INTER- AND INTRA-SPECIFIC DIFFERENCES IN FOLIAR N CONCENTRATIONS OF JUVENILE LOBLOLLY AND SLASH PINE IN NORTH FLORIDA

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Abstract—Differences in foliar N concentrations among species, families, and clones may contribute to variation in relative growth performance under varying environmental conditions. Only limited information exists regarding the importance of genetic vs. environmental controls on the nutritional characteristics of loblolly and slash pine. Knowledge of these processes may provide a better understanding of growth strategies among pine taxa and aid in selection and breeding of superior genotypes. This paper will summarize the results of a study designed to investigate the effects of taxa, genotype, site and silvicultural treatments on levels of foliar N concentrations over an entire leaf cycle. Three different pine taxa were investigated (genetically improved loblolly pine, genetically improved slash pine and unimproved slash pine) at two locations in north Florida. Each study consisted of two silvicultural treatments (non-intensive, intensive), three complete blocks within each treatment, three taxa, and 16 open-pollinated families within each taxon. In these juvenile (3-4 yr old) stands, loblolly pine was the most productive species. In comparison to improved and unimproved slash pine, loblolly pine consistently maintained 1) higher foliar N concentrations over time; and 2) higher family variations in N concentrations.

INTRODUCTION

The productivity of loblolly (*Pinus taeda* L.) and slash pine (*P. elliottii* Engelm. var. *elliottii*) stands has been greatly improved since the 1950's. The increases in production are primarily due to the application of intensive silvicultural treatments and the utilization of genetically improved seedlings that offer increased volume gain and disease resistance. Further increases in stand production may result from an improved understanding of how nutritional characteristics vary among species or genotypes in relation to different environments. 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 (Beets and Jokela 1994). Raupach and Nicholls (1982) observed that some nutrients (N, K, Mg, Zn) were significantly different among radiata pine clones in their study. These studies have demonstrated that foliar nutrient levels were controlled by genetic factors, and that nutritional differences were genotype specific. For nutrient use efficiency (amount of dry weight produced per unit weight of nutrients absorbed), Sheppard and Cannell (1985) found 10 - 30 percent differences among 8-year-old clones of *Picea sitchensis* and *Pinus contorta*, which were closely related to the nutrient concentration of foliage. They proposed an ideotype for high nutrient use efficiency as trees having an inherently low nutrient concentrations in needles. Such trees might be well-suited to grow on nutrient poor sites.

From the standpoint of forest genetics, it would be informative to know whether nutritional traits could be incorporated as direct or indirect selection criteria in tree improvement programs to achieve more genetic gain. Additionally, we need to understand if selection on growth traits (DBH, height, and volume) has any indirect effects on the nutrient status of trees. At present, information regarding the genetic architecture (heritabilities, genetic - environmental interaction, and genetic correlation) for the two southern pine species is limited. The objectives of this study were to 1) Examine temporal foliar N dynamics among three southern pine taxa as influenced by site and silvicultural treatments; and 2) Determine the magnitude of variation in foliar N concentrations among families with a taxon.

METHODS

Two field experiments, previously established by the University of Florida's Cooperative Forest Genetics Research program, were sampled in north central Florida (Dunnellon, Levy County, 29°20' N, 82°50' W and Palatka, Putnam County, 29°40' N, 81°42' W). 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

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using a combination of mechanical and pre- and post-plant directed spray applications of glyphosate applied at labeled rates. Containerized seedlings were planted in December 1994 at a 5 x 11 ft spacing at Palatka, and a 6 10 ft spacing at Dunnellon. Fertilizers were broadcast applied in the high intensity treatment as a balanced mix of macro- and micronutrients during year 1 (250 lbs/ac DAP + 200 lbs/ac KCl) and year 3 (535 lbs/ac 10-10-10 + micronutrients). Insecticides 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.

Two sample trees within a 5-tree row-plot in each family from each block were randomly selected. 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. 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. 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.

Needle N concentrations were measured using the method as outlined in Thomas and others (1967) and Jones and others (1991). Nitrogen concentrations were determined using an Aipkem Flow Solution IV analyzer.

SAS procedures, GLM and MIXED, were used to analyze the data (SAS Institute 1996). Means for foliar N concentrations among the three taxa were compared using the LSMEANS statement in PROC MIXED. A default level of a = 0.05 was used to test significance among the means unless otherwise specified.

RESULTS AND DISCUSSION

Variation of Foliar N Concentrations at the Taxa Level

Nitrogen concentrations generally decreased over a complete leaf life cycle among the three pine taxa (figure 1). Differences in N concentrations were consistent among taxa across locations and treatments, with loblolly pine

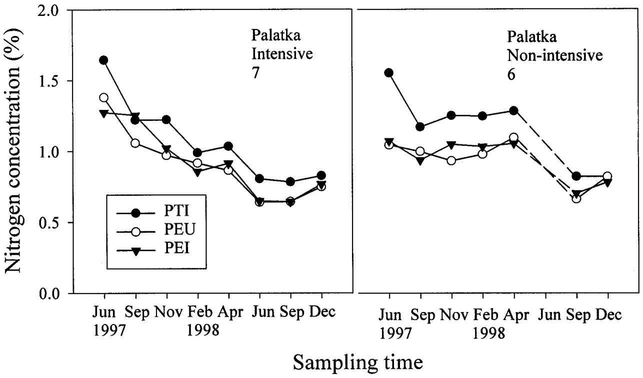

Figure 1—Inter- and Intra-specific Differences in Foliar N concentrations of juvenile loblolly and slash pine in North Florida.

Table 1—Family variation in foliar N concentrations (percent) of the three pine taxa managed under two levels of silvicultural treatments planted at two locations in north-central Florida

Site Treatment Taxa	Interfamily statistics	Mean	Minimum	Maximum
Sampling time: June 1997				
Dunnellon				
High	PTI	1.35	1.02	1.61
	PEU	1.10	0.98	1.20
	PEI	1.21	1.09	1.34
Low	PTI	1.00	0.87	1.12
	PEU	0.90	0.84	0.98
	PEI	0.88	0.73	0.97
Palatka				
High	PTI	1.64	1.38	1.92
	PEU	1.38	1.25	1.47
	PEI	1.28	1.13	1.44
Low	PTI	1.55	1.35	1.80
	PEU	1.05	0.94	1.11
	PEI	1.07	0.98	1.29
Sampling time: December 1998				
Dunnellon				
High	PTI	0.72	0.66	0.77
	PEU	0.74	0.64	0.79
	PEI	0.70	0.64	0.77
Low	PTI	0.81	0.72	0.90
	PEU	0.69	0.63	0.74
	PEI	0.68	0.61	0.74
Palatka				
High	PTI	0.82	0.74	0.91
	PEU	0.75	0.69	0.83
	PEI	0.77	0.68	0.85
Low	PTI	0.82	0.72	0.95
	PEU	0.82	0.74	0.89
	PEI	0.78	0.67	0.90

Note: high = intensive treatment, low = non-intensive treatment; PTI = improved loblolly pine, PEU = unimproved slash pine, PEI = improved slash pine;

having significantly higher concentrations than slash pine. For example, loblolly pine had an average N concentration of 1.64 percent (1.17 and 2.29 percent for minimum and maximum observations, respectively), while improved and unimproved slash pine had N concentrations of 1.28 percent (0.88 - 1.96 percent) and 1.38 percent (1.09 - 1.89 percent), respectively, in June 1997 under the intensive treatment at Palatka. The foliage N concentrations for loblolly pine were significantly higher than either slash pine taxa in seven of the eight sampling periods (88 percent) under the intensive culture treatment and 6 of 8 sampling periods (75 percent) under the non-intensive treatment. Differences in nutrient concentrations for N between improved and unimproved slash pine were generally non-significant. Location × treatment interactions for foliar N concentrations were significant under most sampling periods, showing differential responses among taxa to treatments across locations. Treatments generally did not significantly influence N concentration differences between loblolly and slash pine. 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.

Variation of Foliar N Concentrations at the Family Level

Foliar N concentrations not only showed significant seasonal changes over time at the taxa level, but also varied at the intraspecific (family) level over time (table 1). Family variation in N concentrations (the ratio between the maximum and minimum values of N concentrations) was higher for loblolly than the two slash pine taxa. For example, averaged across locations and treatments, family variation for loblolly, improved and unimproved slash pine was 40, 29, and 19 percent, respectively, in June 1997. Family variation within a taxon decreased from the early fascicle development stage (June 1997) to the later stage (December 1998) for all taxa. Variation in foliar N concentrations among families within a taxon also converged to a similar level for all three taxa. Averaged across locations and treatments, family variation for loblolly, improved and unimproved slash pine was 24, 25, and 20 percent, respectively, in December 1998. The intensive silvicultural treatment increased the foliar N levels at both locations, while loblolly pine still maintained higher N concentrations than the two slash pine taxa across both locations and treatments.

More detailed examination of the relationships between nutrient attributes and growth characteristics at the family level will be helpful to form a better understanding of growth strategies. Estimation of genetic parameters (heritability, genetic-environmental interaction, and genetic correlation coefficients) for various nutritional traits such as nutrient use efficiency, nutrient retranslocation efficiency, and crown nutrient content are planned in the future to quantify the importance of genetic vs. environmental controls on these attributes. Knowledge gained through an understanding of nutritional traits and their relations to growth performance will prove useful in the application of future breeding efforts designed to select superior genotypes for a range of silvicultural management intensities (Xiao 2000).

The potential implications of our findings in the changing nature of foliage N concentrations at the family level suggest that selection could be considered for the two species during the early stages of fascicle development (maturation) if desired in tree improvement programs. For example, N concentrations in the first month that current year foliage attains full length (June, 1997) could be an important sampling period for estimating heritabilities because family variation was most pronounced.

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