WITHIN AND BETWEEN CANOPY VARIABILITY OF FOLIAR NITROGEN CONCENTRATION FOR LOBLOLLY AND SLASH PINE STANDS PLANTED AT DIFFERENT DENSITIES

Rodney E. Will, Greg Barron-Gafford, Robert O. Teskey, and Barry D. Shiver[1]

Abstract—Mid-summer foliar nitrogen concentrations (N) were measured at three canopy positions (upper, middle, lower), two foliage ages per canopy position (current-year and 1-year-old), and two flushes per age class (first flush and second flush) in 4-year-old loblolly (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) stands planted at 740, 2,220, and 3,700 trees ha^{-1} to (1) determine differences in foliar N due to species and planting density, (2) quantify variability within canopies, and (3) determine what factors are important to consider when making comparisons between stands with different canopy structures. Overall, foliar N was greater for loblolly pine than slash pine (11.9 vs. 10.1 mg g^{-1}) and decreased with stand density (12.2, 10.7, and 10.1 mg g^{-1} for stands with 740, 2,220, and 3,700 trees ha^{-1} respectively). Foliar N of current-year foliage (11.9 mg g^{-1}) was greater than 1-year-old foliage (10.2 mg g^{-1}). Several interactions occurred between factors of interest due to changes in the magnitude of differences, not due to changes in the direction of response.

INTRODUCTION

Foliar nitrogen concentration (N) of southern pine stands is influenced by N availability (e.g., Munger and others, in press; Murthy and others 1996; Will and others 2001; Zhang and Allen 1996). N availability is a function of supply (modified by site quality or fertilization) and uptake by the stand (modified by stand density or growth rate). Monitoring foliar N is useful to determine potential deficiencies and possibly to predict growth rate (McNeil and others 1988, Valentine and Allen 1990). However, measuring foliar N is complicated by variability within canopies, e.g., canopy position, foliage age, and flush. Standard procedure is to measure recently developed, sunlit foliage from the upper canopy during midwinter. However, this ignores variability within the canopy and ignores foliar N status during the growing season when N is in greatest demand. As a result, impacts of treatments such as spacing and fertilization on foliar N might not be measured if they are transitory or occur only in certain canopy positions.

Our objectives were to (1) determine differences in growing season foliar N for intensively managed loblolly (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) stands planted at different densities, (2) quantify variability in foliar N within canopies, and (3) determine what factors are important to consider when making comparisons between stands with different canopy structures.

METHODS

An experiment using the factorial combination of species (loblolly pine and slash pine) and stand density (740, 2,220, and 3,700 trees ha^{-1}) was planted in January 1996 at three sites (blocks) on the lower Coastal Plain of south Georgia. Slash pine stands were planted with half-sib family 5-61 (JSC/CCA and Champion Paper) and loblolly pine stands were planted with half-sib family 7-56 (North Carolina State Tree Improvement Cooperative). Stands were kept free of competing vegetation. Stands received 56.1 kg ha^{-1} each of elemental N, P, and K in the spring of 1996. In the spring of 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. Other macronutrients and a suite of 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 in the spring of 1999.

During August of 1999 (fourth growing season), composite foliar samples (10-20 fascicles each) were collected from 10 trees per plot. Separate samples were taken from three canopy positions (upper, middle, and lower), two foliage age classes (1-year-old foliage and current-year foliage), and two flushes per age class (first flush and second flush). Samples were dried at 60 °C and ground. N was determined using an NC2100 CNS analyzer and an NA1500 C/H/N analyzer (CE Elantech Inc., Lakewood, NJ, USA). Data were analyzed using a split-split-split plot analysis to determine the effects of species, stand density, canopy position, age class, and flush as well as all interactions.

RESULTS

Overall, a large amount of variability occurred within the canopies (figs. 1 and 2). Foliar N was consistently greater in loblolly than slash pine, greater in the 740 trees ha^{-1} stands compared to the 2,220 and 3,700 trees ha^{-1} stands, and greater in the current-year than 1-year-old foliage. Several interactions occurred (table 1) that were due to changes in the magnitude of differences, not due to changes in the direction of response. Specifics are listed.

1. Foliar N of loblolly pine (11.9 mg g^{-1}) was greater than slash pine (10.1 mg g^{-1}), but the magnitude depended on foliage year, spacing, and flush (significant species*year, species*spacing*year, species*flush, and species*flush*year interactions).

[1] Assistant Professor, D.B. Warnell School of Forest Resources, University of Georgia, Athens, GA 30602; Research Scientist, Biosphere 2, Oracle, AZ 85623; and Professors, D.B. Warnell School of Forest Resources, University of Georgia, Athens, GA 30602.

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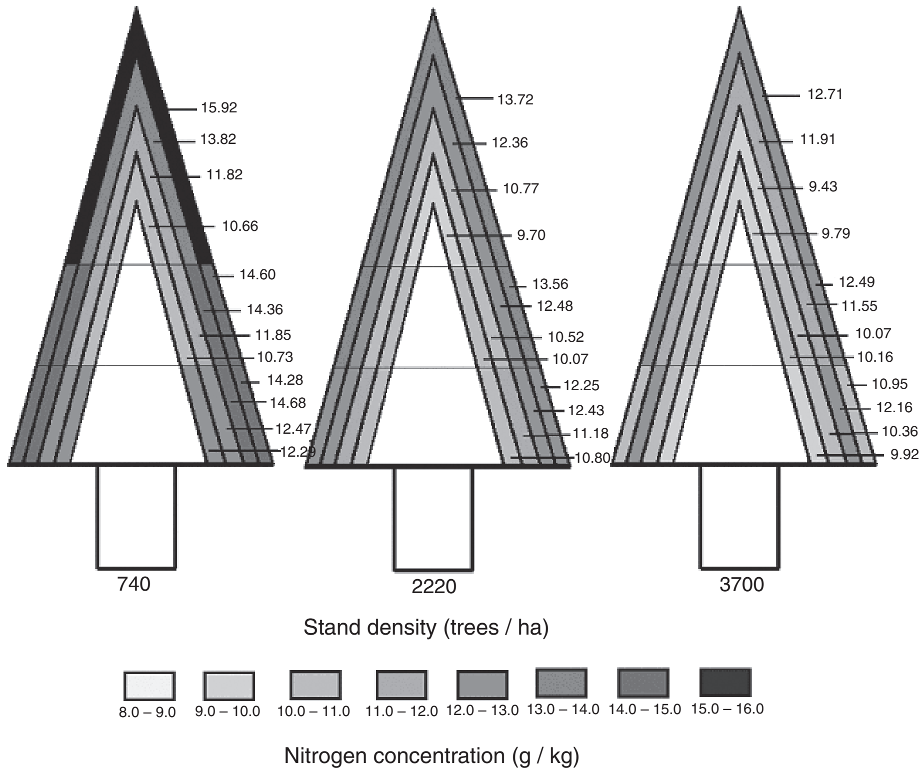

Figure 1—Loblolly pine foliar nitrogen concentrations during the fourth growing season for trees planted at different densities. Foliage was sampled from three canopy positions (upper, middle, lower), two age classes (1-year-old, current-year), and two flushes (first, second). Data are presented in g kg^{-1}.

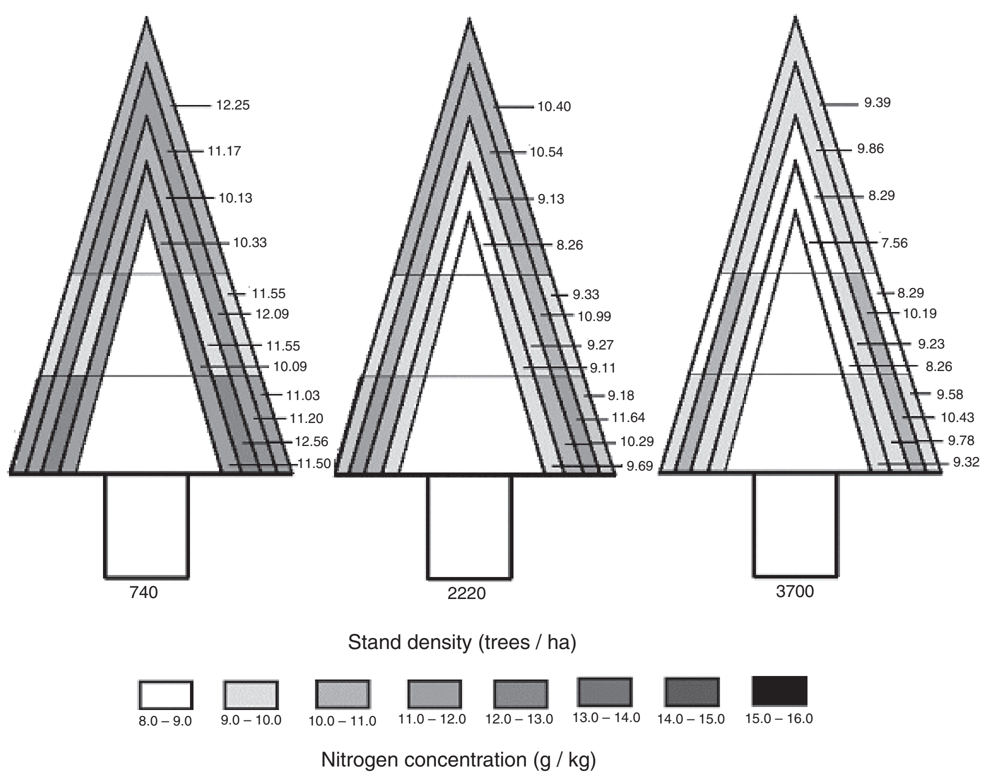

Figure 2—Slash pine foliar nitrogen concentrations during the fourth growing season for trees planted at different densities. Foliage was sampled from three canopy positions (upper, middle, lower), two age classes (1-year-old, current-year), and two flushes (first, second). Data are presented in g kg^{-1}.

Table 1—P values from split-split-split plot analysis

Source	df	p value
Site	2	
Species	1	> 0.0001
Spacing	2	> 0.0001
Spec*Spac	2	0.96
Error1	10	
Position	2	0.22
Spec*Pos	2	0.12
Spac*Pos	4	0.83
Spec*Spac*Pos	4	0.47
Error2	24	
Year	1	> 0.0001
Pos*Year	2	> 0.0001
Spec*Year	1	> 0.0001
Spac*Year	2	0.11
Spac*Pos*Year	4	0.78
Spec*Pos*Year	2	0.67
Spec*Spac*Year	2	0.01
Spec*Spac*Pos*Year	4	0.53
Error3	36	
Flush	1	0.11
Flush*Year	1	> 0.0001
Pos*Flush	2	0.0002
Spec*Flush	1	0.009
Spac*Flush	2	0.002
Pos*Flush*Year	2	> 0.0001
Spec*Flush*Year	1	0.001
Spac*Flush*Year	2	0.19
Spac*Pos*Flush*Year	4	0.15
Spec*Spac*Flush*Year	2	0.08
Spec*Pos*Flush*Year	2	0.22
Spec*Pos*Flush	2	0.14
Spac*Pos*Flush	4	0.74
Spec*Spac*Pos*Flush	4	0.28
Spec*Spac*Flush	2	0.05
Spec*Spac*Pos*Flush*Year	4	0.15
Error4	69	

Species are loblolly and slash pine, spacings are 740, 2,220, and 3,700 trees ha^{-1}, positions are upper, middle, and lower canopy, years are current-year and 1-year-old foliage, and flushes are first and second flush. Significant interactions that occurred were due to changes in the magnitude of differences, not due to changes in treatment rank.

2. Foliar N was greater for the 740 trees ha^{-1} stands (12.2 mg g^{-1}) than for the 2,220 (10.7 mg g^{-1}) or 3,700 (10.1 mg g^{-1}) trees ha^{-1} stands, but the magnitude depended on species, spacing, year, and flush (significant spacing*flush and species*spacing*year interactions).
3. Foliar N of current-year foliage (11.9 mg g^{-1}) was greater than 1-year-old foliage (10.2 mg g^{-1}), but the difference depended on spacing, species, canopy position, and flush (significant position*year, species*year, species*spacing*year, flush*year, and position*year*flush interactions).

DISCUSSION

Clear differences in foliar N were associated with species, stand density, and foliage age. As expected from previous studies, foliar N was lower for slash pine than for loblolly pine (Samuelson 2000, Will and others 2001) and higher in younger foliage (e.g., Munger and others, in press; Will and others 2001; Zhang and Allen 1996).

The decline in foliar N with increasing stand density occurred even though the stands had been fertilized with more than 210 kg ha^{-1} of elemental N. This indicates that the extremely rapid growth rates of the high density stands were exceeding the ability of the soil and supplemental fertilizer to meet the demand for N. Stem growth of the denser stands was becoming limited (Barron-Gafford and others 2003, Burkes and others 2003) and lower foliar N in the dense stands may have been a contributing factor (Barron-Gafford and others 2003). Foliar critical concentration for N is considered to be 12.0 mg g^{-1} in loblolly pine (Jokela and others 1991) and 10.0 mg g^{-1} in slash pine (Fisher and Binkley 2000). For both species, mid-summer estimates of average upper canopy foliar N dipped below critical concentration as stand density increased from 740 to 3,700 trees ha^{-1} (from 13.0 to 10.9 mg g^{-1} for loblolly pine and from 10.9 to 8.8 mg g^{-1} for slash pine). Foliar critical concentrations are based on dormant season measurements and would likely be greater than mid-summer 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 and others 1996, Zhang and Allen 1996).

Unlike other studies that found foliar N to decrease with increasing canopy height (Wells and Metz 1963, White 1954), the main effect of canopy position was not significant in this study. However, canopy position was involved in several interactions such that it decreased with canopy height for the older foliage.

Within a given canopy, the difference in foliar N was as large as 5.3 mg g^{-1}, indicating sampling location had a large impact and that inconsistency in sampling location would mask treatment effects. However, given the general consistency of species and stand density effects within a particular canopy section, the treatment effects on foliar N would have been detected as long as samples were chosen from the same section. This result is particularly robust since stand structure in this experiment was very different between treatments.

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