Tree-Soil Interactions Affect Production of Loblolly and Slash Pine

Christopher A. Dicus and Thomas J. Dean

Abstract: Species-related differences in needle litter nutrient concentrations and subsequent N mineralization were examined in 17-year-old stands of loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) at a common site. Results of this common-garden study indicate that a feedback may exist between foliar litter nutrient concentration and soil N mineralization. Net N mineralization (to 30 cm) was significantly greater in loblolly pine than in slash pine stands, which was attributed to greater litter nutrient concentrations in loblolly pine. Stand volume production was also greater in loblolly pine than in slash pine and was positively correlated with N mineralization. Although lower litter nutrient concentrations may have reduced productivity of slash pine relative to loblolly pine in this study, they may serve as a mechanism to increase the relative fitness of the species by lowering the soil nutrient availability below the optimum of loblolly pine.

Keywords: nitrogen mineralization, needle litter, fitness, *Pinus taeda*, *Pinus elliottii*

LOBLOLLY PINE (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) are two of the most important commercial species in the southeastern United States, covering >25 million ha (Smith et al. 1994). Although both species occur on highly weathered soils that have low N and P availability, loblolly pine produces more merchantable volume than slash pine on many sites (Shoulders 1976, Shiver et al. 2000). Site nutrient availability strongly influences relative production between the species. Generally, slash pine outcompetes loblolly pine on the most nutrient-deficient soils; however, loblolly pine typically outperforms slash pine on areas of relatively higher fertility (Haines et al. 1981). This trend apparently results from slash pine having lower nutrient requirements (Fisher 1983) and greater N and P use efficiencies (Dicus and Dean 2002) than loblolly pine.

Availability of many nutrients in unfertilized soils is largely determined by their rates of mineralization from organic forms. The mineralization rate of a limiting nutrient may influence the composition and production of forest stands (Pastor et al. 1984). In natural stands, species presence is often influenced by the ability to compete for a limiting nutrient; as with loblolly and slash pine, the ability of a species to successfully compete often changes along a gradient of availability. Conversely, stand composition may also directly influence nutrient mineralization (Binkley 1996). Therefore, fitness of a given species could potentially be increased if it is capable of directly or indirectly altering mineralization to an optimal level (Binkley and Giardinia 1998). Thus, loblolly pine fitness would be improved by increasing nutrient mineralization above the optimum of slash pine whereas slash pine fitness would be improved by lowering nutrient mineralization below the optimum of loblolly pine.

Mineralization is strongly influenced by the input of nutrients via litterfall and belowground root turnover. Litter and root nutrient quality affects the total amount of nutrients returned to the soil and also probably the rate of microbial decomposition. Varying mineralization rates under stands of different overstory species have been linked to litter quality in a number of studies (Binkley and Valentine 1991, Gower and Son 1992, Stump and Binkley 1993, Knoepp and Swank 1998, Pérez et al. 1998, Prescott and Zabek 1999, Ste-Marie and Paré 1999). Loblolly pine litter generally has greater N and P concentrations than slash pine litter (Polglase et al. 1992), which could potentially lead to greater N and P input and subsequently greater mineralization in stands of loblolly pine than in slash pine.

Theory suggests that differences in stand composition could potentially alter mineralization of limiting nutrients, which then may alter the fitness of a species on a site (Binkley and Giardinia 1998). However, evidence supporting an interaction between trees and soils is somewhat weak because of a lack of replicated experiments at a common location. In this study we investigated tree-soil interactions and their effect on volume production in midrotation stands of loblolly and slash pine at a single site. Species-related variations in litter quality (defined here as N and P concentrations) were examined as potential mechanisms that influence N mineralization. The three objectives of this study were to determine whether stand volume production was correlated with N mineralization, determine whether N mineralization differed under stands of loblolly and slash pine, and determine whether N mineralization is influenced by needle litter nutrient concentration.

Methods

Site Description

The study was conducted on the Lee Memorial Forest in southeast Louisiana, (latitude 32.8°N, longitude 90.0°W).

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The predominant soil type within the study area is a fine loamy, siliceous, thermic typic Paleudult (Ruston series), which is a well-drained soil of low fertility that characteristically has a high level of exchangeable aluminum. The average daily low and high temperatures at a weather station located approximately 15 km from Lee Memorial Forest are 12.03 and 25.56°C, respectively (pers. comm., Louisiana Office of State Climatology, Feb. 1999). The 30-year mean annual precipitation at the weather station is 1,600 mm.

The study was conducted in a species and spacing trial planted in 1981 on a site that was previously used as a Christmas tree plantation. Loblolly or slash pine was planted in 25 × 25 m plots at spacings of 1.2 × 1.2, 2.4 × 2.4, and 3.7 × 3.7 m. Each species and spacing combination were replicated three times in contiguous blocks at the time of planting. Data were not collected in 3.7 × 3.7 m slash pine plots because of unacceptable levels of mortality of planted trees and subsequent invasion of loblolly pine volunteers across these plots. Therefore, a total of nine loblolly pine plots (three plots per three planting densities) and six slash pine plots (three plots per two planting densities) were examined. Treatment means for standard mensurational data for these plots are shown in Table 1.

Understory woody vegetation on each plot, primarily yaupon holly (*Ilex vomitoria* Ait.) and privet (*Ligustrum japonicum* Thunb.), was cut with a chainsaw ~9 months before data collection to minimize interspecific competition with overstory pine. Felled stems were left on site, and residual stumps were treated with Pathway herbicide, which is a formulation of picloram and 2,4-dichlorophenoxyacetic acid that is commonly used to control sprouting species. To minimize edge effects between treatment plots, measurements were restricted to an inner plot that varied in size to include the total crown of all trees whose boles fell within a 20 × 20 m area. All plot measurements are expressed on a per hectare basis.

N Mineralization

Stand-level soil N mineralization was estimated by a modified sequential coring technique (Raison et al. 1987) that incubated soil in situ in the absence of root uptake and that accounted for downward nutrient flux with water. Two major components in the calculation of stand nutrient mineralization are soil depth and bulk density. The depths of the A- and B-horizons were measured directly on 20 cores per plot to a depth of 30 cm. Horizon depth in each plot was the mean of the 20 samples. Bulk density samples of the A- and B-horizons were collected with a general purpose auger in each quadrant within each plot at the top of each respective

horizon. Bulk density samples were oven-dried at 105°C for 24 hours, weighed, and expressed relative to sample volume.

Mineralization was calculated over two periods of time: July 1997 to January 1998 and January 1998 to September 1998. Twenty samples of the bulk soil were collected in each plot at each sampling date. The 20 samples were separated by horizon (A or B) and mixed thoroughly into a composite sample for each horizon. Three replicate samples were taken from each bulk soil composite sample to account for imperfect mixing of the soil and were transported to the laboratory to be analyzed for extractable N. All soil replicates were stored in the laboratory at approximately 2°C for <24 hours before they were placed in extracting solution.

Soil was incubated in situ in the absence of root uptake by vertically inserting an open 5-cm diameter polyvinyl chloride tube 30 cm into the ground adjacent to each bulk sample. Two holes were drilled in each tube at ground level to prevent standing water in the tube that could result in denitrification and anaerobic mineralization. To account for N flux through the soil column, a nylon mesh bag filled with 8 g of mixed resin was placed in the bottom of each tube. At the end of a measurement period, incubated soil within tubes was collected, combined by horizon and plot, and mixed into a composite sample. Three replicate samples were taken from each incubated composite sample. The resin-filled bags in each tube were also collected at this time.

Mineral N was determined by extracting a 10-g subsample from each replicate with 100 ml of 2 M KCl. A paired 10-g subsample of soil was dried at 105°C for 24 hours to determine relative moisture content. The soil-KCl mixture was mechanically agitated for 1 hour, allowed to settle for 30 minutes, filtered with No. 42 ashless filter paper, and stored under refrigeration for <1 week until analyzed. Extracts were analyzed for total N concentration ($NH4^+$ plus NO_3^-; weight basis) with a conductivity detector (Alltech model 320) and converted to a dry soil concentration using the relative moisture content of the sample. The mineral N content of each composite sample is the mean of the three replicate measurements of N. Stand-level mineral N in each horizon in each plot (kg/ha to 30 cm) was calculated by multiplying the N content in each composite sample by the appropriate values of bulk density and horizon depth.

To determine vertical N flux through the soil column, each resin-filled bag was extracted with 80 ml of 2 M KCl, agitated for 1 hour, filtered with No. 42 ashless paper, and stored in refrigeration until analysis with an $NH4^+$ analyzer.

Table 1. Mean stand characteristics of unthinned 17-year-old stands of loblolly and slash pine planted at various initial spacings near Bogalusa, Louisiana

Species	Initial spacing (m)	Trees/ha	D_q (cm)	Height (m)	Basal area (m²/ha)	SDI
Loblolly	3.7 × 3.7	663 (20)	20.6 (1.1)	13.6 (0.3)	22.3 (2.1)	489 (37)
	2.4 × 2.4	1,276 (45)	17.9 (0.5)	16.2 (0.1)	32.4 (2.5)	752 (50)
	1.2 × 1.2	3,068 (50)	11.7 (0.3)	13.6 (0.1)	33.0 (1.4)	910 (29)
Slash	2.4 × 2.4	1,124 (16)	17.0 (0.4)	13.9 (0.2)	25.5 (0.4)	606 (27)
	1.2 × 1.2	2,891 (114)	12.6 (0.3)	13.5 (0.1)	35.8 (0.5)	959 (13)

SEs are given in parentheses. D_q, quadratic mean diameter; SDI, Reineke's stand density index.

Stand-level estimates of N flux through the columns during the sampling periods are expressed on a per hectare basis. The mean N content of the 20 resin-filled bags represented the stand-level N flux for each combination of sampling period and plot.

Net N mineralization (kg/ha to 30 cm) during each time period in each plot was calculated with

$$\text{Min}_{(N)} = (I_1 - B_0)_{\text{A-horizon}} + (I_1 - B_0)_{\text{B-horizon}} + R_1, \qquad (1)$$

where $\text{Min}_{(N)}$ is the net N mineralization during each time period, I_1 is the N content in incubated soil collected at the end of a time period, B_0 is the stand-level N content in bulk soil collected at the beginning of a time period, A-horizon and B-horizon are horizon designations, and R_1 is stand-level N in resin-filled bags collected at the end of a time period. Total N mineralization from July 1997 to Sept. 1998 (A- and B-horizon to 30 cm) in each plot is the sum of N mineralization over both time periods.

Litter Nutrient Concentration

To determine needle litter nutrient concentrations, needle litter samples were obtained in December 1997 during the apparent peak leaf-off period. Four 1-m^2 plastic sheets were placed on the ground in each plot. Needle litter that fell onto the plastic sheets was collected 1 week later. Needle litter was combined for each plot, oven-dried at 60°C for 48 hours, and ground to pass a 40-mesh screen, and the resulting powder was thoroughly mixed. N and P concentrations were determined on three 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 spectrometry (Huang and Schulte 1985) by the Louisiana State University Agricultural Center Soil Testing and Plant Analysis Laboratory. N and P needle litter concentrations in each plot were the means of the three replicates. Needle litter was not collected again because the observed N and P concentrations were consistent with concentrations that were observed throughout the year in a previous monitoring study on the same site (T. J. Dean, professor, School of Renewable Natural Resources, Louisiana State University, unpublished data, 1993).

Stem Volume and Litter Production

Stem volume and litter production were estimated with regression equations based on outside bark dbh, total height, and height to the base of the live crown, which were measured after the 1996, 1997, and 1998 growing seasons. Standing volume of each loblolly pine tree was calculated using an equation developed by Baldwin and Feduccia (1987) for unthinned stands that incorporates measurements of dbh, tree height, and tree age. Volume of each slash pine tree was calculated with an equation developed by Lohrey (1985) for planted stands that incorporates measurements of dbh and height. Tiarks and Baldwin (1999) validated the equations across a range of sites in Texas, Louisiana, and Mississippi, concluding that the equations can be used with confidence in West Gulf Coast plantations. Annual volume production on each tree was calculated by subtracting the previous-year standing volume from current-year standing volume. Per-tree volume production was summed by plot and expanded to a per hectare basis. Mean annual volume production over is the mean stand-level volume production averaged over 1997 and 1998.

Statistical Analysis

The fixed effects of species and initial spacing on individual variables were analyzed in a randomized complete block design with analysis of variance (Statistical Analysis System version 8.1; SAS Institute, Inc., Cary, NC). Because of the missing cell caused by unacceptable mortality in the 3.7 × 3.7 m spaced slash pine stands, analyses of species and initial spacing effects were limited to the 1.2 × 1.2 and 2.4 × 2.4 m spaced stands, in which initial spacings were common for both species. The general linear model used included a term for block, species, initial spacing, and the interaction of species and initial spacing. The critical value of g for significant effects (determined by examination of type III sum of squares) was set at 0.10. Linear regression of net N mineralization against volume increment also used a general linear model procedure in SAS version 8.1.

Results and Discussion
Species Effects

Annual volume increment for all plots over the 2 years of study ranged from 12.5 to 23.4 $\text{m}^3\,\text{ha}^{-1}\,\text{yr}^{-1}$ and was significantly greater in loblolly pine stands than in slash pine stands (Table 2). Corresponding with volume production, total net N mineralization (to 30 cm) over the 15-month study period, which ranged from 11.91 to 47.93 kg/ha, was also significantly greater in loblolly pine stands than in slash pine stands (Table 2). Thus, species-related differences in N mineralization may have influenced the greater volume production in loblolly pine. Of note, the mean proportion of total N mineralization from resin-filled bags was 51.4% (SE 4.3), and did not vary between species ($P = 0.979$). Also, moisture content was slightly but significantly higher in incubated soil than in bulk soil in both the A-horizon (17.7% versus 14.3%, respectively; $P = 0.026$) and B-horizon (14.1% versus 13.5%, respectively; $P = 0.003$).

Regression of all plots revealed that volume production was positively and linearly related to N mineralization (Figure 1, $P = 0.034$). The linear relationship between N mineralization and volume production is weak ($r = 0.30$), which is somewhat expected as there are many factors that influence stand production. Examination of this relationship for individual species showed no significant relationship in either loblolly pine ($P = 0.154$, $r = 0.267$, $n = 9$) or slash pine ($P = 0.612$, $r = 0.071$, $n = 6$).

Needle litter N and P concentrations were examined to help explain differences between species in N mineralization, which seems to have influenced volume production. N mineralization across all plots was significantly correlated with both N and P concentrations in the needle litter ($P = $

Table 2. Mean values and statistical analyses for 2-year periodic annual volume increment (volume), 15-month net N mineralization (N_{min}, June–September of following year), and needle litter N and P concentration (N_{con} and P_{con}, respectively) in unthinned 17-year-old stands of loblolly and slash pine near Bogalusa, Louisiana

Species	Initial spacing (m)	Volume (m^3 ha^{-1} yr^{-1})	N_{min} (kg/ha)	N_{con} (%)	P_{con} (%)
Loblolly	2.4 × 2.4	20.83	37.23	0.543	0.0235
	1.2 × 1.2	16.02	33.35	0.569	0.0260
Slash	2.4 × 2.4	15.08	20.11	0.342	0.0132
	1.2 × 1.2	14.58	23.77	0.429	0.0172
Root mean square error		2.36	7.66	0.055	0.0029

	df	P values for effect			
Block	2	0.834	0.149	0.645	0.382
Species (S)	1	0.039	0.024	0.002	0.001
Initial spacing (I)	1	0.100	0.980	0.126	0.101
S × I	1	0.164	0.427	0.368	0.675

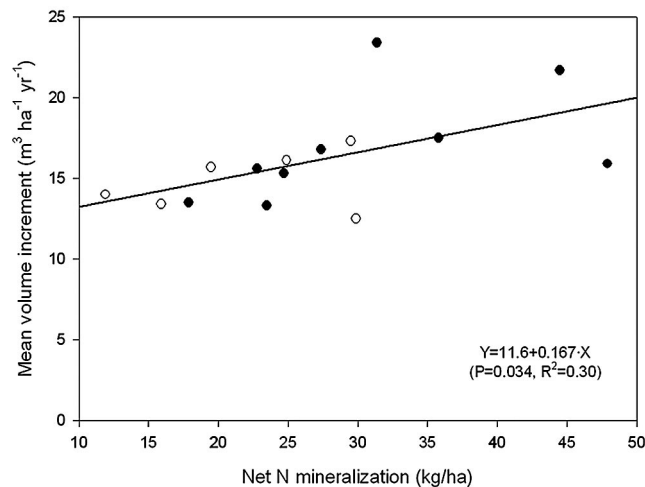**Figure 1.** Annual volume increment (kg ha^{-1} yr^{-1}, 1997–98) as related to net N mineralization from July 1997 to Sept. 1998 (kg/ha) in 17-year-old unthinned stands of loblolly and slash pine near Bogalusa, Louisiana. ●, loblolly pine; ○, slash pine. The line is the least-squares fit.

0.064 and 0.005, respectfully). Needle litter N concentrations, which ranged from 0.32 to 0.65%, and needle litter P concentrations, which ranged from 0.013 to 0.031%, were both significantly greater in loblolly pine than in slash pine (Table 2), which is consistent with results reported by Polglase et al. (1992). Therefore, greater N concentrations in loblolly pine may have led to greater N mineralization (and subsequent production) in those stands. N mineralization has previously been linked to N content in litter in loblolly pine (Vitousek et al. 1992) and across multiple species in Wisconsin (Pastor et al. 1984). Further, Binkley and Ryan (1998) reported that although litter production was equivalent between *Albizia* and *Eucalyptus*, total N input via litter was greater in *Albizia* stands as a result of greater litter N concentration. Scott and Binkley (1997), however, reported poor correlation between N content in litter and N mineralization across many forest types.

It should be noted that although N mineralization was strongly correlated to needle litter nutrient concentration in the present study, no direct causal relationship was tested and other factors might actually be driving differences in mineralization between the species. For example, several studies have reported that decomposition rates of conifer needle litter was closely related to lignin content, which was not measured in the present study, irrespective of N concentration (Stump and Binkley 1993, Fioretto et al. 1998, Murphy et al. 1998, Prescott and Zabek 1999). Prescott et al. (2000) reported that N mineralization was not related to either litter nutrient concentrations or decomposition rates, but rather to the forest floor C/N ratio. Scott and Binkley (1997), using data from many forest types and climatic regimens, reported that N mineralization was more strongly correlated with the ratio of lignin to N than by any other single factor. Scott (1998) demonstrated that N mineralization was most closely related to fungal and bacterial biomass. Gholz et al. (1985) reported that decomposition rates of slash pine litter (and presumably mineralization) were significantly related to needle P concentration but not to N concentration. In light of the previous studies that showed poor correlation of litter decomposition with litter nutrient concentrations, greater N mineralization in loblolly pine may simply result from a greater total amount of organic N available to be mineralized.

Other factors could potentially contribute to differences between species in nutrient supply and subsequent volume production. For example, although fine root production did not vary between species on the study site (Dicus 2000), no estimate of actual nutrient cycling by fine root turnover was measured in the present study. Also, differences in foliar nutrient resorption between loblolly and slash pine (Dicus and Dean 2002) potentially confound the relationship. Regardless of the specific mechanism, evidence here, although not conclusive, suggests that loblolly pine litter had higher nutrient concentrations than that of slash pine, which then led to greater N mineralization and subsequently greater volume production.

Tree-Soil Interaction Effects on Fitness

Binkley and Giardina (1998) hypothesized that tree species may alter soils and directly affect their fitness, a process they termed a "tight weave." Although evidence suggests that lower litter nutrient concentrations may have reduced production of slash pine stands relative to loblolly pine in this study, they may serve as a mechanism to increase the

relative fitness of the species by lowering the soil nutrient availability below the optimum of loblolly pine.

Slash pine has lower nutrient demands than loblolly pine (Fisher 1983). For example, on one highly weathered, nutrient-poor site in northern Florida, 16-year-old slash pine stands had accumulated more stemwood and total biomass than loblolly pine (Jokela and Martin 2000); however, this trend reversed on plots with fertilization and weed control treatments. Slash pine will respond to fertilization (Harding and Jokela 1994), but the magnitude of the response is not as substantial as that for loblolly pine (Jokela and Martin 2000), and unlike loblolly pine decreases as inherent site quality increases (Jokela et al. 2000).

Thus, in the present study, slash pine potentially increased its fitness relative to loblolly pine by recycling fewer nutrients to the soil via litterfall, which effectively lowered the availability of soil nutrients. Conversely, loblolly pine may have raised its fitness relative to slash pine by recycling more nutrients to the soil via litterfall. It is unclear whether production would differ between the species if soil nutrient availability remained equivalent. On soils of equivalent nutrient availability, any production differences between species would depend on how similar the observed mineralization rate was to that of the optimum for each species.

The tree-soil interactions presented here could help elucidate why the natural range of slash pine is typically limited to nutrient poor soils of the Gulf Coastal Plain, whereas the natural range of loblolly pine is much greater. Slash pine tolerates lower soil nutrient availability than loblolly pine partly due to greater nitrogen use efficiency (Dicus and Dean 2002). Another adaptation to poor site quality in slash pine is greater leaf area efficiency than that for loblolly pine (Colbert et al. 1990, Jokela and Martin 2000), which enables slash pine to invest less in nutrient-rich foliage than loblolly pine to obtain equivalent amounts of photosynthate. And the results of this study suggest that slash pine may perpetuate itself on nutrient poor sites by maintaining the nutrient availability below the optimum of loblolly pine, thus supporting the tight-weave hypothesis of Binkley and Giardinia (1998).

It is not clear whether slash pine lowered mineralization rates on these sites below rates that were experienced at the initiation of the stand. It is likely, however, that mineralization rates under both species were lowered because soil nutrients typically decline early in stand development to meet aboveground production demands (Wells and Jorgensen 1975, Binkley et al. 1995). Questions also remain as to whether these differences between species will remain throughout stand development or are a product of ontogeny. Also, the effect on soil nutrient availability in subsequent generations is also unknown. Future research is therefore needed to explore these fundamental questions of forest productivity.

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