Nutrient Concentrations and Contents, and their Relation to Stem Growth, of Intensively Managed *Pinus taeda* and *Pinus elliottii* Stands of Different Planting Densities

Greg A. Barron-Gafford, Rodney E. Will, E. Colter Burkes, Barry Shiver, and Robert O. Teskey

ABSTRACT. Foliar, stem, and fine root nitrogen (N), phosphorus (P), and potassium (K) concentrations were measured, and their contents calculated, to determine the relationship between nutrient acquisition and stem biomass increment on a stand basis in 4-yr-old pine plantations planted at different densities. The study examined stands of loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) in the lower Coastal Plain of the southeastern United States that were intensively managed (i.e., received bedded site preparation, a high level of fertilization, and nearly complete weed control). The stands were planted at densities of 740, 2,220, and 3,700 trees ha^{-1} on three sites, each with a different soil type. Increases in stem biomass growth on a stand basis were not proportional to increases in stand density, indicating that competition for resources was limiting growth at the higher densities. Foliar N and P, stem wood N and K, and fine root N concentrations decreased with increased stand density. For loblolly pine, foliar N concentrations fell from 13.1 mg g^{-1} at 740 trees ha^{-1} to 10.9 mg g^{-1} at 3700 trees ha^{-1} (average of current-year and 1-yr-old foliage), the latter considered below a critical threshold concentration for maintaining high growth rates. Slash pine foliar N concentrations followed a similar pattern, decreasing from 11.2 to 9.1 mg g^{-1}. In both species, foliar P and K concentrations remained above critical concentrations at all planting densities. Overall, foliar N concentration was negatively correlated to stem biomass increment on a stand basis (r = –0.57) whereas foliar N content of 1-yr-old foliage was positively correlated with stem biomass increment (r = 0.59). However, biomass of 1-yr-old foliage was better correlated to total stem biomass growth (r = 0.76) suggesting that amount of foliage, rather than its nutrient content, was a better estimator of growth. For. Sci. 49(2):291–300.

Key Words: Stand density, *Pinus taeda, P. elliottii,* nutrient concentration, nutrient content, nitrogen, phosphorus, potassium.

Greg A. Barron-Gafford, Biosphere II, Oracle, AZ 85623—(800) 828-2462; E-mail: gbarron@bio2.columbia.edu. Rodney E. Will, Warnell School of Forest Resources, University of Georgia, Athens, GA 30602, United States—(706) 542-6821; Fax: (706) 542-8356; E-mail: rwill@smokey.forestry.uga.edu. E. Colter Burkes, 2505 13th St. NW, Washington, DC 20009—Phone: (202) 249-1688; E-mail: colterburkes@hotmail.com. Barry Shiver, Warnell School of Forest Resources, University of Georgia, Athens, GA 30602—(706) 542-3009; E-mail: shiver@smokey.forestry.uga.edu. Robert O. Teskey, Warnell School of Forest Resources, University of Georgia, Athens, GA 30602—(706) 542-5055; E-mail: teskey@arches.uga.edu.

Acknowledgments: The authors thank the Georgia Traditional Industries Program in Pulp & Paper for funding and the Plantation Management Research Cooperative and their industrial cooperators for funding and support. Thanks also to Jeff Price and Mary Anne McGuire for their assistance.

Manuscript received September 21, 2001, accepted July 31, 2002.

At establishment, and during the initial phase of stand development, higher planting densities increase the capture of available resources, such as light, nutrients, and water, and increase growth of the tree crop. As these stands develop, the maximum rate of biomass accumulation will peak and either plateau or decline, with this response occurring sooner in the denser stands (e.g., Harms et al. 1994, Harms and Langdon 1976, Mann and Dell 1971). The plateau or decline in growth rate is an indication that resource acquisition is limiting stand growth. Few studies have attempted to characterize the resource limitations that may be responsible for reduced growth at higher planting densities, but nutrients and water are often considered to be key limiting resources. In the southeastern United States, nutrients are definitely a key limiting resource, with many studies demonstrating increased stand growth following fertilization. In addition, decreased nutrient acquisition and tree growth have been reported with increasing levels of interspecific competition between trees and herbaceous or other woody species (e.g., Morris et al. 1993, Elliot and White 1987).

Water deficits can reduce growth of competing individuals especially in drier regions (Nambiar and Sands 1993). In the southeastern United States, rainfall generally exceeds 1200 mm y^{-1} and is fairly evenly distributed throughout the year. It is somewhat surprising that recent studies in this region have shown very limited improvement in the growth of pine plantations by irrigating to maintain soil moisture near field capacity (Samuelson et al. 2001, Albaugh et al. 1998). This may be due to the sandy soils in the region and deep rooting patterns that allow trees access to water deep in the soil profile or in shallow aquifers. There is some physiological evidence to support this. Tree water status and rates of physiological processes of slash pine (*Pinus elliottii* Engelm.) trees in plantations were not significantly affected by fluctuations in the depth of the water table from 1 to 3 m in the Coastal Plain (Teskey et al. 1994).

Decreased rates of biomass accumulation with increased stand age or increased stand density may be somewhat analogous. As with increases in stand biomass that occur with increased stand density, increased stand age results in greater standing biomass that may increase nutrient demands, increase the amount of nutrients sequestered in the biomass and forest floor, and exacerbate nutrient limitations (Richter et al. 2000, Ryan et al. 1997, Pearson et al. 1987). Chapin et al. (1986) suggested that both leaf area and stem wood production could decline as a result of increasing nutrient limitations with stand age. Binkley et al. (1995) concluded that increasing nutrient limitations in older stands of lodgepole pine (*Pinus contorta* Dougl.) probably accounted for at least part of the decline in stand leaf area and growth. In their study, foliar analysis indicated that N, P, and K all limited growth in older stands. They also found that fertilization with N alone resulted in the greatest basal area response, indicating the importance of N as a limiting nutrient.

The objectives of this study were to investigate the role that nutrients play in controlling growth of different density stands by (1) comparing the N, P, and K concentrations and contents of stems, leaves, and fine roots of loblolly (*Pinus taeda* L.) and slash pine, and (2) determining if N, P, and K concentrations or contents were correlated with growth in stands of different densities. Our hypotheses were: (1) nutrient concentrations would be highest in the least dense stands and would decrease as stand density increased because of a nutrient dilution effect throughout larger canopies and root systems; (2) nutrient contents would be lowest in the least dense stands and would increase as stand density increased because of a greater acquisition of resources and larger biomass in more dense stands; (3) loblolly pine would have greater foliar and fine root nutrient concentrations and contents than slash pine; and (4) stem biomass growth would be better correlated with foliar N content than with leaf biomass because N content combines both the amount of biomass used to capture sunlight and N concentration, which is sometimes related to photosynthetic capacity.

Materials and Methods

Three lower Coastal Plain locations with site-specific differences in soil type were used in this study. The three sites were located in southeastern Georgia and had sandy soils. The Effingham County site had an argillic horizon, but no spodic horizon. The Brantley County site had a spodic horizon, but not an argillic horizon. The site located in Charlton County had both argillic and spodic horizons. Sites had one stand each of loblolly and slash pine planted at densities of 740, 2,220, and 3,700 trees ha^{-1}. Both species and stand density were randomly assigned to plots. The 740 trees ha^{-1} stand had a measurement plot size of 0.12 ha and a gross plot size of 0.23 ha. Stands planted at 2,220 and 3,700 trees ha^{-1} had a measurement plot size of 0.05 ha and gross plot size of 0.13 ha. These plot sizes allowed for a 7 m buffer around the treatment plot for all densities.

Sites were bedded and then received a broadcast application 1.1 kg ha^{-1} Arsenal (imazapyr, BASF), 4.5 l ha^{-1} Garlon (triclopyr amine, Dow Agrosciences LLC), and 2.2 l ha^{-1} Accord (glyphosate, Monsanto) in the autumn of 1995 to completely eliminate competition before planting. All sites were hand-planted in January 1996 with slash pine half-sib family 5-61 (JSC/CCA and Champion Paper) and loblolly pine half-sib family 7-56 (NC State Tree Improvement Cooperative). Beginning in spring 1996, directed sprays of Oust (sulfometuron methyl, DuPont) were applied as needed to keep the plots free of competing vegetation. Tip moth infestations were reduced by application of the insecticide Pounce (permethrin, FMC Corp.) during the first 2 yr of stand development. Plots received 56.1 kg ha^{-1} each of elemental N, P, and K in spring 1996. In spring 1998, stands received 67.3 kg ha^{-1} each of elemental N, P, and K as well as an additional 45 kg ha^{-1} of elemental N applied as NH_4NO_3. Micronutrients were also applied at this time to prevent deficiencies (14 kg Mg ha^{-1}, 27 kg Ca ha^{-1}, 80 kg S ha^{-1}, 0.5 kg B ha^{-1}, 1.4 kg Fe ha^{-1}, 1.7 kg Mn ha^{-1}, 1.7 kg Zn ha^{-1}, and 0.7 kg Cu ha^{-1}). An additional 45 kg ha^{-1} of elemental N was applied as NH_4NO_3 in the spring of 1999.

Survival was excellent, averaging 95% after 3 yr. The vast majority of mortality occurred the year of planting,

i.e., not density dependent. At the end of the fourth growing season, average tree height was 4.5 m for loblolly pine stands and 3.4 m for the slash pine stands. Average dbh at the end of the fourth growing season for loblolly pine stands decreased from 7.9 cm to 6.3 cm as stand density increased from 740 to 3,700 trees h^{-1}. Likewise, dbh for slash pine stands decreased from 7.1 to 6.3 cm with increasing density (Burkes et al. 2003).

Within each of the measurement plots, foliar samples (10–20 fascicles) were collected from ten randomly selected trees during August of their fourth growing season (1999). The canopy height was determined using a height pole and then divided into lower, middle, and upper thirds. Needles from the first and second flushes of both the current (1999) and past year (1998) were collected. Foliage samples were stored on ice for transport to the lab and then oven dried at 64°C and ground. From all plots, stem bark and stem wood samples were taken from five randomly selected buffer trees in August 1999. Stem bark was obtained by scraping a 2×5 cm strip of bark from each tree at breast height. Wood samples were obtained using an increment borer. Samples from the five trees per plot were pooled, placed on ice for transport, and then dried at 64°C and ground.

Ten soil subsamples were collected from each stand in August of the fourth growing season (1999), using a sampling punch tube measuring approximately 2.3 cm inner diameter and 30 cm in length (depth). Of the ten punch tubes, five subsamples were taken within the beds and five were taken between the beds. This subsampling method was used to obtain a representative sample for the entire stand. The subsamples were combined in a plastic bag and stored on ice after collection. In the lab, samples were oven dried at 64°C, sieved through a 0.2 mm sieve to break up all soil aggregates and remove organic debris, and ground using a ball mill grinder.

During August 1999, six root-fans were excavated from the upper 30 cm of the soil surrounding randomly selected trees within each stand to collect fine-root nutrient samples. The six root fans were pooled to form one large sample for each plot. This combined sample was cleansed of soil particles by washing in a bucket of water, placed in paper sacks, and oven-dried at 64°C. After drying, approximately 3 g of fine root material were collected from the pooled sample for each plot and ground using a ball mill grinder.

Soil and tissue nitrogen concentrations were determined using an NC2100 CNS analyzer and an NA1500 C/H/N analyzer (CE Elantech Inc., Lakewood, NJ). Calibration curves were developed using a 2,5-Bis-(5-tert.-butyl-benzoxazol-2-yl)-thiophen (BBOT) standard, and quality control checks were performed after every ten samples. Replicates of samples also were run after every ten samples for additional quality control.

For P and K, a dry ash method was used for inductively coupled plasma (ICP) analysis using a Model 965 Plasma Atomcorp (Thermo-Jarrel Ash, Franklin, MA). Samples were ashed at 500°C for 4 hr, cooled, and then combined with 10 ml of a plant buffer extract, consisting of HCl, HNO_3, molybdenum internal standard, and water. Pine needles (Standard reference material 1575, National Institute of Standards & Technology, Gaithersburg, MD) were used as the standard in this ICP analysis.

Total N, P, and K contents were estimated for the fourth growing season foliar, stem, and fine root biomass. Nutrient contents were calculated by multiplying nutrient concentration by the component biomass. Leaf biomass was estimated from leaf litter collected in traps (each 0.44 m^2) randomly placed throughout each stand. Because the degree of canopy closure varied between plots, more litter traps were placed in the less densely planted plots to ensure representative sampling. Twelve, nine, and seven litter traps were placed in the 740, 2,220, and 3,700 trees ha^{-1} density plots, respectively. Leaf litter was collected every 4 to 6 weeks between March 1999 and March 2001. The litter collected between March 1999 and March 2000 represents the 1998 foliage cohort (developed during 1998, but was on the tree the entire 1999 growing season), while foliage collected between March 2000 and March 2001 represents the 1999 foliage cohort (developed during the 1999 growing season). Litter was oven-dried at 64°C and then weighed. Needle biomass was then converted to fresh needle weight using empirically derived correction factors (Burkes et al. 2003). Foliar nutrient contents were calculated separately for the 1999 cohort (current-year) and 1998 cohort (1-yr-old) based on the concentrations measured for a particular cohort (average of three canopy positions and two flushes within age class) and the estimated foliage biomass.

Stem biomass was partitioned into wood and bark. Stem and bark volume was used to estimate biomass using plot-specific empirically derived volume equations and specific gravity measurements. Stem diameter and bark thickness were sampled at diameter breast height (dbh, 1.37 m) and at 1 m intervals from groundline up to a 2.5 cm diameter top. From these measurements, volume for each meter segment was calculated and summed to find the total tree volume and percent bark by volume. Stem biomass was estimated using height and diameter measurements at the end of the third and fourth growing seasons. All tree diameters were measured, and the number of heights sampled varied inversely with stand density, from every tree to every third tree. Heights of trees not measured were estimated based on diameters using plot-specific regressions.

Fine root biomass was determined using roots collected in soil cores during August 1999. Eight cores, four within beds and four between beds, were taken using a soil corer (5.4 cm diameter by 30 cm depth). Samples were placed on ice for transport to the lab and frozen for storage. Samples later were thawed and washed using a hydropneumatic root elutriator, which uses a mixture of air and water to separate soil from root matter. Recovered root material was stored in whorl pack bags in a 20% methanol and 80% water solution. This cleansed sample was processed using a modification of the Newman's line intercept method so that the length of fine root (< 0.5 mm) could be determined (Newman 1966). Roots greater than 0.5 mm diameter were removed. The dry weight of 50 cm of fine roots was determined to convert fine root length to fine root biomass. Although our estimates of

belowground nutrients were limited, we chose to measure the most biologically active, most nutrient rich root fraction (< 0.5mm diameter) to examine how the changes in stand density were affecting nutrient status of the most sensitive portion of the root system.

Data were analyzed using analysis of variance (ANOVA) and the SAS statistical software package (1996; SAS Institute Inc., Cary, NC). The statistical design for foliar nutrient concentration was a split plot with site as the blocking variable, the factorial combination of species and stand density as the whole plot factors, and foliage age class as the split plot factor. Data from the various crown positions and flushes within age classes were averaged before analysis. The statistical design for other analyses was a randomized complete block design with site serving as a blocking variable and the factorial combination of species and stand density.

Results

Total stem biomass growth and total standing stem biomass increased significantly with increasing stand density; however, these increases were not proportional (Table 1). For example, while there was a three- and five-fold increase in the number of trees ha^{-1} as stand density increased from 740 to 2,220 and from 740 to 3,700 trees ha^{-1}, respectively, total stem biomass growth increased by only 2.5 and 3.5 times across this range of densities. Stem biomass growth did not differ between loblolly and slash pine stands, but total standing stem biomass was significantly greater ($P < 0.05$) for the loblolly pine stands than for slash pine stands, i.e., 19,905 vs. 17,347 kg ha^{-1} for mean standing stem biomass of the three stand densities.

For the 1998 cohort (1-yr-old foliage), stand foliar biomass increased with increasing stand density with biomass in the 2,220 and 3,700 trees ha^{-1} stands significantly higher than that in the 740 trees ha^{-1} stands (Table 1). Foliar biomass of the 1999 cohort was greater than the 1998 cohort and exhibited similar increases with density. Foliar biomass for loblolly and slash pine was not significantly different for either year, nor were there any statistical interactions involving the two species. The amount of fine root biomass also increased significantly with increasing stand density. Loblolly pine stands had significantly greater ($P < 0.05$) amounts of fine root biomass than slash pine stands. Average values of fine root biomass for loblolly and slash pine were 3004 kg ha^{-1} and 2,363 kg ha^{-1}, respectively.

All stands received the same amounts of fertilizer, and even though much more biomass was produced in the denser stands, soil N concentrations in the upper 30 cm of soil were similar for all stands, i.e., there were no significant effects of species or stand density. Average values for the 740, 2,200, and 3,700 trees ha^{-1} stands were 0.48, 0.55, and 0.51 g N kg^{-1}, respectively. Average soil N values for loblolly and slash pine stands were 0.49 and 0.54 g kg^{-1}, respectively.

Foliar N and P concentrations were significantly greater for loblolly pine than for slash pine ($P < 0.05$), while foliar K concentration was significantly greater for slash pine than for loblolly pine ($P < 0.01$) (Figure 1). For all three nutrients, the concentration in current-year foliage was significantly greater than in 1-yr-old foliage ($P < 0.01$). The difference in N concentration between current-year and 1-yr-old foliage was greater for loblolly than for slash pine, although the pattern was reversed for foliar K concentration (significant interaction between species and foliage age). Overall, N concentration significantly decreased with increasing stand density ($P = 0.0005$). Foliar K also decreased with increasing stand density, but the decrease was not as pronounced ($P = 0.04$). Foliar P was not affected by stand density.

Similar to the pattern observed in foliar N concentration, fine root N concentrations decreased with increasing stand density ($P < 0.05$) (Figure 2). In contrast, fine root P and K concentrations were not affected by stand density. Fine root N concentrations were higher in slash pine (11.4 g kg^{-1}) than loblolly pine (10.4 g kg^{-}) ($P = 0.06$), but P and K concentrations did not differ between species. No significant interactions between species and stand density occurred for these three nutrients in fine roots.

Table 1. Stem biomass growth during the fourth growing season (1999), total stem biomass at the end of the fourth growing season, foliar biomass estimated from litterfall for the 1998 and 1999 cohorts, and fine root biomass during the fourth growing season for loblolly and slash pine stands planted at three densities. SE represents standard error of the mean. Different capital letters indicate a significant difference due to density and different lower case letters indicate a significant difference due to species ($P < 0.05$).

			Stand density (trees ha^{-1})					
			740		2220		3700	
Parameter		Species	Mean	SE	Mean	SE	Mean	SE
			A		B		C	
Stem growth (kg ha^{-1})	a	Loblolly pine	5,106	(156)	12,246	(718)	17,539	(725)
	a	Slash pine	4,531	(658)	12,187	(1,214)	16,444	(868)
			A		B		C	
Stem biomass (kg ha^{-1})	a	Loblolly pine	9,314	(538)	21,515	(2,598)	28,887	(2,418)
	b	Slash pine	7,373	(987)	1,8999	(1,805)	25,669	(1,753)
			A		B		B	
1998 Cohort Foliar biomass (kg ha^{-1})	a	Loblolly pine	2,777	(741)	4,050	(516)	4,668	(880)
	a	Slash pine	1,820	(252)	3,614	(295)	4,622	(272)
			A		B		B	
1999 Cohort Foliar biomass (kg ha^{-1})	a	Loblolly pine	4,659	(349)	5,871	(419)	6,184	(342)
	a	Slash pine	3,332	(107)	5,776	(586)	6,214	(707)
			A		B		C	
Fine root biomass (kg ha^{-1})	a	Loblolly pine	1,966	(557)	3,217	(828)	3,830	(1,095)
	b	Slash pine	1,616	(231)	2,300	(771)	3,174	(927)

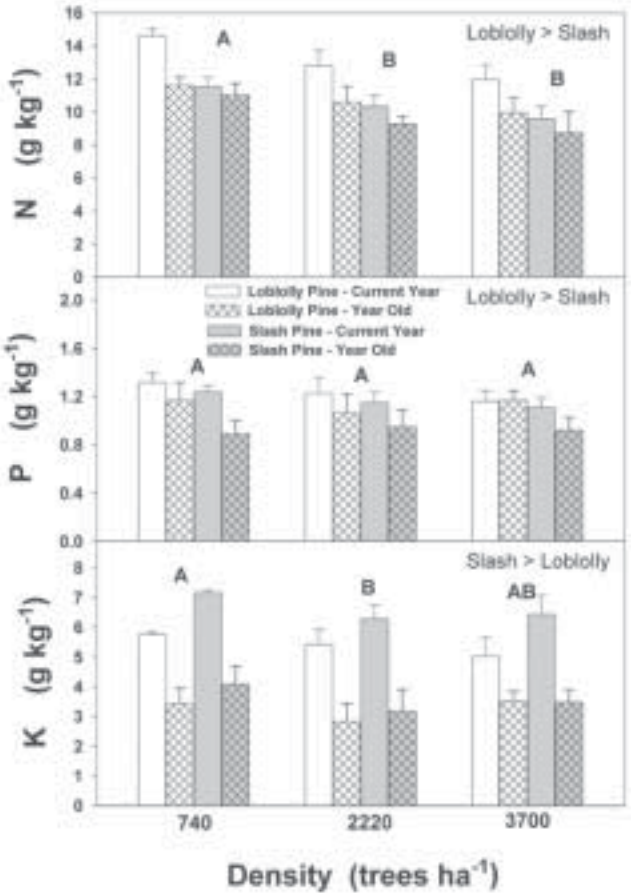

Figure 1. Current-year and 1-yr-old foliage nitrogen (N), phosphorus (P), and potassium (K) concentrations during the fourth growing season for loblolly and slash pine stands planted at three densities. Different letters indicate a significant difference between planting densities ($P < 0.05$). A significant difference between loblolly and slash pine is noted on the graph when it occurred. Vertical bars represent one standard error. Statistical significance was determined from a split plot ANOVA with the factorial combination of species and density serving as the whole plot factors, foliage age serving as the split plot factor, and site serving as the blocking variable.

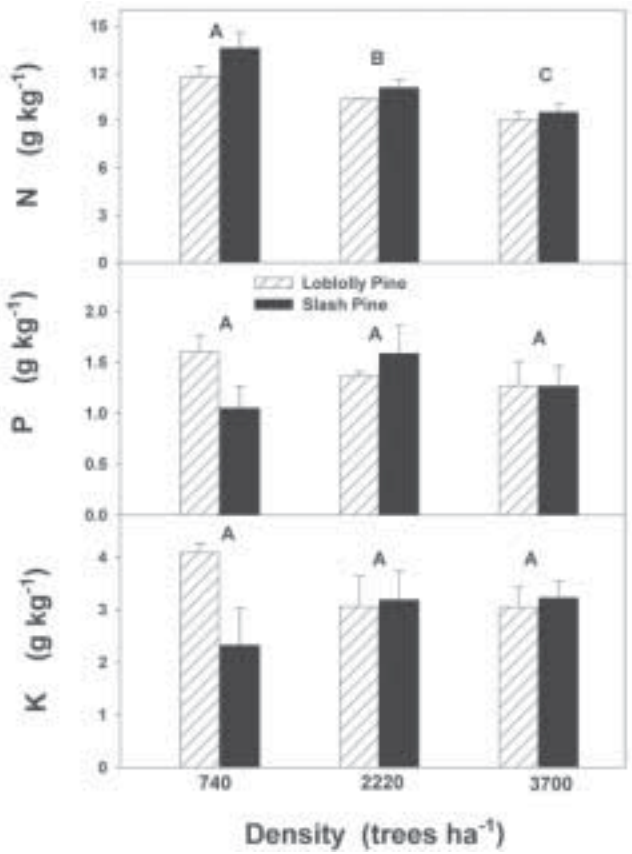

Figure 2. Fine root nitrogen (N), phosphorus (P), and potassium (K) concentrations during the fourth growing season for loblolly and slash pine planted at different densities. Letters indicate a significant difference among planting densities ($P < 0.05$). No difference between loblolly and slash pine occurred. Vertical bars represent one standard error. Statistical significance was determined from a two-way ANOVA with site serving as the blocking variable.

Stem wood N and K concentrations also followed a pattern similar to foliage and root N concentrations, i.e., highest in the lower density stands and decreasing with increasing density (Figure 3). Slash pine had significantly higher stem N and K concentrations than loblolly pine. Stem wood P concentrations were not affected by species or stand density. No significant interactions between species and stand density occurred for these three nutrients. Stand density did not significantly influence stem bark N, P, or K concentrations (Figure 4). Stem bark P concentrations were significantly greater for loblolly than for slash pine.

Foliar N, P, and K contents of the 1998 cohort significantly increased with increasing stand density (Table 2, Table 3). The only species difference (Table 3) was for foliar P contents where loblolly pine stands (4.3 kg ha^{-1}) contained more than slash pine stands (3.1 kg ha^{-1}). Similar to the 1998 cohort foliage, N content increased with increasing stand density for 1999 foliage cohort, but this increase was not statistically significant (Table 3). In addition, N content of loblolly pine stands (72.6 kg ha^{-1}) was significantly greater than for slash pine stands (52.9 kg ha^{-1}). Also for the 1999 foliage cohort, the contents of P and K were significantly greater in the 2,220 and 3,700 trees ha^{-1} stands than in the 740 trees ha^{-1} stands (Table 2, Table 3).

Fine root N content was lower in 740 trees ha^{-1} stands compared with the two higher density stands (Table 2, Table 3). Fine root N content also was significantly higher (Table 3) in loblolly (30.1 kg ha^{-1}) than slash pine (25.4 kg ha^{-1}). Fine root P and K contents also increased with increased stand density (Table 2, Table 3). In both cases, fine roots in the lowest density stands had the lowest nutrient contents, and the fine roots in the higher density stands had the highest contents. Neither fine root P nor K contents were significantly different between the two species (Table 3).

Stem wood N and K contents differed significantly among the three stand densities, and the P content was significantly lower in the 740 trees ha^{-1} stands compared to the two higher density stands (Table 2, Table 3). Slash pine had higher N and P contents in the stem wood than loblolly pine. Stem bark contents of N, P, and K all significantly increased with each increase in stand density (Table 2, Table 3). Stem bark N content of slash pine was significantly greater than for loblolly pine, but stem bark P content was greater for loblolly pine than for slash pine (Table 2, Table 3). A significant interac-

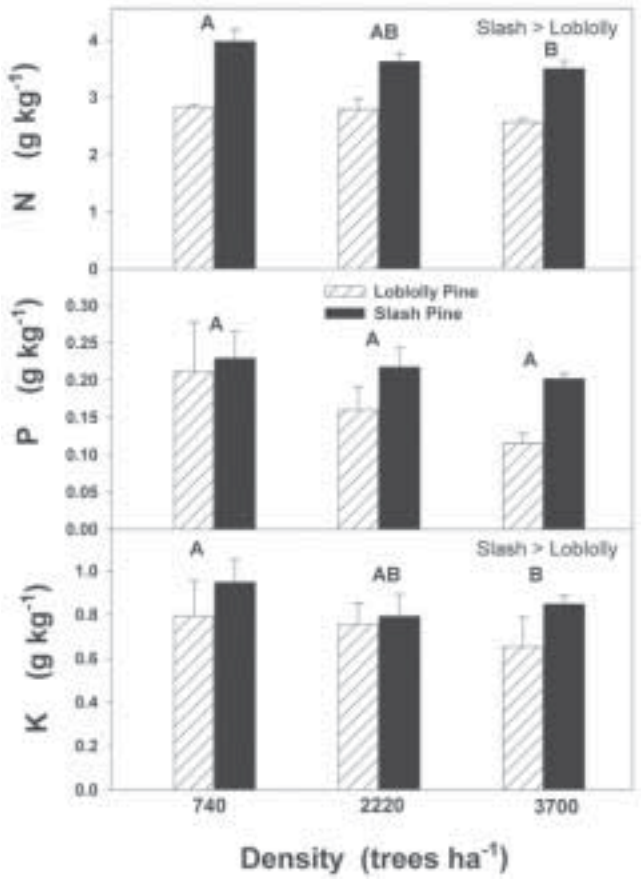

Figure 3. Stem wood nitrogen (N), phosphorus (P), and potassium (K) concentrations during the fourth growing season for loblolly and slash pine planted at three densities. Letters indicate a significant difference among planting densities ($P < 0.05$). A difference between loblolly and slash pine is noted on the graph when it occurred. Vertical bars represent one standard error. Statistical significance was determined from a two-way ANOVA with site serving as the blocking variable.

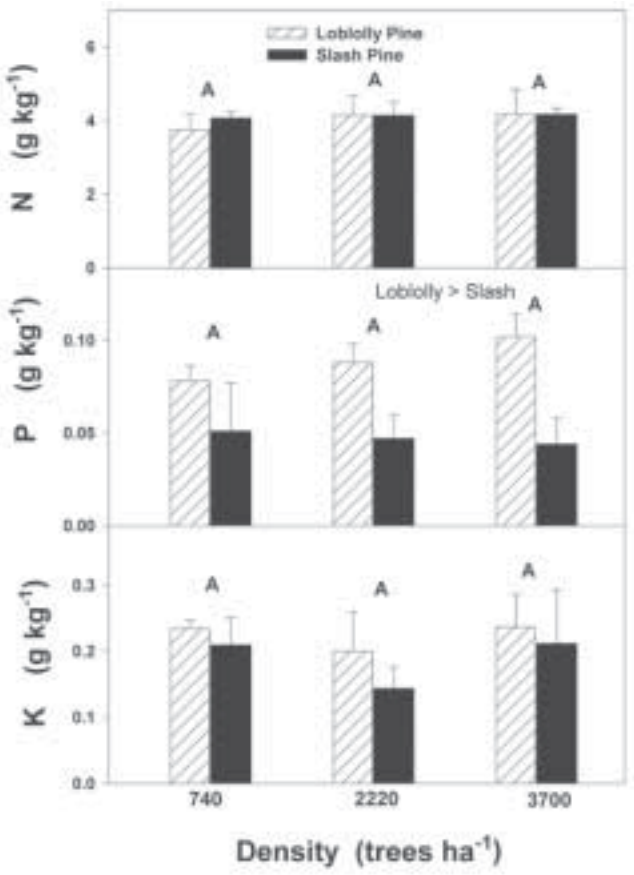

Figure 4. Stem bark nitrogen (N), phosphorus (P), and potassium (K) concentrations during the fourth growing season for loblolly and slash pine planted at three different densities. Letters indicate a significant difference among planting densities ($P < 0.05$). A difference between loblolly and slash pine is noted on the graph when it occurred. Vertical bars represent one standard error. Statistical significance was determined from a two-way ANOVA with site serving as the blocking variable.

tion between species and stand density occurred for stem bark P content (Table 3) because P content increased to a greater extent with increasing stand density for loblolly pine stands than for slash pine stands (Table 2).

Stem growth was negatively correlated (r = -0.57) with foliar N concentration for the 1998 cohort (Figure 5a). The relationship between stem growth and foliar N concentration of the 1999 cohort foliage was similar, but with a lower correlation coefficient (r = –0.50). Foliar N content of the 1998 foliage cohort was positively correlated (r = 0.59) with fourth-year stem biomass growth (Figure 5b). However, foliar biomass of the 1998 cohort was better correlated with fourth year stem growth (r = 0.76) than foliar N content or concentration (Figure 5c). The relationship between N content of the 1999 foliage cohort and stem growth was not significant (P = 0.16). The relationship between the 1999 foliage biomass and stem growth was significant, with a correlation coefficient similar to the 1998 foliage cohort (r = 0.74).

Discussion

On a stand basis, biomass and growth parameters measured in this study increased with stand density. However, the increases were not linear across densities, indicating a resource limitation at the higher densities.

Foliar N, P, and K concentrations, averaged across all stand densities, were within the accepted range for fertilized loblolly and slash pine according to much of the literature (Zhang and Allen 1996, Vose and Allen 1988, Pehl et al. 1984, Shelton 1984, Wells and Metz 1963). Fine root nutrient concentrations generally ran higher than those found in some studies in loblolly pine (Adams et al. 1987, Pehl et al. 1984), but were similar to those found by Shelton (1984). The higher values could have been due, in part, to the fertilization the plots received.

Foliar, fine root, and stem N concentrations decreased significantly with increased stand density, suggesting that N may have limited growth in denser stands. Foliar P and fine root P and K concentrations did not change significantly with increased stand density, suggesting that these two nutrients may not have had as important a role in limiting growth as stand density increased. Further evidence of a possible influence of N, but not P or K, on growth as density increased comes from comparisons of foliar critical concentrations, i.e., established foliar nutrient concentrations below which tree growth has been

Table 2. Fourth growing season (1999) nitrogen (N), phosphorus (P), and potassium (K) contents (kg ha^{-1}) and standard errors (SE) in above- and below-ground biomass components of loblolly and slash pine stands planted at different densities.

			Stand density (trees ha^{-1})					
			740		2220		3700	
	Nutrient	Component	Mean	SE	Mean	SE	Mean	SE
Loblolly pine	N	1998 Cohort	31.5	(7.4)	41.8	(2.2)	45.9	(9.2)
		1999 Cohort	67.8	(4.3)	75.4	(8.7)	74.7	(9.6)
		Stem wood	24.2	(1.0)	55.3	(3.3)	69.3	(7.8)
		Stem bark	4.1	(0.4)	9.6	(0.4)	14.1	(0.6)
		Fine root	23.1	(6.9)	33.3	(8.6)	33.8	(8.1)
	P	1998 Cohort	3.3	(0.9)	4.1	(0.1)	5.4	(1.1)
		1999 Cohort	6.2	(1.2)	7.2	(0.9)	7.3	(0.9)
		Stem wood	1.8	(0.6)	3.2	(0.8)	3.0	(0.3)
		Stem bark	0.09	(0.009)	0.20	(0.004)	0.35	(0.007)
		Fine root	3.3	(1.2)	4.4	(0.2	5.7	(1.1)
	K	1998 Cohort	8.98	(2.1)	10.8	(0.9)	15.9	(2.4)
		1999 Cohort	26.8	(1.7)	31.6	(2.9)	31.9	(5.5)
		Stem wood	6.7	(1.0)	14.9	(1.0)	16.9	(2.2)
		Stem bark	0.25	(0.02)	0.46	(0.06)	0.79	(0.03)
		Fine root	8.2	(2.7)	9.0	(0.9)	12.3	(0.8)
Slash pine	N	1998 Cohort	19.7	(1.7)	33.5	(2.8)	41.1	(8.5)
		1999 Cohort	38.4	(0.7)	60.0	(8.2)	60.4	(12.1)
		Stem wood	26.6	(3.2)	62.5	(3.9)	81.7	(4.4)
		Stem bark	4.1	(0.1)	12.7	(0.6)	14.8	(1.4)
		Fine root	22.1	(4.0)	24.7	(7.2)	29.3	(7.3)
	P	1998 Cohort	1.6	(0.3)	3.4	(0.3)	4.3	(0.5)
		1999 Cohort	4.1	(0.1)	6.6	(0.9)	7.0	(1.3)
		Stem wood	1.5	(0.01)	3.7	(0.3)	4.8	(0.3)
		Stem bark	0.05	(0.016)	0.13	(0.008)	0.14	(0.009)
		Fine root	1.6	(1.1)	3.4	(2.5)	4.3	(1.8)
	K	1998 Cohort	7.2	(2.1)	11.3	(2.1)	16.2	(2.8)
		1999 Cohort	23.9	(0.6)	36.5	(5.0)	41.6	(7.6)
		Stem wood	6.3	(0.3)	13.4	(0.5)	20.0	(0.5)
		Stem bark	0.21	(0.03)	0.40	(0.06)	0.70	(0.14)
		Fine root	3.5	(2.3)	7.0	(4.9)	10.8	(3.8)

found to be limited. Critical concentrations for N, P, and K are considered to be 12.0, 1.0, and 4.0 mg g^{-1}, respectively in loblolly pine (Jokela et al. 1991) and 10.0, 0.9, and 3.0 mg g^{-1}, respectively in slash pine (Fisher and Binkley 2000, p. 294). For both species, foliar P and K concentrations were above these critical concentrations at all densities (average of current-year and 1-yr-old upper canopy foliage), indicating that they probably did not play an important role in limiting growth in these stands. For both species, however, midsummer estimates of upper canopy foliar N decreased, from 13.1 to 10.9 mg g^{-1} for loblolly pine and from 10.9 to 8.8 mg g^{-1} for slash pine, as stand density increased from 740 to 3,700 trees ha^{-1}. Foliar critical concentrations are based on dormant season

Table 3. *P* values associated with the statistical analyses testing for the effects of species, stand density, and the interaction between species and stand density for fourth growing season (1999) nutrient contents in the above- and below-ground biomass components of loblolly and slash pine stand planted at densities of 740, 2220, and 3700 trees ha^{-1}.

		Parameter		
Nutrient	Component	Species	Density	Spec × Den
N	1998 Cohort	0.12	0.04	0.19
	1999 Cohort	0.006	0.10	0.49
	Stem wood	0.007	< 0.0001	0.22
	Stem bark	0.04	< 0.0001	0.10
	Fine root	0.02	0.004	0.23
P	1998 Cohort	0.04	0.009	0.78
	1999 Cohort	0.15	0.04	0.47
	Stem wood	0.09	0.001	0.09
	Stem bark	< 0.0001	< 0.0001	< 0.0001
	Fine root	0.12	0.06	0.91
K	1998 Cohort	0.83	0.01	0.85
	1999 Cohort	0.23	0.03	0.28
	Stem wood	0.66	< 0.0001	0.15
	Stem bark	0.31	< 0.0001	0.94
	Fine root	0.15	0.06	0.72

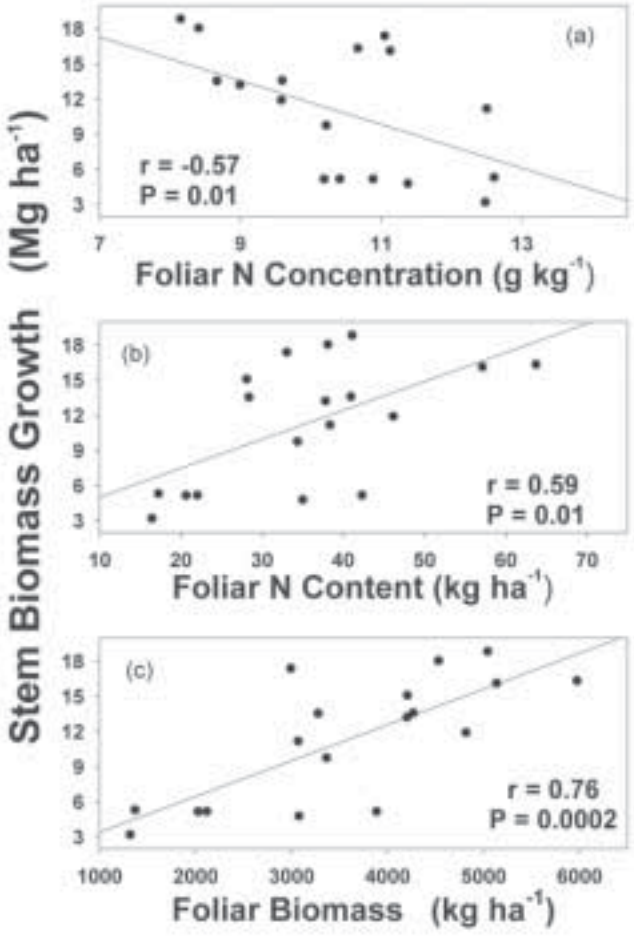

Figure 5. (a) Fourth-year (1999) stem biomass growth: foliar nitrogen (N) concentration of 1-yr-old foliage (1998 cohort). (b) Fourth-year stem biomass growth: foliar nitrogen (N) content of 1-yr-old foliage. (c) Fourth-year stem biomass growth: foliar biomass of 1-yr-old foliage.

measurements and would likely be greater than midsummer concentrations. However, an adjustment for sampling season would probably not be enough to raise foliar concentrations of the densely planted stands above critical concentrations (Murthy et al. 1996, Zhang and Allen 1996).

Although P is most often the limiting nutrient on poorly drained soils in the lower Coastal Plain, fertilization with the amount of P applied in the first 3 yr of this study (120 kg ha^{-1}) is sufficient for an entire rotation. However, even the 210 kg N ha^{-1} added as fertilizer in the first four growing seasons apparently was not enough to meet the demands of these fast growing stands. Not counting branch, coarse root, previous litterfall, or fine root turnover, approximately 238 kg ha^{-1} of N was sequestered in the stem, foliage, and fine roots at the end of the fourth growing season in the highest density stands. Given the exceptional growth rates associated with these intensively managed forests, early, aggressive, and frequent fertilization with N is necessary to maximize stem growth.

Foliar N, P, and K contents fell within the reported range for fertilized pine stands (Zhang and Allen 1996, Shelton 1984, Larsen et al. 1976, Wells et al. 1975, Switzer et al. 1966). Calculated values for fine root N content also were in the generally expected range (Van Lear and Kapeluck 1995, Tuttle 1978, Larsen 1976). While fine root K content values ran a little lower than those found by Tuttle (1978), fine root P and K content values were similar to those of other studies (Van Lear and Kapeluck 1995, Shelton 1984). Foliar and fine root nutrient contents were significantly higher in more dense stands compared to less dense stands as a result of greater acquisition of resources and greater biomass growth. Nutrient contents at the higher densities, however, were either at or approaching a plateau.

While several studies have been published focusing on either stand nutrient dynamics or the effects of stand density on biomass growth, few studies have examined the effects of stand density on nutrient dynamics and the role nutrients may play as an external limiting growth factor. As with our study, Shelton (1984) found that at a young age, higher density stands (4,300 trees ha^{-1}) had higher levels of foliar biomass and foliar N content than less dense stands (1,200 and 1,920 trees ha^{-1}) of loblolly pine. However, the medium spacing had the highest content from ages 15–25. After 25 yr, the N content of all three densities had converged and varied by less than 10%. Even though the trees in our study were only 4 yr old, some contents, such as N content of the 1999 foliage cohort, were fairly similar among densities for loblolly pine.

Foliar N concentration and fourth-year total stem biomass growth were negatively correlated. This does not mean that trees with lower foliar N concentrations will realize more growth, but rather indicates that a dilution effect was occurring over the greater biomass in the denser stands and that less N was available for additional foliage growth at the higher densities. Foliar N content of the 1998 cohort was positively correlated with fourth-year total stem biomass growth. This positive correlation suggests that the stands with greater foliar N content were able to produce more stem biomass growth. Leaf biomass of the 1998 cohort, however, was better correlated to stem biomass growth than foliar N content, suggesting that measures of foliar biomass are better predictors of stem biomass growth. This was contrary to our hypothesis that presumed foliar N content would be better correlated with fourth-year total stem biomass growth because foliar N content encompasses both the amount of sun-intercepting biomass and N concentration. We had presupposed that a possible relationship between N concentration and photosynthetic efficiency might cause foliar N content to be highly correlated with total biomass growth. However, this correlation between N concentration and photosynthesis does not always hold true in southern pines (Samuelson 2001, Will 2001, Teskey et al. 1994). On the stands measured in this study, Will et al. (2001) found that light-saturated net photosynthesis was not different among trees growing at the different densities, even though foliar N concentration decreased with increasing density. The failure to find a significant relationship between fourth year stem growth and foliar N content of the 1999 cohort is further evidence that N content is not as good a predictor of stem growth as is leaf biomass.

In summary, P and K did not appear to be important in these fertilized stands in limiting stem biomass growth. Even though these stands were fertilized, N acquisition may have played an important role in limiting growth as stand density increased. With increased stand density, increases in total stem biomass growth of the stand and N contents were beginning to plateau and N concentrations declined below what are considered critical concentrations. The linkage between stem biomass growth and N was probably the foliage. Increased N availability increases leaf biomass and leaf area, which in turn increases intercepted photosynthetically active radiation (Dewar 1996) and stem growth (e.g., Vose and Allen 1988, Teskey et al. 1987).

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