CROWN STRUCTURE, GROWTH PERFORMANCE, NUTRITIONAL CHARACTERISTICS, AND THEIR GENETIC PARAMETER ESTIMATES IN JUVENILE LOBLOLLY AND SLASH PINE

By

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An understanding of growth, crown structure, nutritional attributes, and their interrelationships can provide valuable information regarding future opportunities for improving forest productivity. This dissertation focused on production ecology, genetics, and nutrition of two important and widely planted commercial timber species in the southeastern United States, loblolly pine and slash pine, as a basis to investigate the interspecific and intraspecific differences in growth strategies. Genetically improved loblolly pine, improved slash pine, and unimproved slash pine were managed under two levels of silvicultural treatments at two locations in north central Florida. Comparisons and contrasts were made at ages 3 and 4 years among the three taxa, while genetic parameters were estimated from 16 loblolly pine and 32 slash pine open-pollinated families to enhance the understanding of genetic architecture of the two species.

Loblolly pine trees had more branches, wider crowns, higher amounts of foliage biomass and leaf area, and overall growth than slash pine at both ages, but produced less volume per unit leaf area (804 cm^3 wood/m^2 leaf area) than improved slash pine (1,106) and unimproved slash pine (1,173). Differences in growth were associated with crown structural and nutritional attributes among taxa. Loblolly pine consistently had higher foliage N and P concentrations over the life cycle of a needle cohort, higher N, K, Mg, and Ca use efficiency for leaf area production, higher crown (foliage) nutrient content, and higher nutrient retranslocation efficiency for N, P, and K than slash pine.

Narrow-sense heritability estimates for most attributes for the two species were low to moderate. Both species had moderate heritabilities in leaf area (h^2 = 0.25 and 0.28, respectively). Loblolly pine had higher heritability (maximum h^2 =0.83) for foliar N concentration, but lower heritabilities for foliar Ca and Mg concentrations than slash pine throughout an entire leaf life cycle. Loblolly pine also had higher heritabilities in N and P use efficiency (loblolly pine h^2 = 0.41 and 0.27, respectively), but was lower for Ca and Mg use efficiency than slash pine (slash pine h^2 = 0.32 and 0.26, respectively). Genotype × environment interactions were not important for most traits except those for crown structure in loblolly pine. Genetic and environmental correlations between growth and crown structural attributes in loblolly pine and between growth and nutritional attributes in slash pine were all positive and low to moderate. Results from this study have provided a comparison of growth strategies that can be used to select species suitable for plantation establishment at different locations and management intensities and to evaluate potential traits for tree improvement programs.

CHAPTER 1
INTRODUCTION

Background

With increasing societal demands for timber products and decreasing access to older timber, modern forestry has begun shifting its harvest to short-rotation plantations. To improve the efficiency of management systems, a better understanding of genetic characteristics and growth strategies of forest trees is necessary. Such information will prove useful in the development of advanced protocols for improving yield and timber quality. Selection of genetically superior trees, efficient utilization of fertilizers, and reduction of competing understory and pests have significantly contributed to the improvement of forest yields. Nevertheless, like many related fields in agriculture, the practical success in forestry far exceeds the theoretical progress. Therefore, an understanding of the mechanisms controlling tree growth and its adaptation to the environmental complexity is critical not only for the future advancement of forestry, but also for the conservation of forest resources and the protection of environmental quality.

Forests are primarily composed of woody plants that vary in size. To increase the productivity of forest stands steadily, the mechanisms involved in stand growth must be fully examined. A better understanding of stand growth as influenced by biological factors and the surrounding environment is essential for continued improvement in growth rates. Many studies have been conducted to address the various issues related to growth, in which close attention has long been paid to the growth characteristics of forest trees and their interaction with the environment for (1) improving the yield and quality of timber and bettering the resistance of trees to pathogens and insects (Ross and Berisford 1990; Ross et al. 1990); (2) increasing the knowledge on general linkages between biological processes and environmental influences (Gholz et al. 1994); and (3) clarifying the growth dynamics of stands by examining the performance of single trees, especially during the seedling and sapling growth stage (Kinerson et al. 1974; Madgwick 1983; Ceulemans et al. 1990; Gower et al. 1993).

In comparison with studies conducted on growth at the stand level, few attempts have been made to comprehensively investigate relationships among growth, nutritional physiology, and genetics in individual trees of a species. In some studies, although individual trees were sampled, analyzed, and scaled to the stand level to estimate overall productivity, the characteristics of the sampled individuals and their relations to one another were mostly unknown (Forrest and Ovington 1971; Kira 1975). One of the difficulties in conducting research at the single tree level is related to selecting representative trees from a spectrum of well-recognized good and poor families of a species and to implement them experimentally in the field while maintaining the uniqueness of family structures.

Interspecific and Intraspecific Differences in Crown Attributes

Canopy structure is one of the most important factors affecting stand growth. A well-developed canopy can efficiently intercept solar energy. Consequently, crown architecture is closely related to forest productivity (Cannell et al. 1987; Wang and Jarvis 1990; Dalla-Tea and Jokela 1991; McCrady and Jokela 1996). For many annual crops, certain morphological traits have been successfully incorporated into breeding programs since the ideotype concept was first proposed by Donald (1968). For example, new and high yield cultivars of wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), maize (*Zea mays*), bean (*Phaseolus vulgaris*) and the others have been bred using ideotype selection techniques (Donald 1968; Mock and Pearce 1975; Adams et al. 1986; Rasmusson 1987). The breeding of crop ideotypes usually assumes significant genetic relationships between crop yield and morphological or physiological traits used as indirect selection criteria (Fakorede and Mock 1978).

Three kinds of ideotypes have been proposed: isolation ideotypes, competition ideotypes, and crop ideotypes (Donald and Hamblin 1976), which could also be applied to forest trees. Isolation ideotypes are expressed in free standing trees that can exploit their surroundings to almost the fullest extent. Such trees have tall, dense and well-developed crowns that spread foliage over a broad area both horizontally and vertically. They grow best when spacing is wide, and will be nonetheless strong competitors if they appear in a forest. Competition ideotypes tend to exceed neighboring trees in height growth and intercept more light at their neighbors’ expense. Stands comprised of this ideotype soon differentiate in crown and stem diameter classes (e.g., dominant, codominant, intermediate, and suppressed trees). Although the dry-matter production of individual trees is higher, the mortality rate of stands is also high, thus making the stand biomass production rates low. Crop ideotypes are individuals that are not strong competitors, and can make efficient use of the limited site resources to which they have access. Such trees have dense and narrow crowns, and produce stands with a minimal differentiation in stem diameters. The biomass production rates are potentially high. Clearly, crop ideotypes are ideal for intensively managed production systems (Donald and Hamblin 1976; Dickmann 1985).

Tree crowns are much more complicated than canopies of annual crops; therefore, it is much more difficult to establish accurate relations between stand productivity and crown structures (Dickmann 1985). Tree canopies not only include structural traits, but also involve phenological characters that can shift between years. Some studies have demonstrated that trees having long narrow crowns (i.e., a higher crown length/crown width ratio) with high leaf area, and relatively few but thin, short branches that are borne at acute angles, will produce higher yields and have higher stem wood allocation percentages. For example, a genotype of *Pinus sylvestris* with a narrow-crowned habit had higher production efficiency, and was likely determined by a single, dominant gene, as shown by the segregation in F_1 and F_2 progenies (Kärki and Tigerstedt 1985).

Some crown traits, such as crown width, branch angle and numbers of branches per whorl, were found to have high heritabilities and significant genetic correlations in *Pinus sylvestris* and *Populus* clones (Kärki and Tigerstedt 1985; Ceulemans et al. 1990). These crown traits may be greatly influenced by environmental factors such as density and competition, and the relations become less useful as the stands age. Structural characteristics, such as number of branches, number of clusters, and branch basal areas, were highly correlated with tree height and diameter at breast height (Forrest and Ovington 1971; Madgwick 1983).

In a series of studies on Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*), it was found that equations predicting component biomass and leaf area differed among open-pollinated families (St. Clair 1993). Narrow-sense heritability estimates were high for biomass components, several biomass partitioning ratios, and stem growth increment. These estimates could be used to select families with favorable partitioning to the stem wood component and, thus, improve stand productivity (St. Clair 1994a). Further, substantial genetic variation was detected for some crown traits such as relative crown size, branch diameter and length, needle size and leaf area.

All of these studies have suggested that it is promising to select crop ideotypes with high yield traits which have high heritabilities that favor more biomass accumulation in pure and closed stands. Moreover, the ideal crown structure may change with environmental conditions and management intensities, or even stages of stand development. Therefore, an understanding of ideotype and environment interactions is a prerequisite for combining the ideotype concept into tree breeding programs. With this knowledge, we can recognize whether crown structure is an adaptive strategy to environments and cultural treatments, or originates from genetic or physiological controls, or alternatively, from genotype× environment interaction.

Soil nutrient supply is also important in determining biomass allocation patterns among different tissue components. More biomass was significantly allocated to roots at high irradiances and low nitrate supplies, causing a lower leaf area ratio and leaf mass ratio in *Mycelis muralis* (Clabby and Osborne 1997). The regulation of canopy nutrients in the production efficiency (stem wood production / unit leaf area) was also determined for some hardwood forest communities (Jose and Gillespie 1996). Canopy nutrient contents showed a strong correlation with production efficiency on a unit leaf area basis rather than on unit leaf mass basis. Further, the authors found that specific leaf area was negatively correlated with the canopy nutrient content per unit leaf area, in contrast to some other studies reported above. Because the study was conducted along a moisture gradient, water was also involved in the relations between nutrient content and specific leaf area. Although all of the above studies have demonstrated that leaf area and nutrients were closely related to growth, few studies have considered the importance of genetics and the interaction between genetics and nutrition on these traits for improving overall growth performance of trees at the intraspecific level.

Nutrient Dynamics and Genetic Variation of Forest Trees

Nutrition of forest trees has been extensively studied in relation to the physiological, ecological and silvicultural aspects influencing the enhancement of growth. Most studies pertinent to the genetic aspects of tree nutrition have only a recent origin, however. In contrast, genetic screening to detect nutritional deficiencies and factors related to abiotic stress, and practices to breed low input cultivars and nutrient use efficient cultivars, have achieved great success in many agronomic plants (Sarif 1981; 1983; Gabelman and Loughman 1987; Bassam et al. 1990). At the intraspecific level, the objective is often to characterize the influence of ancestry on the nutritional status of progeny plants (Rosen and Luby 1987), with the superior parental materials being utilized in the breeding program. However, tree improvement programs have generally paid less attention to genetic differences in nutritional attributes, and have concentrated more on factors relevant to growth, form and pest resistance (Zobel and Talbert 1984). The research in this area has lacked direction, depth and specific goals (Nambiar 1984), although certain outcomes can be found in the genus *Pinus* or *Populus* for intensively managed plantations (Forrest and Ovington 1971; Ceulemans et al. 1990; Li et al. 1991a). To meet the potential needs of tree improvement programs in the future, the amount, cause, and nature of the variation in nutritional traits must be better understood.

About 50% of the yield increase in agriculture in the last few decades has been due to the utilization of fertilizers (Sariƒ 1987) and, thus, the response functions of different crops to nutrients have received widespread attention. Extensive studies have revealed that N, K, and Ca are under strong genetic control; however, exceptions can also be found. For example, P was only genetically controlled in some crop species (Sariƒ 1987). In several wheat cultivars, P accumulation, translocation and utilization efficiency were contingent on the genotype in relation to environmental conditions (Papakosta 1994). Differences were also detected for sorghum (*Sorghum bicolor*) hybrids in response to P levels, with largest differences appearing at low soil P levels (Furlani et al. 1987). Other crops, which included barley and oats (*Avena sativa*), have also varied among cultivars in their grain accumulation of N, P, Ca, Zn, Mn, and Co (Nambiar 1976). These findings suggested that genetic improvement of nutritional traits could lead to the more efficient use of nutrients by crops, which may decrease investments in fertilizer application.

With forest trees, several studies have previously quantified genetic variation in nutritional traits. Full-sib and half-sib families, open-pollinated families from seed origin, and clones from vegetative propagation have been the most common experimental materials used in this research. For example, variability among and within a series of full-sib loblolly pine seedlings from intra-provenance and inter-provenance crosses was found to differ by genotype in nutrient content (P, K, Ca, Mg) of aboveground components, especially in their ability to absorb Ca and Mg (Woessner et al. 1975). Under three levels of nitrogen fertility, genotype × environment interaction was examined in 40 full-sib black spruce (*Picea mariana*) families in greenhouse conditions (Mullin 1985; Mullin and Park 1994). Significant family × nitrogen interactions were found. For other nutrient characteristics, such as nutrient use efficiency, significant variation was detected among 23 open-pollinated loblolly pine families grown under two levels of nitrogen treatment (Li et al. 1991b). Narrow-sense heritability estimates for nutrient use efficiency were 0.84 and 0.69, respectively, under the low and high N levels, suggesting that this trait was under strong genetic control.

Several studies, using clones as experimental materials, have also shown that some nutritional traits are under strong genetic control. Forrest and Ovington (1971) reported large differences in foliar nutrient levels (P, Ca, K, Mg, Mn, and Zn) among six clones of radiata pine (*Pinus radiata*). Broad-sense heritabilities among radiata pine clones for foliar nutrients were higher for K, Mg and Ca than those for N, P, B, Mn, Zn, and Cu (Beets and Jokela 1994). The authors inferred that foliar nutrient levels were controlled by genetic factors, and that nutritional differences were genotype specific. Raupach and Nicholls (1982) observed that few nutrients (N, K, Mg, Zn) were significantly different among radiata pine clones in their study. For nutrient use efficiency (amount of dry weight produced per unit weight of nutrients absorbed), Sheppard and Cannell (1985) found 10 - 30% differences among 8-year-old clones of *Picea sitchensis* and *Pinus contorta*. These differences were closely related to the nutrient concentration of foliage, and an ideotype for high nutrient use efficiency was proposed as trees having an inherently low nutrient concentrations in needles. Such trees might be well-suited to grow on nutrient poor sites.

Genotype (e.g., species, clones or families) × environment interactions will occur whenever genotypes do not achieve consistent performance across a range of environmental conditions. Although many studies have detected significant genotype × environment interactions in the growth characteristics of trees (Sato 1994; Ronnbergwastljung et al. 1994; Isik et al. 1995; Khasa et al. 1995; Johnsen and Major 1995), opposite results have also been reported (Danjon 1995). However, nearly all studies that have detected significant genotype × environment interactions have provided little further information on the underlying environmental factors causing these interactions. Such information is critical for maximizing gains from genetic selection trials (Jackson et al. 1995).

Saulescu and Kronstad (1995) designed a simple approach to describe the specificity of each genotype's response to environmental factors. Environmental variables (e.g., water deficit, minimum temperature of the winter) were directly computed or derived from a simulation model. Simple correlation coefficients between deviations of each genotype from a check (actual yield or simulated yield) and environmental indices were then calculated to describe relations between environments and the performance of each genotype. When genotype × nutrition interactions were found, their patterns often differed from genotype × environment interactions for growth characteristics because significant variation in nutrient traits occurred within a year. New and efficient approaches to deal with nutritional specificity of genotypes under different environmental conditions have not yet been well developed.

Silvicultural treatments can significantly influence growth performance of forest trees, primarily by improving the nutrient conditions for growth. Colbert et al. (1990) reported that fertilizer treatments produced almost the same effects on aboveground biomass production as weed control treatments in juvenile loblolly pine (*Pinus taeda* L.) and slash pine (*P. elliottii* Engelm. var. *elliottii*) plantations. In a study of radiata pine from age 6 to 11 years, Fife and Nambiar (1995) reported that nitrogen fertilization increased foliar nitrogen concentration and significantly affected two physiological indices, predawn foliage water potential and water stress integral (an index of cumulative water stress over time). However, the two indices were not significantly influenced by family or family × nitrogen interactions. Schmidtling (1995) found that when fertilizer rates increased, foliar Mn and B concentrations also increased, while those of Mg and Zn decreased, and other foliar macro- or micro-nutrients were almost not affected in loblolly pine ramets. The effects of genotype are incomparable among most of these studies because of different plantation ages. More important, the impact of silvicultural treatments on nutritional characteristics and nutrient interactions of different families within a species is still unknown, let alone the response features of families in growth to the treatments. If nutrient traits are to be utilized as selection criteria in tree breeding programs, genetic heritabilities of each mineral nutrient must first be identified. Genotype × nutrition effects and genotype × fertilizer interactions should also be taken into consideration and clearly understood for those nutrients with high heritabilities under field conditions.

This dissertation concentrates on the genetics, nutrition and production ecology of loblolly and slash pine, two commercially important and widely planted pine species in the southeastern United States. The focus is on (1) evaluating the relations among growth strategies, crown structure, and nutrient characteristics; (2) examining patterns of genetic interaction of each taxon with growth, crown structure, foliar chemistry and the extent to which they are subjected to genetic control and environmental influence; and (3) comparing growth strategies of individual trees on the basis of families or species. Expected results will positively impact future tree growth modeling and in refining of management prescriptions that involve genotype deployment and silvicultural treatments. The results will also aid in examining genetic and environmental controls on several biological characteristics of trees as a basis for understanding growth strategies and the nutritional physiology of genetically improved loblolly, improved and unimproved slash pine.

CHAPTER 2
EARLY GROWTH PERFORMANCE, CROWN STRUCTURE, AND THEIR RELATIONSHIPS IN JUVENILE LOBLOLLY AND SLASH PINE

Introduction

Crown structure represents an important factor affecting individual tree and stand level growth (Forrest and Ovington 1971; Madgwick 1983; Cannell et al. 1987; Dalla-Tea and Jokela 1991). Many factors, such as inclination and orientation of leaves and geometric properties of twigs and branches, can contribute to variation in crown characteristics and growth performance (Dickmann 1985; Wang and Jarvis 1990). Previous research has suggested that one of the most important factors influencing growth is the amount and distribution of leaf area, as it affects the interception of photosynthetically active radiation (Stenberg et al. 1994; Vose et al. 1994; McCrady and Jokela 1996, 1998). Trees that have long narrow crowns (i.e., a higher crown length/crown width ratio) with high leaf area, and relatively few but thin, short branches borne at acute angles have been reported to produce both high yields and stem wood allocation percentages (Kärki and Tigerstedt 1985). The growth "efficiency" (stem wood production/leaf area) of these trees may be high because they maintain a large crown surface area per unit of growing space (Ford 1985). It follows that as crown width increases, stem wood growth efficiency may decline because the central portion of the crown becomes dominated by supporting branches that produce little photosynthate relative to growth and maintenance respiration demands.

In the southeastern United States, the two most important and widely planted commercial species are loblolly (*Pinus taeda* L.) and slash pine (*P. elliottii* Engelm. var. *elliottii*). Both species in this region are commonly managed under a regime of intensive silvicultural practices that include mechanical and chemical site preparation (Shiver et al. 1990), woody and herbaceous competition control (Miller et al. 1991), genetic tree improvement and fertilization (Neary et al. 1990; Jokela et al. 2000). From a management perspective, species deployment decisions are most often based on estimates of potential site productivity and value accrued at the end of the rotation.

Few comparative studies exist with southern pines that examine species variation in crown structure in relation to growth performance for a range of silvicultural treatments and site types. In one study, loblolly pine demonstrated greater sensitivity than slash pine to fertilizer applications, especially in allocating more carbon to branches and foliage (Jokela and Martin 2000). The crown structure of loblolly pine facilitated greater retention of leaf area than slash pine on those plots receiving fertilizer additions. Establishing a more thorough understanding of the relationships between crown structure and growth efficiency, especially at the interspecific level, will be essential for improving our understanding of growth strategies, development of crop ideotypes and species-site deployment decisions.

The current study utilized two genetics experiments to (1) determine the magnitude of the effects of silvicultural treatments, locations, taxa (genetically improved loblolly pine, improved slash pine, and unimproved slash pine) and their interactions on crown structural characteristics and overall growth performance; (2) ascertain whether significant differences in crown attributes, especially the vertical distribution of leaf area, existed among pine taxa when managed under different silvicultural treatments and site locations; and (3) clarify whether the general relationship between stem wood production and leaf area (growth efficiency) varied among pine taxa and silvicultural treatments.

Materials and Methods

Study Sites

Two locations in north central Florida (Dunnellon in Levy County, and Palatka in Putnam County) were chosen as the experiment sites (Table 2-1). The two sites are part of a larger series of eleven experiments being conducted by the University of Florida's Cooperative Forest Genetics Research Program for genetically testing several pine taxa and their hybrids (Lopez-Upton 1999). Genetically improved loblolly pine, unimproved slash pine, and improved slash pine were selected as experimental materials. Sixteen open-pollinated half-sib families for each of the three taxa were planted across the two sites. Climatic conditions between locations were similar, but the soil types did differ (Table 2-1). The soils at Dunnellon were classified as the Smyrna series (sandy, siliceous, hyperthermic Aeric Alaquods), while the Adamsville series (hyperthermic, uncoated Aquic Quartzipsamments) was dominant at Palatka (Soil Survey Staff 1998).

Experimental Design and Treatments

Within each field site, the experimental design was a randomized complete block split-split plot design, with three complete blocks within each of two silvicultural treatments (intensively-managed treatment, including fertilizer, insecticide, and herbicide utilization; and non- intensively-managed treatment). Each taxon was randomly assigned in each block, and sixteen families were nested within each taxon plot, with five seedlings being planted per family in a row plot.

Table 2-1. Geographic locations, climatic and site conditions of the two experimental sites in north central Florida.

Site	Location	County	Yearly average temperature (°C)	Yearly average precipitation (mm)	Site index[a]	Soil series
Dunnellon	29°20' N 82°50' W	Levy	21	1332	21	Smyrna
Palatka	29°40' N 81°42' W	Putnam	22	1368	22	Adamsville

[a] Site index is expressed as tree height in meters at age 25 years.

All trees were grown in greenhouses before being transplanted to field sites in December, 1994. Site preparation for both locations included bedding and chopping. The seedlings were planted at a 1.5 m × 3.4 m spacing at Palatka, and a 1.8 m × 3.0 m spacing at Dunnellon. Fertilizers, herbicides, and insecticides were applied in the intensively-managed treatment blocks only (Table 2-2).

Sampling Procedures and Inventory

For each location, two sample trees within a family from each five-tree plot were randomly chosen by a SAS procedure (SAS Institute 1990), and then a systematic sampling method was applied to all other families and taxa. All sample trees were healthy and free of disease, and 192 sample trees (2 treatments × 3 blocks × 16 families × 2 trees) were selected for each of the three taxa at each site. Overall, 1,152 trees (2 sites × 2 treatments × 3 blocks × 3 taxa × 16 families × 2 trees) were sampled across the two experimental locations.

In August 1997, an inventory of all 1,152 trees was made. Measurements included DBH, total height, crown height, and crown width. In addition, branch position, branch diameter, and branch angle were measured along the entire stem of each tree. Other factors derived from these records included total branch number per tree, crown shape ratio (CSR = crown height/ crown width), and branch-free stem height (McCrady and Jokela 1996).

Table 2-2. Treatment regimes for intensively-managed and non-intensively-managed blocks at the two research locations.

Culture	Non-intensive management	Intensive management
Bedding	Double (Dunnellon) Single (Palatka)	Double (Dunnellon) Single (Palatka)
Fertilization	None	280 kg/ha DAP + 224 kg/ha KCl 600 kg/ha 10-10-10 + Micronutrients
Herbicide	None	Year 1: Roundup and Atrazine
Insecticide	None	Year 1: Asana, Diomethorate or Pyridine 3 × standard (Dunnellon) 4 × standard (Palatka)

Note: 280 DAP + 224 KCl kg/ha = 50 N, 56 P, 112 K kg/ha, respectively.
macronutrient and micronutrient application rates-
N = 60, P = 24, K = 50, Ca = 20, Mg = 10, S = 13, Fe = 0.5, Zn = 0.06, Mn = 0.5, Cu = 0.06, B = 0.06 (kg/ha)

Similar measurements were made during the fourth growing season in 1998. However, in contrast to sampling 16 families within a taxon, six families were selected based on the first year growth data and long-term breeding values. Within each taxon, three good and three below average families were selected to contrast differences between crown structure and growth performance. A subset of eighteen families totaling 432 trees was measured in 1998.

Biomass and Leaf Area Estimation

In July 1997 and 1998 (ages 3 and 4 years), 1,080 branches (2 locations × 2 treatments × 3 blocks × 3 taxa × 3 crown positions × 5 trees × 2 years) were destructively harvested to develop biomass prediction equations. Individual branches, randomly selected from each of three equally-divided crown positions (upper, middle, and lower), were cut after insertion angle on the stem was measured. All needles from a branch were removed separately by age class (current-year, and one-year-old), and both the needles and branches were weighed after being oven-dried at 70 ^{B}C for at least 48 hours.

In August 1997 and 1998, foliage samples were collected to determine specific leaf area for use in estimating total leaf area per tree. About 20 fascicles in each of the samples by age class and crown position were randomly chosen from one tagged sample tree in each five-tree row plot. Because many trees did not have old foliage in the upper crown, only two positions for old foliage (upper-middle and lower) were sampled. A total of 5,760 foliage samples (2 locations × 2 treatments × 3 blocks × 3 taxa × 16 families × 2 ages × 1 trees × 3 positions [current year foliage] + 2 locations × 2 treatments × 3 blocks × 3 taxa × 16 families × 2 ages × 1 trees × 2 positions [old foliage]) were collected from the trees in 1997, and 2,160 samples were collected from 6 families of each taxa (18 families in total) by the same procedure in 1998.

Fifteen samples from each of the three taxa were collected by location and age class to determine specific leaf area. All-sided leaf surface area was measured in the laboratory using a volume displacement method (Johnson 1984), in which we found a high correlation between fresh foliage weight (g) and volume (cm^3) of the needle samples. Regression methods were used to estimate the volume from fresh needle weight, and then the formula developed by Johnson (1984) was used to estimate leaf surface area of the needle samples. Needle volume estimation equations were combined for taxa, location or age class where statistical results indicated non-significant differences among these effects at " = 0.10. The final equations for the two growing seasons were as follows:

$$\text{Needle volume (cm}^3\text{)} = 0.067 + 1.093 * \text{Weight (g)}$$

$$(r^2 = 0.99,\ n = 180) \text{ – Year 1997}$$

$$\text{Needle volume (cm}^3\text{)} = 0.111 + 1.129 * \text{Weight (g)}$$

$$(r^2 = 0.99,\ n = 180) \text{ – Year 1998}$$

Leaf area at each crown position was calculated as the product of leaf biomass and specific leaf area at that position. Total leaf area per tree was a summation of leaf area at the three different crown positions.

Statistical Analyses

According to the nature and the amount of data collected in this study, biomass equation construction, growth performance evaluation, and crown attribute analyses were divided into two major phases: (1) *a priori* estimation and hypothesis formulation; and (2) *a posteriori* testing and interpretation. In phase 1, main effects and the interactions that could potentially influence tree growth and crown structure were taken into consideration, and a full model was established for each variable (e.g, height, total branch number per tree, total leaf area per tree). At this phase, the likely behavior of the variable was also hypothesized. In phase 2, full models were tested, and main effect and interaction terms that were not significant (5% level by F test) were removed from the models. Final models were developed for each variable that (1) were parsimonious in number of main effects and their interactions; (2) contained only effects that were biologically meaningful and interpretable; and (3) accounted for at least 60% (R^2 \$0.60) of the variation. Predicted results were subsequently justified against the hypothesized outcomes for each variable and all models were checked graphically. If discrepancies existed, the final models were re-analyzed to detect which effect or a set of effects caused unusual behaviors. In such cases, we either re-formulated theory or decomposed the reduced model to develop a new set of functionally efficient models that offered stronger biological interpretations.

Biomass estimation

Biomass prediction equations were developed to estimate branch and foliage biomass using data collected from destructively harvesting 1,080 branches. The prediction equations were applied to the inventory data (branch diameter by crown position) to estimate branch and foliage biomass at the tree level. A full model was formulated for each biomass component (model 2-1). All main effects except branch diameter were discrete variables in the model.

$$Y_{ijklm} = : + "_i + \$_j + (_k + *_l + ._m + b_1D + ("\$)_{ij} + ("()_{ik} + (".)_{im} + ("*)_{il} + (\$()_{jk} + (\$.)_{jm} + ((.)_{km} + D"_i + D\$_j + D(_k + D*_l + D._m + ("\$()_{ijk} + ("\$*)_{ijl} + ((.*)_{kml} + ,_{ijklm} \quad (2\text{-}1)$$

where Y_{ijklm} is the estimates of leaf or branch biomass per branch at position m of taxa l in the treatment k and location j in year i,

: is the overall mean of the model,

$"_{i}$ is the effects of year (Y97 or Y98),

$\$_{j}$ is the effects of location (Dunnellon or Palatka),

$(_{k}$ is the effects of treatment (non-intensive or intensive),

$._{m}$ is the effects of taxa (improved loblolly, improved slash, or unimproved slash pine),

$*_{l}$ is the effects of crown position (lower, middle, or upper),

D is the branch base diameter (mm),

$("\$)_{ij}$ is the year × location interaction,

$("()_{ik}$ is the year × treatment interaction,

$(".)_{im}$ is the year × taxa interaction,

$("*)_{il}$ is the year × position interaction,

$(\$()_{jk}$ is the location × treatment interaction,

$(\$.)_{jm}$ is the location × taxa interaction,

$((.)_{km}$ is the treatment × taxa interaction,

$D"_{i}$, $D\$_{j}$, $D(_{k}$, $D*_{l}$, $D._{m}$ are Diameter × year, diameter × location, diameter × treatment, diameter × taxa, and diameter × position interactions, respectively,

$("\$()_{ijk}$ is the year × location × treatment interaction,

$("\$*)_{ijl}$ is the year × location × taxa interaction,

$((.*)_{kml}$ is the treatment × taxa × position interaction,

$,_{ijklm}$ is the error term.

where i = 1, 2 for years; j = 1, 2 for locations; k = 1, 2 for treatments; l = 1, 2, 3 for crown positions; m = 1, 2, 3 for taxa.

The above model was further tested for the homogeneity of error variances and where necessary logarithmic transformations were performed. After testing, a simplified final model was determined (model 2-2).

$$\log(\hat{Y}_{ijk}) = : + "_{i} + \$_{j} + (_{k} + ("()_{ik} + b_{1}\log(D) \qquad (2\text{-}2)$$

where $\hat{Y}_{ijk}$ is the estimated leaf or branch biomass at crown position k of taxa j in year i,

$:$ is the overall mean of the model,

$"_{i}$ is the effect of year (Y97 or Y98),

$\$_{j}$ is the effect of taxa (improved loblolly, improved slash, or unimproved slash pine),

$(_{k}$ is the effect of crown position (lower, middle, or upper),

$("()_{ik}$ is the year × position interaction,

D is the branch base diameter (mm).

Analyses of mensurational and crown structural attributes

Analysis of variance (ANOVA) was used as the primary method for analyzing the mensurational and crown structure data. Characteristics included diameter at breast height (DBH), total tree height, total branch number per tree, live crown length, crown width, crown shape ratio, and branch-free stem length. All of these attributes were measured on a sample of 1,152 trees at age 3 years and 432 trees at age 4 years. Analyses were conducted separately by year because of sample size differences. A full model with main effects and their interactions was used to test each attribute within a year:

$$Y_{ijklm} = \mu + \alpha_i + \beta_j + \gamma_k + f_{l(k)} + b_{m(j)} + (\alpha\beta)_{ij} + (\alpha\gamma)_{ik} + f\alpha_{il(k)} + (\beta\gamma)_{jk} + f\beta_{jl(k)} + b\gamma_{jkm} + bf_{jklm}$$
$$+ (\alpha\beta\gamma)_{ijk} + f(\alpha\beta)_{ijkl} + \varepsilon_{ijklm} \quad (2\text{-}3)$$

where Y_{ijklm} is the mean of two sample trees at family l of taxa k in block m of treatment j of location i,

μ is the population mean,

α_i is the random variable of location $\sim$ NID $(0, \sigma^2_\alpha)$,

β_j is the fixed effect of treatment (non-intensive or intensive),

γ_k is the fixed effect of taxa (improved loblolly, improved slash, or unimproved slash pine),

$f_{l(k)}$ is the random variable for family nested within taxa $\sim$ NID $(0, \sigma^2_f)$,

$b_{m(j)}$ is the random variable for block nested within treatment $\sim$ NID $(0, \sigma^2_b)$,

$(\alpha\beta)_{ij}$ is the random variable for location × treatment interaction $\sim$ NID $(0, \sigma^2_{\alpha\beta})$,

$(\alpha\gamma)_{ik}$ is the random variable for location × taxa interaction $\sim$ NID $(0, \sigma^2_{\alpha\gamma})$,

$f\alpha_{il(k)}$ is the random variable for location × family(taxa) interaction $\sim$ NID $(0, \sigma^2_{f\alpha})$,

$(\beta\gamma)_{jk}$ is the fixed effect for treatment × taxa interaction,

$f\beta_{jl(k)}$ is the random variable for treatment × family(taxa) interaction $\sim$ NID $(0, \sigma^2_{f\beta})$,

$b\gamma_{jkm}$ is the random variable for taxa × block (treatment) interaction $\sim$ NID $(0, \sigma^2_{b\gamma})$,

bf_{jklm} is the random variable for family(taxa) × block(treatment) interaction $\sim$ NID $(0, \sigma^2_{bf})$,

$(\alpha\beta\gamma)_{ijk}$ is the random variable for location × treatment × taxa interaction $\sim$ NID (0, $\sigma^2_{\alpha\beta\gamma}$),

$f(\alpha\beta)_{ijkl}$ is the random variable for location × treatment × family(taxa) interaction $\sim$ NID (0, $\sigma^2_{f\alpha\beta}$),

ε_{ijklm} is the error term $\sim$ NID (0, σ^2_{ε}).

where i = 1, 2 for locations; j = 1, 2 for treatments; k = 1, 2, 3 for taxa; l = 1, 2, ..., 16 for families per taxa; and m = 1, 2, 3 for blocks.

Variance homogeneity for each variable was examined to ensure appropriate analyses and data transformations (logarithmic transformation) were performed where necessary. If either location × taxa or treatment × taxa interaction was not significant in the full model (i.e., variation in location environments and treatment levels did not translate into significant differences among taxa), but evidence suggested that differences among taxa should exist in these attributes (Nemeth 1973; Vose and Allen 1988; Colbert et al. 1990; Dalla-Tea and Jokela 1991; Zhang et al. 1997; Albaugh et al. 1998; Samuelson 1998; Lopez-Upton 1999), then probable causing effects were examined. To make meaningful biological interpretations, the full model was decomposed into separate models by location, treatment, or both. If the analysis was done within a location but across treatments, the corresponding final model was of the following form for each location:

$$Y_{ijkm} = \mu + \alpha_i + \beta_j + f_{k(j)} + b_{m(i)} + (\alpha\beta)_{ij} + f\alpha_{ijk} + b\beta_{ijm} + \varepsilon_{ijklm} \qquad (2\text{-}4)$$

where Y_{ijkm} is the mean of two sample trees at family k of taxa j in block m of treatment i,

μ is the population mean,

α_i is the fixed effect of treatment (non-intensive or intensive),

β_j is the fixed effect of taxa (improved loblolly, improved slash, or unimproved slash pine),

$f_{k(j)}$ is the random variable for family nested within taxa ~ NID (0, σ^2_f),

$b_{m(i)}$ is the random variable for block nested within treatment ~ NID (0, σ^2_b),

$(\alpha\beta)_{ij}$ is the fixed effect for treatment × taxa interaction,

$f\alpha_{ijk}$ is the random variable for treatment × family(taxa) interaction ~ NID (0, $\sigma^2_{f\beta}$),

$b\beta_{ijm}$ is the random variable for taxa × block (treatment) interaction ~ NID (0, $\sigma^2_{b\beta}$),

ε_{ijkm} is the error term ~ NID (0, σ^2_{ε}).

When the analysis was performed within a combination of locations and treatments, the same principles were used to obtain the final model (i.e., eliminate all terms related to subscript i and keep other terms). The resultant model could be viewed as the full model for analyses by location and treatment.

For pooled or separate analyses, PROC GLM in the SAS® System was utilized to test for significance of random effects, while PROC MIXED was used to test the fixed effects and to perform linear single-degree-of freedom contrasts among taxa (Littell et al. 1996; SAS Institute 1996). The two linear contrasts used to separate taxa differences were (1) loblolly vs. improved slash pine (PTA vs. PEE); and (2) improved slash vs. unimproved slash pine (PEE vs. PEU). A default level of $\alpha = 0.05$ was used to declare significance unless otherwise specified.

Analyses of crown biomass and leaf area attributes

Analytical procedures for crown biomass and leaf area attributes were identical to those described above for mensurational and crown structural variables. The attributes examined included current-year specific leaf area (SLA), one-year-old SLA, current-year leaf biomass, one-year-old leaf biomass, total leaf biomass, branch biomass, total crown biomass, current-year leaf area, one-year-old leaf area, and total leaf area per tree. All attributes were based on measurements from individual trees.

Additional analyses were performed to test for differences in the vertical distribution patterns of leaf area within the crown. Means among the three crown positions were compared to describe vertical crown structure. Similarly, linear contrasts were performed to compare crown position means at " = 0.05.

Relationships between volume increment and leaf area (growth efficiency)

Growth efficiency at the individual tree level was expressed as volume increment (D^2H, age 4 minus age 3 years) per unit leaf area. A similar scheme as employed for the development of biomass estimation equations was also adopted here: a full model including main effects, leaf area, stem volume increment, and their interactions was first proposed, and then tested for variance homogeneity and the significance of each effect. Certain modifications of the model were performed where necessary.

A subset of data at age 3 years corresponding to those families (18 in total for all three taxa) selected for age 4 years were used to calculate volume increment. Leaf area data at age 3 were used as one of the independent variables. A total of 432 sample trees was used in the analysis. Each effect that remained in the final model was significant at " = 0.05.

Results

Biomass Estimation Equations

Separate equations were developed for estimating current-year foliage, one-year-old foliage, total foliage, and branch biomass of individual branches (Table 2-3). Treatment and location effects were not significant and were excluded from all models. Crown position and year × position had a larger influence on leaf biomass than year and taxa, while taxa explained more of the variation in branch biomass than other factors. Significant differences in prediction equations were found among taxa for all variables except one-year-old foliage; however, differences only existed in the intercept, and not in the slope (Appendix A -- Figure A-1). Crown position had the most significant influence on foliage biomass among the discrete variables (Table 2-3). Although only total foliage biomass per branch for loblolly and improved slash pine were reported in Appendix A -- Figure A-1, similar results were found for unimproved slash pine and other biomass components. In general, biomass differences between improved and unimproved slash pine were minor (Table 2-3).

Selection of Models for ANOVA

The full model (2-3) that combined all main effects produced irregular behavior and contradictory results, thus making it necessary to conduct separate analyses by location and treatment. Results also indicated that differences among locations rather than treatments were the main contributor to variation in growth patterns among taxa (Appendix A -- Figure A-2). Two types of differences were found in all attributes across locations: (1) significant treatment × taxa interactions in one location, but not in the other (e.g., crown width); and (2) significant differences in absolute values of taxa (e.g., branch biomass) between

Table 2-3. Model parameter estimates and summary statistics for estimating foliage and branch biomass in loblolly and slash pine.

Model form: log(biomass (g)) = ∶ + (year + taxa + position + year × position) + b_1(log(diameter) (cm))

Factors	Parameters	Current year foliage	One-year-old foliage	Total foliage	Branch
	R^2	0.65	0.70	0.72	0.91
	∶	-1.714	-2.161	-0.862	-3.735
Year	97	-0.082	-0.844	-0.172	-0.203
	98	0	0	0	0
Taxa	PTA[a]	0.260	b	0.140	0.418
	PEU	-0.032		-0.002	-0.016
	PEE	0		0	0
Crown position	Lower	-2.160	1.720	-0.429	0.213
	Middle	-0.840	1.776	0.030	0.189
	Upper	0	0	0	0
Year× Position	97 Lower	1.027	1.169	0.693	c
	97 Middle	0.789	0.130	0.214	
	97 Upper	0	0	0	
	98 Lower	0	0	0	
	98 Middle	0	0	0	
	98 Upper	0	0	0	
	b_1 Diameter	2.175	1.500	1.911	2.708

a PTA = improved loblolly pine
PEE = improved slash pine
PEU = unimproved slash pine

b taxa was not statistically significant and, therefore, was not included in the model.

c year×position was not statistically significant and, therefore, was not included in the model.

locations. Hence, all ANOVA analyses were separately conducted by location using model (2-4) to investigate treatment effects and their interactions with taxa and families.

Genetic effects on most variables were better expressed under the intensive treatment for all taxa at both locations (Appendix A -- Figure A-2). Differences between improved and unimproved slash pine for most variables were not statistically significant under the non-intensive treatment (p $ 0.05), but significant differences were detected under the intensive treatment (p # 0.05). Lopez-Upton (1999) showed similar results for volume when making comparisons among the three taxa.

Mensurational and Crown Structural Characteristics

Interspecific differences existed in some mensurational and crown structural characteristics (Table 2-4). Loblolly pine was more responsive than the two slash pine taxa to the silvicultural treatments at Dunnellon, with DBH responses averaging 103% and 73% at age 3 and age 4 years, respectively. Slash pine also showed a similar trend, but at a diminished level, i.e., the increase in DBH at age 3 and age 4 years was 63% and 44% for improved slash pine, and 47% and 30% for unimproved slash pine, respectively. At Palatka, the same trend followed at age 3 years, but the most noticeable difference was observed in DBH growth at age 4 years. Treatment effects only increased DBH about 17%, 23%, and 28% for loblolly, improved slash, and unimproved slash pine, respectively. Therefore, treatment × taxa interactions for DBH were significant at Dunnellon, but not at Palatka for the years examined (Appendix B).

Height growth was consistently greatest in loblolly pine, but not significantly different from slash pine under the same treatments (Table 2-4). Differences in tree height did not exist between improved and unimproved slash pine. Treatment × taxa interactions were significant at Dunnellon for both ages, but not at Palatka (Appendix B). Loblolly and improved slash pine were most responsive to the intensive treatment at Dunnellon, especially at age 4 years, with height growth responses averaging 48% and 37%, respectively. Corresponding height growth responses at Palatka were 17% and 27%. Height growth responses to the intensive treatment were smaller at age 4 years at Palatka. For example, loblolly pine gained only 17% in height at age 4 years, compared to 41% at age 3 years.

Loblolly pine maintained about 44 and 39 branches per tree at age 3 and 4 years, respectively. Slash pine retained about 10 and 8 branches fewer than loblolly pine (Table 2-4). All three taxa showed decreases in total branch numbers between ages 3 to 4 years under the intensive treatment at both locations, while trees grown under the non-intensive treatment maintained the same number of branches between years.

Live crown length and branch-free stem length showed similar responses to the treatments in all taxa (Appendix B). At this stage of development, almost 90% of the stem contained branches and, therefore, live crown length reflected the same trend as tree height for the respective treatments. An almost constant live crown length between ages 3 and 4 years was observed under the intensive treatment at Palatka, implying that crown closure occurred there at age 4 years.

Crown width followed the same trend as live crown length between ages 3 and 4 years under the intensive treatment at Palatka, presumably due to crown closure (Table 2-4).

Table 2-4. Individual tree growth and crown characteristics for 3- and 4-year-old loblolly and slash pine planted at two locations in north central Florida[a].

Location		Dunnellon						Palatka					
Treatment		Non-intensively managed			Intensively managed			Non-intensively managed			Intensively managed		
Taxa		PTA[b]	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU
Variables:													
DBH (cm)	Year 3	3.0a	3.8b	3.8b	6.1a	6.2a	5.6a	4.9a	5.1a	4.8a	8.1a	8.1a	7.2a
	Year 4	5.2a	6.1b	6.4b	9.0a	8.8a	8.3a	9.2a	8.3ab	7.6b	10.8a	10.3a	9.6a
Height (m)	Year 3	2.9a	2.8a	2.9a	4.3a	3.9ab	3.7b	3.4a	3.1b	3.0b	4.8a	4.4b	4.2c
	Year 4	4.0a	3.8a	4.2a	5.9a	5.2a	5.1a	5.2a	4.4b	4.3b	6.1a	5.7a	5.5a
Branch no. per tree	Year 3	36a	31b	30b	46a	37b	36b	41a	31b	29b	51a	39b	39b
	Year 4	35a	29a	29a	38a	28b	34ab	42a	34b	32b	39a	30b	31b
Live crown length (m)	Year 3	2.6a	2.5a	2.6a	4.0a	3.5ab	3.4b	3.1a	2.8b	2.7b	4.5a	4.0ab	3.9b
	Year 4	3.5a	3.2a	3.6a	4.9a	4.0b	4.1b	4.4a	3.7b	3.4b	4.7a	3.9b	4.1ab

Table 2-4--Continued.

Location		Dunnellon						Palatka					
Treatment		Non-intensively managed			Intensively managed			Non-intensively managed			Intensively managed		
Taxa		PTA[b]	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU
Variables:													
Crown width (m)	Year 3	1.4a	1.2b	1.3b	2.2a	1.8b	1.6b	1.8a	1.4b	1.3b	2.6a	2.2b	1.9b
	Year 4	1.7a	1.6a	1.6a	2.2a	1.9a	2.0a	2.2a	1.9b	1.7b	2.2a	2.3a	2.2a
Crown shape ratio	Year 3	1.9a	2.1b	2.1b	1.9a	2.0a	2.2a	1.8a	2.0ab	2.1b	1.8a	1.9a	2.1b
	Year 4	2.1a	2.3b	2.3b	2.3a	2.2a	2.1a	2.1a	2.0a	2.0a	2.2a	1.7b	1.9ab
Branch-free stem length(m)	Year 3	0.2a	0.3b	0.3b	0.3a	0.4b	0.4b	0.3a	0.3a	0.3a	0.3a	0.3a	0.3a
	Year 4	0.5a	0.6a	0.6a	0.9a	1.2a	1.0a	0.7a	0.8a	0.9a	1.4a	1.9a	1.4a

[a] Taxa means were tested by year, location and treatment separately for each age group. Means among the three taxa for a given variable and year followed by the same letter within a treatment are not statistically significant at the 95% confidence level using linear contrasts of the MIXED procedure.

[b] PTA = improved loblolly pine
PEE = improved slash pine
PEU = unimproved slash pine

Trees at Dunnellon had smaller crowns (crown length and width) than those at Palatka. Loblolly pine consistently had greater crown width than slash pine, and was more responsive and unimproved slash pine (33% vs. 46%). A similar trend was observed at age 4 years, but it was not as significant as at age 3 years, and likely reflected the advent of crown closure.

Crown shape potentially influences the light distribution patterns within the crown and can be viewed as an inherent species' characteristic that reflects adaptation to the prevailing environment. Silvicultural treatments had no significant effects on crown shape ratio (=crown length/crown width), but taxa differences were significant at both ages and locations (Appendix B). At Dunnellon, crown shape ratio steadily increased between years under both silvicultural treatments, except for unimproved slash pine in the intensive treatment. Trees at Palatka exhibited a reverse trend in crown shape ratio between loblolly and slash pine; crown shape ratio for loblolly pine increased from ages 3 to 4 years under both treatments, while this ratio declined in slash pine.

Biomass and Leaf Area Characteristics of Tree Crowns

Tree crowns are most dynamic during early stages of development. Environmental effects (including treatments) can exert significant influence on crown characteristics. As revealed in this study, the intensive treatment significantly affected all crown characteristics at both sites (Appendix C). Significant interspecific (taxa) and intraspecific (families) differences (p # 0.01) were observed in almost all crown characteristics, except at age 4 years at Dunnellon, where significant differences in many crown characteristics diminished.

Specific leaf area

Inconsistent treatment effects were observed across locations for current-year specific leaf area (SLA). At Palatka, current-year SLA increased significantly (p # 0.0004 at age 3, and p # 0.0046 at age 4) in response to the intensive silvicultural treatment. In contrast, current-year SLA decreased at Dunnellon on the intensive plots at age 3 years (p # 0.0161) but increased significantly at age 4 years (p # 0.0295) (Table 2-5). Overall, loblolly pine appeared to have higher current-year SLA (176.6 cm^2/g) than slash pine (146.4 cm^2/g). Improved slash pine consistently had higher current year SLA than unimproved slash pine (147.8 cm^2/g vs. 144.9 cm^2/g).

Among all taxa, one-year-old needles generally had lower SLA than current-year needles (Table 2-5). Loblolly pine had higher SLA (135.6 cm^2/g) in one-year-old needles than slash pine (117.7 cm^2/g).Treatment effects on SLA for older needles were non-significant. For example, treatment effects on this variable across the three taxa diminished at Dunnellon (p # 0.2438 at age 3 years , and p # 0.2000 at age 4 years). Further, treatment × taxa interactions were not significant for SLA at either age (p > 0.10), indicating that all taxa responded similarly to the silvicultural treatments.

Table 2-5. Specific leaf area (SLA), leaf biomass, branch biomass, and leaf area for 3- and 4-year-old loblolly and slash pine planted at two locations in north central Florida[a].

Location		Dunnellon						Palatka					
Treatment		Non-intensively managed			Intensively managed			Non-intensively managed			Intensively managed		
Taxa		PTA[b]	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU
Variables:													
Current-year SLA (cm^2/g)	Year 3	181.1a	148.1b	147.8b	172.5a	143.3b	140.8b	171.4a	134.2b	130.0c	179.4a	149.2b	147.8b
	Year 4	173.2a	151.5b	145.7b	183.3a	158.4b	152.3b	170.0a	145.4b	147.1b	181.6a	152.2b	148.0b
One-year-old SLA (cm^2/g)	Year 3	135.7a	121.9b	119.4b	139.2a	122.6b	119.9b	143.6a	117.3b	114.5b	144.9a	128.6b	125.6b
	Year 4	131.5a	115.7b	114.7b	127.3a	117.4b	109.9b	127.0a	111.7b	110.6b	135.7a	120.9b	113.2b
Current year leaf biomass (kg/tree)	Year 3	0.93a	0.81a	0.80a	2.38a	1.69b	1.39b	1.74a	1.26b	1.07b	3.87a	2.92b	2.15b
	Year 4	1.61a	1.35a	1.50a	3.46a	2.45b	2.40b	4.04a	2.68b	2.16b	4.52a	3.44b	3.11b
One-year-old leaf biomass (kg/tree)	Year 3	0.05a	0.04a	0.04a	0.10a	0.08ab	0.07b	0.07a	0.06ab	0.04b	0.15a	0.13a	0.10ab
	Year 4	0.15a	0.14a	0.15a	0.27a	0.22a	0.23a	0.29a	0.25b	0.21b	0.33a	0.29a	0.27a
Total leaf biomass (kg/tree)	Year 3	0.98a	0.85a	0.84a	2.48a	1.77ab	1.46b	1.81a	1.32b	1.13b	4.02a	3.05b	2.25b
	Year 4	1.76a	1.49a	1.65a	3.73a	2.67b	2.63b	4.35a	2.93b	2.37b	4.85a	3.73ab	3.38b

Table 2-5--Continued.

Location		Dunnellon						Palatka					
Treatment		Non-intensively managed			Intensively managed			Non-intensively managed			Intensively managed		
taxa		PTA[b]	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU
Variables:													
Branch biomass (kg/tree)	Year 3	0.48a	0.33b	0.33b	1.62a	0.85b	0.65b	1.14a	0.63b	0.51b	3.17a	1.87b	1.22b
	Year 4	1.04a	0.70b	0.81ab	2.99a	1.62b	1.44b	3.58a	1.73b	1.28b	4.26a	2.61b	2.25b
Total crown biomass (kg/tree)	Year 3	1.45a	1.17a	1.17a	4.10a	2.62b	2.11b	2.94a	1.95b	1.65b	7.18a	4.91b	3.46b
	Year 4	2.79a	2.18a	2.45a	6.72a	4.30b	4.06b	7.93a	4.66b	3.64b	9.11a	6.34b	5.63b
Current year leaf area (m^2/tree)	Year 3	15.2a	11.0b	10.8b	38.2a	22.6b	18.1b	27.4a	15.9b	13.2b	64.5a	41.2b	29.6b
	Year 4	25.1a	18.1b	19.7b	54.1a	33.8b	31.7b	60.5a	34.8b	28.3b	71.0a	46.4b	40.8b
One-year-old leaf area (m^2/tree)	Year 3	0.6a	0.5a	0.5a	1.4a	1.0b	1.0b	1.1a	0.7b	0.6b	2.2a	1.6ab	1.3b
	Year 4	1.9a	1.6a	1.7a	3.4a	2.5a	2.5a	3.9a	2.7b	2.3b	4.4a	3.4b	3.0b
Total leaf area (m^2/tree)	Year 3	15.8a	11.5b	11.3b	39.6a	23.6b	19.1b	28.5a	16.6b	13.8b	66.7a	42.8b	30.9b
	Year 4	27.0a	19.7b	21.4b	57.5a	36.3b	34.2b	64.4a	37.5b	30.6b	75.4a	49.8b	43.8b

[a] Taxa means were tested by year, location and treatment separately for each age group. Means among the three taxa for a given variable and year followed by the same letter within a treatment were not statistically significant at the 95% confidence level by linear contrasts using the MIXED procedure.

[b] PTA = improved loblolly pine PEE = improved slash pine PEU = unimproved slash pine

Leaf biomass, branch biomass, and total crown biomass

Leaf biomass is a major component of crown biomass at early growth stages. The intensive silvicultural treatment significantly influenced leaf biomass accumulation (Appendix C). At age 3 years, leaf biomass (current year, one-year-old, and total) under the intensive treatment was more than double that under the non-intensive treatment at both sites, except for unimproved slash pine at Dunnellon (Table 2-5). Loblolly pine tended to accumulate more leaf biomass than improved slash pine, regardless of treatments and locations (e.g., 15% and 40% greater under non-intensive and intensive treatment at Dunnellon, respectively). Unimproved slash pine generally accumulated less leaf biomass than improved slash pine. Treatment × taxa interactions were significant in current-year and total leaf biomass, except at age 4 years at Palatka (Appendix C). Differential responses between the three taxa to the silvicultural treatments were the primary cause for this interaction. Further analyses revealed that scale effects rather than rank changes contributed to the interaction (Table 2-5).

Branch biomass generally accounted for less than 50% of the total crown biomass. When branch biomass was compared across locations for a given treatment, trees grown at Palatka had higher amounts than at Dunnellon (Table 2-5). For example, branch biomass at age 3 years under the non-intensive treatment at Palatka was 138% greater than at Dunnellon. In general, the order of branch biomass accumulation among taxa was loblolly pine > improved slash pine > unimproved slash pine. Treatment × taxa interactions were inconsistent across locations and years (Appendix C).

Crown biomass (total leaf and branch biomass) showed similar results to the individual components across locations and treatments (Table 2-5). At age 4 years, crown biomass for loblolly and slash pine grown under the non-intensive treatment at Palatka exceeded that of the intensive treatment at Dunnellon. Loblolly pine increased crown biomass by 170% under the non-intensive treatment at Palatka, but only 27% under the intensive treatment from ages 3 to 4 years. Similar results were found for slash pine (increases of 139% and 29% for improved slash pine, 121% and 63% for unimproved slash pine for the corresponding treatments at ages 3 and 4 years, respectively). Increases in crown biomass over the same period were also observed at Dunnellon, but not as markedly as at Palatka. Interspecific differences were significant, with loblolly pine accumulating more crown biomass than slash pine. Crown biomass for improved and unimproved slash pine showed different trends for the two treatments across locations. Unimproved slash pine accumulated more crown biomass than improved slash pine under the non-intensive treatment, but the reverse was true under intensive treatment at Dunnellon. At Palatka, improved slash pine accumulated more crown biomass than unimproved slash pine for both treatments (Table 2-5). Hence, treatment × taxa interactions represented a rank change at Dunnellon, but a scale effect at Palatka.

Leaf area characteristics

Leaf area is one of the most important variables to influence biomass accumulation and productivity in forest stands. Significant interspecific and intraspecific differences in leaf area were found across locations (Appendix C). Current-year leaf area generally accounted for more than 90% of the total leaf area, indicating that leaf life span was not significantly different among loblolly and slash pine.

The intensive silvicultural treatment significantly increased total leaf area per tree at both locations. For example, leaf area for loblolly pine at age 3 increased from 15.8 m^2/tree under the non-intensive treatment to 39.6 m^2/tree under the intensive treatment at Dunnellon. Similar results were found at Palatka, where total leaf area for loblolly pine increased from 28.5 m^2/tree to 66.7 m^2/tree due to treatment. Slash pine accumulated less leaf area than loblolly pine at both locations, but differences between unimproved and improved slash pine were not the same across locations. Improved slash pine accumulated more leaf area than unimproved slash pine under both treatments at Palatka, but the differences were not significant under most instances at Dunnellon (Table 2-5). On average, trees grown under the non-intensive treatment increased leaf area by 70% at Dunnellon and122% at Palatka between ages 3 and 4 years. In contrast, trees gained 45 - 79% more leaf area due to the intensive management at Dunnellon, and 13 - 42% at Palatka, respectively. Treatment × taxa interactions for other attributes (e.g., total leaf area) were significant (p # 0.05) in the two years at Dunnellon, but only significant (p # 0.10) at age 3 years at Palatka (Appendix C).

Vertical Distribution of Total Leaf Area

The vertical distribution of leaf area can be important in affecting the interception of light energy by leaves within the crown. Previous research has shown that the vertical distribution of leaf area can exert significant influence on light extinction patterns within the crown (Waring and Schlesinger 1985). Vertical differences in total leaf area per tree among taxa were shown in both relative distribution patterns and the absolute amount of leaf area along crown profiles (Figure 2-1). Trees planted at both locations had the most leaf area in the lower and middle crown positions at age 3 years. Loblolly pine tended to have 50% of the total leaf area in the lower crown at Dunnellon, while at Palatka it either had the highest amount of leaf area in the middle crown (non-intensive treatment) or an equal amount between the middle and lower crown positions (intensive treatment). On average, loblolly pine partitioned about 8% of its leaf area in the upper crown, while slash pine partitioned about 13%, as reflected in the significant taxa × position interactions (p # 0.0008).

Location × treatment × position interactions were statistically significant (p # 0.0030), as was the location × treatment × taxa × position interactions (p # 0.0001) for total leaf area. These results demonstrated the complex and significant interactions that occurred among locations, treatments, taxa, and crown positions on the vertical distribution of leaf area. In addition, the vertical distribution of leaf area generally corresponded to the vertical distribution of branch biomass.

Relationships between Volume Increment and Total Leaf Area per Tree (Growth Efficiency)

The rapid growth of forest stands depends on the accumulation of leaf area to intercept light energy for photosynthesis. Thus, the amount of leaf area in a stand can be a direct measure of potential production. A set of linear models with both quantitative and qualitative variables was developed to examine the relationships between leaf area and volume increment between ages 3 and 4 years ($r^2 = 0.77$, p # 0.0001). Based on predicted results, improved and unimproved slash pine were not significantly different in volume

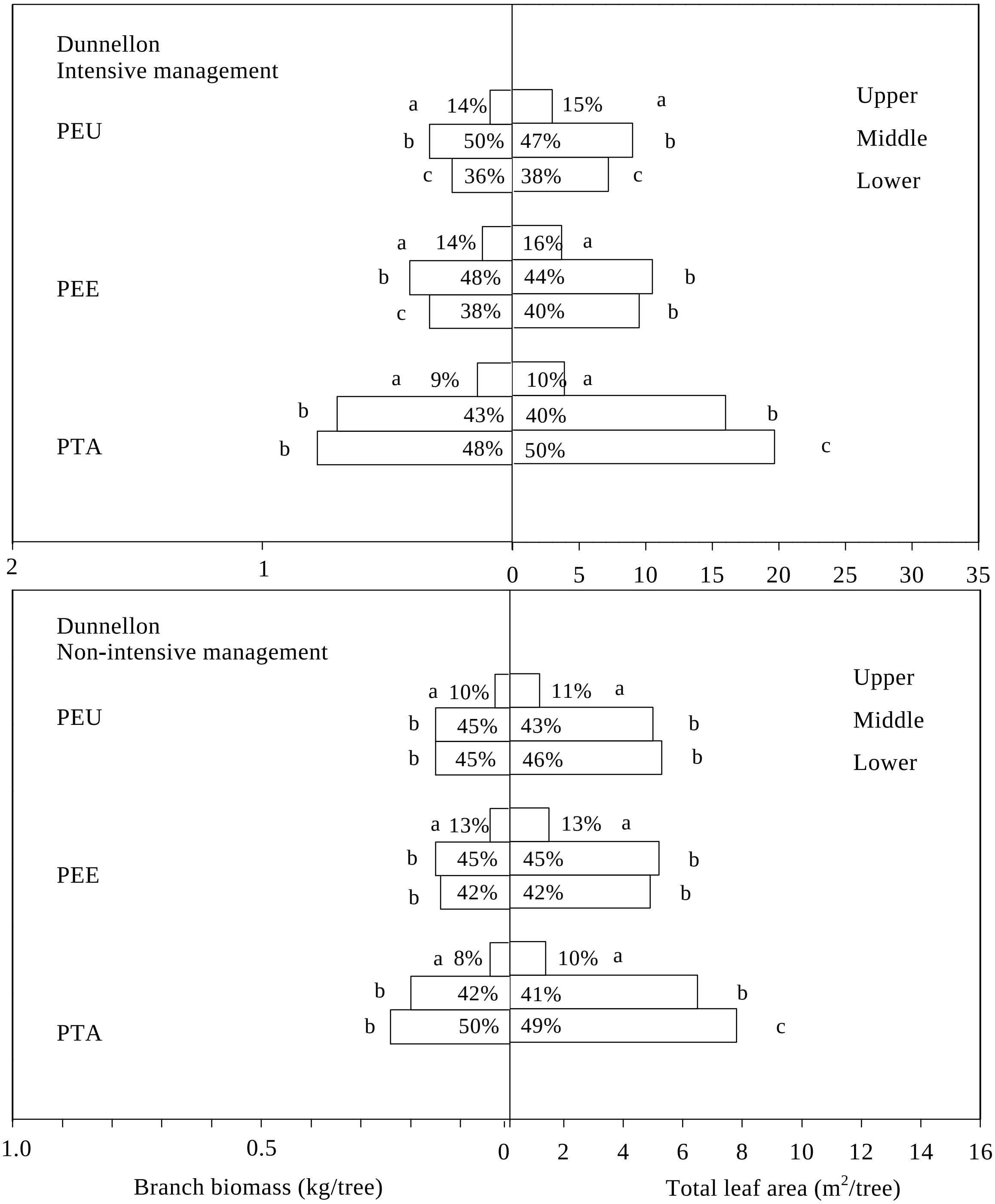

Figure 2-1. Vertical distribution of total leaf area (right) and branch biomass (left) by crown positions at age 3 years for loblolly and slash pine managed under two silvicultural treatment regimes in north central Florida.

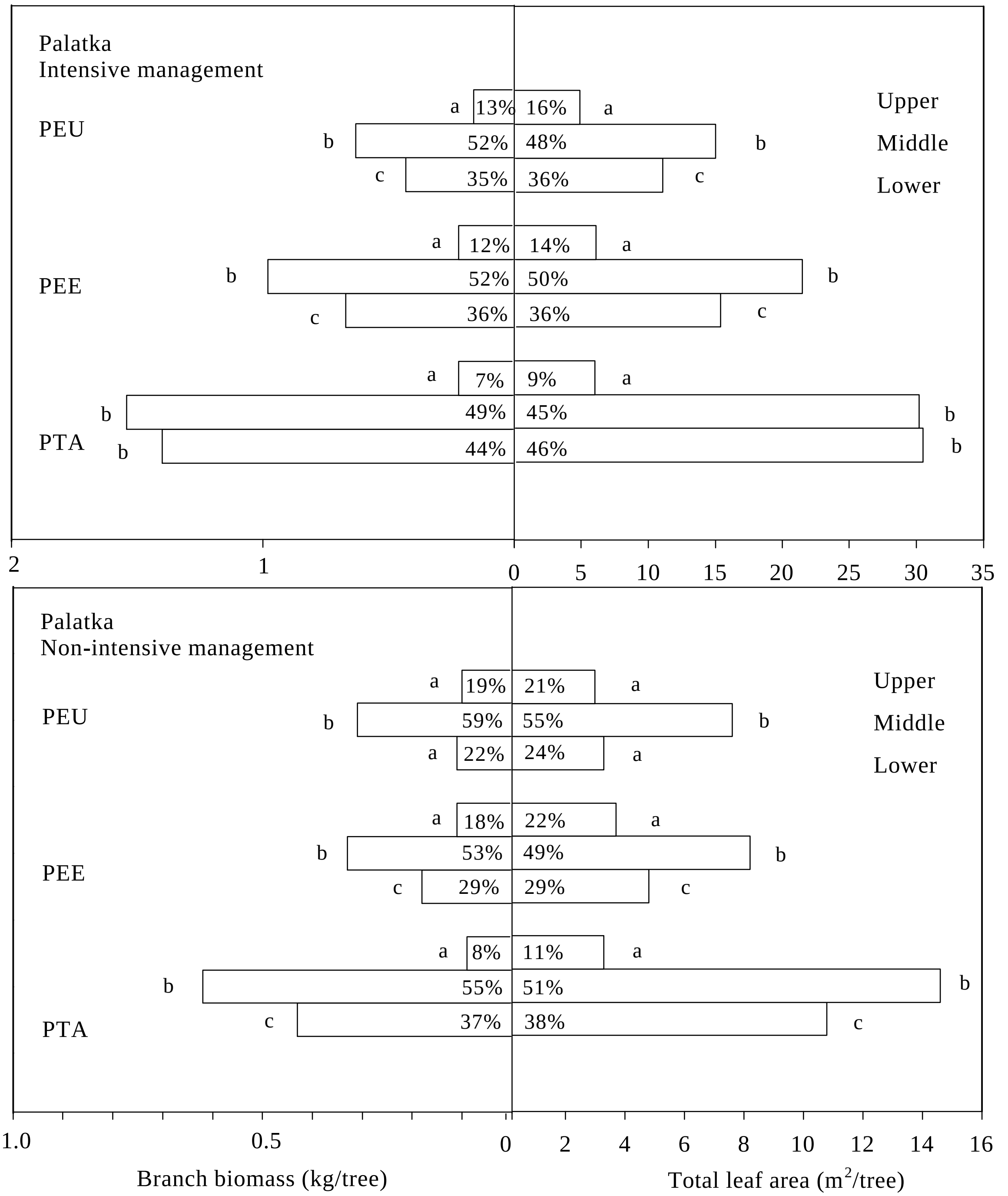

Figure 2-1-- Continued.

Note: PEU = unimproved slash pine, PEE = improved slash pine, PTA = improved loblolly pine

Position means for a given variable of a species followed by the same letter are not significantly different at the 95% confidence level by linear contrasts using the MIXED procedure of SAS.

Percentage numbers around the middle of the bars are the relative partition of leaf area or branch biomass by crown positions.

produced per unit leaf area (1,106 and 1,173 cm^3 stemwood/m^2 leaf area, respectively, averaged across locations and treatments), but differences did exist between loblolly and slash pine (Figure 2-2). Loblolly pine consistently produced less volume per unit leaf area (804 cm^3 wood/m^2 leaf area) than slash pine under the same locations and treatments. Similar results were also reported in a stand-level comparison of growth efficiency between 4-year-old loblolly and slash pine (Colbert et al. 1990).

The intensive silvicultural treatment significantly increased growth efficiency of both taxa at Dunnellon, while the opposite was true at Palatka (p # 0.0001). Additionally, location × treatment effects were significant (p #0.0001), which indicated that the Palatka site provided pine trees with more efficient growth per unit leaf area than the Dunnellon site for the non-intensive treatment (856 vs. 1,357 cm^3 stemwood/m^2 leaf area, averaged across taxa for Dunnellon and Palatka, respectively). In contrast, the Dunnellon site was more favorable for growth efficiency than the Palatka site when intensive silvicultural treatments were applied (1,089 vs. 809 cm^3 stemwood/m^2 leaf area, averaged across taxa for Dunnellon and Palatka, respectively). Further, volume growth rates converged among taxa as leaf area approached 54 m^2/tree under either silvicultural treatment at Dunnellon, and 40 and 55 m^2/tree under the non-intensive and intensive treatments, respectively, at Palatka.

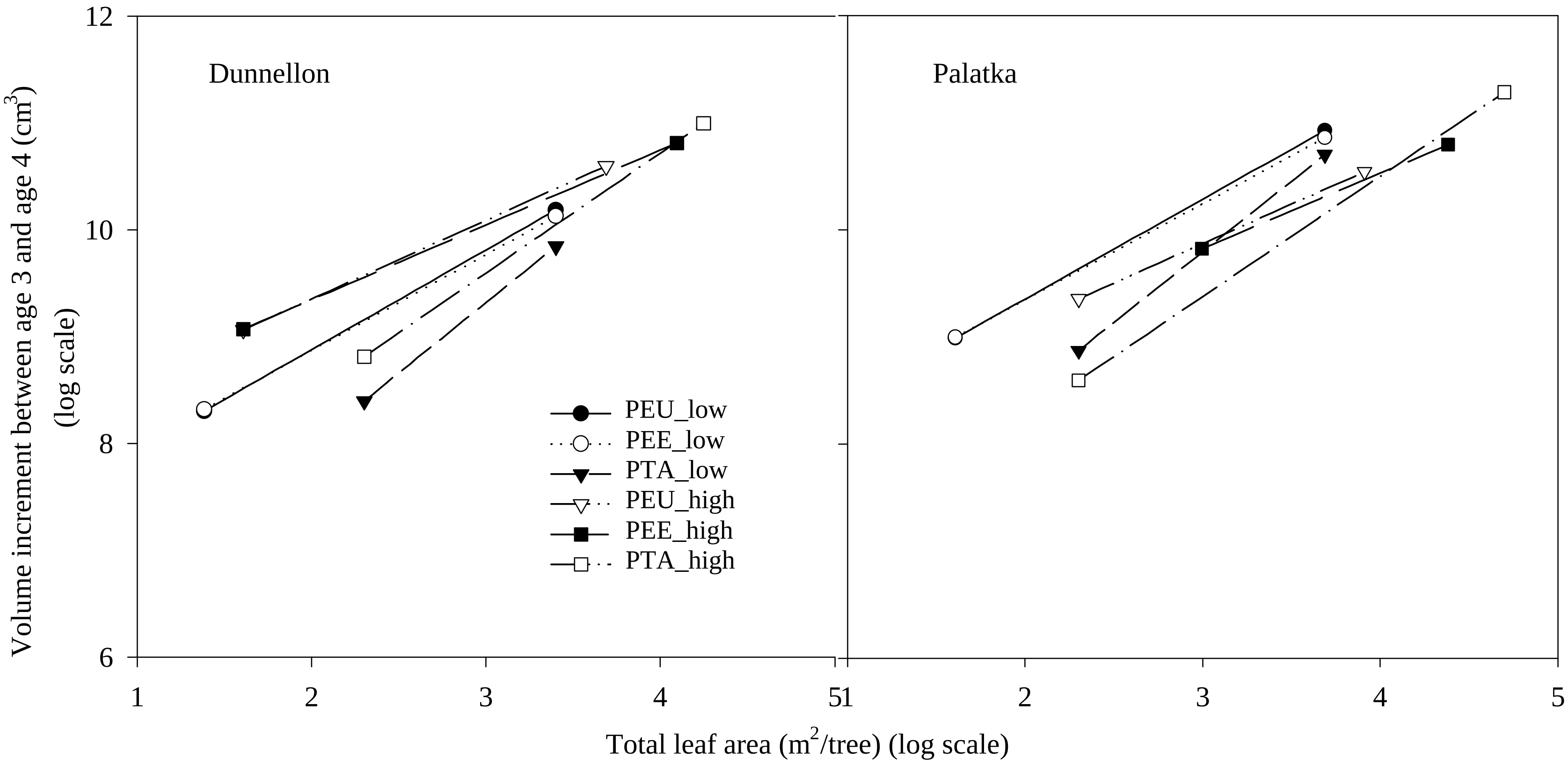

Figure 2-2. Relationship between individual tree volume increment from ages 3 to 4 and total leaf area (all-sided) for loblolly and slash pine managed under two silvicultural treatment regimes in north central Florida.

PEU = unimproved slash pine
PEE = improved slash pine
PTA = improved loblolly pine

low = non-intensive management
high = intensive management

Discussion

Comparisons of Foliage and Branch Biomass Estimation Equations

The foliage-carrying capacity of branches varied significantly among the three crown positions. Leaf biomass per branch, when expressed separately by needle age class, could not be accurately predicted by branch diameter alone ($r^2 = 0.20$ for current year leaves, and $r^2 = 0.11$ for one-year-old leaves). Similar results were found in western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii*), and grand fir (*Abies grandis*) (Kershaw and Maguire 1995). Therefore, equations unique to different crown positions were needed to satisfactorily predict leaf biomass and leaf area distribution within the crown (Gilmore and Seymour 1997). However, total leaf biomass and branch biomass could be predicted satisfactorily using only branch diameter (Table 2-6), though other factors were still important. Model evaluation revealed that leaf biomass was significantly variable under diverse conditions, but branch biomass was relatively independent of external conditions.

Mensurational and Crown Structural Characteristics

Significant differences were observed among taxa for the many mensurational and crown characteristics examined. Loblolly pine generally had greater DBH and height than slash pine. A related study showed that these taxa differences could be partly attributed to lower fusiform rust incidence in loblolly pine (Lopez-Upton 1999). However, studies conducted in rust-free loblolly and slash pine stands suggested that other factors such as canopy structure and growth habit may be more responsible for interspecific differences (Nemeth 1973; McCrady and Jokela 1998). As revealed in this study, branch numbers per tree, crown length and width, and crown shape ratio all showed interspecific variation at this stage of development.

Table 2-6. A comparison (r^2) between estimation models for foliage and branch biomass based on branch diameter alone and multi-factor variables.

Biomass components	Diameter based model[a]	Multiple factor model[b]
Total foliage	0.62	0.72
Current year foliage	0.20	0.65
One-year-old foliage	0.11	0.70
Branch	0.82	0.91

a model constructed using only branch base diameter, i.e., log(biomass) = $b_0 + b_1$(log(diameter)).
b model form was identical to that in Table 2-3.

Crown structure was difficult to model since much variation occurred among individual trees (Doruska and Burkhart 1994). As found in Scots pine (*Pinus sylvestris*), structural attributes related to higher biomass accumulation include higher branch numbers per whorl and longer crowns (Kuuluvainen et al. 1988). Total branch number accounted for 42% of the variation in volume accumulation among Douglas-fir families (King et al. 1992). In the current study, differences in branch numbers could also be related to the superiority of loblolly pine growth relative to slash pine. When both total branch number per tree and crown length were significantly greater than slash pine, loblolly pine generally had greater height growth (Table 2-4). However, when loblolly pine had higher branch numbers per tree but shorter crown length (e.g., under the non-intensive treatment at Dunnellon), its DBH or height growth was less than slash pine.

The distribution of foliage and branches within a crown can influence light penetration and, ultimately, growth potential. Crowns that have a tight branching pattern could reduce light penetration, especially to the lower foliage elements. Sparser crowns could be an important adaptive mechanism that allow trees to optimize growth performance in varying environments (Makela and Vanninen 1998). A simulation study demonstrated that asymmetrical crown development, an expression of phenotypic plasticity of crowns, was advantageous to productivity (Sorrensen et al. 1993). In contrast, Kellomäki et al. (1985) reported that crown shape had little influence on light interception, and that narrower, symmetrical crowns were most efficient in affecting growth potential. Other theories have also been proposed relative to the importance of crown structure on adaptation to harsh environments (Sprugel 1989; Smith and Brewer 1994). In the current study, narrower crowns did not facilitate more rapid growth, as loblolly pine was more productive than slash pine and it also had wider crowns.

Crown dimensional differences have been shown to significantly influence stem biomass partitioning in *Picea abies* and *Picea abies* f. *pendula* (Pulkkinen 1991), aboveground biomass in Scots pine (Kuuluvainen and Kanninen 1992), and height increment in loblolly pine (McCrady and Jokela 1996). Although CSR combined two important crown parameters and was statistically significant among taxa, it appeared to have little ecological significance in this study because the ratio tended to stabilize around 2 (Table 2-4). In a similar study, McCrady (1993) observed significant intraspecific variation in crown shape ratio in young loblolly pine plantations, but did not find an advantage of narrower crowns over wider crowns in height growth. Crown shape ratio may be more of an indication of environment-induced adaptation rather than a significant characteristic that can be used to differentiate functional groups. Although long-term breeding programs have selected progenies of Norway spruce and Scots pine with high crown shape ratios in the cold temperate region (Kellomäki et al. 1985), rapid crown development at early growth stages is one characteristic that distinguishes subtropical pine taxa from other coniferous taxa in the north, temperate regions. As shown in this study and a related stand level study in loblolly pine plantations (McCrady 1993), higher crown shape ratio did not translate into growth advantages at early stages of stand development (r = -0.17, p # 0.0005 between crown shape ratio at age 3 and volume increment).

Crown Biomass, Leaf Area, and Their Vertical Distribution

Crown (branch and leaf) biomass, total leaf area, and their vertical distribution patterns have been closely associated with stand structure, forest productivity, and microclimate of the habitat (Maguire and Bennett 1996). Total leaf area at the tree level and leaf area index at the stand level were both positively associated with the annual productivity of many species (Waring and Schlesinger 1985). Silvicultural treatments increased total leaf area per tree by primarily augmenting leaf biomass rather than changes in specific leaf area (Table 2-5). For example, specific leaf area consistently decreased in all taxa at age 3 years at Dunnellon, while leaf area doubled due to the intensive silvicultural treatment. Similar results were previously reported in loblolly pine (McCrady and Jokela 1996). These results contrast those reported for sweetgum (*Liquidambar styraciflua*), where leaf area increases due to fertilization were largely attributable to leaf size increases (Kuers and Steinbeck 1998).

Biomass allocation between leaves and branches varied markedly among taxa across locations and treatments (Table 2-7). Slash pine allocated more crown biomass to foliage than loblolly pine. Trees at Dunnellon had a higher leaf:branch biomass ratio than at Palatka for all taxa and treatments. Loblolly pine allocated more biomass to branches, which may offer growth advantages by building larger crowns during the early stages of stand development. Consequently, its crown carrying capacity could increase (more leaf area per tree was attained), and mutual shading of leaves could also be avoided. The advantage of this biomass allocation pattern was more pronounced when leaf area was large, suggesting that growth efficiency of loblolly pine, although lower than slash pine at low levels of leaf area, could eventually exceed that of slash pine after crown closure (Figure 2-2). Intensive management tended to favor relative biomass allocation to branches in developing spacious crowns at early growth stages (Table 2-7).

Table 2-7. Variation of leaf:branch biomass ratio as influenced by location, treatment, and tree age in loblolly and slash pine in north central Florida.

Location	Age	Non-intensive management			Intensive Management		
		PTA[a]	PEE	PEU	PTA	PEE	PEU
Dunnellon	3	2.04	2.58	2.55	1.53	2.08	2.25
	4	1.69	2.13	2.04	1.25	1.65	1.83
Palatka	3	1.60	2.09	2.22	1.27	1.63	1.84
	4	1.22	1.69	1.85	1.14	1.43	1.50

[a] PTA = improved loblolly pine
PEE = improved slash pine
PEU = unimproved slash pine

Treatment effects improved growth performance by increasing crown size (Table 2-4), but the vertical distribution of branches and leaves were not significantly affected. For example, intensive management significantly increased total leaf area, foliage and branch biomass, but their relative vertical distribution within the crown largely remained unchanged (Figure 2-1). Gillespie et al. (1994) reported similar results in young loblolly pine, and further indicated that for a given branch size, fertilized plots could carry more leaf biomass than untreated plots. In the current study, treatment effects on leaf carrying capacity of branches were not statistically significant (Table 2-3). Joggi et al. (1983) argued that the vertical distribution of leaf area was less important in determining net photosynthetic rate than LAI and position of leaf age in canopies of red clover (*Trifolium pratense*). However, forest trees are much larger than herbaceous plants and should have developed optimum vertical distribution patterns that could intercept more light energy.

Leaf Area and Growth Efficiency

Variation in leaf area is probably one of the most prominent and dynamic characteristics of forest stands in corresponding to seasonal or yearly changes in environmental conditions. Positive relationships can be found between leaf area and growth rates or total biomass accumulation in many species (Gholz et al. 1991; Gower et al. 1993; McCrady and Jokela 1998). Although annual wood formation per unit leaf area has been reported independent of cultural treatments and species in some studies (Norby 1996), highly significant differences in growth efficiency were detected in relation to silvicultural treatments between loblolly and slash pine (Colbert et al. 1990). Relationships between leaf area and growth efficiency (basal area growth per unit leaf area) also varied in jack pine

(*Pinus banksiana*) and red pine (*P. resinosa*) with different stand origins (Penner and Deblonde 1996). Variability in aboveground net primary production (ANPP) could be largely explained by specific leaf area and leaf area index in some conifer and hardwood stands (Fassnacht and Gower 1997). As shown in this study, growth efficiency differed significantly in relation to silvicultural treatments, taxa, and locations (Figure 2-2), suggesting that growth efficiency is highly variable and it reflects the growing conditions of forest stands.

During the juvenile stages of stand development, slash pine was more efficient in dry-matter production per unit leaf area than loblolly pine (Colbert et al. 1990). However, following peak leaf area accretion, stem wood growth efficiencies of loblolly pine can match that of slash pine (Jokela and Martin 2000). The issue that remains unanswered is the reason behind the changes in growth efficiency between loblolly and slash pine. Because of the enhanced growth impacts caused by intensive management, crown closure was accelerated, especially at Palatka. Under the non-intensive treatment at both Palatka and Dunnellon, crown closure would not be achieved for at least two or more years. These findings, along with similar results from other studies, suggests that crown closure is the period when loblolly pine meets or exceeds slash pine in growth efficiency. Under similar conditions, loblolly pine, having more branches, higher SLA, and larger crown biomass than slash pine, may have more efficient light penetration and interception by foliage after crown closure. However, before crown closure, when light is not a limiting factor, these crown characteristics could not fully provide loblolly pine with higher light use efficiency. Although slash pine had fewer branches, lower SLA, and smaller leaf area in comparison to loblolly pine, its sparser crowns could allow more efficient light penetration in the crown and, therefore, could offset any disadvantage associated with lower leaf amount to gain a more efficient level of stemwood growth. Ford (1985) came to the same conclusion by presenting differences in foliage display schemes and branching patterns among contrasting conifer species.

Biomass allocation to various tree components between loblolly and slash pine trees may also contribute to differences in stemwood growth efficiency for the two species. At early growth stages, loblolly pine preferably allocated more photosynthate to crown (foliage and branch) development than slash pine. On the contrary, slash pine allocated more photosynthate to the stem for storage. For example, slash pine allocated more biomass to the bole (stem + bark) at age 4 years than loblolly pine (58% vs. 44%, respectively) (Colbert et al. 1990). Therefore, slash pine showed more efficient stemwood growth than loblolly pine. After crown closure, loblolly pine started to allocate more photosynthate to stemwood because foliage development peaked, which led to the convergence of growth efficiency for the two species (Figure 2-2). For example, Jokela and Martin (2000) found non-significant differences in stemwood growth efficiency for the two species at age 14 years. Stemwood allocation (percentage of total aboveground biomass) averaged 65.3% for loblolly pine and 62.8% for slash pine. However, more detailed studies should include physiological responses of needles to environment or treatment induced changes to better understand growth strategies for the two species in the future.

Summary

Comparisons and contrasts were made on juvenile growth performance and crown structural characteristics among genetically improved loblolly, unimproved and improved slash pine planted at two locations and managed under two levels of silvicultural intensity in north central Florida. Loblolly pine accumulated more volume and crown biomass than slash pine at both ages 3 and 4 years. Improved slash pine generally grew faster than unimproved slash pine, but a significant treatment × taxa interaction was detected as unimproved slash pine outperformed improved slash pine when the silvicultural treatment intensity was low. Significant differences in growth were associated with variation in crown structure or biomass characteristics among the taxa.

Crown position and branch diameter were the most significant factors influencing foliage biomass per branch. However, location and treatment effects were not statistically significant (p $ 0.10) in determining the foliage biomass carrying capacity of branches. Significant differences in crown structural traits (total branch number per tree, crown width and length) were related to the growth performance between loblolly and slash pine. At early growth stages, loblolly pine had more branches per tree and allocated more biomass to branches than slash pine for crown development. Branch:leaf biomass ratios were closely related to the growth performance among taxa. A greater branch:leaf biomass ratio could represent a growth strategy important for developing spacious crowns that facilitate faster growth due to increased leaf area carrying capacity within the crown.

Treatments significantly increased total leaf area accumulation, but had little impact on the relative distribution of leaf area along the crown profile. Corresponding crown structural changes and biomass accumulation patterns under the intensive treatment led to significant differences in overall growth performance. Specific leaf area (SLA) was one of the adaptation variables sensitive to location, treatment, taxa, crown position, and leaf age. Evidence from this study showed that leaf area increases associated with the intensive silvicultural treatment were primarily attributed to increases in leaf biomass, rather than large changes in SLA. However, the importance of SLA in differentiating interspecific characteristics should not be neglected.

Significant differences in growth efficiency (volume produced per unit leaf area per year), mediated by location and treatment, were detected between loblolly and slash pine. Loblolly pine generally had lower growth efficiency than slash pine, although a convergence among taxa was achieved when leaf area levels became large, and possibly resulted from crown structural changes that facilitated more effective light interception by loblolly pine.

CHAPTER 3

SEASONAL DYNAMICS OF FOLIAR NUTRIENTS, NUTRIENT USE EFFICIENCY, AND RETRANSLOCATION IN JUVENILE LOBLOLLY AND SLASH PINE

Introduction

Nutrient levels in the soil and plant are primary determinants of biological productivity in forest stands. Differences in nutritional physiology (i.e., efficiencies of nutrient uptake, nutrient utilization, and nutrient retranslocation) contribute to the contrasting relative growth rates among species and their ecological responses to environments (Boerner 1984; McGraw and Chapin 1989). A better understanding of nutritional characteristics and their relations is central to the improvement of forest productivity and awareness of ecosystem functioning (Baruah and Ramakrishnan 1988; Knops et al. 1997). In practice, recognition of nutrients in relation to growth performance among species or cultivars can help design conceptual ideotype models for different objectives in breeding programs (Forrest and Ovington 1971; Mehall et al. 1983; Nambiar 1984).

Nutrient levels vary temporally in response to growth requirements and annual physiological cycles (Drossopoulos et al. 1996; Santa et al. 1997). They also vary spatially in adaptation to environmental conditions (e.g., soil fertility, weather) (Miller 1966; Boerner 1985; 1986). Our knowledge of nutrient dynamics for species having multiple cohorts of leaves primarily comes from nutrient comparisons among different leaf age groups sampled in the same year. However, patterns of major leaf nutrients (N and P) are not always closely related in different years (Insley et al. 1981), suggesting that non-standardized sampling procedures may provide inaccurate information or varying interpretations of nutrient dynamics. Therefore, more attention should be paid to the dynamic patterns of nutrients throughout a complete life cycle of the same cohort of leaves.

Nutrient-use efficiency has been most commonly defined in terms of biomass production per unit of nutrient uptake (Gholz et al. 1985; Day 1987; Elliott and White 1993), litterfall production per unit of litterfall nutrient content (Vitousek 1982; Knops et al. 1997; Fassnacht and Gower 1999), or litter produced per unit of nutrient uptake (Garkoti and Singh 1995). The primary consideration in the above definitions is to evaluate ecosystem functioning. Other definitions of nutrient use efficiency encompass physiological aspects of individual tree growth (Kost and Boerner 1985; Reich and Schoettle 1988; Li et al. 1991b). From the standpoint of nutritional and production physiology, absorbed nutrients should meet the demand for foliage development, which in turn affects interception of light energy and overall growth. Therefore, nutrient use efficiency can be defined as the cumulative nutrient use efficiency of dry-matter production, i.e., biomass production per unit of incorporated (uptake + retranslocation) nutrient content (Larcher 1995). Nutrient-use efficiency in terms of leaf area production per unit of nutrient content can serve as the basis for evaluating both nutrient utilization and production efficiency. At present, little information is available about genetic controls on nutrient use efficiency in relation to strategies used by trees to achieve site dominance in growth.

Nutrient retranslocation has been interpreted as mechanisms ranging from increasing plant adaptation to environments to more efficient utilization of nutrients (Nambiar and Fife 1991). Many studies have reported nutrient withdrawals from senescing leaves to young tissues; however, retranslocation efficiency is not related to soil fertility in many species (Chapin and Kedrowski 1983). Nutrient retranslocation not only occurs in senescing leaves, but substantial amounts can also be retranslocated from young leaves throughout the year for meeting growth requirements within the plant (Nambiar 1990). For example, foliar N and P content retranslocated above 40% prior to senescence in many woody species (Reich et al. 1995; Zhang and Allen 1996). Retranslocation of nutrients among growing leaves is probably driven by growth requirements, i.e., nutrient retranslocation from young foliage is closely associated with foliage production (Fife and Nambiar 1984). Strong evidence indicated that N retranslocation was significant in the spring when active shoot elongation was occurring. However, N, P, and K retranslocation was not significant in the fall in *Acer freemanii* (Rose and Biernacka 1999). On the other hand, nutrient retranslocation during senescence is a characteristic of many woody plants, and is controlled by many factors (Nambiar and Fife 1991). Therefore, nutrient retranslocation efficiency and amount could contribute to differences in overall growth performance of trees.

In this study, we consider nutrient issues related to growth strategies of individual trees. Our objectives are to (1) determine patterns of leaf macronutrient (N, P, K, Mg, and Ca) concentrations and content throughout a complete leaf life cycle as influenced by locations and silvicultural treatments; (2) evaluate nutrient use efficiency of leaf area production among several pine taxa; and (3) ascertain variation and significance of nutrient retranslocation efficiency prior to leaf senescence with location, fertilizer treatment, and taxa.

Materials and Methods

Plant Materials and Field Sites

Loblolly pine (*Pinus taeda* L.) and slash pine (*P. elliottii* Engelm. var. *elliottii*) represent two of the most important commercial timber species in the southeastern United States. Long-term studies of the two species have established clear interspecific relations and intraspecific family structures. Three pine taxa (genetically improved loblolly, improved and unimproved slash pine) were chosen for this study.

This study was part of an existing larger series of experiments designed by the University of Florida's Cooperative Forest Genetics Research Program to test growth performance of several pine taxa and their hybrids in relation to location and intensity of silvicultural treatments (Lopez-Upton 1999). The two field sites utilized were in north central Florida (Dunnellon, Levy County, 29°20' N, 82°50' W and Palatka, Putnam County, 29°40' N, 81°42' W). The climate for each location is humid, temperate with a mean annual temperature of 21°C. Annual precipitation averages 1,332 mm at Dunnellon and 1,368 mm at Palatka. The nearly level landscape is underlain by soils classified as sandy, siliceous, hyperthermic Aeric Alaquods (somewhat poorly drained, Smyrna series) at Dunnellon and hyperthermic, uncoated Aquic Quartzipsamments (moderately well drained, Adamsville series) at Palatka (Soil Survey Staff 1998). The site indices for the Smyrna and Adamsville series were 19 m and 20 m (base age 25 years), respectively.

Experimental Layout

Sixteen open-pollinated families from each of three pine taxa (genetically improved loblolly pine, and improved and unimproved slash pine) were planted at both sites in a five-tree row plot in each of three complete blocks using a split-split plot experimental design. Two levels of silvicultural treatments (intensive vs. non-intensive) were applied. Prior to study establishment, each site was chopped and bedded. Understory vegetation in the intensive silvicultural treatment blocks was controlled during the first growing season using a combination of mechanical and pre- and post-plant directed spot spray applications of glyphosate applied at labeled rates. Containerized seedlings were planted in December 1994 at a 1.5 m × 3.4 m spacing at Palatka, and a 1.8 m × 3.0 m spacing at Dunnellon. Fertilizers were broadcast applied in the high intensity treatment during years 1 and 3 as a balanced mix of macro- and micronutrients. Total elemental application rates for plots receiving fertilizer additions at both locations were approximately (kg ha^{-1}): N (110), P (80), K (162), Ca (20), Mg (10), S (13), Fe (0.5), Zn (0.06), Mn (0.5), Cu (0.06), and B (0.06). Insecticides (Asana, Diomethorate or Pyridine) were applied 3-4 times during the first growing season to control tip moth (*Rhyacionia* spp.) on the high intensity treatment. The low intensity treatment did not receive herbicide, fertilizer or insecticide applications. An untreated buffer of at least 21 m separated the high and low intensity treatment.

Sampling Procedures

Two sample trees within a 5-tree row-plot in each family from each block were randomly chosen by a SAS procedure, and then a systematic sampling method was applied to all other families and taxa at the two sites. Sample trees were healthy and free of disease. In total, 192 sample trees (2 treatments × 3 blocks × 16 families × 2 trees) were chosen for each taxa and site. Overall, 1,152 trees (2 locations × 2 treatments × 3 blocks × 3 taxa × 16 families × 2 trees) were sampled across the two sites.

The specific tissues sampled in this study and the timing of collections were consistent among sample trees to avoid likely variation in nutrient concentrations (Bates 1971). Recommended tissue sampling procedures entailed collection of full-length and complete fascicles from the upper third of the crown from representative sample trees (Madgwick and Mead 1990). Because foliage at different ages can vary in nutrient concentration, sample tissues should be age specific (Hom and Oechel 1983; Ernst 1995; Zhang and Allen 1996). Generally, current-year foliage has higher nutrient concentration and lower tree-to-tree variability than older needles and, therefore, it is widely accepted as being most useful for diagnostic purposes (Mead 1984).

Previous research with loblolly and slash pine has shown that foliage nutrients exhibit distinct temporal patterns over the course of a year (CRIFF 1987). To overcome problems with leaf age and season of year, needle samples were collected eight times over a two year period from the same branch of every sample tree through the life cycle of the same needle cohort. Specifically, needle samples were collected from both sites in: June (the first month current year foliage attains full length), September (when needle N concentration is generally lowest during the year), November (a critical stage in retranslocation of some mineral nutrients) in 1997, and February (when needle N concentration is generally at the highest level of a year), April (initial new growth may affect nutrient status of 1-year-old needles), June, September, and December (last month for 1-year-old needles to stay on the tree) in 1998. At each sampling interval, about 50 fascicles were collected from each sample tree. Sample branches were randomly selected from the upper third of the crown in 1997 (the crown position for needle samples became the middle crown in 1998) from a uniform aspect (south). Approximately 9,216 total leaf samples (2 locations × 2 treatment × 3 blocks × 3 taxa × 16 families × 2 trees × 8 times) were processed for chemical analyses.

All tissues were oven-dried at 70 °C for 48 hours or until dry. About 20 complete and full-length fascicles were randomly chosen from each sample to determine total dry weight and the number of needles per fascicle. All dried tissues were ground in a Wiley mill to pass a 2 mm stainless steel screen. The ground dry samples were stored in sealed plastic vials until nutrient analyses were performed.

Nutrient Analyses

Selection of an efficient nutrient digestion method from the many established procedures depends upon the nutrient status of plant materials, which is critical with respect to N. Conifers naturally grow on acid soils where ammonification is the dominant N conversion process (Sarigumba et al. 1977; Pritchett and Smith 1970), and NH_4^+ can be as high as 90% in the mineral soil N pool (Carlyle 1995). Pine trees prefer NH_4^+ as the primary N source from soils (Durzan and Steward 1967; McFee and Stone 1968), largely due to their long-term adaptation to acidic soil environments. Two methods for determining total N in pine foliage were analyzed and compared on a sample subset to determine accuracy and N recovery. A total of 200 samples that included improved loblolly, improved slash and unimproved slash pine that were equally and randomly chosen from the sampling periods were used in the analysis.

Method I: Kjeldahl digestion

To determine foliar N concentrations, a 200 mg sample was weighed into a 50 ml Pyrex test tube, and then 3.2 g of salt catalyst (9:1 K_2SO_4 : $CuSO_4$), 2 glass beads, and 5 ml of concentrated H_2SO_4 were vortexed in the tube under a hood. Two ml of 30% H_2O_2 was added to reduce frothing. Tubes were digested in an aluminum block digester at 380 ^{o}C for 240 minutes (Bremner 1965; Gallaher et al., 1975; Jones et al. 1991). The tubes were capped with small Pyrex funnels which allowed for evolving gases to escape while preserving refluxing action. Cool digested solutions were vortexed with approximately 20 ml of deionized water and allowed to cool to room temperature. Samples were then brought to a 50 ml volume, transferred to 20 ml square Nalgene storage bottles (glass beads were filtered out), sealed, mixed, and stored. Nitrogen that was trapped as $(NH_4)_2$ SO_4 was analyzed. Eight standard pine materials with known N concentration values from National Standard Institute (NSI) were subjected to the same procedures and used as checks.

Method II: wet acid digestion

Needle N concentrations were measured using the method as outlined in Thomas et al. (1967) and Jones et al. (1991), which was similar to the Kjeldahl procedure except that a catalyst was not added. In brief, 100 mg of homogenous tissue was weighed and placed in a 50 ml Pyrex test tube, and then 2 ml of concentrated H_2SO_4 was added. The samples were placed in a digestion block at 380 °C for 30 minutes. All tubes were then removed from the block and allowed to cool. Small amount of 30% H_2O_2 was added into the tubes. Repeated heating and cooling was conducted several times until the solution became clear. In this method, H_2SO_4 was added to raise the temperature of the mixture, while H_2O_2 was used to speed and complete the digestion procedure (Jones et al. 1991). The other macronutrients (P, K, Mg, and Ca) were analyzed using the same digestion procedure. Nutrient concentrations were determined using an inductively-coupled plasma emission spectrometer (ICP or ICAP).

Pairwise sample comparisons for N concentrations indicated that Method I was about 7% lower than Method II in estimating total N concentration, but no significant differences were found between the two methods. To process samples more efficiently, Method II was selected for analyzing all plant tissues. A detailed discussion on advantages and disadvantages of both methods was given by Jones et al. (1991).

Nutritional Variables

Concentrations and fascicle content of N, P, K, Mg, and Ca, and fascicle dry weight over the eight sample periods were included in the statistical analysis. Fascicle nutrient content was calculated as the product of nutrient concentration and average fascicle weight. Nutrient use efficiency of leaf area production (LA_{NUE}) was defined as peak leaf area production per unit nutrient accumulated in current-year foliage and expressed as leaf area (cm^2) / nutrient (mmol). LA_{NUE} was determined using foliar nutrient concentration and specific leaf area estimates from September,1997, with a sample size of 1,152 for that period. Because only current-year needles were analyzed for nutrient concentrations in 1997, LA_{NUE} was computed for current-year foliage only. This index measures peak leaf area production (generally from late August to early September) in terms of total amount of nutrients incorporated in current-year foliage that are available for metabolism.

Nutrient retranslocation efficiency (NRE) was calculated using the following formula (Saur et al. 2000):

$$\text{NRE (\%)} = \frac{FC_1 - FC_2}{FC_1} \times 100$$

where FC_1 was the maximum fascicle nutrient content during the needle cohort life cycle, and FC_2 is nutrient content of green fascicles in early December, 1998, prior to abscission. The term (FC_1 - FC_2) represented the amount of nutrients that were retranslocated. The sample size used in the analyses for nutrient retranslocation totaled 1,152.

Statistical Analyses

All analyses of variance and comparisons of means were conducted using individual tree data. Model selection procedures and criteria were similar to those described in Chapter 2 for growth analyses. Main effects under investigation included location, treatment, taxa, and family, in which all effects except family were regarded as fixed effects. In brief, a full model including all main effects and their interactions (significant at "=0.25) was chosen for preliminary analysis. Non-significant effects and interactions were deleted from the full model, and a final model was then developed. Interaction effects involving family were always kept in the model for appropriate selection of error terms in ANOVA tests, even though they were not significant. SAS procedures GLM and MIXED were used for ANOVA (SAS Institute 1996). Where variance homogeneity was not satisfied, ANOVA was separately performed by locations or treatments. For fascicle nutrient concentrations and content, ANOVA was performed separately by sampling periods.

Means for the various nutrient characteristics (i.e., concentration, content, LA_{NUE}, and nutrient retranslocation efficiency) among the three taxa were compared using the LSMEANS statement in PROC MIXED. A default level of " = 0.05 was used to test significance among the means unless otherwise specified. In presenting the data , means were combined across locations or treatments if scale effects (i.e., no rank changes among the taxa) were detected.

Results

Variation of Leaf Nutrient Concentrations and Fascicle Weight

Nitrogen, P, and K concentrations generally decreased over a complete leaf life cycle among the three pine taxa (Figures 3-1 to Figure 3-3). The decrease was less pronounced for P at the Dunnellon site, while consistent decreases occurred in N and K for both locations and treatments. In contrast, concentrations of less mobile elements, Ca and Mg, generally increased from the beginning to the end of the leaf life cycle (Figure 3-4 and Figure 3-5).

Differences in N and P concentrations were consistent among taxa across locations and treatments, with loblolly pine having significantly higher concentrations than slash pine. For example, loblolly pine had significantly higher N concentrations than either slash pine taxa in 7 out of 8 sampling periods at Palatka, regardless of silvicultural treatment (Figure

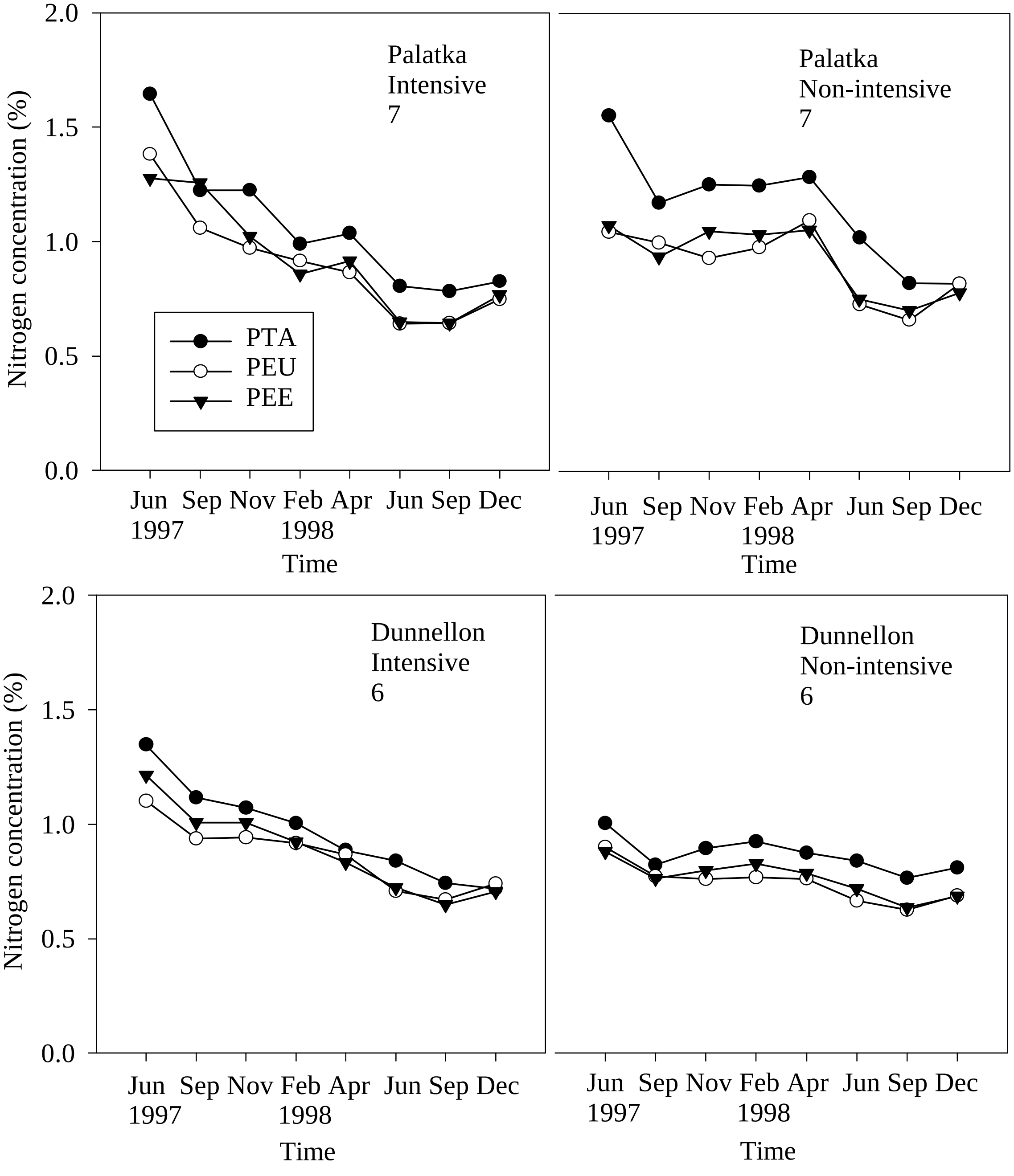

Figure 3-1. Variation in needle N concentration for improved loblolly, improved slash and unimproved slash pine throughout a life cycle of a needle cohort managed under two silvicultural treatment and two locations in north central Florida.
PTA = improved loblolly pine, PEE = improved slash pine, PEU = unimproved slash pine. Integers listed below locations and treatments indicate the number of sampling periods out of eight where significant taxa differences were detected at the 95% confidence level using LSMEANS test of the MIXED procedure.

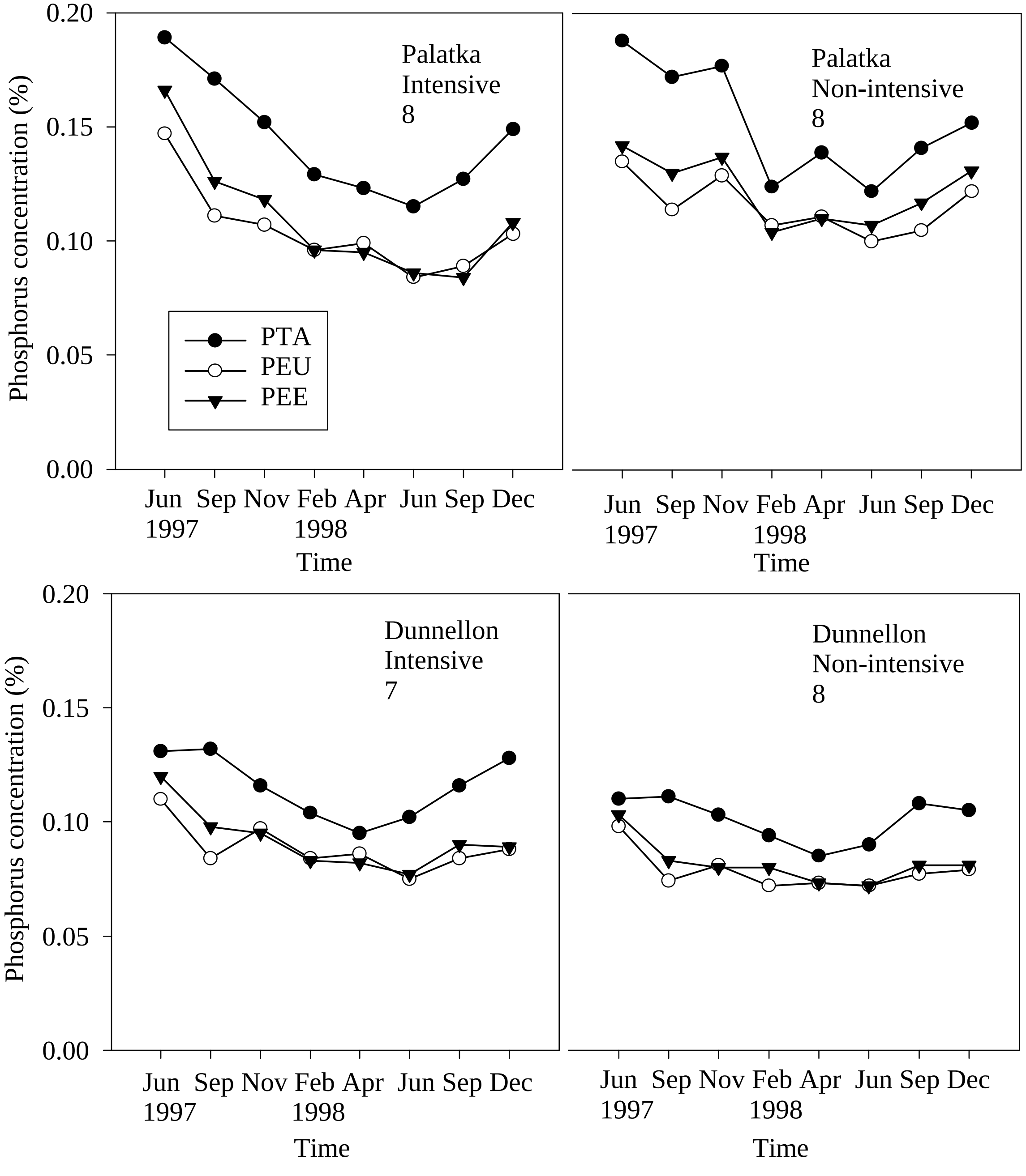

Figure 3-2. Variation in needle P concentration for improved loblolly, improved slash and unimproved slash pine throughout a life cycle of a needle cohort managed under two silvicultural treatment and two locations in north central Florida.

PTA = improved loblolly pine, PEE = improved slash pine, PEU = unimproved slash pine. Integers listed below locations and treatments indicate the number of sampling periods out of eight where significant taxa differences were detected at the 95% confidence level using LSMEANS test of the MIXED procedure.

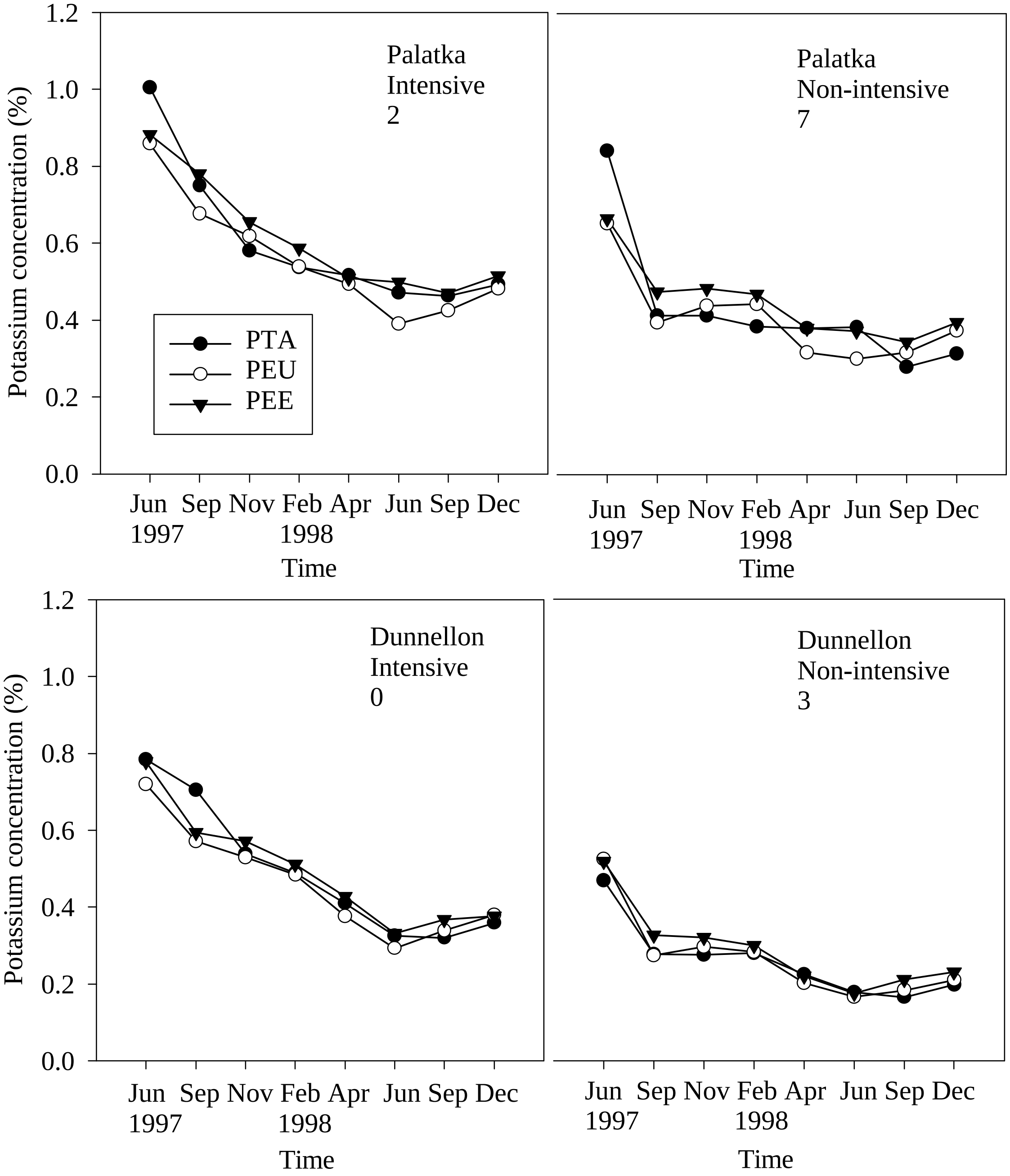

Figure 3-3. Variation in needle K concentration for improved loblolly, improved slash and unimproved slash pine throughout a life cycle of a needle cohort managed under two silvicultural treatment and two locations in north central Florida.

PTA = improved loblolly pine, PEE = improved slash pine, PEU = unimproved slash pine. Integers listed below locations and treatments indicate the number of sampling periods out of eight where significant taxa differences were detected at the 95% confidence level using LSMEANS test of the MIXED procedure.

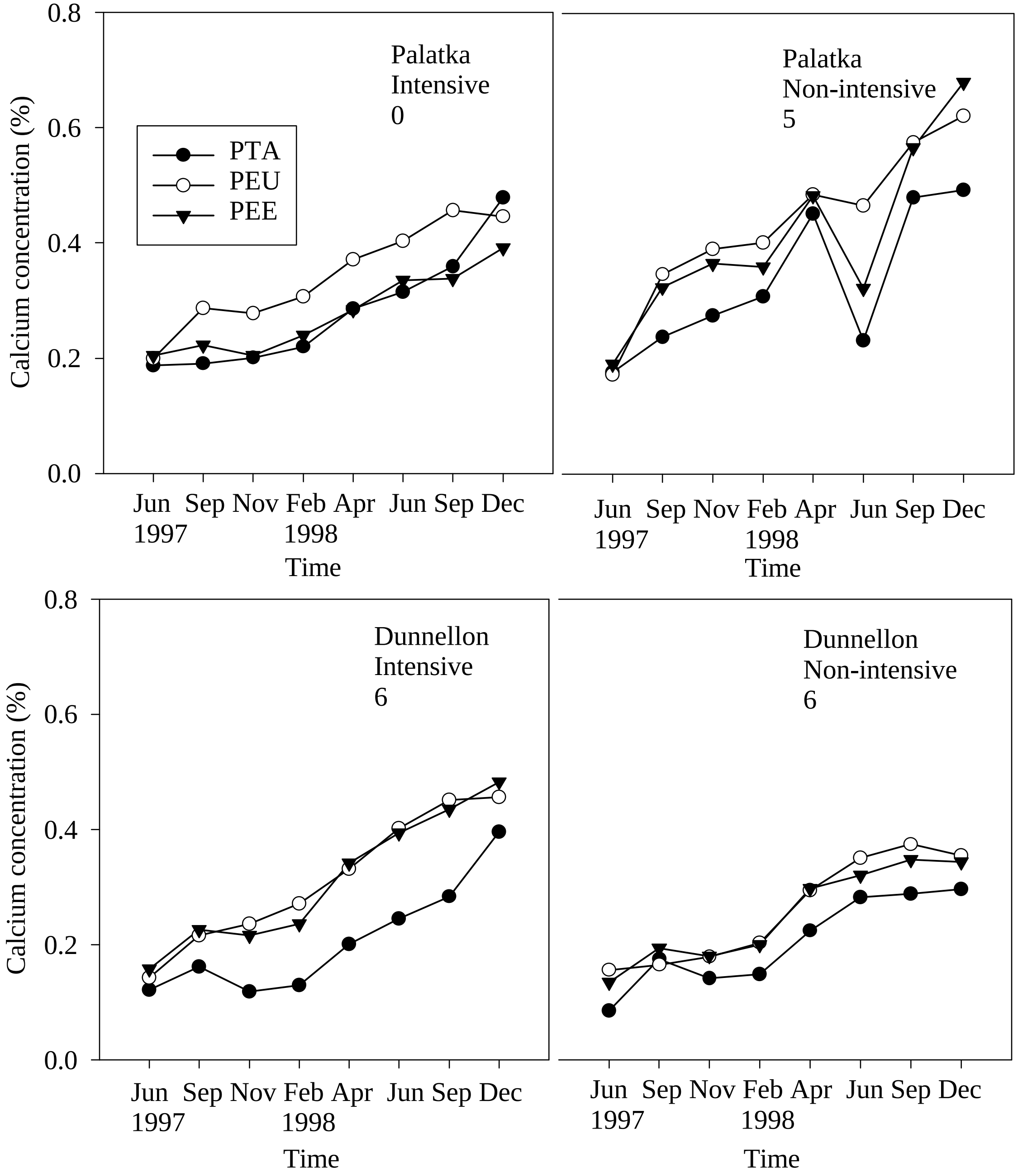

Figure 3-4. Variation in needle Ca concentration for improved loblolly, improved slash and unimproved slash pine throughout a life cycle of a needle cohort managed under two silvicultural treatment and two locations in north central Florida.

PTA = improved loblolly pine, PEE = improved slash pine, PEU = unimproved slash pine. Integers listed below locations and treatments indicate the number of sampling periods out of eight where significant taxa differences were detected at the 95% confidence level using LSMEANS test of the MIXED procedure.

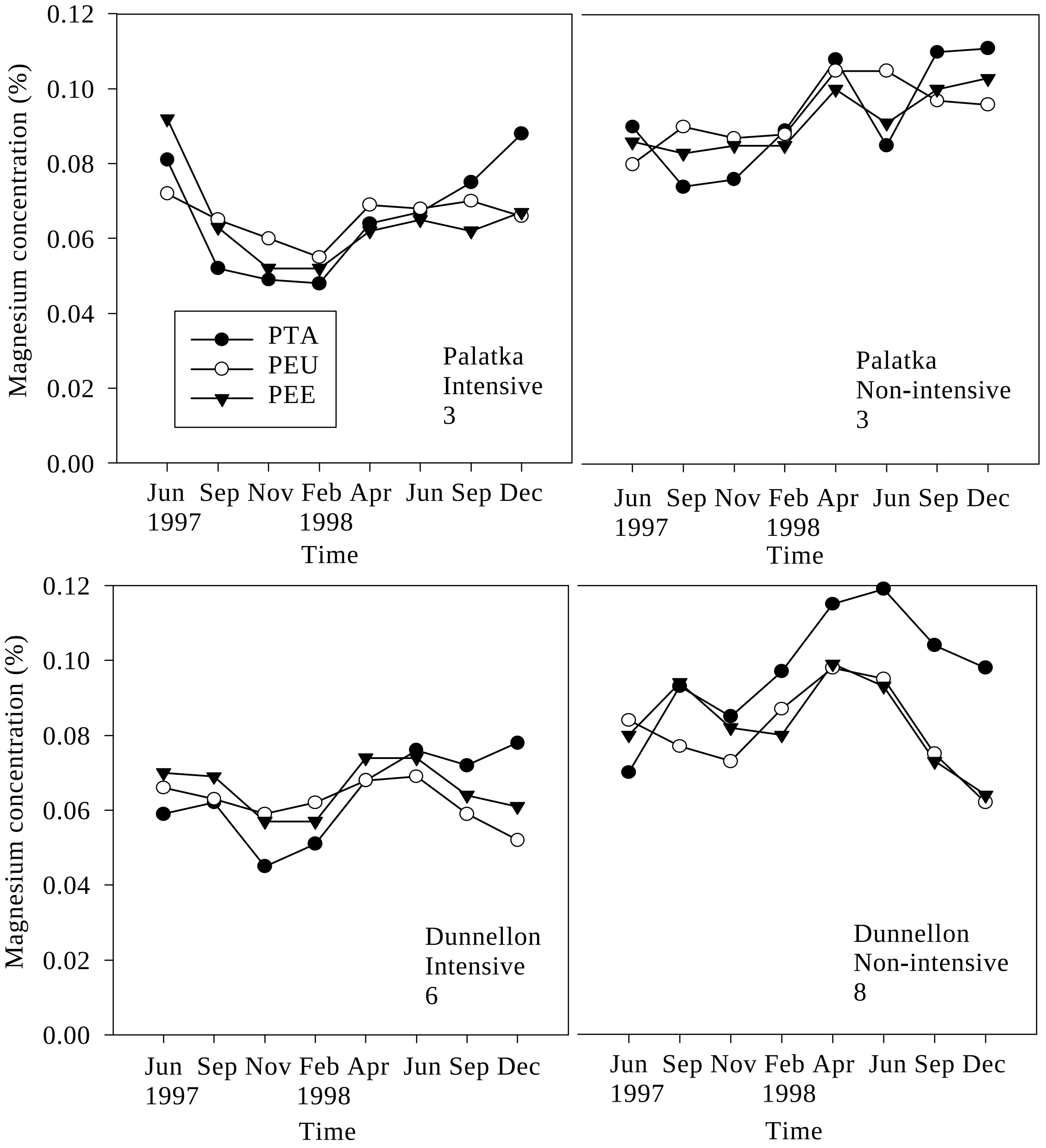

Figure 3-5. Variation in needle Mg concentration for improved loblolly, improved slash and unimproved slash pine throughout a life cycle of a needle cohort managed under two silvicultural treatment and two locations in north central Florida.

PTA = improved loblolly pine, PEE = improved slash pine, PEU = unimproved slash pine. Integers listed below locations and treatments indicate the number of sampling periods out of eight where significant taxa differences were detected at the 95% confidence level using LSMEANS test of the MIXED procedure.

3-1). Differences in nutrient concentrations for N and P between improved and unimproved slash pine were generally non-significant (Appendix D). Less significant differences among the three taxa occurred in K concentrations, except for the non-intensive treatment at the Palatka site (Figure 3-3). Differences among the three taxa and within a taxon were also highly variable for Ca and Mg concentrations. Each taxon had high concentrations in Ca and Mg at some period over the course of the experiment (Appendix E), although loblolly pine tended to have consistently lower Ca concentrations than slash pine at Dunnellon for both the intensive and non-intensive silvicultural treatments.

Both treatment and location generally affected the foliar concentrations of all the macronutrients except for P, where only minor treatment differences were found in 2 out of 8 sampling periods (Appendix D). Location × treatment interactions for foliar concentrations were significant under most sampling periods, showing differential responses among taxa to treatments across locations. Treatments generally did not significantly influence nutrient concentration differences between loblolly and slash pine. The significant treatment × taxa interactions were caused by differential treatment responses between improved and unimproved slash pine, with improved slash pine having lower nutrient concentrations under the non-intensive treatment, but higher concentrations under the intensive treatment compared to unimproved slash pine (Appendix E).

Differences in environmental factors at the two locations also significantly influenced nutrient concentrations in all taxa. Loblolly pine had consistently higher N and P concentrations than slash pine; thus, the significant location × taxa interactions for N and P were primarily caused by rank changes between improved and unimproved slash pine.

However, significant location × taxa interactions in K, Ca, and Mg were involved with rank changes among all three taxa. Loblolly pine had lower concentrations than slash pine for these nutrients during certain sampling periods, and was especially pronounced for Ca (Figure 3-3 to Figure 3-5).

A noticeable change in nutrient concentrations occurred during the final stage of the leaf life cycle, where concentrations of each element among the three taxa tended to converge within a location and treatment. ANOVA also showed that location × taxa interactions and treatment × taxa interactions for all elements (except in Mg) generally became non-significant during the later portion of the leaf life cycle among the three taxa (Appendix D and E).

Fascicle weight of loblolly pine was significantly lower than slash pine, regardless of locations and treatments; an exception occurred during the second sampling period for the intensive treatment at Dunnellon (Figure 3-6). Differences between improved and unimproved slash pine in fascicle weight were not significant (Appendix E). The intensive treatment significantly increased fascicle weight in all taxa, but did not change the rank between loblolly and slash pine. The significant treatment × taxa interactions found for some sampling periods were caused by interactions between improved and unimproved slash pine. Locations also exerted significant influence on fascicle weight, with 7 out of 8 periods showing statistically significant differences between the two experimental locations (Appendix D). Variation in local environments between locations also significantly induced significant location × taxa interactions in 5 out of 8 sampling periods. Additionally, treatment effects on fascicle growth were significantly different across locations in 7 sampling periods (location × treatment interactions were significant). Another noticeable and irregular change over the course of fascicle development occurred in the non-intensive treatment at the Palatka site, where fascicle weight decreased markedly in June 1998, more or less corresponding to the decrease in Ca and Mg concentrations during the same time period (Figures 3-4 to Figure 3-6). Severe drought conditions at Palatka from March to June, 1998 could have contributed to decreased fascicle growth under the non-intensive treatment where the crowns had not yet closed. Total rainfall during that period was only 2.5 mm, or about 6% of the precipitation typically received in a normal year. Trees grown under the intensive treatment may have avoided declines in fascicle growth by shedding lower branches (shaded) to compensate for low soil water availability.

Nutrient dilution can occur in plants when nutrient supply rates cannot match overall biomass accumulation rates. The lowest levels of foliar Mg and Ca concentrations were detected in the intensive treatment in September, following the end of the major portion of the growing season. Especially apparent were large differences in Mg concentrations between the intensive and non-intensive treatments for loblolly pine (Figure 3-7). Treatments obviously decreased needle Mg concentrations for all taxa, but were more severe in loblolly pine than in slash pine. For example, Mg concentrations for loblolly pine for the intensive treatment were well below the minimum critical level (0.07%) (Jokela et al. 1991), while Mg concentrations for slash pine were above the minimum levels. Loblolly and improved slash pine had lower Mg concentrations under both treatments at Palatka than at Dunnellon, while the reverse was true for unimproved slash pine. The dynamics of fascicle nutrient content over the leaf life cycle showed mixed patterns (Appendix F). Loblolly pine

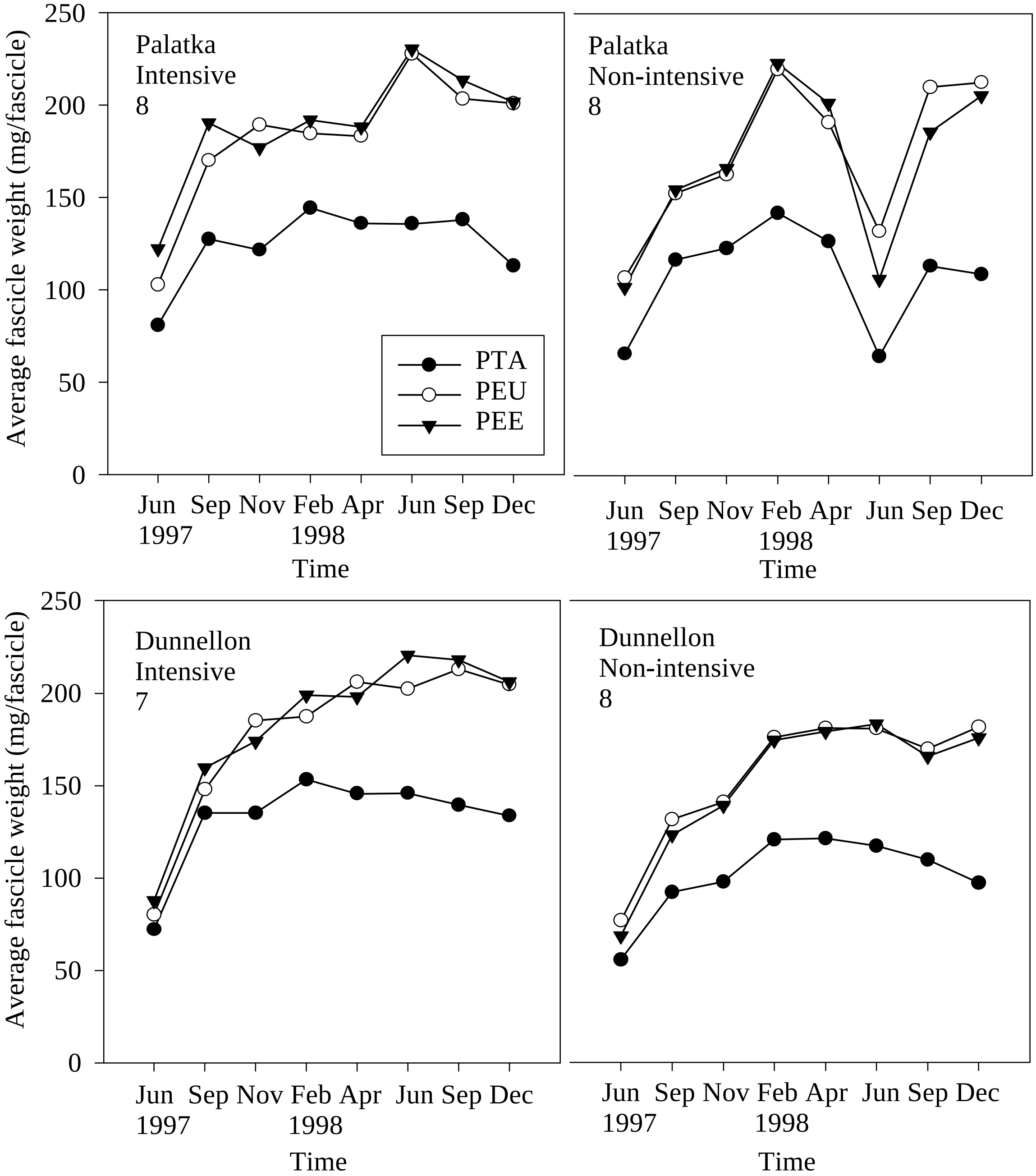

Figure 3-6. Variation in average fascicle weight for improved loblolly, improved slash and unimproved slash pine throughout a life cycle of a needle cohort managed under two silvicultural treatment and two locations in north central Florida.
PTA = improved loblolly pine, PEE = improved slash pine, PEU = unimproved slash pine. Integers listed below locations and treatments indicate the number of sampling periods out of eight where significant taxa differences were detected at the 95% confidence level using LSMEANS test of the MIXED procedure.

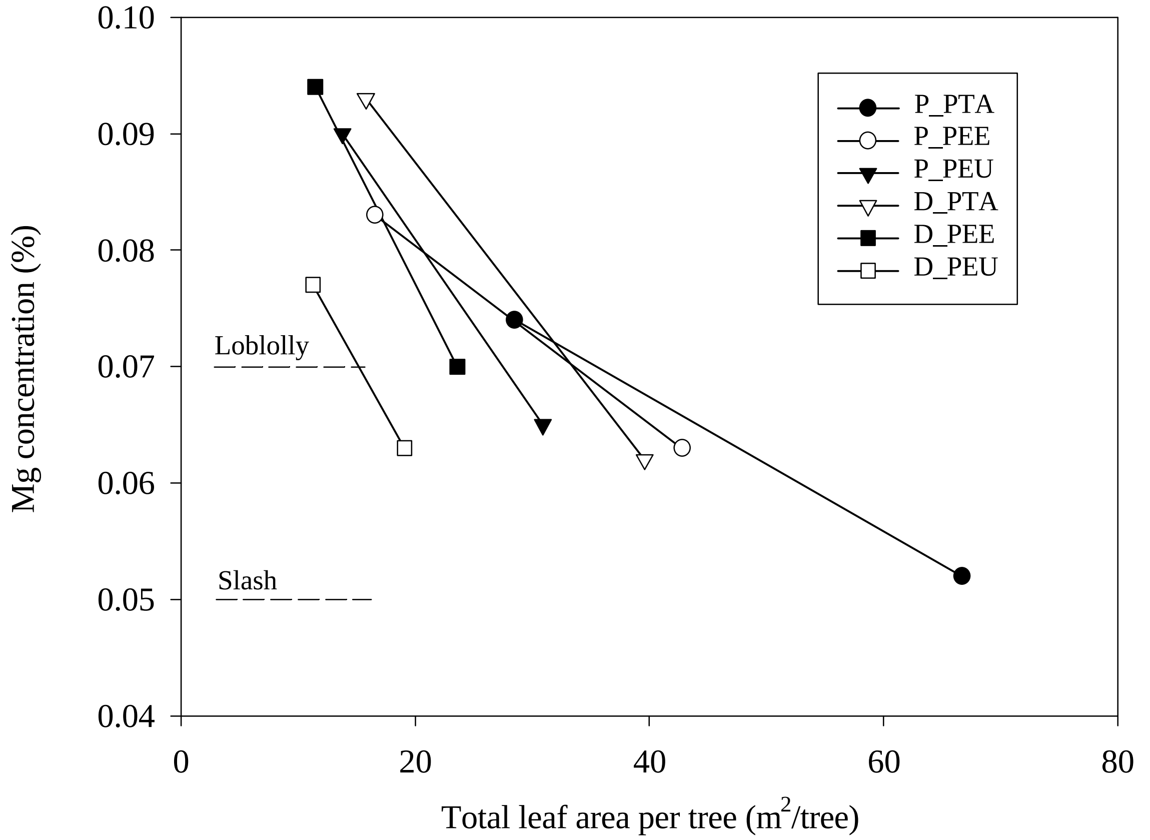

Figure 3-7. Relationships between total leaf area at age 3 years and September Mg concentration for genetically improved loblolly pine (PTA), improved slash (PEE) and unimproved slash pine (PEU) when managed under two silvicultural treatments at two locations in north central Florida. Symbols with higher Mg concentrations (i.e., lower leaf area) were from the non-intensively managed treatment, while those with lower Mg concentrations (i.e., higher leaf area) were from the intensively-managed treatment. The horizontal dashed lines represent critical (minimum) foliar Mg concentrations for loblolly pine (0.07%) and slash pine (0.05%). P = Palatka site, D = Dunnellon site.

generally had significantly lower fascicle nutrient content than slash pine for all elements at different sampling stages . Fascicle content for N, P, and K generally increased over time, peaked, and then decreased (N) or was maintained (P, K) at a steady state in all taxa. Magnesium content showed a similar pattern but peaked much later (after April of second growing season). On the contrary, Ca steadily increased in the fascicles, with the content reaching a maximum before leaf abscission (Appendix E). Analysis of variance was also performed on fascicle nutrient content, and results were similar to those revealed for nutrient concentrations and fascicle weight (Appendix D).

Crown (Leaf) Nutrient Content

Crown nutrient content depends on the accumulation of foliage biomass and leaf nutrient concentration. The amount of nutrients stored in the crown can affect crown development and growth performance. Significant effects of locations and treatments on crown nutrient content were found for all elements among the three taxa (Table 3-1). Trees grown at Palatka tended to accumulate significantly greater amounts of nutrients in the crown than those at Dunnellon when managed under the same silvicultural treatment (Table 3-2).

Differences among taxa in crown nutrient content were statistically significant under most circumstances (Table 3-2). Loblolly pine accumulated significantly greater quantities of all nutrients than slash pine, except under the non-intensive treatment at Dunnellon. Although differences in crown nutrient content between improved and unimproved slash pine were not significant, improved slash pine consistently had higher absolute amounts compared to unimproved slash pine.

Table 3-1. ANOVA for crown nutrient content (g/tree) of loblolly and slash pine at age 3 years. Experimental trees were subjected to two levels of silvicultural treatments and planted at two locations in north central Florida[a].

Source of Variation	N	P	K	Mg	Ca
Location	***	***	***	***	***
Treatment	***	***	***	***	***
Taxa[b]:	***	***	***	***	***
PTA vs. PEE	***	***	***	***	**
PEE vs. PEU	**	**	**	***	**
Location*treatment	***	***	***	***	***
Location*taxa	***	***	***	NS	NS
Treatment*taxa	**	***	***	**	**
Family(taxa)	NS	NS	NS	NS	NS
Block(treatment)	NS	NS	NS	NS	**
Location*family(taxa)	NS	**	NS	NS	NS
Treatment*family(taxa)	NS	NS	NS	NS	NS
Taxa*block(treatment)	***	***	***	***	NS
Location*treatment*taxa	***	***	***	**	NS
Location*treatment* family(taxa)	NS	**	***	***	***

[a] For a given source of variation, main effects and interactions were significant at *** p # 0.01, ** p # 0.05, * p # 0.10. NS = not significant.

[b] PTA = improved loblolly pine
PEE = improved slash pine
PEU = unimproved slash pine

Table 3-2. Nutrient content (g/tree) in the crowns (foliage) of 3-year-old loblolly and slash pine managed under two silvicultural treatments and planted at two locations in north central Florida[a].

Location	Dunnellon						Palatka					
Treatment	Non-intensively managed			Intensively managed			Non-intensively managed			Intensively managed		
Taxa	PTA[b]	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU
Element[c]:												
N	7.9a	5.7a	5.7a	30.4a	17.1b	12.4b	22.6a	11.6b	10.2b	57.0a	39.5b	23.0c
P	1.1a	0.6b	0.5b	3.6a	1.7b	1.1b	3.4a	1.6b	1.2b	8.1a	4.0b	2.4b
K	2.6a	2.5ab	2.0b	19.6a	10.2b	7.7b	8.1a	5.9ab	4.1b	35.3a	24.6b	14.7b
Mg	0.9a	0.7ab	0.5b	1.6a	1.1b	0.8b	1.4a	1.0b	0.9b	2.3a	2.0a	1.4b
Ca	1.6a	1.4a	1.2a	4.3a	3.7ab	2.8b	4.5a	4.0a	3.5a	8.2a	6.9ab	6.0b

[a] Taxa means were analyzed by location and treatment separately. Means among the three taxa for a given variable followed by the same letter were not statistically significant at the 95% confidence level by comparing least square means using the MIXED procedure (SAS Institute 1996).

[b] PTA = improved loblolly pine
PEE = improved slash pine
PEU = unimproved slash pine

[c] Estimates of crown nutrient content were made in September, 1997.

Differences among taxa in crown nutrient content tended to be smaller under the non-intensive treatment than under the intensive treatment at both sites. Therefore, genetic differences among taxa were better expressed under the intensive treatment than under the non-intensive treatment, which led to the significant treatment × taxa interactions for all nutrients (Table 3-1). For example, crown N content at Dunnellon quadrupled, tripled, and doubled under the intensive treatment in comparison to the non-intensive treatment for loblolly, improved and unimproved slash pine, respectively (Table 3-2). Loblolly pine accumulated larger quantities of nutrients in the crown than slash pine under the intensive treatment, while differences among taxa were less pronounced under the non-intensive treatment at both sites for all elements.

Nutrient Use Efficiency of Leaf Area Production

Significant interspecific (species) and intraspecific (family) differences in LA_{NUE} were detected among the three taxa (Table 3-3). This index was calculated based on the leaf area development per unit nutrient accumulated from ages 3 to 4 years. Loblolly pine was significantly more efficient in using N, K, Mg, and Ca to develop leaf area than slash pine, while differences between improved and unimproved slash pine were generally not significant except for K use efficiency. Unimproved slash pine was most efficient in P use efficiency (Figure 3-8).

The intensive silvicultural treatment significantly decreased LA_{NUE} for N, P, and K in all taxa, regardless of differences in locations (Table 3-3). The most significant decrease was found in K use efficiency. When averaged across locations and taxa, K use efficiency decreased markedly from 19.2 cm^2/mmol under the non-intensive treatment to 9.6

Table 3-3. ANOVA for LA_{NUE} (cm^2 leaf area / mmol element) for loblolly and slash pine at age 3 years. Experimental trees were subjected to two levels of silvicultural treatments and planted at two locations in north central Florida[a].

Source of Variation	N	P	K	Mg	Ca
Location	***	***	***	***	***
Treatment	***	*	***	***	NS
Taxa[b]:	***	***	***	***	***
PTA vs. PEE	***	*	***	***	***
PEE vs. PEU	NS	***	***	NS	NS
Location*treatment	***	***	***	***	***
Location*taxa	NS	***	NS	***	***
Treatment*taxa	NS	NS	***	*	NS
Family(taxa)	*	**	NS	**	NS
Block(treatment)	NS	*	**	NS	NS
Location*family(taxa)	NS	NS	NS	NS	NS
Treatment*family(taxa)	NS	NS	NS	NS	NS
Taxa*block(treatment)	***	***	**	***	***
Location*treatment*taxa	***	*	***	NS	*
Location*treatment* family(taxa)	***	*	**	**	***

a For a given source of variation, main effects and interactions were significant at *** p # 0.01, ** p # 0.05, * p # 0.10. NS = not significant.

b PTA = improved loblolly pine
PEE = improved slash pine
PEU = unimproved slash pine

cm^2 /mmol under the intensive treatment. However, taxa responses to the silvicultural treatments were similar in N use efficiency, resulting in non-significant treatment × taxa interactions. Significant treatment × taxa interactions were detected in K use efficiency, but further analysis showed a scale effect instead of a rank change among taxa. For less mobile elements, the intensive silvicultural treatment significantly increased LA_{NUE} in Mg, but not in Ca.

LA_{NUE} was significantly influenced by location and location × treatment interactions (Table 3-3). The Dunnellon site had higher nutrient use efficiencies for all elements except Mg. For example, trees across all three taxa at Dunnellon were 30%, 47%, 45%, and 39% higher than those at Palatka for N, P, K, and Ca use efficiency for leaf area production, respectively. Treatments also showed varied influence on LA_{NUE} at different locations, as location × treatment interactions were highly significant for all elements. Apparently, nutrient use efficiencies for all elements among the three taxa were sensitive to environments, as also shown by the significant location × treatment × taxa and location × treatment × family(taxa) interactions.

Fascicle Nutrient Retranslocation Efficiency

Significant differences occurred in N, P, and K retranslocation efficiencies prior to senescence among taxa, while no differences were found in Mg and Ca retranslocation efficiencies (Figure 3-9). For instance, loblolly pine retranslocated about 45% of the fascicle N prior to abscission, while slash pine only retranslocated 28% during the same period. Differences between improved and unimproved slash pine in nutrient retranslocation were

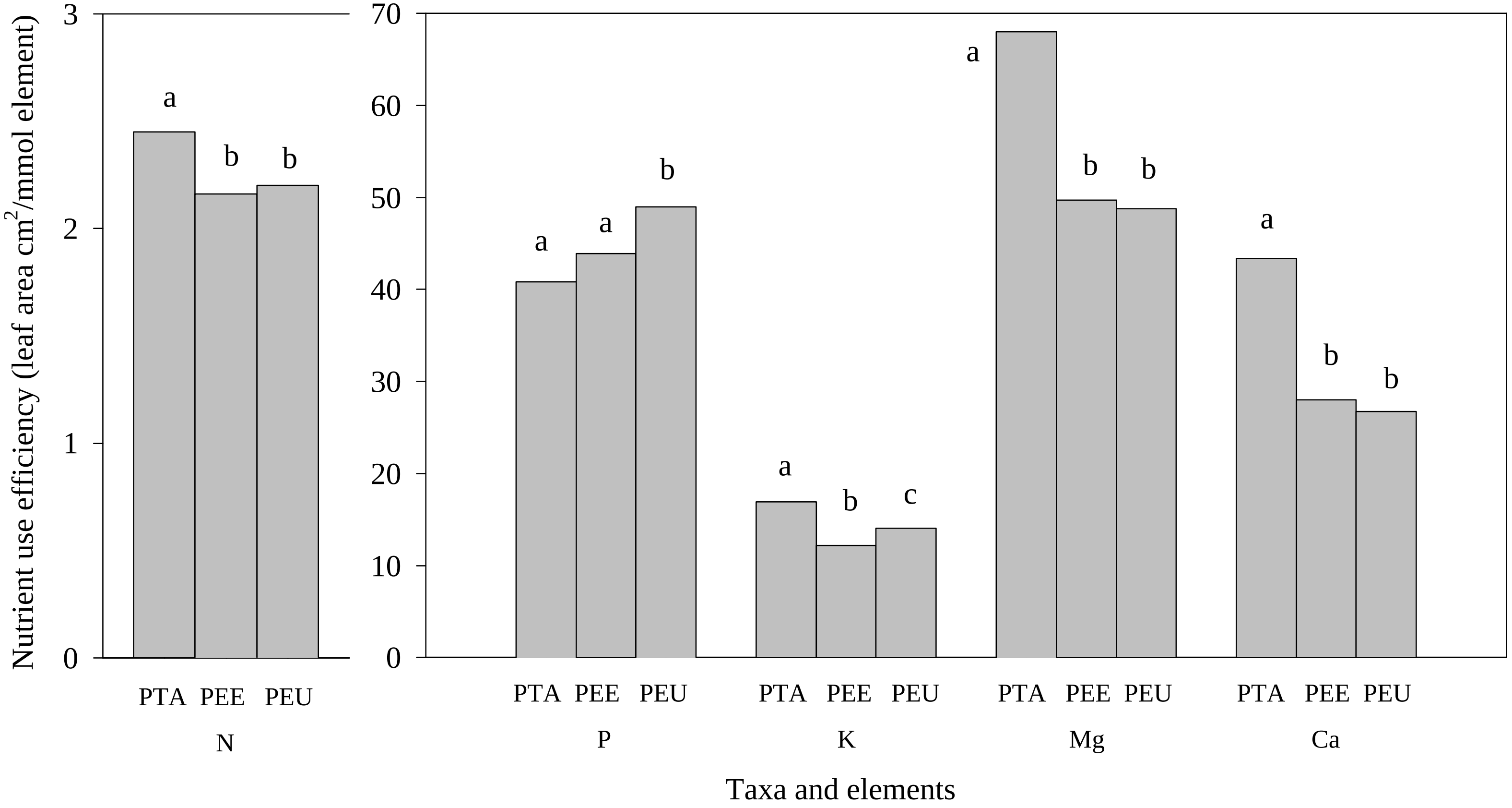

Figure 3-8. Nutrient use efficiency for leaf area development for genetically improved loblolly pine (PTA), improved slash (PEE) and unimproved slash pine (PEU) when managed under two silvicultural treatments at two locations in north central Florida. Means among taxa for a given nutrient followed by the same letter were not statistically significant at the 95% confidence level using the LSMEANS test of PROC MIXED. Note the different scales between N and other elements.

and unimproved slash pine in nutrient retranslocation were not significant, except for N. Large differences among taxa were found in K retranslocation efficiency, where loblolly pine retranslocated 48% of K, in comparison to 21% for improved and unimproved slash pine. Some loss of K from leaching could occur, which would lead to higher K retranslocation estimates.

The silvicultural treatments had no significant effect on nutrient retranslocation efficiencies for all taxa (Table 3-4). Differences among taxa for retranslocation efficiencies were primarily affected by location. The Palatka site had higher levels of nutrient retranslocation efficiency for N, P, K, and Ca than Dunnellon, while the opposite was true for Mg. Significant location × treatment interactions further indicated that location effects on nutrient retranslocation efficiencies (except K) were different across treatments. For example, N retranslocation efficiency in loblolly pine was higher under the intensive treatment (43%) than under the non-intensive treatment (35%) at Dunnellon, while it was higher under the non-intensive treatment (54%) than under the intensive treatment (48%) at Palatka. Slash pine showed a similar trend. In addition, although significant location × taxa interactions were found in retranslocation efficiencies for N, P, and Mg, the mode of influence was different. Scale effects were found in N retranslocation, with loblolly pine having the highest retranslocation efficiency and unimproved slash pine having the lowest. For P retranslocation, loblolly pine consistently had higher efficiencies than slash pine, while rank changes occurred between improved and unimproved slash pine. In Mg retranslocation, the highest efficiencies were found in each taxon at different locations and

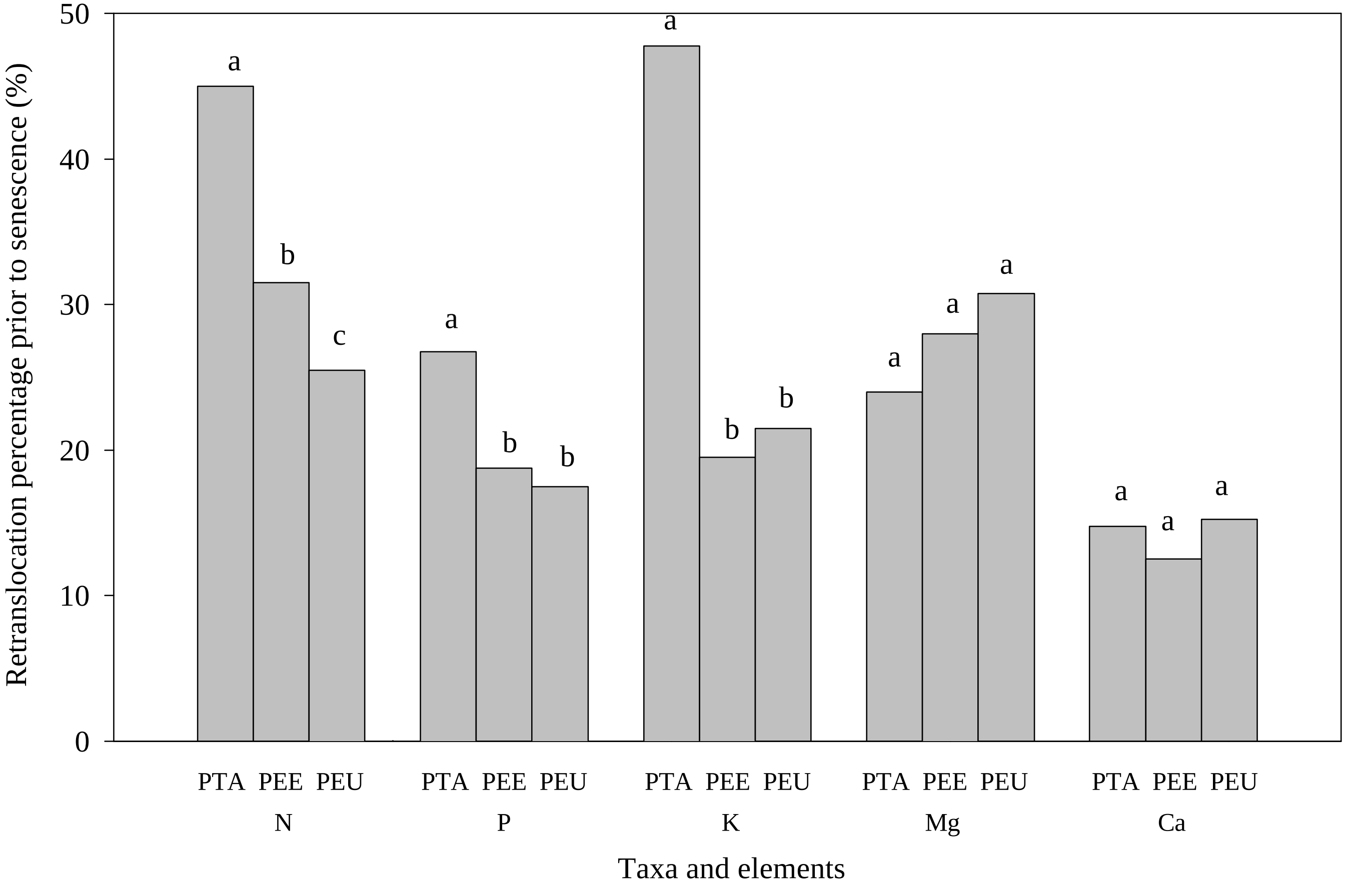

Figure 3-9. Nutrient retranslocation efficiency from fascicles of a single needle cohort prior to senescence for genetically improved loblolly pine (PTA), improved slash (PEE) and unimproved slash pine (PEU) when managed under two silvicultural treatments at two locations in north central Florida. Means among taxa for a given nutrient followed by the same letter were not statistically significant at the the 95% confidence level using the LSMEANS test of the MIXED procedure.

Table 3-4. ANOVA for nutrient retranslocation efficiency (%) and amount retranslocated (mg / fascicle) prior to senescence for a single cohort of needles in loblolly and slash pine at ages 3 to 4 years. Experimental trees were subjected to two levels of silvicultural treatments and planted at two locations in north central Florida[a].

Source of variation	Retranslocation efficiency (%)					Retranslocation amount (mg/fascicle)				
	N	P	K	Mg	Ca	N	P	K	Mg	Ca
Location	***	***	NS	***	**	***	***	***	***	***
Treatment	NS	NS	NS	NS	NS	**	**	***	**	NS
Taxa[b]:	***	***	***	NS	NS	**	NS	*	**	*
PTA vs. PEE	***	***	***	NS	NS	NS	NS	NS	**	*
PEE vs. PEU	**	NS	NS	NS	NS	**	NS	*	NS	NS
Location*treatment	***	**	NS	***	***	***	NS	NS	***	NS
Location*taxa	*	***	NS	***	NS	**	***	*	**	NS
Treatment*taxa	NS	NS	NS	*	***	NS	NS	NS	NS	*
Family(taxa)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

Table 3-4 -- Continued.

Source of variation	Retranslocation efficiency (%)					Retranslocation amount (mg/fascicle)				
	N	P	K	Mg	Ca	N	P	K	Mg	Ca
Block(treatment)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Loc*family(taxa)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Treatment*family(taxa)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Taxa*block(treatment)	***	***	***	***	***	***	***	**	***	***
Location*treatment*taxa	***	NS	NS	NS	NS	***	*	NS	NS	NS
Location*treatment* family(taxa)	**	*	*	NS	*	NS	*	NS	*	NS

a For a given source of variation, main effects and interactions were significant at *** p # 0.01, ** p # 0.05, * p # 0.10. NS = not significant.

b PTA = improved loblolly pine
PEE = improved slash pine
PEU = unimproved slash pine

treatments. Significant interspecific differences (except in P) were found in nutrient retranslocation amount per fascicle prior to needle senescence (Table 3-4). Although loblolly pine had much smaller fascicle weight than slash pine (Figure 3-6), it retranslocated more N, P, and K than slash pine. For example, when averaged across locations and treatments, loblolly pine retranslocated 0.80 mg N/fascicle, while improved and unimproved slash pine only retranslocated 0.73 and 0.58 mg N/fascicle prior to leaf abscission. However, slash pine retranslocated more Mg and Ca than loblolly pine. Further, significant effects of locations and treatments on nutrient retranslocation amounts were found, with the Palatka site and the intensive silvicultural treatment consistently having the highest amounts of nutrient retranslocation prior to leaf senescence.

Discussion

Dynamics of Macronutrients in the Foliage Life Cycle

Temporal and spatial variation in fascicle nutrient concentrations and content reflects periodically different growth demand for nutrients. Cyclic changes in weather conditions affect growth rates and nutrient demands (Miller 1966). Consequently, growth rates of forest stands and foliage nutrient levels are closely correlated in some species (Mahendrappa and Salonius 1982). Seasonal variations in foliage nutrient levels have been reported for many woody plants, such as *Quercus alba* and *Hamamelis virginiana* (Boerner 1984; 1985), *Juglans regia* (Drossopoulos et al. 1996), loblolly pine (Miller 1966; Zhang and Allen 1996), *Pinus strobus* and *Picea glauca* (Munson et al. 1995). However, most previous studies with coniferous species have reported annual variation in nutrient levels for different age classes of needles rather than following a complete life cycle of a specific needle cohort over time. Such information could prove useful in understanding the dynamics of foliar nutrient levels and the possibility of timing fertilizer applications.

Statistical analyses revealed that significant differences between treatments and among taxa occurred in foliar nutrient levels (Appendix D and E). Fertilizer treatments generally increased needle N and K concentrations, decreased needle Ca and Mg concentrations, and had no significant effect on P concentrations over most sampling periods for the three taxa. These results contradict what was found for N and K concentrations between sites with different levels of fertility in *Quercus prinus*, *Q. alba*, and *Acer rubrum* (Boerner 1984), but were similar to those reported for loblolly pine managed under different fertilizer regimes (Zhang and Allen 1996). Although loblolly pine had significantly higher concentrations of N, P, and K than slash pine for most sampling periods, growth rates (DBH and height) measured at this early stage of stand development showed no significant differences between species (Chapter 2). However, differences in crown biomass between loblolly and slash pine were significant, suggesting that growth strategies between the two species may be different. Loblolly pine may initially invest more nutrients in crown development than slash pine, while slash pine may use more nutrients in direct growth of DBH and height.

Fascicle Nutrient Content and Crown Nutrient Content

Fascicle nutrient content represents total accumulation of nutrients over a period of time, and has been used as an indicator of nutrient status when assessing tree growth responses from fertilization (Weetman and Fournier 1982). In comparison with fascicle nutrient content at the time when needles were fully-elongated (June 1997), K was the only nutrient that showed continuous decreases in fascicle content throughout the leaf life cycle at both locations and treatments. Other nutrients generally accumulated in fascicles throughout the leaf life cycle, being especially apparent for Ca and Mg (Appendix E). Fascicle weight also increased from the beginning, peaked, then slightly decreased toward the end of the needle cohort life cycle regardless of locations and treatments. For most sampling periods across locations and taxa, fascicle weight was higher under the intensive treatment than the non-intensive treatment, indicating a significant response to fertilization. Valentine and Allen (1990) proposed that fascicle weight was a better indicator than nutrient concentration in assessing growth responses from fertilization in loblolly pine. Zhang and Allen (1996) suggested that nutrient deficiencies were often associated with increases in both fascicle weight and nutrient concentration following fertilization. Their argument appears correct only if we consider the growing season within a year. For example, in the current study, N, P, and K fertilizers were applied in the intensively-managed blocks only. Trees grown in the intensive treatment at Palatka had higher N and P concentrations during the growing season, but lower concentrations at other times compared to the non-intensive treatment.

Nutrient balance is widely viewed as an important factor affecting plant growth. Dilution in Mg and Ca concentrations across locations were observed over most sampling periods. Because of possible antagonism and interactions between K and Mg, higher K concentrations could result in an induced Mg deficiency. The K/Mg and K/Ca ratios are thus commonly used as DRIS (Diagnosis and Recommendation Integrated System) norms when examining plant nutrient balance (Jones et al. 1991). The declines in Mg and Ca concentrations following fertilization were likely caused by high K concentrations. For example, at Dunnellon the loblolly pine K:Mg ratios in September, 1997 were 100:32 in the non-intensive treatment and 100:9 in the intensive treatment which included K fertilization. Dilution in foliar Mg and Ca concentrations could lead to growth declines if soil supply is inadequate to meet plant demands. Interpretations based solely on nutrient concentrations, however, can lead to incorrect diagnoses and well-designed fertilizer trials involving Mg and Ca applications would be necessary to confirm deficiencies.

Foliage nutrient content in the crown characterizes both leaf biomass accumulation and nutrient concentrations. Silvicultural treatments can significantly increase foliage nutrient content if leaf biomass and nutrient concentrations respond positively to fertilization. However, species may have differential growth responses to enriched environments. Significant differences in crown nutrient content responses to fertilization among genetically improved loblolly, improved slash and unimproved slash pine were found in this study (Table 3-3). In a related study, slash pine was less responsive to fertilization than loblolly pine in volume production and biomass accumulation (Colbert et al. 1990; Jokela et al. 2000). However, improved slash pine tended to be more responsive to fertilization in accumulating certain crown nutrients at this early growth stage compared to loblolly pine. For example, slash pine responded to fertilization with a 3.4:2.5:4.2 times increase in crown N:P:K content, respectively, but a 2.5:2.4:4.4 times increase in crown N:P:K content, respectively, for loblolly pine at the Palatka site was noted. This further indicated that slash pine was less efficient than loblolly pine in nutrient utilization since growth responses in DBH and tree height to fertilization at the same site did not differ significantly between improved slash and loblolly pine (Chapter 2).

Nutrient Use Efficiency of Leaf Area Production

Nutrient use efficiency has been used in several ways to study nutrient cycling, ecosystem functioning and site fertility (Vitousek 1982; Kost and Boerner 1985; Knops et al. 1997). In the current study, we defined nutrient use efficiency as peak leaf area production per unit of nutrient accumulation in current-year foliage. In this case we assumed that the effects of nutrients on growth rates were primarily realized via their direct influence on leaf area development. Because leaf area was closely associated with volume growth in the three taxa (Chapter 2), LA_{NUE} as defined in this study could be a valuable discriminator for understanding inter- and intra-specific growth strategies in southern pines.

Higher soil fertility has generally been associated with lower nutrient use efficiency for biomass production. For example, N and K use efficiency were higher, but P use efficiency was lower in less fertile soils for *Fagus sylvatica* (Minotta and Pinzauti 1996). Phosphorus and Ca use efficiency was higher on infertile sites for *Hamamelis virginiana* (Boerner 1985) and *Cornus florida* (Kost and Boerner 1985), and fertilization reportedly decreased N use efficiency for *Pinus resinosa* (Elliott and White 1993). Mixed results regarding treatment effects on LA_{NUE} were found for the three taxa across locations in this study. Fertilizer treatments decreased K and Mg use efficiency at both sites. However, the treatments decreased N, P, and Ca use efficiency at Dunnellon, but increased them at Palatka. These results suggest that changes in LA_{NUE} across treatments may be related to differences in growth responses due to fertilizer additions. A previous study showed that trees grown at Palatka were more responsive to fertilizer treatments than at Dunnellon (Chapter 2). Additionally, examinations of LA_{NUE} of a single element may not fully characterize the nature of growth responses to site fertility, since some nutrients can compensate for functions in plant metabolism (Jones et al. 1991).

Significant differences in LA_{NUE} between loblolly and slash pine further highlighted different growth characteristics between these two species. Nutrient use efficiency has been suggested as the inverse of nutrient concentrations in plant tissues (Chapin 1980) or aboveground litterfall (Vitousek 1982). Hence, nutrient use efficiency should be negatively related to nutrient concentrations. However, the consistently higher LA_{NUE} and higher nutrient concentrations found in loblolly pine compared to slash pine suggested that these general relationships may not always hold true. Although loblolly pine had lower P use efficiency than slash pine, it had significantly higher nutrient use efficiencies for all other elements. Lower P use efficiency in loblolly pine was compensated for by higher LA_{NUE} in other elements, and higher P concentrations in the needle without significantly reducing growth rates.

Nutrient Retranslocation Efficiency

Various interpretations associated with the importance of nutrient retranslocation on plant growth have been proposed in the literature (Nambiar and Fife 1991). For example, Johnson et al. (1982) suggested the importance of retranslocation as a nutrient conservation mechanism on low fertility soils. However, nutrient uptake, utilization, and retranslocation represent three important processes that influence plant nutrient supply and growth. Nutrient retranslocation is closely related to nutrient uptake and utilization since interactions among these processes can compensate for one another to a certain degree in meeting plant growth requirements (Baruah and Ramakrishnan 1988). For example, nutrient retranslocation may become an important process for meeting plant growth demands when energy expenditure for nutrient uptake exceeds that for remobilization, or when nutrient demands are high but uptake cannot meet requirements. Therefore, nutrient retranslocation is not only associated with leaf senescence during the later stages of foliage development in conifers, but it can also occur at any time during the year.

Reich et al. (1995) reported that 43% of N and 62% of P were retranslocated prior to leaf abscission in 13 woody species in an Amazonian forest. About 47% of N was retranslocated from fascicles of loblolly pine prior to leaf abscission in the current study, which was less than that reported (75%) in another study with loblolly pine (Zhang and Allen 1996). Similar to our results (Figure 3-9), Dalla-Tea and Jokela (1994) reported higher N retranslocation in stands of young loblolly pine (62%) compared to slash pine (57%). The current study showed that nutrient retranslocation also varied by locations and taxa, but at least 20% of foliage N, P, and K were retranslocated prior to abscission. Clearly, nutrients can be retranslocated from foliage regardless of leaf age class, based on growth demands and in relation to nutrient utilization and uptake.

Nutrient retranslocation represents an important physiological process affecting growth of perennial trees, and it can be influenced by many factors. Significant differences between the two silvicultural treatments were not found in retranslocation efficiency for the five nutrients in all taxa across locations. However, the intensive silvicultural treatment increased N, P, and K retranslocation, but decreased Mg and Ca retranslocation prior to leaf abscission when averaged across locations and taxa. Such results suggest that N, P, and K retranslocation for loblolly and slash pine may not be oriented toward nutrient conservation because the fertility gradient imposed in this study had no significant effects on nutrient retranslocation. Similar results of retranslocation responses to fertilization were also reported for these nutrients in loblolly pine (Zhang and Allen 1996) and N in *Ceratonia siliqua* (Correia and Loucao 1997). Related studies indicated that fascicle percent N retranslocated was not influenced by N availability, but total N retranslocated from the stand increased with soil N availability in loblolly pine (Birk and Vitousek 1986). These findings further demonstrate that growth demand for nutrients and annual physiological cycles of growth are two important factors affecting nutrient retranslocation rates in conifers.

Summary

Fascicle macronutrient (N, P, K, Mg, Ca) concentrations, content, utilization efficiency, and retranslocation were assessed throughout a complete life cycle of foliage in 3 to 4 year-old genetically improved loblolly pine, improved and unimproved slash pine managed under two levels of silvicultural treatments at two locations in north central Florida. Foliage concentrations of N, P, and K decreased, while Mg and Ca concentrations increased over the 2-year period. Loblolly pine consistently had higher N and P concentrations than slash pine at any time period, but mixed results were found in K, Mg, and Ca concentrations regarding differences among the three taxa. Slash pine had higher fascicle weight and fascicle nutrient content than loblolly pine at most sampling periods. Loblolly pine also had significantly higher LA_{NUE} (except in P), total crown (foliage) nutrient content, and nutrient retranslocation efficiency prior to leaf abscission (except for

Mg and Ca) than slash pine. Taxa differences for all nutrient characteristics were smaller under the non-intensive treatment than under the intensive treatment at both sites, indicating that stronger expression of genetic differences resulted in a higher fertility environment.

Silvicultural treatment (primarily fertilization) significantly increased fascicle weight, foliage nutrient content, and amount of nutrients retranslocated, but did not significantly affect nutrient retranslocation efficiency (percent nutrient retranslocated from fascicles). Fertilization increased foliar N and K concentrations, decreased Mg and Ca concentrations, but had no significant influence on P concentrations for most sampling periods in all taxa. The silvicultural intensive treatment significantly decreased N, P, and K use efficiency, but increased Mg and Ca use efficiency. Dilution in Mg and Ca concentrations following fertilization may have resulted from rapid leaf area development and antagonistic interactions with K.

$$\begin{aligned} \mathrm{LA_{NUE}}\ (\mathrm{cm}^2/\mathrm{mmol}) &= \frac{\text{Current - year peak leaf area production } \times \mathrm{AW}}{\text{Total nutrient content incorporated in current - year foliage } \times 1000} \\ &= \frac{\text{Current - year foliage biomass } \times \ \mathrm{SLA} \times \mathrm{AW}}{\text{Current - year foliage biomass } \times \ \mathrm{CONC} \times 1000} \\ &= \frac{\mathrm{SLA} \times \mathrm{AW}}{\mathrm{CONC} \times 1000} \end{aligned}$$

where SLA is specific leaf area (cm^2/g), AW is the atomic weight of each element (g/mol), and CONC is the concentration of each nutrient (%).

(back)

CHAPTER 4
GENETIC PARAMETER ESTIMATES FOR CROWN STRUCTURAL AND GROWTH CHARACTERISTICS IN JUVENILE LOBLOLLY AND SLASH PINE

Introduction

Genetic parameters (e.g., heritability, genotype × environment interaction, genetic correlation) have been widely used in making tree breeding and deployment decisions and in predicting breeding values and genetic gain from selection efforts (White 1996). Traits that are easily measured and have high heritabilities are desirable because more genetic gain can be effectively achieved in tree improvement programs. Assessing the magnitude of genotype × environment interactions is also critical to the formation of breeding populations in that low genotype × environment interactions suggest use of a single breeding unit, while high genotype × environment interactions imply that multiple breeding units are needed. In practice, a trait with high heritability and positive genetic correlation with other important traits is desirable because it can be included in a selection program to achieve gains for multiple traits (Haapanen et al. 1997). Thus, for all breeding programs it is important to understand the genetic architecture of the breeding population, which requires precise estimates of: (1) heritabilities and genotype × environment interactions for all traits; and (2) genetic correlations among traits.

Most efforts in the past have been directed at estimating genetic parameters of traits related to volume production and timber quality (Belonger et al. 1996). While it appears that genetic variation exists in some crown structural, morphometric or growth traits at different levels (e.g., leaf, branch, crown) in several species (El Kassaby and Park 1993; St. Clair 1994b; Wu 1994), there is much less information about genetic architecture for the myriad underlying morphological and physiological traits that influence growth performance. Future progress in forest tree improvement programs requires genetic knowledge of these underlying component traits and their effects on volume production for the following reasons: (1) it is important to understand how selection for volume growth affects the component traits to ensure that they are changing in a desired manner; (2) future progress in classical tree improvement programs could be enhanced by selecting for the component traits instead of the aggregate trait of growth; and (3) future applications of biotechnology will require a thorough understanding of the underlying mechanisms controlling commercially-important traits such as growth. For example, higher narrow-sense heritability estimates for several biomass components in Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) suggest that selecting families with favorable partitioning of biomass to stem wood would improve stand productivity (St. Clair 1994a).

The ideotype concept has been proposed for some tree improvement programs (Dickmann 1985; Kärki and Tigerstedt 1985; Martin et al. 2001). Ideotype breeding is a method to improve genetic growth potential by modifying individual morphological, physiological, or phenological characteristics, resulting in a specification of a model plant for potential traits. Breeding for an ideotype requires understanding the genetic architecture of the component traits that control the aggregate traits. This allows breeders to target certain morphological or physiological traits that have significant genetic relationships with growth as indirect selection criteria (Fakorede and Mock 1978).

At present, limited information is available on the heritability and genetic variation of the component traits underlying growth in loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm. var. *elliottii*), the two most important species in the southeastern United States. Since the 1950's tree improvement programs have made substantial progress in improving tree growth (Lowerts 1986; Hodge et al. 1989; 1990). Genetic architecture is thus well known for aggregate growth traits such as height, DBH, and volume (Dieters et al. 1995). However, much less work has been done to understand component traits controlling overall growth (Bridgwater et al. 1985; Williams 1987; Bridgwater 1990). It is critical to understand genetic control of underlying phenological, morphological, and physiological traits controlling growth to allow tree breeding programs and biotechnology efforts to utilize this information.

This study was designed to determine the genetic architecture and genetic parameter estimates of selected growth and crown structural characteristics in loblolly and slash pine in the southeastern United States. The specific objectives of this study were to (1) estimate heritabilities of growth and crown structural traits as references for loblolly and slash pine breeding programs and to evaluate the relative genetic control vs. environmental influence on these traits; (2) evaluate genotype × environment interactions for each growth and crown structural trait; and (3) examine genetic and environmental variances and correlations among selected traits across locations and silvicultural treatments to better understand relationships between growth and crown characteristics.

Materials and Methods

Experiments and Sampling Description

This study was part of an existing large series of experiments designed by the University of Florida's Cooperative Forest Genetics Research Program to test growth performance of several pine taxa and their hybrids in relation to location and intensity of silvicultural treatments (Lopez-Upton 1999). The two field sites utilized were in north central Florida (Dunnellon, Levy County, 29°20' N, 82°50' W and Palatka, Putnam County, 29°40' N, 81°42' W). The climate for each location is humid, temperate with a mean annual temperature of 21°C. Annual precipitation averages 1,332 mm at Dunnellon and 1,368 mm at Palatka. The nearly level landscape is underlain by soils classified as sandy, siliceous, hyperthermic Aeric Alaquods (somewhat poorly drained, Smyrna series) at Dunnellon and hyperthermic, uncoated Aquic Quartzipsamments (moderately well drained, Adamsville series) at Palatka (Soil Survey Staff 1998). The site indices for the Smyrna and Adamsville series were 19 m and 20 m (base age 25 years), respectively.

Sixteen open-pollinated families from each of three pine taxa (genetically improved loblolly pine, and improved and unimproved slash pine) were planted at both sites in a five-tree row plot in each of three complete blocks using a split-split plot experimental design. Two levels of silvicultural treatments (intensive vs. non-intensive) were applied. Prior to study establishment, each site was chopped and bedded. Understory vegetation in the intensive silvicultural treatment blocks was controlled during the first growing season using a combination of mechanical and pre- and post-plant directed spot spray applications of glyphosate applied at labeled rates. Containerized seedlings were planted in December 1994 at a 1.5 m × 3.4 m spacing at Palatka, and a 1.8 m × 3.0 m spacing at Dunnellon. Fertilizers were broadcast applied in the high intensity treatment during years 1 and 3 as a balanced mix of macro- and micronutrients. Total elemental application rates for plots receiving fertilizer additions at both locations were approximately (kg ha^{-1}): N (110), P (80), K (162), Ca (20), Mg (10), S (13), Fe (0.5), Zn (0.06), Mn (0.5), Cu (0.06), and B (0.06). Insecticides (Asana, Diomethorate or Pyridine) were applied 3-4 times during the first growing season to control tip moth (*Rhyacionia* spp.) on the high intensity treatment. The low intensity treatment did not receive herbicide, fertilizer or insecticide applications. An untreated buffer of at least 21 m separated the high and low intensity treatment.

Two sample trees from each five-tree row plot of sixteen families per taxon were randomly chosen in July 1997. Overall, across the two sites, 1,152 trees (2 sites × 2 treatments × 3 blocks × 3 taxa × 16 families × 2 trees) were measured for DBH, total height, crown height, and crown width. Additionally, branch position, branch diameter, and branch angle for each branch were recorded along the entire stem of each tree. Outside-bark volume was calculated using the following formula (Hodge et al. 1996; Sierra-Lucero 1999):

$$\text{VOL (m}^3\text{/tree)} = 0.25 \times 3.14 \times (\text{DBH})^2 \times (1.37 + 0.33 \times (\text{HT} - 1.37))$$

where VOL, DBH, and HT were estimated volume, diameter at breast height, and total tree height, respectively.

In late July 1997 (ages 3 years), 540 branches (2 locations × 2 treatments × 3 blocks × 3 taxa × 5 trees × 3 crown positions per tree) were destructively harvested from randomly selected trees (not identified by families) to develop biomass prediction equations for different crown components. In August 1997, a total of 5,760 foliage samples (2 locations × 2 treatments × 3 blocks × 3 taxa × 16 families × 2 ages × 1 trees × 3 positions [current year foliage] + 2 locations × 2 treatments × 3 blocks × 3 taxa × 16 families × 2 ages × 1 trees × 2 positions [old foliage]) were collected to determine all-sided specific leaf area by age class and crown position on 20 fascicles. Total all-sided leaf area per tree was calculated for each taxon as the product of August foliage biomass and specific leaf area (Chapter 2).

Statistical Analyses

To eliminate scale effects caused by heterogenous variances at different site locations and silvicultural treatments (Falconer and Mackay 1996), all variables were standardized by dividing each observation in a location-treatment-block combination by the corresponding square root of the phenotypic variance for that variable in that block (Visscher et al. 1991; Hodge et al. 1996; Lopez-Upton 1999).

Estimation of variance components

Two analyses (ANOVA) were conducted separately on loblolly and slash pine for each growth or crown structural variable. In the slash pine linear model, taxa differences between improved and unimproved slash pine were maintained as taxa effects. The statistical model for loblolly pine was the same as for slash pine with all of the taxa effects deleted (all effects with subscript l were not present in the loblolly pine linear model). The statistical model for slash pine was of the following form:

$$Y_{ijklmn} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + t_l + \alpha t_{il} + \beta t_{jl} + b_{k(ij)} + f_{m(l)} + \alpha f_{im(l)} + \beta f_{jm(l)} + bf_{k(ij)m(l)} + e_{ijklmn}$$

where Y_{ijklmn} is observation on tree n at family m of taxa l in block k of treatment j of location i,

$:$ is the population mean,

$"_i$ is the fixed effect of location (Dunnellon or Palatka),

$\$_j$ is the fixed effect of treatment (non-intensive or intensive),

$("\$)_{ij}$ is the fixed effect of location × treatment interactions,

t_l is the fixed effect for taxa (improved or unimproved slash pine),

$"t_{il}$ is the fixed effect for location × taxa interactions,

$\$t_{jl}$ is the fixed effect for treatment × taxa interactions,

$b_{k(ij)}$ is the random variable for block nested within location and treatment ~ NID (0, F^2_b),

$f_{m(l)}$ is the random variable for family nested within taxa ~ NID (0, F^2_f),

$"f_{im(l)}$ is the random variable for location × family (taxa) interactions ~ NID (0, $F^2_{"f}$),

$\$f_{jm(l)}$ is the random variable for treat × family (taxa) interactions ~ NID (0, $F^2_{\$f}$),

$bf_{k(ij)m(l)}$ is the random variable for block (location × treatment) × family (taxa) interactions ~ NID (0, F^2_{bf}),

e_{ijklmn} is the random error term ~ NID (0, F^2_e);

where i = 2 for locations, j = 2 for treatment levels, k = 3 for number of blocks, l = 2 for taxa, m = 16 for families per taxon, and n = 2 for trees per plot.

The SAS procedure PROC GLM was utilized to test the significance of random effects using the test option of the RANDOM statement which synthesizes approximate F tests via the Satterthwaite method when exact F tests are not available (SAS Institute 1996). PROC MIXED was used to test the fixed effects and to estimate variance components using the restricted maximum likelihood method (Littell et al. 1996; SAS Institute 1996). Non-significant effects were dropped from the original model such that only effects that were statistically significant at $\alpha = 0.05$ were maintained in the final models for both loblolly and slash pine. A total of 18 growth and crown structural traits were analyzed for each of the two species.

Estimation of genetic parameters

To better understand genetic structure and its relationship to growth performance and characteristics of crown structural traits, three types of parameters were estimated: heritability for each trait, genotype × environment interaction for each trait, and genetic and environmental correlations among traits. Variance components were obtained for all traits across sites and treatments using the SAS PROC MIXED procedure for heritability and genotype × environment interactions.

Narrow-sense heritability for each trait was calculated from analyses pooling data across sites and treatments, to correct upward bias due to the genotype × environment interaction in estimates from a single site or within a single treatment (Dieters 1996; Hodge and White 1992). The variance component for the half-sib families (σ^2_f) is interpreted as an estimate of one quarter of the additive genetic variance (σ^2_A). Thus, heritability for each trait in slash pine was calculated as follows based on the ANOVA model:

$$h^2 = \frac{4\sigma^2_f}{\sigma^2_f + \sigma^2_{bf} + \sigma^2_{\alpha f} + \sigma^2_{\beta f} + \sigma^2_e}$$

where all symbols were the same as those indicated in the ANOVA models. For loblolly pine, one more variance component for the location × treatment × family ($F^{2}_{"\$\mathrm{f}}$) interaction was added in the denominator when these were statistically significant. These terms were never significant for slash pine and were thus pooled with the random error term. The standard error for heritability estimates was calculated using a formula as described by Dickerson (1962).

Two types of genotype × environment interaction (i.e., family × site and family × treatment) were investigated separately for the two species and all 18 traits using the method originally developed by Yamada (1962), and widely used by others thereafter (Burdon 1977; Smith et al. 1993; Dieters et al. 1995):

$$r_{\text{B-treat}} = \frac{s^{2}_{\mathrm{f}}}{s^{2}_{\mathrm{f}} + s^{2}_{b\,\mathrm{f}}}$$

$$r_{\text{B-site}} = \frac{s^{2}_{\mathrm{f}}}{s^{2}_{\mathrm{f}} + s^{2}_{a\,\mathrm{f}}}$$

Estimates of the above type B genetic correlations can be used to evaluate the same trait measured in two different environments (two sites or two treatments) and to examine the stability or consistency of family growth performance and crown structural characteristics across these environments. It has been suggested that a value smaller than 0.67 for $r_{\text{B-treat}}$ or $r_{\text{B-site}}$ implies an important level of genotype × environment interactions (Shelbourne 1972).

Genetic and environmental correlations between two traits were estimated using the Multiple Trait Derivative-Free Restricted Maximum Likelihood (MTDFREML) software program (Boldman et al. 1995). Estimates of genetic correlation coefficients were based on the following formula:

$$r_G = \frac{\text{Cov (X, Y)}}{\sqrt{V_X \cdot V_Y}}$$

where Cov(X, Y) is the additive genetic covariance between two traits X and Y, V_X and V_Y are the additive genetic variances of traits X and Y. Environmental correlation coefficients were calculated similarly by substituting for the additive genetic covariance and variances with environmental covariance and variances, respectively.

Only selected growth and crown structural traits were analyzed for genetic and environmental correlations between two traits across sites and treatments. Selection of these traits was based on the following criteria for the two species separately: (1) moderate heritability estimates; (2) importance in characterization of growth and crown structure; and (3) high application potential in breeding programs.

Results and Discussion

Heritability Estimates

All heritability estimates for the 18 growth and crown structural characteristics in loblolly pine were low to medium (Table 4-1). Some variables, such as volume per tree and branch number per unit (meter) crown length in loblolly pine, had very low genetic variances such that the heritabilities tended to be zero. In particular, the estimates of h^2 =

0.00 for volume was lower than other estimates reported for loblolly pine (Sierra-Lucero 1999; Li et al. 1996) and may be due to (1) the small number of families (16) represented in this study; or (2) high genotype × environment interactions across sites or treatments.

Heritability estimates for slash pine were also low to medium, except those for total branch number and branch number per unit crown length (Table 4-1). Compared to loblolly pine, slash pine had higher heritabilities for volume, branch number, and leaf area measures, but lower heritabilities for crown structure and biomass components. The heritability estimate for volume ($h^2 = 0.12$) was similar to previous estimates at 5 years ($h^2 = 0.07$) from full-sib slash pine tests (Dieters et al. 1995), but lower than results ($h^2 = 0.23$) reported by Dieters (1996) for the wind-pollinated progeny tests of slash pine from ages 6 to 11 years. Generally, narrow-sense heritability estimates for growth factors including volume tend to be low (Cornelius 1994). Thus, these estimates for slash pine are in general agreement with heritabilities found for other species.

Crown structural traits were at least as heritable as growth traits (DBH, height) in loblolly pine. Crown shape ratio (crown length / crown width) had a high heritability estimate ($h^2 = 0.49$), which was very close to the heritability estimate for the same variable ($h^2 = 0.47$) reported by Foster (1986) for loblolly pine. Such results indicated that crown geometry in loblolly pine families showed substantial genetic variation that could be exploited. A similar high degree of inheritance for crown shape was also reported in *Coffea canephora* (Leroy et al. 1993), short-rotation *Populus* clones (Wu 1994), and *Pinus brutia* (Isik and Isik 1999), suggesting that crown form can be incorporated into tree improvement programs in some species, if desired.

Table 4-1. Narrow sense heritability (h^2) estimates and standard errors for growth and crown structural attributes in 3-year-old loblolly and slash pine planted at two locations in north central Florida.

Trait	Loblolly pine	Slash pine
Volume	0.00 ± 0.12	0.12 ± 0.10
Total branch number	0.09 ± 0.15	0.62 ± 0.26
Crown length	0.15 ± 0.16	0.06 ± 0.14
Crown width	0.23 ± 0.24	0.03 ± 0.08
Crown shape ratio	0.49 ± 0.24	0.08 ± 0.08
Height to base of crown	0.00 ± 0.05	0.13 ± 0.09
Branch number per unit crown length	0.00 ± 0.13	0.60 ± 0.21
leaf area per unit crown length	0.22 ± 0.24	0.18 ± 0.12
Current-year leaf biomass	0.14 ± 0.20	0.07 ± 0.10
1-year-old leaf biomass	0.08 ± 0.18	0.23 ± 0.13
Total leaf biomass	0.11 ± 0.19	0.12 ± 0.11
Branch biomass	0.13 ± 0.21	0.00 ± 0.08
Total crown biomass	0.15 ± 0.20	0.07 ± 0.10
Current-year leaf area	0.17 ± 0.22	0.19 ± 0.11
1-year-old leaf area	0.18 ± 0.21	0.32 ± 0.15
Total leaf area	0.25 ± 0.22	0.28 ± 0.12
Current-year specific leaf area	0.16 ± 0.58	0.00 ± 0.48
1-year-old specific leaf area	0.00 ± 0.78	0.00 ± 0.63

As for slash pine, less information regarding the inheritance of crown traits is available. Our preliminary results showed that total branch number per tree ($h^2 = 0.62$) and branch number per unit crown length ($h^2 = 0.60$) were highly heritable and could be considered as selection criteria. These heritability estimates for branch number were higher than previously reported results (h^2 = 0.26 to 0.40) for 1-year-old slash pine seedlings at two levels of silvicultural treatments (Smith 1992). Slash pine also had a lower heritability estimate (h^2 =0.03) for crown width than that of loblolly pine (h^2 = 0.23), which was probably one of the lower estimates when compared with results for Douglas-fir (h^2 = 0.25) (St. Clair 1993) and *Albizia lebbek* (h^2 = 0.24) (Toky et al. 1996). Crown geometry factors (crown width (h^2 = 0.03) and crown length (h^2 = 0.06)) in slash pine appeared less heritable than most growth factors (volume, DBH, and height), and are probably not promising for incorporation into tree improvement programs.

Total leaf area per tree and leaf area per unit crown length were heritable in both loblolly (h^2 = 0.25 and 0.22, respectively) and slash pine (h^2 = 0.28 and 0.18, respectively). St. Clair (1993) reported similar heritability estimates for leaf area measures in Douglas-fir and predicted about 15% genetic gain if leaf area was included in tree improvement programs. However, the drawback for considering leaf area in the selection criteria is that a large amount of field work must be conducted to obtain precise estimates.

Specific leaf area (SLA) has been widely used in ecology for characterizing plant populations and for linking and scaling from individuals to stands in ecosystem studies (Running and Gower 1991; Pierce et al. 1994). If the heritability for SLA is low, it suggests that SLA can be averaged for a single species and compared with that of other species in ecosystem studies. High heritability estimates may imply that the choice of families sampled would influence the species average. Specific leaf area varied significantly within different crown positions of loblolly and slash pine at ages 3 and 4 years (Chapter 2); however, heritability estimates for the two species were very low (h^2 = 0.00 to 0.16). Many studies have examined the intraspecific variation in SLA (Cannell et al. 1983; Magnussen et al. 1986; McCrady and Jokela 1996), but no heritability estimates have been provided for this attribute. Similar to our results, low specific leaf area inheritance ($h^2 = 0.08$) was also reported for Douglas-fir for different crown positions and individual trees as an average (St. Clair 1993). These results may suggest that SLA is primarily controlled by prevailing environmental factors.

<u>Genotype × Environment Interactions</u>

Type B genetic correlation parameters for family × site and family × treatment interactions were estimated for loblolly and slash pine (Table 4-2). Estimates for the family × site interaction can be used to examine consistency of family growth performance and development of crown structural attributes across site locations, while those for the family × treatment interaction can reveal family consistency across silvicultural treatments within a site. Generally, slash pine was more stable than loblolly pine in all the traits for family rankings across sites, indicating that family × site interactions were not important for most traits in slash pine (Table 4-2). For example, 13 out of 18 attributes in slash pine recorded $r_{B\text{-treat}} = 1.00$. Conversely, family × site interactions were important in loblolly pine, since most traits (except crown length, width, crown shape ratio, and current- year SLA) had estimates of $r_{B\text{-treat}}$ below the threshold level of 0.67 (Shelbourne 1972). This result suggests that different families of loblolly pine were sensitive to site changes in developing crown traits and partitioning biomass within the crown. Another reason for the differences observed between species could be experimental error due to the smaller family sample size used to derive estimates for loblolly (n=16) compared to slash pine (n=32).

Table 4-2. Family × site interaction ($r_{B\text{-site}}$), and family × treatment interaction ($r_{B\text{-treat}}$) for growth and crown structural attributes in 3-year-old loblolly and slash pine planted at two locations in north central Florida.

Trait	Loblolly pine		Slash pine	
	$r_{B\text{-site}}$	$r_{B\text{-treat}}$	$r_{B\text{-site}}$	$r_{B\text{-treat}}$
Volume	0.00	0.00	0.82	0.91
Total branch number	0.36	0.50	1.00	1.00
Crown length	1.00	0.39	1.00	0.39
Crown width	0.77	0.64	1.00	1.00
Crown shape ratio	1.00	0.81	1.00	1.00
Height to base of crown	0.00	0.00	0.91	1.00
Branch number per unit crown length	0.00	0.00	1.00	1.00
leaf area per unit crown length	0.47	1.00	1.00	0.48
Current-year leaf biomass	0.29	0.53	1.00	0.42
1-year-old leaf biomass	0.21	0.32	1.00	1.00
Total leaf biomass	0.25	0.44	1.00	0.67
Branch biomass	0.38	0.72	0.00	0.00
Total crown biomass	0.31	0.57	1.00	0.41
Current-year leaf area	0.27	1.00	1.00	0.77
1-year-old leaf area	0.36	0.81	1.00	1.00
Total leaf area	0.30	0.91	1.00	0.88
Current-year specific leaf area	0.81	1.00	0.00	0.00
1-year-old specific leaf area	0.00	0.00	0.00	0.00

Loblolly pine families ranked similarly across treatments in leaf area attributes, as family × treatment interactions were not important for these traits. In contrast, biomass-related attributes and crown structural traits (except crown shape ratio) had significant family × treatment interactions (Table 4-2). In slash pine, family × treatment interactions were not important for most attributes such as growth (volume), crown structural traits (except crown length), and 1-year-old leaf biomass or leaf area. Similar to these results, Smith et al. (1993) examined 21 shoot characteristics of slash pine and reported that almost all attributes had non-significant family × treatment interactions (type B genetic correlation = 0.56 to 0.97) across two levels of N treatment. In this study, only two traits (current-year leaf biomass and total crown biomass across treatments) showed high levels of interactions (type B correlation = 0.42 and 0.41, respectively), indicating that slash pine families responded differently to silvicultural treatments in developing and partitioning current-year leaf and total crown biomass.

Environmental variation affecting genotype responses can originate from two sources: macro- and micro-site variation (Garvilet and Hastings 1994; Li and Wu 1997), which are generally predictable and unpredictable, respectively, in terms of genotype sensitivities to environmental changes (Allard and Bradshaw 1964). Different family responses to site locations and silvicultural treatments can be attributed to the unique macroenvironments associated with this study. Some traits showed significant interactions across the different macroenvironments while others did not for either species. Thus, levels of genotype × environment interactions were trait dependent.

Genetic and Environmental Correlation Analyses

Five attributes, total branch number, crown width, leaf area per unit crown length, branch biomass, and total leaf area were analyzed for genetic and environmental correlations in loblolly pine. These traits were chosen based on criteria stated in the Materials and

Methods section. All five attributes were positively correlated (Table 4-3). Genetic correlations between crown width and leaf area per unit crown length, and between branch biomass and total leaf area were very high (r = 0.97 and 0.96, respectively). Leaf area generally maintained medium to high genetic correlation with other traits, while total branch number had low to medium genetic correlation with other traits. The environmental correlations among these traits showed similar trends to the genetic correlations. Branch biomass was significantly correlated with total leaf area (r = 0.96). Leaf area still maintained medium to high environmental correlation with other traits. Although the genetic correlation between crown width and leaf area per unit crown length was high (r = 0.97), their environmental correlation was low (r = 0.19), implying that these two attributes were genetically controlled by a similar set of genes, but microsite environments that enhance the development of one attribute will not necessarily enhance the other attribute.

Table 4-3. Estimates of genetic (upper triangle) and environmental (lower triangle) correlations among growth and crown structural attributes in 3-year-old loblolly pine planted at two locations in north central Florida.

	Total branch number	Crown width	Leaf area per unit crown length	Branch biomass	Total leaf area
Total branch number	–	0.21	0.39	0.34	0.46
Crown width	0.26	–	0.97	0.81	0.66
Leaf area per unit crown length	0.29	0.19	–	0.84	0.72
Branch biomass	0.32	0.53	0.70	–	0.96
Total leaf area	0.55	0.54	0.74	0.96	–

The environmental proportion of total variance was 81%, 64%, 47%, 62%, and 49%, respectively, for total branch number, crown width, leaf area per unit crown length, branch biomass, and total leaf area.

Five attributes were also selected for genetic and environmental correlation analyses in slash pine: volume per tree, total branch number, branch number per unit crown length, leaf area per unit crown length, and total leaf area. To make comparisons between loblolly and slash pine, it would have been better to select the same set of variables. However, because of the distinct inheritance patterns of the two species, it was difficult to select common attributes that met the three criteria stated previously. For example, volume heritability for loblolly pine was close to zero, thus making it impractical to estimate genetic correlations.

For slash pine, volume showed negative genetic correlation with unit branch number and unit leaf area (r = -0.02 and -0.08, respectively). Generally, volume was most correlated with total leaf area and total number of branches (r = 0.51 and 0.43, respectively), but even these correlations were not high. Thus, it is likely that at least some of the genes that controlled volume growth in slash pine were not associated with those influencing total leaf area or branch numbers.

Environmental correlations between total leaf area and other traits were much higher than genetic correlations in slash pine (Table 4-4). Similar results were also found between volume and other selected traits. The environmental correlation between volume and total branch number per tree was positive (r = 0.49), but volume was also negatively correlated with branch number per unit crown length (r = -0.20), suggesting that fast-growing trees in slash pine were associated with more branches per tree, but fewer branches per unit tree height. Such an outcome may suggest that tall trees with larger internode length favor volume accumulation in slash pine. This analysis is one example of how genetic and environmental correlations can aid in understanding relationships between tree growth and crown structure.

Table 4-4. Estimates of genetic (upper triangle) and environmental (lower triangle) correlations among growth and crown structural attributes in 3-year-old slash pine planted at two locations in north central Florida.

	Volume	Total branch number	Branch number per unit crown length	Leaf area per unit crown length	Total leaf area
Volume	–	0.43	-0.02	-0.08	0.51
Total branch number	0.49	–	0.85	0.32	0.51
Branch number per unit crown length	-0.20	0.55	–	0.26	0.14
Leaf area per unit crown length	0.46	0.56	0.60	–	0.79
Total leaf area	0.72	0.64	0.38	0.92	–

The proportion of total variance attributed to environmental factors for the five attributes in slash pine was 74%, 18%, 22%, 66%, and 52%, respectively, for volume, total branch number, branch number per unit crown length, leaf area per unit crown length, and total leaf area. The most significant difference between loblolly and slash pine for these attributes was genetic vs. environmental control on total branch number. Loblolly pine had low heritability for branch number ($h^2 = 0.09$) and a large proportion of environmental variance (81%). In distinctive contrast, slash pine had high heritability for branch number ($h^2 = 0.62$) and a small proportion of environmental variance (18%). Genetic vs. environmental control on other attributes were less significantly different than that on the total branch number between the two species.

Genetic correlations can be used to estimate the strength and direction in which two traits are correlated through the pleiotropic action of genes. Environmental correlations are measures of microsite environmental fluctuation between the two traits measured from the same individual tree (Falconer and Mackay 1996). Because of different inheritance patterns and the magnitude of genetic control on various traits, genetic and environmental correlations between the same two traits were different in loblolly and slash pine (Tables 4-3 and 4-4). However, most genetic correlations were positive and moderate to high in the two species, indicating that these traits were coheritable to some extent and favorable from the geneticist's point of view. Moderate to strong genetic correlations among selected growth and crown structural traits were also reported in *Eucalyptus globulus* (Volker et al. 1990) and *Pinus sylvestris* (Haapanen et al. 1997). Therefore, tree improvement programs for loblolly and slash pine could take advantage of these positive correlations to make substantial genetic gains from selecting favorable trees with certain crown structural attributes.

Summary

Genetic parameters (heritability, genotype × environment interaction, and genetic and environmental correlation) were estimated for growth and crown structural characteristics in 3-year-old loblolly and slash pine planted at two site locations (Dunnellon and Palatka) and managed under two levels of silvicultural intensity (low and high) in north central Florida. Heritability estimates for the 18 growth and crown structural characteristics for the two species were low to moderate, except for total branch number ($h^2 = 0.62$) and branch number per unit crown length ($h^2 = 0.60$) in slash pine. Most crown and leaf area traits had similar heritability values as growth traits and could be incorporated into tree improvement programs if deemed desirable.

Type B genetic correlations were variable among traits due to the small sample size. Family × treatment interaction analyses indicated that loblolly pine families responded similarly to treatments in leaf area attributes, but biomass-related attributes and crown structural traits (except crown shape ratio) had significant family × treatment interactions. Family × treatment interactions were not important for most attributes in slash pine. A low degree of genetic commonality in current-year leaf biomass and total crown biomass across treatments (type B correlation = 0.42 and 0.41, respectively) indicated that slash pine families responded differently to silvicultural treatments in developing and partitioning current-year leaf and total crown biomass.

Selected growth and crown structural attributes (total branch number, crown width, leaf area per unit crown length, branch biomass, and total leaf area in loblolly pine, and volume, total branch number, branch number per unit crown length, leaf area per unit crown length, and total leaf area in slash pine) were analyzed for genetic and environmental correlations. All five attributes had positive genetic and environmental correlations in loblolly pine, suggesting that large trees were always associated with more branch numbers and biomass, wider crowns, and greater leaf area. Results for slash pine indicated that large trees were generally associated with more branches and leaf area, but few branches per unit tree height. This suggests that tall trees with larger internode length favored greater volume growth in slash pine. The most significant difference between loblolly and slash pine in these attributes was genetic vs. environmental control on total branch number. Loblolly pine had a larger proportion of environmental variance (81%) than slash pine (18%). In conclusion, leaf area and crown traits are under certain genetic control and could be incorporated into tree improvement programs to enhance the growth potential of loblolly and slash pine.

CHAPTER 5
GENETIC AND ENVIRONMENTAL CONTROLS ON NUTRITIONAL CHARACTERISTICS AND CORRELATIONS BETWEEN GROWTH AND NUTRIENT TRAITS IN LOBLOLLY AND SLASH PINE

Introduction

Nutritional characteristics of woody species directly influence forest stand development and growth performance. Previous studies have revealed that substantial variation in many nutrient attributes exist among families within a species, resulting in differences in biomass allocation patterns (Day 1987; Li et al. 1991a) and overall growth performance (Chapin 1980; Boerner 1985; Madgwick and Mead 1990). Knowledge regarding the genetic architecture (i.e., heritability, genotype × environment interaction, genetic correlation) of these nutrient attributes can enhance our understanding of the relative importance of genetic and environmental effects that underlie these quantitative phenotypic traits. Such information can also facilitate the development of advanced breeding and deployment strategies for maximizing growth potential and timber quality in forest tree improvement programs.

Nutritional differences among genotype are generally specified using foliage nutrient concentrations and content (Sarif 1981). Temporal and spatial patterns in foliage nutrient levels have been shown to vary dramatically in response to internal metabolic requirements and external environmental conditions (Boerner 1985; Drossopoulos et al. 1996; Chapter 3). However, less information is available for forest trees regarding the effects of genetic and environmental controls on nutrient levels over an entire leaf life cycle. Although several progeny studies have indicated significant differences in nutritional characteristics among families for various species and also reported heritability estimates (Forrest and Ovington 1971; Li et al. 1991b; Jonsson et al. 1997), the temporal stability of these estimates in relation to time of year is largely unknown. Individual narrow-sense heritability estimates for several growth variables have changed with age (Balocchi et al. 1993; Dieters et al. 1995), indicating that genetic parameters for a given trait are only valid during a specific measurement interval. Therefore, a series of genetic estimates of foliage nutrient levels at different stages of leaf development could present a more complete picture about genetic controls on nutrient dynamics in trees.

Intraspecific differences in mineral nutrients can also be specified through nutritional characteristics in nutrient uptake, transport, distribution (Sarif 1983), utilization efficiency (Li et al. 1991b; Jonsson et al. 1997), and perhaps nutrient retranslocation (Staaf and Stjernquist 1986). Awareness of the magnitude of genetic control of these attributes can contribute to our understanding about physiological processes involving different nutrients through certain periods of a leaf life cycle. Responses of foliage nutrients to different environments (locations or treatments) are important because one of the reasons to specify mineral nutrient requirements by different families within a species is to develop improved or more appropriately adapted families for different soil environments (e.g., productive soils, acidic soils). An experiment designed to allow statistical analyses of genotype × environment interactions could help achieve this objective. Finally, the ultimate goal for examining the genetic basis of mineral nutrients is to achieve improved productivity of forest stands. Thus, a better understanding of genetic and environmental correlations between nutrient status and growth performance could aid the progress of future breeding efforts. Unfortunately, only limited information is currently available on the heritability and genetic variation of nutrient attributes, and their underlying influence on the growth of forest trees.

Loblolly pine (*Pinus taeda* L.) and slash pine (*P. elliottii* Engelm. var. *elliottii*) are the two most important commercial species in the southeastern United States. Tree improvement programs since the 1950s have made considerable progress by directly selecting for rapid growth, i.e., height, DBH, or volume (Lowerts 1986; Hodge et al. 1989; 1990). Thus, genetic architecture is well known for these growth traits (Dieters et al. 1995). Although foliar nutrient concentrations were found to be significantly different among families and each major element showed distinctive patterns to silvicultural treatments (Sword et al. 1998; Chapter 3), less work has been done to estimate the heritability and genetic variation of nutrient attributes and to evaluate genetic correlations with growth. With advanced breeding programs for the two species under way in the southeastern United States (White et al. 1993; McKeand and Bridgwater 1998), an improved understanding of genetic control on nutrient attributes is needed. This study was designed to (1) determine whether heritability estimates of foliage nutrient attributes change during the lifespan of a single needle cohort and whether differences exist between loblolly and slash pine; (2) obtain heritability estimates for nutrient use efficiency of leaf area production, nutrient retranslocation amount and efficiency, and foliage nutrient content as references for future tree improvement programs; (3) evaluate the magnitude of genotype × environment interactions for a variety of nutrient attributes; and (4) examine the degree of genetic and environmental correlations between growth, leaf area development, and selected nutrient attributes.

Materials and Methods

Field Sites and Experimental Layout

The experiment was conducted from April 1997 to December 1998, using two field test sites with distinctively different soil characteristics in north central Florida. At Dunnellon (Levy County, 29°20' N, 82°50' W), the dominant soils belonged to the Smyrna series (sandy, siliceous, hyperthermic Aeric Alaquods), while at Palatka (Putnam County, 29°40' N, 81°42' W) the soils were mapped as the Adamsville series (hyperthermic, uncoated Aquic Quartzipsamments).

A randomized complete block split-split plot design was applied at each site, with three complete blocks under each of two silvicultural treatments (high vs. low intensity). Sixteen open-pollinated half-sib families from each of three taxa (genetically improved loblolly and slash pine, and unimproved slash pine) were planted at both sites in a five-tree row plot with a 1.5 m × 3.4 m spacing at Palatka, and a 1.8 m × 3.0 m spacing at Dunnellon. Each site was chopped and bedded prior to study establishment. Understory vegetation in the intensive silvicultural treatment blocks was controlled during the first growing season using a combination of mechanical and pre- and post-plant directed spot-spray applications of glyphosate applied at labeled rates. Fertilizers were broadcast during years 1 and 3 as a balanced mix of macro- and micronutrients in the high intensity blocks. Total elemental application rates for plots receiving fertilizer additions at both locations were approximately (kg ha^{-1}): N (110), P (80), K (162), Ca (20), Mg (10), S (13), Fe (0.5), Zn (0.06), Mn (0.5), Cu (0.06), and B (0.06). Insecticides (Asana, Diomethorate or Pyridine) were applied 3-4 times during the first growing season to control tip moth (*Rhyacionia* spp.) on the high intensity blocks. The low intensity blocks did not receive herbicide, fertilizer or insecticide applications. An untreated buffer of at least 21 m separated the high and low intensity blocks.

Sampling Procedures

Two sample trees that were healthy and free of disease were randomly chosen from within a 5-tree row-plot in each block for each family by a SAS procedure (SAS Institute 1996). A total of 192 sample trees (2 treatments × 3 blocks × 16 families × 2 trees) for each of the three taxa were selected within each site. Overall, 1,152 trees (2 locations × 2 treatments × 3 blocks × 3 taxa × 16 families × 2 trees) were sampled between both experimental locations.

Growth (DBH, height) and leaf area measurements were conducted in August 1997 and 1998, respectively (Chapter 2). Recommended field sampling procedures for determining foliage nutrient status entailed collection of full-length and complete fascicles from the upper third of the crown (Madgwick and Mead 1990). Temporal and spatial problems related to nutrient variability, due to needle age and crown position, were addressed by collecting samples from an identical branch from the same tree through an entire needle cohort life cycle (i.e., foliage collected over eight sampling periods from 1997 to 1998). About 50 complete fascicles from each tree were collected in: June (the first month that current-year foliage attained full length), September (needle N concentration was generally at the lowest level during the year), November (critical stage in retranslocation for some mineral nutrients) 1997 and February (needle N concentration was generally at the highest level of a year), April (initial new growth may affect nutrient status of 1-year-old needles), June, September, and December (last month for 1-year-old needles to stay on the tree) 1998. Sample branches were randomly selected among all branches within the upper third of the crown, and a uniform aspect (south) was chosen for all foliage collections. Approximately 9,216 total foliage samples (2 locations × 2 treatment × 3 blocks × 3 taxa × 16 families × 2 trees × 8 times) were collected for chemical analyses over the two year period.

All samples were oven-dried at 70 ^{o}C for 48 hours or until dry. About twenty complete and full-length fascicles from each sample were randomly chosen to determine total dry weight, and needles per fascicle. All dried tissues were ground in a Wiley mill to pass a 2 mm stainless steel screen. The ground and dry needle tissues were stored in sealed plastic vials until nutrient determinations were performed.

Nutrient Analyses and Variables

Foliage samples were analyzed for five macronutrients (N, P, K, Mg, and Ca) using the methods as described by Thomas et al. (1967) and Jones et al. (1991). For each sample, 100 mg of homogenous tissue was weighed and placed in a 50 ml Pyrex test tube, and then 2 ml of concentrated H_2SO_4 was added prior to placing the sample into an aluminum block digester at 380 ^{o}C for 30 minutes. All tubes were removed from the block and allowed to cool. A small amount of 30% H_2O_2 was added to the tubes until the solution cleared. Concentrated H_2SO_4 was added to raise the temperature of the mixture, while H_2O_2 was used to speed and complete the digestion process (Jones et al. 1991). Nutrient concentrations were determined using an inductively-coupled plasma emission spectrometer (ICP or ICAP).

Fascicle nutrient content was calculated as the product of nutrient concentration and average fascicle weight. Nutrient use efficiency of leaf area production was defined as the peak amount of leaf area developed per unit nutrient accumulation (leaf area cm^2 / nutrient mmol) and was calculated using the following formula, based on foliage samples collected in September, 1997:

$$\begin{aligned}\mathrm{LA_{NUE}}\ (\mathrm{cm}^2 / \mathrm{mmol}) &= \frac{\text{Current - year peak leaf area production } \times \mathrm{AW}}{\text{Total nutrient content incorporated in current - year foliage } \times 1000}\\ &= \frac{\text{Current - year foliage biomass } \times \text{ SLA } \times \mathrm{AW}}{\text{Current - year foliage biomass } \times \text{ CONC } \times 1000}\\ &= \frac{\mathrm{SLA} \times \mathrm{AW}}{\mathrm{CONC} \times 1000}\end{aligned}$$

where SLA is specific leaf area (cm^2/g), AW is the atomic weight of each element (g/mol), and CONC is the concentration of each nutrient (%).

Nutrient retranslocation efficiency (NRE) was calculated for each sample using the following formula (Zhang and Allen 1996):

$$\mathrm{NRE}\ (\%) = \frac{\mathrm{FC_1} - \mathrm{FC_2}}{\mathrm{FC_1}} \times 100$$

where $\mathrm{FC_1}$ was the maximum fascicle nutrient content during the needle cohort life cycle, and $\mathrm{FC_2}$ is nutrient content of green fascicles in early December, 1998, prior to abscission. The term ($\mathrm{FC_1}$ - $\mathrm{FC_2}$) represented the amount of nutrients retranslocated over time. All calculations were based on a sample size of n = 1,152.

Statistical Analyses

Data standardization and statistical model

All analysis of variance procedures were conducted based on individual tree data. To remove scale effects caused by heterogenous variances in different site locations and silvicultural treatments (Falconer and Mackay 1996), all variables were standardized prior to analysis by dividing each observation within a location-treatment-block combination by the corresponding square root of the phenotypic variance for that variable in that block (Chapter 4).

Analyses of variance for a given nutrient attribute were conducted separately for loblolly and slash pine using different models. Differences between improved and unimproved slash pine were maintained in the model for slash pine, while taxa effects were eliminated in the loblolly pine model. The statistical model for slash pine was of the following form:

$$Y_{ijklmn} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + t_l + \alpha t_{il} + \beta t_{jl} + b_{k(ij)} + f_{m(l)} + \alpha f_{im(l)} + \beta f_{jm(l)} + bf_{k(ij)m(l)} + e_{ijklmn}$$

where Y_{ijklmn} is observation on tree n at family m of taxa l in block k of treatment j of location i,

μ is the population mean,

α_i is the fixed effect of location (Dunnellon or Palatka),

β_j is the fixed effect of treatment (non-intensive or intensive),

$(\alpha\beta)_{ij}$ is the fixed effect of location × treatment interactions,

t_l is the fixed effect for taxa (improved or unimproved slash pine),

αt_{il} is the random variable for location × taxa interactions ~ NID $(0, \sigma^2_{\alpha t})$,

$\$t_{jl}$ is the random variable for treatment × taxa interactions ~ NID (0, $F^{2}_{\$t}$),

$b_{k(ij)}$ is the random variable for block nested within location and treatment ~ NID (0, F^{2}_{b}),

$f_{m(l)}$ is the random variable for family nested within taxa ~ NID (0, F^{2}_{f}),

$''f_{im(l)}$ is the random variable for location × family (taxa) interactions ~ NID (0, $F^{2}_{''f}$),

$\$f_{jm(l)}$ is the random variable for treat × family (taxa) interactions ~ NID (0, $F^{2}_{\$f}$),

$bf_{k(ij)m(l)}$ is the random variable for block (location × treatment) × family (taxa) interactions ~ NID (0, F^{2}_{bf}),

e_{ijklmn} is the random error term ~ NID (0, F^{2}_{e});

where i = 2 for locations, j = 2 for treatment levels, k = 3 for number of blocks, l = 2 for taxa, m = 16 for families per taxon, and n = 2 for trees per plot. A similar linear model as above, but without terms related to taxa effects (i.e., deleting all effects with subscript l), was used for loblolly pine.

The SAS procedure PROC MIXED was used to test the fixed effects and to estimate variance components using REML (restricted maximum likelihood method), while PROC GLM was utilized to test the significance of random effects (Littell et al. 1996; SAS Institute 1996). Those effects that were statistically significant at " = 0.05 were maintained in the final models for the two species. A total of 20 nutrient variables (LA_{NUE}, crown nutrient content, nutrient retranslocation amount, and nutrient retranslocation efficiency for five elements), plus fascicle dry weight, nutrient concentrations and fascicle nutrient content at eight sampling periods, were analyzed for both species.

Estimation of genetic parameters

To better understand the genetic architecture of nutrient attributes and their relationships to growth and leaf area development, three types of genetic parameters were estimated: heritability, genotype × environment interaction, and genetic and environmental correlations. Variance components were obtained for all nutrient variables across sites and treatments using the SAS MIXED procedure.

Narrow-sense heritability was calculated across sites and treatments, which corrects for upward bias due to the genotype × environment interaction when estimated from a single site or within a treatment (Dieters 1996; Hodge and White 1992). The variance component for the half-sib families (F^{2}_{f}) is generally interpreted as an estimate of one quarter of the additive genetic variance (F^{2}_{A}). Heritability estimates for each nutrient variable in slash pine were calculated as follows based on the ANOVA model:

$$h^2 = \frac{4s^{2}_{f}}{s^{2}_{f} + s^{2}_{bf} + s^{2}_{af} + s^{2}_{bf} + s^{2}_{e}}$$

where all symbols representing variance components were the same as those indicated in the linear model. For loblolly pine, one more variance component corresponding to the location × treatment × family ($F^{2}_{"\$f}$) interaction was added in the denominator when statistically significant. These terms were not significant for any variables for slash pine and were pooled with the random error term. Standard errors for heritability estimates were calculated using the formula described by Dickerson (1962).

Family × site and family × treatment interactions were investigated separately for the two species and all variables using the method developed by Yamada (1962), and widely used by other researchers (Burdon 1977; Smith et al. 1993; Dieters et al. 1995):

$$r_{\text{B-treat}} = \frac{\sigma^2_{\text{f}}}{\sigma^2_{\text{f}} + \sigma^2_{b\,\text{f}}}$$

$$r_{\text{B-site}} = \frac{\sigma^2_{\text{f}}}{\sigma^2_{\text{f}} + \sigma^2_{a\,\text{f}}}$$

Estimates of the above type B genetic correlation can be used to evaluate the same trait measured between two sites or two treatments, and to examine consistency of nutrient variables across site locations or silvicultural treatments. It has been suggested that a value smaller than 0.67 in $r_{\text{B-treat}}$ or $r_{\text{B-site}}$ may imply important genotype × environment interaction (Shelbourne 1972).

Genetic and environmental correlations between two variables using data pooled across sites and treatments were estimated using MTDFREML (Boldman et al. 1995). Estimates of genetic correlation coefficients were based on the formula below:

$$r_G = \frac{\text{Cov (X, Y)}}{\sqrt{V_X \cdot V_Y}}$$

where Cov(X, Y) is the additive genetic covariance between two traits X and Y, V_X and V_Y are the additive genetic variances of traits X and Y. Environmental correlation coefficients were calculated similarly by substituting additive genetic covariance and variances with environmental covariance and variances, respectively, in the above formula.

Selected growth and nutrient variables were analyzed for genetic and environmental correlations across sites and treatments. Growth attributes included in the analysis were volume and total leaf area per tree. Nutrient variables that were selected for inclusion in this analysis satisfied the following minimum criteria for the two species: (1) moderate heritability estimates; (2) likely significant effects on growth; and (3) higher potential for inclusion in breeding programs.

Results

Variation of Heritability Estimates over An Entire Leaf Life Cycle

Narrow-sense heritabilities were estimated separately for each sampling period for fascicle weight, nutrient concentrations and fascicle nutrient content for all five macronutrients. In general, heritability estimates for fascicle weight were low in both species. Loblolly and slash pine both displayed a similar decreasing trend of genetic control on fascicle weight from the beginning to the end of the foliage life cycle (Figure 5-1). For example, during the first growing season the heritability for both species approached 0.2 and then declined to less than 0.1 as the needle cohort matured.

Distinctive differences were found in heritabilities for fascicle N concentrations and N content between the two species (Figure 5-2). For N concentration, loblolly pine showed a very high heritability (0.8) during the early stage of fascicle development, while slash pine indicated little additive genetic variance for this attribute. However, the relative genetic control over N concentration increased before foliage abscission in both species. Heritability estimates for fascicle N content were low to moderate (h^2 = 0.15 to 0.20 for loblolly pine, and h^2 = 0.00 to 0.28 for slash pine), but the two species also showed an opposite trend over the entire leaf lifespan; slash pine had higher heritabilities than loblolly pine during the first growing season, while the reverse was true beginning in February 1998 of the second growing season.

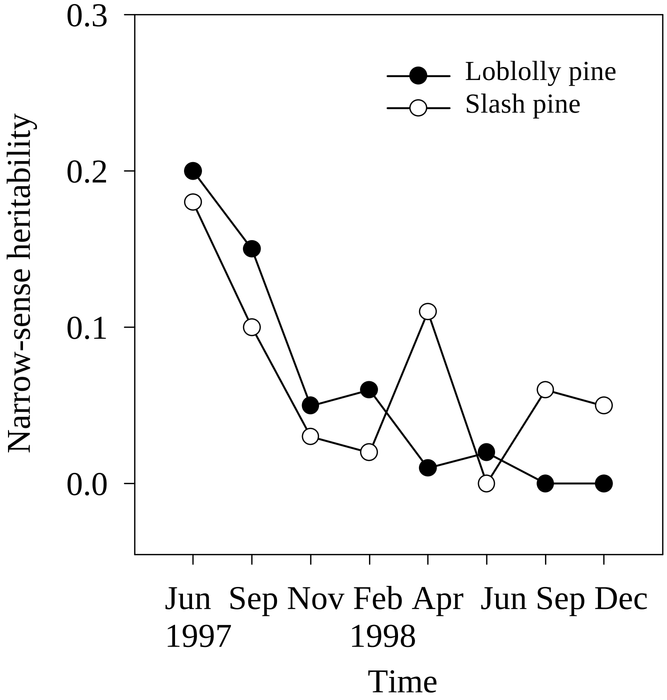

Figure 5-1. Narrow sense heritability for average fascicle weight over an entire lifespan of a needle cohort in loblolly and slash pine planted at two locations in north central Florida.

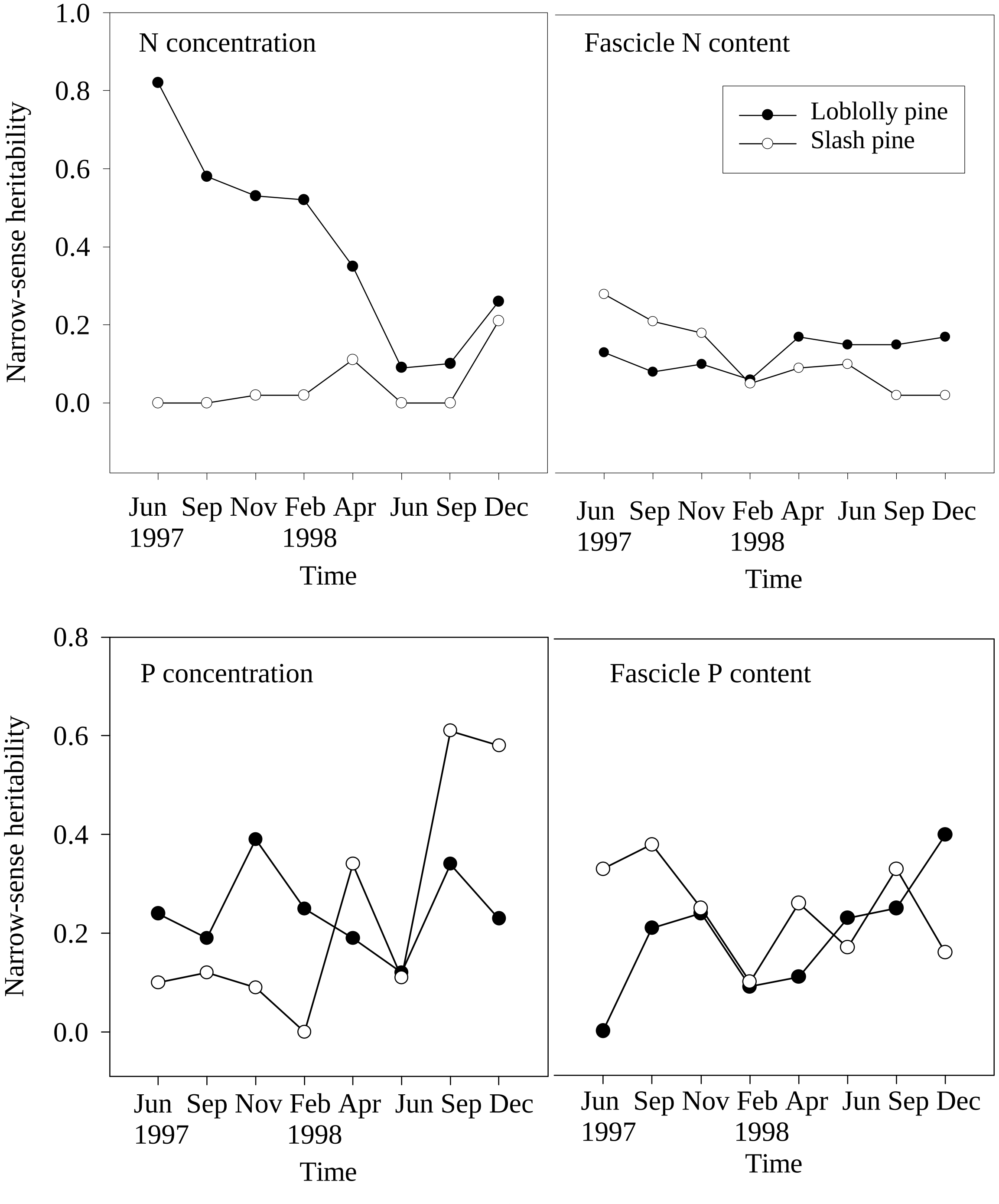

Figure 5-2. Narrow sense heritabilities for macronutrient concentrations and fascicle nutrient content over an entire lifespan of a needle cohort in loblolly and slash planted at two locations in north central Florida

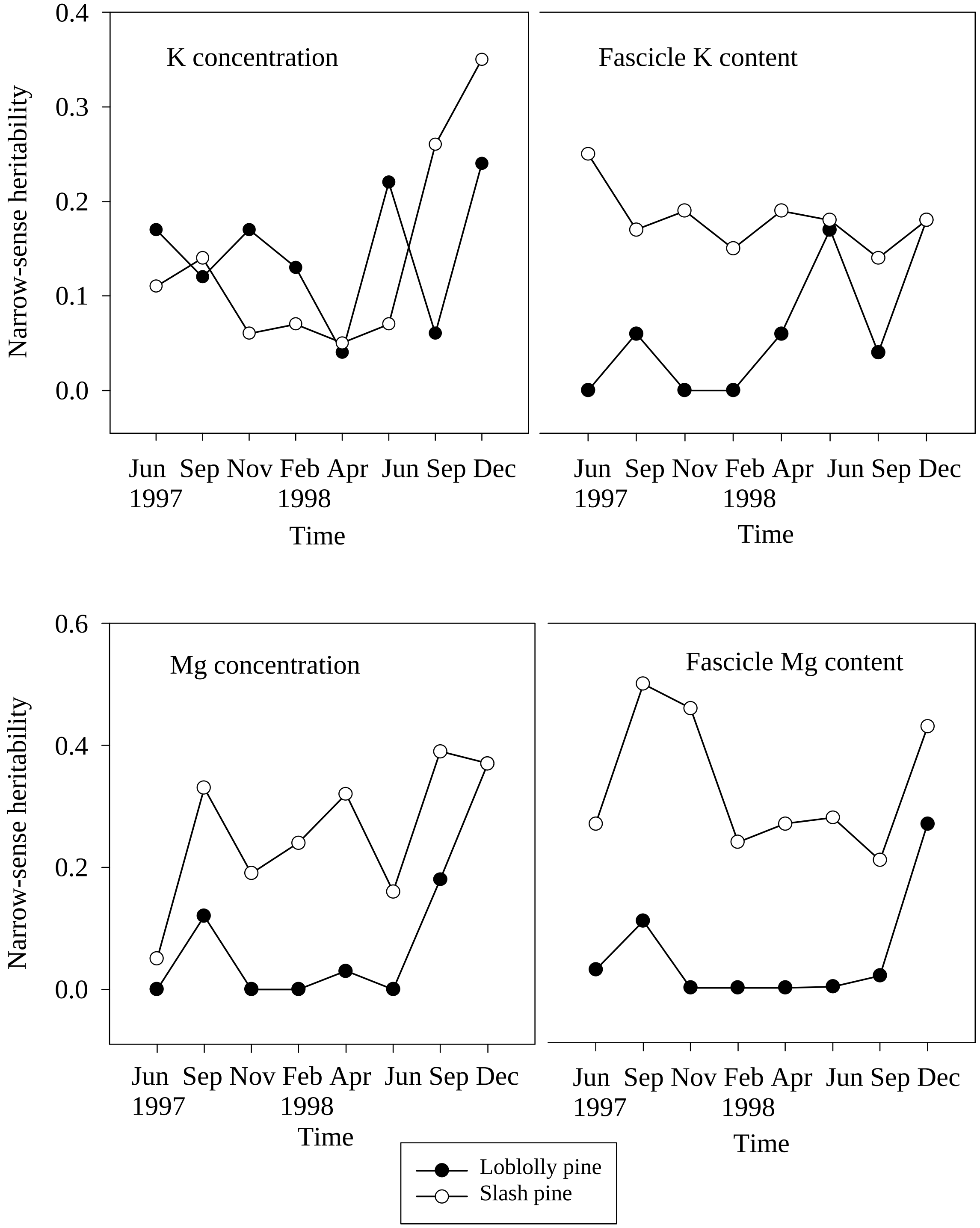

Figure 5-2 -- Continued.

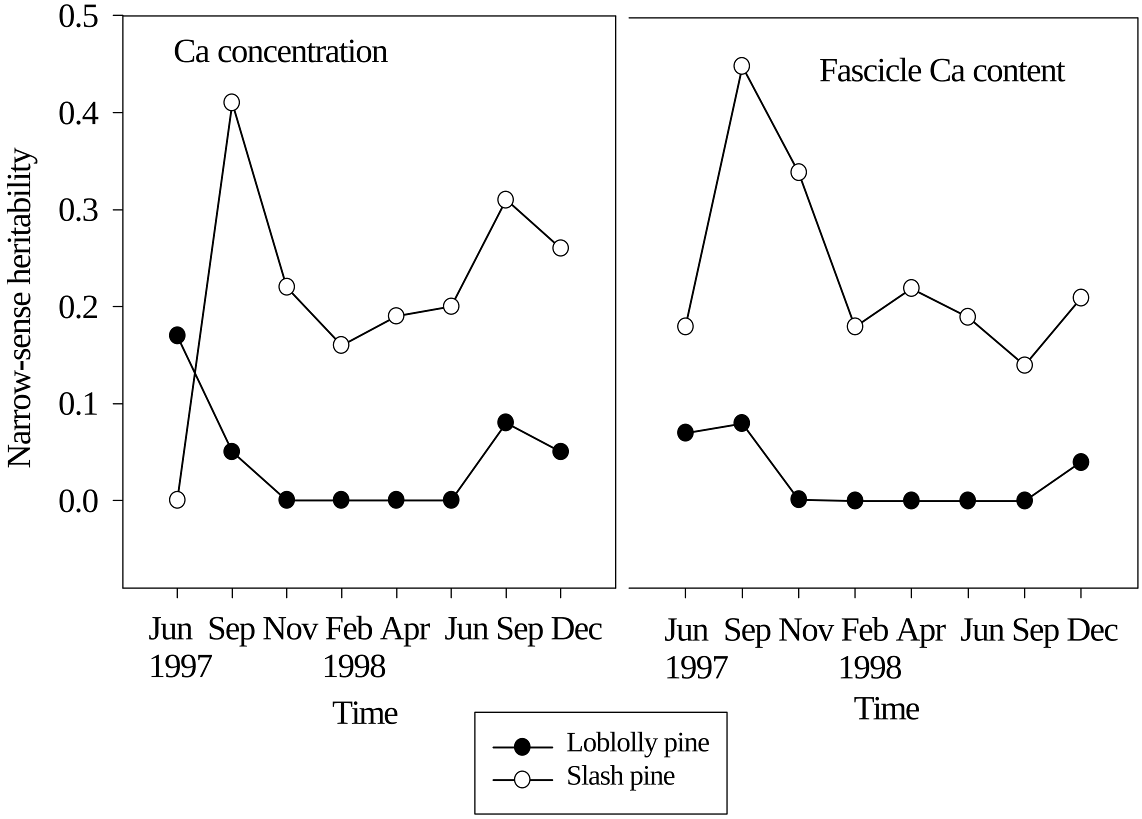

Figure 5-2 -- Continued.

No clear patterns or consistent differences in heritability estimates for P concentrations and fascicle P content were found over time for the two species (Figure 5-2). These estimates were generally low to moderate, with large fluctuation among the different sampling periods (e.g., h^2 = 0.10 to 0.40 for loblolly pine, and h^2 = 0.10 to 0.60 for slash pine for P concentration). Similar results were also detected for variation in K concentration heritability estimates. However, slash pine consistently showed higher heritabilities than loblolly pine in fascicle K content (Figure 5-2) over the entire leaf lifespan. Additionally, an appreciable increase in heritability estimates for the concentration of all elements were generally observed at the final measurement period, just prior to needle abscission.

Slash pine had moderate heritability estimates for concentrations and fascicle content of Mg and Ca. For example, narrow-sense heritabilities for both foliage Ca and Mg concentrations in slash pine exceeded 0.20 in 6 out of 8 sampling periods. In contrast, loblolly pine had a very low level of genetic control for these two elements, with heritabilities close to zero for about one-half of the sampling periods.

Heritability Estimates for Other Selected Nutrient Attributes

Inheritance patterns of LA_{NUE} between loblolly and slash pine showed significant differences (Table 5-1). Nitrogen and P use efficiency was more heritable in loblolly pine (h^2 = 0.41 and 0.27, respectively, for N and P use efficiency) than in slash pine (h^2 = 0.00 and 0.11, respectively, for N and P use efficiency), while Mg and Ca use efficiency was more heritable in slash pine (h^2 = 0.26 and 0.32, respectively, for Mg and Ca use efficiency) than in loblolly pine (h^2 = 0.12 and 0.00, respectively, for Mg and Ca use efficiency). Slash pine had lower heritability estimates for K use efficiency than loblolly pine (h^2 = 0.08 and

0.13, respectively, for slash and loblolly pine). Most noticeably, heritability estimates for N use efficiency for slash pine and Ca use efficiency for loblolly pine were both close to zero. In contrast, the highest heritability estimates were for N use efficiency in loblolly pine ($h^2 = 0.41$) and Ca use efficiency in slash pine ($h^2 = 0.32$).

Heritability estimates for crown (foliage) nutrient content for all five macronutrients were generally low for both species; however, Mg and Ca crown content were more highly heritable in slash pine than in loblolly pine (Table 5-1). Because crown nutrient content was calculated as the product of foliage nutrient concentrations and foliage biomass, and differences between loblolly and slash pine heritability estimates for foliage biomass were small (Chapter 4), nutrient concentrations may contribute more to differences between the two species in the heritability estimates for crown nutrient content than foliage biomass (Figure 5-2).

Nutrient retranslocation amount and efficiency were predominantly controlled by environmental rather than genetic effects for the two species. Genetic variation among families for these nutrient attributes was generally small, thus leading to the low heritability estimates (Table 5-1). For example, nutrient retranslocation amount and efficiency for all five elements were not heritable in loblolly pine ($h^2 = 0.00$ to 0.05), and were only weakly heritable in slash pine ($h^2 = 0.02$ to 0.16).

Table 5-1. Narrow sense heritability (h^2) estimates and standard errors for crown nutrient attributes in 3-year-old loblolly and slash pine planted at two locations in north central Florida[a].

Trait	Loblolly pine	Slash pine
LA_{NUE}:		
N	0.41 ± 0.26	0.00 ± 0.14
P	0.27 ± 0.19	0.11 ± 0.36
K	0.13 ± 0.12	0.08 ± 0.12
Mg	0.12 ± 0.07	0.26 ± 0.20
Ca	0.00 ± 0.13	0.32 ± 0.25
Crown nutrient content:		
N	0.08 ± 0.19	0.08 ± 0.09
P	0.10 ± 0.21	0.12 ± 0.11
K	0.15 ± 0.15	0.14 ± 0.09
Mg	0.00 ± 0.15	0.24 ± 0.11
Ca	0.06 ± 0.16	0.15 ± 0.12
Nutrient retranslocation amount:		
N	0.00 ± 0.06	0.08 ± 0.10
P	0.00 ± 0.47	0.10 ± 1.02
K	0.00 ± 0.15	0.05 ± 0.13
Mg	0.00 ± 0.41	0.09 ± 0.32
Ca	0.00 ± 0.82	0.08 ± 1.19

Table 5-1 – Continued.

Trait	Loblolly pine	Slash pine
Nutrient retranslocation efficiency:		
N	0.00 ± 0.07	0.10 ± 0.11
P	0.01 ± 0.08	0.02 ± 0.05
K	0.05 ± 0.08	0.16 ± 0.08
Mg	0.00 ± 0.07	0.08 ± 0.07
Ca	0.00 ± 0.07	0.11 ± 0.09

a LA$_{NUE}$ and foliage nutrient content were calculated from growth and nutrient measurements conducted in September 1997. Nutrient retranslocation amount and efficiency were computed based on fascicle nutrient content in 1997 (maximum values were used), and December 1998 prior to needle abscission.

Genotype × Environment Interactions

Two types of genotype × environment interaction, family × site and family × treatment, were generally not important for fascicle weight (Appendix G). Family × site and family × treatment interactions were also not important over most sampling periods for nutrient concentrations and fascicle nutrient content, indicating that foliage nutrient levels among families for the two species were not significantly influenced by site environment or silvicultural treatments (Table 5-2). Slash pine was more consistent than loblolly pine in demonstrating constancy in fascicle nutrient concentrations and content among families throughout the entire leaf life cycle across sites and silvicultural treatments.

Family × site and family × treatment interactions were not important in LA$_{NUE}$ for any of the five macronutrients, suggesting a stability among families for the two species in nutrient utilization across sites and treatments (Table 5-2). For total foliage nutrient content, family × site interactions for all elements were very important for loblolly pine, but

Table 5-2. Family × site interaction ($r_{B\text{-}site}$), and family × treatment interaction ($r_{B\text{-}treat}$) for crown nutrient attributes in 3-year-old loblolly and slash pine planted at two locations in north central Florida.

Trait	Loblolly pine		Slash pine	
	$r_{B\text{-}site}$	$r_{B\text{-}treat}$	$r_{B\text{-}site}$	$r_{B\text{-}treat}$
LA_{NUE}:				
N	1.00	1.00	0.00	0.00
P	1.00	1.00	1.00	1.00
K	1.00	1.00	1.00	1.00
Mg	1.00	1.00	1.00	1.00
Ca	0.00	0.00	1.00	1.00
Crown nutrient content:				
N	0.18	0.38	1.00	0.80
P	0.19	0.55	1.00	0.39
K	0.43	1.00	1.00	0.65
Mg	0.00	0.00	1.00	1.00
Ca	0.17	1.00	1.00	0.47
Nutrient retranslocation amount:				
N	0.00	0.00	1.00	1.00
P	0.00	0.00	1.00	1.00
K	0.00	0.00	1.00	1.00
Mg	0.00	0.00	1.00	1.00
Ca	0.00	0.00	1.00	1.00
Nutrient retranslocation efficiency:				
N	0.00	0.00	1.00	1.00
P	1.00	1.00	0.41	1.00
K	1.00	1.00	1.00	1.00
Mg	0.00	0.00	1.00	0.36
Ca	1.00	1.00	1.00	1.00

unimportant for slash pine ($r_{B\text{-site}} = 1$). However, family × treatment interactions were important for loblolly pine in total crown N ($r_{B\text{-treat}} = 0.38$) and P ($r_{B\text{-treat}} = 0.55$) content, and for slash pine in total crown P ($r_{B\text{-treat}} = 0.39$) and Ca ($r_{B\text{-treat}} = 0.47$) content. Because of low genetic variation in nutrient retranslocation amount among families of loblolly pine, meaningful results for genotype × environment interactions were not obtained. Both family × site and family × treatment interactions were unimportant for nutrient retranslocation in slash pine (Table 5-2). Similarly, genotype × environment interactions were also unimportant for the two species in nutrient retranslocation efficiency, except for P retranslocation efficiency across sites ($r_{B\text{-site}} = 0.41$) and Mg retranslocation efficiency across treatments ($r_{B\text{-treat}} = 0.36$) in slash pine (Table 5-2).

Genetic and Environmental Correlations

Loblolly pine

Genetic correlations are generally used to predict correlated responses of two traits to selection, while environmental correlations refer to associations between the proportion of the variance attributed to environmental factors. Total leaf area estimated for September 1997 was the only growth variable for loblolly pine used in this analysis because the heritability for volume was zero (Chapter 4). Foliage macronutrient concentrations for the same period (September 1997) were included in the analysis. Overall, leaf area development in loblolly pine showed variable, low to moderate, but positive genetic correlations with all foliage macronutrients (Table 5-3). Calcium concentrations were genetically the most closely associated with leaf area ($r = 0.61$), followed by K concentrations ($r = 0.42$). Leaf area was not genetically correlated with N and Mg concentrations, suggesting that separate genes may control leaf area development and foliar N or Mg concentrations. Among the five nutrients, Ca concentrations were the least genetically associated with any other element. The negative genetic correlation between Ca and K (r = -0.19) was probably the result of an antagonistic effect between these two cations (Jones et al. 1991). Phosphorus concentrations were the most highly genetically correlated with all other nutrients, except for Ca. Genetic correlations between N and P, between P and K, and between P and Mg concentrations were all highly and positively associated (r = 0.75, 0.68, and 0.56, respectively).

Table 5-3. Estimates of genetic (upper triangle) and environmental (lower triangle) correlations among growth and foliage macronutrient concentrations in 3-year-old loblolly pine planted at two locations in north central Florida.

	Total leaf area	N	P	K	Mg	Ca
Total leaf area	–	0.04	0.25	0.42	0.02	0.61
N	0.10	–	0.75	0.43	0.22	0.10
P	0.03	0.34	–	0.68	0.56	0.01
K	0.07	0.14	0.42	–	0.44	-0.19
Mg	-0.31	0.02	0.01	0.01	–	0.15
Ca	-0.33	0.17	0.07	0.04	0.68	–

Environmental effects on foliar N concentrations in loblolly pine were lower than genetic effects, as the environmental proportion of total variance accounted for only 40% in comparison to the proportion of additive genetic variance (h^2 = 0.56; Figure 5-2). However, the environmental proportion of total variance for P, K, Mg and Ca foliage concentrations was 70%, 77%, 82%, and 73%, respectively. In general, leaf area was not highly correlated environmentally with any macronutrient in loblolly pine, and most notably even negatively associated with Mg and Ca concentrations (r = -0.31 and -0.33, respectively) (Table 5-3), which was probably related to the dilution effects observed for these two nutrients (Chapter 3). Environmental correlations among the five nutrients were generally low, but the correlations between N and P, between P and K, and between Mg and Ca concentrations were moderate (r = 0.34, 0.42, and 0.68, respectively).

Slash pine

Foliar nutrient concentrations were not selected in this analysis for slash pine because heritability estimates for many nutrients were close to zero (Table 5-1). Instead, P, Ca, and Mg use efficiency, and N and K retranslocation efficiency were chosen based on the selection criteria noted previously. Both volume and leaf area per tree had moderate heritabilities (Chapter 4), and were thus included in the analyses. The results for the genetic and environmental correlations in slash pine showed positive associations among all the nutrient attributes examined (Table 5-4).

Volume had a moderate genetic correlation with Ca use efficiency (r = 0.45), but low correlations with other nutrient attributes. Leaf area was also most genetically associated with Ca use efficiency (r = 0.66), indicating that at least some genes controlling volume growth, leaf area development, and Ca use efficiency may be identical in slash pine. As for the five nutrient attributes, genetic correlations between Ca and Mg use efficiency (r = 0.90), between N and K retranslocation efficiency (r = 0.78), and between P and Mg use efficiency (r = 0.57) were among the most noteworthy associations.

Table 5-4. Estimates of genetic (upper triangle) and environmental (lower triangle) correlations among growth and nutrient attributes in 3-year-old slash pine planted at two locations in north central Florida.

	V_1	V_2	V_3	V_4	V_5	V_6	V_7
V_1	–	0.50	0.11	0.45	0.16	0.25	0.34
V_2	0.77	–	0.27	0.66	0.44	0.54	0.49
V_3	0.02	0.05	–	0.36	0.57	0.09	0.11
V_4	0.12	0.09	0.14	–	0.90	0.34	0.27
V_5	0.27	0.30	0.12	0.50	–	0.36	0.20
V_6	0.21	0.17	0.03	0.09	0.12	–	0.78
V_7	0.26	0.25	0.01	0.18	0.18	0.81	–

Note: V_1 = Volume
V_2 = Total leaf area
V_3 = P use efficiency
V_4 = Ca use efficiency
V_5 = Mg use efficiency
V_6 = N retranslocation efficiency
V_7 = K retranslocation efficiency

Environmental correlations between volume or leaf area and nutrient attributes were low but also positive (Table 5-4). Volume was highly environmentally associated with leaf area (r = 0.77). Similar to high genetic correlations, environmental correlations between N and K retranslocation efficiency (r = 0.81), and between Ca and Mg use efficiency (r = 0.50) were also significant (p # 0.001). The environmental proportions of total variance for LA_{NUE} were relatively low, accounting for only 27%, 39%, and 36% for P, Ca, and Mg use efficiency, respectively. In contrast, the environmental proportions of total variance for N and K retranslocation efficiency were high, accounting for 82% and 77%, respectively. Environmental proportions of total variance for volume and leaf area fell in between, accounting for 68% and 57%, respectively.

Discussion

Variation of Genetic Control on Mineral Nutrients over A Complete Foliage Life Cycle

Although numerous studies have revealed the dynamic nature of mineral nutrient levels for various stages of foliage development, less attention has been paid to quantifying sources of variation (genetic vs. environmental control) for different nutrients within a species. Similar to other studies, our results with loblolly and slash pine have confirmed the dynamic nature of macronutrients through an entire life cycle of a foliage cohort; concentrations of N, P, and K decreased from the beginning to the end of the foliage life cycle, while Mg and Ca concentrations increased over the same period (Chapter 3). Clearly, the dynamics of each nutrient depend upon its mobility. However, phenotypic analyses of nutrient concentrations and content had little power in revealing the underlying forces shaping different growth characteristics in the two species.

It appears that changes in heritability estimates for N concentrations were more uniform over time than for the other elements. Whether this originated from the genetic nature of each nutrient or differential environmental effects is unknown. However, N exists in the foliage primarily in the organic form, with 70-80% of N being located in chloroplasts (Morita and Kono 1974; Makino and Osmond 1991). This may have contributed to the regular pattern of heritability estimates observed throughout the foliage life cycle because leaching losses of N are relatively uniform and less influenced by precipitation. On the contrary, about 50% or more of P in foliage in some tree species is in the inorganic form (Chapin and Kedrowski 1983; Carlyle and Malcolm 1986). Polglase et al. (1992) reported that inorganic P was about 75% of total P in freshly fallen needles after fertilization in loblolly and slash pine stands, and was thus readily leachable. In comparison, only 20% of total N in the Oi horizon needles of the forest floor was labile. To a certain extent, the degree of variation in heritability estimates corresponds to the order of nutrient losses from leaching: K > P > N > Ca (Waring and Schlesinger 1985). Magnesium could be positioned in front of or behind N (Waring and Running 1998). Therefore, variation in heritability estimates for the nutrients may be partly related to leaching intensities before each of the eight sampling periods. For example, the total rainfall at Palatka in 1998 was only about 68% of precipitation in a normal year, while the rainfall at Dunnellon over the same period was about 14% above normal.

Interspecific differences between loblolly and slash pine were clearly evident in the heritability estimates for the five macronutrients throughout the foliage life cycle. Foliage N concentrations were more heritable in loblolly than in slash pine, while the reverse was true for foliage Mg and Ca concentrations. No obvious differences or patterns were detected in P and K concentrations between the two species (Figure 5-2). A review of heritability estimates from previous studies have generally indicated that traits more important to survival and fitness (e.g., height, DBH) have lower heritabilities than others (e.g., wood specific gravity) (Zobel and Talbert 1984; Cornelius 1994). It is too early to conclude that Ca and Mg are more important than N in nutrient metabolism in loblolly pine, or to conclude that the opposite is true for slash pine based on only one study. Because of the lack of related information, it is not clear why the two species are more genetically variable for different foliage nutrients. However, this could be one of the significant differences in genetic control on the nutritional physiology between the two species. Future experiments should be designed to investigate mechanisms of selective utilization of different nutrients between the two species.

The implications of our findings in the changing nature of foliage nutrient heritability estimates suggest that different nutrient attributes should be considered for the two species during the early stages of fascicle development (maturation) if desired in tree improvement programs. It appears that heritability estimates of all macronutrients are variable at different sampling periods and, therefore, family screening based on nutrient characteristics for a species should be conducted at the time when heritability is high.

Heritabilities of Nutrient Attributes

LA_{NUE} has been shown to be under stronger genetic control than nutrient retranslocation in both species (Table 5-1). Significant interspecific differences were very clear in N use efficiency ($h^2 = 0.41$ and 0.00 for loblolly and slash pine, respectively). Li et al. (1991b) reported a high heritability estimate ($h^2 = 0.84$) for nutrient use efficiency (defined as stem biomass produced per unit N applied per plant) in loblolly pine seedlings. The heritability for N productivity (defined as the slope of the linear regression between foliage N concentration and relative biomass increase rate) was estimated to be approximately 0.20 in Scots pine (*Pinus sylvestris*) seedlings (Jonsson et al. 1997). Although all these heritability estimates regarding N utilization have different definitions, it seems that N utilization is highly heritable in loblolly pine, moderately heritable in Scots pine, and less so if at all in slash pine.

Loblolly pine was associated with higher heritabilities for N and P use efficiency for leaf area production, while slash pine had higher heritabilities for Mg and Ca utilization efficiency. Such outcomes are in general agreement with differences found for foliage nutrient concentration heritabilities between the two species. Our previous results indicated that loblolly pine was significantly higher than slash pine in N, K, Mg, and Ca use efficiency, but lower in P use efficiency (Chapter 3). These findings suggest that loblolly pine may have higher Ca and Mg use efficiency than slash pine, but the variation in the two attributes was low among families in loblolly pine. On the contrary, slash pine had lower N and K use efficiency than loblolly pine, and also had lower variation among families for the two attributes.

One implication of our results relates to the selection of different LA_{NUE} attributes for tree improvement programs for the two species. Loblolly pine had lower P use efficiency and higher heritability than slash pine, which may provide opportunities for further improvement in loblolly pine breeding programs. Similarly, N use efficiency could be an important selection trait for increasing loblolly pine productivity because most pine plantations in Florida are deficient in N and P, but not in Ca and Mg (Jokela et al. 1988). For slash pine, the potential traits may only include Mg and Ca use efficiency. The other three attributes do not appear promising because of low heritabilities. From the perspective of LA_{NUE}, more genetic gains could probably be obtained from loblolly pine than from slash pine in that tree growth generally requires larger quantities of N, P, and K than Mg and Ca. It may also prove beneficial to improve LA_{NUE} for N and P in loblolly pine. However, it is still important for further studies to determine if higher nutrient use efficiencies lead to higher growth rates for the two species. Additionally, studies with more families should be conducted to confirm the differences in LA_{NUE} between loblolly and slash pine as only 32 families for slash pine and 16 families for loblolly pine were involved in the current study.

Heritability estimates for foliage nutrient content, nutrient retranslocation amount and retranslocation efficiency prior to needle senescence were low for loblolly pine. Therefore, these attributes may offer little potential for tree improvement programs. In contrast, the heritability of these same attributes for slash pine were generally as high as those for growth (e.g., foliage Mg content $h^2 = 0.24$, K retranslocation efficiency $h^2 = 0.16$) and, therefore, they may warrant further consideration in future breeding efforts.

Genotype × Environment Interactions in Nutritional Attributes

The objective of genotype × environment interaction analyses is to explore performance patterns produced by genotypes across sites or treatments. Most studies on genotype × environment interaction have focused on the production stability of various species at different locations, while less information is known about consistency of the foliage nutritional status across environments, which could be related to growth stability at different environments. It appeared that foliar macronutrient concentrations had significant family × site and family × treatment interactions over some sampling periods in both loblolly and slash pine. However, it was difficult to conclude that the nutritional stability of families was associated with their growth stability without finding a consistent pattern of nutrient levels at the different life cycle across sites or treatments (Appendix G). In comparison with loblolly pine, slash pine families maintained more consistent nutrient levels across sites or treatments. Given the significant family × site and family × treatment interactions in some growth and biomass attributes (Chapter 4), further studies should be conducted to examine interspecific differences between loblolly and slash pine in genotype × environment interactions and the stability of the relationships between growth and nutritional attributes across environments.

Little information is available to explain the biological nature and causes of genotype × environmental interactions. Genotype × environmental interaction studies require the experimental control of various environmental components (Federer and Scully 1993), which implies that resultant genotype × environment interactions are useful only after we know what factors cause the genotype differentiation. Lin and Binns (1994) suggested that genotype × environment interaction studies are incomplete unless researchers determine the underlying biological factors. For example, temperature during the critical growth stage was concluded to cause much of the genotype × environmental interaction in perennial ryegrass (*Lolium perenne* L.) (Eeuwijk and Elgersma 1993). Recognition of the underlying genetics in genotype × environmental interactions is difficult because environmental factors are complex and several genes may be involved in the response of an attribute to a specific environmental factor (Perez 1996). However, information about the biological nature and environmental components causing significant genotype × environment interactions is important since more potential gains could be realized if superior families were deployed based on their responses to different environments. In this study, the cause of genotype × environmental interactions in some nutritional traits might be attributed to differences in soil environments (Spodosol vs. Entisol and their features), as climatic conditions at the two locations were similar. Therefore, soil characteristics, especially those influencing nutritional status, should be further investigated to explore the cause of genotype × environment interactions for both species.

Genetic and Environmental Correlations between Growth and Nutrient Traits

Understanding the relationships between plant growth and foliage nutrient characteristics has been one of the contemporary research questions in production ecology. Most studies have only reported results of phenotypic correlations between the two traits. However, trait associations can result from both environmental factors and genes that affect both traits simultaneously. Environmental correlations can provide information about environmental factors (including treatment measures) that influence both traits similarly. Genetic correlations represent associations between the breeding values of two traits and indicate the strength of the genetic relationship between the two traits. Genetic correlations are also of great importance because they can result in changes across generations in traits that are not originally targeted by selection.

All environmental correlations between growth and nutritional attributes were positive for both species, except for the correlations between leaf area and foliar Ca or Mg concentrations in loblolly pine (Table 5-3). Sword et al. (1998) reported different responses in foliar Ca and Mg concentrations of loblolly pine families to treatments, and our previous results (Chapter 3) also revealed statistically significant interspecific differences in the dilution effects of Mg due to rapid leaf area development, especially under the intensive treatment. We primarily attributed the dilution effects to the antagonistic interactions between K and Mg. The current study showed that leaf area and Ca or Mg concentrations were environmentally negatively associated (r = -0.33 and -0.31 for leaf area with Ca and

Mg, respectively), suggesting that the negative relationships between leaf area and Mg concentrations could be induced by silvicultural treatments. Presumably, fertilization increased leaf area development but did not supplement sufficient Mg to meet further requirements. It remains to be seen if the trees will outgrow this apparent induced deficiency, as the root systems occupy greater soil volume and access higher levels of Mg supply.

LA_{NUE} and retranslocation rates in trees represent important nutritional physiological characteristics that have been intensively studied. Their relationships to stand production capacity in different forest ecosystems have led to the development of several theories regarding their biological mechanisms (Vitousek 1982; Chapin and Kedrowski 1983; Birk and Vitousek 1986; Nambiar and Fife 1991; Knops et al. 1997). However, most studies have focused on the functional ecology of these nutrient attributes, and less attention has been given to genetically correlated responses of growth and nutrient use efficiency or retranslocation rates in different environments, which would be more useful for selection activities used in tree improvement programs. Albrektson et al. (1995) reported high phenotypic correlations between volume yield capacity and mineral nutrient efficiency, but low correlations between yield capacity and N retranslocation rates in Scots pine (*Pinus sylvestris*) and lodgepole pine (*P. contorta*) stands; genetic correlations were unknown. Our results from loblolly pine (Table 5-3) and slash pine (Table 5-4) indicate that genetic correlations between growth (volume or leaf area) and all nutrient attributes were low to moderate and positive, suggesting that selection for growth factors will not cause correspondent decreases in a tree's capacity to utilize or retranslocate nutrients (i.e., negative selection pressure).

Because of the distinctly different inheritance patterns between loblolly and slash pine for most growth and nutritional attributes, direct species comparisons based on a common set of variables was not possible in the current study. Additional studies are required to better understand the underlying mechanisms of correlated genetic or environmental control on growth and nutritional traits for each of these species.

Summary

Genetic parameters (heritability, genotype × environment interactions, and genetic and environmental correlations) for fascicle macronutrient (N, P, K, Mg, Ca) concentrations, fascicle nutrient content, nutrient utilization efficiency of leaf area production, and retranslocation were estimated throughout an entire foliage cohort life cycle in 3- to 4-year-old loblolly and slash pine stands managed under two levels of silvicultural treatment at two locations in north central Florida. Narrow-sense heritability estimates for all nutrient attributes were low to moderate. Loblolly pine showed a higher but decreasing trend in foliar N concentration heritabilities over time than slash pine, which had little additive genetic variance for N concentration. Conversely, slash pine showed higher heritabilities in Ca and Mg concentrations than loblolly pine throughout the entire foliage life cycle. Nitrogen and P use efficiency was more heritable in loblolly pine than in slash pine, while Mg and Ca use efficiency was more heritable in slash pine than in loblolly pine. Further, nutrient retranslocation amounts and efficiencies were primarily controlled by environmental effects in both species. Some nutritional attributes (e.g., N and P use efficiency for loblolly pine, and Mg and Ca use efficiency for slash pine) have the potential to be included in tree improvement programs.

Family × site and family × treatment interactions were not significant in most sampling periods for macronutrient concentrations and fascicle content. Similarly, genotype × environment interactions were not important for LA_{NUE}, suggesting that for both species, families were consistent in nutrient utilization across sites and treatments. Genotype × environment interactions observed for most nutrients in retranslocation amount and efficiency were unimportant.

Genetic and environmental correlations among total leaf area and concentrations of N, P, K, Ca, and Mg in loblolly pine, and among volume, total leaf area, P, Ca and Mg use efficiency, and N and K retranslocation efficiency in slash pine, were estimated and analyzed. Leaf area in loblolly pine showed variable, low to moderate but positive genetic correlations with all macronutrients ($r = 0.02$ to 0.61). Leaf area was not highly environmentally correlated with any macronutrient in loblolly pine, and even negatively associated with foliar Mg ($r =-0.31$) and Ca ($r = -0.33$) concentrations. In slash pine, volume and leaf area were highly genetically associated with Ca use efficiency ($r = 0.45$ and 0.66, respectively), suggesting that at least some of the genes controlling volume growth, leaf area development, and Ca use efficiency may be identical.

CHAPTER 6
SUMMARY AND CONCLUSIONS

Crown structural and nutritional characteristics of forest trees are closely associated with growth performance. Genetic and environmental effects both play important roles in shaping characteristics of crown structure, foliage nutrition physiology and, ultimately, distinctive growth patterns among species or within a species. An understanding of these characteristics and their relationships is essential to improve our knowledge of mechanisms of tree growth. Additionally, an awareness of the effects of silvicultural treatments and locations are critical to the appropriate selection of superior and adaptive genotype for different treatment regimes and locations. This dissertation has focused on the genetics, nutrition and production ecology of two important and widely planted commercial timber species in the southeastern United States, loblolly pine and slash pine.

This study was overlaid on a larger progeny test consisting of seven pine species or hybrids conducted by the Cooperative Forest Genetics Research Program at the University of Florida. Sixteen families each from genetically improved loblolly and slash pine, and unimproved slash pine were selected as experimental materials. Two experimental sites, located at Dunnellon and Palatka, Florida, and consisting of a common study design, were chosen for this research project. Two levels of silvicultural treatments (high and low intensity) were applied at both sites. A total of 1,152 trees were repeatedly measured and sampled for the determination of crown structural, nutritional and growth characteristics from 1997 to 1998 when the trees were 3 and 4 years old, respectively.

This dissertation consists of five chapters. Chapter 1 reviewed relevant research findings and presented a broad overview on current issues pertinent to the growth and nutrition of forest trees. Based on the objectives of this study, interspecific and intraspecific differences in crown structure and nutrient dynamics were addressed. At the interspecific level, individual investigations dealt with (1) growth performance, crown structure, and their relationships in juvenile loblolly and slash pine; and (2) seasonal dynamics of foliar nutrients, nutrient use efficiency of leaf area production, and retranslocation in juvenile loblolly and slash pine. At the intraspecific level, the research focused on (1) genetic parameter estimates and correlations between crown structure and growth performance in loblolly and slash pine; and (2) genetic and environmental controls on nutritional characteristics and their correlations with growth in juvenile loblolly and slash pine. These topics corresponded to the main subjects reported in Chapters 2 to 5.

Interspecific Level Conclusions

At the taxa level, DBH and height growth were consistently greater in loblolly pine, but not significantly different from slash pine when averaged across study locations and treatments. Loblolly pine maintained about 44 and 39 branches per tree at age 3 and 4 years, respectively, about 10 and 8 branches more for each year than slash pine. Loblolly pine at Dunnellon had greater crown size (57%) than at Palatka (44%) at age 3 years, while the reverse was true for improved slash (50% vs. 57%) and unimproved slash pine (33% vs. 46%).

Loblolly pine had higher current-year needle SLA (176.6 cm^2/g) than improved slash pine (147.8 cm^2/g) and unimproved slash pine (144.9 cm^2/g). In addition, loblolly pine tended to accumulate more leaf biomass than either of the slash pine taxa, regardless of treatments and locations. Similar trends followed for branch biomass and total crown biomass (branches plus foliage): loblolly pine > improved slash pine > unimproved slash pine. Current-year leaf area generally accounted for more than 90% of the total leaf area among all taxa, but slash pine accumulated less leaf area than loblolly pine at both locations; however, differences between unimproved and improved slash pine were not significant. Vertical differences among taxa in total leaf area per tree were shown in both the relative distribution patterns and the absolute amount of leaf area along crown profiles. Most notably, loblolly pine partitioned 8% of the total leaf area in the upper crown, while slash pine partitioned about13% and, thereby, contributed to a significant taxa × position interaction (p # 0.0008).

Similar to other published reports, loblolly pine at this juvenile stage of development consistently produced less volume per unit leaf area (804 cm^3 wood/m^2 leaf area) than improved slash pine (1,106 cm^3 wood/m^2 leaf area) and unimproved slash pine (1,173 cm^3 wood/m^2 leaf area), within a given location and treatment. However, volume increments of individual trees converged among taxa as leaf area approached 54 m^2/tree(both treatments) at Dunnellon, and 40 and 55 m^2/tree for the non-intensive and intensive silvicultural treatments, respectively, at Palatka.

Nutritional characteristics also showed both similarities and differences among taxa. For example, foliar N, P, and K concentrations generally decreased, while Ca and Mg concentrations increased over an entire leaf life cycle for all the three taxa. However, the magnitude of change in foliar nutrient concentrations, fascicle nutrient content, and fascicle weight was different in terms of taxa, location, and treatment. Loblolly pine consistently and significantly had higher N and P concentrations than slash pine, regardless of locations and treatments. Differences among the three taxa in K concentrations was not significant, while Ca and Mg concentrations were highly variable among taxa and dependent upon experimental location (Mg) and treatment (Ca).

Significant differences in LA_{NUE} were found among taxa and within a taxon. Loblolly pine had significantly higher N, K, Mg, and Ca utilization efficiency for developing leaf area than slash pine, while differences between improved and unimproved slash pine were not significant except for K use efficiency. Loblolly pine also had significantly higher crown nutrient content for all five elements compared to slash pine. Although differences between improved and unimproved slash pine in crown nutrient content were not significant, improved slash pine consistently had higher absolute amounts than unimproved slash pine. Additionally, loblolly pine displayed significantly higher nutrient retranslocation efficiency for N, P, and K than either slash pine taxa, while no differences were found in Mg and Ca retranslocation efficiency among taxa. Differences between improved and unimproved slash pine in nutrient retranslocation efficiencies were not significant except for N (32% vs. 25% for improved and unimproved slash pine, respectively).

The intensive silvicultural treatment significantly increased fascicle weight, foliage nutrient content, and nutrient retranslocation amount, but did not affect nutrient retranslocation efficiency (percent nutrient retranslocated from fascicles). The intensive silvicultural treatment increased foliar N and K concentrations and decreased Mg and Ca concentrations, but had no significant influence on P concentrations at most sampling periods among the three taxa. The intensive treatment also significantly decreased N, P, and K use efficiency, but increased Mg and Ca use efficiency.

Intraspecific Level Conclusions

Intraspecific studies in this dissertation concentrated on examining genetic variation and related characteristics of crown structure, growth, and nutritional attributes. Genetic parameter estimates (e.g., heritability, genotype × environment interaction, genetic correlation) were determined to achieve these objectives. A total of 18 growth and crown structural characteristics (i.e., volume, total branch number, crown length and width, crown shape ratio, height to base of crown, branch number per unit crown length, leaf area per unit crown length, current-year and 1-year-old leaf biomass, total leaf biomass, branch biomass, crown biomass, current-year and 1-year-old leaf area, total leaf area, and current-year and 1-year-old specific leaf area) were analyzed.

Heritability estimates for the above attributes were generally low to moderate for both species ($h^2 = 0.00$ to 0.49). Two noteworthy exceptions with slash pine were for total branch number ($h^2 = 0.62$) and branch number per unit crown length ($h^2 = 0.60$). Most crown and leaf area traits were under certain genetic control and had similar heritability values as growth traits and, therefore, could be incorporated into tree improvement programs.

Genotype × environment interactions for most attributes (type B genetic correlations) were variable, primarily due to the small sample size. Family × site or family × treatment interaction results for these crown structural and growth traits indicated differential family responses to sites or treatments in loblolly and slash pine. With loblolly pine, more than half of the total traits had significant family × site interaction, while only biomass-related attributes and crown structural traits (except crown shape ratio) had significant family × treatment interactions. Family × treatment interactions were not significant for most attributes in slash pine. Significant family × treatment interactions in current-year leaf biomass and total crown biomass across treatments (type B correlation = 0.42 and 0.41, respectively) showed that slash pine families differed in developing and partitioning current-year leaf and total crown biomass across treatments.

Selected growth and crown structural attributes for loblolly pine (total branch number, crown width, leaf area per unit crown length, branch biomass, and total leaf area) and slash pine (volume, total branch number, branch number per unit crown length, leaf area per unit crown length, and total leaf area in slash pine) were analyzed for genetic and environmental correlations to further understand relationships among these traits. Genetic and environmental correlations were all positive in loblolly pine, revealing that larger trees were more associated with wider crowns, more branch numbers, and higher amounts of branch biomass and leaf area than small trees. Results for slash pine indicated that large trees were associated with more branches and leaf area, but few branches per unit tree height. This suggests that tall trees with larger internode length favor greater volume growth in slash pine. Loblolly pine differed most significantly from slash pine in total branch number. Loblolly pine had a larger proportion of environmental variance (81%) than slash pine (18%) for branch number.

Nutritional attributes that were investigated in relation to intraspecific variation included concentrations and fascicle content of N, P, K, Ca, and Mg at eight sampling periods throughout an entire foliage life cycle, total foliage nutrient content in the crown, LA_{NUE}, and nutrient retranslocation amount and efficiency for all five macronutrients. Heritability estimates for most nutrient attributes were low to moderate ($h^2 = 0.00$ to 0.41). Loblolly pine showed a higher but decreasing trend of heritabilities in foliage N concentrations through the foliage life cycle than slash pine, which had little additive genetic variance in N concentration. Conversely, slash pine showed higher heritabilities in Ca and Mg concentrations than loblolly pine through the foliage life cycle. Nitrogen and P use efficiency was more heritable in loblolly pine ($h^2 = 0.41$ and 0.27 for N and P, respectively) than in slash pine ($h^2 = 0.00$ and 0.11 for N and P, respectively), while Mg and Ca use efficiency was more heritable in slash pine ($h^2 = 0.26$ and 0.32 for Mg and Ca, respectively) than in loblolly pine ($h^2 = 0.12$ and 0.00, respectively). It appeared that nutritional attributes related to N and P were more heritable in loblolly pine, while nutritional attributes related to Ca and Mg were more heritable in slash pine. The magnitude of heritability estimates for some nutritional attributes (i.e., LA_{NUE}) was similar to that of crown structural traits and could be considered in tree improvement programs.

Family × site and family × treatment interactions were not important in most sampling periods for nutrient concentrations and fascicle nutrient content of the five elements in both species. Similarly, genotype × environment interactions were not important in LA_{NUE}, retranslocation amount and efficiency of all five elements, indicating that families in each species were stable in the expression of these nutrient traits across sites and treatments.

Genetic and environmental correlations among leaf area and concentrations of N, P, K, Ca, and Mg in loblolly pine, and among volume, leaf area, P, Ca and Mg use efficiency, and N and K retranslocation efficiency in slash pine, were estimated and analyzed. Leaf area in loblolly pine showed variable, low to moderate, but positive genetic correlations with all macronutrients (r = 0.02 to 0.61). However, leaf area was negatively associated with Mg and Ca concentrations (r =-0.31 and -0.33, respectively). In slash pine, volume and leaf area were highly genetically associated with Ca use efficiency (r = 0.45 and 0.66, respectively), suggesting that at least some of the genes controlling volume growth, leaf area development, and Ca use efficiency may be identical.

Major results regarding the differences in crown structure, nutritional attributes, and their genetic architecture were summarized across locations and treatments for the two species (Table 6-1). Results from these investigations highlight potentially important differences in growth performance, crown structural development, and nutritional processes among improved loblolly pine, and improved and unimproved slash pine that may contribute to long-term growth differentials. At the current development stage (3 to 4 years old), loblolly pine tended to be the most productive taxon, especially on the intensively-managed plots. Genetic variation at the intraspecific level also indicate significant differences among families in growth, crown structure, and nutritional attributes, suggesting that these attributes could be considered in tree improvement programs for the two species.

Table 6-1. A comparison of growth characteristics in crown structure and nutritional attributes for loblolly and slash pine at ages 3 and 4 years old.

Characteristics	Loblolly pine	Slash pine
Crown Structure		
Total branch number per tree	greater (35 to 51)	fewer (28 to 39)
Live crown length	greater (> 4.0 m)	smaller (< 4.0 m)
Crown width	greater (> 2.0 m)	smaller (< 2.0 m)
Specific leaf area (cm^2/g)	current-year (> 170) one-year-old (> 130)	current-year (< 160) one-year-old (< 130)
Branch biomass (kg/tree)	greater (> 2.5)	smaller (< 2.0)
Leaf:branch biomass ratio	smaller (< 2.0)	greater (> 2.0)
Total leaf area per tree (m^2/tree)	age 3 years > 35 age 4 years > 50	age 3 years < 20 age 4 years < 35
Vertical distribution of leaf area	greater in middle and lower positions, smaller in upper crown (c. 8%)	greater in upper crown (c. 13%)
Stemwood growth efficiency (cm^3 wood/m^2 leaf area)	smaller (c. 800)	greater (> 1100)
Dry weight per fascicle (g)	smaller (< 140)	greater (> 180)
Nutritional attributes		
Nutrient concentrations	higher in N and P, lower in Ca	higher in Ca, lower in N and P
Nutrient content (g/tree) of crowns	higher for all 5 macronutrients	lower for all 5 macronutrients
Nutrient use efficiency for leaf area development (cm^2 leaf area/mmol nutrient)	higher in N, K, Mg, and Ca, lower in P	higher in P, lower in N, K, Mg, and Ca
Nutrient retranslocation efficiency (%)	higher in N, P, and K	lower in N, P, and K

Table 6-1– Continued.

Genetic architecture in crown structure and nutrients		
Heritabilities for crown structure	moderate in crown length, width, crown shape ratio, total leaf area, and leaf area per unit crown length	moderate to high in total branch number per tree, branch number per unit crown length, and total leaf area per tree
Heritabilities for nutritional attributes	moderate to high in N concentrations, low in Ca and Mg concentrations, moderate in N and P use efficiency for leaf area development, low in Ca and Mg use efficiency	moderate in Ca and Mg concentrations, low in N concentrations, moderate in Ca and Mg use efficiency for leaf area development, low in N and P use efficiency
Genotype × environment interaction	important for crown structure, crown biomass, and leaf area; not important for nutritional attributes	not important for almost all crown structure and nutritional attributes
Genetic and environmental correlation	large trees associated with wider crowns, more branch numbers, and large amount of branch biomass and leaf area; leaf area had low to moderate, but positive genetic correlations with all macronutrients	large trees associated with more branch numbers, large amount of leaf area, and few branches per unit crown height; volume and leaf area were highly associated with Ca use efficiency for leaf area development

Note: For heritability estimates, only levels of the values are given: low ($h^2 < 0.20$), moderate ($0.20 \# h^2 \# 0.40$), high ($h^2 > 0.40$).

APPENDIX A

RELATIONSHIPS BETWEEN BRANCH DIAMETER AND PREDICTED FOLIAGE BIOMASS, AND RESPONSES OF SELECTED CROWN ATTRIBUTES TO SILVICULTURAL TREATMENTS FOR IMPROVED LOBLOLLY, IMPROVED SLASH AND UNIMPROVED SLASH PINE AT TWO LOCATIONS IN NORTH CENTRAL FLORIDA

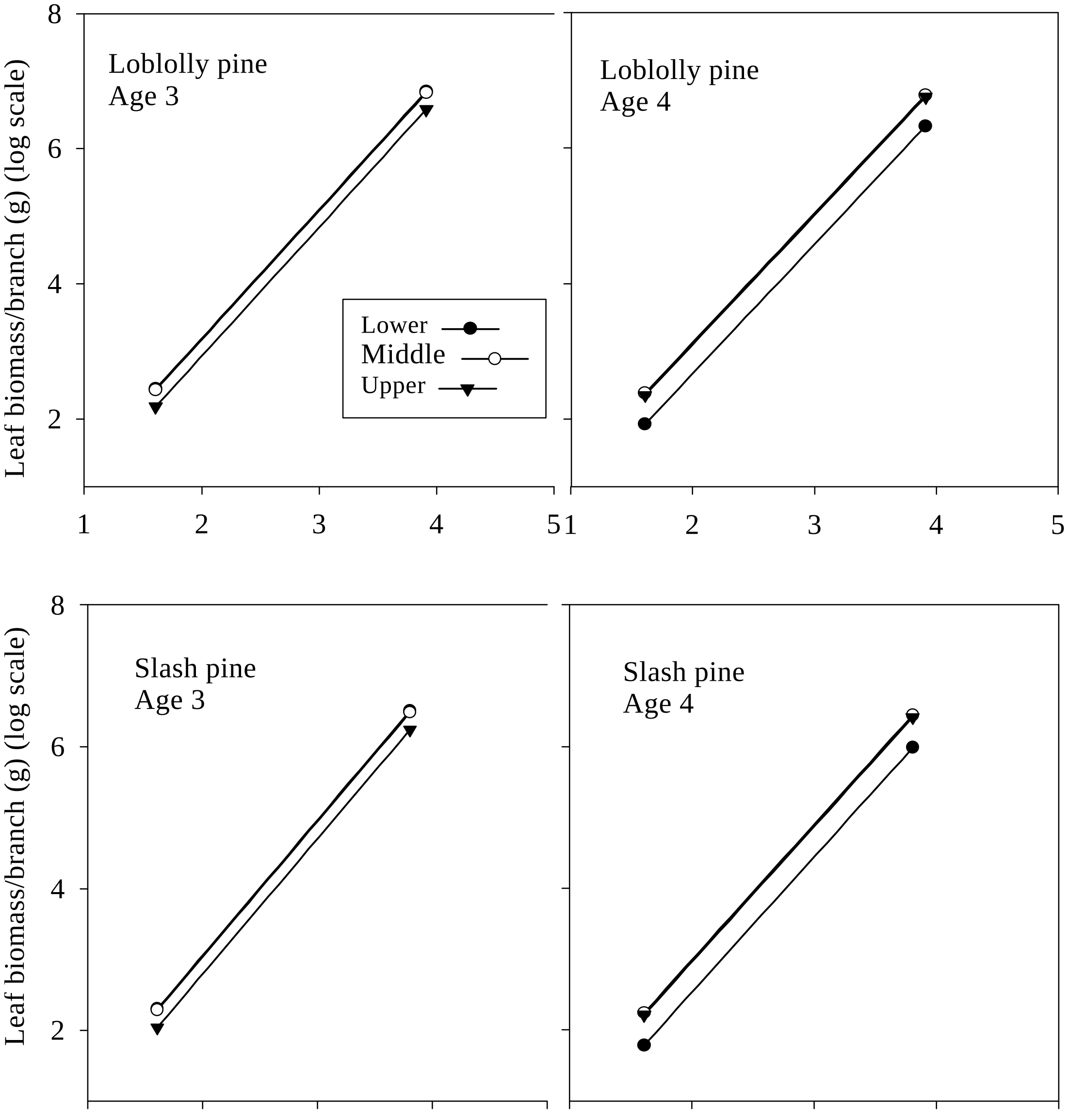

Figure A-1. Relationships between branch diameter and predicted total foliage biomass at different crown positions in loblloly and slash pine at ages 3 and 4 years.

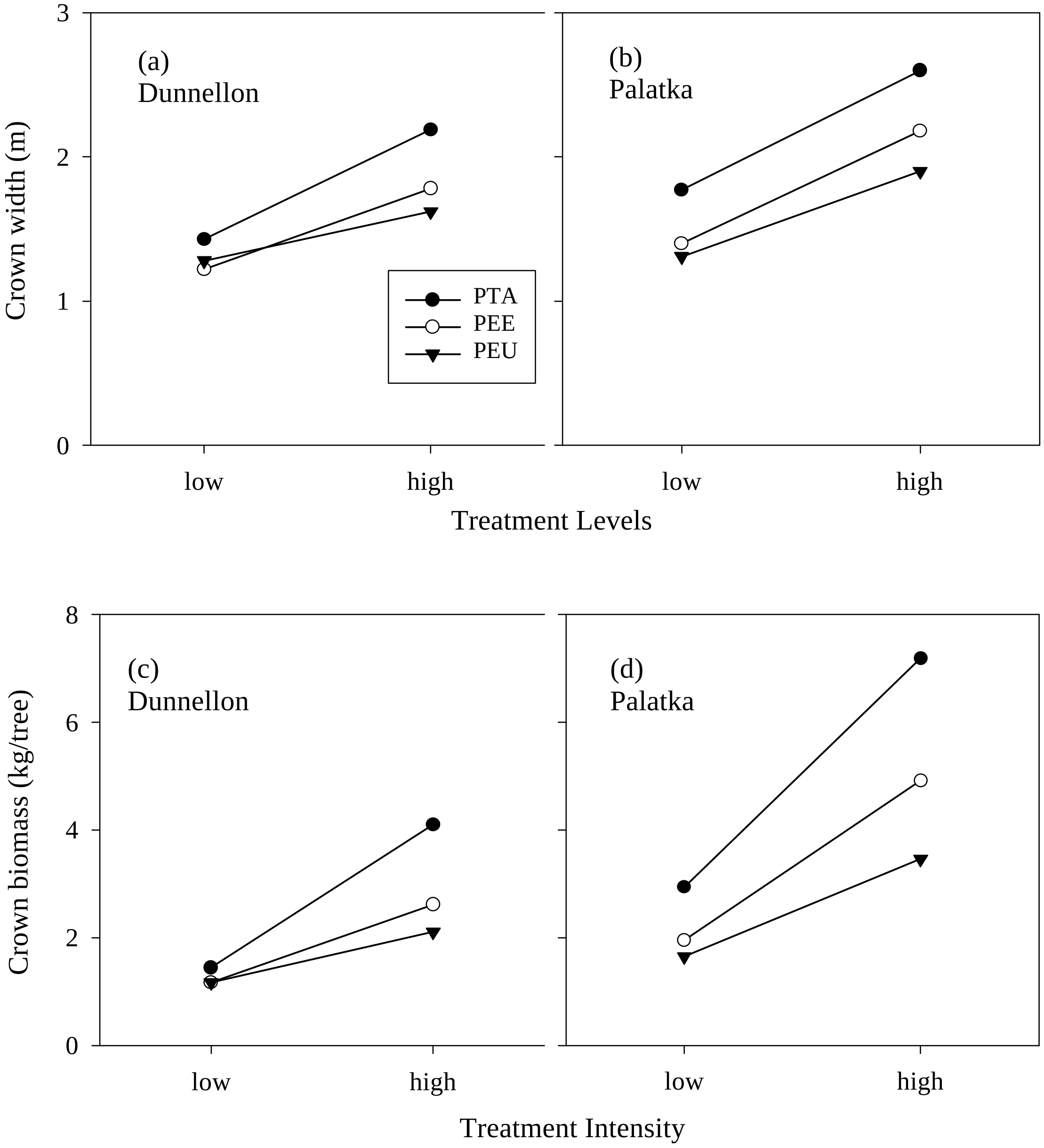

Figure A-2. Responses among taxa at age 3 years in crown width (a and b) and total crown biomass (c and d) to silvicultural treatments at two locations in north central Florida.

Note: PTA = improved loblolly pine	low = non-intensive treatment
PEE = improved slash pine	high = intensive treatment
PEU = unimproved slash pine	

APPENDIX B

ANOVA FOR MENSURATIONAL AND CROWN STRUCTURAL ATTRIBUTES FOR 3- AND 4-YEAR-OLD LOBLOLLY AND SLASH PINE PLANTED AT TWO LOCATIONS IN NORTH CENTRAL FLORIDA[a].

Source of variation	Age	DBH	Height	Branch no. per tree	Live crown length	Crown width	Crown shape ratio	Branch-free stem length
				Location = Dunnellon				
Treatment	Year 3	***	***	***	***	***	NS	***
	Year 4	***	***	*	***	*	NS	***
Taxa[b]	Year 3	NS	*	***	*	***	***	***
	Year 4	NS	NS	*	**	NS	NS	NS
PTA vs. PEE	Year 3	*	*	***	**	***	***	***
	Year 4	NS	NS	**	***	*	NS	NS
PEU vs. PEE	Year 3	NS	NS	NS	NS	NS	**	NS
	Year 4	NS	NS	NS	NS	NS	NS	NS
Treatment*Taxa	Year 3	*	*	NS	*	***	NS	NS
	Year 4	*	**	NS	**	NS	**	NS
Family(Taxa)	Year 3	NS	*	***	*	**	*	NS
	Year 4	*	**	***	*	NS	*	*
Treatment*Family(Taxa)	Year 3	NS	NS	NS	NS	NS	NS	NS
	Year 4	NS	**	NS	NS	NS	NS	*
Block(Treatment)	Year 3	NS	NS	NS	NS	*	*	NS
	Year 4	NS	NS	NS	NS	**	***	NS
Taxa*Block(Treatment)	Year 3	***	***	***	***	NS	*	**
	Year 4	***	*	NS	NS	NS	NS	NS

APPENDIX B--Continued.

Source of variation	Age	DBH	Height	Branch no. per tree	Live crown length	Crown width	Crown shape ratio	Branch-free stem length
Location = Palatka								
Treatment	Year 3	***	***	***	***	***	NS	NS
	Year 4	***	***	*	**	**	NS	***
Taxa[b]	Year 3	NS	**	***	**	***	**	NS
	Year 4	*	**	***	***	*	**	NS
PTA vs. PEE	Year 3	NS	**	***	**	***	**	NS
	Year 4	NS	**	***	***	NS	**	*
PEU vs. PEE	Year 3	*	NS	NS	NS	*	NS	NS
	Year 4	NS	NS	NS	NS	NS	NS	NS
Treatment*Taxa	Year 3	NS	NS	NS	NS	NS	NS	NS
	Year 4	NS	NS	NS	NS	***	NS	NS
Family(Taxa)	Year 3	NS	**	***	NS	NS	*	***
	Year 4	***	***	***	***	***	NS	NS
Treatment*Family(Taxa)	Year 3	**	**	NS	**	**	*	NS
	Year 4	NS	NS	NS	NS	NS	NS	NS
Block(Treatment)	Year 3	NS	NS	**	NS	NS	NS	NS
	Year 4	NS	NS	NS	NS	*	NS	NS
Taxa*Block(Treatment)	Year 3	***	***	NS	***	***	***	***
	Year 4	***	***	NS	***	NS	**	**

a Analyses were conducted separately by year and location. For a given source of variation, main effects and interactions were significant at *** p # 0.01, ** p # 0.05, * p # 0.10. NS = not significant.

b PTA = improved loblolly pine PEE = improved slash pine PEU = unimproved slash pine

APPENDIX C

ANOVA FOR CROWN BIOMASS AND LEAF AREA ATTRIBUTES FOR 3- AND 4-YEAR-OLD LOBLOLLY AND SLASH PINE PLANTED AT TWO LOCATIONS IN NORTH CENTRAL FLORIDA[a].

Source of variation	Age	Current year leaf biomass	One-year-old leaf biomass	Total leaf biomass	Branch biomass	Total crown biomass	Current year leaf area	One-year-old leaf area	Total leaf area	Current/ total ratio in leaf area
					Location = Dunnellon					
Treatment	Year 3	***	***	***	***	***	***	***	***	*
	Year 4	***	***	***	***	***	***	***	***	***
Taxa[b]	Year 3	***	*	**	***	***	***	***	***	***
	Year 4	***	NS	**	***	***	***	*	***	***
PTA vs. PEE	Year 3	***	NS	**	***	***	***	**	***	***
	Year 4	***	NS	**	***	***	***	**	***	**
PEU vs. PEE	Year 3	NS	NS	NS	NS	NS	NS	NS	NS	**
	Year 4	NS	NS	NS	NS	NS	NS	NS	NS	*
Treatment*Taxa	Year 3	**	*	**	***	**	***	**	**	**
	Year 4	**	NS	**	***	**	**	NS	**	**
Family(Taxa)	Year 3	**	**	**	**	**	***	***	***	***
	Year 4	NS	*	NS	NS	NS	NS	*	NS	NS

APPENDIX C--Continued.

Source of variation	Age	Current year leaf biomass	One-year-old leaf biomass	Total leaf biomass	Branch biomass	Total crown biomass	Current year leaf area	One-year-old leaf area	Total leaf area	Current/ total ratio in leaf area
					Location = Dunnellon					
Treatment*Family (Taxa)	Year 3	NS	NS	NS	NS	NS	NS	NS	NS	NS
	Year 4	NS	*	NS	NS	NS	NS	NS	NS	NS
Block(Treatment)	Year 3	NS	NS	NS	NS	NS	NS	NS	NS	*
	Year 4	*	*	*	NS	*	NS	NS	NS	NS
Taxa*Block (Treatment)	Year 3	***	***	***	***	***	***	***	***	NS
	Year 4	NS	NS	NS	NS	NS	*	NS	NS	**

APPENDIX C--Continued.

Source of variation	Age	Current year leaf biomass	One-year-old leaf biomass	Total leaf biomass	Branch biomass	Total crown biomass	Current year leaf area	One-year-old leaf area	Total leaf area	Current/ total ratio in leaf area
					Location = Palatka					
Treatment	Year 3	***	***	***	***	***	***	***	***	***
	Year 4	**	**	**	**	**	***	**	***	*
Taxa[b]	Year 3	***	***	***	***	***	***	***	***	***
	Year 4	***	***	***	***	***	***	***	***	***
PTA vs. PEE	Year 3	***	**	***	***	***	***	***	***	**
	Year 4	***	**	***	***	***	***	***	***	NS
PEU vs. PEE	Year 3	**	**	**	*	**	*	**	*	***
	Year 4	NS	NS	NS	NS	NS	NS	NS	NS	***
Treatment*Taxa	Year 3	**	NS	*	**	**	**	NS	*	**
	Year 4	NS	NS	NS	NS	NS	NS	NS	NS	*
Family(Taxa)	Year 3	*	*	*	*	*	**	**	**	NS
	Year 4	**	*	**	***	**	*	*	**	NS

APPENDIX C--Continued.

Source of variation	Age	Current year leaf biomass	One-year-old leaf biomass	Total leaf biomass	Branch biomass	Total crown biomass	Current year leaf area	One-year-old leaf area	Total leaf area	Current/ total ratio in leaf area
					Location = Palatka					
Treatment*Family (Taxa)	Year 3	NS	NS	NS	NS	NS	NS	**	*	***
	Year 4	NS	NS	NS	NS	NS	NS	NS	NS	NS
Block(Treatment)	Year 3	NS	NS	NS	NS	NS	NS	NS	NS	NS
	Year 4	NS	NS	NS	NS	NS	NS	NS	NS	NS
Taxa*Block (Treatment)	Year 3	***	***	***	***	***	***	***	***	NS
	Year 4	NS	NS	NS	NS	NS	NS	NS	NS	NS

---

[a] Analyses were conducted separately by year and location. For a given source of variation, main effects and interactions were significant at *** p # 0.01, ** p # 0.05, * p # 0.10. NS = not significant.

[b] PTA = improved loblolly pine
PEE = improved slash pine
PEU = unimproved slash pine

APPENDIX D

ANOVA FOR NUTRIENT CONCENTRATION, NUTRIENT CONTENT PER FASCICLE, AND AVERAGE FASCICLE WEIGHT IN LOBLOLLY AND SLASH PINE AT AGE 3 AND 4 YEARS. EIGHT SAMPLING PERIODS CORRESPONDED TO THE LIFE CYCLE OF THE SAME NEEDLE COHORT. ALL EXPERIMENTAL TREES WERE SUBJECTED TO TWO LEVELS OF SILVICULTURAL TREATMENTS AND PLANTED AT TWO LOCATIONS IN NORTH CENTRAL FLORIDA[a].

Superscript notations in this appendix indicate:

a Analyses were conducted separately by location, treatment and sampling period. For a given source of variation, main effects and interactions were significant at *** p # 0.01, ** p # 0.05, * p # 0.10. NS = not significant.

b sampling periods:
p1 = June 1997
p2 = September 1997
p3 = November 1997
p4 = February 1998
p5 = April 1998
p6 = June 1998
p7 = September 1998
p8 = December 1998.

c PTA = improved loblolly pine
PEE = improved slash pine
PEU = unimproved slash pine.

Table D-1. N concentration (%).

Source of variation	p1[b]	p2	p3	p4	p5	p6	p7	p8
Location	***	***	***	***	***	***	***	***
Treatment	***	***	***	NS	***	**	NS	NS
Taxa[c]:	***	**	***	***	***	***	***	***
PTA vs. PEE	***	**	***	***	***	***	***	***
PEE vs. PEU	NS	NS	**	NS	NS	*	NS	NS
Location * treatment	***	*	***	***	***	***	***	NS
Location * taxa	***	*	***	***	***	***	***	NS
Treatment * taxa	NS	*	NS	**	NS	***	NS	NS
Family(taxa)	***	**	***	***	***	NS	**	***
Block(treatment)	NS	NS	NS	NS	NS	*	NS	NS
Location * family (taxa)	NS	NS	*	NS	**	NS	NS	NS
Treatment * family(taxa)	NS	NS	NS	NS	**	NS	NS	NS
Taxa * block(treatment)	***	***	***	***	***	***	***	***
Location * treatment * taxa	***	***	***	***	NS	***	**	***
Location * treatment * family(taxa)	NS	NS	NS	NS	NS	**	NS	NS

Table D-2. P concentration (%).

Source of variation	p1[b]	p2	p3	p4	p5	p6	p7	p8
Location	***	***	***	***	***	***	***	***
Treatment	***	*	NS	NS	NS	NS	NS	NS
Taxa[c]:	***	***	***	***	***	***	***	***
PTA vs. PEE	***	***	***	***	***	***	***	***
PEE vs. PEU	**	***	NS	NS	NS	NS	NS	NS
Location * treatment	**	***	***	***	***	***	***	***
Location * taxa	***	***	***	***	***	NS	NS	NS
Treatment * taxa	NS	NS	NS	**	NS	NS	NS	NS
Family(taxa)	**	**	***	**	***	**	***	***
Block(treatment)	NS	NS	NS	**	NS	NS	NS	NS
Location * family (taxa)	NS	NS	**	**	**	NS	**	NS
Treatment * family(taxa)	NS	NS	NS	NS	NS	**	NS	NS
Taxa * block(treatment)	***	***	***	**	***	***	***	***
Location * treatment * taxa	***	NS	NS	***	NS	NS	***	NS
Location * treatment * family(taxa)	*	*	NS	NS	NS	NS	NS	NS

Table D-3. K concentration (%).

Source of variation	p1[b]	p2	p3	p4	p5	p6	p7	p8
Location	***	***	***	***	***	***	***	***
Treatment	***	***	***	***	***	***	***	***
Taxa[c]:	**	**	***	**	**	***	**	**
PTA vs. PEE	**	NS	***	**	NS	NS	**	**
PEE vs. PEU	NS	**	*	*	**	***	NS	NS
Location * treatment	***	*	***	***	***	***	***	***
Location * taxa	***	***	*	***	NS	***	NS	NS
Treatment * taxa	NS	*	NS	NS	NS	NS	NS	NS
Family(taxa)	**	*	NS	**	NS	*	**	**
Block(treatment)	NS	NS	NS	NS	NS	NS	NS	NS
Location * family (taxa)	NS	NS	NS	NS	NS	NS	**	NS
Treatment * family(taxa)	NS	NS	NS	NS	**	NS	**	*
Taxa * block(treatment)	***	***	***	***	***	***	***	***
Location * treatment * taxa	***	***	NS	*	***	NS	***	***
Location * treatment * family(taxa)	NS	*	*	**	NS	NS	NS	NS

Table D-4. Ca concentration (%).

Source of variation	p1[b]	p2	p3	p4	p5	p6	p7	p8
Location	***	***	***	***	***	NS	***	***
Treatment	NS	**	**	**	***	NS	**	NS
Taxa[c]:	**	***	***	***	***	***	**	**
PTA vs. PEE	**	***	***	***	***	**	**	*
PEE vs. PEU	NS	NS	*	*	NS	**	NS	NS
Location * treatment	NS	***	***	***	***	NS	***	***
Location * taxa	***	***	***	***	***	***	***	NS
Treatment * taxa	NS	NS	NS	NS	NS	NS	NS	NS
Family(taxa)	NS	NS	*	NS	NS	NS	**	**
Block(treatment)	NS	NS	NS	NS	NS	NS	NS	NS
Location * family (taxa)	NS	NS	NS	NS	NS	NS	NS	NS
Treatment * family(taxa)	NS	NS	NS	NS	NS	NS	NS	NS
Taxa * block(treatment)	***	***	***	***	***	***	***	***
Location * treatment * taxa	***	***	NS	NS	***	***	***	***
Location * treatment * family(taxa)	NS	**	**	**	**	*	**	**

Table D-5. Mg concentration (%).

Source of variation	p1[b]	p2	p3	p4	p5	p6	p7	p8
Location	***	***	NS	***	**	***	***	***
Treatment	***	***	***	***	***	***	***	***
Taxa[c]:	**	**	*	NS	NS	*	***	***
PTA vs. PEE	**	**	*	NS	NS	*	***	***
PEE vs. PEU	**	NS	NS	NS	NS	NS	NS	NS
Location * treatment	***	NS	NS	**	**	NS	***	***
Location * taxa	***	***	***	*	***	***	***	***
Treatment * taxa	***	NS	NS	*	*	NS	NS	NS
Family(taxa)	NS	**	NS	*	**	*	***	**
Block(treatment)	NS	NS	NS	NS	NS	*	NS	NS
Location * family (taxa)	NS	NS	NS	NS	NS	*	NS	NS
Treatment * family(taxa)	NS	NS	*	**	NS	NS	NS	NS
Taxa * block(treatment)	**	***	***	***	***	**	***	***
Location * treatment * taxa	***	***	***	***	**	***	***	***
Location * treatment * family(taxa)	**	NS	NS	NS	NS	NS	NS	NS

Table D-6. Average fascicle weight (mg/fascicle).

Source of variation	p1[b]	p2	p3	p4	p5	p6	p7	p8
Location	***	***	***	***	NS	***	***	**
Treatment	***	***	***	NS	NS	***	***	***
Taxa[c]:	***	***	***	***	***	***	***	***
PTA vs. PEE	***	***	***	***	***	***	***	***
PEE vs. PEU	NS	NS	NS	NS	NS	NS	NS	NS
Location * treatment	NS	**	***	***	***	***	***	***
Location * taxa	***	***	NS	**	NS	***	NS	**
Treatment * taxa	***	NS	NS	***	NS	NS	**	NS
Family(taxa)	***	**	***	*	*	NS	NS	NS
Block(treatment)	NS	NS	NS	***	**	*	NS	NS
Location * family (taxa)	NS	NS	NS	NS	NS	NS	NS	NS
Treatment * family(taxa)	NS	NS	NS	NS	NS	NS	NS	NS
Taxa * block(treatment)	**	***	***	NS	***	***	NS	NS
Location * treatment * taxa	NS	***	NS	*	NS	***	***	NS
Location * treatment * family(taxa)	NS	NS	NS	NS	NS	NS	NS	**

Table D-7. N content (mg/fascicle).

Source of variation	p1[b]	p2	p3	p4	p5	p6	p7	p8
Location	***	***	***	***	***	***	***	***
Treatment	***	***	***	NS	NS	***	***	**
Taxa[c]:	*	***	***	***	***	***	***	***
PTA vs. PEE	*	***	***	***	***	***	***	***
PEE vs. PEU	NS	*	NS	*	NS	NS	NS	NS
Location * treatment	NS	**	***	***	***	***	***	***
Location * taxa	*	***	NS	*	*	***	NS	***
Treatment * taxa	*	**	NS	*	NS	NS	NS	NS
Family(taxa)	**	*	*	NS	**	NS	NS	NS
Block(treatment)	NS	NS	NS	NS	NS	NS	NS	NS
Location * family (taxa)	NS	NS	NS	NS	NS	NS	**	NS
Treatment * family(taxa)	NS	NS	NS	NS	NS	NS	NS	NS
Taxa * block(treatment)	***	***	***	NS	NS	***	**	NS
Location * treatment * taxa	**	***	*	**	***	*	***	***
Location * treatment * family(taxa)	NS	NS	NS	NS	NS	*	NS	*

Table D-8. P content (mg/fascicle).

Source of variation	p1[b]	p2	p3	p4	p5	p6	p7	p8
Location	***	***	***	***	***	NS	***	***
Treatment	***	***	*	NS	NS	***	*	NS
Taxa[c]:	***	***	NS	***	**	***	**	***
PTA vs. PEE	***	NS	NS	***	**	***	**	***
PEE vs. PEU	**	***	NS	NS	NS	NS	NS	NS
Location * treatment	NS	***	***	***	***	***	***	***
Location * taxa	***	**	*	**	NS	***	NS	***
Treatment * taxa	***	NS	NS	***	NS	NS	NS	**
Family(taxa)	*	**	**	NS	**	*	**	*
Block(treatment)	NS	NS	NS	**	NS	NS	NS	NS
Location * family (taxa)	NS	NS	NS	NS	NS	NS	*	NS
Treatment * family(taxa)	NS	NS	NS	NS	NS	NS	*	NS
Taxa * block(treatment)	***	***	***	NS	***	***	***	***
Location * treatment * taxa	***	***	NS	***	**	NS	***	***
Location * treatment * family(taxa)	**	NS	NS	NS	NS	NS	NS	**

Table D-9. K content (mg/fascicle).

Source of variation	p1[b]	p2	p3	p4	p5	p6	p7	p8
Location	***	***	***	***	***	***	***	***
Treatment	***	***	***	***	***	***	***	***
Taxa[c]:	***	***	***	***	***	***	***	***
PTA vs. PEE	***	***	***	***	***	***	***	***
PEE vs. PEU	NS	***	NS	**	*	***	NS	NS
Location * treatment	NS	NS	***	***	***	***	***	***
Location * taxa	**	***	***	***	*	***	**	***
Treatment * taxa	*	NS	*	NS	NS	***	NS	NS
Family(taxa)	*	*	*	*	*	*	NS	NS
Block(treatment)	NS	NS	NS	NS	NS	NS	NS	NS
Location * family (taxa)	NS	NS	NS	NS	NS	NS	*	NS
Treatment * family(taxa)	NS	NS	*	NS	*	NS	*	NS
Taxa * block(treatment)	***	***	***	**	***	*	***	***
Location * treatment * taxa	NS	***	NS	NS	**	***	***	**
Location * treatment * family(taxa)	NS	NS	NS	NS	NS	NS	NS	*

Table D-10. Ca content (mg/fascicle).

Source of variation	p1[b]	p2	p3	p4	p5	p6	p7	p8
Location	***	***	***	***	***	**	***	***
Treatment	**	NS	NS	**	**	**	NS	NS
Taxa[c]:	***	***	***	***	***	***	***	***
PTA vs. PEE	***	***	***	***	***	***	***	***
PEE vs. PEU	NS	NS	NS	*	NS	NS	*	NS
Location * treatment	NS	***	***	***	***	***	***	***
Location * taxa	***	***	***	***	NS	***	*	***
Treatment * taxa	*	NS	NS	NS	NS	NS	NS	**
Family(taxa)	NS	**	**	*	NS	*	NS	NS
Block(treatment)	NS	NS	NS	NS	NS	NS	NS	NS
Location * family (taxa)	NS	NS	NS	NS	NS	NS	*	NS
Treatment * family(taxa)	NS	NS	NS	NS	NS	NS	NS	NS
Taxa * block(treatment)	***	***	***	***	NS	***	***	***
Location * treatment * taxa	NS	**	***	***	NS	NS	***	***
Location * treatment * family(taxa)	***	**	**	***	***	NS	NS	***

Table D-11. Mg content (mg/fascicle).

Source of variation	p1[b]	p2	p3	p4	p5	p6	p7	p8
Location	***	***	***	***	***	***	***	***
Treatment	NS	*	***	***	***	NS	**	***
Taxa[c]:	***	***	***	***	***	***	***	***
PTA vs. PEE	***	***	***	***	***	***	***	***
PEE vs. PEU	***	NS	NS	NS	NS	NS	NS	NS
Location * treatment	***	***	***	***	***	***	***	***
Location * taxa	***	***	***	***	NS	***	***	***
Treatment * taxa	***	NS	NS	NS	NS	NS	NS	**
Family(taxa)	NS	**	***	**	NS	**	*	**
Block(treatment)	*	NS	NS	**	***	**	NS	NS
Location * family (taxa)	NS	NS	NS	NS	NS	NS	NS	NS
Treatment * family(taxa)	NS	NS	NS	NS	NS	NS	NS	NS
Taxa * block(treatment)	NS	**	***	**	NS	***	**	***
Location * treatment * taxa	***	NS	**	***	***	NS	***	***
Location * treatment * family(taxa)	***	***	NS	NS	***	NS	NS	NS

APPENDIX E
TAXA MEANS BY EXPERIMENTAL LOCATION, SILVICULTURAL TREATMENT AND SAMPLING PERIOD FOR FASCICLE NUTRIENT CONCENTRATION, CONTENT, AND WEIGHT IN LOBLOLLY AND SLASH PINE IN NORTH CENTRAL FLORIDA[a].

Superscript notations in this appendix indicate:

a Taxa means were analyzed separately by silvicultural treatment and sampling period that corresponded to the life cycle of a needle cohort. Means among three taxa for a given variable followed by the same letter were not statistically significant at the 95% confidence level by comparisons of least square means using the LSMEANS test of the MIXED procedure.

b PTA = improved loblolly pine
PEE = improved slash pine
PEU = unimproved slash pine

Table E-1. Sampling time: June 1997.

Location	Dunnellon						Palatka					
Treatment	Non-intensively managed			Intensively managed			Non-intensively managed			Intensively managed		
Taxa	PTA[b]	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU
Concentration (%)												
N	1.00a	0.88a	0.90a	1.35a	1.21ab	1.10b	1.55a	1.07b	1.05b	1.64a	1.28b	1.38b
P	0.11a	0.10ab	0.10b	0.13a	0.12b	0.11c	0.19a	0.14b	0.14b	0.19a	0.17b	0.15b
K	0.47a	0.52a	0.52a	0.78a	0.78a	0.72a	0.84a	0.67b	0.65b	1.00a	0.89a	0.86a
Mg	0.07a	0.08b	0.08b	0.06a	0.07b	0.07b	0.09a	0.09ab	0.08b	0.08a	0.09a	0.07b
Ca	0.08a	0.13b	0.16b	0.12a	0.16a	0.14a	0.18a	0.19a	0.17a	0.19a	0.20a	0.20a
Fascicle weight (mg/fascicle)	56a	68b	77b	72a	88b	80ab	66a	102b	107b	81a	122b	103c
Content (mg/fascicle)												
N	0.55a	0.60a	0.69a	0.98a	1.07a	0.88a	1.01a	1.08a	1.12a	1.32a	1.55a	1.43a
P	0.06a	0.07a	0.07a	0.10a	0.10a	0.09b	0.12a	0.14a	0.14a	0.15a	0.20b	0.15ab
K	0.26a	0.35b	0.40b	0.57a	0.68b	0.57ab	0.54a	0.66a	0.69a	0.81a	1.06b	0.88a
Mg	0.03a	0.05b	0.06b	0.04a	0.06b	0.05ab	0.06a	0.09b	0.09b	0.07a	0.11b	0.07a
Ca	0.05a	0.09b	0.12c	0.09a	0.14a	0.12a	0.12a	0.20b	0.19b	0.15a	0.25b	0.21b

Table E-2. Sampling time: September 1997.

Location	Dunnellon						Palatka					
Treatment	Non-intensively managed			Intensively managed			Non-intensively managed			Intensively managed		
Taxa	PTA[b]	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU
Concentration (%)												
N	0.82a	0.76a	0.77a	1.12a	1.01a	0.94b	1.17a	0.94b	1.00b	1.22a	1.26a	1.06b
P	0.11a	0.08b	0.07b	0.13a	0.10b	0.08c	0.17a	0.13b	0.11c	0.17a	0.13b	0.11b
K	0.28a	0.33a	0.27a	0.70a	0.59a	0.57a	0.41a	0.47a	0.39a	0.75a	0.78ab	0.68b
Mg	0.09a	0.09a	0.08b	0.06a	0.07b	0.06b	0.07a	0.08ab	0.09b	0.05a	0.06b	0.07b
Ca	0.17a	0.19b	0.16a	0.16a	0.23b	0.22b	0.24a	0.32b	0.35b	0.19a	0.22a	0.29a
Fascicle weight (mg/fascicle)	92a	123b	132b	135a	160a	148a	117a	155b	153b	128a	190b	170b
Content (mg/fascicle)												
N	0.74a	0.94b	1.01b	1.51a	1.61a	1.39a	1.37a	1.45a	1.52a	1.55a	2.38b	1.80ab
P	0.10a	0.10a	0.10a	0.18a	0.16ab	0.12b	0.20a	0.20a	0.17a	0.22a	0.24a	0.19a
K	0.25a	0.40b	0.36b	0.95a	0.96a	0.85a	0.49a	0.75b	0.60ab	0.97a	1.47b	1.16a
Mg	0.08a	0.11b	0.10b	0.08a	0.11a	0.09a	0.09a	0.13b	0.14b	0.07a	0.12b	0.11b
Ca	0.16a	0.24b	0.22b	0.22a	0.37b	0.32b	0.28a	0.50b	0.53b	0.24a	0.42a	0.48a

Table E-3. Sampling time: November 1997.

Location	Dunnellon						Palatka					
Treatment	Non-intensively managed			Intensively managed			Non-intensively managed			Intensively managed		
Taxa	PTA[b]	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU
Concentration (%)												
N	0.89a	0.80b	0.76b	1.07a	1.01ab	0.94b	1.25a	1.05b	0.93b	1.23a	1.02b	0.97b
P	0.10a	0.08b	0.08b	0.12a	0.09b	0.10b	0.18a	0.14b	0.13b	0.15a	0.12b	0.11b
K	0.27a	0.32a	0.30a	0.54a	0.57a	0.53a	0.41a	0.48b	0.44ab	0.58a	0.66a	0.62a
Mg	0.08a	0.08a	0.07b	0.05a	0.06b	0.06b	0.08a	0.08a	0.09a	0.05a	0.05a	0.06a
Ca	0.14a	0.18a	0.18a	0.12a	0.22b	0.24b	0.28a	0.37b	0.39b	0.20a	0.20a	0.28a
Fascicle weight (mg/fascicle)	98a	139b	141b	135a	174b	185b	123a	166b	163b	122a	177b	189b
Content (mg/fascicle)												
N	0.87a	1.10b	1.06b	1.44a	1.74a	1.75a	1.54a	1.74a	1.51a	1.49a	1.78a	1.82a
P	0.10a	0.11a	0.11a	0.16a	0.16a	0.18a	0.22a	0.23a	0.21a	0.18a	0.21a	0.20a
K	0.27a	0.45b	0.42b	0.72a	0.99b	0.99b	0.51a	0.81b	0.71b	0.71a	1.15b	1.15b
Mg	0.08a	0.11b	0.10ab	0.06a	0.10b	0.11b	0.09a	0.14b	0.14b	0.06a	0.09ab	0.11b
Ca	0.14a	0.25b	0.25b	0.16a	0.37b	0.44b	0.34a	0.60b	0.64b	0.24a	0.37ab	0.53b

Table E-4. Sampling time: February 1998.

Location	Dunnellon						Palatka					
Treatment	Non-intensively managed			Intensively managed			Non-intensively managed			Intensively managed		
Taxa	PTA[b]	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU
Concentration (%)												
N	0.92a	0.83b	0.77c	1.00a	0.92b	0.92b	1.25a	1.03b	0.98b	0.99a	0.86b	0.92ab
P	0.09a	0.08b	0.07c	0.10a	0.08b	0.08b	0.12a	0.10b	0.11b	0.13a	0.10b	0.10b
K	0.28a	0.30a	0.28a	0.49a	0.51a	0.48a	0.38a	0.47b	0.44b	0.54a	0.59a	0.54a
Mg	0.10a	0.08b	0.09b	0.05a	0.06b	0.06b	0.09a	0.09a	0.09a	0.05a	0.05a	0.06a
Ca	0.15a	0.20b	0.20b	0.13a	0.24b	0.27b	0.31a	0.36b	0.40b	0.22a	0.24a	0.31a
Fascicle weight (mg/fascicle)	121a	174b	176b	153a	199b	187b	142a	223b	220b	144a	192b	185b
Content (mg/fascicle)												
N	1.11a	1.43b	1.34b	1.54a	1.82b	1.71ab	1.74a	2.29b	2.14b	1.41a	1.63b	1.69b
P	0.11a	0.14b	0.13b	0.16a	0.16a	0.16a	0.17a	0.23b	0.23b	0.18a	0.18a	0.18a
K	0.34a	0.52b	0.50b	0.74a	1.02b	0.91b	0.54a	1.04b	0.97b	0.76a	1.12b	0.99b
Mg	0.12a	0.14b	0.15b	0.08a	0.11b	0.11b	0.12a	0.19b	0.19b	0.07a	0.10b	0.10b
Ca	0.18a	0.35b	0.36b	0.20a	0.47b	0.51b	0.43a	0.80b	0.89b	0.30a	0.47ab	0.56b

Table E-5. Sampling time: April 1998.

Location	Dunnellon						Palatka					
Treatment	Non-intensively managed			Intensively managed			Non-intensively managed			Intensively managed		
Taxa	PTA[b]	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU
Concentration (%)												
N	0.87a	0.78b	0.76b	0.89a	0.83a	0.88a	1.29a	1.05b	1.10b	1.04a	0.91b	0.86b
P	0.09a	0.07b	0.07b	0.10a	0.08a	0.09a	0.14a	0.11b	0.11b	0.12a	0.10b	0.10b
K	0.22a	0.22a	0.20a	0.41a	0.43a	0.38a	0.38a	0.38a	0.32b	0.52a	0.51a	0.49a
Mg	0.11a	0.10b	0.10b	0.07a	0.07a	0.07a	0.11a	0.10a	0.10a	0.06a	0.06a	0.07a
Ca	0.22a	0.30b	0.29b	0.20a	0.34b	0.33b	0.45a	0.48a	0.48a	0.29a	0.28a	0.37a
Fascicle weight (mg/fascicle)	121a	179b	181b	146a	198b	206b	127a	201b	191b	136a	188b	183b
Content (mg/fascicle)												
N	1.05a	1.40b	1.37b	1.28a	1.64ab	1.79b	1.62a	2.11b	2.08b	1.40a	1.70b	1.58ab
P	0.10a	0.13b	0.13b	0.14a	0.16a	0.18a	0.18a	0.22b	0.21b	0.17a	0.18a	0.18a
K	0.27a	0.39b	0.36b	0.60a	0.84b	0.78ab	0.48a	0.77b	0.61c	0.70a	0.95b	0.91b
Mg	0.14a	0.18b	0.18b	0.10a	0.15b	0.14b	0.14a	0.20b	0.20b	0.09a	0.12b	0.13b
Ca	0.27a	0.54b	0.54b	0.29a	0.68b	0.67b	0.57a	0.96b	0.94b	0.38a	0.54ab	0.67b

Table E-6. Sampling time: June 1998.

Location	Dunnellon						Palatka					
Treatment	Non-intensively managed			Intensively managed			Non-intensively managed			Intensively managed		
Taxa	PTA[b]	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU
Concentration (%)												
N	0.84a	0.72b	0.66c	0.84a	0.72b	0.71b	1.02a	0.75b	0.73b	0.81a	0.65b	0.64b
P	0.09a	0.07b	0.07b	0.10a	0.08b	0.08b	0.12a	0.11b	0.10b	0.12a	0.09b	0.08b
K	0.18a	0.18a	0.17a	0.33a	0.33a	0.29a	0.38a	0.37a	0.30b	0.47ab	0.50a	0.39b
Mg	0.12a	0.09b	0.09b	0.08a	0.07a	0.07a	0.08a	0.09ab	0.10b	0.07a	0.06a	0.07a
Ca	0.28a	0.32a	0.35a	0.25a	0.39b	0.40b	0.23a	0.32a	0.47b	0.31a	0.33a	0.40a
Fascicle weight (mg/fascicle)	117a	183b	181b	146a	220b	202b	65a	106ab	132b	136a	230b	228b
Content (mg/fascicle)												
N	0.98a	1.30b	1.20b	1.22a	1.58b	1.42ab	0.65a	0.79a	0.93a	1.08a	1.49b	1.46b
P	0.11a	0.13b	0.13b	0.15a	0.17a	0.15a	0.08a	0.11a	0.13a	0.16a	0.20b	0.19b
K	020a	0.32b	0.30b	0.47a	0.74b	0.60c	0.24a	0.37a	0.37a	0.65a	1.15b	0.89c
Mg	0.14a	0.17b	0.17b	0.11a	0.16b	0.14b	0.06a	0.10ab	0.14b	0.09a	0.15b	0.15b
Ca	0.33a	0.59b	0.64b	0.35a	0.86b	0.81b	0.16a	0.39ab	0.69b	0.42a	0.78a	0.92a

Table E-7. Sampling time: September 1998.

Location	Dunnellon						Palatka					
Treatment	Non-intensively managed			Intensively managed			Non-intensively managed			Intensively managed		
Taxa	PTA[b]	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU
Concentration (%)												
N	0.76a	0.63b	0.62b	0.74a	0.65b	0.67b	0.82a	0.70b	0.66b	0.78a	0.64b	0.64b
P	0.11a	0.08b	0.08b	0.12a	0.09b	0.08b	0.14a	0.12b	0.11b	0.13a	0.08b	0.09b
K	0.17a	0.21b	0.18ab	0.32a	0.37a	0.34a	0.28a	0.34b	0.32ab	0.46a	0.47a	0.43a
Mg	0.10a	0.07b	0.07b	0.07a	0.06b	0.06b	0.11a	0.10a	0.10a	0.07a	0.06a	0.07a
Ca	0.29a	0.35b	0.37b	0.28a	0.43b	0.45b	0.48a	0.57a	0.58a	0.36a	0.34a	0.46a
Fascicle weight (mg/fascicle)	110a	165b	170b	140a	218b	213b	113a	186b	210b	138a	213b	203b
Content (mg/fascicle)												
N	0.83a	1.05b	1.05b	1.03a	1.41b	1.42b	0.91a	1.27b	1.37b	1.07a	1.36b	1.31b
P	0.12a	0.13a	0.13a	0.16a	0.19a	0.18a	0.16a	0.22b	0.22b	0.18a	0.18a	0.18a
K	0.18a	0.35b	0.31b	0.45a	0.80b	0.73b	0.32a	0.62b	0.66b	0.64a	1.00b	0.86b
Mg	0.11a	0.12a	0.13a	0.10a	0.14b	0.13b	0.12a	0.19b	0.21b	0.10a	0.13ab	0.14b
Ca	0.32a	0.57b	0.64b	0.40a	0.95b	0.96b	0.55a	1.12b	1.26b	0.49a	0.74ab	0.92b

Table E-8. Sampling time: December 1998.

Location	Dunnellon						Palatka					
Treatment	Non-intensively managed			Intensively managed			Non-intensively managed			Intensively managed		
Taxa	PTA[b]	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU	PTA	PEE	PEU
Concentration (%)												
N	0.81a	0.68b	0.69b	0.72a	0.70a	0.74a	0.82a	0.78a	0.82a	0.83a	0.77a	0.75a
P	0.10a	0.08b	0.08b	0.13a	0.09b	0.09b	0.15a	0.13ab	0.12b	0.15a	0.11b	0.10b
K	0.20a	0.23b	0.21ab	0.36a	0.38a	0.38a	0.31a	0.40b	0.37b	0.49a	0.52a	0.48a
Mg	0.10a	0.06b	0.06b	0.08a	0.06b	0.05b	0.11a	0.10a	0.10a	0.09a	0.07b	0.07b
Ca	0.30a	0.34b	0.35b	0.40a	0.48a	0.46a	0.49a	0.68b	0.62b	0.48a	0.39a	0.45a
Fascicle weight (mg/fascicle)	97a	176b	181b	134a	206b	205b	109a	205b	213b	113a	202b	201b
Content (mg/fascicle)												
N	0.77a	1.19b	1.24b	0.96a	1.44b	1.51b	0.87a	1.59b	1.74b	0.93a	1.54b	1.49b
P	0.10a	0.14b	0.14b	0.17a	0.18a	0.18a	0.17a	0.27b	0.26b	0.17a	0.22a	0.21a
K	0.19a	0.40b	0.38b	0.48a	0.78b	0.78b	0.34a	0.80b	0.80b	0.56a	1.05b	0.96b
Mg	0.10a	0.11a	0.11a	0.10a	0.12a	0.11a	0.12a	0.21b	0.20b	0.10a	0.13b	0.13b
Ca	0.29a	0.60b	0.64b	0.52a	0.98b	0.93b	0.55a	1.41b	1.35b	0.53a	0.80ab	0.91b

APPENDIX F

DYNAMICS IN FASCICLE NUTRIENT CONTENT OVER THE COURSE OF A NEEDLE COHORT LIFE CYCLE FOR IMPROVED LOBLOLLY, IMPROVED SLASH AND UNIMPROVED SLASH PINE FROM AGES 3 TO AGE 4 YEARS. ALL INDIVIDUAL TREES WERE SUBJECTED TO TWO LEVELS OF SILVICULTURAL TREATMENTS AND PLANTED AT TWO LOCATIONS IN NORTH CENTRAL FLORIDA

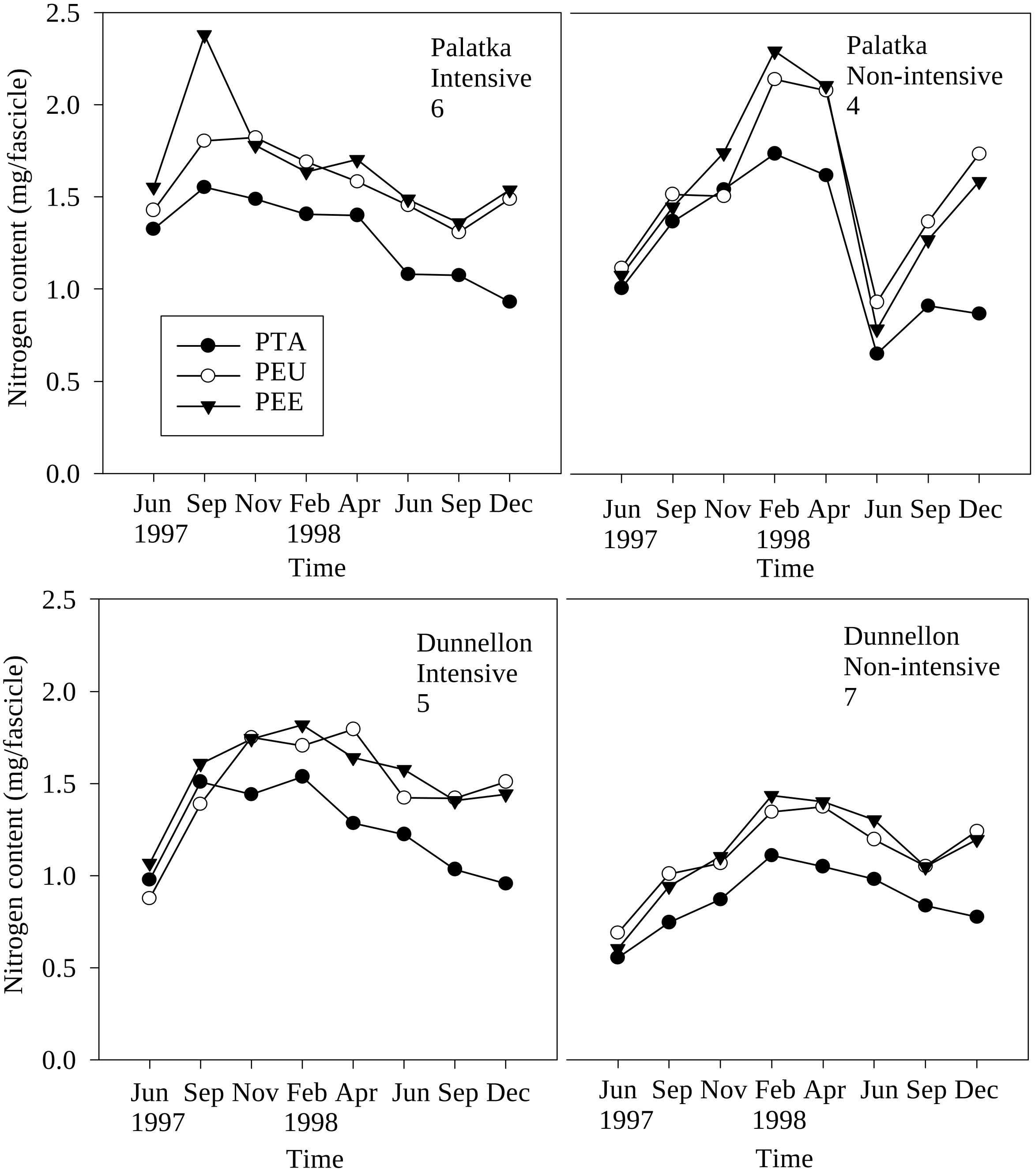

Figure F-1. Variation in fascicle N content for improved loblolly, improved slash and unimproved slash pine throughout a life cycle of a needle cohort managed under two silvicultural treatment and two locations in north central Florida. PTA = improved loblolly pine, PEE = improved slash pine, PEU = unimproved slash pine. Integers listed below locations and treatments indicate the number of sampling periods out of eight where significant taxa differences were detected at the 95% confidence level using LSMEANS test of the MIXED procedure.

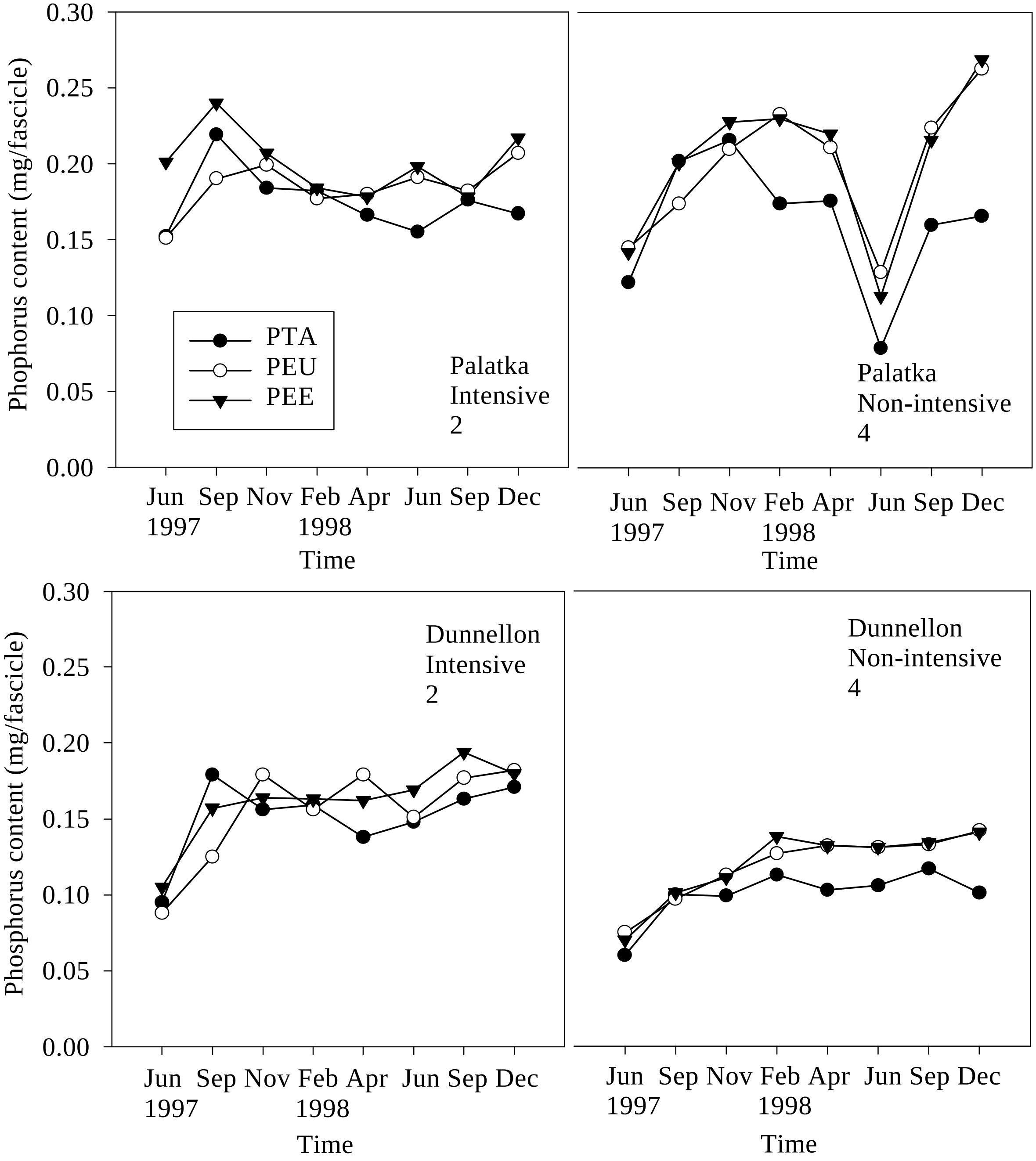

Figure F-2. Variation in fascicle P content for improved loblolly, improved slash and unimproved slash pine throughout a life cycle oh a needle cohort managed under two silvicultural treatment and two locations in north central Florida.
PTA = improved loblolly pine, PEE = improved slash pine, PEU = unimproved slash pine.
Integers listed below locations and treatments indicate the number of sampling periods out of eight where significant taxa differences were detected at the 95% confidence level using LSMEANS test of the MIXED procedure.

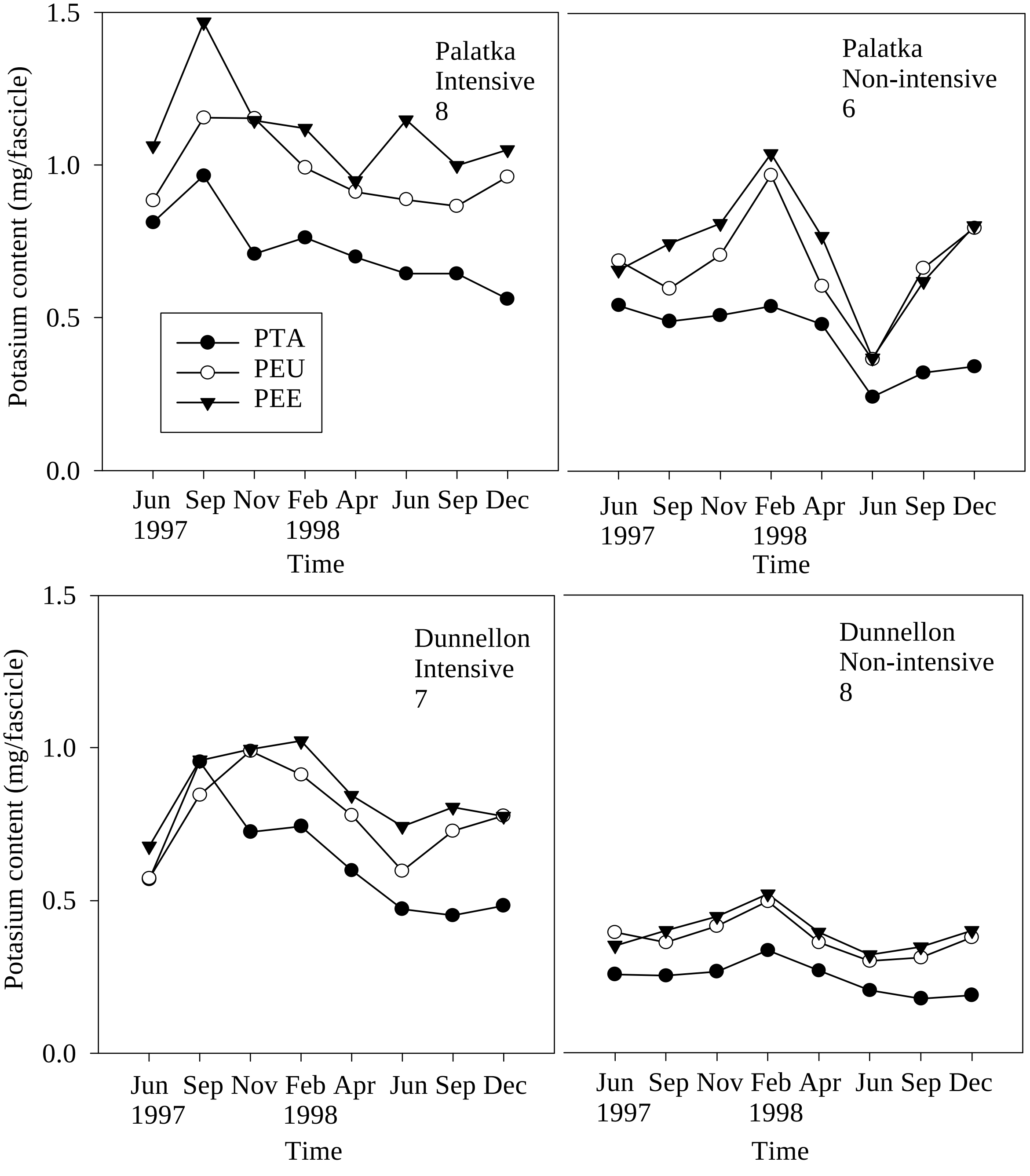

Figure F-3. Variation in fascicle K content for improved loblolly, improved slash and unimproved slash pine throughout a life cycle of a needle cohort managed under two silvicultural treatment and two locations in north central Florida. PTA = improved loblolly pine, PEE = improved slash pine, PEU = unimproved slash pine. Integers listed below locations and treatments indicate the number of sampling periods out of eight where significant taxa differences were detected at the 95% confidence level using LSMEANS test of the MIXED procedure.

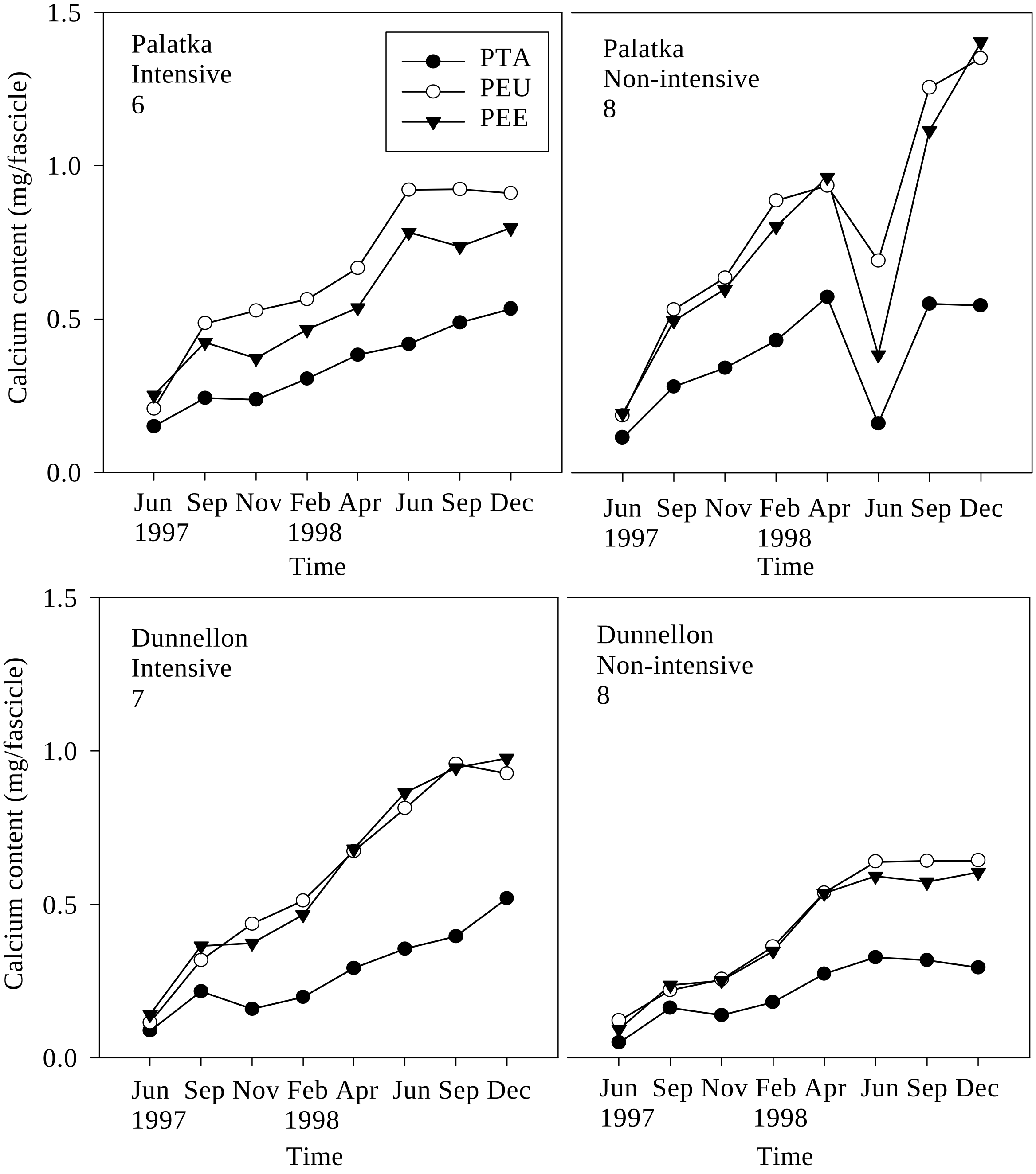

Figure F-4. Variation in fascicle Ca content for improved loblolly, improved slash and unimproved slash pine throughout a life cycle of a needle cohort managed under two silvicultural treatment and two locations in north central Florida. PTA = improved loblolly pine, PEE = improved slash pine, PEU = unimproved slash pine. Integers listed below locations and treatments indicate the number of sampling periods out of eight where significant taxa differences were detected at the 95% confidence level using LSMEANS test of the MIXED procedure.

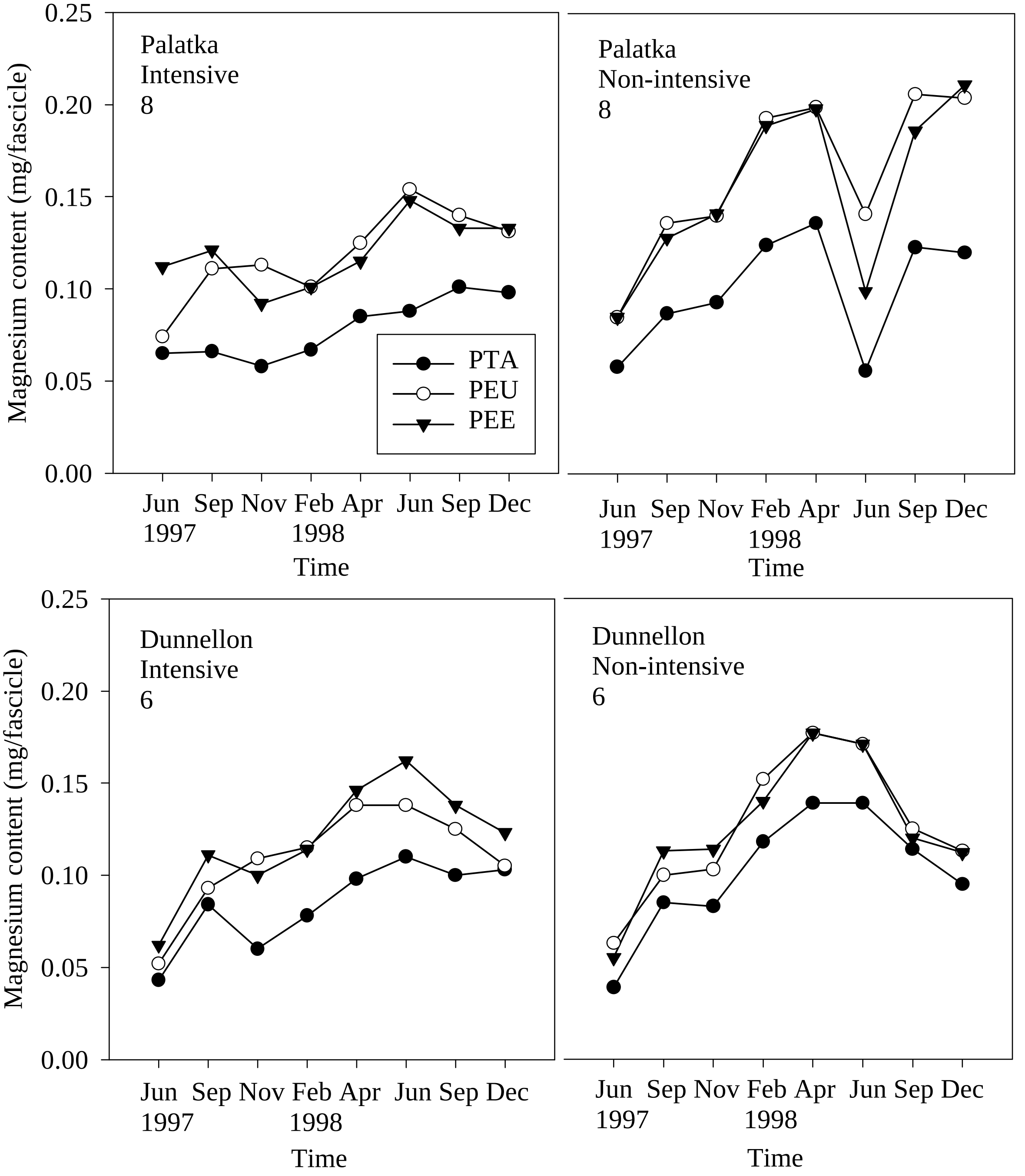

Figure F-5. Variation in fascicle Mg content for improved loblolly, improved slash and unimproved slash pine throughout a life cycle of a needle cohort managed under two silvicultural treatment and two locations in north central Florida.
PTA = improved loblolly pine, PEE = improved slash pine, PEU = unimproved slash pine. Integers listed below locations and treatments indicate the number of sampling periods out of eight where significant taxa differences were detected at the 95% confidence level using LSMEANS testof the mixed procedure.

APPENDIX G

FAMILY × SITE ($r_{B\text{-site}}$), AND FAMILY × TREATMENT INTERACTIONS ($r_{B\text{-treat}}$) FOR AVERAGE FASCICLE WEIGHT, NUTRIENT CONCENTRATIONS AND NUTRIENT CONTENT OVER AN ENTIRE LIFE CYCLE OF A NEEDLE COHORT FROM AGES 3 TO 4 YEARS IN LOBLOLLY AND SLASH PINE PLANTED AT TWO LOCATIONS IN NORTH CENTRAL FLORIDA.

Superscript notations for sampling periods in this appendix indicate:

a p1 = June 1997
p2 = September 1997
p3 = November 1997
p4 = February 1998
p5 = April 1998
p6 = June 1998
p7 = September 1998
p8 = December 1998.

APPENDIX G – CONTINUED.

Attributes	Sampling periods[a]	Loblolly pine		Slash pine	
		$r_{B\text{-site}}$	$r_{B\text{-treat}}$	$r_{B\text{-site}}$	$r_{B\text{-treat}}$
Average fascicle weight (mg/fascicle)	p1	1.00	1.00	0.64	1.00
	p2	0.88	0.71	0.85	0.90
	p3	1.00	1.00	1.00	1.00
	p4	0.53	0.95	1.00	1.00
	p5	1.00	1.00	1.00	1.00
	p6	0.26	1.00	0.00	0.00
	p7	0.00	0.00	1.00	1.00
	p8	0.00	0.00	1.00	0.63
N concentration (%)	p1	1.00	0.98	0.00	0.00
	p2	1.00	1.00	0.00	0.00
	p3	0.92	1.00	1.00	1.00
	p4	1.00	0.92	1.00	1.00
	p5	0.50	1.00	1.00	1.00
	p6	1.00	0.30	0.00	0.00
	p7	0.52	0.84	0.00	0.00
	p8	1.00	0.59	1.00	1.00

APPENDIX G – CONTINUED.

Attributes	Sampling periods[a]	Loblolly pine		Slash pine	
		$r_{B\text{-site}}$	$r_{B\text{-treat}}$	$r_{B\text{-site}}$	$r_{B\text{-treat}}$
Fascicle N content (mg/fascicle)	p1	0.55	0.66	1.00	1.00
	p2	1.00	0.80	0.68	1.00
	p3	1.00	0.30	1.00	1.00
	p4	0.73	0.36	1.00	1.00
	p5	0.65	1.00	1.00	1.00
	p6	0.78	1.00	1.00	1.00
	p7	1.00	1.00	0.40	1.00
	p8	0.56	1.00	1.00	1.00
P concentration (%)	p1	0.95	0.80	1.00	1.00
	p2	0.66	1.00	1.00	1.00
	p3	0.68	0.99	1.00	1.00
	p4	0.58	1.00	0.00	0.00
	p5	0.38	1.00	1.00	1.00
	p6	0.88	0.42	1.00	1.00
	p7	1.00	0.90	0.96	1.00
	p8	1.00	1.00	0.89	1.00
Fascicle P content (mg/fascicle)	p1	0.00	0.00	1.00	1.00
	p2	1.00	0.93	0.87	1.00
	p3	1.00	0.53	1.00	1.00
	p4	1.00	1.00	1.00	1.00
	p5	0.79	1.00	1.00	1.00
	p6	1.00	0.68	1.00	1.00
	p7	1.00	0.71	0.95	1.00
	p8	1.00	1.00	0.82	1.00

APPENDIX G – CONTINUED.

Attributes	Sampling periods[a]	Loblolly pine		Slash pine	
		$r_{B\text{-site}}$	$r_{B\text{-treat}}$	$r_{B\text{-site}}$	$r_{B\text{-treat}}$
K concentration (%)	p1	0.74	1.00	1.00	1.00
	p2	1.00	1.00	0.77	0.82
	p3	1.00	1.00	1.00	1.00
	p4	1.00	1.00	1.00	1.00
	p5	1.00	0.14	1.00	1.00
	p6	0.57	0.88	1.00	1.00
	p7	0.39	0.23	1.00	1.00
	p8	1.00	0.46	1.00	1.00
Fascicle K content (mg/fascicle)	p1	0.00	0.00	1.00	1.00
	p2	1.00	0.69	1.00	1.00
	p3	0.00	0.00	1.00	1.00
	p4	0.00	0.00	1.00	1.00
	p5	1.00	0.23	1.00	1.00
	p6	1.00	1.00	1.00	1.00
	p7	1.00	0.20	0.55	1.00
	p8	1.00	0.88	0.93	1.00
Ca concentration (%)	p1	1.00	1.00	0.00	0.00
	p2	1.00	1.00	1.00	1.00
	p3	0.00	0.00	0.87	1.00
	p4	0.00	0.00	0.62	0.75
	p5	0.00	0.00	1.00	0.83
	p6	0.00	0.00	1.00	1.00
	p7	1.00	1.00	1.00	1.00
	p8	1.00	1.00	1.00	1.00

APPENDIX G – CONTINUED.

Attributes	Sampling periods[a]	Loblolly pine		Slash pine	
		$r_{B\text{-site}}$	$r_{B\text{-treat}}$	$r_{B\text{-site}}$	$r_{B\text{-treat}}$
Fascicle Ca content (mg/fascicle)	p1	0.89	0.73	1.00	1.00
	p2	1.00	1.00	1.00	1.00
	p3	1.00	0.00	1.00	1.00
	p4	0.00	0.00	0.76	1.00
	p5	0.00	0.00	1.00	0.79
	p6	0.00	0.00	1.00	1.00
	p7	0.00	0.00	0.51	1.00
	p8	0.23	1.00	1.00	1.00
Mg concentration (%)	p1	0.00	0.00	0.19	1.00
	p2	1.00	1.00	1.00	1.00
	p3	0.00	0.00	1.00	1.00
	p4	0.00	0.00	1.00	1.00
	p5	1.00	0.15	1.00	1.00
	p6	0.00	0.00	1.00	1.00
	p7	0.66	0.49	0.96	1.00
	p8	1.00	1.00	0.98	1.00
Fascicle Mg content (mg/fascicle)	p1	0.35	0.37	1.00	1.00
	p2	1.00	0.47	1.00	1.00
	p3	0.00	0.00	1.00	1.00
	p4	0.00	0.00	1.00	1.00
	p5	0.00	0.00	1.00	1.00
	p6	0.00	0.04	1.00	1.00
	p7	0.08	1.00	0.73	1.00
	p8	0.89	1.00	0.98	1.00

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BIOGRAPHICAL SKETCH

Yu Xiao was born on January 22, 1962, in Beijing, People's Republic of China. His family moved to Xian, Shaanxi province, in 1966, where he graduated from Applied Optics Institute High School in July 1978. He was admitted to the Northwest China College of Forestry in September 1978, and there he received his Bachelor of Science in forestry in July 1982. He began his graduate study in September 1982 at the same college with an emphasis on forest plantation productivity. He received his Master of Science in forestry in October 1985.

Yu Xiao started to work as a research scientist from March 1986 in the Northwest Plateau Institute of Biology, Chinese Academy of Sciences. He participated in research programs in forest productivity, spring wheat ecology and breeding, and rangeland management until November 1994. He came to the Department of Biological Sciences, Texas Tech University, in December 1994 as a visiting scientist, primarily working on the mechanistic models in ecosystem processes. He entered the Ph.D. program in the School of Forest Resources and Conservation, University of Florida, in January 1996.