GENOTYPE X ENVIRONMENT INTERACTIONS IN SELECTED LOBLOLLY (*Pinus taeda* L.) AND SLASH PINE (*P. elliottii* Engelm. var. *elliotttii*) PLANTATIONS IN THE SOUTHEASTERN UNITED STATES.

By

BRIAN EDWARD ROTH

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
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Man always kills the thing he loves, ... and so we the pioneers have killed our wilderness. Some say we had to. Be that as it may, I am glad I shall never be young without wild country to be young in.

–Aldo Leopold, *A Sand County Almanac. 1949*

I'm truly sorry man's dominion,
Has broken nature's social union,

–Robert Burns, *To A Mouse, On Turning Her Up In Her Nest With The Plough*. 1785

What do we know?
How do we know it?
And how do we apply it?

–Congressman Greg Walden (R-OR), *Subcommittee on Forests and Forest Health Chairman*.
24th February 2006

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By

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Few studies have quantified the combined effects of silvicultural treatment, planting density, and genetic improvement in full-sib family blocks of loblolly (*Pinus taeda* L.) and slash pine (*P. elliottii* Engelm. var. *elliottii*). This information is critical for the proper deployment of improved genotypes of southern pine and ultimately how they respond to specific silvicultural treatments in a changing climate across a range of soils. This study employed a series of replicated factorial experiments and family block plantings in Florida and Georgia which manipulated gradients in planting density (1334 versus 2990 trees ha^{-1}), understory competition and soil nutrient availability.

Age-two loblolly pine accumulation and distribution of biomass and nitrogen were more responsive to treatment than slash pine. Total slash pine biomass accumulation varied from 4.7 to 11.6 Mg ha^{-1} with responses limited to the main effects of silviculture, density, and family. Loblolly pine total biomass accumulation varied from 8.6 to 15.5 Mg ha^{-1}, with several interactions: silviculture x density, silviculture x location, and family x density. Loblolly pine distribution of biomass was influenced by: family x density, family x silviculture and silviculture x density x location. Total nitrogen content ranged from 33.0 to 83.3 kg ha^{-1} and varied with silviculture, family and density x location for slash pine. Loblolly pine total N accumulation ranged from 23.3 to 101.5 kg ha^{-1} with two interactions: family x density and silviculture x density x location.

At age five, families varied in needlefall, leaf area index, fraction of light intercepted, light extinction coefficient, intercepted photosynthetically active radiation (IPAR) and radiation use efficiency (RUE). There were small differences among families in RUE (1.08 to 1.16 g MJ^{-1} PAR), although they were stable across locations.

Age five basal area and standing volume for both species demonstrated significant interactions: family x location, family x silviculture and silviculture x density. Family x silviculture interactions were positive and the best overall families responded the greatest to intensive silviculture. This research demonstrates that genotype x environment interactions exist in certain southern pine families. These results reinforce the need for understanding the biotic and abiotic mechanisms that drive these interactions.

CHAPTER 1
INTRODUCTION

Background

The southeastern United States contains some of the most intensively managed pine plantations in the world (Fox *et al.*, 2007). Considerable gains in the productivity of loblolly (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Englm. var. *elliottii*) plantations have been achieved over the past 30 years and these plantations now produce a wide range of ecosystem services, such as fiber, carbon sequestration, and biofuels. Growth responses to intensive silvicultural practices (Fox *et al.*, 2007) typically range from 2- to 3.5-fold for loblolly pine in the southeastern USA (Jokela *et al.*, 2004). While the absolute amount of biomass produced is important, so too is the distribution of biomass and nutrients to various components such as the foliage, branches, bark, bole, and belowground, particularly when new sources of bioenergy are concerned (Scott and Dean, 2006).

Demonstrated increases in unit area production have been realized through combinations of silvicultural treatments such as site preparation, fertilization, competition control, and density management (Colbert *et al.*, 1990; Albaugh *et al.*, 1998; Martin and Jokela, 2004b; Fox *et al.*, 2007). Preparation of the planting site prior to plantation establishment has demonstrated benefits on seedling survival in the short-term and stand growth and development in the long-term (Nilsson and Allen, 2003). On flatwood sites in the southeastern United States, site preparation treatments generally involve combinations of bedding and chemical control of competing vegetation. Collectively, these treatments have had a substantial effect on long-term growth responses (Jokela *et al.*, 2000; Zhao *et al.*, 2008). From a mechanistic perspective, post-planting management of associated vegetation has led to large gains in plantation productivity as site resources , such as soil moisture and nutrient supply is made available to the crop trees (Roth and Newton, 1996; Miller *et al.*, 2003). Competing vegetation can be controlled either mechanically or chemically and long-term gains in wood volume in southern pine plantations have ranged from 14 to 5840% (Wagner *et al.*, 2006).

Since the early 1970's, forest fertilization has been a common management practice throughout much of the southern United States. During the period from 1969 to 2004, over 6.5 million ha of southern pine stands were fertilized in the southeastern United States, mainly with nitrogen and phosphorus (Albaugh *et al.*, 2007). Fertilization treatments are aimed at meeting the nutrient demands of rapidly growing plantations on sites where inherent nutrient supplies are low (Comerford *et al.*, 2006). Nutrient availability is often adequate during the first few years following plantation establishment because of enhanced decomposition and mineralization of organic matter. However, by the time of crown closure, nutrients become limiting due to decreases in soil supplies and immobilization of nutrients in microbial biomass and woody vegetation, in addition to the increased demands of these rapidly growing trees. Loblolly pine tends to be more responsive to fertilization treatments than slash pine plantations (Jokela *et al.*, 2000).

Historically, southern pine plantations have been established at densities ranging from about 1500 to 2240 trees ha^{-1} and subsequently thinned to between 625 and 1000 trees ha^{-1} at around age 10 to 14 years. Recently, there has been a trend in the southeastern United States towards the establishment of plantations at lower densities with the goal of producing chip-n-saw or sawtimber without thinning (Huang and Kronrad, 2004). However, associated with these shifts in initial planting density, come implications for nutrient management (Barron-Gafford *et al.*, 2003), the efficiency of resource use (Will *et al.*, 2001), and the deployment of elite genotypes (Fang *et al.*, 1999).

Advances in tree breeding over the past 50 years have been focused on improving volume growth, disease resistance, tree form and wood quality (White *et al.*, 2007). Plantations established with first-generation seed developed by tree breeding programs have demonstrated 8 to 12% gains in unit area volume production at harvest age (Squillace, 1989). Gains in volume production due to the establishment of plantations with second-generation seed sources are estimated to be in the range of 10 to 30% over unimproved sources (Li and McKeand, 1989; McKeand *et al.*, 2003a). When a combination of elite genetic materials are combined with site-specific silvicultural treatments, mean annual increments of up to 20 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ have been documented (Allen *et al.*, 2005c). Most plantations in the Southeast are currently established using open pollinated, half-sib families; however, full-sib family blocks are becoming more common and deployment of clones via rooted cuttings or somatic plantlets are moving to become an operational reality (Sutton, 2002).

Problem

Genotypes may respond differentially to silvicultural treatments, locations and climatic conditions. This 'genotype x environment' interaction is more likely to occur given increasing levels of tree improvement (i.e. second-generation breeding cycles), the deployment of more uniform genotypes (i.e. full-sib families and clonal materials) (McKeand *et al.*, 2006), and especially when deployed in combinations of intensive silvicultural management (Roth *et al.*, 2007a). These genotype x environment interactions may be manifest as rank changes among genotypes when deployed across natural or man-made environmental gradients in resource availability, or as "scale effects" in which the absolute differences among genotypes change with environment (Knight, 1970).

Tree breeding programs have recognized that genotype x environment interactions are a possibility, which could dictate a need for site-specific breeding efforts (McKeand *et al.*, 1997b).

The general approach has been the deployment of a large number of genotypes across a wide range of sites, under fairly uniform silvicultural treatments aimed at minimizing within site variation. In this situation it is important to test how genotypes respond to environmental variation due to localized edaphic, climatic and disease conditions, since there is a desire to move genotypes long distances from their origins in order to increase yields (Lambeth *et al.*, 2005). Often these tests are evaluating the performance of progeny in single-tree plots and rarely has the field performance of these elite genotypes been verified using pure family block plantation trials (Vergara *et al.*, 2004; Dean, 2007).

Research studies aimed at quantifying the response of southern pines with the combined effects of silvicultural treatments and genetic improvement in loblolly and slash pine in pure-family block plantings are limited and documented genotype x silviculture interactions on stand level attributes have not always been evident. For example, in a 12-year-old loblolly pine family x vegetation control study in Georgia, no genotype x environment interaction was found for total standing volume (Martin and Shiver, 2002). Also, loblolly pine whole tree biomass at age five in a genotype x fertilization experiment in North Carolina did not demonstrate a significant interaction (Retzlaff *et al.*, 2001). However, in a 5-year-old loblolly pine experiment, families interacted with silviculture, planting density and location for basal area, unit area stem volume and aboveground biomass (Roth *et al.*, 2007a) and in the same trial there was a family x density interaction for wood quality traits (Roth *et al.*, 2007b).

The current research effort is driven by the need to supply information to resource managers who are faced with difficult decisions about where to deploy elite genetic materials, given the understanding that these genotypes may respond differently to silvicultural treatments, locations, and changing climatic conditions. Given this information, site-specific and silviculture-specific treatment prescriptions for individual genotypes could be developed. In addition, this information may influence breeding strategies in order to capture the full advantage of unique genotypes that respond differentially with environmental conditions. The work described in this investigation is aimed at partially filling this need by examining how genotype x environment interactions influence biomass accretion, distribution, nitrogen content, stem volume, basal area, and radiation use efficiency in selected full-sib families of loblolly and slash pine in the southeastern United States.

Approach and Objectives

The approach taken in this investigation was to use various subsets of a large series of replicated factorial experiments which were established on multiple locations in Florida and Georgia to provide insight into understanding genotype x environment interactions in southern pines. The experimental design was unique in that it used large full-sib family block plots, where stand level attributes could be investigated across combinations of silvicultural management intensity, planting density, and locations. The larger trial series consisted of: contrasting silvicultural treatment intensities (operational versus intensive), planting densities (1334 versus 2990 trees ha^{-1}) and elite full-sib families (seven for loblolly and six for slash pine). These treatments were designed to provide large contrasts in planting density, competition from associated vegetation, soil nutrient availability and genetic selection.

The overall objectives of this study were to investigate and quantify the magnitude and nature of genotype x environment interactions for selected elite full-sib families of loblolly and slash pine across a range of contrasting locations on stand level traits. Specific objectives were to document significant interactions between the factors of: genotype x silviculture, genotype x density, genotype x location, silviculture x density, silviculture x location, location x density, and any higher level interactions among these factors for biomass accretion, distribution, nitrogen content, stem volume, basal area, and radiation use efficiency. Results are presented in three main chapters: Chapter two - biomass production, distribution and nitrogen content at age two, Chapter three - interception and efficiency of PAR at ages four and five, and Chapter four - basal area, stem volume and biomass production at age five.

This research provides a valuable contribution towards the management of intensively managed loblolly and slash pine plantations in the southeastern United States, in that it is the only one of its kind where the combined effects of genotype, silviculture, and planting density can be examined singly or in combination across a range of site conditions in a family block planting design. This information will aid resource managers through an understanding of how elite genotypes respond on a unit area basis to intensive silvicultural treatments when deployed across man-made and naturally occurring environmental gradients.

CHAPTER 2

INFLUENCE OF GENOTYPE AND ENVIRONMENT ON BIOMASS ACCUMULATION, DISTRIBUTION AND NITROGEN CONTENT IN SELECTED LOBLOLLY (*Pinus taeda* L.) AND SLASH PINE (*P. elliotti* ENGELM. VAR. *elliotttii*) PLANTATIONS IN THE SOUTHEASTERN UNITED STATES

Introduction

The forested portion of the southeastern United States contains almost one-half of the world's industrial forest plantations and produces more industrial timber than any other region of the world (Allen *et al.*, 2005c). Combinations of species selection, silvicultural management intensity, planting density, and deployment of improved genotypes have greatly improved the productivity of these plantations over the past several decades (Jokela *et al.*, 2004). These managed plantations now produce a wide range of ecosystem services, such as fiber, carbon sequestration, and biofuels. Much of the response to these treatments occurs early in the development of these stands when rapid shifts in the accumulation and distribution of biomass among tree components occurs (Adegbidi *et al.*, 2005). During this early stage of stand development, biomass is preferentially accumulated in the foliage (FOL) and belowground (BELOW) components, at the expense of stemwood (BOLE) (Adegbidi *et al.*, 2002). As stand development progresses this trend reverses, with the bole becoming a more significant component over time (Martin and Jokela, 2004b).

Quantification of accumulation and distribution of biomass and nutrients in various tree components such as the FOL, branches (BRANCH), bark (BARK), BOLE, and BELOW is important for predicting and managing alternative sources of bioenergy (Scott and Dean, 2006) and in the development of process based growth models (Landsberg and Waring, 1997; Zhang and Borders, 2004). Nitrogen is the most common nutrient limiting in these systems and was examined in this study. Much of the early research on the distribution of biomass in southern pine species has been focused on individual seedlings (Ledig *et al.*, 1970; Johnson, 1990; Li *et al.*, 1991b; Jose *et al.*, 2003), or trees (Neary *et al.*, 1990), and where unit area production has been examined (Jokela *et al.*, 1989), it often does not include the BELOW component (Jokela and Martin, 2000), with a few exceptions (Gholz and Fisher, 1982; Adegbidi *et al.*, 2005).

Shifts in biomass distribution over time have been attributed to several factors, including inherent site productivity (Keyes and Grier, 1981; Stape *et al.*, 2004), soil properties (Burkes *et al.*, 2003), nutrient additions (Keyes and Grier, 1981; Axelsson and Axelsson, 1986; Gower *et al.*, 1992; Haynes and Gower, 1995; Albaugh *et al.*, 1998; du Toit, 2008), irrigation (Axelsson and Axelsson, 1986; Gower *et al.*, 1992; Samuelson *et al.*, 2004), stand density (Litton *et al.*, 2003; Burkes *et al.*, 2003), weed control (Britt *et al.*, 1990), stand structure (Vanlear and Kapeluck, 1995; Dean, 2001), species (Johnson, 1990; Griffin *et al.*, 1995), and genotype within species (Bongarten and Teskey, 1987; Crawford *et al.*, 1991; St Clair, 1994).

Previous work has documented how biomass accumulation and distribution can be affected by single factors such as fertilization and genotype; however, studies investigating the effects of these factors in combination are limited, especially for southern pines (Crawford *et al.*, 1991; Li *et al.*, 1991b; Gower *et al.*, 1993; Retzlaff *et al.*, 2001). It has been demonstrated that much of the response to these treatments occurs early in the development of these intensively managed stands, when rapid shifts in the accumulation and distribution of biomass among tree components occurs. The strength of the current investigation was that stand level attributes were examined on a unit area basis in pure family blocks across species, contrasting soil types, and silvicultural treatments. In this investigation biomass accumulation, distribution and N content as influenced by the combined effects of silvicultural management intensity, planting density, and family in two-year-old family block plantings of loblolly (*Pinus taeda* L.) and slash pine (*P. elliottii*

Engelm. var. *elliotttii*) across a range of locations was examined. The main objective of this study was to examine the nature and extent of any genotype x environment interactions in loblolly and slash pine such as: genotype x silviculture, genotype x density, genotype x location, silviculture x density, silviculture x location, location x density, and any higher level interactions among these factors. Within this larger framework, specific objectives were to: 1) quantify the accumulation of biomass and N content within the components of FOL, BARK and BRANCH, BOLE, and BELOW components, 2) quantify the distribution of biomass and N content in the FOL, BOLE and BELOW components, and 3) determine if family performance and biomass distribution was stable across combinations of locations, silvicultural management intensities, and planting densities.

Treatment Descriptions

Five trials, three with loblolly and two with slash pine, were installed at locations previously supporting southern pine plantations (Table 2-1). The topography is nearly flat, with less than a 1% slope. Soil series for the five sites were: Sanderson, FL - Leon (sandy, siliceous, thermic Aeric Alaquods); Waverly, GA - Bladen (mixed, semiactive, thermic Typic Albaquults); Bunnell, FL - Myakka (sandy, siliceous, hyperthermic Aeric Alaquods); Perry, FL - Leon (sandy, siliceous, thermic Aeric Alaquods); Waldo, FL - Newnan (sandy, siliceous, hyperthermic Ultic Haplohumods). Trials were installed on sites that held recently harvested southern pine plantations. Associated woody vegetation common to all sites included sawtooth palmetto [*Serenoa repens* (B.) Small.], wax myrtle (*Myrica ceriferea* L.), runner oak (*Quercus pumila* Walt.), blueberries (*Vaccinium* spp.), gallberry [*Ilex glabra* (L.) Gray], and St. John's-wort [*Hypericum fasciculatum* (Lam.)]. Herbaceous plants in the understory commonly included bluestem grasses (*Andropogon* spp.), panic grasses (*Panicum* spp.), sedges (*Carex* spp. and *Cyperus* spp.), and dogfennel [*Eupatorium capillifolium* (Lam.) Small.]. All study locations shared a subtropical and humid climate with long hot wet summers and mild dry winters. Long-term (1931 – 2000) precipitation has averaged 1384 mm yr^{-1} (NOAA, 2002).

Each installation was double bedded using separate passes following 2.75 meter spacing between planting rows. All installations were treated in the late summer/early fall of 1999 with pre-plant herbicides consisting of Chopper® (imazapyr) at 1.02 ℓ·ha^{-1} and Garlon (triclopyr) at 7.02 ℓ·ha^{-1}, with the goal of removing all woody competition and reducing initial levels of herbaceous vegetation. The operational silvicultural treatment was representative of a management regime commonly utilized by forest industry throughout the southeastern United States. These plots also received a single banded, or broadcast, application of 280 kg·ha^{-1} diammonium phosphate at the time of planting.

In contrast, the intensive treatment received annual fertilizer additions following early vegetation control. For two years following planting, competing vegetation was controlled using directed applications of Arsenal® (imazapyr) at 0.28 ℓ·ha^{-1} (limited to loblolly pine installations) and Oust® (sulfometuron methyl) at 0.14 ℓ·ha^{-1} on all installations. At the time of planting, the intensive plots were fertilized with 560 kg·ha^{-1} of 10-10-10 plus micronutrients, and was followed by site specific annual applications of macro- and micronutrient fertilizers using prescriptions based on foliar analyses. The total amounts of nutrients applied to each installation through age two are presented in Table 2-2.

Planting density was the second treatment factor applied at the whole-plot level: 1334 trees·ha^{-1} planted at a spacing of 2.75 m x 2.75 m, and 2990 trees·ha^{-1} planted at a spacing of 1.22 m x 2.75 m. Within the 2990 trees·ha^{-1} sub-plots, trees were arranged in eight beds of 16 planting positions, for a total of 128 trees per gross treatment plot. A two tree border existed around the perimeter, resulting in a 48 tree interior measurement plot that was 0.016 ha in size.

The 1334 trees·ha^{-1} sub-plots of each genetic entry were arranged in eight beds of 10 planting positions each, for a total of 80 trees per gross plot. This arrangement, with a single tree buffer around the perimeter, resulted in a 48 tree interior measurement plot of 0.036 ha. Tree survival was over 95% in all treatments at the end of the first growing season, despite an ongoing drought at the time of establishment.

At the sub-plot level, genetic entries consisted of first generation elite full-sib families. On loblolly pine sites, there were seven entries of full-sib families and on slash pine sites there were six entries, each including a poor grower. In order to reduce confounding effects of disease, all genetic entries in the study were selected *a priori* based on knowledge from breeding programs and progeny tests from sources exhibiting average to excellent resistance to fusiform rust [*Cronartium quercum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*]. Seedlings were grown in 66 ml cell^{-1} Ray Leach 'Cone-tainer'™ cells (Stuewe and Sons, Inc Corvallis, OR), and were planted in January of 2000.

Insecticides were uniformly applied across all treatments on loblolly pine installations in an effort to control damage from Nantucket pine tip moth (*Rhyacionia frustrana* [Comstock]). Treatments were applied on a monthly basis over the first two growing seasons, beginning in March and ending in September. Alternating applications of the following chemicals and application rates were applied aerially or by hand: Pounce® 3.2EC (62 ml product ℓ^{-1} water), Warrior T® (39 ml product ℓ^{-1} water), Dimilin® 25W (62 ml product ℓ^{-1} water), and Mimic® 2LV (125 ml product ℓ^{-1} water).

A fungicide was uniformly applied across all treatments on slash pine installations in order to control for the confounding effects of potential fusiform rust infection. Treatments were applied by ground application on a monthly basis over a four-month period (beginning in March) during the first two growing seasons. The fungicide product and rate consisted of 12 g of 50% concentrated DF Bayleton® with 65ml of Agri-Dex in 18.9 ℓ of water.

Sampling Procedures

Biomass estimation

Biomass prediction equations were developed using data collected from a destructive harvest completed at the end of the second growing season in November 2001. The sample trees were located in border rows which surrounded the sub-plots. Three loblolly and two slash pine experimental trials were sampled. At the loblolly pine locations, three replicates from each of two predetermined families (families L2 and L4), on each of the four silviculture x density whole plots, were sampled. A total of 70 trees were harvested across three locations. The slash pine experimental trials were sampled (families S1 and S6) in a similar manner, with the exception that four replicates were chosen for a total of 60 trees across two locations. Sample trees were free of damage and disease and were selected utilizing random sampling stratified by diameter class within each treatment and location. Prior to harvest, an inventory was completed on each sample tree consisting of total height, diameter at breast height, diameter at ground line, and crown width at the widest point parallel to and perpendicular to the bed (Figure 2-1).

Sample trees were felled at ground line using a hand saw, placed on a tarp and separated into aboveground components: FOL, BRANCH, BARK and BOLE; there were no dead branches on these trees due to their young age. The total fresh weight of each component was measured in the field. To determine the fraction of BARK to BOLE, a 6 cm disk of wood was cut from the base of each of three equally spaced stem segments along the full length of the stem. The BARK component was separated from each disk and the fresh weight of each was determined in the field. There was no sub-sampling; all tissue samples were transported from the field and dried to a constant weight at 70^0C.

Due to the considerable effort involved in belowground sampling, loblolly pine harvests for these components were limited to two out of three replicates, while slash pine was sampled on all three replicates, both from the same trees that were sampled for the aboveground components (n=32 slash, n=21 loblolly). Entire taproots were extracted and included coarse roots within one square meter that were greater than two millimeters in diameter to a depth of 40 cm. Entire samples were dried and weighed; there was no sub-sampling. Biomass components for taproot and coarse roots were pooled and the combined component was identified as BELOW.

Nitrogen concentrations were determined using a sub-sample of ground tissue from each biomass component. Tissue samples were chipped, following drying, using a small gas powered chipper. A homogenized sample of chips was then processed through a Wiley mill using a 2 mm sieve and then analyzed using a NCS 2500 Elemental Analyzer (Fisons Instrument, Milan, Italy). There was one exception, at the Bunnell, FL location, where the foliar tissue samples were lost. As a substitute, a sample of foliage was collected during the same month as the biomass sampling from eight random living trees across each family and plot that was sampled.

Logarithmically transformed linear allometric equations were developed for each biomass component according to the base model (Equation 2-1) (Crow, 1988):

$$\ln(\mathrm{Y}) = \ln(\beta_0) + \beta_1 \ln X_1 + \ln(\varepsilon) \qquad (2\text{-}1)$$

where ln is the natural logarithm, Y is the dry weight of each biomass component (FOL, BRANCH. BARK, BOLE, BELOW) expressed in kg tree^{-1}, (β_0) is the mean of the tree within each species, X_1 is the product of the combined variables of DBH squared times HT for each tree expressed in dm^3, and ε is the random error associated with estimating the weight of the aboveground biomass for each tree.

The need for separate groups of equations by species, locations, silvicultural management intensity, families, and planting density was examined utilizing PROC MIXED (Littel *et al.*, 1996) in SAS. These were evaluated by beginning with a pooled dataset and systematically decomposing the general model by entering treatment variables and their interactions. At each step, slopes and intercepts of the resulting equations were evaluated through covariate analysis. Probability plots of the residuals indicated that the normality assumption were satisfied and plots of residuals versus predicted values showed no obvious pattern, suggesting that the assumptions of independence and equal variance were met. Corrections for bias in the transformation of logarithmic units to arithmetic units, were completed (Baskerville, 1972). Species specific equations for each biomass component (Table 2-3) were applied to the age two individual tree inventory data and summed for each plot (expressed in Mg ha^{-1} of dry matter). Percentage FOL, BOLE, and BELOW were calculated using the sum of all individual biomass components (TOTAL) in the denominator. Nitrogen contents were determined as the product of nitrogen concentration and the dry weight for each component. Components were pooled and summed to obtain N content for the FOL, aboveground (ABOVE), BELOW and TOTAL components.

Analysis

All analyses were performed using PROC MIXED (Littel *et al.*, 1996) in SAS. To test for differences in stand level attributes among treatments, separate analyses of variance (ANOVA) were performed for loblolly and slash pine using a mixed linear model for data pooled across sites within each species (Equation 2-2):

$$\begin{aligned} Y_{ijklmn} = {} & \mu + S_i + b(s)_{ij} + C_k + D_l + CD_{kl} + F_m + CF_{km} + DF_{lm} + CDF_{klm} + SC_{ik} + SD_{il} + CD_{ikl} + \\ & SF_{im} + SCF_{ikm} + SDF_{ilm} + SCDF_{iklm} + b(s)C_{ijk} + b(s)D_{ijl} + b(s)CD_{ijkl} + b(s)F_{ijm} + b(s)CF_{ijkm} + \\ & b(s)DF_{ijlm} + b(s)CDF_{ijklm} + b(s)S_{ij} + b(s)SC_{ijk} + b(s)SD_{ijl} + b(s)CD_{ijkl} + b(s)SF_{ijm} + b(s)SCF_{ijkm} + \\ & b(s)SDF_{ijlm} + w_{ijklmn} \end{aligned} \tag{2-2}$$

where Y_{ijklmn} is the response variable (FOL, BRANCH, BARK, BOLE, or TOTAL) of the *n*th plot of the *m*th family of the *l*th planting density of the *k*th silvicultural intensity of the *j*th block of the *i*th location ($i = 1,2,$; $j = 1,2, \ldots, 4$; $k = 1,2$; $l = 1,2$; $m = 1,2,\ldots, 6$ for slash and 7 for loblolly pine; and $n = 1$); μ is the overall mean; S_i is the fixed effect of the *i*th location; $b(s)_{ij}$ is the random interaction effect of the *j*th block within the *i*th location; C_k is the fixed effect of the *k*th silvicultural intensity; D_l is the fixed effect of the *l*th planting density; F_m is the fixed effect of the *m*th family and w_{ijklmn} is the random error. Blocks were nested within locations, while the factors of silvicultural management intensity (C), planting density (D), and genotype (F) were crossed. All terms containing $b(s)_{ij}$ were considered to be random effects in the model and were pooled as appropriate for each variable tested using the procedure described by Bancroft and Han (1983). The only exception was $b(s)CD_{ijkl}$, which was never pooled as it was used as the error term to test the main effects of S_i, C_k and D_l. Individual variance components were pooled when the probability of a greater *F* statistic was 0.25 or larger. As noted by Bancroft and Han (1983), the significance level for the *F* test is much higher than conventional levels of 0.01 or 0.05 and is a conservative measure of the relative efficiency of pooling the sources of variation.

Results

Biomass Accumulation

Slash pine

Slash pine TOTAL biomass accumulation varied significantly at age two-years by the main effects of silvicultural intensity ($p=0.0021$), planting density ($p<0.0001$) and family ($p<0.0001$), with no interactions among these factors or locations (Table 2-4). Total above- and belowground biomass (TOTAL) accumulation under intensive silviculture, when averaged across both densities and all families, was 14% greater than the operational treatment (7.6 vs. 8.7 Mg ha^{-1}). As expected, a near doubling of the number of stems planted per ha from 1334 to 2990 trees ha^{-1}

(44%) resulted in a 1.46-fold increase in TOTAL biomass accumulation (4.7 vs. 11.6 Mg ha^{-1}). There was considerable variation among slash pine families in TOTAL biomass accumulation. The absolute differences in accumulation between the two bottom and the single top performing families were around 18% (7.6 versus 8.9 Mg ha^{-1}, families S3 and S4, versus S2, respectively) (Figure 2-2).

Similar to the TOTAL component, slash pine biomass accumulation in the components of FOL, BRANCH, BARK, BOLE and BELOW varied by the main effects of silvicultural intensity ($p<0.0024$), planting density ($p<0.0001$), and family ($p<0.0001$), with no interactions among these factors or between locations (Table 2-4). Silvicultural intensity increased the accumulation of biomass to the BELOW, FOL, and BOLE components by 11, 13 and 17%, respectively. The effect of increasing planting density, from 1334 to 2990 trees ha^{-1}, increased the FOL component the least (1.44-fold) and the BOLE component the most (1.48-fold). There were large differences among the two bottom and the top performing families in the accumulation of biomass for the various tree components; BOLE was the most responsive at 21% (1.2 versus 1.4 Mg ha^{-1}, families S3 and S4, versus S2) and BELOW the least responsive at 16% (1.8 versus 2.1 Mg ha^{-1}; families S3 and S4, versus S2) (Figure 2-2).

Loblolly pine

There were three strong and significant ($p<0.001$) two-way interactions for loblolly pine biomass accumulation at age 2 for all components: silviculture x density, silviculture x location, and family x density (Table 2-4). The effect of silvicultural intensity on TOTAL biomass accumulation was not stable as planting density increased from 1334 to 2990 trees ha^{-1} (i.e. silviculture x density). The response to the intensive silvicultural treatment was most pronounced on the high density plots (13.9 versus 17.2 Mg ha^{-1}) (Figure 2-3a). The form of this interaction was a non-proportional response between planting densities to increasing silvicultural intensity. Under the operational silviculture treatment, a near doubling of the planting density resulted in a 2.2-fold increase in TOTAL biomass, compared to a 2.4-fold increase under the intensive silvicultural treatment.

Total biomass accumulation was influenced by a combination of silvicultural intensity and location (silviculture x location). The most productive combination occurred under the intensive silviculture treatment at the Sanderson, FL location (15.5 Mg ha^{-1}), with the least productive under the operational treatment at Bunnell, FL (8.6 Mg ha^{-1}) (Figure 2-3b). Within each of the Bunnell, FL and Waverly, GA locations, there was no significant difference in TOTAL biomass accumulation between the silvicultural treatments; however, at the SA location there was a statistically significant 36% difference in TOTAL biomass accumulation (11.3 versus 15.5 Mg ha^{-1}, operational and intensive treatments, respectively).

Family performance for TOTAL biomass accumulation was not stable across densities (i.e., a significant interaction of family x density). In general, families with high growth rates at low densities performed better than expected at higher densities (Figure 2-4). The form of this interaction was a non-proportional response among families with increasing planting densities, with the exception of families L4 and L8. These two families were top performers for biomass accumulation and demonstrated a rank change. Family L4 outperformed L8 at 1334 trees ha^{-1}, averaged across locations (7.7 vs. 7.3 Mg ha^{-1}); however, this trend was reversed at 2990 trees ha^{-1} (17.2 vs. 17.6 Mg ha^{-1}).

Biomass Distribution to Foliage, Bole, and Belowground

Slash pine

The main effects of silvicultural intensity ($p<0.0017$) and family ($p<0.0001$) were statistically significant in slash pine for the distribution of biomass to all components (Table 2-5). Intensive silvicultural treatments minutely increased the distribution of biomass to BOLE

(15.2 to 15.7%, operational and intensive treatments, respectively). By contrast, biomass distribution in the FOL (38.5 and 38.1%) and BELOW components (24.3 and 24.0%) decreased in response to the intensive silvicultural treatments. Families varied significantly in their distribution of biomass to FOL (38.0 to 38.4%, families S2 and S5, respectively), BOLE (15.5 to 15.8%, families S2 and S6, respectively) and the BELOW (23.9 to 24.2%, families S2 and S6, respectively) (Figure 2-5). The effects of silviculture and family did not interact and were stable across planting densities and locations.

Loblolly pine

The distribution of loblolly pine biomass among FOL, BOLE, and BELOW components demonstrated a main effect of family ($p<0.0001$) and a three-way interaction of silviculture x density x location ($p<0.0001$) (Table 2-5). Families varied in their distribution of biomass to FOL (19.6 to 20.8%, families L6 and L4, respectively), BOLE (30.0 to 30.9%, families L4 and L6, respectively) and BELOW (25.7 to 26.6%, families L4, and L6, respectively) (Figure 2-6). The three-way interaction was complex and involved a differential response in biomass distribution between silvicultural intensity and planting density across locations. In general, this interaction was driven by an anomaly which occurred at the Bunnell, FL location within the 1334 trees ha^{-1} planting density. At this planting density, the intensive silvicultural treatment had less biomass distributed to the BELOW component (18.7 versus 19.7%, intensive and operational respectively), and greater distribution to FOL (31.7 versus 30.9%) and BOLE (27.3 versus 26.5%) (Figure 2-7c).

Nitrogen Content

Slash pine

Two years after planting, there was a significant and strong main effect of silvicultural treatment intensity on N content for all slash pine biomass components ($p<0.0001$). On average, total N accumulation in the above- and belowground tissue components increased by about 40% under the intensive silvicultural treatment (from 46.8 to 65.5 kg ha^{-1} under operational and intensive treatments, respectively). Foliar N accumulations averaged 30.9 and 40.7 kg ha^{-1} (operational and intensive) and N accumulation in the ABOVE component were 39.4 kg ha^{-1} for the operational and 54.0 kg ha^{-1} for the intensive treatments, respectively.

There were significant differences among slash pine families for N contents of all biomass components: FOL (p=0.0481), ABOVE (p=0.0479), BELOW (p=0.0462), and TOTAL (p=0.0490) (Table 2-6). Family variation in total N content ranged from a low of 52.0 kg ha^{-1} for family S3 to a high of 61.3 kg ha^{-1} for family S2 (Table 2-6). Families were stable and did not vary in combination with any other treatment factors for N content.

Significant interactions between planting density and location for N content of the FOL, ABOVE and TOTAL components (p<0.0001) were detected. At 1334 trees ha^{-1}, total N content averaged 33.0 kg ha^{-1} for each of the Perry, FL and Waldo, FL locations independently. However, when the planting density was increased at the same conditions to 2990 trees ha^{-1}, the Perry, FL location was more responsive than the Waldo, FL location (88.3 versus 70.5 kg ha^{-1} of N, respectively) (Table 2-7). There was a three-way interaction for N content in the BELOW component between silvicultural intensity, planting density, and location (Figure 2-8). The N content for the BELOW component at the Waldo, FL location, under the 2990 trees ha^{-1} treatment, was considerably higher than that at the Perry, FL location (11.4 versus 9.6 kg ha^{-1}, respectively, both under the intensive silvicultural treatment).

Loblolly pine

Nitrogen content in all biomass components demonstrated two types of interactions: genotype x density, and silviculture x density x location. Families were not stable across the two planting densities tested in this experiment for N content for FOL (p=0.0235), ABOVE (p=0.0364), BELOW (p=0.0057), and TOTAL (p=0.0250) (i.e., a family x density interaction). In general, this interaction was due to scale effects among families, with the notable exception of two families (L4 and L8), which changed rank in N content between planting densities. For example, at the 2990 trees ha^{-1} density, N contents for families L4 and L8 by component were as follows: FOL (59.4 and 60.3 kg ha^{-1}), ABOVE (79.3 and 80.8 kg ha^{-1}), BELOW (15.1 and 15.3 kg ha^{-1}), and TOTAL (94.3 and 96.1 kg ha^{-1}). Nitrogen contents for families L4 and L8 by component at the 1334 trees ha^{-1} planting density were as follows: FOL (27.4 and 26.0 kg ha^{-1}), ABOVE (37.5 and 35.7 kg ha^{-1}), BELOW (6.4 and 6.0 kg ha^{-1}), and TOTAL (43.9 and 41.7 kg ha^{-1}) (Table 2-8).

The three-way interaction (silviculture x density x location) was caused by an unequal response to silvicultural management intensity between planting densities at the three locations examined (FOL, p<0.0001; ABOVE, p<0.0001; BELOW, p=0.0001; TOTAL, p<0.0001). At the Bunnell, FL location, there were much lower than expected N contents in the FOL, ABOVE, and TOTAL components in the intensive silvicultural treatment combination at the 1334 trees ha^{-1} planting density (Table 2-9). For each component, with the exception of BELOW, the intensive silviculture treatment had lower values of N than the operational silvicultural treatment (FOL – 14.5 and 19.7 kg ha^{-1}, ABOVE – 18.1 and 24.1 kg ha^{-1}, BELOW – 5.2 and 5.0 kg ha^{-1}, and TOTAL – 23.3 and 29.1 kg ha^{-1}, respectively). This was not observed at either the Sanderson, FL or Waverly, GA locations.

Discussion

Understanding genotype x environment interactions is becoming increasingly important as the level of genetic selection in southern pines increases in combination with the intensity of silvicultural management. Questions remain as to how best to deploy this elite genetic material, given uncertainty in predicting its response to a wide variety of anthropogenic and abiotic environmental factors (Fox, 2000). The experimental design in the current study provided a powerful opportunity to examine unit-area biomass accumulation, N content, and distribution in selected elite families of loblolly and slash pine as influenced by a combination of silvicultural management intensities, planting densities, and locations.

After two growing seasons significant interactions were evident for biomass accumulation, N content and distribution to various stand components. Generally, loblolly pine demonstrated a greater number of and higher-level interactions than did slash pine. This was not unexpected, since loblolly pine has been shown to be considerably more responsive than slash pine to silvicultural treatments, such as weed control and fertilization than slash pine (Xiao *et al.*, 2003; Cobb *et al.*, 2008). Significant interactions in this study included: genotype x location, genotype x density, and silviculture x density x location. The ability to detect these interactions was a function of the high statistical power of the experimental design and the precision associated with the intensity of sample measurements.

Biomass accumulation in slash pine at age-two was responsive to the main effects of silvicultural intensity, planting density, and family with no interactions. Age-two total biomass accumulation was in the range of 6 Mg ha^{-1}and was consistent with that published by others when extrapolated from age-four data (Colbert *et al.*, 1990; Jokela and Martin, 2000). Since the response to these treatments did not interact in slash pine, the accumulation of biomass should be predictable at an early age; however, this stability may be influenced over time as stands develop and are subjected to a variety of biotic and abiotic factors such as disease and catastrophic weather events (Roth *et al.*, 2007a). As reported previously by others, slash pine response to intensive silviculture was mostly evidenced by increases in BOLE biomass, despite modest increases in FOL biomass (Colbert *et al.*, 1990). The greatest variation among the families in this experiment occurred in the BOLE component.

Total biomass accumulation values for loblolly pine at age-two-years in this region were in general agreement with previously published estimates of around 10 Mg ha^{-1} (Adegbidi *et al.*, 2002). There were three types of interactions evident for loblolly pine biomass accumulation at age-two: silviculture x density, silviculture x location, and genotype x density.

Loblolly pine response in biomass accumulation to silvicultural management intensity was not stable across planting densities; and the largest response occurred under the narrowest spacing. While the mechanism behind this effect could not be tested in this investigation, there may be a synergistic effect of increased resource availability with increasing stand density. Increases in individual tree biomass with increasing stand density have been documented (Scott *et al.*, 1998); however, this was not observed in the current study on the individual tree level. Several mechanisms have been proposed to explain this, including micro-site availability of water and nutrients (Woodruff *et al.*, 2002), and early signaling of intra-tree competition (Ritchie, 1997; Ballaré, 1999).

The silviculture x location interaction was interesting in that it was driven by a single location: Sanderson, FL. The two locations were contrasting in water availability and soil characteristics (see Appendix B and C). The Sanderson location has lower water availability and the soil type at this location was a Spodosol, which tends to be infertile, and is in contrast to the Ultisol at the Waverly, GA location which tends to have available nutrients concentrated near the soil surface. It has been well documented that loblolly pine productivity is highly dependant on nutrient availability (Jokela *et al.*, 2000) and on the nutrient poor Sanderson, FL location, the intensive silvicultural treatment created a large contrast in biomass accumulation due to nutrient addition, when compared to the relatively nutrient rich Waverly, GA location.

The genotype x density interaction for TOTAL biomass accumulation observed in this investigation was surprising. Previous research has shown that stand density has no effect on the growth performance of individual loblolly pine families (McCrady and Jokela, 1996); however, there are limited exceptions and these were generally of the scale type effects for a few genotypes grown at very high densities (Land *et al.*, 2004). While much of the interaction observed in the current investigation was of the scale type, there was a rank change between the two top producing families (L4 and L8) as planting density increased. The fact that a limited number of highly reactive families were responsible for this effect is consistent with most genotype x environment interactions described in the literature (Zas *et al.*, 2004; Roth *et al.*, 2007a). Of interest, is that these two families have been identified as putative crop and competition ideotypes (L8 and L4, respectively) at age 6 in this same study series (Staudhammer *et al.*, 2009). Family L4 tends to have a large and deep crown structure (Chmura and Tjoelker, 2008), which may have provided a competitive advantage in the widely spaced 1334 trees ha^{-1} treatment. If this contrast between putative ideotypes continues to hold over time, then the results documented in this investigation would suggest that competition dynamics between these genotypes began at an extremely early stage of stand development.

Shifts in biomass distribution among tree components occur as trees and stands develop (Ledig *et al.*, 1970; Jokela and Martin, 2000; King *et al.*, 2007). For example, soon after plantation establishment, biomass accumulation was primarily distributed in the FOL and BELOW components, but as trees grow in size the BOLE component becomes an increasingly larger and more significant component (Adegbidi *et al.*, 2005). Treatments such as silvicultural management intensity, plantation density, and family also influence the distribution of biomass among tissue components, but the separation of these treatment effects from developmental effects is difficult since these treatments simultaneously increase growth and advance stand development (Coyle and Coleman, 2005). This investigation does not attempt to separate these effects, since the primary goal was to examine genotype x environment interactions among combinations of treatments, rather than make inferences about the causation of differences in biomass distribution between treatments.

Slash pine biomass distribution was influenced by the main effects of family and silvicultural treatment. Family differences in biomass distribution within various components were relatively small, less than one percent; however, at this early stage of stand development small differences can lead to a competitive growth advantage in the long-term. Increasing the intensity of silvicultural treatments had the effect of greater biomass distribution to BOLE in relation to FOL, which was supported by the work of others (Colbert *et al.*, 1990). However, in this study, distribution of biomass to BOLE was not influenced by increasing planting density as was found in a four-year-old slash pine experiment in GA (Burkes *et al.*, 2003).

Loblolly pine family distribution of biomass to various components was stable across all treatments and locations. This finding is supported by that documented in a five-year-old loblolly pine family block experiment where biomass allocation of fast- and slow-growing families were similar across fertilizer treatments (Retzlaff *et al.*, 2001). However, others have found that selected loblolly pine families (Li *et al.*, 1991b) and clones (Tyree *et al.*, 2009) distribute biomass differentially between roots and shoots under contrasting fertilization regimes. Among the limited number of families examined in this investigation, those with the highest amount of TOTAL biomass accumulation had the least amount of biomass allocated to FOL and the greatest to BOLE, which may reflect ontogenetic effects.

There was a significant three-way interaction influencing the distribution of loblolly pine biomass, which involved a combination of silvicultural intensity, planting density, and location. The Bunnell, FL location was the primary driver behind this interaction. The topography at this location is nearly flat and soils are deep, sandy Spodosols. On September 14th, 2001, after the first growing season, tropical storm Gabrielle traversed the study area with large amounts of precipitation and sustained high winds. From observational data following the storm, it was evident that the effects of this storm influenced biomass distribution in the year following, especially in the treatment combination of wide spacing and intensive silviculture. Trees in this treatment combination appeared to be most affected (primarily root damage) by the effects of wind, since fertilization produced larger crowns and the heavy precipitation contributed to erosion of the beds and instability of the root systems. The patterns of biomass distribution in these treatments demonstrated a higher distribution to FOL and BOLE, which ran contrary to the patterns observed for the same treatment combinations at the other two locations. Presumably, these factors collectively influenced the expression of this three-way interaction in loblolly pine.

Nitrogen accumulation in slash pine components demonstrated two main effects (silvicultural treatment intensity and family) and one significant three-way interaction: silviculture x density x location for N content to the BELOW component. For slash pine, the addition of around 240 kg ha^{-1} of N above that added in the operational silvicultural intensity treatment was associated with an increase in total N content by about 20 kg ha^{-1} over the two years following planting. As has been reported previously in the literature, the families with the greatest biomass production also tended to have the greatest N contents (Crawford *et al.*, 1991). There was a two-way interaction between location and planting density. The cause was at the Perry, FL location, which had larger total N content at the 2990 trees ha^{-1} density than at Waldo, FL. While nutritional inputs were similar between locations, with the exception of sulfur (Table 2-2), responses to this difference should have been evidenced via a silviculture x location interaction, which was not detected. To complicate this, there was a three-way interaction for N content in the BELOW component between silvicultural treatment intensity, planting density and location, which may be a statistical anomaly. For some yet unexplained reason, N accumulation in the BELOW component was greater at Waldo, FL than at Perry, FL. This occurred despite similar biomass accumulations, under the operational silvicultural treatment intensity at the 2990 trees ha^{-1} planting density.

Nitrogen contents of loblolly pine biomass components were within 10% of those reported for stands of similar age (Adegbidi *et al.*, 2005) and varied in combination with the factors of families, locations, planting densities and silvicultural treatments. This was especially evident at the inherently nutrient poor Bunnell, FL location, where the influence of the intensive silvicultural treatment had a negative impact on N accumulation at the 1334 trees ha^{-1} planting density. This effect was driven more by a lower accumulation of biomass than N concentration, and possibly reflective of hurricane damage from the previous season.

The genotype x density interaction for N content offered insight into why particular genotypes responded differentially to intra-specific competition. The genotype x density interaction was similar as observed in the accumulation and distribution of biomass; the two families involved in the rank change for N content were the same (families L4 and L8). While subtle, it appears that the two families responsible for the differences in N content may have differential uptake rates between planting densities, which were not explained by belowground biomass, excluding fine roots. While this current investigation did not examine fine roots, this may be worthy of future research efforts in an attempt to better understand N uptake.

Conclusions

After two growing seasons, biomass accumulation, N content and distribution were influenced by combinations of silvicultural intensity, planting density, family and locations in plantations of loblolly and slash pine. Significant genotype x density, silviculture x density, and silviculture x location interactions existed for loblolly pine biomass accumulation, yet none existed for slash pine. When distribution of this accumulated biomass to various components was examined, the only interaction that was significant was silviculture x density x location for loblolly pine. Nitrogen accumulation and distribution was influenced by significant genotype x density and silviculture x density x location interactions for loblolly pine and density x location interactions for slash pine.

Evidence of these complex interactions, as early as age two, serves to underscore the importance of understanding how to best deploy elite genotypes of loblolly and slash pine, given the uncertainty in predicting its response to a wide variety of man made and abiotic environmental factors. For example, the only three-way interaction occurring for slash pine may have been due to the effects of a hurricane after the first growing season. While distribution of accumulated biomass did not appear to be involved in driving these interactions, variation in crown structure (McCrady and Jokela, 1996) or resource use efficiency may play a role (McKeand *et al.*, 1997a) and deserves further investigation.

Table 2-1. Characteristics of the five PPINES experimental locations in southeast Georgia and northeast Florida.

Site location	Species	Latitude (^{0})	Longitude (^{0})	Soil order	Elevation (m)
Sanderson, FL	Loblolly	30.28	-82.33	Spodosol	45
Waverly, GA	Loblolly	31.13	-81.75	Ultisol	10
Bunnell, FL	Loblolly	29.28	-81.31	Spodosol	8
Perry, FL	Slash	30.17	-83.73	Spodosol	15
Waldo, FL	Slash	29.80	-82.21	Spodosol	50

PPINES: Pine Productivity Interactions on Experimental Sites.

Table 2-2. Elemental application rates ($kg \cdot ha^{-1}$) of fertilizers supplied to the PPINES locations through the end of the second growing season (intensive silvicultural management treatments only).

Site location	N	P	K	Mg	Ca	S	B	Zn	Mn	Fe	Cu
Sanderson, FL	290	103	121	45	45	28	0.9	2.7	2.2	5.4	1.5
Waverly, GA	290	103	121	45	45	28	0.9	2.7	2.2	5.4	1.5
Bunnell, FL	236	100	125	34	34	40	0.9	2.2	2.2	5.3	0.9
Perry, FL	298	90	116	56	45	132	1.1	3.0	3.0	7.3	1.5
Waldo, FL	292	103	124	63	56	27	1.7	2.5	2.7	3.4	1.0

Operational silviculture treatments all received 45 $kg \cdot ha^{-1}$ N and 50 $kg \cdot ha^{-1}$ of P in the form of diammonium phosphate at the time of planting only.

Table 2-3. Parameter estimates and standard errors of the estimates for foliage, bole and belowground biomass (kg·tree^{-1}) equations for two-year-old loblolly and slash pine. Equations were generated using destructive harvest data.

Component/	B_0			β_1			Overall Model Estimates		
Species	Estimate	SE	p-value	Estimate	SE	p-value	R^2	RMSE	n
FOL									
Loblolly	-0.06034	0.04752	0.2065	0.44997	0.03387	<0.0001	0.582	0.31682	130
Slash	0.01654	0.04622	0.7209	0.44997	0.03387	<0.0001	0.582	0.31682	130
BRANCH									
Loblolly	-0.69577	0.05997	<0.0001	0.55626	0.04275	<0.0001	0.658	0.39985	130
Slash	-1.18661	0.05833	<0.0001	0.55626	0.04275	<0.0001	0.658	0.39985	130
BARK									
Loblolly	-1.88773	0.03359	<0.0001	0.48311	0.02378	<0.0001	0.806	0.22095	129
Slash	-1.36949	0.03227	<0.0001	0.48311	0.02378	<0.0001	0.806	0.22095	129
BOLE									
Loblolly	-0.54397	0.03351	<0.0001	0.59587	0.02337	<0.0001	0.866	0.22042	130
Slash	-0.93778	0.03220	<0.0001	0.59587	0.02337	<0.0001	0.866	0.22042	130
BELOW									
Loblolly	-0.19065	0.06869	0.0077	0.44718	0.04403	<0.0001	0.694	0.27061	53
Slash	-0.42350	0.05038	<0.0001	0.44718	0.04403	<0.0001	0.694	0.27061	53

Regression model: $\ln Y = \beta 0 + \beta 1 \ln X$, where ln= natural logarithm, Y = biomass component total dry weight (kg·tree^{-1}), β0 and β1 = regression coefficients (intercept and slope, respectively), X = DBH^2 x HT in dm^3. Abbreviations for biomass components are as follows: FOL = foliage, BRANCH = branches, BARK = bark, BOLE = stemwood, and BELOW = belowground. The belowground component consists of taproot plus coarse roots greater than 2 mm in diameter. Fine roots were excluded.

Table 2-4. Summary of statistical significance (prob. >F) and associated degrees of freedom from ANOVA to test loblolly and slash pine foliage, branches, bark, stemwood, belowground, and total biomass accumulation at age two-years.

Source of Variation	Num. df	Den. df	Foliage p-value	Branches p-value	Bark p-value	stemwood p-value	Belowground p-value	Total p-value
Loblolly								
Silviculture (C)	1	9	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
Density (D)	1	9	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
C x D	1	9	**0.0003**	**0.0003**	**0.0003**	**0.0003**	**0.0003**	**0.0003**
Family (F)	6	54	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
C x F	6	154	0.9598	0.9252	0.9517	0.9052	0.9604	0.9445
D x F	6	154	**0.0212**	**0.0175**	**0.0199**	**0.0164**	**0.0213**	**0.0192**
C x D x F	6	154	0.7393	0.7188	0.7336	0.7096	0.7398	0.7293
Location (S)	2	9	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
S x C	2	9	**0.0007**	**0.0004**	**0.0006**	**0.0003**	**0.0007**	**0.0005**
S x D	2	9	0.0519	0.0553	0.0527	0.0571	0.0519	0.0534
S x C x D	2	9	0.0524	0.0658	0.0568	0.0701	0.0520	0.0596
S x F	12	54	0.1136	0.1035	0.1119	0.0970	0.1137	0.1094
S x C x F	12	154	0.7983	0.7881	0.7970	0.7799	0.7983	0.7933
S x D x F	11	154	0.2319	0.2991	0.2524	0.3250	0.2302	0.2663
S x C x D x F	11	154	0.8269	0.7915	0.8159	0.7784	0.8278	0.8086
Slash								
Silviculture (C)	1	18	**0.0024**	**0.0017**	**0.0021**	**0.0016**	**0.0024**	**0.0021**
Density (D)	1	18	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
C x D	1	18	0.1448	0.1269	0.1385	0.1215	0.1454	0.1370
Family (F)	5	119	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
C x F	5	119	0.6414	0.6066	0.6305	0.5931	0.6423	0.6277
D x F	5	119	0.4192	0.3432	0.3965	0.3135	0.4210	0.3883
C x D x F	5	119	0.8823	0.8705	0.8789	0.8652	0.8825	0.8778
Location (S)	1	6	0.7625	0.7919	0.7716	0.8026	0.7617	0.7746
S x C	1	18	0.8989	0.8950	0.8974	0.8940	0.8991	0.8973
S x D	1	18	0.4731	0.4363	0.4607	0.4244	0.4741	0.4574
S x C x D	1	18	0.8746	0.8876	0.8794	0.8908	0.8742	0.8798
S x F	5	119	0.1622	0.1658	0.1631	0.1673	0.1621	0.1637
S x C x F	5	119	0.8304	0.8590	0.8400	0.8682	0.8296	0.8425
S x D x F	5	119	0.6339	0.6525	0.6396	0.6595	0.6334	0.6415
S x C x D x F	5	119	0.9980	0.9982	0.9981	0.9982	0.9980	0.9981

P-values significant at the 95% level of confidence are shown in bold type.

Table 2-5. Summary of statistical significance (prob. >F) and associated degrees of freedom from ANOVA to test loblolly and slash pine distribution of biomass to foliage, stemwood, and belowground components at age two-years.

Source of Variation	Num. df	Den. df	Percent foliage p-value	Percent stemwood p-value	Percent belowground p-value
Loblolly					
Silviculture (C)	1	121	**<0.0001**	**<0.0001**	**<0.0001**
Density (D)	1	114	0.1585	0.1763	0.1539
C x D	1	121	**0.0066**	**0.0072**	**0.0065**
Family (F)	6	114	**<0.0001**	**<0.0001**	**<0.0001**
C x F	6	121	0.9964	0.9963	0.9963
D x F	6	114	0.4562	0.4743	0.4510
C x D x F	6	121	0.4958	0.5062	0.4926
Location (S)	2	9	**0.0002**	**0.0002**	**0.0002**
S x C	2	121	**<0.0001**	**<0.0001**	**<0.0001**
S x D	2	114	**<0.0001**	**<0.0001**	**<0.0001**
S x C x D	2	121	**<0.0001**	**<0.0001**	**<0.0001**
S x F	12	114	0.2868	0.2765	0.2898
S x C x F	12	121	0.8920	0.8938	0.8913
S x D x F	11	114	0.0550	0.0550	0.0550
S x C x D x F	11	121	0.5210	0.5159	0.5223
Slash					
Silviculture (C)	1	12	**0.0016**	**0.0014**	**0.0016**
Density (D)	1	6	0.1587	0.1620	0.1549
C x D	1	12	0.9003	0.8960	0.9017
Family (F)	5	30	**<0.0001**	**<0.0001**	**<0.0001**
C x F	5	89	0.1854	0.1832	0.1860
D x F	5	89	0.6592	0.6697	0.6554
C x D x F	5	89	0.3632	0.3586	0.3648
Location (S)	1	6	0.8900	0.8954	0.8880
S x C	1	12	0.9454	0.9455	0.9455
S x D	1	6	0.3675	0.3623	0.3691
S x C x D	1	12	0.9030	0.9049	0.9023
S x F	5	30	0.1510	0.1465	0.1525
S x C x F	5	89	0.7210	0.7814	0.7674
S x D x F	5	89	0.8835	0.8828	0.8837
S x C x D x F	5	89	0.9895	0.9897	0.9894

P-values significant at the 95% level of confidence are shown in bold type.

Table 2-6. Least squared means for slash pine nitrogen accumulation (kg ha^{-1}) among various biomass components as influenced by full-sib family at age two-years.

	Family					
	S1	S2	S3	S4	S5	S6
FOL	37.0 ab	38.8 a	33.2 b	33.7 b	34.7 ab	37.3 ab
ABOVE	48.3 abc	50.9 a	43.3 c	43.9 bc	45.1 abc	48.6 ab
BELOW	9.8 ab	10.3 a	8.8 b	8.9 b	9.3 ab	9.9 ab
TOTAL	58.1 ab	61.3 a	52.0 b	52.9 b	54.4 ab	58.5 ab

Values within biomass components (rows) having the same letter are not significantly different at the 95% level of confidence using Bonferroni's least significant difference (LSD). Abbreviations and p-values for the percent distribution by component are as follows: FOL = foliage (p=0.0481), ABOVE = aboveground (p=0.0479), BELOW = belowground (p=0.0462), and TOTAL = total (p=0.0490). The belowground component consists of taproot plus coarse roots greater than 2 mm in diameter. Fine roots were excluded.

Table 2-7. Slash pine nitrogen accumulation in foliage, aboveground and total biomass components by planting density and location at two-years (kg ha^{-1}). There was a significant two-way interaction ($p<0.0001$) between planting density and location for each component.

Component/ Location	2990 trees ha^{-1}	1334 trees ha^{-1}
FOL		
Perry, FL	57.5 a	21.2 c
Waldo, FL	44.2 b	20.5 c
ABOVE		
Perry, FL	74.4 a	28.0 c
Waldo, FL	57.5 b	26.9 c
TOTAL		
Perry, FL	88.3 a	33.0 c
Waldo, FL	70.5 b	33.0 c

Values within each biomass component (i.e. two rows following each component) having the same letter are not significantly different at the 95% level of confidence using Bonferroni's least significant difference (LSD). Abbreviations by component are as follows: FOL = foliage, ABOVE = aboveground, and TOTAL = total.

Table 2-8. Loblolly pine nitrogen accumulation in foliage, aboveground, belowground, and total biomass components by family and planting density at two-years (kg ha^{-1}). There was a significant two-way interaction between family and density (p=0.0235, p=0.0364, p=0.0057, and p=0.0250 for each component, respectively).

Component/ Planting density	Family						
	L1	L2	L4	L5	L6	L7	L8
FOL							
1334 trees ha^{-1}	22.3 f	24.6 def	27.4 d	22.8 ef	21.0 f	25.8 de	26.0 de
2990 trees ha^{-1}	50.5 bc	55.6 ab	59.4 ab	52.2 abc	44.4 c	55.9 ab	60.3 a
ABOVE							
1334 trees ha^{-1}	30.2 ef	33.3 de	37.5 d	30.8 ef	28.2 f	35.0 de	35.7 d
2990 trees ha^{-1}	66.9 bc	73.7 abc	79.3 a	69.6 abc	59.1 c	74.5 ab	80.8 a
BELOW							
1334 trees ha^{-1}	5.3 fg	5.8 defg	6.4 d	5.4 efg	5.0 g	6.2 de	6.0 def
2990 trees ha^{-1}	12.8 bc	14.1 ab	15.1 a	13.2 abc	11.3 c	14.2 ab	15.3 a
TOTAL							
1334 trees ha^{-1}	35.5 fg	39.2 def	43.9 d	36.2 efg	33.2 g	41.2 de	41.7 de
2990 trees ha^{-1}	79.7 bc	87.8 ab	94.3 a	82.8 abc	70.4 c	88.7 ab	96.1 a

Values within each biomass component (i.e. two rows following each component) having the same letter are not significantly different at the 95% level of confidence using Bonferroni's least significant difference (LSD). Abbreviations for each component are as follows: FOL = foliage, ABOVE = aboveground, BELOW = belowground, and TOTAL = total.

Table 2-9. Loblolly pine nitrogen accumulation in foliage, aboveground, belowground, and total biomass components by silvicultural treatment, planting density, and location at age two-years (kg ha^{-1}).

Component/	2990 trees ha^{-1}		1334 trees ha^{-1}	
Location	Intensive	Operational	Intensive	Operational
FOL				
Bunnell, FL	53.7 bc	43.8 d	14.5 g	19.7 fg
Sanderson, FL	62.7 a	43.9 cd	33.0 e	21.2 f
Waverly, GA	62.2 ab	57.7 ab	32.4 e	24.8 f
ABOVE				
Bunnell, FL	66.4 bc	53.5 de	18.1 g	24.1 g
Sanderson, FL	86.5 a	60.1 cd	47.4 e	29.5 fg
Waverly, GA	85.8 a	79.5 ab	44.7 e	33.9 f
BELOW				
Bunnell, FL	13.5 abc	11.8 abc	5.2 cd	5.0 d
Sanderson, FL	14.2 ab	6.5 c	11.1 abc	4.4 d
Waverly, GA	15.7 ab	7.7 bc	16.0 a	5.7 cd
TOTAL				
Bunnell, FL	79.9 a	65.3 ab	23.3 d	29.1 d
Sanderson, FL	100.7 a	71.2 a	53.8 b	33.8 cd
Waverly, GA	101.5 a	95.5 a	52.4 b	39.6 c

There was a significant three-way interaction between silvicultural management intensity, planting density and location. Abbreviations and p-values for N content by component are as follows: FOL = foliage ($p<0.0001$), ABOVE = aboveground ($p<0.0001$), BELOW = belowground ($p=0.0001$), and TOTAL = total ($p<0.0001$). Values within each biomass component (i.e. two rows following each component) having the same letter are not significantly different at the 95% level of confidence using Bonferroni's least significant difference (LSD).

Figure 2-1. Typical two-year-old slash pine that was harvested from the intensive silviculture treatment at the Waldo, FL location, demonstrating the rapid development at this early age.

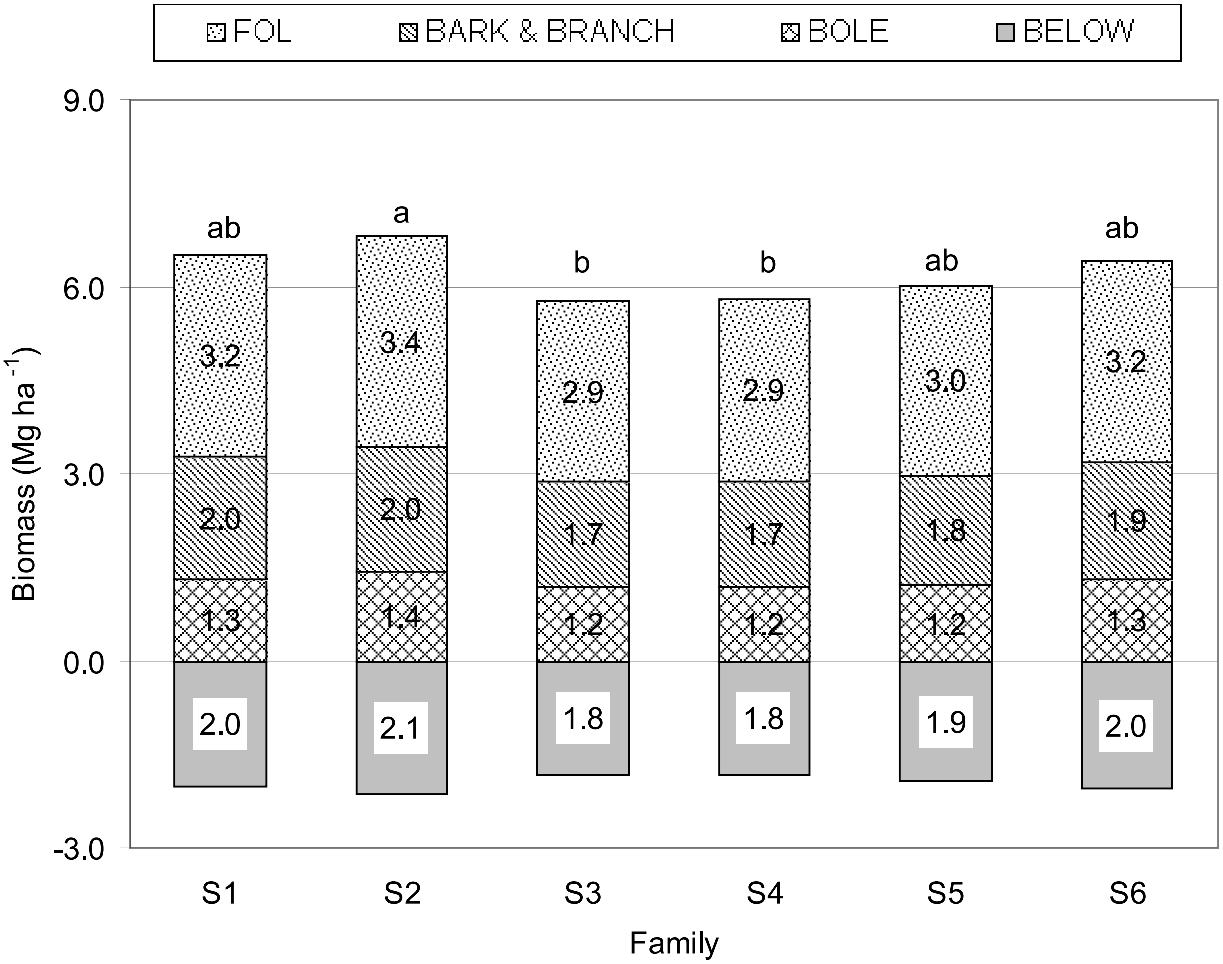

Figure 2-2. Least squares means for the main effect of full-sib family ($p<0.0001$) on slash pine biomass accumulation (Mg ha^{-1}) in foliage (FOL), bark and branches (BARK & BRANCH), stemwood (BOLE), and belowground (BELOW) components at age two years when averaged across two locations and planting densities. For each family with the same letter, each biomass components was not significantly different at the 95% level of confidence using Bonferroni's least significant difference (LSD).

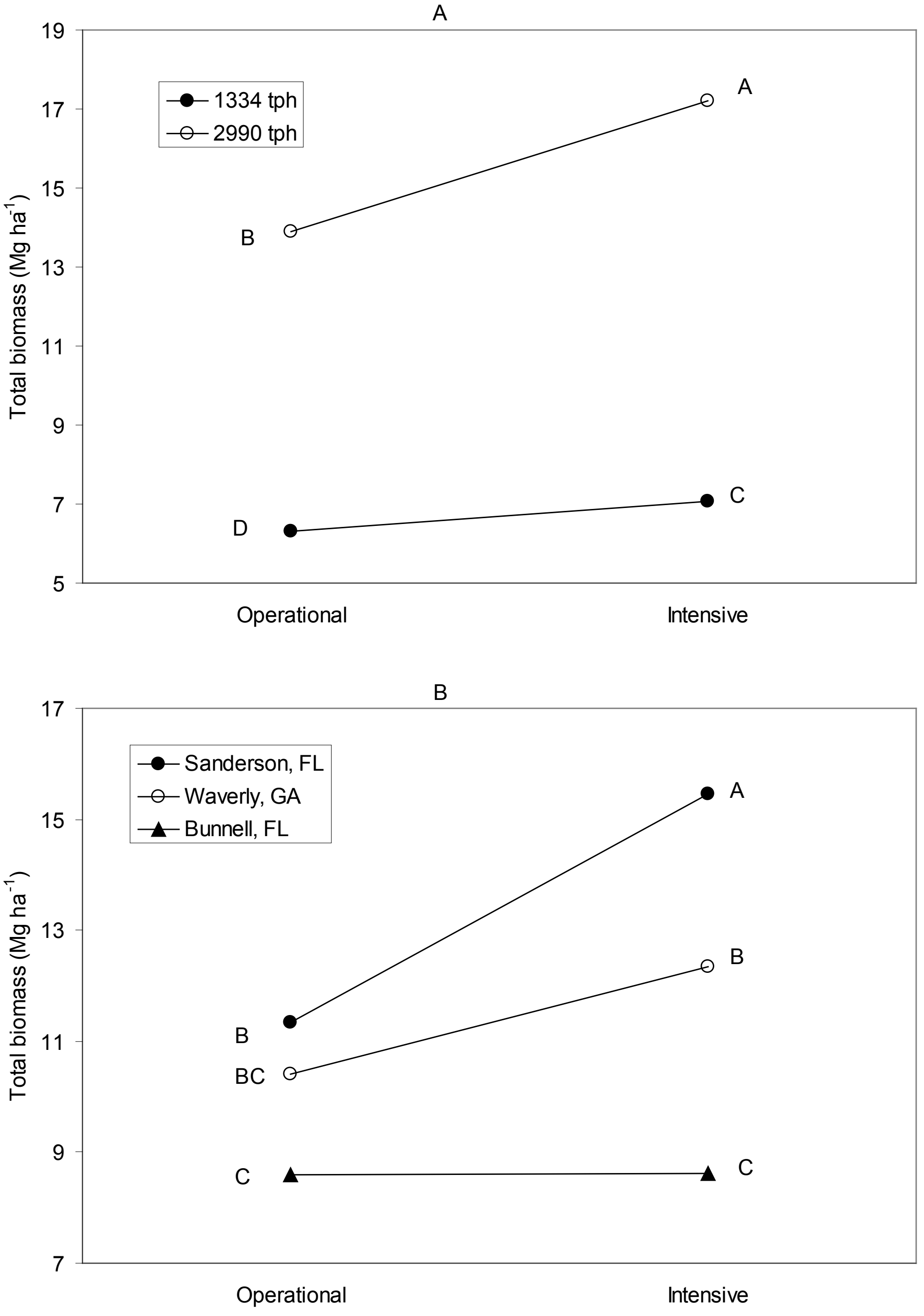

Figure 2-3. Least squares means for the effect of silvicultural intensity on loblolly pine total biomass accumulation as influenced by A) planting density (p=0.0003) and B) location (p=0.0005). Data points within graphs followed by the same letter are not significantly different at the 95% level of confidence using Bonferroni's least significant difference (LSD). Trees ha^{-1} is abbreviated as tph.

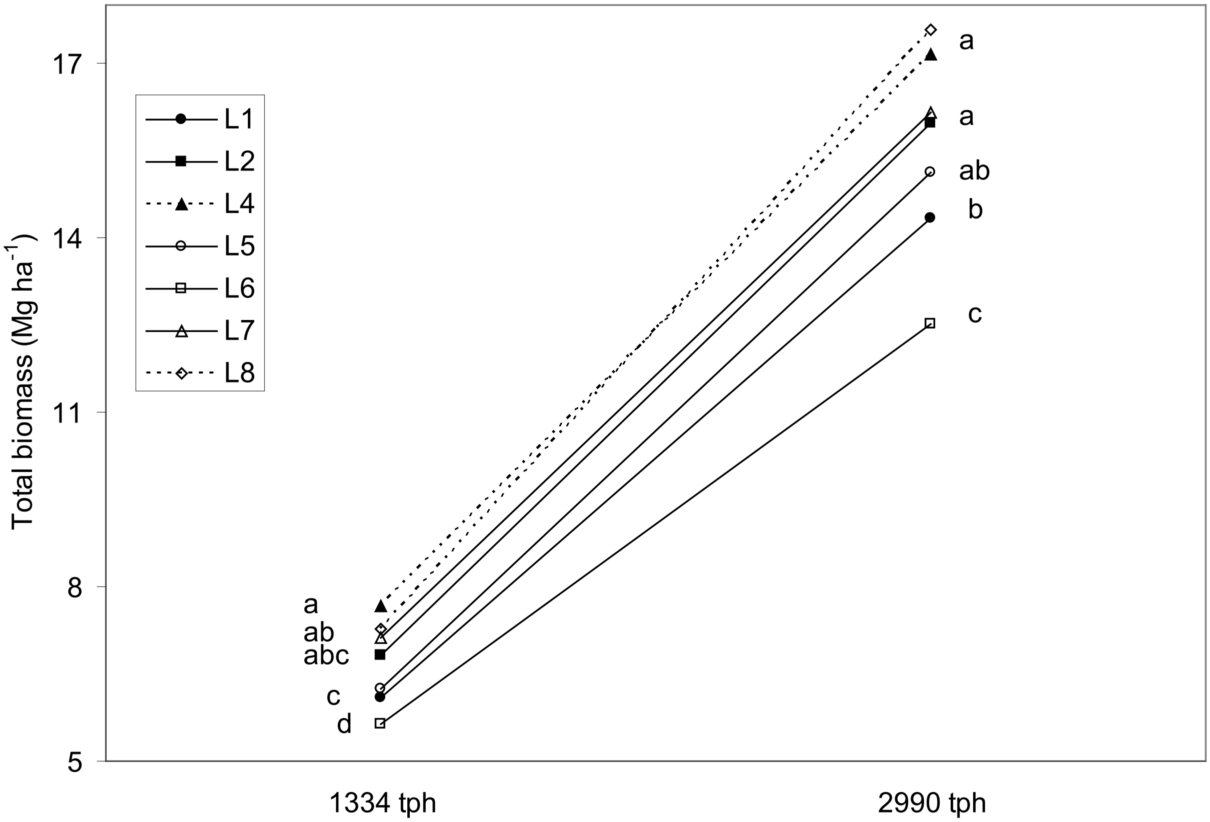

Figure 2-4. Least squares means for loblolly pine total biomass accumulation demonstrating an interaction between family and planting density (p=0.0192). Each data point is averaged across two silvicultural treatment intensities and three locations. While not statistically significant, notice the rank change between families L4 and L8 when planting density increased from 1334 to 2990 trees ha^{-1}. Trees ha^{-1} is abbreviated as tph. Data points within planting densities followed by the same letter are not significantly different at the 95% level of confidence using Bonferroni's least significant difference (LSD).

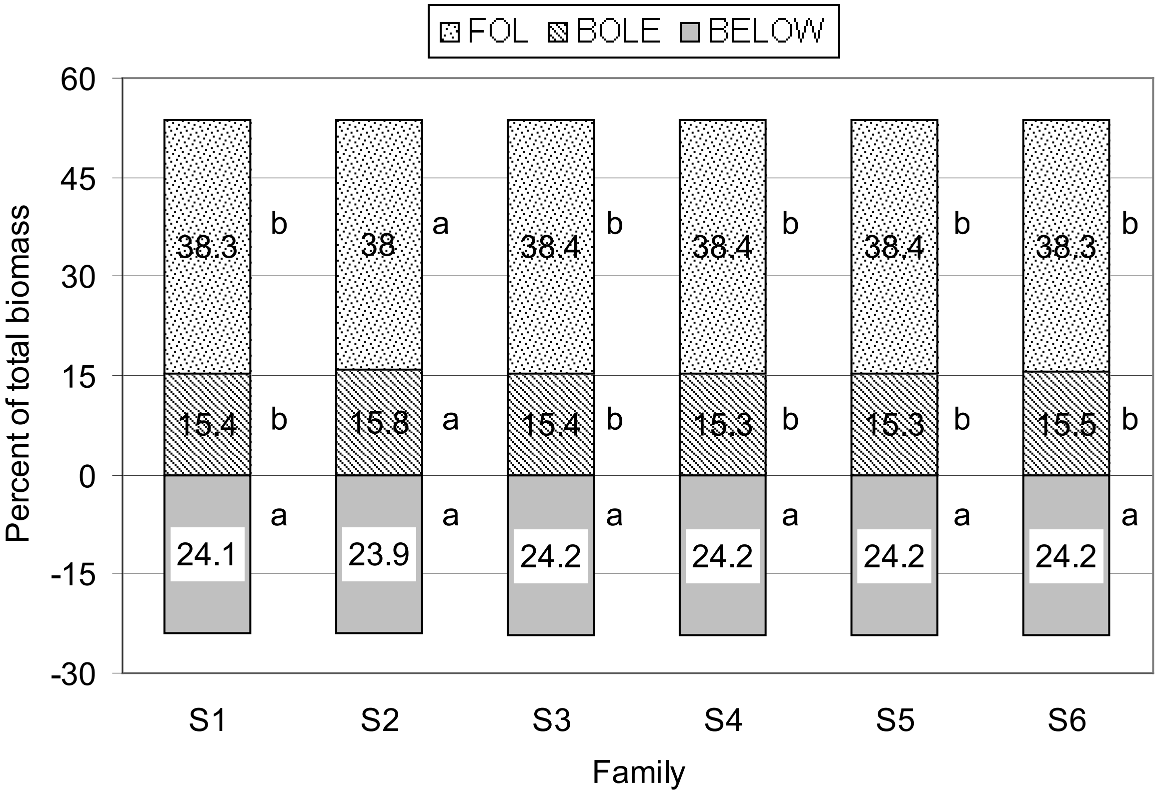

Figure 2-5. Least squares means for the main effect of full-sib family ($p<0.0001$) on slash pine biomass distribution to foliage (FOL), stemwood (BOLE), and belowground (BELOW) components expressed as a percentage of total biomass. Branch and bark data followed similar patterns and are not shown for simplicity. Data are at age two years and was averaged across two locations and planting densities. For each family having the same letter, biomass components were not significantly different at the 95% level of confidence using Bonferroni's least significant difference (LSD).

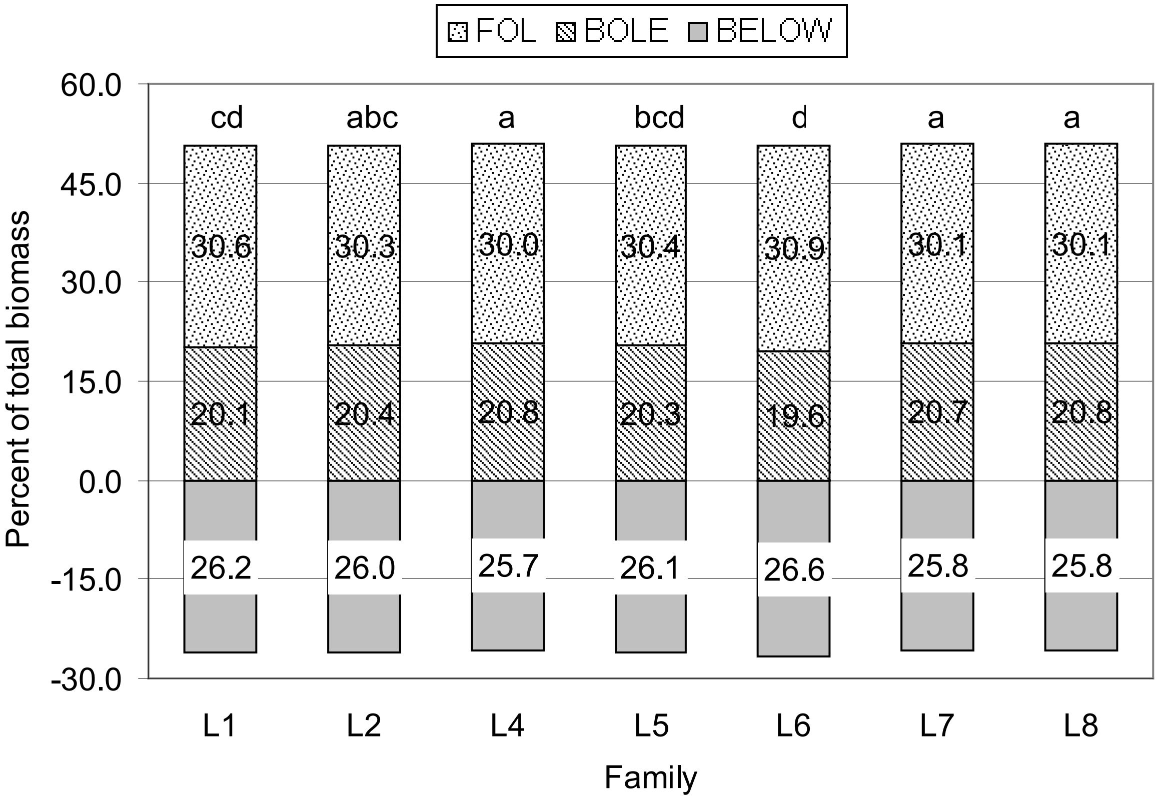

Figure 2-6. Least squares means for the main effect of full-sib family (p<0.0001) on loblolly pine biomass distribution to foliage (FOL), stemwood (BOLE), and belowground (BELOW) components expressed as a percentage of total biomass. Branch and bark data followed similar patterns and are not shown for simplicity. Data are at age two-years and was averaged across two locations and planting densities. For each family having the same letter, biomass components were not significantly different at the 95% level of confidence using Bonferroni's least significant difference (LSD).

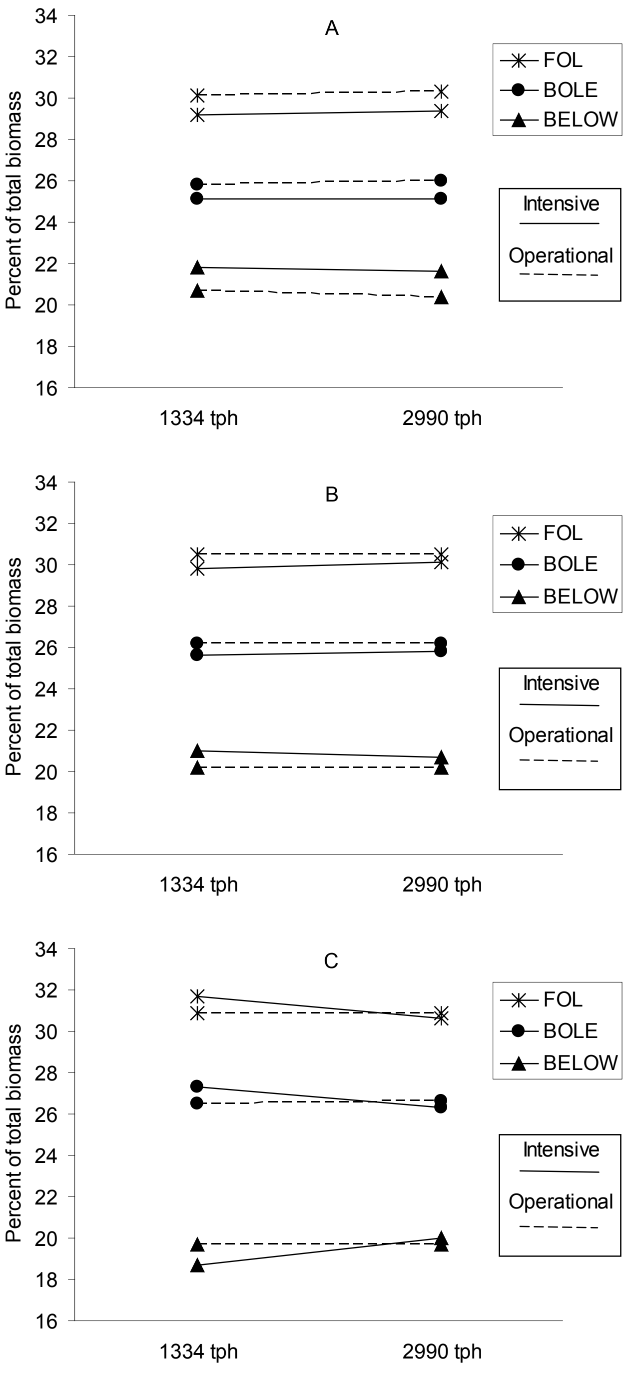

Figure 2-7. Loblolly pine biomass distribution to foliage (FOL), stemwood (BOLE) and belowground (BELOW) components demonstrating a three-way interaction (p<0.0001) between silvicultural management intensity, planting density, and location: A) Sanderson, FL B) Waverly, GA and C) Bunnell, FL. Planting density was expressed in trees ha-1 (tph)

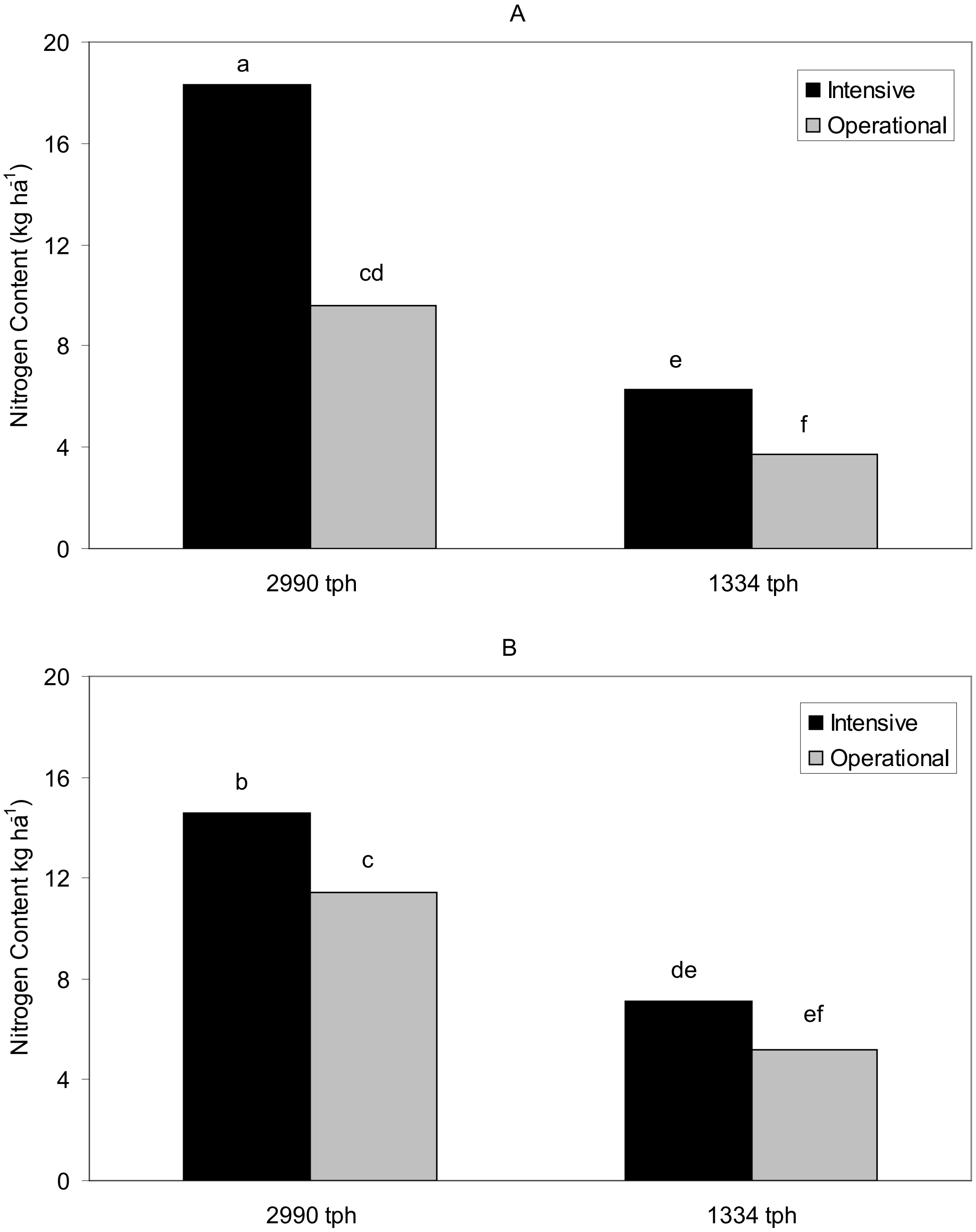

Figure 2-8. Belowground nitrogen content at age two-years demonstrating a significant three-way interaction (p=0.0012) between silvicultural intensity, planting density, and location: A) Perry, Fl, and B) Waldo, FL. Data were averaged across six full-sib families. Bars with the same letter across both locations were not significantly different at the 95% level of confidence using Bonferroni's least significant difference (LSD).

CHAPTER 3

FAMILY DIFFERENCES IN LIGHT INTERCEPTION AND RADIATION USE EFFICIENCY IN SELECTED LOBLOLLY (*Pinus taeda* L.) PLANTATIONS IN THE SOUTHEASTERN UNITED STATES

Introduction

Over the past three decades plantation forest productivity in the southeastern United States has been enhanced significantly through the active management of nutrition, weed control, genetic improvement and density management (Colbert *et al.*, 1990; Borders and Bailey, 2001; Jose *et al.*, 2003; Jokela *et al.*, 2004; Martin and Jokela, 2004b; Allen *et al.*, 2005c; Fox *et al.*, 2007). The aim has been to increase aboveground net primary productivity (ANPP) through rapid development of site occupancy and canopy leaf area index (LAI). Aboveground net primary productivity has been shown to be positively and linearly related to the amount of photosynthetically active radiation intercepted (IPAR) by the crowns (Cannell et al., 1987; Dalla-Tea and Jokela, 1991; McCrady and Jokela, 1998; Will et al., 2005). Forest managers can manipulate LAI through a combination of genetic selection and the application of silvicultural treatments that ameliorate site resource deficiencies. There is evidence that specific crown attributes in individual trees may make them more efficient at resource use and these traits could be exploited in tree breeding and production purposes (Martin *et al.*, 2001; Emhart *et al.*, 2007). While this approach has been successfully implemented in the case of annual cereal crops (Green, 1989; Siddique et al., 1989), it has yet to be demonstrated in forested plantations (Cannell, 1989).

The amount of photosynthetically active radiation (PAR) intercepted by a canopy is largely determined by the amount of foliage, as well as its distribution and orientation in the canopy (Sinclair and Knoerr, 1982; Colbert *et al.*, 1990; McCrady and Jokela, 1996). The slope of the relationship between ANPP and IPAR describes the efficiency of IPAR use in biomass production (Waring, 1983; Jarvis and Leverenz, 1983; Cannell *et al.*, 1987; Cannell *et al.*, 1988; Landsberg and Wright, 1989; Green *et al.*, 2001; Binkley *et al.*, 2004)(Equation 3-1) and is often referred to as Radiation Use Efficiency (RUE) (expressed in g MJ^{-1} of PAR intercepted) (Monteith, 1977; Sinclair and Muchow, 1999).

$$ANPP = IPAR \times RUE \tag{3-1}$$

As LAI and IPAR in forest plantations approaches a maximum, through the combination of deployment of elite genotypes and intensive silvicultural management, information about the efficiently of IPAR will become increasingly important.

Recently, there has been evidence that RUE is influenced by canopy structural properties in forest plantations (Chmura et al., 2007; Duursma and Makela, 2007, Duursma et al., 2010). The deep crowns of trees means that the relationship between individual leaf photosynthesis and absorbed light is strongly non-linear and any increase in incident radiation should theoretically lead to a decrease in RUE as a greater proportion of individual leaves in the canopy become light saturated (Monteith, 1977; Hollinger, 1989). However, in practice, this does not occur since not all the leaves in the canopy are light saturated due to shading from leaves higher in the canopy (Wang and Jarvis, 1990; Hilker et al., 2008). Therefore, in order to influence RUE the entire canopy light environment should be optimized via a combination of leaf acclimation to the light environment (Dewar et al., 1998) and a modification of canopy structure (Jarvis and Leverenz, 1983; Leverenz and Hinckley, 1990). This 'optimization' theory states that the greatest number of leaves should receive sufficient non-saturating energy to function near their photosynthetic potential (Hollinger, 1989). This has been demonstrated in tropical trees in South America, where leaf physiology, morphology and orientation were optimized such that leaf level RUE was maximized (Posada, 2003).

A quantifiable measure of leaf orientation and canopy structure is the light extinction coefficient (k), which describes the rate of decreased irradiance vertically through a canopy (Kira *et al.*, 1969; Falster and Westoby, 2003). This variable is influenced by leaf orientation, foliage clumpiness and canopy structure (Okerblom and Kellomaki, 1983; Gower *et al.*, 1999; de Castro and Fetcher, 1999). An erect display of foliage homogenizes the penetration of light through the canopy, which is especially effective at high levels of leaf area (Terashima and Hikosaka, 1995). In theory, RUE should increase with declining values of k (i.e. trending towards an erectophile orientation of leaves). Previous research in agricultural systems has demonstrated this effect in cultivars of wheat (*Triticum aestivum*) in Western Australia (Siddique et al., 1989) and rice (*Oryza sativa*) in Japan (Hayashi and Ito, 1962). It follows that the light extinction coefficient should play an important role in determining how much PAR is intercepted by a forested canopy (Gholz et al., 1991) and therefore should influence RUE in forest plantations (Dalla-Tea and Jokela, 1991; Sands, 1996; McCrady and Jokela, 1998; Medlyn, 1998). This theory was supported in a study comparing native and hybrid poplar clones grown at high densities in southern Wisconsin (Green et al., 2001). However, canopy structure and light interception are often difficult to measure in detail, especially across wide areas and short time periods. Emerging remote sensing technologies such as Lidar (light detection and ranging) have advanced to the stage where detailed measurements of crown structure (Roth *et al.*, 2007c) and light interception are now possible (Ahl et al., 2004; Lee et al., 2009) and should allow for more detailed investigations of variation in RUE in forested ecosystems.

Radiation use efficiency in forests is known to be influenced by site conditions such as water availability, fertility, and climatic conditions (Monteith, 1977; Runyon *et al.*, 1994; Prince and Goward, 1995; Balster and Marshall, 2000), which vary in time, elevation, soil type, and geographic location (Ares and Fownes, 2001; Stape, 2002; Stape *et al.*, 2004; Pangle *et al.*, 2009). Process based growth models modify RUE according to the stresses imposed by site resource limitations and climatic extremes in order to generate accurate estimates of production (Esprey *et al.*, 2004). For example, drought stress has been shown to reduce RUE in sweetgum (*Liquidambar styaciflura*) and sycamore (*Platanus occidentalis*) in Georgia (Allen et al., 2005a; Allen et al., 2005b), tropical ash (*Fraxinus uhdei* [Wenzing] Lingelsh) and Eucalyptus (*Eucalyptus camaldulensis*) in Hawaii (Harrington and Fownes, 1995; Ares and Fownes, 2001) and *E. grandis* x *urophylla* in Brazil (Stape et al., 2004).

Likewise, nutrition has been shown to have a positive influence on RUE in forests globally. For example, significant gains in RUE have been attributed to increased soil nutrient availability in loblolly pine (*Pinus taeda* L.) in the southeastern United States (Martin and Jokela, 2004a), Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) in British Columbia (Balster and Marshall, 2000), *Eucalyptus grandis* in South Africa (du Toit and Dovey, 2005; du Toit, 2008), and Sitka spruce (*Picea sitchensis* [Bong.] Carr.) in Central Scotland (Wang *et al.*, 1991). However, in contrast, some investigations concluded that RUE was not influenced by nitrogen fertilization. For example, while nitrogen inputs increased aboveground productivity in stands of sweetgum and sycamore in Georgia, it did not influence RUE (Allen et al., 2005b). The same effect was reported in an experiment with loblolly and slash pine (*P. elliottii* Engelm. var. *elliotttii*) in north central Florida (Dalla-Tea and Jokela, 1991). In these studies, the authors concluded that changes in growth following fertilization were due to increased LAI and light capture, rather than changes in RUE.

Genotype x environment studies of RUE are uncommon in forested ecosystems and results have been inconclusive. Radiation use efficiency did not vary between a mixed species deciduous and a coniferous plantation forest type along a 260 meter elevation gradient in North Carolina (Pangle et al., 2009). While there were significant differences among forest types along a transect in Oregon, the experimental design did not allow for the examination of the stability of RUE among these genotypes across environmental gradients (Runyon et al., 1994). Radiation use efficiency was not stable among four tropical species in Hawaii when grown under contrasting plantation establishment regimes (i.e., planted versus coppiced) (Harrington and Fownes, 1995). Similarly, RUE among four species (loblolly pine, slash pine, sweetgum, and sycamore) was dependant upon the treatments of fertilization and irrigation (i.e. species x silviculture) in a trial in Georgia (Allen et al., 2005a). In that study, fertilization and irrigation increased RUE in sycamore, yet sweetgum was only influenced by fertilization, and the pines were not affected. In a factorial species x irrigation x fertilization study in north central Florida, there were differences in RUE between loblolly and slash pine, but these did not interact with irrigation nor fertilization at age 6-years (Martin and Jokela, 2004a).

The current investigation of light interception, crown attributes and RUE builds on that of McCrady and Jokela (1998), who found differences in RUE among loblolly pine families, but did not test for the stability of these traits across an environmental gradient. The current investigation is unique, in that it is the first to examine the stability of loblolly pine performance grown under intensive silviculture in large full-sib family block plots across locations of contrasting site properties. The main objective of this study was to detect and describe the nature and extent of genotype x location interactions in loblolly pine IPAR and RUE at age four-and five-years. Within this larger framework, specific objectives were to: 1) quantify NF, LAI and *k* among families and between locations 2) quantify ANPP, the fraction of light intercepted (*f*), and IPAR among families and between locations, 3) quantify RUE among families and between locations, and 4) determine if family performance in these parameters was stable across locations.

Materials and Methods

Experimental Site and Design

This investigation was carried out at two study locations in Sanderson, FL (29.28 ^{0}N, 82.33 ^{0} W) and Waverly, GA (31.28 ^{0}N, 81.75 ^{0} W). The topography at both locations was nearly flat with slopes less than 1%. The soils at the Sanderson, FL and Waverly, GA locations were mapped as the Leon (sandy, siliceous, thermic Aeric Alaquods; formed in thick beds of acid sandy marine sediments) and Bladen series (mixed, semiactive, thermic Typic Albaquults; formed from deposits of clayey fluvial or marine sediments), respectively. The sandy soils at the Sanderson, FL location were generally poor in fertility and trees responded well to nutrient additions. The clay loam soils at the Waverly, GA location were acutely phosphorus deficient, but supported high and sustained levels of productivity when fertilizer additions were made (Pritchett and Comerford, 1982; Jokela *et al.*, 1989). The climate varied little between locations and was characterized as humid and sub-tropical, with average annual temperatures ranging from 19 to 21 ^{0} C. Long-term annual precipitation, from 1931 to 2000, averaged 1384 mm across locations (NOAA, 2002).

The field experiments used in this investigation were part of a larger set of genotype x silviculture x planting density studies (Roth *et al.*, 2007a). In this analysis, four complete blocks per location were sampled and consisted of six full-sib loblolly pine families grown under intensive silvicultural management and at an initial planting density of 2990 trees ha^{-1}. Trees within a family block were planted at a 1.22 m x 2.75 m spacing and were arranged in eight beds of 16 planting positions each, for a total of 128 trees per gross treatment plot. A two tree border around the perimeter resulted in a 48 tree interior measurement plot of 0.016 ha. Prior to planting, the study sites were double bedded on separate passes following a 2.75 meter spacing. In the late summer/early fall of 1999, each location was treated with pre-plant herbicides consisting of Chopper® (imazapyr) at 1.02 $\ell \cdot \text{ha}^{-1}$ and Garlon® (triclopyr) at 7.02 $\ell \cdot \text{ha}^{-1}$, with the goal of removing all woody competition and reducing initial levels of herbaceous vegetation. The objective was to minimize within location environmental variation caused by competition for site resources from associated vegetation. For two years following planting, competing vegetation was controlled using directed applications of Arsenal® (imazapyr) at 0.28 $\ell \cdot \text{ha}^{-1}$ and Oust® (sulfometuron methyl) at 0.14 $\ell \cdot \text{ha}^{-1}$, with the objective of maintaining ground cover below a 30% threshold. At the time of planting, the plots were fertilized with 560 kg ha^{-1} of 10-10-10 plus micronutrients, which was followed by annual applications of macro- and micronutrient fertilizers based on prescriptions developed from foliar analyses. The total amounts of nutrients applied on each installation through age five are presented in Table 3-1.

All genetic entries in the study were selected from sources exhibiting moderate to excellent resistance to fusiform rust [*Cronartium quercum* (Berk.) Miyabe ex Shirai f. sp. fusiforme] based upon a priori knowledge from tree breeding programs and progeny tests. This was done in order to reduce the confounding effects of disease incidence. Seedlings were grown in Ray Leach 'Cone-tainer'TM cells (Stuewe and Sons, Inc Corvallis, OR), consisting of 66 ml cell^{-1} and were hand planted over a two day period in January 2000. Overall survival following planting was greater than 95%, with low mortality rates in the subsequent years.

Insecticides were uniformly applied across all treatments on loblolly pine installations in an effort to control damage from the Nantucket pine tip moth (*Rhyacionia frustrana* [Comstock]). Treatments were applied on a monthly basis over the first two growing seasons, beginning in March and ending in September. Alternating applications of the following chemicals and application rates were applied aerially or by hand: Pounce® 3.2EC (62 ml product ℓ^{-1} water), Warrior T® (39 ml product ℓ^{-1} water), Dimilin® 25W (62 ml product ℓ^{-1} water), and Mimic® 2LV (125 ml product ℓ^{-1} water).

Inventory and Aboveground Biomass Estimates

Diameter (DBH) was measured annually at ages three (2003), four (2004) and five (2005) years on all trees in the 48 tree measurement plots. Total height (HT) was measured on all trees at age 3 and a random 20% sub-sample at ages 4 and 5. Individual tree HT at ages 4 and 5 were estimated using site specific HT vs. DBH regression models developed from this sub-sample. Aboveground biomass estimates (AGB), expressed in units of Mg ha^{-1} of dry matter, were developed using linear allometric equations developed from these same studies (Roth *et al.*, 2007a). Additional variables such as surviving tree density, height to live crown, crown ratio, and projected crown area at age five years were measured in order to help explain any associations with treatment related differences via covariate analysis.

Needlefall, Leaf Area Index, and Aboveground Net Primary Production

Needlefall (NF) was collected an average of six times per year over a three year period (June 2003 to February 2007) to estimate leaf area index (LAI). Within each family measurement plot, six circular littertraps (1.0 m^2 each) were deployed, with half randomly positioned along the bed and inner bed positions. Litter was almost exclusively pine foliage (> 98%) and was separated from other pine material (branch, bark, twigs and cones), oven dried at 70^{0}C and weighed to the nearest 0.1 g.

Foliar biomass accretion was modeled using logistic equations fitted to measured NF data (Kinerson *et al.*, 1974; Dougherty *et al.*, 1995). This approach assumed that: (1) within a given year all needles that formed had died and senesced from the tree by February 28, two calendar years following their formation (i.e. maximum needle lifespan was no greater than two years), and (2) that the accretion curve was not affected by family or location, (3) and the phenological year for foliage accretion began on March 1 (Martin and Jokela, 2004a). Therefore, total NF in a given phenological year (March 1 - February 28) represented total needle production in the previous year. In this study, we were able to calculate foliage biomass accretion over a two year period (ages 4 to 5 yrs). Needlefall data were corrected for losses due to senescence, which were estimated to be 14% for loblolly pine (Dalla-Tea and Jokela, 1991). Projected LAI was calculated as the product of NF mass (based on 1.0 m^2 litter traps) and family level specific leaf areas (SLA) measured within each location. Specific leaf area (m^2 g^{-1}) was determined using the volume displacement method (Johnson, 1984) on foliar samples that were collected from individual families in the fall of 2003. Aboveground net primary productivity (ANPP) was calculated as the difference between unit-area standing biomass (AGB) on an annual basis, which included annual NF (Equation 3-2):

$$ANPP = \sum AGB_{t2} - \sum AGB_{t1} + \sum_{t1}^{t2} NF \tag{3-2}$$

While mortality was accounted for, herbivory was assumed to be insignificant in these young trees during this period, and was not included in this calculation of ANPP (Clark *et al.*, 2001).

Fraction of PAR Intercepted, Light Extinction Coefficient

The fraction of PAR intercepted (*f*) was calculated from measurements of above and below canopy PAR (Equation 3-3):

f = 1 – (PAR transmitted through canopy/ PAR incident at top of canopy). (3-3)

The amount of PAR transmitted through the canopy was measured using a handheld Sunfleck Ceptometer (Decagon Devices 1987), which measured below canopy PAR of each family block plot (at 1.37 meter elevation). Incident PAR above the canopy was measured in an adjacent open area using a quantum light sensor (LI-COR 190SA) linked to a data recorder which continuously recorded PAR on a 5 second interval, and stored averages per minute. At regular intervals during the sampling period, measurements of PAR with the two sensors were conducted side by side to ensure concurrence. Six permanent transects running perpendicular to the beds were sampled and recorded for each plot, which included gaps in the canopy. A mean of eight sub-samples were averaged along each transect and the six transects averaged to obtain a per plot value. Data were collected on a regular interval during the growing seasons (March through October) of 2004 and 2005 under cloud free conditions between 1100 and 1400 h solar time (Table 3-2).

The light extinction coefficient (k) was empirically determined using an equation derived from the Beer-Lambert law (Equation 3-4) and measured values of projected LAI (all-sided/pi;(Grace, 1987) and f):

$$k = (\log(1-f))/\mathrm{LAI} \tag{3-4}$$

Since k varies by the angle of the sun (Stenberg *et al.*, 1994), season specific sun-angle values of the extinction coefficient k were cosine corrected ($k/\cos 50^0$) for the solar zenith noon at each sampling date. The Beer-Lambert law assumes a homogenous uniform distribution of leaves along the path of light (Kira *et al.*, 1969). This assumption is easily violated in pine forests, especially in mature stands where the canopy is highly aggregated (Gholz *et al.*, 1991). However, given that the current investigation was carried out in dense young stands planted to a regular spacing with a uniform canopy, it was assumed that the Beer-Lambert assumptions were met and that the estimates of k were valid for comparing relative family and silvicultural treatment effects (Gower *et al.*, 1999; de Castro and Fetcher, 1999). In a related study, the methodology for estimating IPAR and k using the Beer-Lambert law was validated in a young loblolly pine experiment in north central Florida (Martin and Jokela, 2004a).

Amount of PAR Intercepted and Radiation Use Efficiency

Estimates of intercepted PAR over each growing season (MJ m^{-2} y^{-1}) were calculated by summing monthly estimates of incoming shortwave radiation (total direct and diffuse solar radiation received on a horizontal surface) and multiplying by the plot level fraction of PAR intercepted (*f*), centered around each sampling period (monthly values interpolated) (Table 3-2). The satellite-derived solar estimates were obtained for each study site using 10 km modeled grid data available from the National Solar Radiation Data Base (NSRDB), 1991 – 2005 update (ftp://ftp.ncdc.noaa.gov/pub/data/nsrdb-solar Last accessed March 2009). We assumed that incoming PAR was 50% of the total incoming shortwave radiation (Landsberg and Waring, 1997; Waring and Running, 1998). Growing season (March to October) PAR interception was used since ceptometer measurements were problematic when the sun angle was low during the winter months. The consequence of this was that values of RUE would be slightly higher than published estimates of RUE using year-long IPAR data. Aboveground radiation use efficiency of each family was determined annually by dividing ANPP by the sum of intercepted PAR over the growing season (March - October) and was expressed as g MJ PAR^{-1}.

Statistical Analyses

Analysis of variance (ANOVA) was used to test for stand level differences in the variables of interest between locations and among families, including their interactions at ages 4 and 5 years using PROC MIXED (Littel *et al.*, 1996) in SAS. Two forms of the mixed linear model were used, since some variables were measured on a monthly basis and others on an annual basis. The response variables of LAI, *k*, and *f* were examined utilizing Equation 3-5:

$$Y_{ijklmn} = \mu + L_i + b(l)_{ij} + F_k + Y_l + LF_{ik} + LY_{il} + b(l)F_{ijk} + b(l)Y_{ijl} + FY_{kl} + M_m + FM_{km} + LM_{im} + w_{ijklmn} \qquad (3\text{-}5)$$

where Y_{ijklmn} is the response variable (LAI, k, and f) of the nth plot of the mth month of the lth year of the kth family of the jth block of the ith location ($i = 1,2$; $j = 1,2, \ldots, 4$; $k = 1,2, \ldots, 6$; $l = 1,2$; $m = 1,2, \ldots, 4$; and $n = 1$); μ is the overall mean; L_i is the fixed effect of the ith location; $b(l)_{ij}$ is the random interaction effect of the jth block within the ith location; F_k is the fixed effect of the kth family; Y_l is the fixed effect of the lth year; M_m is the fixed effect of the mth month; and w_{ijklmn} is the random error.

The response variables of NF, ANPP, and RUE were examined utilizing Equation 3-6:

$$Y_{ijklm} = \mu + L_i + b(l)_{ij} + F_k + Y_l + LF_{ik} + LY_{il} + b(l)F_{ijk} + b(l)Y_{ijl} + LFY_{ikl} + COV_{ijklm} + w_{ijklm} \qquad (3\text{-}6)$$

where Y_{ijklm} is the response variable (NF, ANPP, and RUE) of the mth plot of the lth year of the kth family of the jth block of the ith location ($i = 1,2$; $j = 1,2, \ldots, 4$; $k = 1,2,\ldots, 6$; $l=1,2$; and $m = 1$); μ is the overall mean; L_i is the fixed effect of the ith location; $b(l)_{ij}$ is the random interaction effect of the jth block within the ith location; F_k is the fixed effect of the kth family; Y_l is the fixed effect of the lth year; COV is the covariate of interest where applicable; and w_{ijklm} is the random error.

For both models, blocks were nested within locations. Block within locations $b(l)_{ij}$ was considered a random effect, as are all terms containing $b(l)_{ij}$. Where a covariate was significant at $p=0.05$ it was included in the model, otherwise it was excluded (the only significant covariate was age five stand density on RUE). Where assumptions of normality and constant variance were not met the variables were log transformed prior to analysis. Significant effects were examined comparing least squares means using Bonferroni's adjusted significance level.

Results

Needlefall, Leaf Area Index, and Aboveground Net Primary Production

Variation in annual NF was dependant on the combined effects of location and year ($p < 0.0001$, location x year interaction), and to a lesser degree for the main effect of family ($p=0.1054$). In 2004, the greatest NF occurred at the Sanderson, FL location (5.12 versus 3.88 Mg ha^{-1} yr^{-1} for Sanderson, FL and Waverly, GA, respectively); however, in 2005 this trend had reversed, with the Waverly, GA location producing the greatest NF (3.72 versus 5.05 Mg ha^{-1} yr^{-1} for Sanderson, FL and Waverly, GA, respectively). Differences in family level NF were stable across years ($p=0.1332$, genotype x year) and locations ($p=0.7533$, genotype x location). Needlefall amounts among families, averaged across both locations and years, varied relatively little and ranged from 4.05 to 4.63 Mg ha^{-1} yr^{-1} for families L1 and L7, respectively (Table 3-3).

There were significant location x year and location x month interactions for mean projected LAI ($p=0.0002$ and $p<0.0001$, respectively). The location x year interaction was caused by differences in LAI at the Sanderson, FL location between years. While LAI in 2004 was similar between locations, the amount of LAI in 2005 had declined by approximately 20% at the Sanderson, FL location (Table 3-4). Plotting the trend over time (Figure 3-1a) demonstrated that this decline at the Sanderson, FL location began in September 2004. By the following year (2005), the decline in LAI at Sanderson, FL had stabilized and then tracked parallel to the trends observed at the Waverly, GA location. The significant location x month interaction was caused by a steeper decline in LAI at the Sanderson location in the fall months (Figure 3-1b).

Additionally, mean projected LAI between years was not stable among families ($p=0.0218$, genotype x environment interaction). While LAI decreased for all families, LAI significantly deceased in 2005 for families L5, L7 and L2 (19, 17, and 14%, respectively) (Table 3-5). In contrast, family L1 was the most stable with an LAI of 1.9 m^2 m^{-2} in 2004 vs. 1.7 m^2 m^{-2} in 2005.

Unlike NF and LAI response, there were no interactions between factors for ANPP; only the main effects of year (p=0.0079) was statistically significant. There was a 10% decline in overall ANPP from year to year (20.9 to 18.8 Mg ha^{-1} yr^{-1} for 2004 and 2005, respectively). Family performance for ANPP remained stable across locations and years, with subtle differences (10%) between the top producing and poorest growing family (Table 3-3).

Fraction of PAR Intercepted, Light Extinction Coefficient

There were location x year (p=0.0001), location x month (p=0.0007), and family x month (p=0.0053) interactions for the fraction of PAR intercepted. As with LAI, the variable response in *f* across time occurred at a single location (Sanderson, FL). When averaged across families, the fraction of PAR intercepted at the Sanderson, FL location had declined from 0.739 in 2004 to 0.667 in 2005 (Table 3-4). Averaged across years, the Sanderson, FL location had a steeper decline in *f* in the month following peak LAI (August) than did the Waverly, GA location (Figure 3-4a). Families were not stable across months averaged between years, with the overall greatest instability occurring in March and the least in September. Overall, family L4 was the most stable, with families L1 and L2 the least and families L5, L7, and L8 intermediate (Figure 3-5).

Locations were unstable across years and months for the sun angle cosine corrected light extinction coefficient (*k*) (p<0.0001). The location x year interaction was again influenced by the Sanderson, FL location, where significantly higher *k* values existed in 2005 than at the contrasting Waverly, GA location (0.83 versus 0.44) (Table 3-4). Values of *k* between locations in 2004 were similar averaging between 0.42 and 0.44. The location x month interaction was also due to instability at the Sanderson, FL location. Averaged across both years, *k* was significantly higher in the month of May at the Sanderson, FL location (0.88) than at the Waverly, GA location (0.60) (Figure3-4b). There were large differences in growing season *k* among families, which ranged from 0.43 for family L4 and 0.67 for family L1 (Table 3-3). Low values of *k* (tending toward an erectophile display of foliage) allow for a deeper penetration of light through the canopy than higher values (tending toward planophile).

Amount of PAR intercepted and Radiation Use Efficiency

The total amount of PAR intercepted by the canopy during the growing season varied by the main effect of family (p=0.0291) and demonstrated a location x year interaction (p=0.0002). Family variation in IPAR ranged from 1719 to 1857 MJ m^{-2} yr^{-1} for families L1 and L8, respectively (Table 3-3). Family L7 performance was similar to L8 and it intercepted 1856 MJ m^{-2} yr^{-1}. The Sanderson, FL location was the most reactive across years for IPAR (Table 3-4). At this location, a reduction in the amount of PAR intercepted occurred in 2005 (from 1639 to 1819 MJ m^{-2} yr^{-1} from 2004 to 2005, respectively).

Aboveground net primary productivity was positively related to IPAR (Figure 3-2) and the slope of this relationship (RUE) was different among families (p=0.0161), with efficiency values ranging from 1.08 to 1.16 g MJ^{-1} (families L8 and L4, respectively) (Table 3-3). For a given amount of IPAR, family L4 produced more aboveground biomass than did family L8 when averaged across locations and years. There were no location x year interactions for RUE and families did not vary in RUE across locations or years. However, covariate analysis indicated a strong positive influence of surviving tree density in 2005 on RUE (p=0.0005) (Figure 3-3). This was the only covariate that was significant for any variable examined. Radiation use efficiency increased by about 0.2 g MJ^{-1} across the range of observed tree density (1334 to 2990 trees ha^{-1}) in this study at age five.

Discussion

This investigation provided the unique opportunity to examine the stability of PAR interception and RUE in selected elite full-sib families of loblolly pine when deployed in uniform blocks and grown under an intensive silvicultural treatment regime over time and contrasting locations (see Appendix B and C). This study provided information about the extent that genotype x environment interactions influenced RUE, which can be particularly useful in the development and utilization of process-based growth models (Landsberg and Hingston, 1996; Landsberg and Waring, 1997; Esprey *et al.*, 2004). While there was variation among families, there was no evidence for genotype x environment interactions (i.e. genotype x location, genotype x year, or genotype x month) in RUE.

The annual NF observed in this investigation ranged from 3.7 to 5.1 Mg ha^{-1}, which corresponds with published literature for loblolly pine: 4.6 Mg ha^{-1} at age six (Dalla-Tea and Jokela, 1991; Jokela and Martin, 2000) and 4.7 to 5.7 Mg ha^{-1} among selected families at age five (McCrady and Jokela, 1998). Annual NF at age four was about 5.0 Mg ha^{-1} for family L4 in a separate experiment (Adegbidi *et al.*, 2005). There was a large decline in NF at the Sanderson, FL location in 2005, and climatic conditions have been shown to alter levels of annual NF (Dougherty *et al.*, 1995). This effect was most likely due to early leaf senescence related to the effects of hurricanes Frances and Jeanne in 2004. Since the Waverly, GA location was further away from the storm paths, it was largely unaffected by these severe windstorm events (Roth *et al.*, 2007a). The effect of declining NF following these hurricanes was also observed and documented in another trial in Florida (Li *et al.*, 2007).

Projected LAI varied among years and locations and ranged from a low of 1.7 to a maximum of 3.3 m^2 m^{-2}. These values were lower than those reported for loblolly pine of around 4.0 m^2 m^{-2} at a similar stage of stand development (Allen *et al.*, 2005a) and yet were within the upper limit of 3.2 m^2 m^{-2} observed in a series of intensively managed loblolly pine plantations at age four years (Adegbidi *et al.*, 2002). Following the normal pattern of leaf accretion over a growing season, values of LAI increased to a maximum in August and declined to a minimum in March. However, as with the observed pattern of NF, the decline in LAI in the fall at the Sanderson, FL location was much more dramatic than at Waverly, GA. Since the Sanderson, FL location is inherently less fertile, this may be due in part to the curtailment of fertilization in 2003 and the hurricanes in 2004 (fertilization was resumed in 2005). In a nearby trial, loblolly pine LAI declined significantly within a year following curtailment of fertilization, and declined by as much as 12.6% after four years (Martin and Jokela, 2004b). It follows that the amounts of nutrients added in 2003 may have also been insufficient to meet the demands of these rapidly developing crowns and stands, especially on the inherently nutrient poor site at Sanderson, FL. Examination of LAI on the family level between years, demonstrated that certain families were able to hold higher levels of LAI despite the overall decline in 2005 across both locations. As predicted by McCrady and Jokela (1998), it follows that these were the most productive families, and could be characterized as having the crown structural properties of 'crop ideotypes' as described by Martin and others (2001).

Crown structural properties influence the amount of light intercepted by individual trees within a forest canopy and play important roles in determining the competitiveness of individual trees (Cannell, 1978). Traits such as the distribution of leaves within the canopy are under some level of genetic control (Emhart *et al.*, 2007; Chmura and Tjoelker, 2008). For example, in a companion study, which compared elite families of loblolly and slash pine in the Western Gulf region of the United States, family L4 exhibited the largest number of flushes and had a different crown shape with longer branches in the mid-crown position (Chmura *et al.*, 2007). The authors suggested that this most likely led to better light-capture and greater carbon assimilation and aboveground biomass accumulation.

The current investigation examined differences in the light extinction coefficient *k* and how it was influenced by the combined effects of family, location and year. Cosine corrected values of *k* averaged about 0.44 across locations and years, with the exception of a significantly high value which occurred at the Sanderson, FL location in 2005 (*k*=0.83). With the exception of this outlying value, these estimates were in general agreement with the published literature. A mean of 0.33 was documented among five loblolly pine families in a four-year-old experiment (McCrady and Jokela, 1998). In a 14-year-old loblolly pine experiment, *k* values ranged from 0.36 to 0.64 (Sampson and Allen, 1998), while a *k* of 0.46 was documented in a 15-year-old loblolly pine plantation in North Carolina (Sinclair and Knoerr, 1982). Across several lodgepole pine stands in Wyoming, *k* varied from 0.3 to 0.7 for a wide range of stand and site conditions, with lower *k* values associated with higher values of LAI (Sampson and Smith, 1993). This was also documented among five elite families of loblolly pine, where families with the largest LAI also had the lowest values of *k* (McCrady and Jokela, 1998). In theory, low values of *k* will allow for a deeper penetration of light into the canopy and therefore greater RUE given similar amounts of IPAR. In support of this theory, variation in *k* has been shown to be related to RUE among five cultivars of wheat (Green, 1989) and five hybrid poplar clones (Green *et al.*, 2001). In these experiments, RUE was greatest in cultivars and clones with lower values of *k*, despite similar amounts of IPAR. There was some evidence in the current investigation to support this trend as family L4 exhibited the greatest values of RUE combined with the lowest *k*.

Aboveground net primary productivity was similar among the families examined in this investigation. This likely resulted because the families were all chosen for superior performance in growth. Similarly, the silvicultural treatments applied in this experiment, which combined high planting density with intensive silvicultural management, likely evened the inherent differences in site quality between the locations. Presumably, this may account for the lack of observed differences in ANPP between locations. The lack of a genotype x location interaction in ANPP was supported in a recent study which compared deciduous and pine forest types along an elevational gradient in North Carolina (Pangle *et al.*, 2009). The authors noted no differences between forest types for ANPP; however, there were large differences in RUE.

Individual families varied in their RUE, but were stable between locations and years (i.e. no genotype x environment interaction). Family level growing season RUE values in this study ranged from 1.08 to 1.16 g MJ^{-1}; however, due to differences in methodology in the calculation of IPAR (most studies report RUE on an annual basis), direct comparisons of RUE among other studies requires interpolation. With this in mind, the RUE values reported in this investigation were generally consistent with others reported for loblolly pine. They were bounded by annual estimates reported by Martin and Jokela (2004a) and Dalla-Tea and Jokela (1991) of 0.40 g MJ^{-1} and 0.81 g MJ^{-1}, respectively in north central Florida. The values of RUE in the current investigation were also greater than those reported for loblolly pine in Georgia of 0.795 g MJ^{-1} (Allen *et al.*, 2005a). In contrast, McCrady and Jokela (1998) documented RUE ranging from 1.33 to 1.48 g MJ^{-1} among five loblolly pine families in South Carolina, and Allen *et al.* (2005b) reported values ranging from 1.39 to 1.74 g MJ^{-1} for sycamore and sweetgum in Georgia, respectively. The total amount of variation in RUE among the families tested in this experiment was marginal. A similar effect was found among poplar clones; however, those were from random sources which had not been selected for improved growth (Landsberg and Wright, 1989). The lack of large differences in RUE among the families in the current experiment may be due to the highly productive nature of the elite loblolly pine families that were selected for inclusion in the experiment, which did not vary in ANPP. At a species level, RUE and growth efficiency among genotypes tends to vary the greatest where contrasting species (Allen *et al.*, 2005a; Cobb *et al.*, 2008) and families (McCrady and Jokela, 1998) were tested.

Evidence from other studies suggests the greatest responses in RUE have occurred where the most limiting site resources have been manipulated (Stape, 2002; du Toit, 2008). For example, fertilization increased RUE of stemwood production of Douglas-fir across a series of locations with wide range of site quality in the interior region of the Pacific Northwest USA (Balster and Marshall, 2000) and in an eight-year-old loblolly pine experiment on a nutrient poor, deep sandy soil in North Carolina (Albaugh *et al.*, 2004). However, there was no effect of fertilization and weed control on the RUE of loblolly and slash pine on three locations in the Western Gulf of the United States (Chmura and Tjoelker, 2008), possibly since all three were productive sites. In contrast, this hypothesis was not supported for two experiments growing on nutrient poor locations where fertilization did not influence RUE (Dalla-Tea and Jokela, 1991; Allen *et al.*, 2005a).

Similar to anthropogenic manipulations of site resources, natural variation along resource gradients can influence RUE in forests (Stape *et al.*, 2004). While RUE was stable along a 260 m elevational gradient in two deciduous and pine forest types (Pangle *et al.*, 2009), this was not the case along a much steeper elevational gradient in Hawaii (Ares and Fownes, 2001). In this latter investigation conducted with tropical ash, RUE was reduced at the higher elevations where site resources were most limited. In keeping with the theory that the greatest interactions for RUE occur under conditions where resources are most limiting, RUE varied the most on nutrient poor Andisols, as compared to the relatively nutrient rich Histosols (Ares and Fownes, 2001). The stability of RUE across locations documented in the current investigation, despite inherent differences in productivity between the soil types, may be due to the leveling effects of the intensive silviculture treatments which ameliorated limiting site resources on the least productive site (see chapter 2).

The current investigation noted a trend of increasing RUE with increasing tree density after five years from planting (Figure 3-3). This effect has been documented previously where closely spaced stands tended to be more efficient at capturing and utilizing PAR than widely spaced stands (Burkes *et al.*, 2003), perhaps due to less variation in horizontal needle distribution (Smith and Long, 1989; Smith *et al.*, 1991; Smith and Long, 2001). Part of this phenomenon may be that stands growing at higher densities tend to have a more even distribution of foliage within their canopies, which leads to increased efficiency in light interception (Will *et al.*, 2001; Will *et al.*, 2005). However, it has also been demonstrated that growth efficiency varies with changes in biomass allocation due to increasing planting densities (Burkes *et al.*, 2003). Yet, in older stands, RUE in loblolly pine was found to decrease with stand basal areas exceeding 18 m^2 ha^{-1} (Martin and Jokela, 2004a). The authors demonstrated that this association was driven by decreases in woody biomass increment due to stand aging at full stocking. This was also demonstrated among poplar clones in China, where growth efficiency declined at the highest planting densities (Fang *et al.*, 1999). Results from the current study suggest that there is room to exploit differences in RUE among selected families of loblolly pine and that RUE may be stable across years and locations when grown under intensive silvicultural management. It follows that, as LAI reaches a biological maxium, due to the combined effects of the deployment of elite genotypes grown under intensive silvicultural treatments, manipulation of RUE may become more important for forest production, and therefore the mechanisms behind this phenomenon warrant further investigation.

Conclusions

This investigation examined the influence of location and year on NF, LAI, *k*, *f*, IPAR, ANPP, and RUE among six elite full-sib loblolly pine families grown in full-sib family blocks grown under close spacing and intensive silvicultural management tested at two unique locations and soil types. Genotype by environment interactions were evident: i.e., there was a genotype x year interaction for LAI and also a genotype x month interaction for the fraction of light intercepted. Trends over time were not stable between locations, with location x year interactions evident for all variables, with the exception of ANPP and RUE. Additionally, f and k were not stable across months between locations (i.e. location x month interaction). Radiation use efficiency among families was stable across time and locations, which is in general agreement with results from other studies where RUE was stable across a range of environmental conditions (Pangle *et al.*, 2009). The current investigation makes an important contribution to the field by documenting family level loblolly pine stability of RUE through time and across locations of contrasting soil types. Future investigations at these locations should examine the interacting influence of silvicultural intensity, planting density, family and locations on canopy structure and RUE. Investigations which link specific canopy structural traits involved in light capture and photosynthesis with variation in natural and anthropogenic factors that influence RUE would be informative decisions regarding the deployment of elite southern pine genotypes.

Table 3-1. Cumulative elemental nutrient application rates for the PPINES intensive silvicultural treatments through five growing seasons (kg ha^{-1}).

Location	N	P	K	Mg	Ca	S	B	Zn	Mn	Fe	Cu
Sanderson, FL	369	128	121	45	45	35	0.9	2.7	2.2	14.7	3.9
Waverly, GA	369	128	121	45	45	35	0.9	2.7	2.2	14.7	3.9

Table 3-2. Summation of incoming monthly shortwave radiation per month in MJ m^{-2}, for two locations (Sanderson, FL and Waverly, GA) and two years (2004 and 2005). Each location is part of a larger family block study investigating the effects of silvicultural treatment intensity and planting density on the performance of full-sib loblolly pine families.

Location	Year	March	April	May	June	July	August	September	October
Sanderson, FL	2004	592	662	756	650	655	537	413	447
	2005	490	654	691	573	680	589	554	414
Waverly, GA									
	2004	607	669	777	649	684	551	419	462
	2005	489	665	710	639	709	618	555	408

Data were obtained for each study site using the 10 km modeled grid data available from the NSRDB (The National Solar Radiation Data Base) (1991 - 2005). ftp://ftp.ncdc.noaa.gov/pub/data/nsrdb-solar Last accessed March 2009.

Table 3-3. Least squares means for needlefall, light extinction coefficient, amount of PAR intercepted, aboveground net primary productivity, and radiation use efficiency for six full-sib loblolly pine families averaged across two locations (Sanderson, FL and Waverly, GA) and two years (2004-2005). Families were stable across locations and years (i.e. no genotype x environment interactions).

Family	NF	*k*	IPAR	ANPP	RUE
L4	4.58 a	0.43 a	1808 ab	21.0 a	1.16 a
L1	4.05 a	0.67 c	1719 b	19.3 a	1.12 ab
L2	4.33 a	0.60 bc	1798 ab	19.6 a	1.09 ab
L5	4.46 a	0.52 abc	1791 ab	19.5 a	1.09 ab
L8	4.60 a	0.47 ab	1857 a	20.2 a	1.08 ab
L7	4.63 a	0.51 ab	1856 a	19.5 a	1.08 b

NF is mean annual needlefall in Mg ha^{-1}, *k* is cosine corrected light extinction coefficient, IPAR is the sum of PAR intercepted by the canopy (MJ m^{-2}), and ANPP is expressed in Mg ha^{-1}. Radiation use efficiency (RUE) is expressed in g MJ^{-1}PAR and is adjusted for the covariate of tree density which was fixed at 2840 trees ha^{-1}. Values with the same letter within columns are not significantly different at the 95% level of confidence using Bonferroni's LSD.

Table 3-4. Least squares means for needlefall, leaf area index, light extinction coefficient, fraction of PAR intercepted, amount of PAR intercepted, aboveground net primary productivity for the interaction between location (Sanderson, FL and Waverly, GA) and year (2004 and 2005).

Location	Year	NF	LAI	*k*	*f*	IPAR
Sanderson, FL	2004	5.12 a	2.08 a	0.44 a	0.739 a	1819 a
	2005	3.72 b	1.66 b	0.83 b	0.667 b	1639 b
Waverly, GA	2004	3.88 b	2.22 a	0.42 a	0.735 a	1888 a
	2005	5.05 a	3.26 ab	0.44 a	0.740 a	1872 a

Needlefall (NF) is mean annual needlefall in Mg ha^{-1}, LAI is mean growing season projected, *k* is cosine corrected light extinction coefficient, f is the mean fraction of light intercepted during the growing season, and IPAR is the sum of PAR intercepted by the canopy expressed in MJ m^{-2}. Values with the same letter within columns are not significantly different at the 95% level of confidence using Bonferroni's LSD.

Table 3-5. Least squares means for Leaf Area Index (LAI) for six full-sib loblolly pine families in 2004 and 2005, averaged across two locations (Sanderson, FL and Waverly, GA). Families were stable across locations (i.e. no genotype x location interaction).

Family	2004	2005
L4	2.1 ab	1.8 bc
L8	2.2 ab	1.9 abc
L5	2.1 ab	1.7 c
L7	2.3 a	1.9 bc
L2	2.1 ab	1.8 c
L1	1.9 abc	1.7 c

Leaf area index is on a projected basis. Values with the same letter within variables are not significantly different at the 95% level of confidence using Bonferroni's LSD.

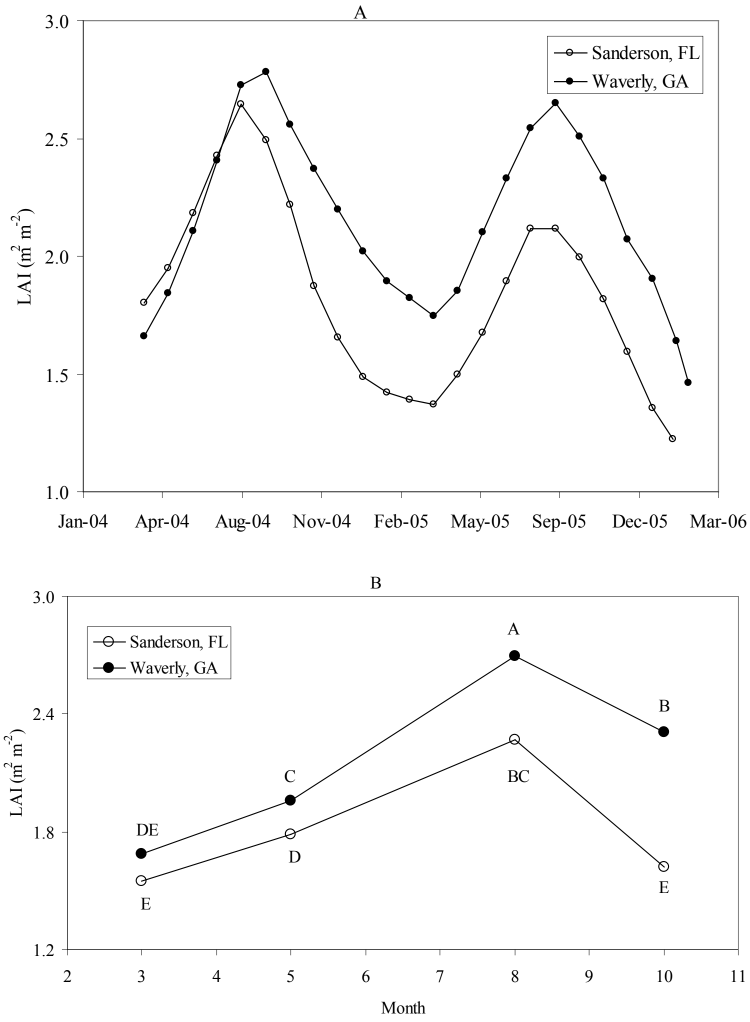

Figure 3-1. A) Projected leaf area index (LAI) over a two year period for the Sanderson, FL and Waverly, GA locations. Within each location, the data were averaged across six full-sib loblolly pine families. The location x year interaction for mean LAI was significant at $p < 0.0001$. Note the effects of hurricanes Frances and Jeanne were evident for the periods immediately following the September 2004 data point at the Sanderson, FL location. B) Relationship between projected leaf area and month demonstrating the location by month interaction ($P<0.0001$). Each data point represents a single location averaged across six families and two years (2004 and 2005).

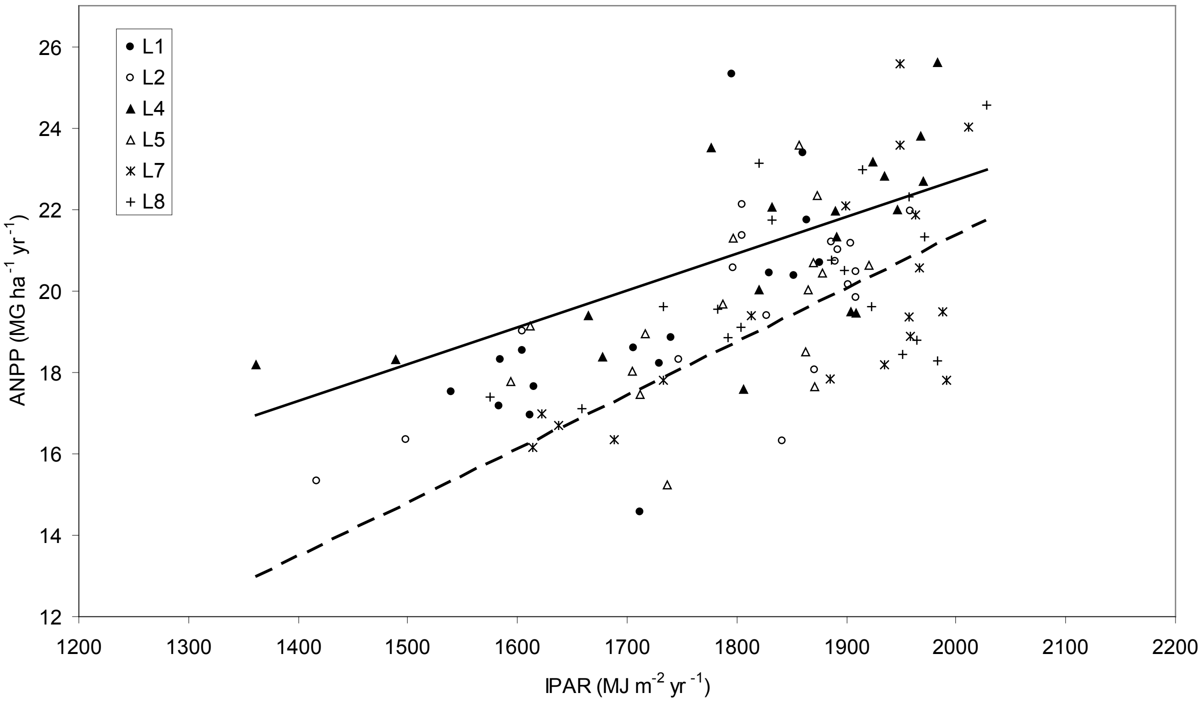

Figure 3-2. Relationship between annual aboveground net primary production and intercepted radiation for loblolly pine full-sib families L4 (solid line) and L7 (dotted line). Each data point with the same symbol represents a single full-sib family plot (n=6) at one of two years (2004 and 2005) and two locations (Sanderson, FL and Waverly, GA). There was a statistically significant difference in the slopes (RUE) between families L4 and L7 (see Table 3-3).

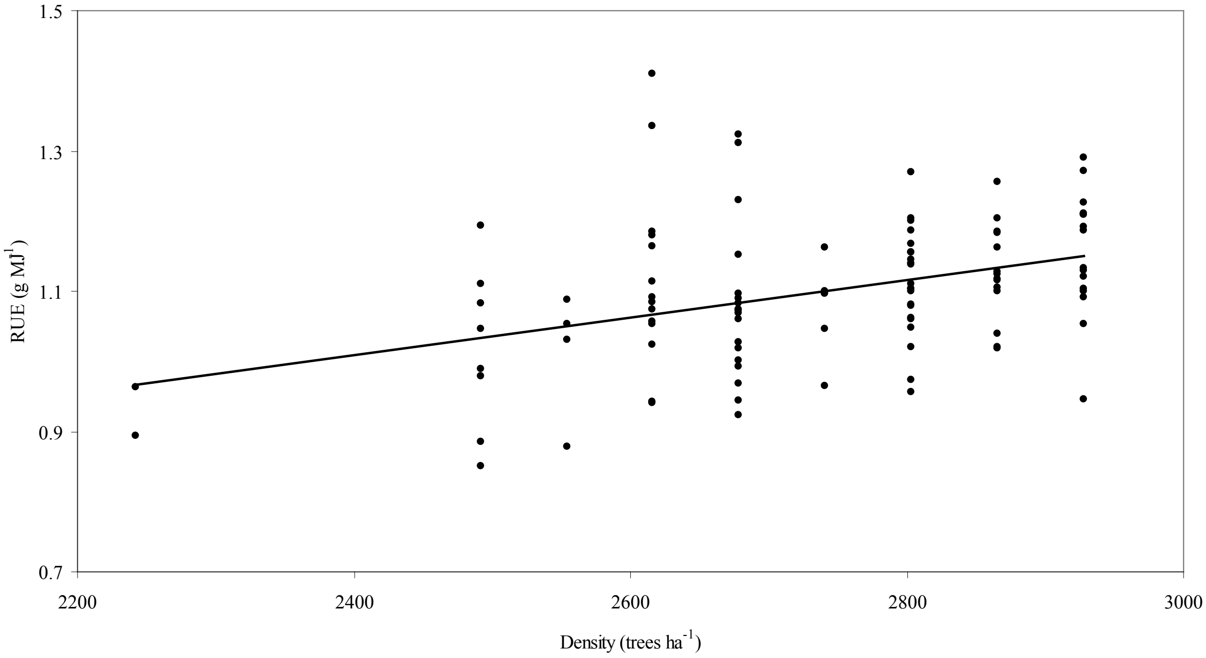

Figure 3-3. Relationship between RUE and tree density at age-five-years for loblolly pine. Each data point represents a single family plot at one of two locations (Sanderson, FL and Waverly, GA) and the solid line represents the least-squared regression. RUE = 0.0003 (density) + 0.3606 ($r^2 = 0.1507$).

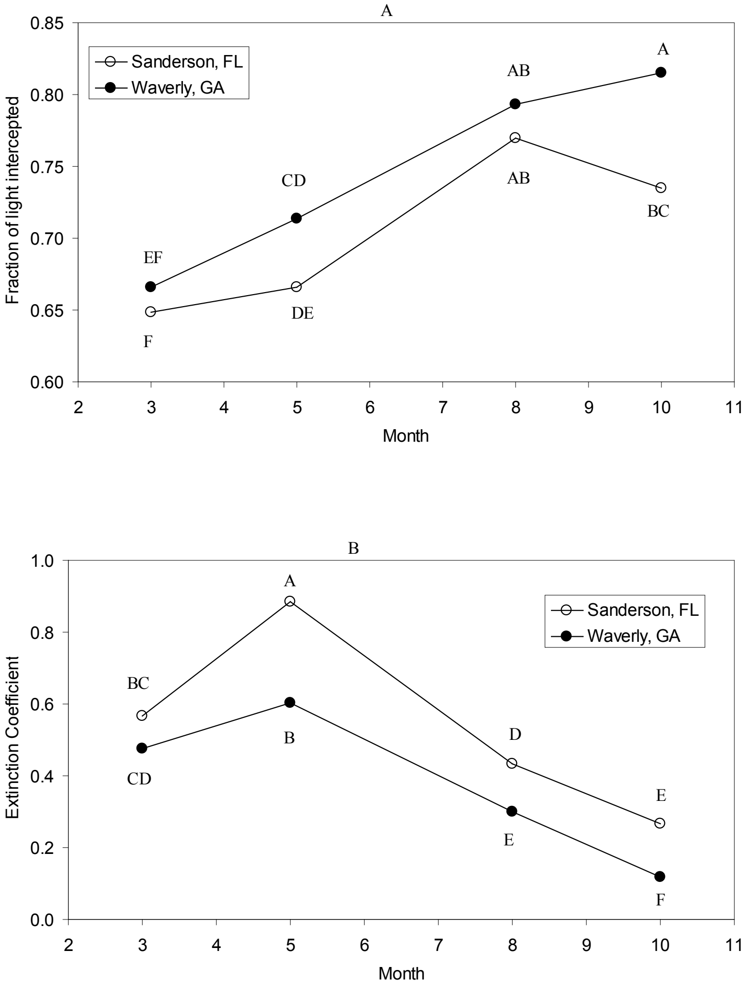

Figure 3-4. Relationship between: A) fraction of light intercepted (*f*), and B) light extinction coefficient (*k*), by month of year for two locations ($p<0.0007$ and $p=0.0001$ respectively). Each data point represents a single location averaged across six families and two years (2004 and 2005).

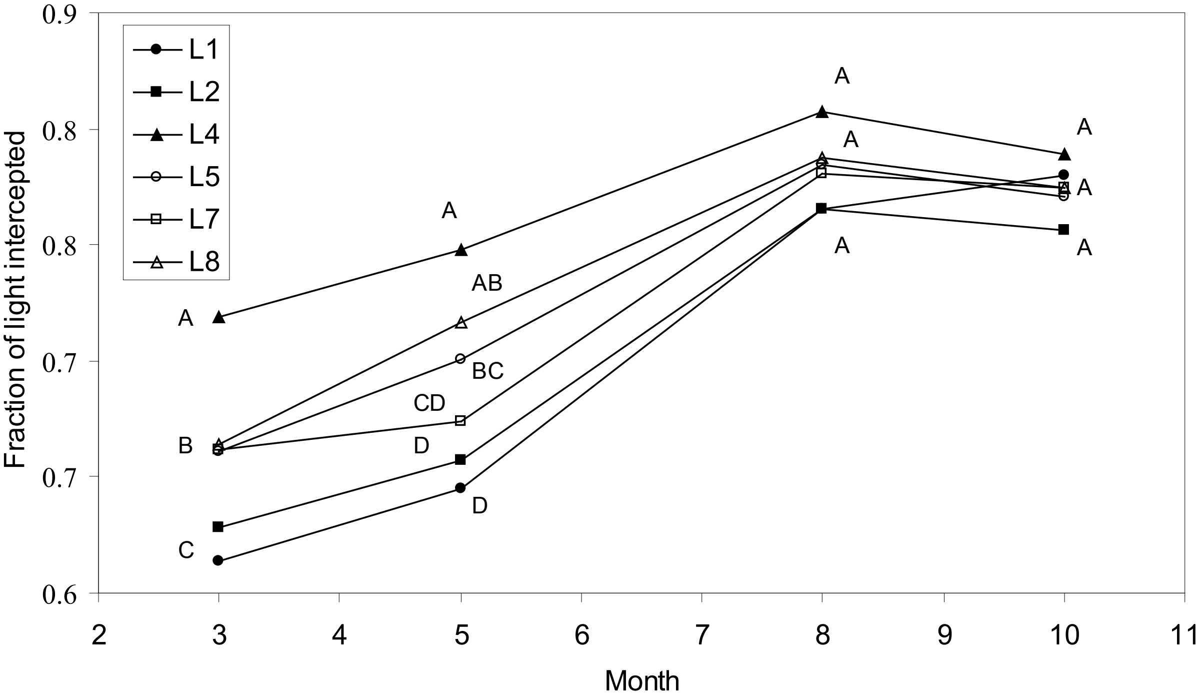

Figure 3-5. Relationship between the fraction of light intercepted (*f*) by month of year for six loblolly pine families (p=0.0053). Each data point represents a single family averaged across two locations (Sanderson, FL and Waverly, GA) and two years (2004 and 2005). RUE and tree density at age-five-years for loblolly pine.

CHAPTER 4

GENOTYPE X ENVIRONMENT INTERACTIONS IN SELECTED LOBLOLLY (*Pinus taeda* L.) AND SLASH PINE (*P. elliottii* ENGLM. VAR. *elliottii*) PLANTATIONS IN THE SOUTHEASTERN UNITED STATES[1].

Introduction

Considerable gains in the productivity of loblolly (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Englm. var. *elliottii*) plantations in the southeastern United States have been achieved over the past 30 years. Demonstrated increases in unit area production have been realized through silvicultural inputs of fertilization, competition control, and density management. These treatments were designed to relieve site resource limitations in order to focus growth on crop trees (Colbert *et al.*, 1990; Jokela *et al.*, 2000; Borders and Bailey, 2001; Martin and Jokela, 2004b). Growth responses to intensive silvicultural practices range from 2- to 3.5-fold at age 15 for loblolly pine in the southeastern USA (Jokela *et al.*, 2004). Additionally, tree breeding programs have increased volume production by 10 to 30% over unimproved sources (Li and McKeand, 1989; McKeand *et al.*, 2003a). When a combination of elite genetic materials are combined with site-specific silvicultural treatments, mean annual increments of up to 20 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ have been documented (Allen *et al.*, 2005c). However, as resource managers begin to deploy selected full-sib families or clones (Bridgwater *et al.*, 2005), there is a greater likelihood that genotype x environmental (GxE) interactions will occur, especially under conditions of increased silvicultural intensity (McKeand *et al.*, 2006). These interactions may be manifest as rank changes among genotypes when grown under different environments/treatment conditions,

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[1] Reprinted with permission from Roth,B.E., Jokela,E.J., Martin,T.A., Huber,D.A., White,T.L., 2007. Genotype x environment interactions in selected loblolly and slash pine plantations in the southeastern United States. Forest Ecology and Management 238, 175-188.

or as “scale effects” in which the absolute differences among genotypes change with environment.

Research studies aimed at quantifying the combined effects of silvicultural treatments and genetic improvement on unit area production in loblolly and slash pine are rare. Earlier studies indicate that GxE would not be of major consequence for the majority of genotypes being deployed under traditional silvicultural systems (McKeand *et al.*, 2006). For example, no GxE was found for total standing volume at age 12 in a loblolly pine genotype x vegetation control study in Georgia, USA (Martin and Shiver, 2002), and none was found at age four for five open-pollinated loblolly pine families grown under two spacings in South Carolina, USA (McCrady and Jokela, 1996). Likewise, an analysis of whole tree biomass of five-year-old loblolly pine from two seed sources did not demonstrate GxE using a factorial genotype x fertilization experiment in North Carolina, USA (Retzlaff *et al.*, 2001).

Tree improvement programs have historically assessed GxE interactions for determining the need for site specific breeding efforts (McKeand *et al.*, 1997b). Generally, in these investigations, a large number of genotypes are tested across a range of sites. Environmental variance in these breeding programs is due to localized climatic, edaphic and disease conditions, rather than to specific silvicultural treatments that manipulate site resources. Few studies have documented GxE interactions among silvicultural treatments, but available evidence suggests that when GxE did occur in these situations, it was caused by a limited number of genotypes in the population that were highly sensitive to environmental variation (Zas *et al.*, 2004). For example, (Duzan *et al.*, 1988) found modest rank changes in family performance across a variety of sites in the southeastern USA, while (Yeiser *et al.*, 2001) showed instability in volume production at ages five and ten among loblolly pine families from some, but not all, seed zones in the Western Gulf region of the United States. Similarly, a large GxE was documented for growth traits in loblolly pine families from Florida sources when moved northward one USDA (United States Department of Agriculture) Plant Hardiness Zone (Atwood *et al.*, 2002; Sierra-Lucero *et al.*, 2002); yet, none was observed for other provenances (McKeand *et al.*, 1990; Sierra-Lucero *et al.*, 2002). It appears that GxE may become significant only under extremes in seed source movement and/or site productivity and that relatively few genotypes from the population contribute to this response.

The intensity of genetic selection and silvicultural treatments is expected to increase in the future as resource managers move seed-sources long distances in an effort to increase yields (Lambeth *et al.*, 2005). Likewise, the probability of GxE becoming significant in the future is real and site/genotype specific silvicultural prescriptions may be needed to maximize volume and value production (Allen *et al.*, 2005c). It follows that resource managers will benefit from an understanding of how elite genotypes respond across naturally occurring and man-made environmental gradients (*i.e.*, fertilization, density management and associated vegetation control), as well as how soil physical, chemical and biological processes affect productivity (Fox, 2000).

The overall objectives of this study were to investigate and quantify the magnitude and nature of GxE in full-sib families of loblolly and slash pine. This was accomplished by using a series of replicated factorial experiments and family block plantings established in Florida and Georgia that manipulated gradients in planting density, understory competition and soil nutrient availability.

Methods

Study Description

In January of 2000, the Forest Biology Research Cooperative (http://www.sfrc.ufl.edu/fbrc/index.html. Last accessed February 2009), located at the University of Florida, established a series of field research installations that were designed to examine the interactions of full-sib loblolly and slash pine families with several environmental factors, such as: location, silvicultural treatment intensity, and planting density (Roth *et al.*, 2002). This trial series, referred to as PPINES (Pine Productivity INteractions on Experimental Sites), is the only one of its kind where the combined effects of species, genotype, silviculture and planting density can be examined singly or in combination across a range of site conditions in the southeastern United States. Large family-block plots, combined with contrasting treatments provide a unique opportunity to examine GxE using stand level variables (*i.e.*, basal area, stem volume, and aboveground biomass).

Four study locations were included in this trial series representing two distinctly contrasting soil types (Table 4-1). The topography is nearly flat, with less than a 1% slope. Soil series for the four sites were: Sanderson, FL - Leon (sandy, siliceous, thermic Aeric Alaquods); Waverly, GA - Bladen (mixed, semiactive, thermic Typic Albaquults); Perry, FL - Leon (sandy, siliceous, thermic Aeric Alaquods); Waldo, FL - Newnan (sandy, siliceous, hyperthermic Ultic Haplohumods). Trials were installed on sites that held recently harvested southern pine plantations. Associated woody vegetation common to all sites included sawtooth palmetto [*Serenoa repens* (B.) Small.], wax myrtle (*Myrica ceriferea* L.), runner oak (*Quercus pumila* Walt.), blueberries (*Vaccinium* spp.), gallberry [*Ilex glabra* (L.) Gray], and St. John's-wort [*Hypericum fasciculatum* (Lam.)]. Herbaceous plants in the understory commonly included bluestem grasses (*Andropogon* spp.), panic grasses (*Panicum* spp.), sedges (*Carex* spp. and

Cyperus spp.), and dogfennel [*Eupatorium capillifolium* (Lam.) Small.]. All study locations shared a subtropical and humid climate with long hot wet summers and mild dry winters. Long-term (1931 – 2000) precipitation has averaged 1384 mm yr^{-1} (NOAA, 2002).

Experimental Design

The PPINES series was composed of two installations each of loblolly and slash pine. Within each installation, the experimental design was a 2 x 2 x 8 (silviculture x planting density x genetic entry) factorial which is planted in a randomized complete block, split-plot design. Each site had four complete blocks which consisted of four silviculture-density whole plots. At the whole-plot level, the two contrasting silvicultural treatments were operational versus intensive, while the two planting density treatments were 1334 $trees \cdot ha^{-1}$ versus 2990 $trees \cdot ha^{-1}$. Within each of these whole plot treatment combinations, there were eight sub-plots representing the genetic entries. Throughout this chapter, genetic entries are alpha numerically coded using the prefix letter L for loblolly and S for slash pine. Each installation had 13 312 trees, on 128 plots, which were distributed on approximately 10 ha of experimental area.

Treatment Descriptions

Prior to planting, each installation was double bedded on separate passes following a 2.75 m spacing pattern. In the late summer/early fall of 1999, all installations were treated with pre-plant herbicides consisting of Chopper® (imazapyr) at 1.02 $\ell \cdot ha^{-1}$ and Garlon® (triclopyr) at 7.02 $\ell \cdot ha^{-1}$ with the goal of removing all woody competition and reducing initial levels of herbaceous vegetation. The objective was to provide a site with resources suitable for optimum growth while minimizing the variation within individual study sites. The operational silviculture treatment represented a typical regime utilized by forest industry throughout the southeastern USA at the time. After receiving a common site preparation treatment, the operationally treated plots received a single banded, or broadcast, application of 280 kg·ha^{-1} diammonium phosphate at the time of planting.

The contrasting intensive treatment was mainly driven by early vegetation control and annual fertilization. On these plots, competing vegetation was controlled for two years following planting using directed applications of Arsenal® (imazapyr) at 0.28 ℓ·ha^{-1} (limited to loblolly pine installations) and Oust® (sulfometuron methyl) at 0.14 ℓ·ha^{-1} on all installations. For the follow-up treatments ground cover was kept below a 30% threshold through age three. By age five, the tree crowns had closed canopy and the herbaceous component was limited due to light availability. The intensive plots were fertilized with 560 kg·ha^{-1} of 10-10-10 plus micronutrients at the time of planting, which was followed by annual applications of macro- and micronutrient fertilizers using prescriptions based on foliar analyses. The total amounts of nutrients applied on each installation through age five are presented in Table 4-2.

The second treatment factor at the whole-plot level was contrasting planting density: 1334 trees·ha^{-1} planted at a spacing of 2.75 m x 2.75 m, and 2990 trees·ha^{-1} planted at a spacing of 1.22 m x 2.75 m. The 2990 trees·ha^{-1} sub-plots of each genetic entry were arranged in eight beds of 16 planting positions each, for a total of 128 trees per gross treatment plot. A two tree border around the perimeter resulted in a 48 tree interior measurement plot of 0.016 ha. The 1334 trees·ha^{-1} sub-plots of each genetic entry were arranged in eight beds of 10 planting positions each, for a total of 80 trees per gross plot. A single tree buffer around the perimeter resulted in a 48 tree interior measurement plot of 0.036 ha. Despite an ongoing drought at the time of establishment, survival was over 95% in all treatments at the end of the first growing season.

At the sub-plot level, genetic entries consisted of first generation elite full-sib families. On loblolly sites there were seven entries of full-sib families, which included a previously identified poor grower, and an intimate mixture of the top six full-sib families. The entries were similar for the slash pine sites, with the exception of one less full-sib family to make room for the loblolly mixture in addition to a slash mixture. This allowed for a direct comparison of species performance across spacing and silvicultural treatments on these two slash locations.

All genetic entries in the study were selected from sources which exhibited moderate to excellent resistance to fusiform rust [*Cronartium quercum* (Berk.) Miyabe ex Shirai f. sp. f*usiforme*] based upon *a priori* knowledge from breeding programs. This was done in order to reduce the confounding effects of disease incidence. Seedlings were grown in 66 ml·cell^{-1} Ray Leach 'Cone-tainer'™ cells (Stuewe and Sons, Inc Corvallis, OR). Each site was hand planted over a two day period in January 2000.

Insecticides were uniformly applied across all treatments on loblolly pine installations in an effort to control damage from Nantucket pine tip moth (*Rhyacionia frustrana* [Comstock]). Treatments were applied on a monthly basis over the first two growing seasons, beginning in March and ending in September. Alternating applications of the following chemicals and application rates were applied aerially or by hand: Pounce® 3.2EC (62 ml product ℓ^{-1} water), Warrior T® (39 ml product ℓ^{-1} water), Dimilin® 25W (62 ml product ℓ^{-1} water), and Mimic® 2LV (125 ml product ℓ^{-1} water).

A fungicide was uniformly applied across all treatments on slash pine installations in order to control for the confounding effects of potential fusiform rust infection. Treatments were applied by ground application on a monthly basis over a four-month period (beginning in March) during the first two growing seasons. Treatments a rates consisted of 12 g of 50% concentrated DF Bayleton® with 65ml of Agri-Dex in 18.9 ℓ of water.

Inventory, Yield and Biomass Estimates

Annual measurements of DBH were made at ages two-, three-, and five-years on all trees in the measurement plots. Total height (HT) was measured on every tree at ages two and three, but was limited to a representative 20% sub-sample at age five. Individual tree HT at age five was determined from site and treatment specific HT versus DBH relationships developed from this sub-sample. Abiotic and biotic tree damage was assessed at the time of measurement. Basal area (BA) was calculated on a per family-plot basis ($m^2 \cdot ha^{-1}$), which accounts for variation due to mortality. Since the trees were relatively small at these ages, a simple index of individual tree stem volume was utilized: the sum of a cylinder from the tree base to breast height (BH = 1.37 m) and of a cone from BH to the top if the tree. Individual surviving trees per plot were summed to yield total standing stem volume per plot (VOL) and was expressed in m^3 ha^{-1}.

Aboveground biomass equations were developed using a treatment specific dataset from this experiment along with supplemental data from previous regional studies of similar age and treatment history (Table 4-3). Biomass harvests on PPINES were conducted at age two and five and covered the full range of locations and silvicultural treatments. Due to resource limitations, allometric equations were developed that were common to the full-sib families represented in the study. This was done in order to increase the power to detect differences between species, locations, densities and silvicultural intensities. Two families were harvested within each species at age two. At age five, due to further resource limitations, the harvest was restricted to two locations of loblolly pine and further limited to a subset of silvicultural treatments and families. Trees selected for each harvest originated from border rows. These border rows were buffering the effects of genotype only since there were additional buffers separating the density and silvicultural intensity treatments. The age two harvest consisted of 47 loblolly pine (families L2 and L4) and 60 slash pine (S1 and S6) trees, which were harvested across each of the four culture/density whole plots on two sites from each species. The age five harvest consisted of 54 loblolly pine trees from the 2290 trees·ha^{-1} planting density over both contrasting silvicultural intensities at Sanderson, FL and the intensive cultural treatment at Waverly, GA.

Within each harvest year, sample trees free of damage and disease, were selected at random from across the diameter distribution representative of each treatment and site. Prior to harvest, an inventory was completed on each sample tree which consisted of HT, DBH, diameter at ground line, and crown width at the widest point parallel to, and perpendicular to the planting bed. Sample trees were felled at ground line using a hand saw, placed on a tarp and separated into four aboveground components: foliage, branches, stem and dead branches. The total fresh weight of each component was measured separately in the field. The fraction of bark to stem components were estimated from six cm disks of wood, cut from the base of each of three equally spaced stem segments along the full length of the stem. Bark was separated from each disk and the fresh weight of each was determined in the field. Tissue samples were transported from the field and dried to a constant weight at 70^{0}C.

Logarithmically transformed linear allometric equations were developed using a combination of the biomass harvests and the regional data set according to the base model (Equation 4-1) (Crow, 1988).

$$\ln(Y_i) = \ln(\beta_0)_{i0} + \beta_1 \ln X_{i1} + \ln(\varepsilon_i) \qquad (4\text{-}1)$$

Where ln is the natural logarithm, Y_i is the dry weight of the unit area aboveground biomass (AGB) of the *i*th sample tree expressed in kg·tree^{-1}, $(\beta_0)_{i0}$ is the mean of the *i*th sample tree within each species, X_{i1} is the product of the combined variables of DBH squared times HT for the *i*th sample tree expressed in dm^3, and ε_i is the random error associated with estimating the weight of the aboveground biomass of the *i*th sample tree. The need for separate groups of equations by species, location, silviculture, and density was examined utilizing PROC MIXED (Littel *et al.*, 1996) in SAS. These were evaluated by beginning with a pooled dataset and systematically decomposing the general model by entering treatment variables and their interactions. At each step slopes and intercepts of the resulting equations were evaluated through covariance analysis. The large sample size in the pooled regional dataset (n = 432 harvest trees) yielded tests with many degrees of freedom, thereby increasing the power to detect differences in parameters between treatments. Variables were included in the development of the model if they were significant at $\alpha = 0.05$. However, there were some instances where various combinations of treatments in the PPINES trial resulted in individual trees of much larger size than those from the regional dataset. Therefore, results could not be extrapolated for those individual treatment combinations. As a result, only the variable of species was included in the allometric relationships (Table 4-4). Probability plots of the residuals indicated that the normality assumption was satisfied and plots of residuals versus predicted values showed no obvious pattern, suggesting that the assumptions of independence and equal variance were met. Corrections for bias in the transformation of logarithmic units to arithmetic units were applied (Equation 4-2) (Baskerville, 1972):

$$\hat{Y} = e^{(\hat{\mu} + \hat{\sigma}^2/2)} \qquad (4\text{-}2)$$

where $\hat{Y}$ is the estimated aboveground biomass in arithmetic units of the skewed Y distribution at X (Equation 4-1). AGB was calculated for each plot and is expressed in $\mathrm{Mg \cdot ha^{-1}}$ of dry matter.

Analysis

All analyses were performed using PROC MIXED (Littel *et al.*, 1996) in SAS. To test for differences in stand level attributes among treatments, separate analyses of variance (ANOVA) were performed for loblolly and slash pine using a mixed linear model for data pooled across two sites within each species (Equation 4-3):

$$Y_{ijklmn} = \mu + S_i + b(s)_{ij} + C_k + D_l + CD_{kl} + F_m + CF_{km} + DF_{lm} + CDF_{klm} + SC_{ik} + SD_{il} + CD_{ikl} + SF_{im} + SCF_{ikm} + SDF_{ilm} + SCDF_{iklm} + b(s)C_{ijk} + b(s)D_{ijl} + b(s)CD_{ijkl} + b(s)F_{ijm} + b(s)CF_{ijkm} + b(s)DF_{ijlm} + b(s)CDF_{ijklm} + b(s)S_{ij} + b(s)SC_{ijk} + b(s)SD_{ijl} + b(s)CD_{ijkl} + b(s)SF_{ijm} + b(s)SCF_{ijkm} + b(s)SDF_{ijlm} + w_{ijklmn} \tag{4-3}$$

where Y_{ijklmn} is the response variable (BA, VOL, or AGB) of the *n*th plot of the *m*th family of the *l*th planting density of the *k*th silvicultural intensity of the *j*th block of the *i*th site ($i = 1,2$; $j = 1,2, \ldots, 4$; $k = 1,2$; $l = 1,2$; $m = 1,2,\ldots, 6$ for slash and 7 for loblolly pine; and $n = 1$); μ is the overall mean; S_i is the fixed effect of the *i*th location; $b(s)_{ij}$ is the random interaction effect of the *j*th block within the *i*th location; C_k is the fixed effect of the *k*th silvicultural intensity; D_l is the fixed effect of the *l*th planting density; F_m is the fixed effect of the *m*th family and w_{ijklmn} is the random error. Blocks were nested within locations, while the factors of silviculture (C), planting density (D), and genotype (F) were crossed. All terms containing $b(s)_{ij}$ were considered to be random effects in the model and were pooled as appropriate for each variable tested using the procedure described by (Bancroft and Han, 1983). The only exception was $b(s)CD_{ijkl}$, which was never pooled as it is used as the error term to test the main effects of S_i, C_k and D_l. Individual variance components were pooled when the probability of a greater *F* statistic was 0.25 or larger. As noted by (Bancroft and Han, 1983), the significance level for the *F* test is much higher than conventional levels of 0.01 or 0.05 and is a conservative measure of the relative efficiency of pooling the sources of variation.

Since the analysis of each variable has a differing model construct, the variance components for each model are presented in a separate table subsequent to the traditional ANOVA tables in the results section. Assumptions of equal variance between the two planting density treatments were violated for all variables examined. This was due to heterogeneity in the covariance structure associated with planting density; there was greater variation within the 2290 trees·ha^{-1} treatment. To account for this heterogeneous variance, the residual was grouped by the fixed effect of density (Bozivich *et al.*, 1956). Where significant effects were found, least squares means were generated between levels of the factors of interest. Where multiple non-planned comparisons were made, a Bonferroni's adjusted significance level was used. Single degree of freedom contrasts were performed to test for differences between species (mixed loblolly vs. mixed slash pine plots) and also method of deployment (mixed vs. pure plots).

Results

Strong and significant GxE in BA, VOL, and AGB was apparent in this experiment for both species. The strength of the experimental design enabled the detection of three types of unit area production interactions: genotype x site, genotype x silviculture, and silviculture x density (Tables 4-5, 4-6 and 4-7). There were no significant three-way interactions involving genotype, site and silviculture. Some combinations of treatments interacted as early as age two and all increased in significance with time. Despite the high statistical power to detect interactions, there was no evidence for genotype x density interactions of any kind, despite the extremes in planting density combined with the contrasting silvicultural treatments and locations.

Genotype x Site Interactions

At age two there were strong and significant interactions between sites and loblolly pine families for BA, VOL and AGB (p=0.0474, p=0.0390, p=0.0440, respectively); by age five the significance of these interactions had increased (p=0.0271, p=0.0224, 0.0388) (Table 4-5). For slash pine, GxE between sites was not evident at age two but became significant for BA, VOL and AGB by age three (p=0.0039, p=0.0046, p=0.0158, respectively) and gained in significance over those for loblolly by age five (p=0.0127, p=0.0157, p=0.0158) (Table 4-6). The varying performance of families across sites was largely due to scale effects, with certain families performing better or worse than their peers when grown together on contrasting sites. For example, at age five, the difference between sites in AGB for loblolly pine family L5 was 13%

(versus a 19% average for all other families) (Figure 4-1a). In terms of absolute production, family L4 was the top performer across both sites. Similar effects were observed for slash pine families between sites. Generally, these can be split into three groups based on their performance. The first group (S4 and S6) was the most sensitive across locations, and despite varying yields, both families had similar slopes representing the degree of performance across locations (Figure 4-1b). The second group had intermediate sensitivities despite a wide range of yields in AGB (S1, S2, and S3). Family S5 had similar levels of AGB at both locations which resulted in a rank change (Figure 4-1b).

Genotype x Silviculture Interactions

Genotype x silviculture interactions were not as strong as the interactions of genotype x location. Significant GxE became apparent by age three among the loblolly pine families for VOL (p=0.0421) (Table 4-5) and grew stronger with time (p=0.0019 at age five). The significance of the interaction for loblolly pine in BA (p=0.0541) and AGB (p=0.0502) at age five was not as strong as was for VOL. In contrast, elite families of slash pine were not as responsive to silviculture as was loblolly pine. Similarly, the performance among slash pine families was more stable when grown under contrasting silvicultural regimes. In slash pine, GxE (as driven by silvicultural treatment intensity) was not significant until age five and then only for VOL (p=0.0126); BA was weakly significant at p=0.0589 (Table 3-6).

As with genotype x location interactions, the instability of family performance across contrasting silvicultural treatments was mainly the result of scale effects, where certain families either outperformed or underperformed their peers with increasing intensity of silvicultural treatment. Examination of least squares means for VOL at age five showed that loblolly family L4 was most responsive to increasing silvicultural intensity (75% increase), while family L5 was one of the least responsive families (55% increase) (Figure 4-2a). Family L5 was also the family that exhibited the least difference in volume growth across contrasting locations (13% difference). All other families were intermediate in their response. For slash pine, families S2 and S6 were the most responsive in VOL at age five to increasing intensity of silvicultural treatment (63% increase), with all other families exhibiting a lower response (combined 55% increase) (Figure 4-2b).

Silviculture x Density Interactions

Interactive effects of silvicultural treatment intensity and planting density for loblolly pine were highly significant ($p<0.0001$) for all growth metrics at age two, and continued through age five. Similar effects were noted for slash pine, but they did not become significant until age three ($p<0.005$). In all cases, the interactions were due to larger responses to increasing silvicultural treatment intensities under conditions of increasing planting density. For example, on the slash pine sites, the intensive silvicultural treatment increased AGB by 5.7 $\mathrm{Mg \cdot ha^{-1}}$ at 1334 $\mathrm{trees \cdot ha^{-1}}$, versus 12 $\mathrm{Mg \cdot ha^{-1}}$ at 2990 $\mathrm{trees \cdot ha^{-1}}$ (Figure 4-3c). However, there was one case where this two-way interaction at age five for loblolly AGB was dependent on location (three-way interaction, $p = 0.0007$). In this case (Sanderson, FL), the 2990 $\mathrm{trees \cdot ha^{-1}}$ operational treatment produced a much lower than expected response in AGB than that at the Waverly, GA location (Figures 4-3a and 4-3b). All other combinations of silvicultural treatment intensity and planting density between locations had similar responses for AGB at age five.

Location x Density Interactions

There were significant location x density interactions for all variables at ages three and five for slash pine ($p< 0.05$) (Table 4-6) but not for loblolly pine (Table 4-5). In general, mortality was greatest in slash pine, with the majority occurring between ages three and five. Despite similar survival between the two slash pine locations (Table 4-8), the Perry, FL location had greater VOL at age five than the Waldo, FL location at the 2990 trees·ha^{-1} planting density ($p<0.0197$).

Species and Deployment Interactions

There were strong and significant species x location interactions ($p<0.0001$) for all variables. Loblolly pine was more responsive in aboveground biomass than slash pine on the two locations where a direct comparison was possible (Figure 4-4). Top performing full-sib loblolly pine families expressed similar yields at age five whether grown in intimate mixtures or pure blocks. However, slash pine tended to have greater BA, VOL, and AGB on a unit area basis when grown in mixtures, as compared to pure plots of the same full-sib families (Table 4-9).

Effects of Disease and Hurricanes

Plot level incidence of fusiform rust and wind damage at age five was examined in an attempt to partially explain genotype x location interactions. Despite the fact that all families in the study were selected to have some level of fusiform rust resistance, based on *a priori* knowledge, there were significant rank changes among slash pine families in fusiform rust occurrence between locations at age five ($p=0.0189$). Similar results have been previously documented in slash pine (Schmidt and Allen, 1998). Of the six slash pine families in the experiment, three (S4, S5, and S6) demonstrated GxE in fusiform rust incidence, with the Waldo, FL location having the highest incidence levels (Figure 4-5a). The other three families had a similar, but low overall incidence of fusiform rust between locations. Loblolly pine families generally had low incidence of fusiform rust and no significant interactions were found.

In the summer of 2004 two hurricanes, Frances and Jeanne, passed in close proximity to the Waldo, FL location. While damage was not extensive, there were a substantial proportion of trees toppled or leaning at varying degrees throughout the study area. Damage from these storms was minimal at the Perry, FL location and barely evident at either of the two loblolly pine locations. There was significant GxE for wind damage in slash pine between locations ($p<0.0001$) (Figure 4-5b). Trees on the slash pine locations may have toppled due to indirect effects of weak root systems in combination with relatively large canopies. Diseased trees may have broken due to fusiform rust galls located on tree stems.

Discussion

This experiment provided the opportunity to quantify the combined effects of silvicultural treatments and genetic improvement on unit area production in selected full-sib loblolly and slash pine families. The GxE observed in this study occurred at the two-way level: genotype x location and genotype x silviculture. While the genotype x density interactions were not significant, as reported for another loblolly pine experiment (McCrady and Jokela, 1996), there were significant silviculture x density interactions for unit area production, which occurred independent of mortality. The variety of interactions evident in this study was not surprising given the range of contrasting elite genotypes, silvicultural treatments and study locations established. When combined with the high statistical power associated with the complex experimental design, we had the ability to detect significant differences in the responses of these elite genotypes to various environmental conditions in plantations of loblolly and slash pine in the southeastern United States.

Genotype x Silviculture

Genotype x environment issues in southern forestry will not be of importance unless silviculture or propagule type changes significantly from those currently in use (McKeand *et al.*, 2006). Therefore, it was somewhat surprising that the genotype x location interactions were more significant and consistent than the genotype x silviculture interactions. This is even more striking given the extremes in the silvicultural treatment intensities employed in this study.

However, the magnitude increase in productivity with increasing silviculture likely overpowered the statistical significance of this interaction, as certain families tended to show a greater response than others. One example was loblolly family L4 which is widely deployed operationally across the southeastern United States. Its plasticity with regard to intensive management demonstrates responsiveness considerably greater than its peers. While not of the same magnitude, the same is true for select families of slash pine in this experiment (S2 and S6). This effect of similar relative differences in yield, yet larger absolute differences with increasing silvicultural intensity has been previously demonstrated in loblolly pine (McKeand *et al.*, 1997a). It follows that this variation in GxE across locations and silvicultural treatments could potentially be exploited if the relatively few ‘responding’ genotypes were to be identified and deployed on the proper sites in combination with appropriate site-specific silvicultural treatments.

Genotype x Location

The strongly significant genotype x location interaction, even after accounting for the extremes in silvicultural treatments, is an indication that variation in soils, climate, edaphic variables, and pests (even across relatively short distances) are important regardless of the level of silvicultural intensity. As other researchers have suggested, soil conditions that regulate the ability to supply moisture and nutrients (Fox, 2000), may be partly responsible for the GxE observed in this experiment (see Appendix B and C). Growth response to nutrition has been shown to vary by family, especially for loblolly pine (Li *et al.*, 1991b; Samuelson, 2000). There is also evidence that carbon allocation to aboveground and belowground tissues is sensitive to soil fertility and varies with provenance and family (Crawford *et al.*, 1991; Wu *et al.*, 2004). For example, in an loblolly pine fertilization experiment, families varied in the production of fine roots under low nitrogen (N) treatments, but not under high N levels (Samuelson, 2000).

Examination of foliar nutrition at age five on the current experiment did not explain the GxE observed in production at age five (unpublished data).

Genetic variability within a population allows for the potential to buffer against the effects of disease and weather, and is an important aspect of family stability. This becomes critical in areas where there are extremes in localized climatic conditions and/or pathogen populations. In the current study, through examination of damage codes made at the time of inventory, we were able to partially explain the GxE across locations for slash pine, but not for loblolly pine. In slash pine, the occurrence of fusiform rust and hurricane damage influenced the genotype x location interaction. Two of the three families responsible for the age five GxE in fusiform rust occurrence (S4 and S6) (Figure 4-5a) corresponded to the GxE between locations in AGB (Figure 4-1b). It was somewhat surprising that fusiform rust incidence did not explain the genotype x location interactions in loblolly pine given that the performance of resistant families of this species are the most unpredictable across sites (McKeand *et al.*, 2003b).

Since all test locations were located within USDA Plant Hardiness Zone 8b, adaptation problems across sites should not be expected in this experiment (Schmidtling, 2001; Lambeth *et al.*, 2005). One anomaly is the single family (S5), which had a greater incidence of fusiform rust occurrence at Waldo, FL (Figure 4-5a), yet similar biomass production when compared across locations (Figure 4-1b). The explanation for this anomaly may lie with its relative stability to the severe winds of 2004 (Figure 4-5b). In contrast, family S6 had the highest incidence of weather damage at the Waldo, FL location (42.4%), in combination with a fairly high occurrence of fusiform rust (30.1%). While there were large scale effects from wind damage, there were no changes in rank among the slash pine families (Figure 4-5b). Occurrence of pitch canker, insect damage, and forking was examined, but did not explain the GxE observed in this study.

The significant genotype x location interactions as demonstrated in this study, with limited genotypes and locations, serves to emphasize the importance of carefully considering deployment and management of elite genotypes in the future. In some cases, existing expert local knowledge of site conditions, including those not foreseen such as catastrophic insect, disease or climatological variation, may provide critically important information needed to make successful deployment decisions. For locations with extreme site conditions or unknown climate variability, it may be desirable to emphasize pest resistance over growth when selecting genotypes to deploy, which could minimize the risk of unexpected growth performance.

Silviculture x Density

Interactions between silvicultural treatments and stand density are well known to occur and have been described using several conceptual models that link silviculture with ecology (Long *et al.*, 2004). We noted significant silviculture x density interactions, with the greatest response in production occurring under conditions of intensive silviculture and high initial planting density (Figure 4-3). This interactive effect is due to better and earlier site resource capture at higher planting densities. Treatments planted at 2990 trees$\cdot$ha^{-1} closed canopy a minimum of two years earlier than the lower densities. The low density plots were not able to take full advantage of the extra resources made available through the intensive silvicultural treatment, which was applied to both planting densities. The location x silviculture x density interaction noted for loblolly AGB is likely a function of differences in the inherent productivity of the two contrasting locations examined in combination with the relatively high nutrient demands of loblolly pine (Jokela *et al.*, 2000). Inherent productivity differences between locations are demonstrated using a surrogate of average tree height at age five (averaged across families and densities) on the operational treatments (6.64 m at Sanderson, FL versus 7.65 m at Waverly, GA). The nutrient poor, sandy soil at Sanderson, FL is clearly unable to supply the nutrients demanded for maximum growth in the absence of nutrient additions, and has been documented in other studies (Adegbidi *et al.*, 2005). Nutrient limitations are exacerbated when tree density, and resulting unit area AGB, is dramatically increased to levels approaching 2990 trees·ha^{-1} (Burkes *et al.*, 2003). Resource managers will need to be aware that plantations in the southeastern United States growing on nutrient poor sites at higher densities will be in critical need of nutrient amendments much earlier in their rotations than previously thought. As seen in other experiments, where limiting site resources were ameliorated through combinations of competing vegetation control and nutrient applications, loblolly pine productivity was close to it's predicted biological maximum, regardless of the inherent site quality (Jokela *et al.*, 2004; Sayer *et al.*, 2004).

Species and Deployment Interactions

It is curious that loblolly performance was similar regardless of deployment in mixtures or pure plots, while slash pine performed better when grown in mixtures. It has been documented in other ecosystems that contrasting species can exploit different resource strata and therefore have greater yields when grown together on the same site. Perhaps the families chosen for the slash pine installations are truly an example of this. A more likely explanation is that there may be differential pest or environmental stress between the mixed and pure plots.

Conclusions

The significant genotype x location interactions that were found in this study, despite limited genotypes and locations, serves to emphasize the importance of carefully considering deployment strategies of improved genotypes of loblolly and slash pine in the southeastern United States. As resource managers make decisions about where to deploy this elite genetic material, they also will need to know how these genotypes will respond to intensive silvicultural treatments in association with localized pest and climatic conditions. For example, as silvicultural treatments become more effective at ameliorating limiting site resources, the efficiency of nutrient uptake and utilization among genotypes will likely play a larger role in their differentiation of performance (Li *et al.*, 1991a). Variation in crown structure could also lead to significant GxE (McCrady and Jokela, 1996).

This issue is certain to increase in importance as advances in clonal forestry occur (McKeand *et al.*, 2003a; Bouvet *et al.*, 2005). In certain cases where intensive silviculture and advanced breeding strategies are combined, it may become necessary to develop site specific silvicultural treatments for particular genotypes or to modify breeding strategies in order to capture the full advantage of the GxE interaction.

Table 4-1. Characteristics of the PPINES experimental locations.

Site location	Species	Latitude	Longitude	Soil order	Elevation (m)
Sanderson, FL	Loblolly	30.28 ^{0}	-82.33 ^{0}	Spodosol	45
Waverly, GA	Loblolly	31.13 ^{0}	-81.75 ^{0}	Ultisol	10
Perry, FL	Slash	30.17 ^{0}	-83.73 ^{0}	Spodosol	15
Waldo, FL	Slash	29.80 ^{0}	-82.21 ^{0}	Spodosol	50

PPINES - Pine Productivity INteractions on Experimental Sites. All locations were planted in January of 2000.

Table 4-2. Cumulative elemental nutrient application rates for the PPINES intensive silvicultural treatments through five growing seasons (kg ha^{-1}).

Site location	N	P	K	Mg	Ca	S	B	Zn	Mn	Fe	Cu
Sanderson, FL	369	128	121	45	45	35	0.9	2.7	2.2	14.7	3.9
Waverly, GA	369	128	121	45	45	35	0.9	2.7	2.2	14.7	3.9
Perry, FL	373	112	115	56	45	139	1.1	3.0	3.0	15.5	5.2
Waldo, FL	370	124	124	63	56	33	1.7	2.5	6.1	6.1	4.4

Operational silviculture treatments all received 45 kg ha^{-1} N and 50 kg ha^{-1} of P in the form of diammonium phosphate at the time of planting only.

Table 4-3. Description of biomass harvest data used to develop the allometric equations displayed in Table 4-4.

Silvicultural intensity [*]	Planting density [†]	Age [‡]	Year [§]	Sample (n)	Reference
Loblolly					
Intensive	495	2	2003	24	FBRC 2004
Intensive	540	2	2001	17	This chapter
Intensive	608	4	1999	8	Adegbidi et al 2002
Intensive	625	4	1986	27	Colbert et al. 1990
Intensive	1200	2	2001	18	This chapter
Intensive	1200	5	2004	72	This chapter
Operational	495	2	2003	24	FBRC 2004
Operational	540	2	2001	16	This chapter
Operational	608	3	2000	24	Adegbidi et al 2002
Operational	608	4	1999	24	Adegbidi et al 2002
Operational	625	4	1986	6	Colbert et al. 1990
Operational	1200	2	2001	18	This chapter
Operational	1200	5	2004	36	This chapter
Slash					
Intensive	495	2	2003	12	FBRC 2004
Intensive	540	2	2001	14	This chapter
Intensive	625	4	1986	27	Colbert et al. 1990
Intensive	1200	2	2001	14	This chapter
Operational	495	2	2003	12	FBRC 2004
Operational	540	2	2001	16	This chapter
Operational	625	4	1986	7	Colbert et al. 1990
Operational	1200	2	2001	16	This chapter

[*] Silvicultural intensity is a generalized grouping of cultural treatments found in the individual studies that closely approximates that found in the current PPINES investigation: The operational treatment represents silviculture best practices in the southeast at the end of the 20th century, receiving a common site preparation treatment and single banded application of 280 kg·ha^{-1} Diammonium Phosphate at the time of planting. The contrasting intensive treatment is driven mainly by early complete vegetation control and annual fertilization. [†] Planting density is expressed as the number of trees·ha^{-1}. [‡] Age is the age in years of the trees at time of the biomass harvest. [§] Year is year of the biomass harvest.

Table 4-4. Parameter estimates and standard errors of the estimate aboveground biomass ($kg \cdot tree^{-1}$) equations for loblolly and slash pine. Data used to develop equations were generated from regional trials in FL and GA, two to five years in age.

	β_0			β_1		
Species	Estimate	SE	p-value	Estimate	SE	p-value
Loblolly	0.63065	0.02679	<0.0001	0.53480	0.00774	<0.0001
Slash	0.56723	0.02678	<0.0001	0.53480	0.00774	<0.0001

Regression model: $\ln Y = \beta_0 + \beta_1 \ln X$, where ln= natural logarithm, Y = aboveground total dry weight ($kg \cdot tree^{-1}$), β_0 and β_1 = regression coefficients (intercept and slope, respectively), $X = DBH^2 \cdot HT$ in dm^3. Overall model $R^2 = 0.929$, RMSE = 0.26574, n = 432.

Table 4-5. Summary of statistical significance (prob. >F) and associated degrees of freedom from ANOVA to test loblolly pine basal area, stem volume and aboveground biomass at age two-, three- and five-years.

Source of variation	Basal area[†]			Stem volume[‡]			Aboveground biomass[§]		
	Num. df	Den. df	p-value	Num. df	Den. df	p-value	Num. df	Den. df	p-value
Age 2									
Silviculture (C)	1	76	**<0.0001**	1	76	**<0.0001**	1	76	**<0.0001**
Density (D)	1	6	**<0.0001**	1	6	**<0.0001**	1	6	**<0.0001**
C x D	1	72	**<0.0001**	1	72	**<0.0001**	1	72	**<0.0001**
Family (F)	6	76	**<0.0001**	6	76	**<0.0001**	6	76	**<0.0001**
C x F	6	76	0.3689	6	76	0.2596	6	76	0.4582
D x F	6	72	0.1361	6	72	0.1015	6	72	0.1785
C x D x F	6	72	0.4031	6	72	0.3705	6	72	0.3433
Location (S)	1	6	**0.0263**	1	6	**0.0219**	1	6	**0.0276**
S x C	1	76	**<0.0001**	1	76	**<0.0001**	1	76	**0.0002**
S x D	1	6	0.1887	1	6	0.1672	1	6	0.1537
S x C x D	1	72	**0.0097**	**1**	**72**	**0.0094**	**1**	**72**	**0.0055**
S x F	6	76	**0.0474**	**6**	**76**	**0.0390**	**6**	**76**	**0.0440**
S x C x F	6	76	0.8238	6	76	0.7674	6	76	0.8742
S x D x F	5	72	0.7599	5	72	0.7067	5	72	0.5411
S x C x D x F	5	72	0.2597	5	72	0.2553	5	72	0.2679
Age 3									
Silviculture (C)	1	6	**<0.0001**	1	6	**<0.0001**	1	6	**<0.0001**
Density (D)	1	6	**<0.0001**	1	6	**<0.0001**	1	6	**<0.0001**
C x D	1	72	**<0.0001**	1	6	**0.0024**	1	72	**<0.0001**
Family (F)	6	70	**<0.0001**	6	70	**<0.0001**	6	70	**<0.0001**
C x F	6	70	0.0701	6	70	0.0421	6	70	0.1081
D x F	6	72	0.5611	6	66	0.6152	6	72	0.8293
C x D x F	6	72	0.4365	6	66	0.3392	6	72	0.3136
Location (S)	1	6	**0.0023**	1	6	**0.0042**	1	6	**0.0061**
S x C	1	6	0.1132	1	6	0.2190	1	6	**0.0290**
S x D	1	6	0.1526	1	6	0.1837	1	6	0.1664
S x C x D	1	72	0.0715	1	6	0.2083	1	72	**0.0178**
S x F	6	70	0.0550	6	70	0.1195	6	70	0.1899
S x C x F	6	70	0.7820	6	70	0.7901	6	70	0.9084
S x D x F	5	72	0.8857	5	66	0.9280	5	72	0.6851
S x C x D x F	5	72	0.4151	5	66	0.3647	5	72	0.4449
Age 5									
Silviculture (C)	1	6	**<0.0001**	1	6	**<0.0001**	1	6	**<0.0001**
Density (D)	1	6	**<0.0001**	1	6	**<0.0001**	1	6	**<0.0001**
C x D	1	6	**0.0014**	1	6	**0.0011**	1	142	**<0.0001**
Family (F)	6	136	**<0.0001**	6	136	**<0.0001**	6	142	**<0.0001**
C x F	6	136	0.0541	6	136	**0.0019**	6	142	0.0502
D x F	6	136	0.1022	6	136	0.1149	6	142	0.4576
C x D x F	6	136	0.8249	6	136	0.6683	6	142	0.5154
Location (S)	1	6	**0.0021**	1	6	**0.0028**	1	6	**0.0032**
S x C	1	6	**0.0056**	1	6	**0.0038**	1	6	**0.0005**
S x D	1	6	0.1092	1	6	0.1314	1	6	0.0708
S x C x D	1	6	0.4445	1	6	0.2368	1	142	**0.0007**
S x F	6	136	**0.0271**	6	136	**0.0224**	6	142	**0.0388**
S x C x F	6	136	0.3847	6	136	0.2075	6	142	0.5364
S x D x F	5	136	0.4779	5	136	0.5922	5	142	0.4878
S x C x D x F	5	136	0.6594	5	136	0.5897	5	142	0.4361

Table 4-5 Continued.

Different models were constructed for each variable within each age with varying random affects in the variance terms; hence the need for different numerator and denominator degrees of freedom in the mixed model. [†] Basal area is expressed in $m^2 \cdot ha^{-1}$. [‡] Stem volume is expressed in $m^3 \cdot ha^{-1}$ and is calculated as the sum of per tree measurements of the volume of a cylinder to 1.37 m and the volume of a cone from 1.37 m to the top if the tree. [§] Aboveground biomass is expressed in metric tons per hectare and was calculated using individual tree allometric equations. P-values significant at the 95% level of confidence are shown in bold type.

Table 4-6. Summary of statistical significance (prob. >F) and associated degrees of freedom from ANOVA to test slash pine basal area, stem volume and aboveground biomass at age two-, three- and five-years.

Source of variation	Basal area[†]			Stem volume[‡]			Aboveground biomass[§]		
	Num. df	Den. df	p-value	Num. df	Den. df	p-value	Num. df	Den. df	p-value
Age 2									
Silviculture (C)	1	18	**0.0002**	1	18	**0.0004**	1	18	**0.0018**
Density (D)	1	18	**<0.0001**	1	18	**<0.0001**	1	18	**<0.0001**
C x D	1	18	0.0659	1	18	0.0760	1	18	0.1300
Family (F)	5	119	**<0.0001**	5	119	**<0.0001**	5	119	**<0.0001**
C x F	5	119	0.4326	5	119	0.4252	5	119	0.6137
D x F	5	119	0.1267	5	119	0.1027	5	119	0.3591
C x D x F	5	119	0.8362	5	119	0.8065	5	119	0.8731
Location (S)	1	6	0.9236	1	6	0.9826	1	6	0.7859
S x C	1	18	0.7668	1	18	0.8279	1	18	0.8956
S x D	1	18	0.2432	1	18	0.2885	1	18	0.4431
S x C x D	1	18	0.7714	1	18	0.8336	1	18	0.8855
S x F	5	119	0.1953	5	119	0.1890	5	119	0.1649
S x C x F	5	119	0.9212	5	119	0.9251	5	119	0.8537
S x D x F	5	119	0.7424	5	119	0.7318	5	119	0.6487
S x C x D x F	5	119	0.9946	5	119	0.9951	5	119	0.9982
Age 3									
Silviculture (C)	1	18	**<0.0001**	1	18	**<0.0001**	1	18	**<0.0001**
Density (D)	1	18	**<0.0001**	1	18	**<0.0001**	1	18	**<0.0001**
C x D	1	18	**0.0003**	1	18	**0.0007**	1	18	**0.0037**
Family (F)	5	119	**<0.0001**	5	119	**<0.0001**	5	119	**<0.0001**
C x F	5	119	0.1182	5	119	0.0797	5	119	0.4432
D x F	5	119	0.0641	5	119	0.0559	5	119	0.1259
C x D x F	5	119	0.6940	5	119	0.6627	5	119	0.7740
Location (S)	1	6	**0.0257**	1	6	**0.0410**	1	6	0.0937
S x C	1	18	**0.0121**	1	18	**0.0240**	1	18	0.1037
S x D	1	18	**0.0118**	1	18	**0.0159**	1	18	**0.0369**
S x C x D	1	18	0.1990	1	18	0.2184	1	18	0.3651
S x F	5	119	**0.0039**	5	119	**0.0046**	5	119	**0.0158**
S x C x F	5	119	0.0549	5	119	0.0608	5	119	0.2363
S x D x F	5	119	0.4222	5	119	0.4083	5	119	0.4500
S x C x D x F	5	119	0.9283	5	119	0.9148	5	119	0.9953
Age 5									
Silviculture (C)	1	6	**<0.0001**	1	6	**<0.0001**	1	6	**<0.0001**
Density (D)	1	12	**<0.0001**	1	12	**<0.0001**	1	12	**<0.0001**
C x D	1	12	**0.0007**	1	12	**0.0002**	1	12	**0.0037**
Family (F)	5	116	**<0.0001**	5	116	**<0.0001**	5	116	**<0.0001**
C x F	5	116	0.0589	5	116	**0.0126**	5	116	0.4432
D x F	5	116	0.2837	5	116	0.1763	5	116	0.1259
C x D x F	5	116	0.4665	5	116	0.5684	5	116	0.7740
Location (S)	1	6	**0.0024**	1	6	**0.0037**	1	6	**0.0937**
S x C	1	6	0.1441	1	6	0.1880	1	6	0.1037
S x D	1	12	**0.0439**	1	12	**0.0197**	1	12	**0.0369**
S x C x D	1	12	0.2945	1	12	0.2869	1	12	0.3651
S x F	5	116	**0.0127**	5	116	**0.0157**	5	116	**0.0158**
S x C x F	5	116	0.0510	5	116	0.0790	5	116	0.2363
S x D x F	5	116	0.7333	5	116	0.5427	5	116	0.4500
S x C x D x F	5	116	0.9229	5	116	0.8777	5	116	0.9953

Table 4-6. Continued.

Different models were constructed for each variable within each age with varying random affects in the variance terms; hence the need for different numerator and denominator degrees of freedom in the mixed model. † Basal area is expressed in $m^2 \cdot ha^{-1}$. ‡ Stem volume is expressed in $m^3 \cdot ha^{-1}$ and is calculated as the sum of per tree measurements of the volume of a cylinder to 1.37 m and the volume of a cone from 1.37 m to the top if the tree. § Aboveground biomass is expressed in metric tons per hectare and was calculated using individual tree allometric equations. P-values significant at the 95% level of confidence are shown in bold type.

Table 4-7. Variance components and associated statistical significance (prob. > |Z|) for individual model results in tables 4-5 and 4-6. Random variance components and their interactions were pooled when the P-value was greater than 0.25 and are either left blank or not shown in this table.

Source of Variation [*]	Slash Pine			Loblolly Pine		
	Basal area[†]	Stem volume[‡]	Aboveground biomass[§]	Basal area[†]	Stem volume[‡]	Aboveground biomass[§]
Age2						
Location (Block)	0.0928	0.0965	0.0967	0.1129	0.1205	0.1442
S x D(Block)				0.1177	0.1164	0.1192
S x C x D(Block)	0.0268	0.0245	0.0311			
S x C x F(Block)				0.0647	0.0609	0.0364
Residual at 3440 tph	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Residual at 1240 tph	<0.0001	<0.0001	<0.0001	0.0090	0.0103	0.0415
Age3						
Location (Block)	0.0915	0.0908	0.1037	0.2663	0.2733	0.2539
S x C(Block)				0.1119	0.1691	0.1380
S x D(Block)				0.1024	0.1654	0.0978
S x C x D(Block)	0.0153	0.0131	0.0197		0.2337	
S x C x F(Block)				0.2404	0.1763	0.2309
Residual at 3440 tph	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Residual at 1240 tph	<0.0001	<0.0001	<0.0001	0.0026	0.0038	0.0143
Age5						
Location (Block)	0.3690	0.3663	0.3769	0.1579	0.1594	0.1661
S x C(Block)	0.1667	0.1468	0.2149	0.1374	0.1356	0.1026
S x D(Block)				0.1707	0.1746	0.0992
S x C x D(Block)	0.0736	0.0688	0.1142	0.2415	0.2037	
Residual at 3440 tph	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Residual at 1240 tph	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Sources of variation are Location (S), planting density (D), silvicultural intensity (C), and family (F). Due to heterogeneity in the covariance structure with respect to the fixed effect of planting density and greater variation within the 2290 trees$\cdot$ha^{-1} treatment, the residual was grouped according to the planting density treatment. [†] Basal area is expressed in $m^2 \cdot ha^{-1}$. [‡] Stem volume is expressed in $m^3 \cdot ha^{-1}$ and is calculated as the sum of per tree measurements of the volume of a cylinder to 1.37 m and the volume of a cone from 1.37 m to the top if the tree. [§] Aboveground biomass is expressed in metric tons per hectare and was calculated using individual tree allometric equations

Table 4-8. Summary of mensurational characteristics by species, silvicultural treatment * and planting density † at age two-, three- and five-years. (n = 56 plots for loblolly and n = 48 plots for slash pine when averaged across sites and families). Values in parentheses are one standard error of the mean.

	Silvicultural Treatments *					
	Operational			Intensive		
Age and planting density	DBH (cm)	Height (m)	trees·ha^{-1} †	DBH (cm)	Height (m)	trees·ha^{-1} †
Loblolly pine						
Age 2						
1334 TPH †	2.8(0.06)	2.68(0.04)	1328(1)	3.5(0.07)	2.88(0.04)	1329(0)
2990 TPH †	2.7(0.06)	2.76(0.04)	2990(1)	3.3(0.07)	2.97(0.04)	2990(0)
Age 3						
1334 TPH †	6.5(0.12)	4.24(0.06)	1324(3)	8.5(0.10)	4.66(0.05)	1328(0)
2990 TPH †	5.7(0.12)	4.27(0.07)	2984(2)	7.3(0.07)	4.67(0.05)	2984(3)
Age 5						
1334 TPH †	11.0(0.21)	7.10(0.08)	1232(9)	13.9(0.10)	7.73(0.05)	1227(8)
2990 TPH †	8.6(0.18)	6.78(0.10)	2769(21)	11.1(0.10)	7.77(0.05)	2742(20)
Slash pine						
Age 2						
1334 TPH †	2.4(0.07)	2.00(0.03)	1325(2)	2.7(0.07)	2.04(0.03)	1324(2)
2990 TPH †	2.6(0.06)	2.10(0.02)	2985(3)	2.9(0.05)	2.10(0.02)	2982(4)
Age 3						
1334 TPH †	5.5(0.12)	3.14(0.05)	1309(6)	6.2(0.14)	3.24(0.05)	1317(4)
2990 TPH †	5.1(0.09)	3.32(0.04)	2973(8)	6.1(0.12)	3.43(0.04)	2973(6)
Age 5						
1334 TPH †	10.5(0.17)	6.22(0.06)	1072(45)	13.1(0.10)	6.50(0.03)	1107(23)
2990 TPH †	8.7(0.11)	6.31(0.04)	2690(35)	10.9(0.14)	6.81(0.04)	2608(36)

*The operational treatment represents silviculture best practices in the southeast at the end of the 20th century, receiving a common site preparation treatment and single banded application of 280 kg·ha^{-1} diammonium phosphate at the time of planting. The contrasting intensive treatment is driven mainly by early complete vegetation control and annual fertilization. † Planting density and subsequent density are expressed as the number of trees·ha^{-1}.

Table 4-9. Age five contrasts between slash pine families grown in mixtures versus grown in pure plots.

	Deployment		
Variable	Mixed	Pure	p-value
Basal Area[†]	17.2	16.7	0.1016
Stem Volume[‡]	54.1	52.5	0.1089
Aboveground Biomass [§]	38.4	37.4	0.0754

Intimate mixtures of all top performing slash pine full-sib families (S1, S2, S4, S5 and S6) were contrasted with the average of the same full-sib families grown in pure blocks across two locations (Waldo and Perry), two planting densities, and two silvicultural intensities. [†] Basal area is expressed in $m^2 \cdot ha^{-1}$. [‡] Stem volume is expressed in $m^3 \cdot ha^{-1}$ and is calculated as the sum of per tree measurements of the volume of a cylinder to 1.37 m and the volume of a cone from 1.37 m to the top if the tree. [§] Aboveground biomass is expressed in metric tons per hectare and was calculated using individual tree allometric equations.

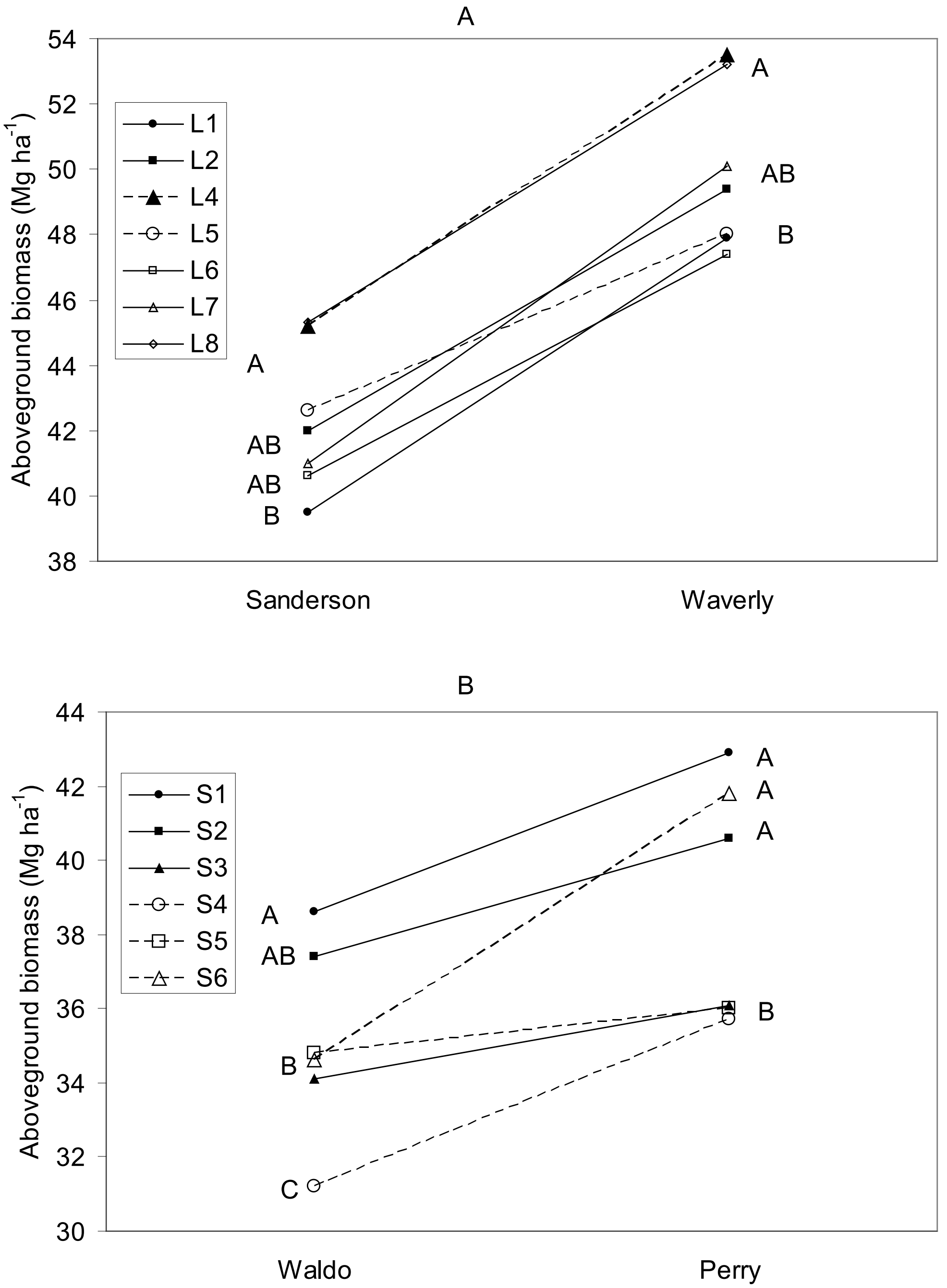

Figure 4-1. Standing crop biomass (metric tons per hectare) at age five demonstrating a genotype x location interaction for: A) loblolly pine (p=0.0388) and B) slash pine (p=0.0158). Data points within sites with the same letter are not significantly different at the 90% level of confidence using Bonferroni's Least Significant Difference (LSD).

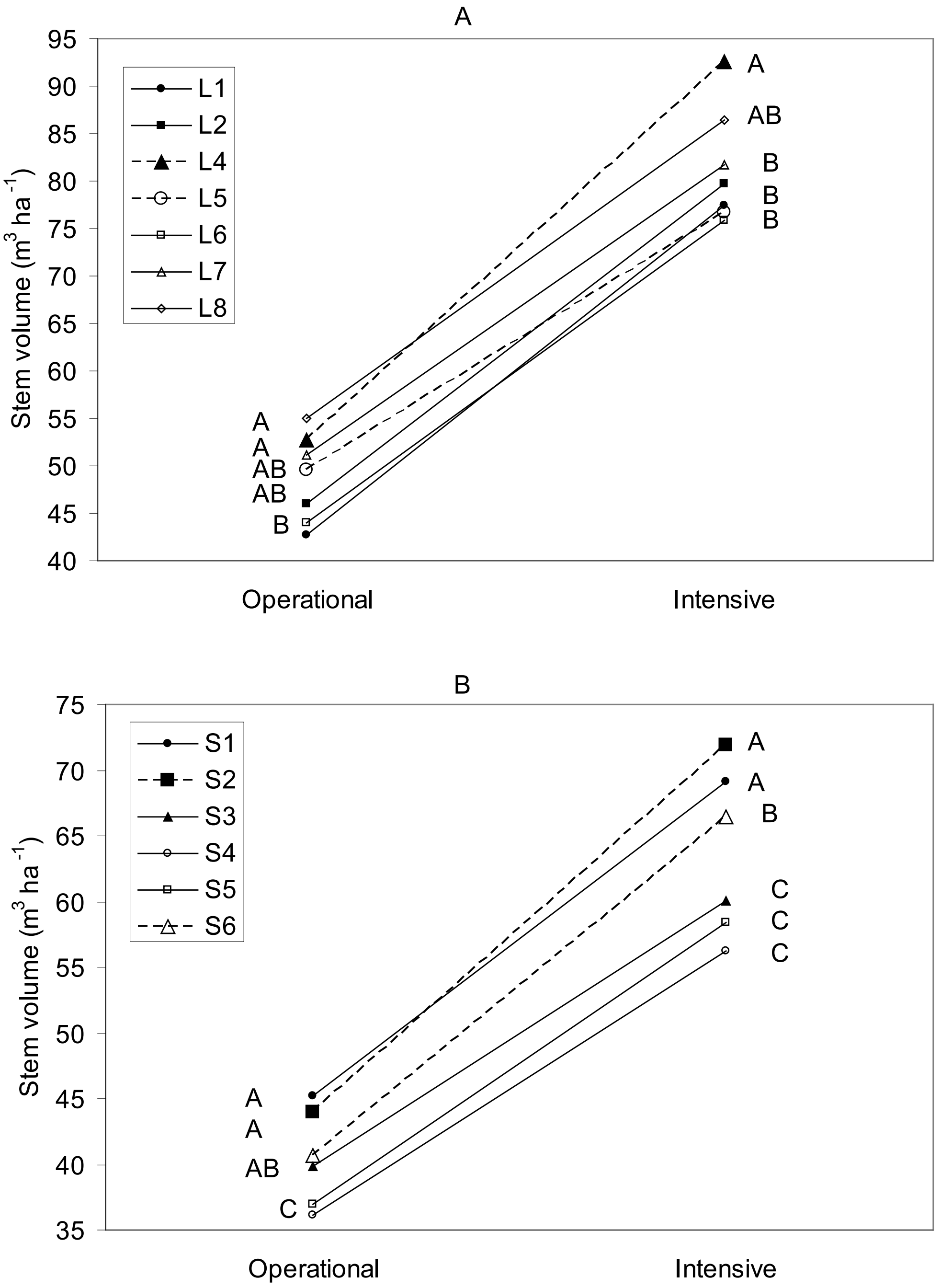

Figure 4-2. Standing volume ($m^3 \cdot ha^{-1}$) at age five demonstrating a genotype x silviculture interaction for:A) loblolly pine ($p=0.0019$) and B) slash pine ($p=0.0126$). Data points within species and cultures having the same letter are not significantly different at the 90% level of confidence using Bonferroni's Least Significant Difference (LSD).

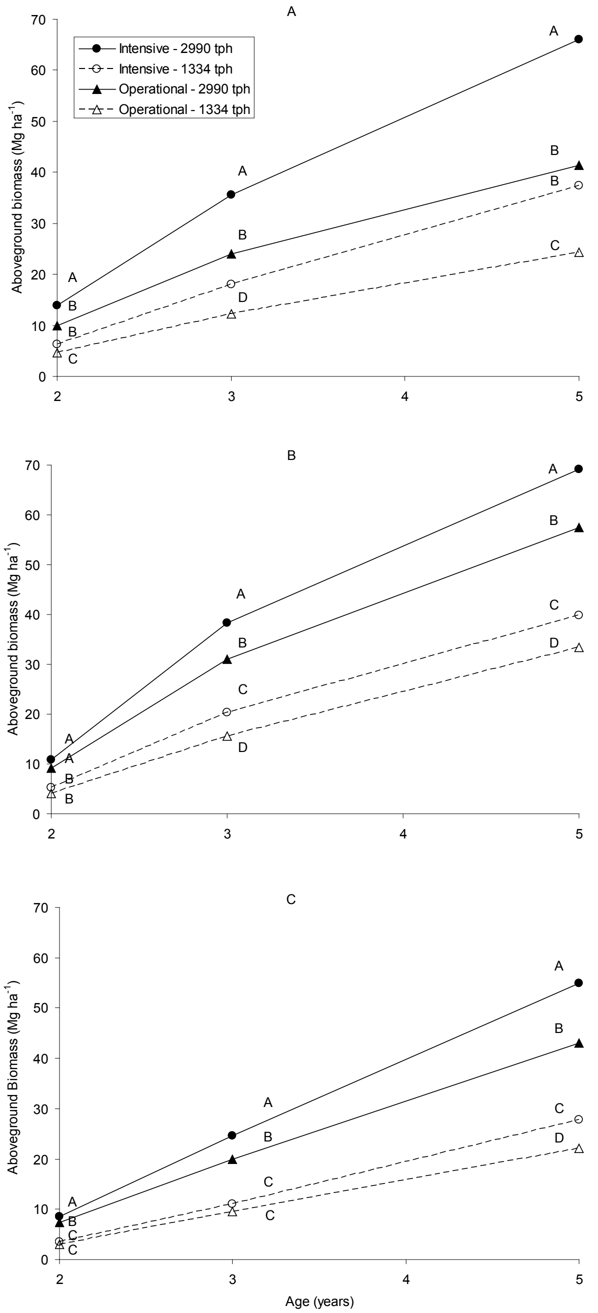

Figure 4-3. Aboveground biomass accretion by silvicultural treatment for loblolly pine at A) Sanderson, FL, B) Waverly, GA, and C) slash pine across both locations with slash pine. Loblolly pine is expressed by location for ease of presentation due to a three-way, location x silviculture x density interaction. There was no three-way interaction for slash pine. Data points within ages on each graph having the same letter are not significantly different at the 90% level of confidence using Bonferroni's Least Significant Difference (LSD).

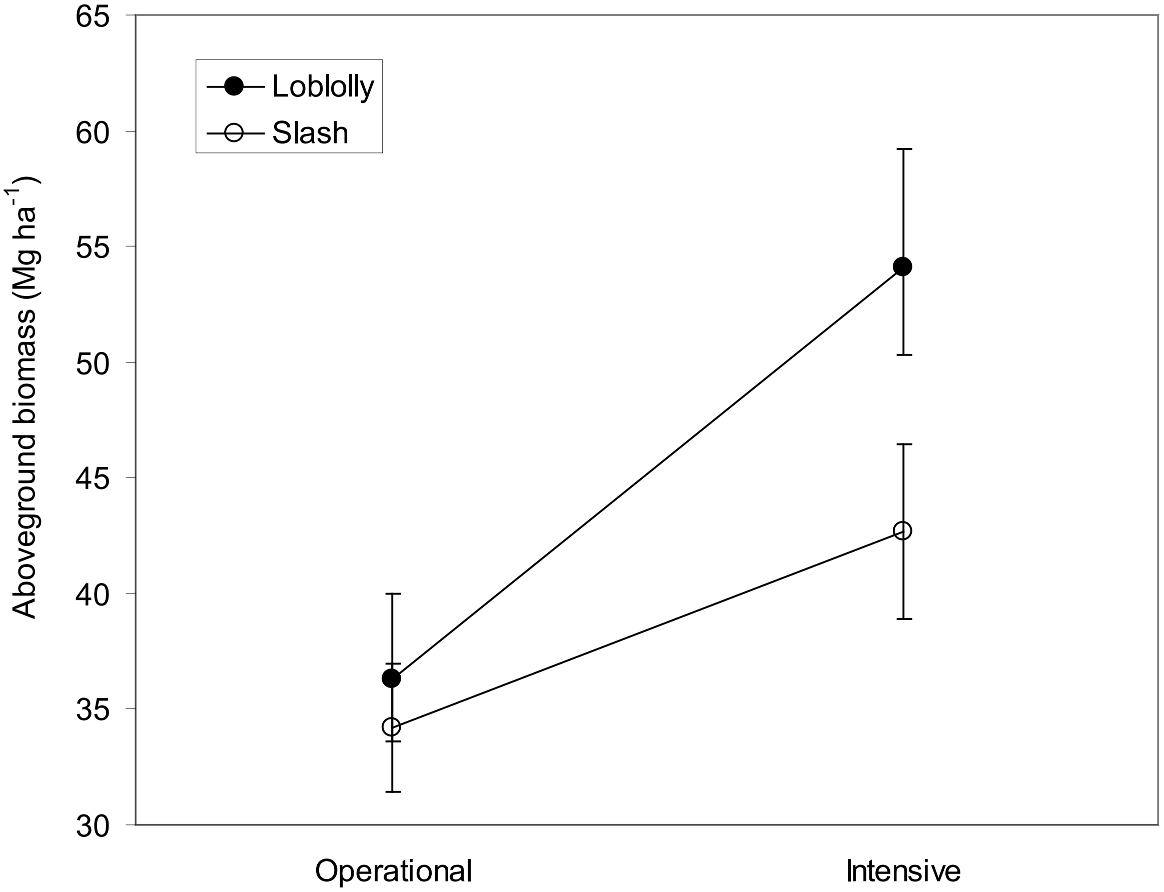

Figure 4-4. Standing crop biomass (metric tons per hectare) at age five demonstrating a species x silviculture interaction for loblolly and slash pine ($p<0.0001$). Mixed family plots across two locations and two levels of silvicultural treatment intensity were compared. Y error bars represent plus and minus one standard error of the mean.

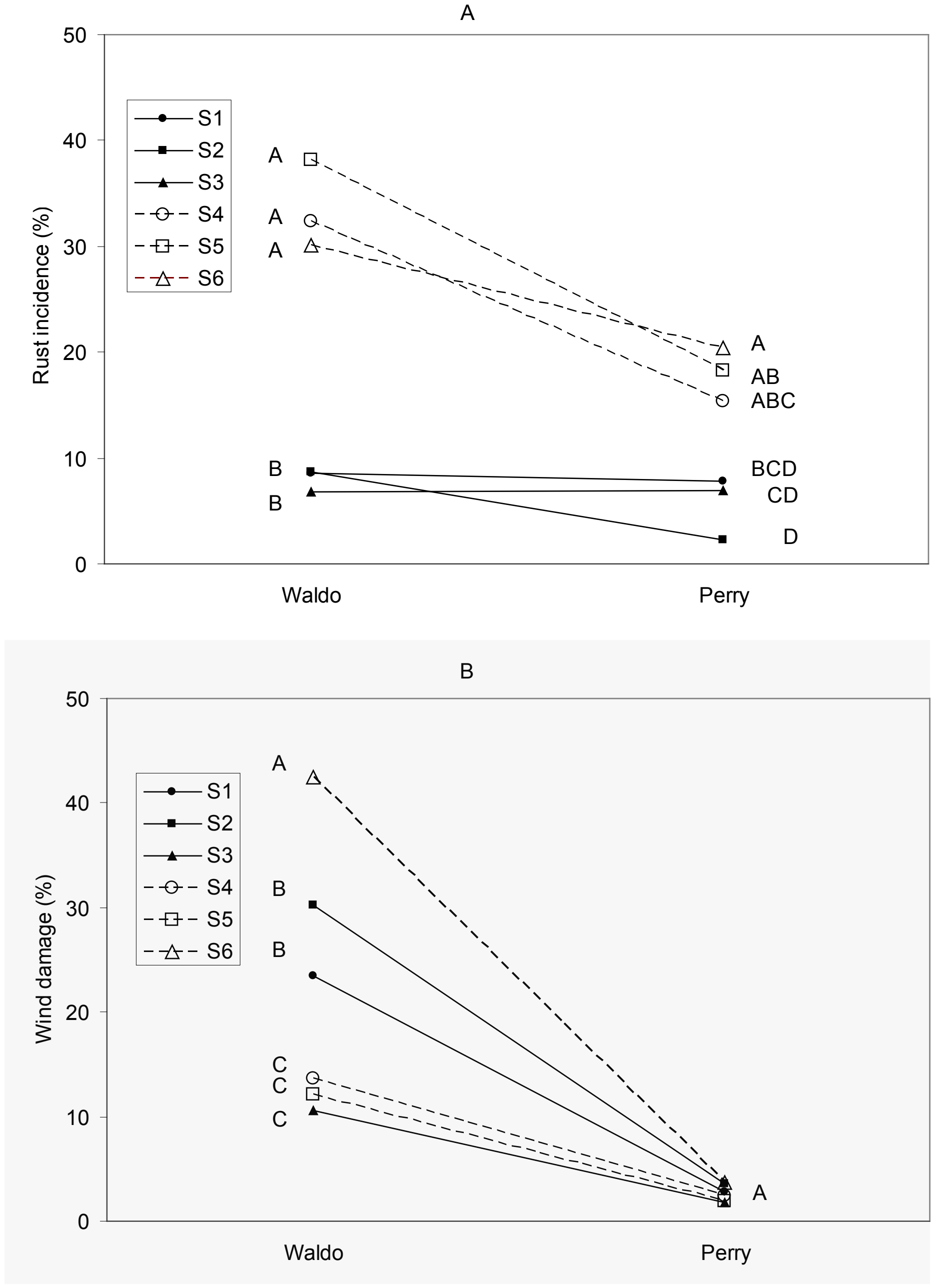

Figure 4-5. A) Percent incidence of fusiform rust per plot at age five demonstrating a genotype x location interaction for slash pine (p=0.0189). Trees were considered infected if galls were noted on the branches or the main stem. B) Percent incidence of wind damage per plot at age five, also demonstrating a significant genotype x location interaction for slash pine (p<0.0001). Trees were considered to be impacted by wind if they were leaning by more than 22 degrees from vertical or had a broken top. Data points within sites with the same letter are not significantly different at the 90% level of confidence using Bonferroni's Least Significant Difference (LSD).

CHAPTER 5
SUMMARY AND FUTURE RESEARCH

Summary

Research studies aimed at quantifying the response of southern pines with the combined effects of silvicultural treatments and genetic improvement in loblolly and slash pine in pure-family block plantings are very limited and documented genotype x silviculture interactions have not always been evident. The main goal of this investigation was to examine the stability of loblolly and slash pine full-sib family performance across a contrasting range of locations, planting densities, and silvicultural management intensities. Performance variables measured included: aboveground and belowground biomass accumulation and distribution, nitrogen content, unit-area stem volume, leaf area index, light extinction coefficient, interception of photosynthetically active radiation and radiation use efficiency. This study makes use of a series of replicated factorial experiments and family block plantings established in Florida and Georgia that manipulated gradients in planting density, understory competition and soil nutrient availability. Results for genotype x environment interactions (Table 5-1) were presented in three main chapters: Chapter two - biomass production, distribution and nitrogen accumulation at age two, Chapter three - interception and efficiency of PAR at ages four and five, and Chapter four - basal area, stem volume and biomass production at age five.

Biomass Production, Distribution, and Nitrogen Content at Age Two

Chapter two makes usage of the full complement of five experimental locations in southeastern Georgia and northeastern Florida (three loblolly and two slash pine), two levels of silvicultural management intensity (operational and intensive), seven loblolly and six slash pine families (L1, L2, L4, L5, L6, L7, L8 and S1, S2, S3, S4, S5, S6), two levels of planting density (1334 and 2990 trees ha^{-1}). Biomass accumulation of the foliage, branch & bark, bole and belowground components were examined. In addition, the nitrogen accumulation of the foliage, aboveground and belowground, and total components were quantified and tested across treatments. The distribution of this biomass among the components was also examined. The objective was to determine for each species independently, if there were interactions between the factors of location, family, silvicultural management intensity, and planting density.

After two growing seasons, biomass accumulation, N content and distribution were influenced by the combinations of silvicultural intensity, planting density, family, and locations in plantations of loblolly and slash pine. Significant genotype x density, silviculture x density, and silviculture x location interactions existed for loblolly pine biomass accumulation, yet none were evident for slash pine. Total biomass accumulation in slash pine ranged from 4.7 to 11.6 Mg ha^{-1} across planting densities. Loblolly pine TOTAL biomass effects of silviculture were not stable across planting density or locations. The response to the intensive silvicultural treatment was most pronounced on the high density plots (13.9 versus 17.2 Mg ha^{-1}, operational and intensive, respectively) and at the Sanderson, FL location (15.5 Mg ha^{-1}).

When distribution of this accumulated biomass to various components was examined, the only interaction that was significant was a three-way silviculture x density x location for loblolly pine. This interaction was driven by a differential response to silviculture and planting density at the Bunnell, FL location. At this location, the pattern of biomass distribution within the low density treatment was the inverse of those expected for the intensive silvicultural treatment which had less biomass distributed to the BOLE component. Loblolly pine families varied in their distribution of biomass to FOL (19.6 to 20.8%, families L6 and L4 respectively), BOLE (30.0 to 30.9%, families L4 and L6) and BELOW (25.7 to 26.6%, families L4 and L6)

Nitrogen accumulation in all biomass components demonstrated two types of interactions: genotype x density, and silviculture x density x location. Families were not stable across the two planting densities tested in this experiment for N content for FOL ($p=0.0235$), ABOVE ($p=0.0364$), BELOW ($p=0.0057$), and TOTAL ($p=0.0250$) (i.e. a family x density interaction). In general, this interaction was due to scale effects among families, with the notable exception of two families (L4 and L8) which changed ranks in N content between planting densities. The three-way interaction (silviculture x density x location) was caused by an unequal response to silvicultural management intensity between planting densities at the three locations examined (FOL, $p<0.0001$; ABOVE, $p<0.0001$; BELOW, $p=0.0001$; TOTAL, $p<0.0001$). At the Bunnell, FL location, there were much lower than expected N contents in the FOL, ABOVE, and TOTAL components in the intensive silvicultural treatment combination at the 1334 trees ha^{-1}

Taken together, evidence of these complex interactions as early as age-two, serves to underscore the importance of understanding how to best deploy elite genotypes of loblolly and slash pine, given the uncertainty in predicting its response to a wide variety of man made and abiotic environmental factors. For example the only three-way interaction occurring for slash pine may have been due to the effects of a hurricane after the first growing season. While distribution of accumulated biomass did not appear to be involved in driving these interactions, variation in crown structure (McCrady and Jokela, 1996) or resource use efficiency may play a role (McKeand *et al.*, 1997a) and was investigated in Chapter three.

Interception and Efficiency of PAR at Ages Four and Five

Chapter three examines the stability of IPAR and RUE in selected elite full-sib families of loblolly pine deployed in uniform blocks grown under intensive silviculture over time and locations. This chapter utilizes a subset of the experimental material from Chapter two since logistical constraints limited the experimental design to two loblolly pine locations (Sanderson, FL and Waverly, GA), six full-sib families (L1, L2, L4, L5, L6, L7, and L8), at a combination of 2990 trees ha^{-1} and the intensive silvicultural treatment. While there was variation among families, there was no evidence for genotype x environment interactions (i.e. genotype x location or genotype x year). However, there were significant interactions for location x year.

The annual NF observed in this investigation ranged from 3.7 to 5.1 Mg ha^{-1} across years and locations. There was a large decline in NF at the Sanderson, FL location in 2005 which was thought to be due to early leaf senescence related to the effects of hurricanes Frances and Jeanne in 2004. Projected LAI varied among years and locations from a low of 1.7 to a maximum of 3.3 m m^{-2}. Cosine corrected values of *k* averaged about 0.44 across locations and years, with the exception of a significantly high value which occurred at the Sanderson, FL location in 2005 (*k*=0.83). Aboveground net primary productivity was similar among families and likely due to the fact that they were all chosen for superior performance in growth. Similarly, the silvicultural treatment combination applied in this experiment, which combined high planting density with intensive silvicultural management, likely evened the inherent differences in site quality between the locations; hence, the lack of significant differences in ANPP between locations. There was a statistically significant effect of family on growing season RUE and values ranged from 1.08 to 1.16 g MJ^{-1} (families L8 and L4, respectively). The more densely spaced plots tended to be more efficient at capturing and utilizing PAR. Results from this experiment suggest that RUE in full-sib families of loblolly pine was stable across contrasting soil types early in the stage of stand development.

Basal Area, Stem Volume and Biomass Production at Age Five

The fourth chapter examined genotype x environmental responses in biomass production and stem volume through age five-years. This investigation utilized two locations from within each species, combining silvicultural treatment intensity (operational versus intensive), planting density (1334 versus 2990 trees·ha^{-1}) and full-sib families (seven loblolly and six slash pine families).

Age five unit-area aboveground biomass (AGB) and stem volume (VOL) varied significantly in response to several treatment combinations: genotype x location, genotype x silviculture, and silviculture x density for BA and VOL. Family interactions with silvicultural intensity were positive and the best overall performing families responded the most under the intensive silvicultural treatment. For slash pine, families S2 and S6 were the most responsive in VOL (63% increase due to silvicultural intensity). Loblolly pine family L4 was the most responsive to silvicultural treatment (75% increase in VOL), while L5 was the least responsive (55% increase). Accumulation of biomass at age five interacted with silvicultural management intensity and planting density. Response to silvicultural treatment was the greatest under the narrowest planting density. This was evidenced for slash pine where the intensive silvicultural treatment increased aboveground standing biomass by 5.7 Mg ha^{-1} at 1334 trees ha^{-1} versus 12 Mg ha^{-1} at 2990 trees ha^{-1}. There was a three-way interaction for loblolly pine aboveground biomass. At the Sanderson, FL location, the 2990 trees ha^{-1} density under the operational silviculture treatment produced a much lower response than the same treatment combination at the Waverly, GA location. This was attributed to the Sanderson, FL location having a lower inherent level of productivity than the Waverly, GA location. No three-way interactions, which included family, were evident and all genetic sources were stable across the contrasting planting densities.

However, there were changes in slash pine family rankings between locations, which were partly explained by reductions in growth associated with a combination of fusiform rust infection [*Cronartium quercum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*] and wind damage from the 2004 hurricane season. Loblolly pine generally had a low incidence of rust infection and no significant interactions were found. At age five, loblolly pine outperformed slash pine in aboveground biomass accumulation, especially under the intensive silvicultural management intensity. While loblolly performance was similar, whether deployed in mixtures or pure family blocks, slash pine tended to be more productive in intimate mixtures than when grown in pure family blocks.

Focus of Future Research

Future research should build on the strengths and limitations of this investigation and provide insight into the biological mechanisms that drive genotype x environment interactions in southern pines. The strengths of this study were the large contrasts within the treatments of silvicultural treatment intensity and planting density, across locations with contrasting soil types. Also, elite full-sib families were deployed in large family block plantings allowing for unit-area estimates over time. Moreover, the experimental design had a high statistical power for the detection of interactions among these multiple treatment combinations. However, the study could have been more informative if a larger number of families were tested, especially those which had contrasting traits for biomass accumulation, distribution, and resource use efficiency. A wider distribution of locations across regions may have also provided more information as to how these elite families may vary with local climate and disease conditions.

Informative research investigations of genotype x environment interactions could focus on particular biological mechanisms of forest plantation productivity, such as nutrient uptake or light capture, in large block planting experiments. These experiments should incorporate a wide range of genotypes which have been selected for contrasting traits which have been identified as having an influence on these biological mechanisms. For example, genotypes with a large contrast in the distribution and structure of fine roots could provide insight into genotype x environment interactions for nutrient uptake. Similarly, genotypes with contrasting crown architecture could yield valuable information regarding the mechanisms driving light capture and use. Additionally, increasing the uniformity within genotypes (i.e. full-sib families to clones within families), while increasing the uniformity of experimental material, is thought to lead to increased genotype x environmental interactions and should be utilized in future studies where appropriate.

While this investigation tested several genotypes across contrasting soil types (Spodosols versus Ultisols), these were were in close geographic proximity to each other with similar environmental conditions. Despite this, there were large genotype x environment interactions which were driven by the effects of localized disease incidence and hurricane proximity. Future research should test selected genotypes (clones) across a wider range of contrasting physical and environmental conditions. Environmental and physical attributes should contrast: soil types (i.e. rooting volume, physical properties, and nutrient availability), climate (i.e. temperature, relative humidity, light regime, and the distribution of annual precipitation), and pest incidence (i.e. fusiform rust and Nantucket tip moth incidence). This wide gradient of environmental conditions could be achieved by establishing trials across contrasting regions where southern pine has been deployed, such as Hawaii, South America, and the southeastern United States).

Table 5-1. Significant interactions for loblolly and lash pine by variable and year as described in this investigation.

Trait	Ages	Interaction
Loblolly pine		
Total biomass accumulation	2	silviculture x density, silviculture x location, genotype x density
Biomass distribution	2	silviculture x density x location
Nitrogen accumulation	2	genotype x density, silviculture x density x location
Needlefall	4&5	location x year
Leaf area index	4&5	location x year
Fraction of PAR intercepted(*f*)	4&5	location x year
Light extinction coefficient (*k*)	4&5	location x year
Intercepted PAR	4&5	location x year
Basal area	2,3&5	genotype x location, silviculture x density x family
Stem volume accumulation	3&4	silviculture x density
Stem volume accumulation	2&5	genotype x location
Stem volume accumulation	2	silviculture x density x location
Aboveground biomass accumulation	3	silviculture x density x location
Aboveground biomass accumulation	2,3,& 5	genotype x location
Slash pine		
Aboveground nitrogen accumulation	2	density x location
Belowground nitrogen accumulation	2	silviculture x density x location
Basal area	3&5	silviculture x density, location x density
Basal area	3	silviculture x location
Basal area	3&5	genotype x location
Stem volume accumulation	3&5	silviculture x density, location x density
Stem volume accumulation	3	silviculture x location
Stem volume accumulation	3&5	genotype x location
Stem volume accumulation	5	genotype x silviculture
Aboveground biomass accumulation	3&5	genotype x location, silviculture x density, location x density

APPENDIX A
GLOSSARY OF TERMS, UNITS AND DESCRIPTIONS

Table A-1. Glossary of terms, units and descriptions.

Term	Unit	Description
Diameter at breast height	cm	The diameter of individual trees measured (DBH).
Height	m	Total height of individual trees (HT).
Stem volume	m^3 ha^{-1}	Unit area volume of the bole component (VOL).
Basal area	m^2 ha^{-1}	The cross sectional area of all trees per hectare measured at 1.37 meters above the ground level (BA).
Biomass	Mg ha^{-1}	Unit area biomass of various tree components (foliage, branches & bark, bole, aboveground, belowground and total).
Nitrogen content	kg ha^{-1}	Nitrogen content of various tree components (foliage, branches & bark, bole, aboveground, belowground and total).
Aboveground net primary productivity	Mg ha^{-1} yr^{-1}	Aboveground unit area biomass production including needlefall (ANPP).
Needlefall	Mg ha^{-1} yr^{-1}	Amount of needles senesced per unit area over time (NF).
Leaf area index	m^2 m^{-2}	Measure of the projected surface area of leaves per unit area of ground (LAI).
Fraction of photosynthetically active radiation	fraction	Fraction of photosynthetically active radiation below the canopy to that above the canopy (f).
Intercepted photosynthetically active radiation	MJ m^{-2} yr^{-1}	Sum of photosynthetically active radiation (400 to 700 nm wavelength) intercepted per unit area over time (IPAR).
Light extinction coefficient	unit-less	A quantitative description of the rate of decreased irradiance vertically through a canopy (k).
Radiation Use Efficiency	g MJ^{-1}	The weight of biomass produced per unit input of intercepted photosynthetically active radiation (RUE).

APPENDIX B
HISTORICAL ANNUAL RAINFALL, AVERAGE TEMPERATURE, MINIMUM TEMPERATURE, MAXIMUM TEMPERATURE DATA BY LOCATION

Table B-1. Historical annual rainfall, average temperature, minimum temperature, maximum temperature data by location.

Variable/Year		Sanderson, FL	Waverly, GA	Bunnell, FL	Perry, FL	Waldo, FL
Annual Precipitation (mm yr^{-1})	2000	802	1118	1076	895	872
	2001	1075	1073	1948	1051	1070
	2002	1355	1094	1594	1578	1405
	2003	1610	933	1327	2076	1184
	2004	1914	1119	1906	1521	1483
	mean 1961 to 1990	1409	1260	1424	1477	1316
Average temperature (^{0}C)	2000	20.2	19.5	21.2	19.9	20.1
	2001	20.6	20.2	21.4	20.2	20.6
	2002	20.7	20.5	21.7	20.4	20.7
	2003	20.2	19.6	21.8	21.3	20.4
	2004	20.3	19.9	21.3	20.3	20.7
	mean 1961 to 1990	19.9	19.8	21.1	20.4	20.3
Minimum temperature (^{0}C)						
	2000	-6.7	-5.0	-5.6	-9.4	-7.2
	2001	-5.0	-5.0	-4.4	-7.8	-5.6
	2002	-5.0	-3.3	-3.3	-7.8	-5.0
	2003	-7.8	-7.2	-7.8	-7.2	-6.7
	2004	-5.0	-2.8	-3.9	-6.7	-5.0
Maximum temperature (^{0}C)						
	2000	38.3	39.4	36.7	37.8	42.2
	2001	36.7	36.1	35.6	36.7	35.6
	2002	37.2	36.7	36.1	37.2	37.2
	2003	35.0	35.0	35.6	35.0	34.4
	2004	35.6	35.6	38.3	36.1	36.7

Noaa: Sanderson = Lake City 2B, Waverly = Brunswick McKinnon AP, Bunnell = Deland 1 SSE, Perry = Perry, Waldo = Gainesville Regional AP. (NOAA National climatic data center http://www.ncdc.noaa.gov/oa/ncdc.html . Last accessed April 22nd 2009).

Table B-2. Palmer Drought Severity Index (PDSI) annual values for three regions in FL and GA.

Year	Waverly, GA	Sanderson, Perry, and Waldo, FL	Bunnell FL
2000	-2.64	-2.96	-3.63
2001	-2.37	-2.38	-1.79
2002	-2.15	-0.59	0.83
2003	0.82	1.20	2.19
2004	0.24	0.60	0.89

Note: This index quantifies the severity of a wet or dry spell. This is based on the principles of a balance between moisture supply and demand. Man-made changes were not considered in this calculation. The index generally ranges from -6 to +6, with negative values denoting dry spells and positive values indicating wet spells. There are a few values in the magnitude of +7 or -7. PDSI values 0 to -.5 = normal; -0.5 to -1.0 = incipient drought; -1.0 to -2.0 = mild drought; -2.0 to -3.0 = moderate drought; -3.0 to -4.0 = severe drought; and greater than -4.0 = extreme drought. Similar adjectives are attached to positive values of wet spells. This is a meteorological drought index used to assess the severity of dry or wet spells of weather.

APPENDIX C
GENERAL SOIL PROPERTIES OF THE FIVE PPINES EXPERIMENTAL LOCATIONS IN SOUTHEAST GEORGIA AND NORTHEAST FLORIDA

Table C-1. General soil properties of the five PPINES experimental locations in southeast Georgia and northeast Florida.

	Sanderson, FL	Waverly, GA	Bunnell, FL	Perry, FL	Waldo, FL
Soil order	Spodosol	Ultisol	Spodosol	Spodosol	Spodosol
Soil series	Leon sand (sandy, siliceous, thermic Aeric Alaquods)	Bladen (mixed, semiactive, thermic Typic Albaquults)	Myakka sand (sandy, siliceous, hyperthermic Aeric Alaquods)	Leon (sandy, siliceous, thermic Aeric Alaquods)	Newnan (sandy, siliceous, hyperthermic Ultic Haplohumods)
Depth class	Very deep	Very deep	Deep, to very deep	Very deep	Very deep
Drainage class	Poorly, to very poorly drained	Poorly drained	Poorly, to very poorly drained	Poorly, to very poorly drained	Somewhat poorly drained
Reactivity	Extremely acidic, to slightly acidic	Extremely acidic, to strongly acidic	Acidic, to strongly acidic	Extremely acidic, to slightly acidic	Extremely, to moderately acidic

USDA-NRCS Soil Survey Division, Official soil series descriptions. PPINES: Pine Productivity Interactions on Experimental Sites.

APPENDIX D
RAW DATA UTILIZED TO DEVELOP ALLOMETRIC EQUATIONS

Table D-1. Raw data utilized to develop allometric equations from the Bunnell, FL location at age 2.

DENSITY	CULTURE	FAM	BLOCK	TREE	HT	DBH	HTLC	GLD	CWAL	CWAC	FOLIAGE	BRANCH	BARK	BOLE	CROOTS	TAP
1334	Intensive	L2	1	70	2.42	3.8	0.20	10.2	2.08	2.15	1.9993	1.4494	0.375104	1.517796		
1334	Intensive	L2	3	77	2.20	2.7	0.20	7.9	1.64	1.52	1.3489	0.7946	0.238550	0.838150		
1334	Intensive	L2	4	7	1.94	1.5	0.01	6.9	1.65	1.51	1.1313	0.6240	0.159060	0.472940	0.4160	0.6910
1334	Operational	L2	1	73	2.25	1.9	0.30	6.9	1.28	1.29	0.6434	0.4233				
1334	Operational	L2	3	79	2.80	3.2	0.19	8.3	1.82	1.62	1.2531	0.7825	0.180360	1.161240		
1334	Operational	L2	4	1	2.31	1.8	0.21	7.5	1.61	1.76	1.2195	0.6061	0.199396	0.783704	0.2853	0.5816
2990	Intensive	L2	1	12	3.32	4.3	0.37	10.0	1.70	1.55	1.2563	0.9118	0.460987	1.750213	0.6858	0.9406
2990	Intensive	L2	3	4	2.58	3.7	0.23	9.3	1.73	1.67	1.4409	1.0869	0.311846	1.471054		
2990	Intensive	L2	4	6	2.32	1.8	0.21	7.2	1.43	1.62	0.9580	0.4584	0.199242	0.642358		
2990	Operational	L2	1	6	3.21	3.2	0.23	7.6	1.45	1.50	1.0635	0.5740	0.311367	1.159533		
2990	Operational	L2	3	127	2.04	1.5	0.46	4.8	0.88	0.86	0.2103	0.1331	0.100299	0.293601		
2990	Operational	L2	4	125	2.49	2.6	0.21	8.5	1.86	1.98	1.4054	0.9211	0.243090	0.909410	0.7699	0.9218
1334	Intensive	L4	1	20	2.90	4.2	0.05	10.8	2.36	2.08	2.6396	1.6890	0.353197	1.752203		
1334	Intensive	L4	3	5	2.20	1.9	0.32	8.2	1.70	1.38	1.4466	0.8720	0.232867	1.039833		
1334	Operational	L4	1	9	2.05	1.7	0.01	6.6	1.35	1.64	1.2691	0.8082	0.153526	0.486474		
1334	Operational	L4	3	41	2.95	3.3	0.41	8.5	1.75	1.59	1.0709	0.8363	0.285786	1.095514		
1334	Operational	L4	4	7	2.23	1.8	0.27	7.3	1.20	1.32	0.8104	0.3953	0.177883	0.573817	0.1556	0.3609
2990	Intensive	L4	1	81	3.44	4.4	0.25	9.8	1.90	2.35	1.8884	1.6298	0.372667	2.060933	0.3749	1.0445
2990	Intensive	L4	3	3	2.27	2.0	0.25	7.8	1.60	2.02	1.3426	0.9867	0.159796	0.686904		
2990	Intensive	L4	4	115	2.32	2.1	0.28	6.7	1.36	1.62	0.8189	0.4482	0.124543	0.650657		
2990	Operational	L4	1	122	3.48	3.6	0.21	7.7	1.80	1.72	1.0685	0.8756	0.290712	1.477088		
2990	Operational	L4	3	115	2.54	2.9	0.39	6.9	1.36	1.79	0.5080	0.4693	0.258857	0.735943		
2990	Operational	L4	4	11	2.03	1.5	0.32	6.6	1.35	1.42	0.6676	0.3894	0.156072	0.461528	0.2889	0.3794

Note: For all tables in Appendix D; DENSITY is expressed in trees per hectare, FAM refers to Family (L is loblolly and S is slash pine), TREE is tree number, HEIGHT is total height in meters, DBH is in centimeters, HTLC is the height to the base of the live crown in meters, GLD is groundline diameter in centimeters, CWAL is crown width along the beds in meters and CWAC is crown width across the beds in meters, FOLIAGE is the total dry weight of green foliage in kilograms, BRANCH is the total dry weight of branches in kilograms, BARK is the total dry weight of bark in kilograms, BOLE is the total dry weight of the bole wood in kilograms, CROOT is the total dry weight of roots greater than 2 millimeters in diameter centered on a 1 square meter section to 40 centimeters depth in kilograms, and TAP is the total dry weight of the taproot in kilograms.

Table D-2. Raw data utilized to develop allometric equations from the Perry, FL location at age 2.

DENSITY	CULTURE	FAM	BLOCK	TREE	HT	DBH	HTLC	GLD	CWAL	CWAC	FOLIAGE	BRANCH	BARK	BOLE	CROOTS	TAP
1334	Intensive	S6	1	96	1.99	2.5	0.30	8.4	1.25	1.50	2.1453	0.8269	0.301743	0.547257		
1334	Intensive	S6	2	4	2.50	4.1	0.30	8.9	1.45	1.95	2.2553	0.7892	0.540589	0.911011	0.4005	0.8964
1334	Intensive	S6	3	72	3.23	4.9	0.21	9.6	1.79	2.11	3.0797	1.2585	0.694913	1.472187	0.7344	1.0651
1334	Operational	S6	1	2	2.51	3.3	0.25	7.2	1.44	1.71	1.6580	0.4443	0.307644	0.805956		
1334	Operational	S6	2	1	2.08	3.2	0.39	6.6	1.36	1.43	1.1660	0.4177	0.378365	0.407935	0.1735	0.5498
1334	Operational	S6	3	74	1.84	2.1	0.41	6.0	1.12	0.99	0.6873	0.2600	0.205840	0.319160	0.1278	0.3591
1334	Operational	S6	4	2	2.61	3.7	0.51	8.1	1.64	1.71	1.7699	0.6999	0.469514	0.708886		
2990	Intensive	S6	1	116	1.85	2.4	0.45	6.9	1.24	1.40	0.9379	0.2818	0.217668	0.460232		
2990	Intensive	S6	2	121	2.29	3.0	0.21	8.3	1.90	2.00	2.0256	0.7007	0.356322	0.740278	0.4097	0.7402
2990	Intensive	S6	3	127	2.98	4.3	0.23	9.3	1.57	1.80	2.0559	0.7573	0.569735	1.196065	0.7409	0.8588
2990	Operational	S6	1	12	1.58	1.3	0.30	5.4	1.10	1.08	0.4652	0.1507	0.126927	0.154173		
2990	Operational	S6	2	113	2.69	4.5	0.30	10.0	1.73	2.03	3.0237	1.4440	0.597148	1.329352	0.5761	1.3678
2990	Operational	S6	3	15	2.46	4.1	0.29	9.3	1.56	1.40	1.7066	0.7060	0.488642	0.837158	0.4557	0.8823
2990	Operational	S6	4	6	2.29	3.4	0.24	8.2	1.79	1.69	1.4725	0.6223	0.385816	0.626684		
1334	Intensive	S1	1	126	1.79	2.0	0.35	6.6	1.14	1.22	0.8270	0.2408	0.191367	0.345933		
1334	Intensive	S1	2	3	1.80	2.7	0.31	8.0	1.44	1.39	1.5151	0.4442	0.317754	0.452846	0.3869	0.5581
1334	Intensive	S1	3	5	2.74	4.5	0.19	8.6	1.84	1.81	2.4361	0.8204	0.615309	1.093291	0.5377	0.8622
1334	Operational	S1	1	32	2.30	3.1	0.24	8.6	1.64	1.74	1.4823	0.5066	0.374399	0.714601		
1334	Operational	S1	2	10	1.70	1.6	0.19	6.2	1.15	1.02	0.7542	0.1615	0.182176	0.236924	0.1895	0.3045
1334	Operational	S1	3	31	2.32	3.7	0.18	9.0	1.35	1.37	1.4716	0.4939	0.439875	0.804725	0.2190	1.1023
1334	Operational	S1	4	75	2.46	3.4	0.20	9.3	1.47	1.64	1.6562	0.7018	0.409141	0.664759		
2990	Intensive	S1	1	3	1.74	2.2	0.28	6.2	1.12	1.51	0.8940	0.2096	0.194299	0.337801		
2990	Intensive	S1	2	13	2.54	4.1	0.23	8.9	1.74	1.76	1.9971	0.6639	0.575313	0.959287	0.5628	0.9062
2990	Intensive	S1	3	13	2.60	4.2	0.30	9.4	1.70	1.90	2.0986	0.6860	0.628359	0.990141	0.3803	0.7521
2990	Operational	S1	1	124	2.50	3.6	0.23	7.9	1.18	1.42	1.1744	0.3590	0.470901	0.679999		
2990	Operational	S1	2	5	1.66	1.9	0.39	5.7	1.17	1.14	0.5927	0.1621	0.149687	0.215313	0.0750	0.2642
2990	Operational	S1	3	3	2.07	3.1	0.24	8.1	1.54	1.70	1.4365	0.5125	0.334085	0.641515	0.4098	0.6234
2990	Operational	S1	4	126	2.55	3.5	0.24	7.8	1.51	1.48	1.2111	0.3375	0.388529	0.777771		

Table D-3. Raw data utilized to develop allometric equations from the Waldo, FL location at age 2.

DENSITY	CULTURE	FAM	BLOCK	TREE	HT	DBH	HTLC	GLD	CWAL	CWAC	FOLIAGE	BRANCH	BARK	BOLE	CROOTS	TAP
1334	Intensive	S6	1	10	2.20	4.0	0.17	9.0	2.00	1.60	3.0356	1.2928	0.520445	0.907655	0.4454	0.8535
1334	Intensive	S6	2	74	2.45	3.3	0.38	7.5	1.59	1.65	2.0905	0.6763	0.561258	1.015342		
1334	Intensive	S6	3	71	1.77	2.1	0.22	6.2	1.60	1.75	1.3901	0.4907	0.190888	0.406612	0.1111	0.3983
1334	Intensive	S6	4	8	2.10	3.5	0.19	9.1	1.60	1.90	2.0303	0.6720	0.388469	0.654631		
1334	Operational	S6	1	74	2.20	2.6	0.05	6.9	1.90	1.50	1.4639	0.4683	0.247864	0.531136	0.2465	0.5603
1334	Operational	S6	2	123	2.61	3.2	0.10	7.1	1.74	1.19	1.3896	0.5240	0.440034	0.707166		
1334	Operational	S6	3	3	1.91	2.1	0.29	5.3	1.22	1.15	0.6997	0.1994	0.216668	0.302732	0.1823	0.2682
1334	Operational	S6	4	9	2.18	2.6	0.10	6.8	1.40	1.30	0.9933	0.3173	0.356395	0.447005		
2990	Intensive	S6	1	126	2.02	3.2	0.04	7.7	1.90	1.70	2.0282	0.9394	0.237175	0.509125	0.4734	0.5047
2990	Intensive	S6	2	30	1.83	2.0	0.24	6.1	1.19	1.20	0.8180	0.2029	0.206956	0.308944		
2990	Intensive	S6	3	117	2.69	4.0	0.27	8.3	1.63	1.50	2.0611	0.7134	0.576441	1.001759	0.3921	0.8283
2990	Intensive	S6	4	8	2.55	4.1	0.10	8.7	1.60	1.80	1.9619	0.6508	0.626494	1.077106		
2990	Operational	S6	1	3	2.29	3.3	0.02	8.1	1.60	1.90	1.7945	0.7292	0.411277	0.844523	0.5452	0.5278
2990	Operational	S6	2	11	2.51	2.6	0.02	7.3	1.40	1.15	1.2500	0.6663	0.347706	0.628894		
2990	Operational	S6	3	9	1.66	1.9	0.12	5.0	1.00	0.98	0.4264	0.1144	0.140267	0.213333	0.0449	0.1802
2990	Operational	S6	4	4	2.56	3.0	0.25	6.8	1.64	1.59	1.1806	0.3170	0.342947	0.606753		
1334	Intensive	S1	1	4	2.08	3.5	0.18	8.2	1.90	2.00	2.2294	0.8992	0.444257	0.656243	0.4862	0.7035
1334	Intensive	S1	2	80	2.63	4.0	0.21	8.0	1.79	1.68	2.1209	0.6998	0.552539	1.037061		
1334	Intensive	S1	3	6	2.20	3.6	0.18	8.3	1.37	1.39	1.5683	0.4347	0.450499	0.730001	0.2928	0.5950
1334	Intensive	S1	4	10	1.55	1.6	0.35	5.1	1.00	0.80	0.4784	0.0802	0.142004	0.179696		
1334	Operational	S1	1	78	2.21	3.4	0.20	8.5	1.70	2.00	2.0702	0.7119	0.414243	0.709157	0.3604	0.8613
1334	Operational	S1	2	20	1.61	1.3	0.17	5.1	1.03	1.04	0.5805	0.1069	0.150655	0.175545		
1334	Operational	S1	3	76	2.38	3.5	0.15	8.0	1.57	1.69	1.9282	0.7629	0.525205	0.783095	0.4418	0.8052
1334	Operational	S1	4	5	2.10	2.2	0.30	5.9	0.90	1.00	0.7130	0.1463	0.225553	0.321547		
2990	Intensive	S1	1	126	1.45	1.3	0.02	6.2	1.30	1.30	0.9496	0.2259	0.188882	0.238618	0.1602	0.2887
2990	Intensive	S1	2	41	2.31	2.7	0.15	7.1	1.60	1.60	1.2378	0.3772	0.411945	0.535155		
2990	Intensive	S1	3	123	2.60	3.9	0.03	7.8	1.16	1.80	1.4101	0.3549	0.420664	0.724836	0.4343	0.5717
2990	Intensive	S1	4	1	2.55	3.6	0.35	7.5	1.50	1.40	1.5596	0.4690	0.460796	0.801904		
2990	Operational	S1	1	3	1.75	2.0	0.08	7.0	1.30	1.90	1.0707	0.4046	0.266551	0.384949	0.3382	0.3761
2990	Operational	S1	2	2	2.36	3.6	0.07	7.4	1.40	1.35	1.2435	0.3661	0.458898	0.619702		
2990	Operational	S1	3	11	2.17	2.6	0.19	7.0	1.06	1.30	0.8249	0.1820	0.335544	0.524456	0.1717	0.3276
2990	Operational	S1	4	15	2.80	4.1	0.22	7.4	1.46	1.21	1.3039	0.4125	0.540188	0.816012		

Table D-4. Raw data utilized to develop allometric equations from the Sanderson, FL location at age 2.

DENSITY	CULTURE	FAM	BLOCK	TREE	HT	DBH	HTLC	GLD	CWAL	CWAC	FOLIAGE	BRANCH	BARK	BOLE	CROOTS	TAP
1334	Intensive	L2	1	4	2.95	3.5	0.25	8.7	1.64	1.84	2.0391	0.9833	0.193595	1.701805		
1334	Intensive	L2	2	2	3.80	4.3	0.25	9.8	2.12	2.31	3.0527	2.2758	0.570441	1.965059	0.9270	1.6907
1334	Intensive	L2	3	40	2.09	1.6	0.16	6.6	1.50	1.52	1.1152	0.6210	0.084507	0.578693		
1334	Operational	L2	1	5	3.64	3.8	0.18	9.3	2.40	2.32	2.4474	1.8532	0.500576	1.478524		
1334	Operational	L2	2	8	3.07	3.6	0.22	9.8	2.10	1.78	2.0887	1.2268	0.261541	1.715159	0.2953	1.3505
1334	Operational	L2	3	1	2.52	2.3	0.19	6.9	1.60	1.65	1.3519	0.8934	0.161003	0.745697		
2990	Intensive	L2	1	10	3.22	3.6	0.51	7.8	1.28	1.80	1.4088	0.6836	0.299616	1.792484		
2990	Intensive	L2	2	126	2.72	2.4	0.40	8.2	1.95	1.49	1.4938	0.6870	0.248792	0.792008	0.5125	0.6553
2990	Intensive	L2	3	4	3.56	4.3	0.23	9.7	1.83	2.24	2.0789	1.2958	0.489258	2.462842		
2990	Operational	L2	1	125	2.61	2.4	0.19	6.6	1.24	1.64	1.1350	0.4955	0.129914	0.673286		
2990	Operational	L2	2	14	3.04	2.9	0.19	7.0	1.35	1.38	1.1446	0.5655	0.216974	0.804326	0.3200	0.6055
2990	Operational	L2	3	124	3.09	3.3	0.23	10.9	1.67	1.85	1.2378	0.8821	0.322140	1.459460		
1334	Intensive	L4	1	8	3.93	5.7	0.22	11.5	2.70	2.55	3.9940	2.9101	0.562096	3.771904		
1334	Intensive	L4	2	76	3.14	2.8	0.31	8.5	1.76	1.90	1.9891	1.3182	0.193095	0.988005		
1334	Intensive	L4	3	8	2.96	3.6	0.22	8.9	2.33	2.10	2.6945	1.8854	0.348360	1.878540		
1334	Operational	L4	1	73	2.84	3.4	0.25	8.4	1.85	1.82	2.4216	1.4661	0.250277	1.675123		
1334	Operational	L4	2	71	2.76	2.5	0.02	7.1	1.46	1.47	1.1628	0.6002	0.143202	0.628898	0.3760	0.8027
1334	Operational	L4	3	6	3.34	3.6	0.32	9.0	2.45	2.42	2.3765	1.9574	0.31695	1.382050		
2990	Intensive	L4	1	126	3.50	4.6	0.02	9.5	2.35	1.80	3.1121	1.8500	0.491626	2.906674		
2990	Intensive	L4	2	2	3.94	5.0	0.28	9.8	2.05	2.30	2.4143	1.6231	0.51932	2.040580	0.6239	1.1592
2990	Intensive	L4	3	128	2.85	3.3	0.38	7.9	1.44	1.46	1.2372	0.7529	0.204887	1.050213		
2990	Operational	L4	1	120	3.58	4.3	0.14	8.6	1.68	2.15	1.9006	1.2712	0.280100	1.367800		
2990	Operational	L4	2	117	2.60	2.1	0.22	6.6	1.35	1.58	0.8465	0.5332	0.180528	0.542572	0.8747	0.5137
2990	Operational	L4	3	12	2.03	1.8	0.12	5.8	1.17	1.28	0.7130	0.3459	0.082600	0.416900		

Table D-5. Raw data utilized to develop allometric equations from the Waverly, GA location at age 2.

DENSITY	CULTURE	FAM	BLOCK	TREE	HT	DBH	HTLC	GLD	CWAL	CWAC	FOLIAGE	BRANCH	BARK	BOLE	CROOTS	TAP
1334	Intensive	L2	1	8	2.11	1.8	0.23	5.9	1.12	1.23	1.1391	0.8627	0.096729	0.417871		
1334	Intensive	L2	2	3	2.95	3.1	0.14	8.7	1.55	1.69	2.2978	1.1845	0.361774	1.247126	0.5656	1.0484
1334	Intensive	L2	3	73	2.34	2.8	0.17	7.2	1.23	1.35	1.4804	0.6997	0.179847	0.675153		
1334	Operational	L2	2	9	3.14	3.3	0.15	7.9	1.38	1.49	1.9240	0.6339	0.308182	1.173318	0.2690	0.8558
1334	Operational	L2	3	73	2.99	3.5	0.17	7.0	1.20	1.13	1.2734	0.5590	0.155815	0.709185		
2990	Intensive	L2	1	2	2.60	3.3	0.26	8.1	1.88	1.45	2.1357	1.1878	0.195979	0.925121		
2990	Intensive	L2	2	125	2.24	2.1	0.35	5.7	1.14	1.34	0.6316	0.2473	0.148617	0.387783	0.2052	0.3724
2990	Intensive	L2	3	9	2.82	3.3	0.15	7.8	1.55	1.73	1.2008	0.7586	0.232510	0.953290		
2990	Operational	L2	1	125	2.30	2.3	0.21	5.2	1.04	1.19	0.5506	0.2421	0.106025	0.318075		
2990	Operational	L2	2	120	2.95	2.9	0.25	6.9	1.36	1.67	1.4353	0.7634	0.221482	0.884018	0.5576	0.5380
2990	Operational	L2	3	124	3.39	3.5	0.21	7.4	1.38	1.40	1.3602	0.5697	0.200931	1.142569		
1334	Intensive	L4	1	77	3.27	4.4	0.13	9.8	1.98	2.10	2.4741	1.7733	0.459487	1.688713		
1334	Intensive	L4	2	72	2.91	2.9	0.34	8.2	1.64	1.72	2.1399	0.7920	0.244071	1.015429		
1334	Intensive	L4	3	2	3.44	4.5	0.23	10.0	1.88	1.82	2.4949	1.7038	0.407901	1.716099		
1334	Operational	L4	1	5	3.24	3.4	0.19	7.0	1.66	1.41	1.6942	0.8265	0.209492	0.801308		
1334	Operational	L4	2	78	2.53	2.2	0.02	5.6	1.36	1.31	0.8475	0.3751	0.151125	0.468875	0.1405	0.5245
1334	Operational	L4	3	8	2.88	3.1	0.19	6.8	1.37	1.42	0.7140	0.4606	0.241195	0.853005		
2990	Intensive	L4	1	8	3.12	3.5	0.27	7.2	1.39	1.58	1.6439	0.9477	0.238393	0.954707		
2990	Intensive	L4	2	116	3.55	3.9	0.36	8.3	1.50	1.60	1.8904	0.9539	0.274692	1.291208	0.4717	0.9361
2990	Intensive	L4	3	4	2.41	2.5	0.35	6.8	1.22	1.36	1.0046	0.4967	0.147010	0.525290		
2990	Operational	L4	1	5	2.72	3.2	0.14	7.2	1.43	1.54	1.2515	0.5328	0.172311	0.702089		
2990	Operational	L4	2	122	3.04	3.0	0.21	6.5	1.40	1.33	1.3144	0.5920	0.155577	0.849323	0.5117	0.5961
2990	Operational	L4	3	3	2.71	2.7	0.24	7.2	1.52	1.63	1.8726	0.8959	0.252374	0.758826		

Table D-6. Raw data utilized to develop allometric equations from the Sanderson, FL location at age 5, operational silviculture and family L4.

DENSITY	CULTURE	FAM	BLOCK	TREE	HT	DBH	HTLC	GLD	CWAL	CWAC	FOLIAGE	BRANCH	BARK	BOLE	CROOTS	TAP
2990	Operational	L4	1	117	8.90	10.9	4.0	15.1	1.7	2.1	2.956490	4.089143	2.543035	13.55602	2.0684	4.030
2990	Operational	L4	1	119	8.70	9.5	3.8	13.1	1.2	1.9	1.319228	1.712753	1.935347	9.597816	1.5594	3.120
2990	Operational	L4	1	124	8.60	11.1	3.6	16.0	1.9	2.2	2.397552	3.003228	2.725137	11.71901	2.0003	4.030
2990	Operational	L4	2	2	7.30	8.7	2.7	13.4	1.0	1.3	1.773862	2.318415	1.602432	7.561728	1.2511	3.085
2990	Operational	L4	2	7	6.60	7.5	3.3	10.5	0.9	1.6	0.835146	1.163054	1.128934	4.595382	0.9319	1.795
2990	Operational	L4	2	10	7.20	9.4	3.2	14.0	0.9	2.3	1.364494	2.465949	1.918021	7.986881	0.9411	3.200
2990	Operational	L4	3	3	6.70	8.5	1.2	13.0	1.6	2.6	1.863535	2.598732	1.816049	5.918531	1.8901	2.455
2990	Operational	L4	3	8	6.60	8.2	2.3	12.2	1.3	1.8	1.362917	1.757734	1.222061	5.475812	1.1872	1.935
2990	Operational	L4	3	10	5.20	6.2	2.1	10.0	1.2	1.3	0.700546	0.642764	0.711522	3.098149	0.8232	0.980
2990	Operational	L4	1	117	8.90	10.9	4.0	15.1	1.7	2.1	2.956490	4.089143	2.543035	13.55602	2.0684	4.030
2990	Operational	L4	1	119	8.70	9.5	3.8	13.1	1.2	1.9	1.319228	1.712753	1.935347	9.597816	1.5594	3.120
2990	Operational	L4	1	124	8.60	11.1	3.6	16.0	1.9	2.2	2.397552	3.003228	2.725137	11.71901	2.0003	4.030
2990	Operational	L4	2	2	7.30	8.7	2.7	13.4	1.0	1.3	1.773862	2.318415	1.602432	7.561728	1.2511	3.085
2990	Operational	L4	2	7	6.60	7.5	3.3	10.5	0.9	1.6	0.835146	1.163054	1.128934	4.595382	0.9319	1.795
2990	Operational	L4	2	10	7.20	9.4	3.2	14.0	0.9	2.3	1.364494	2.465949	1.918021	7.986881	0.9411	3.200
2990	Operational	L4	3	3	6.70	8.5	1.2	13.0	1.6	2.6	1.863535	2.598732	1.816049	5.918531	1.8901	2.455
2990	Operational	L4	3	8	6.60	8.2	2.3	12.2	1.3	1.8	1.362917	1.757734	1.222061	5.475812	1.1872	1.935
2990	Operational	L4	3	10	5.20	6.2	2.1	10.0	1.2	1.3	0.700546	0.642764	0.711522	3.098149	0.8232	0.980

Table D-7. Raw data utilized to develop allometric equations from the Sanderson, FL location at age 5, operational silviculture and family L7.

DENSITY	CULTURE	FAM	BLOCK	TREE	HT	DBH	HTLC	GLD	CWAL	CWAC	FOLIAGE	BRANCH	BARK	BOLE	CROOTS	TAP
2990	Operational	L7	1	1	7.30	10.2	3.3	14.2	1.6	2.1	1.463778	1.885822	2.091422	8.969746	0.9572	2.980
2990	Operational	L7	1	5	6.50	7.0	2.6	10.8	1.1	1.3	1.165500	1.291080	1.104800	4.366182	1.0887	1.935
2990	Operational	L7	1	11	7.90	10.1	3.4	14.5	1.3	1.8	2.081492	2.928984	2.279269	10.58874	2.5761	4.550
2990	Operational	L7	2	7	7.00	9.3	3.4	12.6	1.4	1.5	1.221102	1.701700	1.719716	7.117963	1.4154	2.610
2990	Operational	L7	2	10	5.60	7.0	2.2	11.5	0.8	1.5	0.848667	1.335285	1.119273	3.873030	0.8682	1.680
2990	Operational	L7	2	12	6.70	10	3.0	13.2	1.4	1.6	1.694390	2.316637	2.080382	7.018864	1.0027	2.955
2990	Operational	L7	3	116	5.40	6.8	2.1	10.2	1.2	1.7	0.878688	0.887750	0.958651	2.858964	0.8464	1.525
2990	Operational	L7	3	120	4.30	4.7	1.7	7.7	1.1	0.8	0.504060	0.438053	0.561154	1.109500	0.3732	0.820
2990	Operational	L7	3	125	5.70	7.0	2.2	11.1	1.5	1.8	1.375891	1.405923	1.221622	3.507611	0.8432	1.735
2990	Operational	L7	1	1	7.30	10.2	3.3	14.2	1.6	2.1	1.463778	1.885822	2.091422	8.969746	0.9572	2.980
2990	Operational	L7	1	5	6.50	7.0	2.6	10.8	1.1	1.3	1.165500	1.291080	1.104800	4.366182	1.0887	1.935
2990	Operational	L7	1	11	7.90	10.1	3.4	14.5	1.3	1.8	2.081492	2.928984	2.279269	10.58874	2.5761	4.550
2990	Operational	L7	2	7	7.00	9.3	3.4	12.6	1.4	1.5	1.221102	1.701700	1.719716	7.117963	1.4154	2.610
2990	Operational	L7	2	10	5.60	7.0	2.2	11.5	0.8	1.5	0.848667	1.335285	1.119273	3.873030	0.8682	1.680
2990	Operational	L7	2	12	6.70	10.0	3.0	13.2	1.4	1.6	1.694390	2.316637	2.080382	7.018864	1.0027	2.955
2990	Operational	L7	3	116	5.40	6.8	2.1	10.2	1.2	1.7	0.878688	0.887750	0.958651	2.858964	0.8464	1.525
2990	Operational	L7	3	120	4.30	4.7	1.7	7.7	1.1	0.8	0.504060	0.438053	0.561154	1.109500	0.3732	0.820
2990	Operational	L7	3	125	5.70	7.0	2.2	11.1	1.5	1.8	1.375891	1.405923	1.221622	3.507611	0.8432	1.735

Table D-8. Raw data utilized to develop allometric equations from the Sanderson, FL location at age 5, intensive silviculture and family L4.

DENSITY	CULTURE	FAM	BLOCK	TREE	HT	DBH	HTLC	GLD	CWAL	CWAC	FOLIAGE	BRANCH	BARK	BOLE	CROOTS	TAP
2990	Intensive	L4	1	2	9.70	14.7	3.1	21.7	1.9	3.0	4.365611	6.154241	4.193221	22.68302	3.1143	8.185
2990	Intensive	L4	1	10	10.20	12.0	5.0	17.8	1.6	2.3	2.273807	3.483918	2.725506	17.49223	1.7567	5.695
2990	Intensive	L4	1	14	9.50	10.7	4.6	16.0	1.7	1.9	2.473326	3.329021	2.314326	14.56822	2.3031	4.075
2990	Intensive	L4	2	4	9.10	12.5	4.5	17.5	0.1	1.5	2.353397	4.592274	3.343303	15.32264	2.3967	4.950
2990	Intensive	L4	2	9	8.50	10.1	3.0	14.1	1.5	1.9	2.348419	2.641727	2.092892	10.37911	1.6156	4.375
2990	Intensive	L4	2	16	8.70	11.6	3.3	16.3	1.6	2.0	2.805349	4.603774	2.295119	13.76613	2.1191	4.030
2990	Intensive	L4	3	5	9.80	13.4	3.9	19.0	2.1	3.3	3.749350	5.815700	2.729314	20.02824	3.2440	8.370
2990	Intensive	L4	3	8	9.10	10.6	3.9	14.7	1.7	2.8	2.751041	4.683094	1.975358	11.60802	1.6952	4.395
2990	Intensive	L4	3	12	8.20	8.6	3.9	13.0	1.3	2.2	1.647227	2.840481	1.258580	7.105862	1.8196	2.520
2990	Intensive	L4	1	2	9.70	14.7	3.1	21.7	1.9	3.0	4.365611	6.154241	4.193221	22.68302	3.1143	8.185
2990	Intensive	L4	1	10	10.20	12.0	5.0	17.8	1.6	2.3	2.273807	3.483918	2.725506	17.49223	1.7567	5.695
2990	Intensive	L4	1	14	9.50	10.7	4.6	16.0	1.7	1.9	2.473326	3.329021	2.314326	14.56822	2.3031	4.075
2990	Intensive	L4	2	4	9.10	12.5	4.5	17.5	0.1	1.5	2.353397	4.592274	3.343303	15.32264	2.3967	4.950
2990	Intensive	L4	2	9	8.50	10.1	3.0	14.1	1.5	1.9	2.348419	2.641727	2.092892	10.37911	1.6156	4.375
2990	Intensive	L4	2	16	8.70	11.6	3.3	16.3	1.6	2.0	2.805349	4.603774	2.295119	13.76613	2.1191	4.030
2990	Intensive	L4	3	5	9.80	13.4	3.9	19.0	2.1	3.3	3.749350	5.815700	2.729314	20.02824	3.2440	8.370
2990	Intensive	L4	3	8	9.10	10.6	3.9	14.7	1.7	2.8	2.751041	4.683094	1.975358	11.60802	1.6952	4.395
2990	Intensive	L4	3	12	8.20	8.6	3.9	13.0	1.3	2.2	1.647227	2.840481	1.258580	7.105862	1.8196	2.520

Table D-9. Raw data utilized to develop allometric equations from the Sanderson, FL location at age 5, intensive silviculture and family L7.

DENSITY	CULTURE	FAM	BLOCK	TREE	HT	DBH	HTLC	GLD	CWAL	CWAC	FOLIAGE	BRANCH	BARK	BOLE	CROOTS	TAP
2990	Intensive	L7	1	115	8.70	12.6	3.8	16.7	1.7	2.0	2.225849	3.273179	3.076216	16.27494	2.5520	6.950
2990	Intensive	L7	1	121	7.90	11.8	2.4	16.3	1.6	1.7	2.108314	4.298014	2.827464	11.91885	2.0844	4.780
2990	Intensive	L7	1	127	9.80	12.5	3.9	19.5	1.7	2.2	3.181229	4.871542	3.515428	20.98008	3.1436	8.545
2990	Intensive	L7	2	115	8.60	12.2	3.7	16.2	1.2	1.9	3.328359	4.565272	3.140607	16.50768	2.3114	6.285
2990	Intensive	L7	2	119	7.60	10.6	2.4	14.5	1.5	2.3	2.138471	3.443857	2.147685	10.78626	1.9542	3.585
2990	Intensive	L7	2	122	8.40	12.6	3.0	17.1	0.8	2.0	2.820264	4.374569	2.959585	13.57723	2.3371	5.390
2990	Intensive	L7	3	118	6.90	9.4	3.0	13.5	0.9	2.1	1.291142	2.451272	1.516088	6.812977	1.8101	3.410
2990	Intensive	L7	3	120	7.70	12.6	2.9	17.1	1.8	1.7	3.051658	4.498341	2.743148	13.54697	2.5773	5.440
2990	Intensive	L7	3	123	8.60	13.8	3.5	18.7	1.6	1.5	3.079408	4.314661	3.339809	18.57347	3.6666	6.770
2990	Intensive	L7	1	115	8.70	12.6	3.8	16.7	1.7	2.0	2.225849	3.273179	3.076216	16.27494	2.5520	6.950
2990	Intensive	L7	1	121	7.90	11.8	2.4	16.3	1.6	1.7	2.108314	4.298014	2.827464	11.91885	2.0844	4.780
2990	Intensive	L7	1	127	9.80	12.5	3.9	19.5	1.7	2.2	3.181229	4.871542	3.515428	20.98008	3.1436	8.545
2990	Intensive	L7	2	115	8.60	12.2	3.7	16.2	1.2	1.9	3.328359	4.565272	3.140607	16.50768	2.3114	6.285
2990	Intensive	L7	2	119	7.60	10.6	2.4	14.5	1.5	2.3	2.138471	3.443857	2.147685	10.78626	1.9542	3.585
2990	Intensive	L7	2	122	8.40	12.6	3.0	17.1	0.8	2.0	2.820264	4.374569	2.959585	13.57723	2.3371	5.390
2990	Intensive	L7	3	118	6.90	9.4	3.0	13.5	0.9	2.1	1.291142	2.451272	1.516088	6.812977	1.8101	3.410
2990	Intensive	L7	3	120	7.70	12.6	2.9	17.1	1.8	1.7	3.051658	4.498341	2.743148	13.54697	2.5773	5.440
2990	Intensive	L7	3	123	8.60	13.8	3.5	18.7	1.6	1.5	3.079408	4.314661	3.339809	18.57347	3.6666	6.770

Table D-10. Raw data utilized to develop allometric equations from the Waverly, GA location at age 5, intensive silviculture and family L4.

DENSITY	CULTURE	FAM	BLOCK	TREE	HT	DBH	HTLC	GLD	CWAL	CWAC	FOLIAGE	BRANCH	BARK	BOLE	CROOTS	TAP
2990	Intensive	L4	2	115	7.40	13.4	2.9	17.2	1.6	1.7	4.710800	5.812981	2.393065	13.12115	3.024	4.650
2990	Intensive	L4	2	118	7.80	11.1	3.5	16.5	0.9	1.7	2.385796	2.601123	1.742230	12.12738	1.132	3.885
2990	Intensive	L4	2	125	8.20	14.5	3.2	19.5	1.5	1.7	4.038553	4.951684	3.290382	17.85689	2.677	4.500
2990	Intensive	L4	3	117	7.80	11.0	3.1	15.6	0.9	1.5	2.816326	3.501507	1.639230	10.32345	1.164	3.630
2990	Intensive	L4	3	120	7.80	11.5	3.2	15.5	1.2	1.7	3.644605	3.752476	1.910576	11.58636	2.873	4.190
2990	Intensive	L4	3	125	9.30	13.1	3.6	18.8	1.3	1.8	4.654730	5.814757	2.607345	18.63877	3.620	5.985
2990	Intensive	L4	4	102	8.70	12.0	3.2	14.5	1.2	2.2	2.203734	3.052889	2.255072	10.13622	1.917	2.785
2990	Intensive	L4	4	113	9.50	13.1	3.9	17.1	1.4	3.0	3.919030	5.868425	2.980239	17.35341	2.705	4.055
2990	Intensive	L4	4	116	8.80	13.1	3.5	16.7	1.6	1.9	4.641446	5.521206	3.479358	18.14702	1.862	3.975
2990	Intensive	L4	2	115	7.40	13.4	2.9	17.2	1.6	1.7	4.710800	5.812981	2.393065	13.12115	3.024	4.650
2990	Intensive	L4	2	118	7.80	11.1	3.5	16.5	0.9	1.7	2.385796	2.601123	1.742230	12.12738	1.132	3.885
2990	Intensive	L4	2	125	8.20	14.5	3.2	19.5	1.5	1.7	4.038553	4.951684	3.290382	17.85689	2.677	4.500
2990	Intensive	L4	3	117	7.80	11.0	3.1	15.6	0.9	1.5	2.816326	3.501507	1.639230	10.32345	1.164	3.630
2990	Intensive	L4	3	120	7.80	11.5	3.2	15.5	1.2	1.7	3.644605	3.752476	1.910576	11.58636	2.873	4.190
2990	Intensive	L4	3	125	9.30	13.1	3.6	18.8	1.3	1.8	4.654730	5.814757	2.607345	18.63877	3.620	5.985
2990	Intensive	L4	4	102	8.70	12.0	3.2	14.5	1.2	2.2	2.203734	3.052889	2.255072	10.13622	1.917	2.785
2990	Intensive	L4	4	113	9.50	13.1	3.9	17.1	1.4	3.0	3.919030	5.868425	2.980239	17.35341	2.705	4.055
2990	Intensive	L4	4	116	8.80	13.1	3.5	16.7	1.6	1.9	4.641446	5.521206	3.479358	18.14702	1.862	3.975

Table D-11. Raw data utilized to develop allometric equations from the Waverly, GA location at age 5, intensive silviculture and family L7.

DENSITY	CULTURE	FAM	BLOCK	TREE	HT	DBH	HTLC	GLD	CWAL	CWAC	FOLIAGE	BRANCH	BARK	BOLE	CROOTS	TAP
2990	Intensive	L7	2	7	7.20	10.5	3.3	14.5	0.6	0.8	1.895508	1.987311	1.906627	8.523747	0.760	2.445
2990	Intensive	L7	2	10	7.90	14.0	2.7	19.0	1.6	1.5	4.931632	5.993063	3.864070	17.62493	2.933	5.605
2990	Intensive	L7	2	16	7.80	10.9	3.2	15.6	0.9	1.1	1.863997	2.037190	1.935102	9.755023	1.602	2.370
2990	Intensive	L7	3	3	8.30	12.3	3.2	15.5	1.2	1.4	3.811197	4.731141	2.734752	14.83388	1.523	4.175
2990	Intensive	L7	3	7	6.20	8.0	3.7	11.5	0.6	0.6	0.924774	1.010446	1.046071	4.566710	0.848	2.035
2990	Intensive	L7	3	13	8.10	13.1	3.2	17.9	1.0	1.3	3.585558	5.289763	2.885409	17.25368	3.422	5.100
2990	Intensive	L7	4	6	7.70	12.8	3.0	16.7	1.0	1.4	3.062652	4.871665	2.897013	14.69069	2.960	3.965
2990	Intensive	L7	4	9	8.00	15.2	2.9	22.1	1.6	1.6	5.274806	8.861452	4.011820	19.44468	3.864	5.410
2990	Intensive	L7	4	13	7.00	11.0	2.8	15.0	1.1	1.5	2.711424	3.156577	2.576949	9.253309	1.677	3.155
2990	Intensive	L7	2	7	7.20	10.5	3.3	14.5	0.6	0.8	1.895508	1.987311	1.906627	8.523747	0.760	2.445
2990	Intensive	L7	2	10	7.90	14.0	2.7	19.0	1.6	1.5	4.931632	5.993063	3.864070	17.62493	2.933	5.605
2990	Intensive	L7	2	16	7.80	10.9	3.2	15.6	0.9	1.1	1.863997	2.037190	1.935102	9.755023	1.602	2.370
2990	Intensive	L7	3	3	8.30	12.3	3.2	15.5	1.2	1.4	3.811197	4.731141	2.734752	14.83388	1.523	4.175
2990	Intensive	L7	3	7	6.20	8.0	3.7	11.5	0.6	0.6	0.924774	1.010446	1.046071	4.566710	0.848	2.035
2990	Intensive	L7	3	13	8.10	13.1	3.2	17.9	1.0	1.3	3.585558	5.289763	2.885409	17.25368	3.422	5.100
2990	Intensive	L7	4	6	7.70	12.8	3.0	16.7	1.0	1.4	3.062652	4.871665	2.897013	14.69069	2.960	3.965
2990	Intensive	L7	4	9	8.00	15.2	2.9	22.1	1.6	1.6	5.274806	8.861452	4.011820	19.44468	3.864	5.410
2990	Intensive	L7	4	13	7.00	11.0	2.8	15.0	1.1	1.5	2.711424	3.156577	2.576949	9.253309	1.677	3.155

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BIOGRAPHICAL SKETCH

Brian Edward Roth was born in Edmonton, Alberta, Canada in 1969 and learned to appreciate nature at an early age. He joined Junior Forest Wardens, a forestry youth program similar to 4-H, when he was nine, which fostered his interest in forestry and outdoor activities.

Brian enrolled at the University of Alberta in 1987 in the newly founded Biotechnology program, but transferred to the Forestry program a year later. While an undergrad, he took every advantage of summer work opportunities to gain a variety of experience in his chosen field. This included a summer as a helicopter rappel forest firefighter and cruising timber for the province of Alberta. He also spent a summer in northern Sweden working for the Swedish University of Agricultural Sciences on a National Forest Inventory.

Brian left Alberta for Oregon State University in Corvallis in the Spring of 1991, where he studied forest regeneration and forest herbicides. He purchased and rehabilitated 6.5 acres of degraded forestland in the Coastal Mountain Range and eventually earned a M.S. in forest science in 1994. Over the following several years, Brian worked as a field forester in an old-growth logging camp on Vancouver Island for MacMillan Bloedel, Inc. and in Seattle, Washington as a research forester for Weyerhaeuser Company.

In 2000, Brian left Washington State for Gainesville, Florida to work at the School of Forest Resources and Conservation. While employed as the Program Manager for the Forest Biology Research Cooperative and later as an independent forestry consultant, Brian labored toward the lofty goal of a Doctorate in the area of forest production ecology.