodie 2000) and was shown to be well correlated with static MOE measured on wood sticks in species such as radiata pine at age 11 (Kumar et al. 2002). Somewhat lower correlations between the same traits were reported for loblolly pine measured at age 6, (Eckard et al. 2010), and for 25 year old Douglas-fir (Cherry et al. 2008). In another radiata pine study consisting of trials ranging from 10-15 years in age, Kumar (2004) found generally moderate correlations between density and acoustics. Chauhan & Walker (2006) found generally weak relationships between density and acoustic velocity when looking at *Pinus radiata* grouped in different age classes.

Lowe et al. (1999) outline the potential for improving wood density to increase the profit for certain pulp industries. Properties like pulp yield correlate with specific gravity (Bowyer et al. 2003), even though there are also some recent contradictory results concerning the degree of direct correlations (White et al. 2009). Nevertheless, wood density is important for yield and end-product properties (Zobel & Jett 1995) and affects costs in the entire chain from harvesting to logistics and processing at the mill.

The genetic control of many wood properties is generally high (Zobel & Jett 1995), and many studies have shown high heritability values for density compared to many other economically important traits (Cornelius 1994). High individual-tree heritability values were reported for open-pollinated families of loblolly pine planted across different regions of the southeast at age 12 (Jett et al. 1991). Based on measurements on 12 mm breast height

increment cores, Isik et al. (2008a) found high half-sib family mean heritabilities in loblolly pine progeny trials, 6-18 years of age and planted across a number of sites.

Silvicultural treatments at stand establishment such as application of herbicides (Allen et al. 1990), nitrogen fertilization (Allen 1987) and/ or applications of phosphorous on appropriate soils generally have positive effects on total volume production (Allen 1987; Nilsson & Allen 2003). In a study comparing different southern pines, wood quality traits such as specific gravity were not found to be negatively affected by intensive treatments (cultivation and different levels of fertilization) applied at stand establishment and later through the stands 9-year development (Schmidtling 1973). In a study with loblolly pine, Mora (2003) looked at a number of regeneration trials with different levels of early intensive silviculture and found large responses in volume 20 years after treatments. Despite these growth responses, only small treatment-induced changes in specific gravity and transition age between juvenile and mature wood were found and only for some sites and for some treatment combinations (Mora 2003).

Imposed treatments later during the rotation (after the establishment phase) often include applications of nitrogen and phosphorous fertilizers (Allen 1987; Allen et al. 2005), and potassium and micronutrients are frequently included in these applications (Allen et al. 2005). Treatment effects from repeated fertilization of loblolly pine starting at age 8 and maintained for a number of years was studied by Albaugh et al. (2004) who found significant effects of fertilization on wood specific gravity; fertilized trees had lower specific gravity.

After application, the impacts of fertilization on specific gravity gradually levels off (Love-Myers et al. 2009). Similar results have been reported in different studies of loblolly pine, even though the magnitude and significance of these kinds of treatment effects vary with stand age, site conditions, water supply, and level of silvicultural input (Megraw 1985; Albaugh et al. 2004; Love-Myers et al. 2010). Treatment effects can also vary at different positions within the tree (Megraw 1985). Antony et al. (2009) found that specific gravity was lowered in the rings formed during the years following application of high levels of fertilizer in mid-rotation loblolly pine. Compared to trees in stands receiving intensive mechanical site preparation only, Clark et al. (2004) reported 6-10 percent lower stem specific gravity on 12-year-old loblolly pine stands subjected to a combination of frequent applications of fertilizer and vegetation control treatments. Effects on specific gravity from vegetation control treatments only were not significant in their study. Even though short-term reductions in specific gravity can be observed after fertilization, these are usually offset in terms of total dry substance produced due to larger volume production (Megraw 1985).

Studies of the interactions between genetics and fertilization and /or weed control treatments for wood quality are not common. In a study of slash pine, Rockwood et al. (1985) found no overall significant GxE interaction for specific gravity. Schmidting (1973) did not find GxE interactions for specific gravity in a rather small material and Williams & Megraw (1994) found very low GxE in a 2-3 year-old loblolly pine material consisting of families subjected to fertilization and irrigation as treatments versus no treatment. Byram & Lowe (1988) reported that loblolly pine seed sources could behave differently in terms of specific gravity

when planted in different regions even though rank changes between families generally did not occur at different sites in their material. Jett et al. (1991) looked at the specific gravity variation in juvenile wood for a number of selected open-pollinated loblolly pine families from diverse provenances planted across diverse regions and found significant GxE for a small subset of the families. The variation in specific gravity did not follow the pattern of variation reported for natural stands (Megraw 1985) as well as for plantations (Jordan et al. 2008) with generally increasing density when moving towards the east and south. Jokela et al. (2004) found different patterns in the specific gravity variation when looking at effects of weed control and fertilization at different sites across the southern U.S. At some sites specific gravity increased with intensive treatments compared to the control, and at some sites the opposite happened. The authors thought the results were confounded by climate and different genetics at different sites.

MOE has been shown to be heritable in many studies of species using SilviScan measurement technology as for example in radiata pine (Kumar et al. 2006) and Norway spruce (Gräns et al. 2009). Also laboratory bending tests have proven useful when estimating genetic parameters in species such as Douglas-fir (Cherry et al. 2008). For squared acoustic velocity, (Jayawickrama et al. (2011) reported moderate individual narrow-sense heritabilities based on data from trials of mid-rotation coastal Douglas fir, and Kumar et al. (2002) reported high narrow-sense heritability values for acoustic velocity in a material of 12 year-old *Pinus radiata* families. In 8-year-old slash pine, Li et al. (2007) found high narrow-sense heritability for squared acoustic velocity and Roth et al. (2007) reported significant

family effects on squared velocity when measuring a limited number of loblolly pine full-sib families at age six.

Effects of silviculture on MOE have been investigated in a rather limited number of studies. Based on laboratory bending tests, juvenile wood MOE was lower after intensive fertilization with loblolly pine (Clark et al. 2004). Roth et al. (2007) reported significant effects of planting density on squared velocity with higher velocity values in the denser stands of 6-year old loblolly pine. They also found significant family and culture effects on squared acoustic velocity with especially one individual full-sib family responding differently to intensive levels of fertilization and vegetation control compared to operational levels. Cherry et al. (2008) found no significant family x site interactions for acoustic velocity in 25 year old coastal Douglas-fir stands with a large number of families. Li et al. (2007) reported that family rankings for squared acoustic velocity were “moderately repeatable” for the investigated sites with type B genetic correlation 0.68. The study consisted of 139 slash pine families sampled on six sites. Kumar (2004) observed low GxE for acoustic velocity for open-pollinated families of *Pinus radiata*. When comparing different results from softwood species it is important to keep in mind at which ages the measurements were made. Age-age correlations for these traits vary in different studies, and the juvenile wood is different from mature wood in many respects (Zobel & Jett 1995).

Specific gravity is seldom closely associated with growth rate in loblolly pine and has generally low genetic correlations with these categories of traits (Megraw 1985). In *Pinus*



*radiata*, Burdon & Low (1992) found a negative association between density and ring width but a positive correlation with tree height. Harding (1995) working with loblolly pine concluded that if selection for density was made early, it did not negatively affect later radial growth. Belonger (1998) reported low to medium negative genetic correlations between stem volume and wood density but also showed that selection of individual families within provenances could be successful in terms of potential for finding families that combine fast growth and high wood density. Williams & Megraw (1994) found some rather weak positive correlations between specific gravity and height at different ages, and Cherry et al. (2008) found density estimated from wood discs to have moderate negative correlations with growth traits in several trials of coastal Douglas-fir. Johnson & Gartner (2006) also working with coastal Douglas-fir found moderate negative genetic correlations between velocity and diameter at breast height. Li et al. (2007) found no correlations between juvenile wood velocity and volume in slash pine and concluded that selection based on acoustic measurements could be included in tree improvement programs as a way to improve corewood stiffness. A significant but small positive correlation between stiffness and height was found in their material however. Based on data from 347 Douglas-fir families at 14 sites Jayawickrama et al. (2011) reported negative correlations between squared acoustic velocity and height and diameter at breast height for large parts of their material. Roth et al. (2007) found that height in relation to diameter was strongly related to acoustic velocity in their studied material with higher velocity values in more slender trees. Toulmin & Raymond (2007) found low correlation between velocity and diameter at breast height for *radiata* pine.

The objectives of the study were to:

- 1) investigate the effect of fertilization and herbicide treatments on wood quality traits of loblolly pine
- 2) investigate effects of treatments on different families and possible interactions between silvicultural treatments and genetics for the studied traits
- 3) estimate genetic parameters for all traits
- 4) estimate genetic and phenotypic correlations among traits
- 5) examine the relationship between wood quality traits and growth traits

## **Materials and Methods**

### *Field trial*

The study was based on a loblolly pine genetics by culture field trial. See Chapter 2 of this dissertation for a detailed description of the experimental layout, genetic material, and silvicultural treatments applied, as well as for more information about the background concerning the sampling schedule.

### *Acoustic velocity measurements*

Acoustic velocity was measured on 2150 trees representing 25 half-sib families in four silvicultural treatment combinations using TreeSonic (Fakopp Enterprise website 2011). The acoustic velocity data was collected in October 2006 (after 16 growing seasons).

Measurements were performed by applying a sensor probe 0.5 m above breast height and another sensor 0.5 m below breast height so that the sensors were 1 m apart. In an attempt to lower the amount of compression wood measured, the sensors were placed on the side of the stem where the least branches and defects were found (by visual inspection). By using a timer to record the time for an acoustic stress wave (induced by a hitting with a metal hammer on the upper sensor probe) to go from the upper to the lower sensor probe, velocity could be calculated. The sensors were only applied once per tree. Trees with severe damage and dead trees were not sampled. Three stable (extra readings were made in case numbers changed dramatically from one time to another) readings were taken at each tree and then averaged into one value recorded in  $\mu\text{s}/\text{m}$  and later converted and squared into  $\text{km}^2/\text{s}^2$ .

This method, based on measurements on standing trees builds on the relationship described by the following equation:

$$MOE = \rho v^2 \quad (\text{Eq. 3.1})$$

where *MOE* is dynamic modulus of elasticity,  $\rho$  is the green density of the sampled material, and  $v$  is the velocity of the stress wave when moving through the sampled material (Andrews 2002b). If  $\rho$  is set to be constant, it follows that squared velocity will offer an indirect or surrogate estimation of MOE and several studies have estimated genetic parameters using squared velocity data (see introduction for references).

#### *Wood sample collection and X-ray wood density measurements*

Gas-powered drills were used to obtain bark-to-bark clear wood increment cores at breast height from the same trees as those that were sampled for acoustic velocity. The sampling was done in January of 2007 (after 16 growing seasons). The wood cores were 12 mm in diameter, and a large effort was made to avoid defects such as reaction wood, branches or large resin deposits in the wood samples. In many cases, trees had to be drilled repeatedly to obtain acceptable samples. Also, if the core did not go through the pith, a new sample had to be taken. Trees with severe damage were not sampled. The wood cores were tagged and put in individual bags, then immediately put on ice and then moved to a freezer. After a period of storage in about -29° C, the samples were prepared for X-ray densitometry. Wood cores were thawed in room temperature for 12 hours, and then split at the pith into two separate samples.

The cores were then dried in a forced-air drying oven for approximately 48 hours in a temperature around +50° C. One of the two pith-to-bark samples from each tree was glued to sticks made of poplar wood and from the glued sticks 2 mm thick radial wood samples were cut using a circle saw. The X-ray scanning was performed in a QTRS-01X Tree Ring Analyzer using a QMS model (QMC, Knoxville, TN). Measurements were obtained for ring width and average ring basic density, earlywood and latewood percent. Focus in this paper was to analyze basic density.

### *Statistical analysis*

After initial examination of the combined acoustic velocity and the X-ray densitometry data, a very limited number of outliers were removed. The ring closest to the pith was excluded from the analysis. Plots of the data indicated that no transformations were needed. Area-weighted density values were calculated for the whole wood core as well as for two core sections. Since different year rings had different areas, values for ring density had to be area-weighted using the same equation as previously described in Chapter 1 of this dissertation:

$$\text{Weighted wood density} = \frac{\sum_{i=\min}^{\max} a_i * b_i}{\sum_{i=\min}^{\max} a_i} \quad (\text{Eq. 3.2})$$

where  $a_i$  is the basal area of ring  $i$ ,  $b_i$  is the wood density of year ring  $i$ , and min and max correspond to the lowest and highest year ring number of the core section.

The year rings were grouped into one section consisting of rings 2-6 and one section consisting of rings 7-16. Based on plots of density development from pith to bark (see Figure 3.1 and Figure 3.2), the 6<sup>th</sup> year ring was chosen to represent the last ring of the ring 2-6 wood core section. (This also corresponded to the first year ring from the pith containing on average more than 50% latewood, see Figure 3.3). This method was somewhat similar to the one used in for example Aspinwall et al. (2010) and Cumbie (2002) who used 40% latewood as the cutoff point. We modified this somewhat after inspecting the shape of the plots of density and latewood percentage and its development from pith to bark for this material.

The calculated values of the core sections were used to test differences between means for different treatment combinations, to obtain variance components, look for significant interactions, obtain genetic parameter estimates, and phenotypic as well as genetic correlations.

A general linear mixed model was used to evaluate the effects of the treatment combinations and their interactions.

$$Y_{ijk} = \mu + B_i + T_j + BT_{ij} + e_{ijk} \quad (\text{Eq. 3.3})$$

Where:

$Y_{ijk}$  = the observation of the  $k$ th tree of the  $j$ th treatment level of the  $i$ th block

$\mu$  = the overall mean

$B_i$  = the fixed effect of the  $i$ th block ( $i = 1, 2, \dots, 5$ )

$T_j$  = the fixed effect of the  $j$ th level of treatment ( $j = 1, 2, \dots, 4$ )

$BT_{ij}$  = the fixed interaction effect between block and treatment

$e_{ijk}$  = the error, assumed to be independent and normally distributed with the expected mean zero and variance  $\sigma_e^2$ .

The RANDOM statement and the TEST option were used to obtain correct F-tests.

Differences between the four treatment combination means were investigated using Tukey's studentized range test. The GLM procedure of SAS Software (SAS Institute Inc. 2004-2008) was used to run the model.

To investigate the effects of treatments on genetic variances and heritabilities and to look for significant genetics by culture interactions the following linear mixed model was used:

$$Y_{ijkl} = \mu + B_i + T_j + BT_{ij} + F_k + FB_{ik} + FT_{jk} + FBT_{ijk} + e_{ijkl} \quad (\text{Eq. 3.4})$$

Where:

$Y_{ijkl}$  = the observation of the  $l$ th tree of the  $k$ th family in the  $j$ th treatment combination in the  $i$ th block

$\mu$  = the overall mean

$B_i$  = the fixed block effect ( $i = 1, 2, \dots, 5$ )

$T_j$  = the fixed treatment effect ( $j = 1, 2, \dots, 4$ )

$F_k$  = the random family effect ( $k= 1, 2, \dots, 25$ ), expected to be  $\sim \text{NID}(0, \sigma_f^2)$

$BT_{ij}$  = the fixed block by treatment interaction

$FT_{jk}$  is the random family by treatment combination interaction, with expectations  $\sim \text{NID}(0, \sigma_{ft}^2)$ ,

$FB_{ik}$  = the random family by block interaction, expected to be  $\sim \text{NID}(0, \sigma_{bf}^2)$

$FBT_{ijk}$  = the random family by block by treatment combination interaction, expected to be  $\sim \text{NID}(0, \sigma_{fbt}^2)$

$e_{ijk}$  = random error term with expectations  $\sim \text{NID}(0, \sigma_e^2)$ .

When fitting the model, we used Log Likelihood ratio tests to see if additional terms were significant.

Individual tree narrow-sense heritability ( $h^2_i$ ) and family mean heritability ( $h^2_F$ ) values were estimated as follows:

$$h^2_i = 4 \sigma_f^2 / (\sigma_f^2 + \sigma_{fb}^2 + \sigma_{ft}^2 + \sigma_{fbt}^2 + \sigma_e^2) \quad (\text{Eq. 3.5})$$

Where:

$\sigma_f^2$  = the family variance component

$\sigma_{fb}^2$  = the family by block interaction variance component

$\sigma_{ft}^2$  = the family by treatment interaction variance component

$\sigma_{fbt}^2$  = the family by block by treatment interaction variance component



$\sigma_e^2$  = the error variance component.

Family mean heritability ( $h^2_F$ ) values were estimated as follows:

$$h^2_F = \sigma_f^2 / (\sigma_f^2 + \sigma_{fb}^2/b + \sigma_{ft}^2/t + \sigma_{fbt}^2/bt + \sigma_e^2/btn) \quad (\text{Eq. 3.6})$$

Where:

$\sigma_f^2$  = the family variance component

$\sigma_{fb}^2$  = the family by block interaction variance component

b = the number of blocks in the trial (5)

$\sigma_{ft}^2$  = the family by treatment interaction variance component

t = the number of treatments (4)

$\sigma_{fbt}^2$  = the family by block by treatment interaction variance component,

n = the average number of trees of each family in each block and treatment combination (4.3)

$\sigma_e^2$  = the error variance component.

The ASReml software was used to obtain variance components and to calculate functions of variance components (Gilmour et al. 2009). The open-pollinated families were not independent since there was some relatedness among them (See Appendix 3.1). To account for relatedness in the estimation of variance components, a pedigree file was used in the analysis. Standard errors of heritabilities were estimated using the Delta method (Isik et al. 2008b).

Pearson's product-moment correlations were calculated based on family means of phenotypic wood quality data using PROC CORR in SAS (SAS Institute Inc. 2004-2008). Also genetic correlations were obtained by utilizing BLUP for GCA values of families. Phenotypic and genetic correlations were also calculated between wood quality traits and growth, form, and stem quality traits measured on the same trees and presented previously in Chapter 2 of this dissertation.

## Results

Survival was high in all treatment plots, between 80 and 88 % and we did not include further analysis of survival data. Due to the extra buffer rows included around some plots the data were still somewhat unbalanced in terms of number of observations per treatment combination and family. The minimum amount of observations for one family was 73 for ring 7-16 core density and the maximum was 94 for squared acoustic velocity (Appendix 3.2). The number of observations in each treatment combination varied from 412 for ring 7-16 core section density in the control plots to 581 for velocity in the fertilization only plots. There were still a very large number of observations (more than 2000 in total for every trait) which compensated for the unbalance.

Means for treatment combinations and pooled means across treatments (with standard errors within parenthesis) are presented in Table 3.1. Squared acoustic velocity ranged from 14.5  $\text{km}^2/\text{s}^2$  in the fertilization only plots to 16.4  $\text{km}^2/\text{s}^2$  in the herbicides only plots, and there were significant differences between the control plot mean, the herbicide only plot mean, and the combined fertilization and herbicides plots mean. Average core density varied from 465  $\text{kg}/\text{m}^3$  in the control plots to 450  $\text{kg}/\text{m}^3$  in the combined fertilization and herbicide plots, and the control plot mean was significantly different from the fertilization only plots mean and the fertilization and herbicide plots mean. The herbicides only plot mean was also significantly different from the fertilization plot mean as well as the fertilization and herbicides plot mean for this trait. Ring 2-6 core section density varied from 445  $\text{kg}/\text{m}^3$  in the

control plot to 435 kg/m<sup>3</sup> on average in the fertilization and herbicide plots. The control plot mean was significantly different from the means in the fertilization plots and the fertilization plus herbicides plots. The herbicide only plot mean was also significantly different from the combined fertilization and herbicides plots. The ring 7-16 core section density varied from 590 kg/m<sup>3</sup> in the herbicide only plots to 538 kg/m<sup>3</sup> in the fertilization only plots and all treatment combination means were significantly different. Fertilizer and herbicide main effects as well as their interactions were also analyzed (See Appendix 3.3-3-4). The main effect of herbicides was significant for squared velocity and ring 7-16 core section density. The fertilization effect was significant for whole core density and ring 7-16 core section density, and also close to significant ( $p=0.059$ ) for ring 2-6 core section density. There was no significant fertilization x herbicide interaction effect for any of the included traits.

In Figure 3.1 the radial development of average ring density, pooled across treatment combinations was plotted from pith to bark for the 2049 measured trees. The first year measurements often result in somewhat unreliable data and were excluded from further analysis. The average value for density started around 400 kg/m<sup>3</sup> and increased rather sharply approximately until around ring 7 at density level 550 kg/m<sup>3</sup>. Then the curve evened out from there on. There was a large spread of individual values around the average curve in the figure. Density values for each treatment combination from pith to bark were plotted in Figure 3.2. Differences between treatment combinations were not dramatic. There were some fluctuations across rings observed, especially between rings four to seven for the fertilization

and the fertilization plus herbicide treatment plots, while the trends for the control and the herbicides only plots were more stable.

The average number of rings per tree at breast height varied very little between the treatments (from 12.7 rings per tree in the control plots to 13.7 rings per tree in the fertilizer only plots, and 14.0 rings per tree in the herbicides and the combined fertilization and herbicides plots). In Figure 3.4 the radial development of average ring width, pooled across treatment combinations was plotted from pith to bark. The initial rings were around 10 mm and the width gradually decreased moving from pith to bark and reached the 5 mm level around year 7, and then continued to decrease in width but at a slower pace. Ring width for each treatment combination was plotted in Figure 3.5 and a similar trend as in Figure 3.4 could be observed.

Treatment effects, block effects, and their interactions were evaluated and results from F-tests are given in Table 3.2. Treatment effects were significant for squared acoustic velocity ( $p=0.0002$ ), whole core density ( $p=0.047$ ), and ring 7-16 section density ( $p<.0001$ ), but not for ring 2-6 section density ( $p=0.279$ ). Block effects were also significant for squared acoustic velocity and ring 7-16 section density. The block by treatment interaction effects were significant for all traits.

Genetic effects were significant for all traits (Table 3.3), and there was a range in family means for each trait (See Appendix 3.2). Family means for squared acoustic velocity varied

from 13.8 km<sup>2</sup>/s<sup>2</sup> to 16.8 km<sup>2</sup>/s<sup>2</sup>. Variance components for family with standard errors, as well as components for family by treatment, family by block, and error, based on pooled data from all treatment combinations are given in Table 3.3. The percent variance explained by family varied from 19.6% for ring 7-16 section density to 7.0 % for ring 2-6 section density. No family by treatment or family by block interaction were significant based on Log Likelihood ratio tests. Heritability estimates with corresponding standard errors are also presented in Table 3.3. When pooled across treatments, individual-tree heritability values were 0.41 for squared velocity, 0.32 for whole core weighted density, 0.28, for ring 2-6 core section density, and 0.78 for ring 7-16 core section density. Pooled family mean heritability values were 0.90 for squared velocity, 0.88 for whole core weighted density, 0.86 for ring 2-6 core section density, and 0.95 for ring 7-16 core section density (Table 3.3).

Even though a few families changed ranking slightly, the family rankings across treatment combinations were rather stable for the investigated traits (Figures 3.6-3.9). Pooled arithmetic means across treatment combinations for all families and the number of observations on each family are given in Appendix 3.2.

Phenotypic correlations between pairs of traits based on family means were presented above the diagonal in Table 3.4 and were found to be significant for whole core density vs. ring 2-6 section density and between ring 7-16 section density and squared acoustic velocity, and ring 7-16 section density and whole core density, as well as ring 7-16 section density and ring 2-6 section density. Genetic correlations pooled across treatments and based on family BLUP-

values were presented below the diagonal in Table 3.4. Significant genetic correlations were found between squared acoustic velocity and ring 7-16 section density and a bit weaker correlation was found for squared acoustic velocity and whole core density. Genetic correlations between whole core density and ring 2-6 section density as well as whole core density and ring 7-16 section density were also significant as well as the correlation between ring 2-6 section density and ring 7-16 section density.

Phenotypic correlations (Table 3.5) and genetic correlations (Table 3.6) between wood quality traits and growth and form traits measured in the same trial (presented in Chapter 2) were also investigated. Generally, correlations were low and non-significant. One significant phenotypic correlation between squared acoustic velocity and height was found; taller trees had higher squared acoustic velocity (Table 3.5). Also the genotypic correlation between those two traits was significant (Table 3.6). Forking defect was weakly correlated with squared acoustic velocity, and volume was weakly negatively genetically correlated with ring 2-6 core section density.

## Discussion

### *Acoustic velocity*

The overall mean for squared acoustic velocity was  $15.3 \text{ km}^2/\text{s}^2$ , and the means for the treatment combinations ranged between  $14.5 \text{ km}^2/\text{s}^2$  in the fertilization only treatment plots to  $16.4 \text{ km}^2/\text{s}^2$  in the herbicides only plots (Table 3.1). If the green density is kept constant in the formula for MOE (Eq. 3.1), the MOE increases with increased squared velocity. The numbers for squared velocity were rather high compared to another recent study on 8-year-old loblolly pine (Eckard et al. 2010) and a study on 8-year-old slash pine (Li et al. 2007). The reason for the higher values in this study could be related to the age of the sampled wood. Since the trees in the present study were about twice the age of the trees in the studies cited above, and since the outermost rings are primarily measured in acoustic stress-wave studies performed on standing trees (Wang et al. 2002; Gorman et al. 2003), the wood section measured in this study most likely consisted of relatively older year rings, and thereby had less juvenile characteristics compared to the studies of younger trees mentioned above. Juvenile wood usually has lower density and higher microfibril angle, resulting in lower wood stiffness compared to mature wood (Larson et al. 2001). Correlations between inner and outer sections of the stem have been found in earlier studies. For radiata pine the correlation between standing tree acoustics data and acoustic measurements in wood from sections close the pith were 0.74 (Grabianowski et al. 2006). The methodology is still under development and Mora et al. (2009) suggested the use of calibrations for adjusting acoustic velocity data to be able to improve the precision of MOE estimates. Mahon et al. (2009)



reported that accuracy could be improved if the TreeSonic probes were placed on opposite sides of the stem. Following these recommendations could have resulted in somewhat different numbers, but the methods were not tested in this study.

Overall treatment combination effects were significant for squared acoustic velocity (Table 3.2). Differences for squared acoustic velocity were found between the control plots and the herbicides only plots and between the control plots and combined herbicides and fertilization plots when using Tukey's studentized range test. Herbicides only and fertilization only were also different. The test indicated no significant difference between the control plots and the fertilizer only plots however (Table 3.1). Also when breaking out the main effects (herbicides and fertilization) the herbicides main effect for squared acoustic velocity was significant ( $p=0.003$ ) but not the fertilization main effect (Appendix 3.4). The reasons behind this were not clear. Effects of silviculture on modulus of elasticity or its surrogate trait acoustic velocity (or squared acoustic velocity) have been previously reported for loblolly pine where Clark et al. (2004) reported significantly lower stiffness (measured in the laboratory on wood samples) in the corewood but not in the outer wood after fertilization or fertilization in combination with herbicides in a twelve year old field trial. Roth et al. (2007) reported decreased squared velocity with intensified silviculture treatments for parts of their 6-year-old loblolly pine material consisting of a rather limited number of full-sib families. In a combined radiata pine thinning and fertilization study, Downes et al. (2002) found somewhat lower MOE-values after treatment.

The slower growing control treatment plots had lower values for squared acoustic velocity than the trees in the faster growing herbicides plots and fertilization plus herbicides plots. The values for the control plots and the fertilization plots only were very similar however (Table 3.1). In Li et al. (2007), the authors discussed possible reasons why a slower growing tree could have somewhat lower acoustic velocity for juvenile wood in slash pine. They assumed that if the ratio of earlywood to latewood was kept constant, acoustic velocity measurements could be lower in slower grown plantations since a fixed area of wood would have been measured in both cases, which in turn would have resulted in more wood formed by a younger cambium included in the measurement zone for the slower growing tree compared to a tree with wider rings.

Obviously, it would have been good to have had more acoustic velocity data from this trial measured at different stages of stand development, especially at younger ages, to be able to make comparisons regarding possible variations in treatment effects over time as well as to check for the presence of age-age correlations.

It is very important to sample enough trees per family when trying to estimate genetic parameters and family ranks for indirect measures of wood stiffness (Matheson et al. 2002). For example, Williams & Megraw (1994) suggested that in loblolly pine, 20-30 open-pollinated families with 2-5 trees per family could be enough to make a distinction. In this material heritability values for squared acoustic velocity were high (0.41 for individual-tree heritability, and 0.90 for family mean heritability) which is common for many wood quality

traits, (Table 3.3). For 8-year old slash pine material consisting of 139 families at six different sites, Li et al. (2007) found high narrow-sense heritabilities (0.42) for squared acoustic velocity, and Kumar et al. (2002) reported high narrow-sense heritability values for acoustic velocity in a material of 12 year-old *Pinus radiata* families. In a Douglas-fir material, individual narrow-sense heritabilities were reported to range from 0.24 to 0.40 (Jayawickrama et al. 2011). There could be issues when interpreting heritability estimates based on data from tools such as TreeSonic since the measurements should mainly be reflecting the outermost year rings. This concern was raised by Jayawickrama et al. (2011), but the authors did not observe any indications of lower heritabilities when comparing numbers from older trees with younger trees that had been included in their study material.

It could also be a question of the degree of age-age correlations for MOE or its surrogate trait acoustic velocity. For radiata pine, using SilviScan estimated MOE, Dungey et al. (2006) and Kumar et al. (2006) found high heritability values of rings rather close to the pith, but a decrease then followed when moving towards the bark. However, this pattern was not as obvious in the radiata pine study by Wu et al. (2007) or in the Norway spruce clonal material investigated by Gräns et al. (2009).

Family by treatment interaction effects were very low and non-significant for squared acoustic velocity (Table 3.3). There are no comparable studies where acoustic velocity has been evaluated for a large number of families and for a wide range of silvicultural treatments. In a study of full-sib families in different management intensity, Roth et al. (2007) reported

mixed results regarding squared acoustic velocity for a limited number (seven) families. Some families interacted, as an example one family was very sensitive to treatment changes while another family was very stable. Li et al. (2007) reported that family rankings for squared acoustic velocity were “moderately repeatable” with type B genetic correlation of 0.68 across six sites for 139 slash pine families, and Cherry et al. (2008) found no significant family x site interactions for acoustic velocity when measuring a large number of families of coastal Douglas-fir.

There was one close to significant genetic correlation between squared acoustic velocity and whole core density, and a significant genetic correlation between squared acoustic velocity and ring 7-16 core section density (Table 3.4). Genetic correlations were somewhat higher than phenotypic correlations. Eckard et al. (2010) reported low correlations between acoustic velocity and wood density in a 8-year old loblolly pine trial. For radiata pine, Chauhan & Walker (2006) also found poor association between the traits, but they also found that the correlation improved somewhat with age. Cherry et al. (2008) reported weak correlations between velocity and density in Douglas-fir. The correlations in this material were higher between the ring 7-16 wood core section density and squared velocity than for the whole core density and squared velocity. There are indications suggesting that for variations in outer wood stiffness, MFA is not quite as closely associated with stiffness as it is in corewood, and therefore density should become more important determining outerwood stiffness (Cown et al. 1999).

There were no significant correlations between wood quality traits and growth traits except between squared acoustic velocity and height and squared acoustic velocity and forking defect (Tables 3.5-3.6). Li et al. (2007) also reported low but positive correlations between height and acoustic velocity in slash pine. They hypothesized that it had a connection with greater elongation of the tracheids (Li et al. 2007), and this appears to be a reasonable explanation for our study as well. Cherry et al. (2008) reported weak, non-significant height vs. velocity correlations for their Douglas-fir material.

### *Wood density*

For all traits, the majority of the treatment combination means were significantly different (Table 3.1). The pooled mean across all treatment combinations and families was 457 kg/m<sup>3</sup>, which is a typical value for loblolly pine at age 16 years (Bowyer et al. 2003). The pooled average ring width curve (Figure 3.4) had a shape somewhat opposite to the overall density curve (Figure 3.1), and the radial development of ring width plotted by treatment combination (Figure 3.5) showed that the most intensive treatments (fertilization as well as fertilization plus herbicides) initially displayed considerably wider year rings compared to the control plots and the herbicide only plots. This corresponds to the differences in stem diameter development and the resulting individual tree volume differences between treatment combinations discussed in Chapter 2.

The decrease in whole core density was somewhat lower than reported by for example Clark et al. (2004) who found that annual fertilization only or combined with herbicides reduced

stem specific gravity by 6 to 10 percent compared to the control plots. In our trial, treatments had not been applied annually, and there were also a number of years since the last application, so the fertilizer and herbicide treatment effects on whole core density had probably diminished somewhat (See Figure 3.2). Previous research has indicated that reductions in breast height specific gravity between 5 and 10% could be expected after adding 200-400 kg/ha of nitrogen to a loblolly pine stand, if the trees are not too young (in that case a smaller effect could be expected), and the effect usually last for a number of years (Megraw et al. 1985). Also Love-Myers et al. (2010) reported significant fertilization effects (reduced density) on whole core, juvenile section and mature section density. For herbaceous weed control plots, Antony et al. (2011) reported a significant reduction in whole disc specific gravity and even though no change in juvenile period was found, the diameter of the juvenile core increased.

Megraw (1985) discussed the mechanisms behind the temporary decrease in density after fertilization, mentioning lower latewood percentage as well as more complicated shifts within the density profile of each year ring, resulting in lower maximum ring density. In a loblolly pine trial, Love-Myers (2010) found reductions in latewood percentage due to fertilization. Earlier studies such as the one by Mora (2003) also indicated potential changes in transition age when trees were subjected to different treatments.

Individual-tree heritability values were moderate to high for wood density, ranging from 0.28 for the ring 2-6 core section to 0.78 for the ring 7-16 core section and the range in values for

family mean heritability was from 0.86 to 0.95 (Table 3.3). High numbers were expected for these kinds of wood quality traits which have been studied extensively previously (Megraw 1985; Zobel & Jett 1995). It has also been shown before in loblolly pine that heritability values for density can vary between different groups of year rings (Belonger 1998).

The interaction effects for wood density between family and treatment combination were very low and non-significant in this material (Table 3.3), and family rankings were generally stable across treatments (Figures 3.7-3.9). There are few studies to compare with regarding the interactions between genetics and fertilization and /or weed control treatments for wood density. Often low and non-significant effects have been reported for southern pines (Schmidting 1973; Rockwood et al. 1985). Jokela et al. (2004) found different patterns in the specific gravity variation, but the authors thought the results were confounded by climate and different genetics at different sites. Jett et al. (1991) found some interacting families for specific gravity in different geographic areas but did not look at trials with contrasting treatments.

The genetic correlation between ring 2-6 core section density and ring 7-16 core section density (Table 3.4) was rather high (0.75) and significant ( $p < .001$ ). The phenotypic correlations (Table 3.4) were in some cases somewhat lower than the genetic correlations as could be expected. High age-age correlations would be favourable for early selection. Ring 2-6 section wood density was weakly (-0.29) negatively genetically correlated with volume (Table 3.6). Also Belonger (1998) reported a negative genetic correlation of -0.31 between

volume and wood density based on four trials of 12 year-old loblolly pine from 49 open-pollinated families from different provenances. Williams & Megraw (1993) reported a somewhat positive correlation between height and specific gravity in loblolly pine however. No phenotypic correlations between growth, form, and stem quality traits versus wood density were found in this material (Table 3.5). It would have been interesting to expand the study and look at variation in wood density at different levels along the stem. It is important to keep in mind that wood properties vary considerably within a tree from pith to bark and at different heights along the stem (Megraw 1985; Burdon et al. 2004; Jayawickrama et al. 2009). When making assumptions about whole stem properties based only on breast-height increment cores, there are few studies to rely on. However, Aspinwall et al. (2010) found favourable correlations between wood density values for wood cores taken at breast height and whole-stem wood density in a recent study on loblolly pine.

#### *Conclusions and practical implications*

There were large and significant family effects and treatment combination differences for the wood quality traits in this study, but there were no significant silviculture by genetics interactions found; family rankings were quite stable across cultural regimes. Therefore, for similar stands, with similar genetic material and subjected to the same kinds of treatments, there should generally not be any value improvement from matching silvicultural treatments to specific half-sib families. The risk of affecting wood quality in a negative way through intensive silviculture should not be overlooked. Wood density is important for yield and product quality (Zobel & Jett 1995; Bowyer et al. 2003), and even small changes in this trait



could have large impacts. Also, the overall degree of uniformity of the wood within the tree is an important characteristic (Zobel & Sprague 1998; Gartner et al. 2005), which could also be at least partly manipulated using silviculture and genetics. Treatment means for squared acoustic velocity ranged between 14.5 km<sup>2</sup>/s<sup>2</sup> and 16.4 km<sup>2</sup>/s<sup>2</sup>, while family means for the same trait varied from 13.8 km<sup>2</sup>/s<sup>2</sup> to 16.8 km<sup>2</sup>/s<sup>2</sup> when pooled across treatments. Significant increases in wood stiffness could be expected when applying certain treatments to the best families.

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## TABLES

**Table 3.1.** Overall means and treatment combination means for wood quality traits. Different letters in a column indicate significant differences between treatment combination means at the  $p \leq 0.05$  level.

Treatment combination	Velocity <sup>2</sup> (km <sup>2</sup> /s <sup>2</sup> )	Whole core dens. (kg/m <sup>3</sup> )	Ring 2-6 dens. (kg/m <sup>3</sup> )	Ring 7-16 dens. (kg/m <sup>3</sup> )
Control	14.7 <b>c</b>	464.6 <b>a</b>	445.2 <b>a</b>	570.1 <b>b</b>
Herbicides	16.4 <b>a</b>	459.8 <b>a</b>	442.3 <b>ab</b>	589.5 <b>a</b>
Fertilization	14.5 <b>c</b>	453.8 <b>b</b>	437.4 <b>bc</b>	537.9 <b>d</b>
Fert.+ Herb.	15.7 <b>b</b>	450.0 <b>b</b>	435.4 <b>c</b>	552.2 <b>c</b>
Overall mean*	15.3 (2.8)	456.5 (33.5)	439.7 (32.8)	561.4 (48.3)

\*Standard errors (SE) for overall means are given within parenthesis.

**Table 3.2.** F-values and probabilities of F-tests for block, silvicultural treatment effects, and their interactions for wood quality traits\*.

Source	Velocity <sup>2</sup>		Whole core dens		Ring 2-6 dens.		Ring 7-16 dens.	
	F	Pr>F	F	Pr>F	F	Pr>F	F	Pr>F
Block	12.0	<b>0.0004</b>	1.5	0.2550	0.7	0.6059	4.6	<b>0.0178</b>
Treatment	15.1	<b>0.0002</b>	3.6	<b>0.0474</b>	1.4	0.2786	27.7	<b>&lt;.0001</b>
Block x Treatment	5.0	<b>&lt;.0001</b>	4.6	<b>&lt;.0001</b>	5.4	<b>&lt;.0001</b>	5.2	<b>&lt;.0001</b>

\*Probabilities of  $\leq 0.05$  were considered significant. The degrees of freedom for Block, Treatment, and Block x Treatment were 4, 3, and 12 respectively. The degrees of freedom for Residual ranged from 2039 (Ring 7-16 section dens.) to 2092 (Velocity<sup>2</sup>).

**Table 3.3.** Variance components for family, family by treatment (FT), family by block (FB) and residual (Error), individual-tree ( $h^2_i$ ), and family mean ( $h^2_f$ ) heritability values for different wood quality traits. The t-value in the table is the ratio of the family variance component and its standard error. Percent (%) variance explained by family effect in the total variance is also included. Standard errors (SE) associated with family variance and heritabilities are reported.

Trait	Family (SE)	t	%	FT*	FB*	Error	$h^2_i$ (SE)	$h^2_f$ (SE)
Velocity <sup>2</sup>	0.66 (0.22)	2.98	10.3	0.58E-06	0.36E-01	5.81	0.41 (0.12)	0.90 (0.03)
Whole core dens.	85.3 (29.4)	2.90	8.0	0.16E-03	0.99E-04	975.7	0.32 (0.10)	0.88 (0.04)
Ring 2-6 section dens.	72.8 (25.5)	2.85	7.0	0.96E-04	0.96E-04	951.2	0.28 (0.09)	0.86 (0.04)
Ring 7-16 section dens.	377.4 (117.6)	3.18	19.6	15.2	2.22	1533.7	0.78 (0.20)	0.95 (0.02)

\* No family by treatment or family by replication interaction was significant based on Log Likelihood ratio tests.

**Table 3.4.** Pearson product-moment correlation coefficients based on phenotypic family means (above diagonal) and genetic correlations based on family BLUP values (below diagonal) pooled across treatments for different wood quality traits\*. Probability values of correlation coefficients (H0: r=0) were also reported. Probabilities of  $\leq 0.05$  were considered significant.

	Velocity <sup>2</sup>	Whole core dens.	Ring 2-6 dens.	Ring 7-16 dens.
Velocity <sup>2</sup>	-	0.23 (.274)	0.07 (.739)	<b>0.44 (.028)</b>
Whole core dens.	<b>0.27 (.051)</b>	-	<b>0.97 (&lt;.001)</b>	<b>0.84 (&lt;.001)</b>
Ring 2-6 dens.	0.11 (.419)	<b>0.97 (&lt;.001)</b>	-	<b>0.74 (&lt;.001)</b>
Ring 7-16 dens.	<b>0.49 (&lt;.001)</b>	<b>0.84 (&lt;.001)</b>	<b>0.75 (&lt;.001)</b>	-

\*For the Pearson product moment phenotypic correlations based on family means the sample size (# of families) was 25. Sample size for genetic correlation coefficients was 54.

**Table 3.5.** Pearson product-moment phenotypic correlation coefficients based on family means pooled across treatments for different wood quality traits\*. Probability values of correlation coefficients (H0: r=0) were also reported. Probabilities of  $\leq 0.05$  were considered significant.

	Velocity <sup>2</sup>	Whole core dens.	Ring 2-6 dens.	Ring 7-16 dens.
Height	<b>0.53 (.006)</b>	0.03 (.889)	-0.16 (.443)	0.06 (.780)
Volume	0.25 (.235)	-0.09 (.678)	-0.27 (.120)	-0.07 (.757)
Sweep	-0.09 (.679)	0.20 (.347)	0.23 (.263)	0.16 (.459)
Branch angle	-0.23 (.274)	-0.14 (.500)	-0.11 (.617)	-0.20 (.341)
Forking defect**	<b>0.39 (.052)</b>	0.14 (.519)	0.07 (.743)	0.25 (.221)
Rust	-0.06 (.783)	0.23 (.270)	0.21 (.311)	0.23 (.279)

\*For the Pearson product-moment phenotypic correlations based on family means the sample size was 25. \*\*Forking defect is a combination of forking and ramicorn branching.

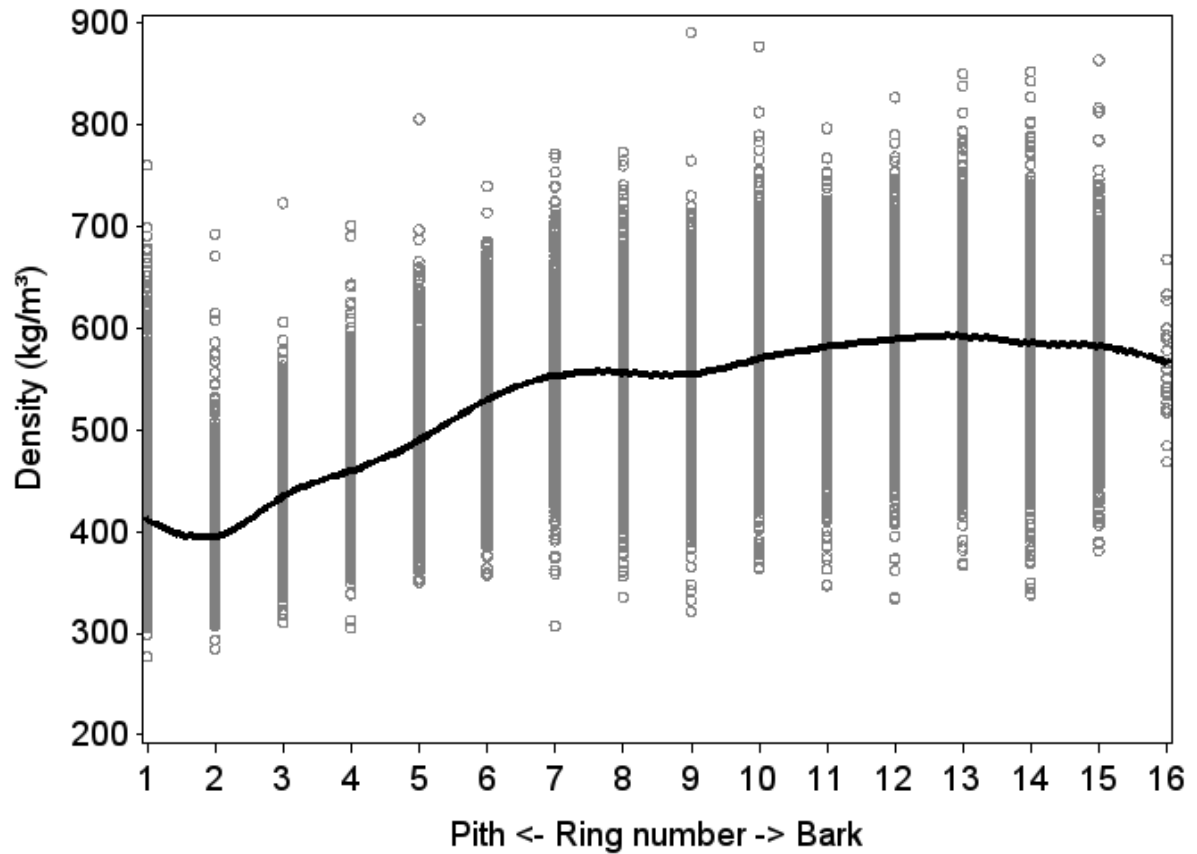
**Table 3.6.** Genetic correlations based on family BLUP values pooled across treatments for different growth, form, stem quality, and wood quality traits\*. Probability values of correlation coefficients (H0: r=0) were also reported. Probabilities of  $\leq 0.05$  were considered significant.

	Velocity <sup>2</sup>	Whole core dens.	Ring 2-6 dens.	Ring 7-16 dens.
Height	<b>0.46 (&lt;.001)</b>	-0.02 (.908)	-0.20 (.142)	0.00 (.987)
Volume	0.20 (.145)	-0.12 (.381)	<b>-0.29 (.031)</b>	-0.12 (.384)
Sweep	-0.03 (.812)	0.20 (.139)	0.24 (.083)	0.15 (.283)
Branch angle	-0.25 (.073)	-0.18 (.203)	-0.14 (.306)	-0.24 (.075)
Forking defect**	<b>0.40 (.003)</b>	0.20 (.158)	0.14 (.325)	0.26 (.057)
Rust	-0.04 (.768)	0.18 (.206)	0.16 (.253)	0.16 (.249)

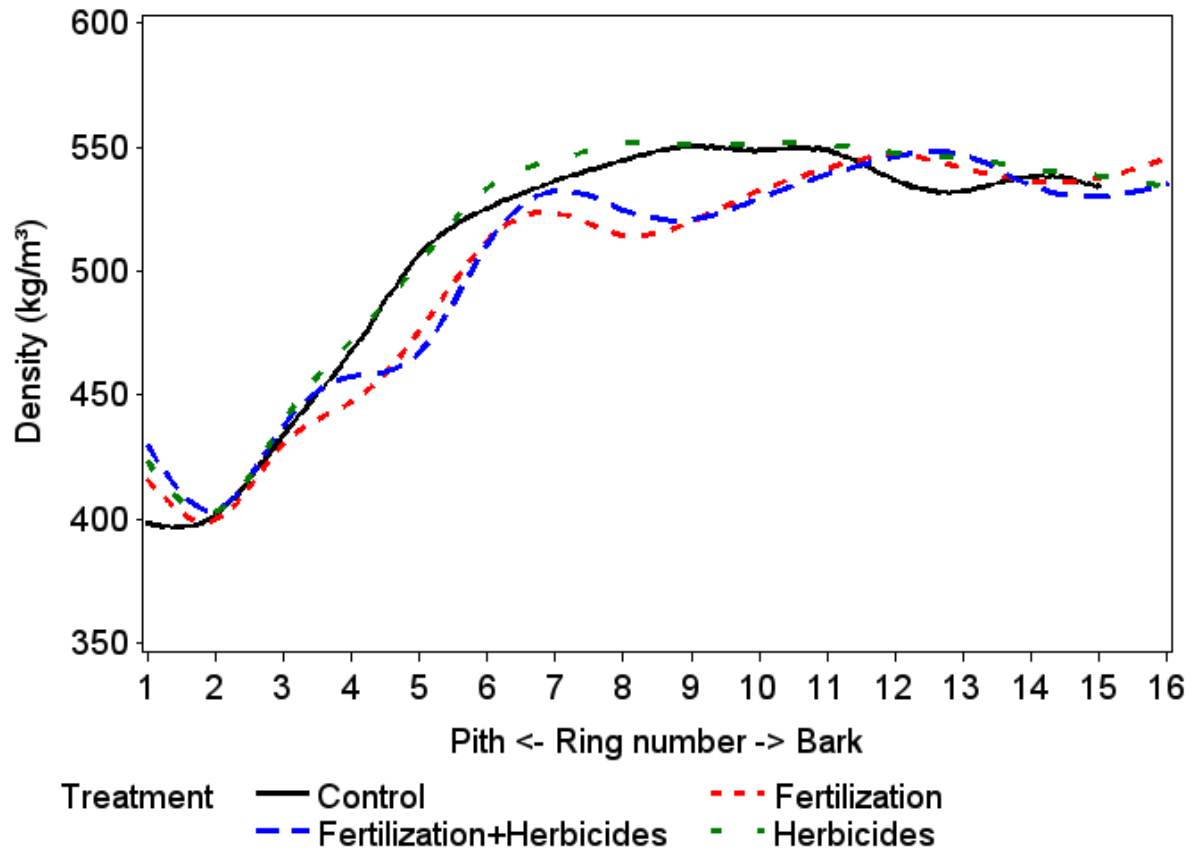
\* Sample size (# of families) for genetic correlation coefficients was 54. \*\*Forking defect is a combination of forking and ramicorn branching.



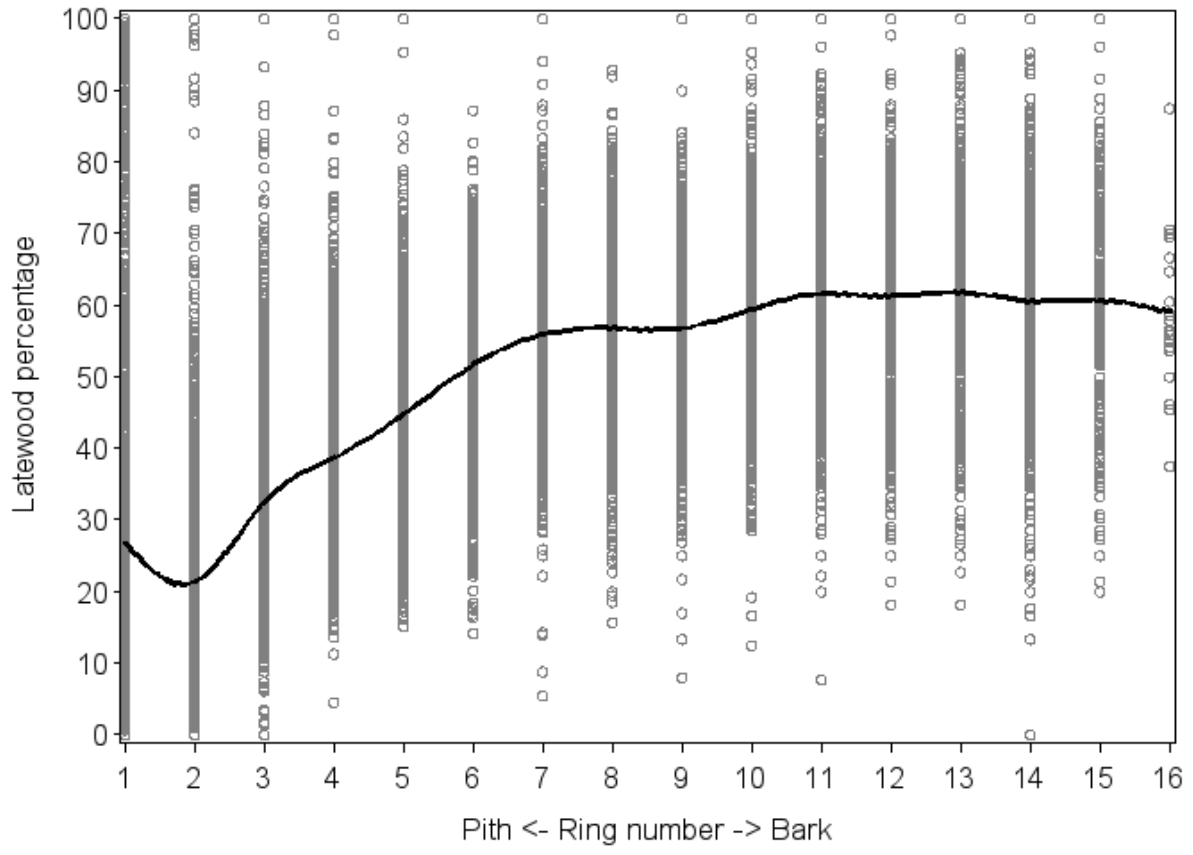
## FIGURES



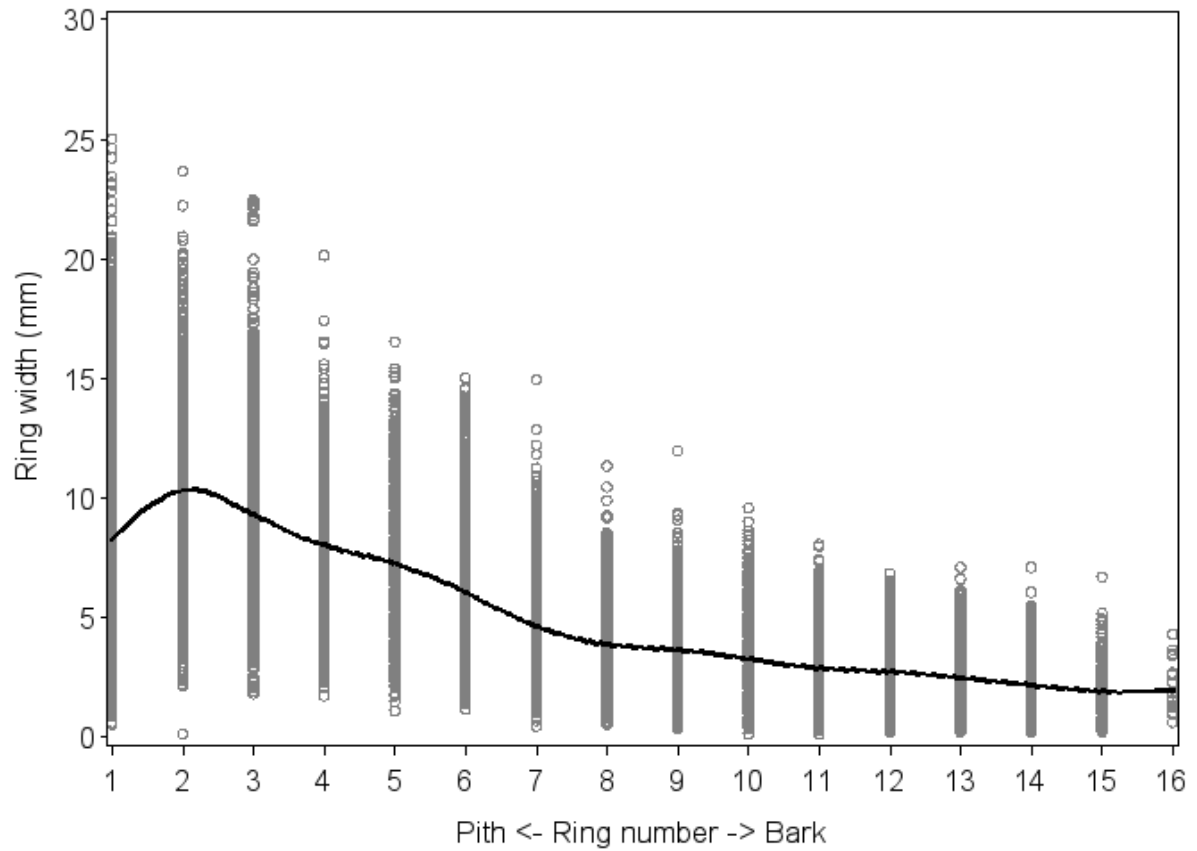
**Figure 3.1.** Average density ( $\text{kg/m}^3$ ) by year ring number pooled across the four different treatment combinations. Individual observations are symbolized by circles, and the overall mean is represented by a line.



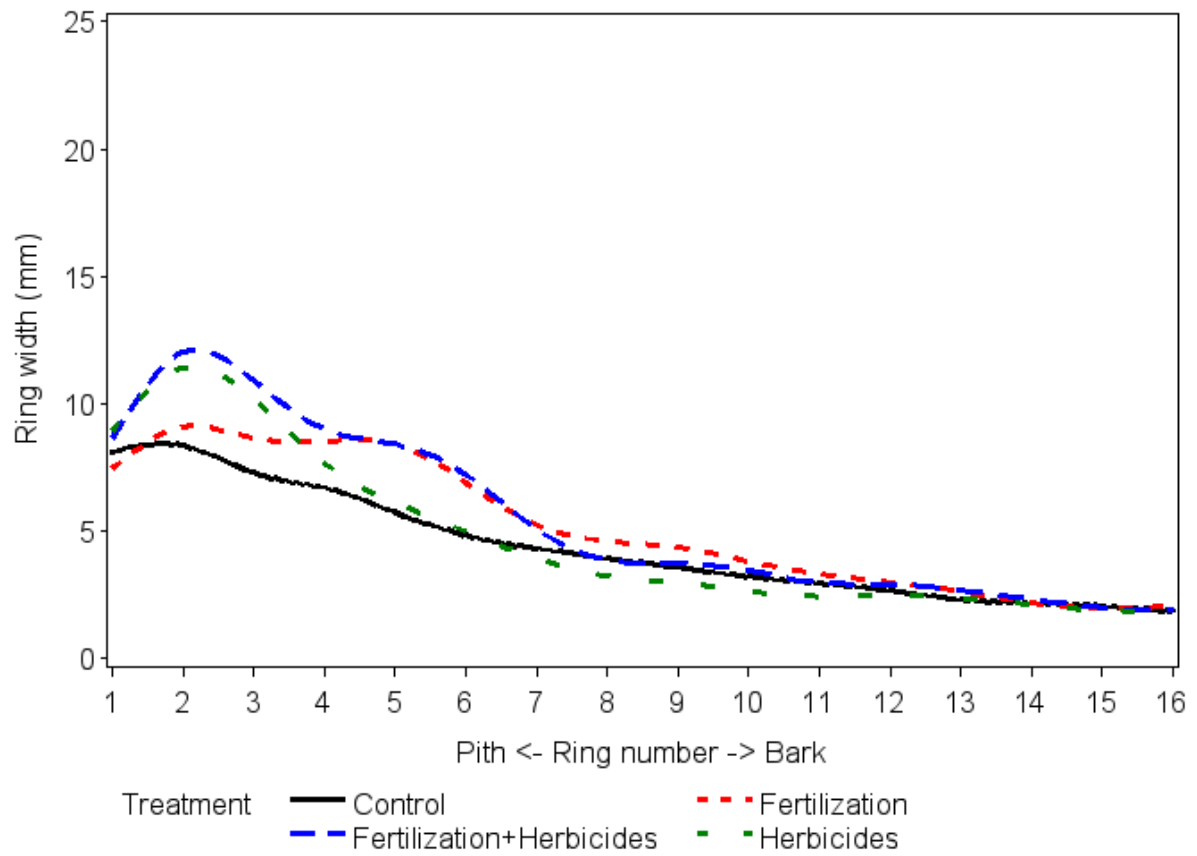
**Figure 3.2.** Average density ( $\text{kg/m}^3$ ) by year ring number for the four different treatment combinations (represented by four different lines).



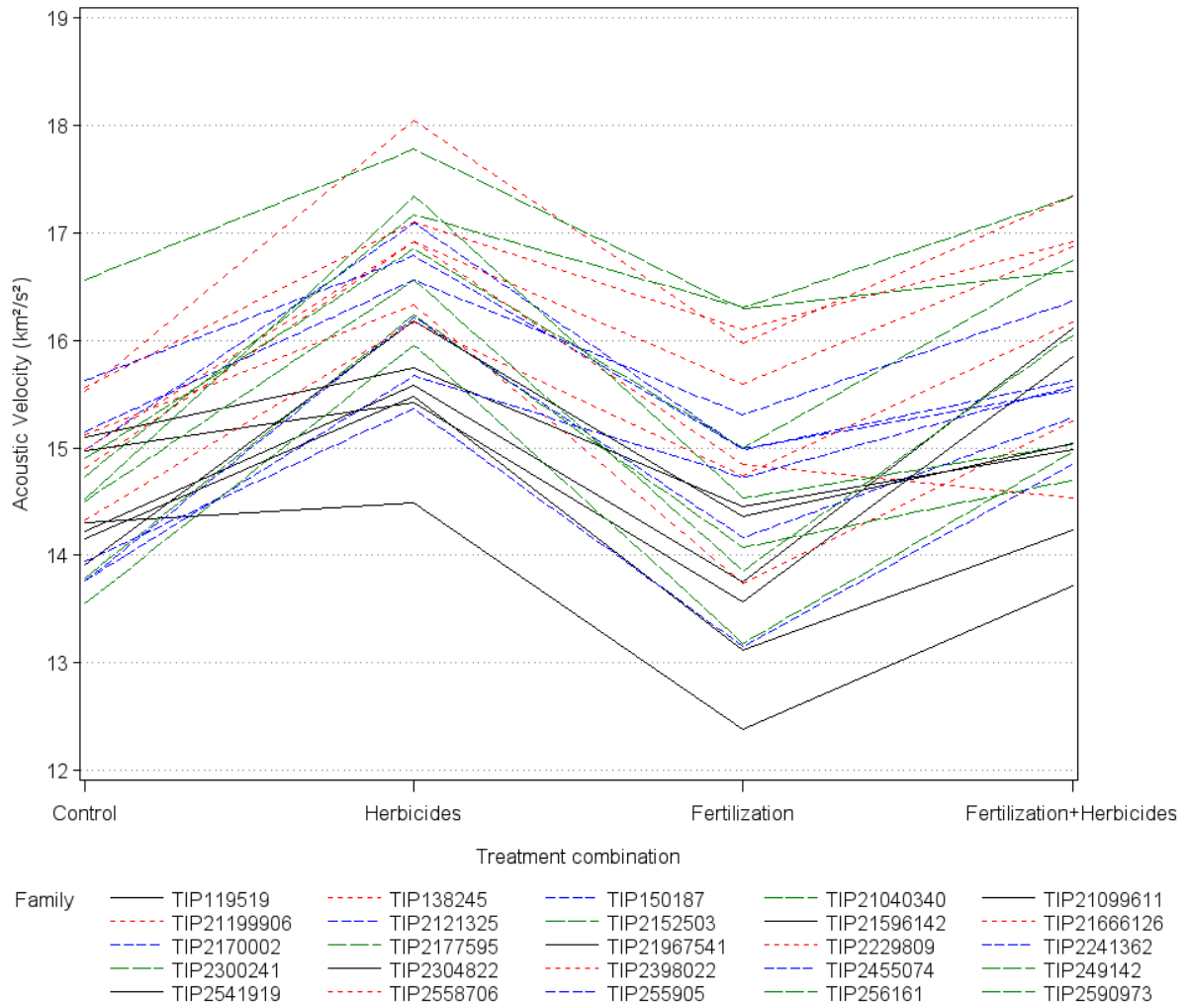
**Figure 3.3.** Average latewood percentage by year ring number pooled across the four different treatment combinations. Individual observations are symbolized by circles and the overall mean is represented by a line.



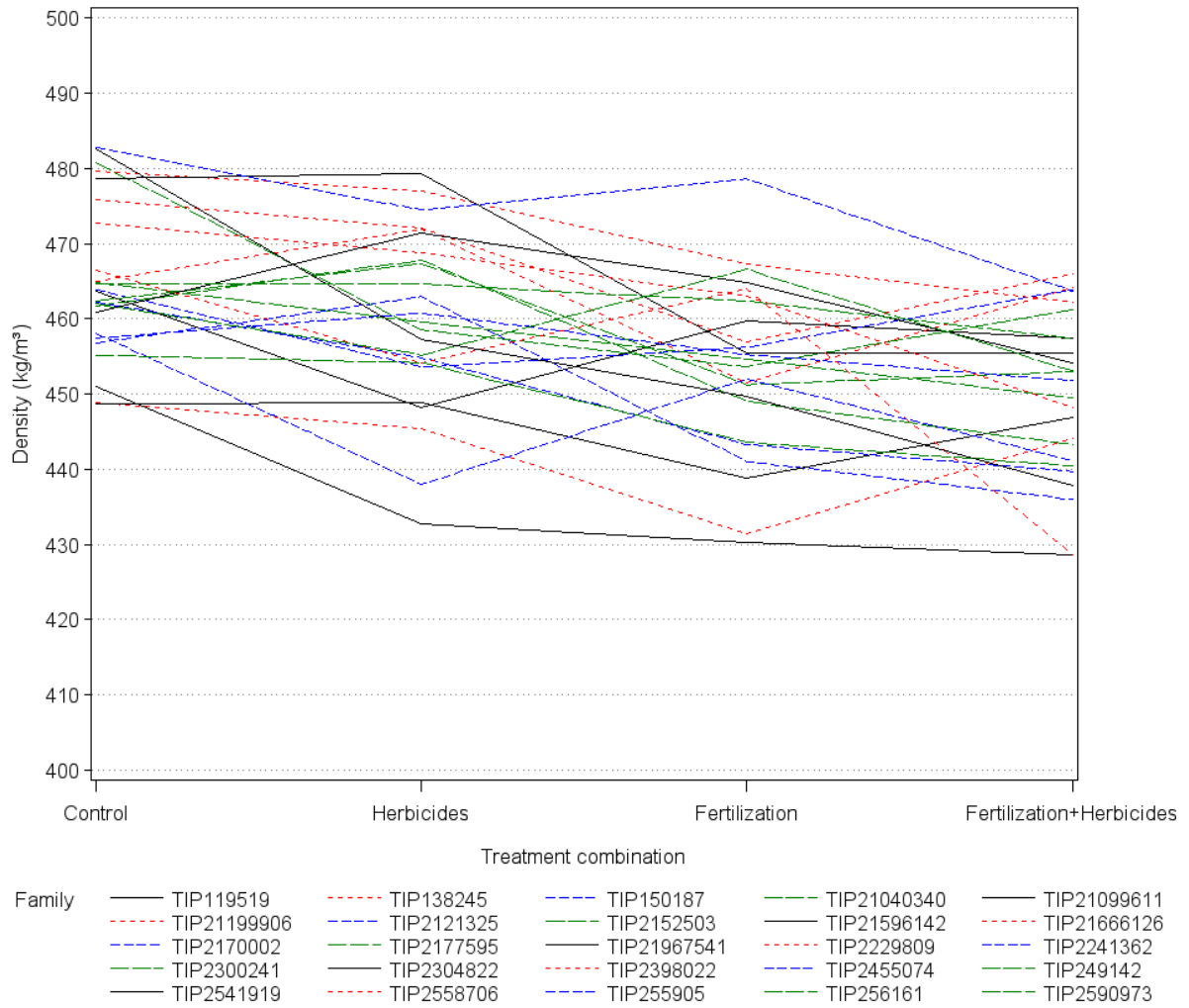
**Figure 3.4.** Average ring width (mm) by year ring number pooled across the four different treatment combinations. Individual observations are symbolized by circles and the overall mean is represented by a line.



**Figure 3.5.** Average ring width (mm) by year ring number for the four different treatment combinations (represented by four different lines).

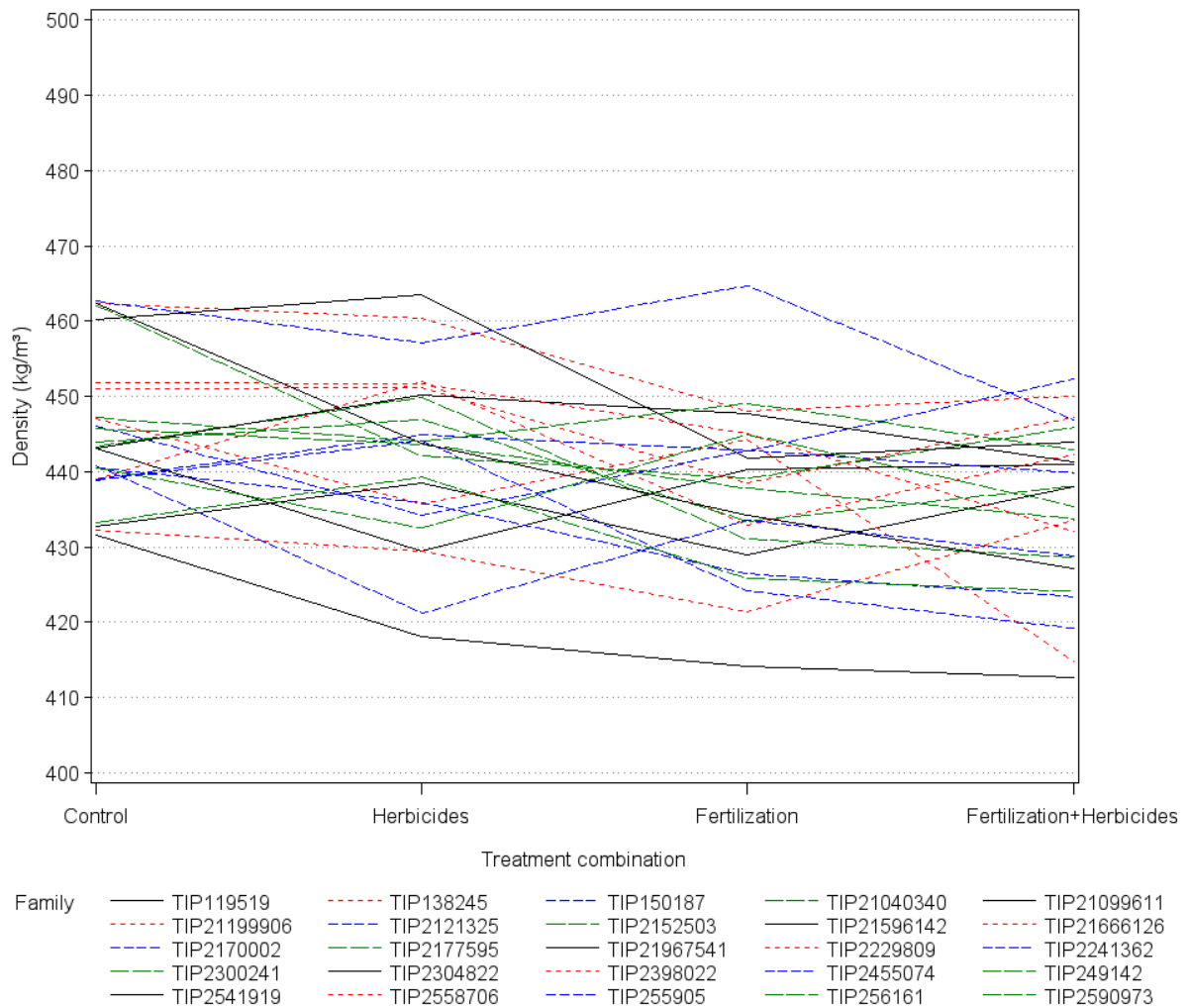


**Figure 3.6.** Family means for squared acoustic velocity ( $\text{km}^2/\text{s}^2$ ) in different treatment combinations.

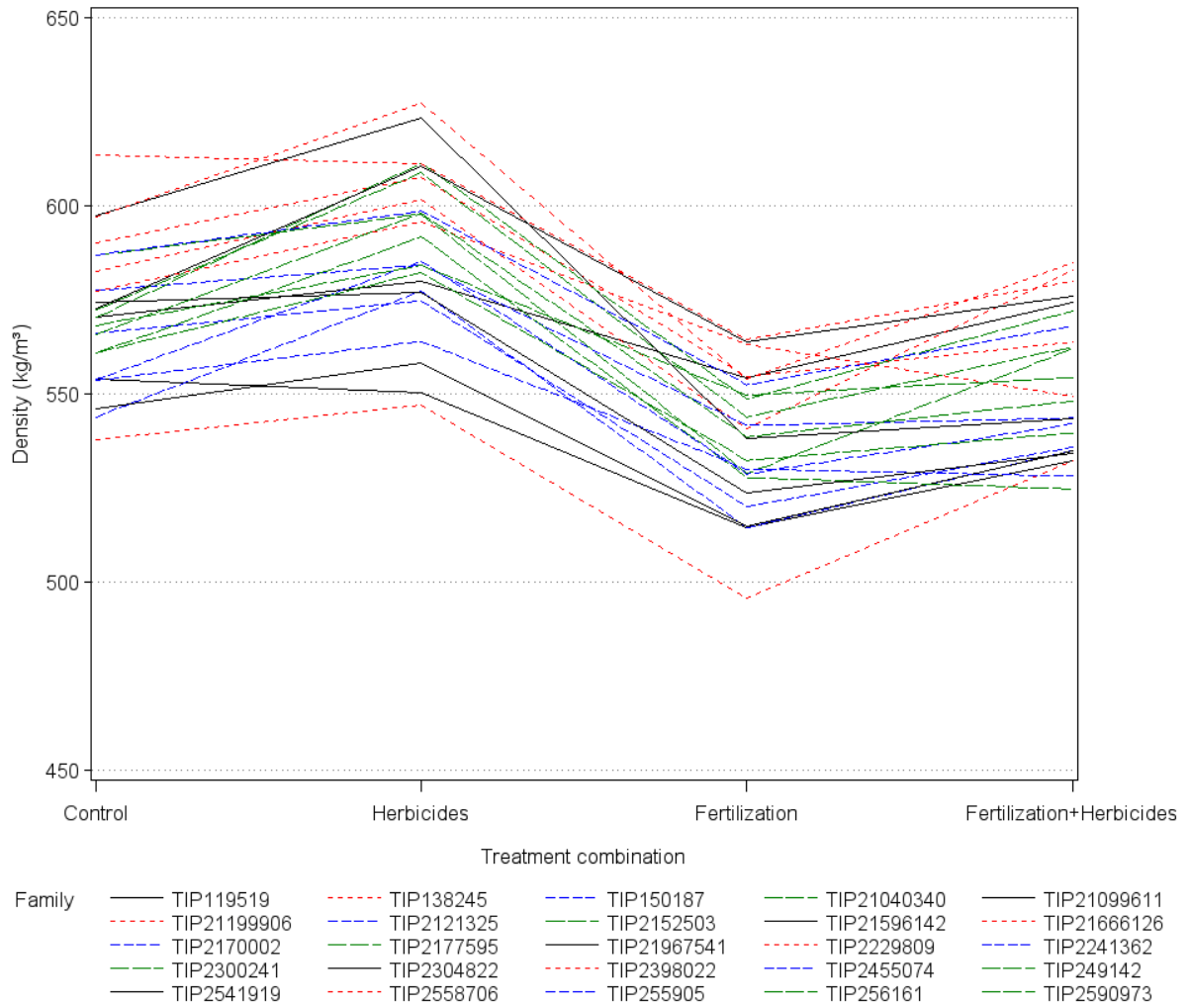


**Figure 3.7.** Family means for area-weighted whole core density (kg/m<sup>3</sup>) in different treatment combinations sampled at breast height.





**Figure 3.8.** Family means for area-weighted wood density ( $\text{kg/m}^3$ ) for the core section consisting of year rings 2-6 from the pith sampled at breast height in different treatment combinations.



**Figure 3.9.** Family means for area-weighted wood density ( $\text{kg/m}^3$ ) for the core section consisting of year rings 7-16 from the pith sampled at breast height in different treatment combinations.

## APPENDICES

**Appendix 3.1.** Ancestry table including a list of families used in the trial and relationships between parents and grandparents. Families that appear more than once are marked with an\*.

OP Family (coded ID)	Selection cycle	ID Parent 1 (coded ID)	ID Parent 2 (coded ID)
TIP2300241	Second	TIP1174558	TIP1159174
TIP119519*	First	Unknown	Unknown
TIP138245*	First	Unknown	Unknown
TIP150187*	First	Unknown	Unknown
TIP2170002	Second	TIP138245*	TIP1389204*
TIP2590973	Second	TIP1440382*	TIP1389204*
TIP2398022	Second	TIP1487936	TIP119519*
TIP21040340	Second	TIP11038493	TIP1857822
TIP21666126	Second	TIP1879215	TIP1440382*
TIP256161	Second	TIP150484	TIP1609597*
TIP255905	Second	TIP157854	TIP1440382*
TIP2121325	Second	TIP138245*	TIP1609597*
TIP2177595	Second	TIP150187*	TIP119519*
TIP249142	Second	TIP181745	TIP119519*
TIP2558706	Second	TIP143184	TIP1672933
TIP21199906	Second	TIP11563990*	TIP1218280*
TIP21967541	Second	TIP1685530	TIP1218280*
TIP21596142	Second	TIP166526	TIP1158645
TIP2152503	Second	TIP189053	TIP1218280*
TIP2304822	Second	TIP1321927	TIP11563990*
TIP2455074	Second	TIP170699	TIP176296
TIP2541919	Second	TIP1536913	TIP1213202
TIP21099611	Second	TIP1587442	TIP1136373
TIP2229809	Second	TIP138245*	TIP1243915*
TIP2241362	Second	TIP1243277	TIP1243915*

**Appendix 3.2.** Pooled means across treatment combinations for squared acoustic velocity, area-weighted wood quality traits, average ring width, and number of year rings per tree.

Standard errors of means are within parentheses, N=number of observations

Family	Velocity <sup>2</sup> (km <sup>2</sup> /s <sup>2</sup> )	Whole core dens. (kg/m <sup>3</sup> )	Ring 2-6 dens. (kg/m <sup>3</sup> )	Ring 7-16 dens. (kg/m <sup>3</sup> )	Whole core average ring width (mm)	Average number of year rings per tree
TIP119519	14.95 (2.97) N=92	457.1 (31.79) N=92	438.4 (30.49) N=92	569.6 (38.64) N=92	5.60 (1.28) N=92	13.72 (1.73) N=92
TIP138245	16.21 (2.35) N=90	462.7 (33.91) N=88	441.6 (34.45) N=88	575.96 (45.04) N=88	5.81 (2.30) N=88	14.00 (1.21) N=88
TIP150187	15.72 (2.53) N=90	459.1 (32.44) N=86	443.6 (33.41) N=86	561.1 (46.72) N=86	5.11 (1.16) N=86	13.74 (1.31) N=86
TIP21040340	15.90 (2.96) N=76	457.93 (33.11) N=74	440.16 (33.21) N=74	570.26 (48.21) N=73	5.28 (1.08) N=74	13.62 (1.31) N=74
TIP21099611	14.95 (2.55) N=85	435.78 (27.99) N=84	419.21 (26.43) N=84	537.97 (39.26) N=84	4.98 (1.14) N=84	13.60 (1.26) N=84
TIP21199906	15.09 (3.13) N=82	441.83 (31.62) N=81	428.71 (30.72) N=81	527.06 (45.41) N=81	5.07 (1.06) N=81	13.60 (1.45) N=81
TIP2121325	15.64 (2.28) N=86	446.86 (30.78) N=85	429.43 (30.65) N=85	538.92 (43.65) N=85	5.48 (1.25) N=85	13.80 (1.32) N=85
TIP2152503	14.73 (2.78) N=77	462.32 (34.43) N=74	446.24 (33.26) N=74	567.38 (55.84) N=74	5.24 (1.17) N=74	13.69 (1.33) N=74
TIP21596142	13.76 (2.96) N=83	446.06 (26.36) N=82	434.81 (25.58) N=82	539.19 (34.09) N=80	4.69 (0.96) N=82	13.13 (1.54) N=82
TIP21666126	15.32 (2.98) N=91	470.93 (35.96) N=89	454.53 (35.32) N=89	577.27 (48.44) N=89	4.62 (1.14) N=89	13.43 (1.57) N=89
TIP2170002	14.85 (2.59) N=87	449.54 (36.37) N=87	431.21 (34.71) N=87	547.9 (53.06) N=87	5.81 (1.28) N=87	13.76 (1.23) N=87
TIP2177595	15.46 (2.63) N=92	455.00 (30.53) N=91	437.85 (30.71) N=91	550.75 (47.65) N=91	5.48 (1.33) N=91	13.84 (1.19) N=91
TIP21967541	14.18 (3.17) N=79	465.77 (31.54) N=78	451.17 (29.46) N=78	571.28 (52.83) N=77	4.82 (1.10) N=78	13.44 (1.48) N=78

**Appendix 3.2. (continued).** Pooled means across treatment combinations for squared

acoustic velocity, area-weighted wood quality traits, average ring width, and number of year rings per tree. Standard errors of within parentheses, N=number of observations.

Family	Velocity <sup>2</sup> (km <sup>2</sup> /s <sup>2</sup> )	Whole core density (kg/m <sup>3</sup> )	Ring 2-6 dens. (kg/m <sup>3</sup> )	Ring 7-16 dens. (kg/m <sup>3</sup> )	Whole core average ring width (mm)	Average number of year rings per tree
TIP2229809	16.71 (2.00) N=81	466.84 (31.86) N=80	446.28 (29.08) N=80	589.10 (48.39) N=80	5.09 (1.09) N=80	13.83 (1.13) N=80
TIP2241362	14.31 (2.62) N=85	456.31 (37.12) N=82	441.82 (36.78) N=82	552.02 (50.74) N=82	4.92 (1.11) N=82	13.54 (1.29) N=82
TIP2300241	16.82 (2.37) N=79	457.18 (26.10) N=77	440.29 (26.02) N=77	575.24 (45.02) N=77	4.60 (1.03) N=77	13.62 (1.26) N=77
TIP2304822	14.94 (2.59) N=80	463.03 (30.13) N=78	445.86 (28.79) N=78	581.46 (44.05) N=77	4.62 (0.90) N=78	13.54 (1.50) N=78
TIP2398022	15.37 (2.58) N=80	452.08 (35.45) N=77	434.41 (34.10) N=77	569.46 (42.51) N=77	4.96 (0.10) N=77	13.75 (1.29) N=77
TIP2455074	15.85 (2.19) N=83	447.02 (31.24) N=80	430.68 (29.44) N=80	544.03 (39.28) N=80	5.42 (0.89) N=80	13.94 (1.12) N=80
TIP249142	16.62 (2.27) N=78	458.41 (29.84) N=76	437.77 (29.52) N=76	563.91 (41.50) N=76	5.62 (1.28) N=76	13.96 (0.81) N=76
TIP2541919	15.05 (3.07) N=76	454.26 (35.33) N=74	439.78 (33.78) N=74	549.42 (48.19) N=74	4.71 (1.09) N=74	13.57 (1.41) N=74
TIP2558706	16.52 (2.56) N=78	461.38 (32.94) N=76	443.73 (31.35) N=76	587.64 (41.57) N=75	5.01 (1.05) N=76	13.62 (1.64) N=76
TIP255905	15.04 (2.79) N=94	474.23 (37.51) N=91	457.46 (38.09) N=91	575.51 (42.09) N=90	5.10 (1.11) N=91	13.52 (1.49) N=91
TIP256161	14.35 (2.92) N=83	448.19 (31.25) N=80	430.50 (30.72) N=80	552.88 (47.85) N=80	5.67 (1.27) N=80	13.76 (1.35) N=80
TIP2590973	15.30 (2.26) N=86	462.08 (32.53) N=85	445.63 (34.05) N=85	562.84 (46.82) N=85	5.11 (1.15) N=85	13.72 (1.24) N=85

### Appendix 3.3. Analysis of fertilization and herbicide main effects.

Main effects were analyzed separately for squared acoustic velocity, whole core density, ring 2-6 section density, and ring 7-16 section density, using a linear model:

$$Y_{ijkl} = \mu + B_i + N_j + W_k + NW_{jk} + BN_{ij} + BW_{ik} + BNW_{ijk} + e_{ijkl} \quad (\text{Eq. 3.7})$$

Where:

$Y_{ijkl}$  = the dependent variable (the observation of the  $l$ th tree of the  $k$ th herbicide treatment level of the  $j$ th fertilization level in the  $i$ th block)

$\mu$  = the overall mean

$B_i$  = the fixed effect of the  $i$ th block ( $i = 1, 2, \dots, 5$ )

$N_j$  = the fixed effect of the  $j$ th level of fertilization ( $j = 1, 2$ )

$W_k$  = the fixed effect of the  $k$ th level of herbicide treatment ( $k = 1, 2$ )

$NW_{jk}$  = the fixed interaction effect between the fertilizer and herbicide treatment

$BN_{ij}$  = the fixed interaction effect between block and fertilization

$BW_{ik}$  = the fixed interaction effect between block and herbicide treatment

$BNW_{ijk}$  = the fixed interaction effect between block, fertilization, and herbicide treatment

$e_{ijkl}$  = the random error, assumed to be independent and normally distributed with the expected mean zero and variance  $\sigma_e^2$ .

The GLM procedure of SAS Software (SAS Institute Inc. 2004-2008) was used to run the model and the RANDOM statement and the TEST option was used to get the correct F-tests.

Results are shown in Appendix 3.4. There was no significant fertilization by herbicides treatment interaction in the plots. Herbicide effects were significant on squared acoustic velocity ( $p=0.003$ ) and for the ring 7-16 core section density ( $p=0.051$ ) while significant fertilization effects were found for whole core density ( $p=0.007$ ) and ring 7-16 core section density ( $p<0.001$ ). Fertilization effects were close to significant for ring section 2-6 density ( $p=0.059$ ). The remaining traits displayed no significant effects at the  $p\leq 0.05$  level.



**Appendix 3.4.** Probability of F-tests for the treatment main effects and their interactions for investigated wood quality traits\*.

Source	Velocity <sup>2</sup>	Whole core dens.	Ring 2-6 dens.	Ring 7-16 dens.
Herbicides	<b>0.003</b>	0.311	0.557	<b>0.051</b>
Fertilization	0.402	<b>0.007</b>	0.059	<b>&lt;.001</b>
Fertilization x Herbicides	0.107	0.940	0.936	0.433

\*Fertilization, herbicides, and the interaction term had 1 DF. The denominator degrees of freedom were 4 for all the terms. P-values  $\leq 0.05$  were considered significant.