NITROGEN AND PHOSPHORUS USE EFFICIENCY IN STANDS OF LOBLOLLY AND SLASH PINE

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Abstract—Nitrogen and phosphorus use efficiency (NUE and PUE, respectively), the annual amount of stemwood produced per unit net N or P used in total aboveground production, were examined in 17-year-old pure stands of unthinned loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Englem.) planted at two spacings. Slash pine stands had a greater NUE and PUE than loblolly pine, which was attributed to greater relative allocation of aboveground production to stemwood, lower foliar N and P concentrations, and greater foliar retranslocation of N and P by slash pine. Compared to 2.4 x 2.4 meter spaced stands, denser 1.2 x 1.2m spaced stands had lower NUE and PUE, which may be related to a sustained drought. Results of this study imply that nutrient management should differ in stands of varying composition and structure.

INTRODUCTION

In the southeastern United States, stand production of loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) forests are often limited due to highly weathered soils that have low N and P base saturation. Potential production of southern pine plantations has been estimated to be twice that which is currently realized (Albaugh and others 1998, Sampson and Allen 1998). To increase production, nutrient management has become increasingly common. For example, 650,000 hectares of southern pine forests were fertilized in 1999, a 35 percent increase over the previous year[1]. While the effects of increased nutrient supply on forest production are readily recognized, there is a need to better understand the underlying mechanisms of nutrient dynamics so as to maximize returns on nutrient management investments.

N and P use efficiency (NUE and PUE, respectively), the amount of stemwood produced per unit N or P used in total aboveground production, is a quantitative measure of how effectively stands use these often-limiting nutrients to produce merchantable stemwood. Knowledge of how NUE and PUE vary could facilitate more sound nutrient management decisions. Any factor that influences stemwood production also likely affects NUE and PUE. For example, the inherently greater percentage of aboveground production allocated to stemwood by slash pine compared to loblolly pine (Colbert and others 1990) could potentially contribute to greater NUE and PUE by slash pine if nutrient uptake was equivalent between species. Likewise, any factor that influences the amount of N or P used to produce new aboveground biomass, such as differences in N or P concentration among the various biomass components or differences in the foliar retranslocation of these nutrients, could also affect NUE or PUE. This study investigated the effects of species and spacing on NUE and PUE in midrotation stands of loblolly and slash pine. Further, differences in biomass allocation, nutrient concentrations, and foliar retranslocation were examined as potential factors that influence NUE and PUE.

METHODS

Site

The study was conducted in a species and spacing trial planted in 1981 on the Lee Memorial Forest in southeast Louisiana. The predominant soil type within the study area is a fine-loamy, siliceous, thermic typic Paleudult (Ruston series). Loblolly or slash pine was planted in 25 x 25 meter plots at spacings of 1.2 x 1.2 meters and 2.4 x 2.4 meters. Each species and spacing combination was replicated 3 times in contiguous blocks.

Understory woody vegetation on each plot was cut with a chainsaw prior to data collection to minimize interspecific competition with overstory pine. Felled stems were left on-site and residual stumps were treated with the herbicide picloram. Measurements were restricted to an inner plot approximately 20 x 20 meters to minimize edge effects between treatment plots. Actual inner measurement plot boundaries varied by plot to include the total crown of all trees whose boles fell within a 20 x 20 meter area. All plot measurements were converted to a per hectare basis.

Nitrogen and Phosphorus Use Efficiency

Aboveground biomass production was estimated with regression equations. Each tree in each plot was numbered in 1996 and was measured for outside bark diameter at breast height (1.37 meters), total height and height to the base of the live crown after the 1996, 1997,

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and 1998 growing seasons. Using these measurements, standing first-year foliage, second-year foliage, stemwood, and branchwood mass for each loblolly pine tree were estimated with equations developed by Baldwin (1987) and Baldwin and others (1997). Slash pine biomass components were calculated with regression equations developed by Lohrey (1984). Lohrey (1984) did not distinguish between first-year and second-year foliage; therefore, to obtain an estimate of first-year foliage, the estimated total foliage on each slash pine tree was multiplied by 53.62 percent, the mean percentage of total loblolly pine foliage that consisted of first-year foliage.

Annual foliage production on each tree for a given year was the first-year foliage in the current year. Annual needle litter production for each year (used to calculate foliar retranslocation) was the second-year foliage in the current year. Annual stemwood and branchwood production on each tree were calculated by subtracting the previous-year standing biomass in each respective component from current-year standing biomass. Per-tree biomass production for each respective component was summed by plot and expanded to a per hectare basis. Two-year periodic mean annual production by component is the mean stand-level biomass production for each respective component averaged over 1997 and 1998.

To obtain N and P concentrations, first-year foliage, second-year foliage, and branchwood samples were collected in mid-September 1997 by shooting a midcanopy branch from 4 trees in each plot with a 12-gauge shotgun and #4 shot. Stemwood samples were obtained by coring four trees in each plot at breast height during December 1997. Needle litter samples were obtained in December 1997 by placing four 1 x 1 meter plastic sheets on the ground in each plot and collecting needle litter after 1 week.

Each component type was combined for each plot, oven-dried at 60°C for 48 hours, ground to pass a 40-mesh screen, and the resulting powder thoroughly mixed. N and P concentration were determined on 3 replicates of the mixture. N concentration was determined with the Dumas-method with a Leco FP-428 Analyzer. P concentration was determined with inductively coupled plasma (ICP) spectrometry (Huang and Schulte 1985). N and P concentration for each component in each plot was the mean of the 3 replicates.

Annual stand-level N and P in new biomass production for each component in each plot in each year was calculated by multiplying the periodic mean annual biomass production in each component in each plot by its corresponding nutrient concentration. A portion of N and P in new biomass production was assumed to have been supplied by foliar retranslocation. The total amount of retranslocated N and P was assumed to come partially from first-year foliage before its second year and partially from second-year foliage before senescence. Thus, the annual per-hectare N and P supplied by foliar retranslocation in each plot in each year was calculated as the difference in N content in first-year foliage from the previous year and N content in second-year foliage from the current year plus the difference in N content in second-year foliage in the previous year and N content in needle litter that fell in the previous year.

Net N and P used in total aboveground production were calculated as the difference between N or P in new aboveground biomass minus N or P that was supplied by foliar retranslocation. NUE and PUE were calculated as mean annual stemwood production (kg/ha per year) per unit net N or P used in total aboveground production (kg/ha per year).

Analysis

Species and initial spacing effects on individual variables were analyzed in a randomized complete block design by analysis of variance with a general linear model procedure (Statistical Analysis System Version 8, SAS Institute Inc., Cary, NC, USA). The general linear model included a variable for block, species (loblolly or slash pine), initial spacing (2.4 x 2.4 meters or 1.2 x 1.2 meters), and the interaction between species and initial spacing. The critical value for significant effects was set at 0.10.

RESULTS AND DISCUSSION

Slash pine had a greater NUE than loblolly pine, producing more stemwood per unit net N used in total aboveground production (figures 1a). There were no significant species by initial spacing interactions for any of the variables measured. Several factors contributed to greater NUE by slash pine. First, while absolute production of stemwood did not vary between species (P = 0.233), slash pine allocated a greater percentage of total aboveground production to stemwood than loblolly pine (67 percent and 63 percent, respectively; P = 0.072). This pattern is apparently manifested early in development as Colbert (1990) reported similar results for 4-year-old seedlings. A

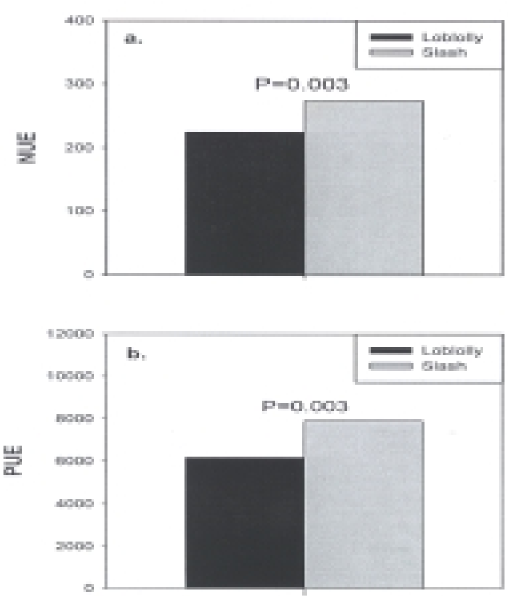

Figure 1—Nitrogen use efficiency (NUE) (a) and phosphorus use efficiency (PUE) (b) by species calculated as mean annual stemwood production (kg/ha per yr) per unit net N or P used in total aboveground production (kg/ha per yr). Data are from 17-year-old pure, unthinned stands of loblolly and slash pine in southeastern Louisiana.

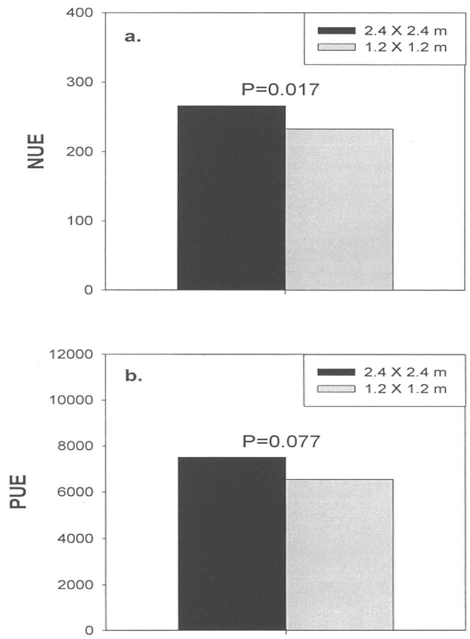

Figure 2—Nitrogen use efficiency (NUE) (a) and phosphorus use efficiency (PUE) (b) by initial spacing calculated as mean annual stemwood production (kg/ha per year) per unit net N or P used in total aboveground production (kg/ha per year). Data are from 17-year-old pure, unthinned stands of loblolly and slash pine in southeastern Louisiana.

lower N cost in new aboveground biomass also contributed to a greater NUE by slash pine as slash pine had lower N concentrations than loblolly pine in both first-year foliage (0.93 percent and 1.15 percent, respectively; P = 0.004) and branchwood (0.36 percent and 0.40 percent, respectively; P = 0.068). Further, slash pine foliage retranslocated a greater percentage of N during its lifespan than loblolly pine foliage (58.2 percent and 51.6 percent, respectively; P = 0.040).

Slash pine also had a greater PUE than loblolly pine (figure 1b). As with N, greater PUE by slash pine resulted in part from greater relative allocation to stemwood than loblolly pine. Again, slash pine had a lower P concentration in first-year foliage than loblolly pine (0.062 percent and 0.073 percent, respectively; P = 0.004). Although slash pine had greater P concentration in stemwood than loblolly pine (0.0045 percent and 0.0037 percent; P = 0.015), the relatively low concentration of stemwood did not appreciably affect total annual P demands. Slash pine foliage also had a greater percentage of P retranslocated during its lifetime than loblolly pine foliage (75.3 percent and 66.0 percent, respectively; P = 0.007).

Comparisons of initial spacing showed that NUE and PUE was greater in the 2.4 x 2.4 meter spaced stands than in the denser 1.2 x 1.2 meter spaced stands (figure 2), which was unexpected. Generally, foliar efficiency at producing stemwood increases with increasing stand density (Smith and Long 1989, Long and Smith 1990), and NUE and PUE were expected to follow a similar pattern. The decline in NUE and PUE in the denser 1.2 x 1.2 meter spaced stands may be related to a sustained drought that occurred during the study that likely caused intense intraspecific competition for water, particularly in the denser stands. As evidence for increased competition in the denser stands, 1.2 x 1.2 meters spaced stands had a significantly greater percentage of total volume lost each year to mortality than 2.4 x 2.4 meter spaced stands (1.32 percent and 0.08 percent per year, respectively; P = 0.001).

CONCLUSIONS

Slash pine stands had a greater NUE and PUE than loblolly pine, which was attributed to slash pine allocating a greater percentage of total aboveground production to stemwood, having lower foliar N and P concentrations, and retranslocating a greater percentage of N and P from foliage before senescence than loblolly pine. Both NUE and PUE declined with closer initial spacing, which was attributed to a drought that occurred during the study.

The results of this study illustrate how nutrient use efficiencies differ between stands of varying composition and structure. Thus, in light of the investment into intensive silviculture, it is apparent that forest managers must consider many variables in a sound nutrient management regime and a "one size fits all" approach is inappropriate.

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