The Relationship of Biomass Allocation and Nutrient Dynamics in Loblolly and Slash Pine Forests.

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THE RELATIONSHIP OF BIOMASS ALLOCATION AND NUTRIENT DYNAMICS IN LOBLOLLY AND SLASH PINE FORESTS

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The School of Forestry, Wildlife, and Fisheries

by

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B.S., Louisiana Tech University, 1992
M.S., Utah State University, 1995
December 2000
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\[ M_{res}=5-\left(-3596.65+66.52\cdot SI\right)/(-8.56+15.91\cdot SI) \]
\[ +(-3596.65+66.52\cdot SI)/(T_b+(-855.59+15.91\cdot SI)) \]
where \( M_{res} \) is residual root weight, SI is site index (base age 50), and \( T_b \) is number of days buried. Residual root mass for medium roots in Block 2 are estimated by the equation 
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ABSTRACT

Aboveground biomass allocation and its effect on various aspects of N and P dynamics were investigated in loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) stands planted at different spacings. Further, the relationship of nutrient demand and root production was investigated to validate the functional balance hypothesis in forest stands.

N mineralization was greater in loblolly pine stands than slash pine, corresponding with greater needle litter N concentration. Both N and P mineralization increased in loblolly pine stands with increasing stand density, the result of greater nutrient input through increased litterfall.

There were no species differences in total standing N at wider spacings, but slash pine had greater standing N at narrower spacings. There were no species differences in total standing P at any spacing. With increasing stand density in loblolly pine, total N and P increased then decreased. The majority of standing N and P was located in the crown. Loblolly pine had more standing N and P in the crown than slash pine. With increasing stand density, the fraction of total standing biomass, N, and P in the crown decreased.

There were no species differences in apparent N and P demand (total N and P in annual aboveground production minus retranslocation). Apparent N and P demand in loblolly pine stands increased with stand density then decreased. Retranslocation minimized variation in apparent N and P demand between species and densities.
Conflicting with apparent N and P demand, actual N and P uptake were greater in loblolly pine, and actual N uptake was positively and linearly related to stand density.

Fine root production did not differ between species. The proportion of total net primary production allocated to fine roots was lower than reported in other studies and may be related to a drought that forced roots below the maximum sampling depth. For loblolly pine, stand density appears to have influenced annual aboveground biomass allocation and subsequent N demand and uptake which was positively and linearly related to fine root production, thus supporting the functional balance hypothesis. However, there was no evidence for the functional balance hypothesis in slash pine.
CHAPTER 1

INTRODUCTION

The underlying mechanisms of biomass allocation are fundamental to the study of forest productivity. Aboveground biomass allocation is affected by factors such as genotype (Li et al. 1991, McCrady and Jokela 1996), soil water and nutrient status (King et al. 1999), canopy dominance (Naidu et al. 1998), and stand age (Alban 1988, Beets and Whitehead 1996). Of interest to this study, differences between species and stand density may also affect aboveground biomass allocation. For example, loblolly pine (Pinus taeda L.) generally allocates a greater percentage of total aboveground biomass to the crown than slash pine (Pinus elliottii Engelm.), a closely related species (Colbert 1990). And increasing stand density generally results in increasing stand-level production of stem wood (Long 1985) and foliage (Dean and Baldwin 1996), but decreasing production of branch wood (Assman 1970, Jack and Long 1991).

While the mechanisms that control aboveground allocation are becoming clearer, belowground allocation is less understood as a result of the difficult nature of obtaining belowground data and the various techniques of estimating belowground production that often do not produce consistent trends. One modeling approach to explain allocation to fine roots was forwarded by Davidson (1969) who hypothesized that a functional balance existed between the size and activity of the photosynthetic system (shoots) and the size and activity of the nutrient acquisition system (roots). In general, the functional balance hypothesis states that photosynthate is allocated to
foliage production when there is a shortage of carbon, and conversely, photosynthate is allocated to fine roots when nutrients are limiting.

The functional balance hypothesis was developed to describe root to shoot ratios in simple annuals. Due to the complexity of forest systems, it is not appropriate for use in making quantitative predictions about biomass allocation in forest systems. However, the functional balance hypothesis provides a framework in which general predictions can be made. Of interest to this study, the functional balance hypothesis suggests that fine root production may be linked to demands for a limiting nutrient. According to the functional balance hypothesis, changes in nutrient demand, as influenced by aboveground biomass allocation, may subsequently affect belowground production.

Aboveground biomass allocation patterns likely affect nutrient demands. Large differences in nutrient concentrations may exist between the various aboveground components (foliage, stem wood, branch wood) that make up total aboveground production. For example, Switzer et al. (1968) showed that foliar N concentration of 18-year-old loblolly pine was 14 times greater than stem wood N concentrations. Because of large differences in nutrient concentration between components, differences in biomass allocation, as influenced by species and stand density, should therefore also affect the accumulation and demand for nutrients.

This study examined aboveground biomass allocation and its subsequent effect on various aspects of nutrient dynamics. Further, the relationship of nutrient demand, as influenced by biomass allocation, and root production was investigated. The study
was conducted in stands of loblolly pine and slash pine, two commercially important species in the southeast United States that are commonly limited by N and P. The two main objectives of this study were to determine (1) if aboveground structure, as influenced by species and stand density, affected N and P mineralization, accumulation, and uptake, and (2) if belowground production corresponded with N or P demand and uptake, thereby providing a mechanism for belowground production in pines.
2.1. Introduction

Nutrient mineralization (particularly of N and P) is important in the loblolly pine (Pinus taeda L.) and slash pine (Pinus elliottii Engelm.) forests of the southeastern United States because stands are often located on Ultisols that have low base saturation. Hence, silvicultural treatments that increase mineralization rates without degrading soil structure should also increase nutrient availability and subsequent production.

Silvicultural treatments such as harvest and site preparation often result in short-term increases in nutrient mineralization (Burger and Pritchett 1984, Vitousek and Matson 1985). N mineralization was documented at rates three times higher in recently harvested sites than in adjacent mid-rotation loblolly pine stands (Piatek and Allen 1999). This increase is likely caused by a combination of mixing logging slash and mineral soil (Gent et al. 1984) and increased post-harvest soil temperatures (Vitousek and Matson 1985). The magnitude of the increase in mineralization is related to the intensity of both the harvest (Prescott 1997) and site preparation (Burger and Pritchett 1984, Vitousek and Matson 1985, Vitousek et al. 1992, Lundmark-Thelin and Johansson 1999). The effects of silvicultural treatments may be long lasting; changes in mineralization have been detected 20-40 years after treatment (Morris and Boerner 1998, Piatek and Allen 1999).
Selection of planted species at stand establishment may affect long-term nutrient mineralization. Mineralization rates often vary under stands of different overstory species, which may be related to litter quality and subsequent rates of decomposition (Binkley and Valentine 1991, Gower and Son 1992, Knoepp and Swank 1998, Pérez et al. 1998, Ste-Marie and Paré 1999). N mineralization rates are generally higher under stands of deciduous broadleaves (Stump and Binkley 1993) compared with evergreen conifers (Miller et al. 1979, Prescott et al. 1992a,b). This corresponds with greater litter N concentrations in broadleaves than conifers (Vogt et al. 1986). N mineralization rates also vary by conifer species as well, which again is related to litter quality. For example, litter decomposition and subsequent N mineralization rates under stands of western red cedar, firs, and hemlocks were related to the C:N ratio in the litter (Prescott and Zabek 1999).

Litter quantity may also be positively correlated with nutrient mineralization rates. For a given litter quality, increases in litter production should be associated with increases in nutrient input and subsequent mineralization. A positive relationship between stand density and litter production has been reported for radiata pine (Pinus radiata (D. Don)) (Raison et al. 1992) and loblolly pine (Hennessey et al. 1992). A link between litter quantity and nutrition is supported by the increased rates of production of both the overstory and understory after direct application of litter to loblolly pine plantations (Haywood et al. 1997).

This study examined the effect of species and stand density on N and P mineralization. Specifically, the three objectives of this study were to (1) determine if
N and P mineralization rates differed under stands of loblolly and slash pine, (2) determine if N and P mineralization rates differed under stands of increasing stand density, and (3) determine if N and P mineralization rates were correlated with stand volume production. Differences in litter quality and quantity were also measured as they are commonly related to mineralization.

2.2. Methods

2.2.1. Site Description

The study was conducted 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). The average daily low and high temperatures at the Franklinton 3 SW weather station, located approximately 15 km from Lee Memorial Forest, are 12.03°C and 25.56°C, respectively (Southern Regional Climate Center, Louisiana Office of State Climatology). The 30-year mean annual precipitation at the weather station is 1600 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. Pure stands of loblolly or slash pine were planted in 25 x 25 m plots at spacings of 1.2 x 1.2 m (narrowly spaced), 2.4 x 2.4 m (medium-spaced), and 3.7 x 3.7 m (widely spaced). Each species and spacing combination was replicated three times in contiguous blocks that represented a perceived fertility gradient. Data collection was limited in slash pine plots to the medium and narrowly spaced plots as a result of unacceptable mortality of planted trees and subsequent invasion of loblolly pine volunteers in the widely spaced 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 2.1.

Understory woody vegetation on each plot, primarily yaupon holly (*Ilex vomitoria* Aiton) and Privet (*Ligustrum japonicum* Thunberg.), 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 a smaller plot approximately 20 x 20 m to minimize edge effects between treatment plots. Actual inner measurement plot boundaries varied by plot and were expanded from 20 x 20 m to include the total crown of all trees whose boles fell within a 20 x 20 m area. All plot measurements were converted to a per-hectare basis.

### 2.2.2. Soil Nutrient Mineralization

Stand-level soil N and P 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. To estimate mean depth of the A- and B-horizons, twenty soil cores were taken in each plot. A-horizon depths were measured directly, while B-horizon depths were the residual depth to 30 cm. Horizon depth in each plot was the mean of the twenty samples.
Table 2.1. Mean stand characteristics (1997 and 1998) in unthinned 17-year-old stands of loblolly and slash pine planted at various spacings near Franklinton, LA, USA. Standard errors are given in parentheses.

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<th>Trees per hectare</th>
<th>$^{2}$Dq (cm)</th>
<th>Height (m)</th>
<th>Basal area ($m^2$ ha$^{-1}$)</th>
<th>$^{3}$SDI</th>
</tr>
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<tr>
<td>$S_L I_W$</td>
<td>663 (20)</td>
<td>20.6 (1.1)</td>
<td>13.6 (0.3)</td>
<td>22.3 (2.1)</td>
<td>489 (37)</td>
</tr>
<tr>
<td>$S_L I_M$</td>
<td>1,276 (45)</td>
<td>17.9 (0.5)</td>
<td>16.2 (0.1)</td>
<td>32.4 (2.5)</td>
<td>752 (50)</td>
</tr>
<tr>
<td>$S_L I_N$</td>
<td>3,068 (50)</td>
<td>11.7 (0.3)</td>
<td>13.6 (0.1)</td>
<td>33.0 (1.4)</td>
<td>910 (29)</td>
</tr>
<tr>
<td>$S_S I_M$</td>
<td>1,124 (16)</td>
<td>17.0 (0.4)</td>
<td>13.9 (0.2)</td>
<td>25.5 (0.4)</td>
<td>606 (27)</td>
</tr>
<tr>
<td>$S_S I_N$</td>
<td>2,891 (114)</td>
<td>12.6 (0.3)</td>
<td>13.5 (0.1)</td>
<td>35.8 (0.5)</td>
<td>959 (13)</td>
</tr>
</tbody>
</table>

$^{1}$Treatment levels for the Species (S) variable are denoted by L (loblolly pine) or S (slash pine). Treatment levels for the Initial spacing (I) variable are denoted by W (widely spaced, 3.7 x 3.7 m spacing), M (medium-spaced, 2.4 x 2.4 m spacing) or N (narrowly spaced, 1.2 x 1.2 m).

$^{2}$Quadratic mean diameter.

$^{3}$Reineke's stand density index.
To obtain mean bulk density of the A-horizon in each plot, the organic litter layer was pushed aside at four locations within each plot and a 6-cm diameter, 6.5-cm long steel tube was carefully inserted vertically into the top of the mineral soil to avoid compaction. Soil within the tube was extracted and stored. B-horizon bulk density samples were obtained in like manner after gently excavating mineral soil to the top of the B-horizon. Samples were dried at 105°C for 24 hours, weighed, and converted to a weight to volume basis.

Mineralization was sampled over two periods of time: July 1997 to January 1998 and January 1998 to September 1998. Twenty soil cores (bulk samples) 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. Three replicate samples were taken from each composite sample to account for imperfect mixing of the soil and were transported to the laboratory to be analyzed for extractable N and P. All soil replicates were stored in the laboratory in refrigeration at approximately 2°C for less than 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 PVC 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 gm of mixed resin was placed in the bottom of each tube. At the end of a measurement period, soil within tubes was collected, combined by horizon and plot, and mixed into a composite sample (incubated
samples. Three replicate samples were taken from each 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 N KCl. A paired 10 g subsample of soil was dried at 105°C for 24 hours to determine dry weight. The soil-KCl mixture was mechanically agitated for one hour, allowed to settle for 30 minutes, filtered with No. 42 ashless filter paper, and stored in refrigeration until analyzed. Extracts were analyzed for total N concentration (NH$_4^+$ plus NO$_3^-$; weight basis) with an NH$_4^+$ analyzer (Alltech 320 Conductivity Detector) and converted to a dry soil concentration using the weight of dried subsamples. 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$^{-1}$ 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 N KCl, agitated for one hour, filtered with No. 42 ashless paper, and stored in refrigeration until analysis with an NH$_4^+$ analyzer. Stand-level estimates of N flux through the columns during the sampling periods are expressed on a per hectare basis. The mean of twenty resin-filled bags was used as the stand-level N flux for each combination of sampling period and plot.

Mineral P content was determined by extracting a 5-g subsample from each soil replicate with 50 ml of Mehlich-3 solution. The soil and solution were mechanically agitated for one hour, allowed to settle for 30 minutes, filtered with No. 42 ashless
Extracts were analyzed for total P concentration (weight basis) colorimetrically (Hewlett Packard HP 8453 UV-visible Spectrophotometer) and converted to a dry soil content using the weight of dried subsamples. The P content of each composite sample is the mean of the 3 replicate measurements of P. Stand-level mineral P (kg ha\(^{-1}\)) in each horizon in each plot was calculated by multiplying the P content in each composite sample by the respective values of bulk density and horizon depth.

Net N and P mineralization (kg ha\(^{-1}\) to 30 cm) during each time period in each plot was calculated with the equation

\[ \text{Min}_{(N, P)} = (I_{i+1} - B_i)_{A\text{-horizon}} + (I_{i+1} - B_i)_{B\text{-horizon}} + R_{i+1} \]

where \( \text{Min}_{(N, P)} \) is the net N or P mineralization between two time periods, \( I_{i+1} \) is the N or P content in incubated soil collected at the end of a time period, \( B_i \) is the stand-level N or P content in bulk soil collected at the beginning of a time period, A-horizon and B-horizon are horizon designations, and \( R_{i+1} \) is stand-level N in resin-filled bags collected at the end of a time period. \( R_1 \) was set to zero in the calculation of P mineralization because of the relative immobility of P in soils (Tisdale et al. 1993). Total N and P mineralization from July 1997 to September 1998 (A- and B-horizon to 30 cm) in each plot is the sum of N and P mineralization from both measurement periods.
2.2.3. Litter Nutrient Concentration

Needle litter samples were obtained in December 1997. Four 1-m² plastic sheets were placed onto the ground in each plot. Needle litter that fell onto the plastic sheets were collected one week later.

Needle litter 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 three replicates of the mixture. Phosphorus concentration was determined with inductively-coupled plasma (ICP) spectrometry (Huang and Schulte 1985), and nitrogen concentration was determined with the Dumas-method with a Leco FP-428 Analyzer. N and P needle litter concentration in each plot was the mean of the three replicates.

2.2.4. Litter Production

Litter production was estimated with allometric equations. Because loblolly and slash pine needles senesce and abscise after two growing seasons, current-year needle litter production was assumed to be directly correlated to the amount of previous-year second-year foliage. Each tree in each plot was numbered and measured for outside bark DBH, total height and height to the base of the live crown after the 1996 and 1997 growing seasons to obtain estimates of litter production in 1997 and 1998. Using these measurements, standing first-year and second-year foliage for each loblolly pine tree in each year was estimated using allometric equations developed by Baldwin et al. (1997). Total foliage for each slash pine tree for each year was estimated using allometric equations developed by Lohrey (1984). Lohrey (1984) did
not distinguish between first-year and second-year foliage, and therefore, estimated total foliage on each slash pine tree was multiplied by 0.4638 (the mean percentage of total loblolly pine foliage that consisted of second-year foliage) to obtain an estimate of second-year foliage. The assumption that the proportion of first- to second-year foliage in slash pine stands trees was the same as in loblolly pine trees has not been verified. Per-tree, second-year foliage was summed by plot for each year and expanded to a per hectare basis to obtain an estimate of stand-level second-year foliage. Annual needle litter production was the mean of total second-year foliage in each respective plot in 1996 and 1997.

2.2.5. Statistical Analysis

Separate methods were used in the analyses of species and initial spacing effects and of current stand density effects. Species and initial spacing effects on individual variables were analyzed in a randomized complete block by analysis of variance with a general linear model procedure (Statistical Analysis System Version 6.12, SAS Institute Inc., Cary, NC, USA). This approach examined the discreet variables to investigate the long-term effects of treatments made at stand establishment. Because of the missing cell caused by unacceptable mortality in the widely spaced slash pine stands, analyses of species and initial spacing effects were limited to the medium and narrowly spaced stands, where initial spacings were common for both species. The model used was

\[ Y_{jk} = \mu + B_i + S_j + I_k + (SI)_{jk} + e_{ijk}, \]
where \( Y_{ijk} \) is the observation for the \( i^{th} \) block, \( j^{th} \) species (loblolly or slash pine) and \( k^{th} \) initial spacing (medium or narrow), \( \mu \) is the population mean, \( B \) is effect of block, \( S \) is the effect of species, \( I \) is the effect of planting density, and \( \epsilon_{ijk} \) is the random error associated with each observation.

The effects of current stand density on individual variables were analyzed by linear regression (Statistical Analysis System Version 6.12, SAS Institute Inc., Cary, NC, USA). Reineke's stand density index (SDI) was used to quantify current stand density and was calculated with the equation

\[
[2.3] \quad \text{SDI} = \text{TPH} \cdot (D_q/25)^1.6
\]

where \( D_q \) is quadratic mean diameter (cm) and \( \text{TPH} \) is the number of trees per hectare (Daniel and Sterba 1980). The regression approach examined the continuous variable to elucidate a relationship between current stand conditions and N and P accumulation. Analyses of slash pine would have been limited to only two clusters of points (medium- and narrowly spaced stands) thereby making all relationships suspect. Therefore, only loblolly pine stands were used in the analyses of current stand density effects. The full linear model used was

\[
[2.4] \quad Y = \beta_0 + \beta_1 \cdot \text{SDI} + \epsilon
\]

where \( Y \) is the predicted value for each observation, \( \beta_0 \) and \( \beta_1 \) are regression coefficients, \( \text{SDI} \) is Reineke's stand density index, and \( \epsilon \) is the random error associated with each observation.

Linear regression was also used to relate periodic annual volume increment over 1997 and 1998 (the two years that N and P mineralization were calculated) with N
and P mineralization. All loblolly and slash pine stands were used in the analysis (n=15). The linear model used was

\[ V_i = \beta_0 + \beta_1 \cdot M_{(N,P)} + \varepsilon \]

where \( V_i \) is the predicted periodic annual volume increment for 1997 and 1998, \( \beta_0 \) and \( \beta_1 \) are regression coefficients, \( M_{(N,P)} \) is either net N or P mineralization, and \( \varepsilon \) is the random error associated with each observation.

Because of the large amount of variability inherent in forest stands, the critical value of \( \alpha \) for significant effects was set at 0.10.

2.3. Results and Discussion

2.3.1. Species and Initial Spacing Effects

There were no significant species by planting density interactions for any of the variables measured (Table 2.2). N mineralization was significantly affected by species with greater N mineralization in loblolly pine stands than in slash pine stands (Figure 2.1). P mineralization was negative during the study period (Table 2.2) indicating net immobilization. P mineralization was not significantly affected by species in this study. Planting density had no significant effect on either N or P mineralization.

Needle litter N and P concentrations were similar to those reported in other studies (Table 2.2, cf. Switzer et al. 1968, Adams et al. 1987). Species was a significant factor in both needle litter N and P concentration (Table 2.2) with greater concentrations of both nutrients in loblolly pine litter than slash pine (Figure 2.2). Planting density had no effect on either N or P concentration (Table 2.2).
Table 2.2. Mean values and statistical analyses for net N mineralization from June 1997 to September 1998 (N_{min}), total net P mineralization from June 1997 to September 1998 (P_{min}), fraction of needle litter that consisted of N (f_N), fraction of needle litter that consisted of P (f_P), and estimated mean annual litter production that fell in 1997 and 1998 (Litter). Data are from unthinned 17-year-old stands of loblolly and slash pine near Franklinton, LA, USA.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>N_{min} (kg ha^{-1})</th>
<th>P_{min} (kg ha^{-1})</th>
<th>f_N (%)</th>
<th>f_P (%)</th>
<th>Litter (kg ha^{-1} yr^{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>S_{LM}</td>
<td>37.23</td>
<td>-0.1564</td>
<td>0.543</td>
<td>0.0235</td>
<td>3,170</td>
</tr>
<tr>
<td>S_{LN}</td>
<td>33.35</td>
<td>-0.0888</td>
<td>0.569</td>
<td>0.0260</td>
<td>3,198</td>
</tr>
<tr>
<td>S_{SM}</td>
<td>20.11</td>
<td>-0.2618</td>
<td>0.342</td>
<td>0.0132</td>
<td>3,410</td>
</tr>
<tr>
<td>S_{SN}</td>
<td>23.77</td>
<td>-0.4720</td>
<td>0.429</td>
<td>0.0172</td>
<td>3,425</td>
</tr>
</tbody>
</table>

Root MSE 7.66 0.2928 0.055 0.0029 285

P values for effect

<table>
<thead>
<tr>
<th>Effect</th>
<th>Block P</th>
<th>S P</th>
<th>I P</th>
<th>SxI P</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.149</td>
<td>0.024</td>
<td>0.980</td>
<td>0.427</td>
</tr>
<tr>
<td></td>
<td>0.483</td>
<td>0.199</td>
<td>0.688</td>
<td>0.443</td>
</tr>
<tr>
<td></td>
<td>0.645</td>
<td>0.002</td>
<td>0.126</td>
<td>0.368</td>
</tr>
<tr>
<td></td>
<td>0.382</td>
<td>0.001</td>
<td>0.101</td>
<td>0.675</td>
</tr>
<tr>
<td></td>
<td>0.114</td>
<td>0.205</td>
<td>0.900</td>
<td>0.971</td>
</tr>
</tbody>
</table>

1^ Treatment levels for the Species (S) variable are denoted by L (loblolly pine) or S (slash pine). Treatment levels for the Initial spacing (I) variable are denoted by M (medium-spaced, 2.4 x 2.4 m spacing) or N (narrowly spaced, 1.2 x 1.2 m).

2^ Mean square error.
Figure 2.1. Mean net N mineralization (kg ha\(^{-1}\)) by species in 17-year-old unthinned stands of loblolly and slash pine near Franklinton, LA, USA. Vertical line represents least significant difference (\(a=0.10, n=12\)). Mineralization values were calculated from July 1997 through September 1998.
Figure 2.2. Mean N concentration (%) by species (a) and mean P concentration (%) by species (b) of needle litter in 17-year-old unthinned stands of loblolly and slash pine near Franklinton, LA, USA. Vertical line represents least significant difference ($\alpha=0.10$, $n=12$). Needle litter was collected in December 1997.
Greater needle litter N concentration in loblolly pine stands corresponded with greater N mineralization in loblolly pine stands. Although not measured, it is likely that lower needle litter C:N ratios in loblolly pine allowed more rapid microbial decomposition of litter and subsequent N mineralization, a relationship documented in other species (Pastor et al. 1984, Stohlgren 1988). A relationship between needle litter P concentration and P mineralization was less evident as higher needle litter P concentrations in loblolly pine did not translate into elevated P mineralization. The results suggest that decomposition of needle litter in these stands are more closely associated with N concentration than P concentration. This conflicts with Gholz et al. (1985) who reported that percent weight loss of needle litter in slash pine was related to P concentration, but not N concentration. The difference may be attributable to varying degrees of N and P limitations in the soils of the two studies.

Needle litter decomposition rates are not necessarily directly related to C:N and C:P ratios. In several studies (Stump and Binkley 1993, Fioretto et al. 1998, Murphy et al. 1998, Prescott and Zabek 1999), decomposition of conifer needle litter was most closely related to lignin content (which decreases decomposition rates) irrespective of N concentration. However, Scott and Binkley (1997) showed that N mineralization in 11 previous studies was most closely related to litter lignin:N ratio, and that there was a negative relationship between litter lignin content and litter N concentration; this might lead to a positive relationship between litter N concentration and N mineralization. Although direct causality cannot be attributed here, evidence suggests that the choice
of species at stand establishment affected future N mineralization through its effects on litter quality.

Neither species nor planting density had a significant effect on estimated litter production (Table 2.2). Therefore, litter quantity does not appear to explain the differences in N mineralization between the species. However, total N input via litter would be greater in loblolly pine stands as a result of greater needle litter N concentrations. This agrees with Binkley and Ryan (1998) who observed that although litter production was equivalent in stands of *Albizia* and *Eucalyptus*, total N input via litter was greater in *Albizia* stands as a result of greater litter N concentration.

Estimates of litter production using allometric equations must be used with caution, however. Although it has been verified that foliage mass is directly correlated with needle litter (Gholz et al. 1985), partitioning to foliage biomass may change as soil nutrient and water resources change (King et al. 1999). Rainfall was below normal during the study period and therefore the potential exists that estimated foliage production was overestimated by the equations. The effects of any drought-induced reductions in litter production would be greatest in the narrowly spaced stands (Vose and Allen 1991).

**2.3.2. Current Stand Density Effects on Nutrient Mineralization**

Both N and P mineralization significantly increased with stand density in the loblolly pine plots (Figure 2.3). Linear regression explained 60 and 63% of variation in N and P mineralization, respectively. There was no correspondence between stand density and either needle litter N or P concentration. Slopes between the
Figure 2.3. N mineralization (kg ha⁻¹) (a) and P mineralization (kg ha⁻¹) (b) from June 1997 to September 1998 as functions of Reineke's stand density index (SDI). Lines are least-squares fit. Data are from 17-year-old unthinned stands of loblolly pine planted at various densities near Franklinton, LA, USA. Mineralization values were calculated from July 1997 through September 1998.
mineralization variables and SDI were not significant (P=0.435 and P=0.148 respectively) indicating that needle litter N and P concentrations were nearly constant with stand density in this study. Therefore, litter quality does not appear to explain the increase in N or P mineralization with stand density.

Needle litter production significantly increased with stand density (Figure 2.4). Linear regression indicated that 85% of the variation in needle litter production could be explained with stand density. This suggests, therefore, that current stand density in the loblolly pine stands affected N and P mineralization through its effects on litter quantity. This contrasts with the results of Scott and Binkley (1997) who found in one broad examination of eleven previous studies that litter quantity was not related to N mineralization, but instead was most closely related to litter quality. Because litter quality did not significantly covary with stand density in this study, it appears that increases in litter production led to increased N and P input and subsequent mineralization of those nutrients.

2.3.3. Nutrient Mineralization and Volume Production

Linear regression of all loblolly and slash pine stands showed that two-year periodic annual volume increment was significantly and positively related to N mineralization (Figure 2.5). The relationship is somewhat weak (R²=0.22) which is not unexpected as there are many physical factors that influence stand production. P mineralization was not significantly related to volume production (P=0.191). This indicates that while P is extremely low in these soils, volume production seems more
Figure 2.4. Estimated mean annual needle litter production (1997 and 1998) in 17-year-old unthinned stands of loblolly at varying levels of Reineke's stand density index (SDI) near Franklinton, LA, USA. Line is least-squares fit. Needle litter was estimated with allometric equations by Baldwin et al. (1997). Estimates of second-year foliage in the previous year were used as a surrogate for current-year needle litter production.
Figure 2.5. Two-year, periodic annual volume increment (kg ha$^{-1}$ yr$^{-1}$, 1997-98) as related to net N mineralization from July 1997 to September 1998 (kg ha$^{-1}$) in 17-year-old unthinned stands of loblolly and slash pine near Franklinton, LA, USA. Line is least-squares fit.
limited by N. Stands with the greatest N input via litter appear to have the greatest N mineralization and subsequent production.

Aboveground production has been previously linked to changes in litter. For example, aboveground production in both chestnut and oak stands was related to the amount of nutrient input via litter (Gallarado et al. 1998a, b). Also, application of needle litter in loblolly pine stands resulted in increased stand volume production (Haywood et al. 1987).

Shiver et al. (2000) found that for many soil types in the southeastern Gulf Coastal Plain, loblolly pine stands had significantly greater stand volume at 14 years than slash pine stands. In this study, volume production was positively related to N mineralization, which was often greater in loblolly pine stands (Figure 2.5). Therefore, greater volume production in loblolly pine stands could be attributable to greater N input via litter. It follows that some type of N amendment may be needed in slash pine stands to attain volume increment comparable to loblolly pine. Slash pine allocates a greater percentage of N to stemwood than loblolly pine (Chapter 3), immobilizing the nutrient from recycling. Therefore, the effectiveness and longevity of fertilization may be less in slash pine stands compared to loblolly pine, an outcome confirmed by Jokela et. al (2000). Multiple fertilization treatments throughout the rotation of slash pine stands may consequently be needed to attain production levels inherent to loblolly pine.
2.4. Conclusions

Choice of species at stand establishment and the level of current stand density affect rates of N and P mineralization, likely through changes in litter quality and quantity. N mineralization was significantly greater in loblolly pine stands than slash pine, corresponding with greater needle litter N concentration in loblolly pine. There were no differences in P mineralization between the loblolly pine and slash pine stands despite greater P concentration of needle litter in loblolly pine on average. Both N and P mineralization increased in the loblolly pine stands with increasing stand density, but this increase does not appear related to needle litter N and P concentration. Instead, increased litter production with increasing stand density apparently led to greater N and P-input and subsequent N and P mineralization.

Stand volume production was positively correlated with N mineralization, but not P mineralization. The species and density of a stand apparently produces secondary effects on soil productivity through its effects on litter quality and quantity. Because slash pine stands typically had lower rates of N mineralization, N fertilization may be needed to increase production levels to those inherent in loblolly pine.
CHAPTER 3
ABOVEGROUND N AND P DISTRIBUTION IN STANDS OF LOBLOLLY
AND SLASH PINE AT VARYING STAND DENSITIES

3.1. Introduction

Nutrient accumulation affects many aspects of forest productivity. Nutrient
take and accumulation have been positively correlated with growth rate in species
and in geographic areas as diverse as birch in Alaska and eucalypts in Australia (Miller
1984, 1989). Rates of nutrient accumulation typically increase during stand
development, attain a maximum near canopy closure, then slowly decline (Pearson et
al. 1987, Miller 1995). Early in stand development, most nutrients are accumulated in
foliage (Smith et al. 1971); however, with time and in the absence of disturbance, the
proportion of nutrients in stem wood and branch wood biomass increases while the
proportion in foliage decreases (Switzer et al. 1968, Gholz and Fisher 1982).
Accumulation and retention of nutrients in aboveground biomass has been linked to
declines in available soil nutrients and subsequent declines in stand production
(Binkley et al. 1995, Murty et al. 1996), although this phenomenon has been
questioned recently (Olsson et al. 1998).

Nutrient accumulation is a function of dry matter production and the nutrient
concentration of that dry matter. Large differences in nutrient concentrations may exist
between the various aboveground components (foliage, stem wood, branch wood) that
make up total aboveground production. For example, Switzer et al. (1968) showed that
foliar N concentration of 18-year-old loblolly pine (Pinus taeda L.) was 14 times
greater than stem wood N concentrations. Thus, not only total production of biomass, but also the distribution of aboveground biomass into the various components can have a considerable effect on total nutrient accumulation.

Factors such as genotype (Li et al. 1991, McCrady and Jokela 1996), soil water and nutrient status (King et al. 1999), canopy dominance (Naidu et al. 1998), and stand age (Alban 1988, Beets and Whitehead 1996) may affect biomass allocation patterns and subsequent nutrient accumulation. It is also likely that silvicultural treatments have varying effects on the distribution of nutrients into the various aboveground components as well as total nutrient accumulation.

The choice of species at stand establishment may affect nutrient accumulation. For example, red pine (Pinus resinosa Ait.) accumulates more N and P over time than jack pine (Pinus banksiana Lamb.) due to greater biomass production and also higher tissue nutrient concentrations (Alban 1988). Two commercially important species in the southeastern United States are loblolly pine and slash pine (Pinus elliottii Engelm.). These closely related species vary in biomass allocation patterns with loblolly pine generally accumulating more biomass in crown components than slash pine (Colbert et al. 1990). Because aboveground components vary in nutrient concentration, differences in biomass allocation patterns between these species are likely manifested in differences in nutrient accumulation and distribution.

Within a species, the choice of stand density may also influence biomass allocation (Long and Smith 1984) and likely the subsequent accumulation of nutrients. Stand density influences crown development and morphology (Jack and Long 1991,
Dean and Baldwin 1996), which in turn affects aboveground carbon allocation patterns to the stem, foliage, and branches (Ford 1985). Because each of these components vary in nutrient concentration, stand density should therefore also influence the distribution and total amount of accumulated nutrients in a forest stand.

In many forest sites in the southeast United States, production is limited by low soil nutrient availability, particularly nitrogen and phosphorus. Long-term nutrient management decisions by forest managers thus require a knowledge of the demands for these nutrients in forest stands so as to discern potential consequences of silvicultural treatments on nutrient capital. While total aboveground N has been documented for loblolly pine (Switzer and Nelson 1972, Larsen et al. 1976), no study has compared the distribution of N and P between loblolly and slash pine as has been done for other similar species of pine (Alban 1988). And while the role of stand density in aboveground biomass allocation is well documented, its effects on nutrient accumulation in the various components is less understood. This study was therefore conducted to investigate the distribution and total accumulation of aboveground N and P in loblolly and slash pine stands at varying stand densities. Specifically, the two objectives of this study were (1) to determine if stands of loblolly and slash pine planted at different initial spacings varied in the distribution and total aboveground accumulation of biomass, N, and P, and (2) to determine if current stand density affected the distribution and total aboveground accumulation of biomass, N, and P.
3.2. Methods

3.2.1. Site Description

The study was conducted on the Lee Memorial Forest in southeast Louisiana in a species and spacing trial planted in 1981 on a site that was previously used as a Christmas tree plantation. Data were collected in pure, unthinned stands of loblolly or slash pine planted at spacings of 1.2 x 1.2 m (narrowly spaced), 2.4 x 2.4 m (medium-spaced), and 3.7 x 3.7 m (widely spaced). Each species and initial spacing combination was replicated three times in contiguous blocks that represented a perceived fertility gradient. Data were not collected in widely spaced slash pine stands because of unacceptable mortality of planted trees and subsequent invasion of loblolly pine volunteers. The physical characteristics of the study site and attributes of the plots at the time of measurement are described in Chapter 2.

3.2.2. Standing Biomass

Aboveground biomass was estimated with regression equations. Each tree in each plot was numbered and measured for outside bark diameter at breast height (DBH, 1.37 m), total height and height to the base of the live crown after the 1996 and 1997 growing seasons. Using these measurements, standing first-year foliage, second-year foliage, stem wood, and branch wood mass for each loblolly pine tree in each year were estimated with equations developed by Baldwin (1987) and Baldwin et al. (1997). Estimates of slash pine component biomass were estimated with regression equations developed by Lohrey (1984). Lohrey (1984) did not distinguish between first-year and second-year foliage; therefore, estimated total foliage on each slash pine
tree was multiplied by 0.5362 (the mean percentage of total loblolly pine foliage that consisted of first-year foliage) to obtain an estimate of first-year foliage. Second-year foliage on slash pine trees was the residual of total foliage minus first-year foliage. The assumption that the percentage of first- to second-year foliage in slash pine stands was the same as in loblolly pine stands was not tested; however, both loblolly and slash pine foliage live for two years before senescence, and it is therefore reasonable to assume that the percentage of total foliage that consisted of a given year would be near 50%. Per-tree biomass by component was summed by plot and expressed on a per-hectare basis.

### 3.2.3. Nutrient Accumulation

First-year foliage, second-year foliage, and branch wood samples were obtained in mid-September 1997 (when leaf area was assumed to be at or near maximum) by shooting a mid-canopy branch from four trees in each plot with a 12-gauge shotgun and #4 shot. Branches were selected to minimize damage to the residual canopy. There is a significant linear relationship of foliar N concentration and canopy depth in the loblolly pine stands examined in this study (P<0.001, T.J. Dean, unpublished data). However, because the relationship is weak (R²=0.14) and foliage samples were obtained from mid-canopy branches, the bias was assumed negligible. Stem wood samples were obtained by coring four trees in each plot at breast height during December 1997.

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
into a composite sample. N and P concentration were determined on three replicates of each composite sample to account for imperfect mixing of the powder. Phosphorus concentration was determined with inductively-coupled plasma (ICP) spectrometry (Huang and Schulte 1985), and nitrogen concentration was determined with the Dumas-method with a Leco FP-428 Analyzer. N and P concentration for each component in each plot was the mean of the three replicates of each composite sample. Mean stand-level N and P accumulation for each component in each plot was calculated by multiplying the per-hectare estimate of biomass in each component in each plot by its corresponding nutrient concentration.

3.2.4. Statistical Analysis

Separate methods were used in the analyses of species and initial spacing effects and of current stand density effects. Species and initial spacing effects on individual variables were analyzed in a randomized complete block by analysis of variance with a general linear model procedure (Statistical Analysis System Version 6.12, SAS Institute Inc., Cary, NC, USA). This approach examined the discreet variables to investigate the long-term effects of treatments made at stand establishment. Because of the missing cell caused by unacceptable mortality in the widely spaced slash pine stands, analyses of species and initial spacing effects were limited to the medium and narrowly spaced stands, where initial spacings were common for both species.

The effects of current stand density on individual variables were analyzed by linear regression (Statistical Analysis System Version 6.12, SAS Institute Inc., Cary,
NC, USA). Reineke's stand density index (SDI) was used to quantify current stand density and was calculated with the equation

\[ SDI = \frac{TPH \cdot (D_q/25)^{1.6}}{} \]

where \( D_q \) is quadratic mean diameter (cm) and TPH is the number of trees per hectare (Daniel and Sterba 1980). The regression approach examined the continuous variable to elucidate a relationship between current stand conditions and N and P accumulation. Analyses of slash pine would be limited to only two clusters of points (medium- and narrowly spaced stands) thereby making all relationships suspect. Therefore, only loblolly pine stands were used in the analyses of current stand density effects.

Because of the large amount of variability inherent in forest stands, the critical value of \( \alpha \) for significant effects was set at 0.10. Detailed methods of species and initial spacing analyses and of current density analyses are described in Chapter 2.

3.3. Results and Discussion

3.3.1 Species and Initial Spacing Effects

Both species and initial spacing affected the distribution of biomass into the various components and also total aboveground biomass (Table 3.1). Significant interactions between species and initial spacing effects were detected for stem wood and branch wood mass; no significant main effects or significant interactions were detected for foliage mass. Stem wood mass did not significantly vary between species in medium-spaced stands but was greater in slash pine in the narrowly spaced stands. The greater stem wood production by slash pine on these well-drained soils was unexpected given that loblolly pine generally outproduces slash pine on all but very
Table 3.1. Mean values and results from analyses of variance for biomass accumulated (Mg ha\(^{-1}\)) in stem wood \((\text{Stem}_B)\), branch wood \((\text{Branch}_B)\), foliage \((\text{Foliage}_B)\), and total aboveground components \((\text{stem wood} + \text{foliage} + \text{branch wood}, \text{Total}_B)\) in relation to species and initial spacing. Data are from unthinned 16-year-old stands of loblolly and slash pine near Franklinton, LA, USA.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Stem(_B)</th>
<th>Branch(_B)</th>
<th>Foliage(_B)</th>
<th>Total(_B)</th>
</tr>
</thead>
<tbody>
<tr>
<td>S(_L)I(_M)</td>
<td>83.4</td>
<td>13.8</td>
<td>7.2</td>
<td>104.5</td>
</tr>
<tr>
<td>S(_L)I(_N)</td>
<td>73.5</td>
<td>8.0</td>
<td>6.9</td>
<td>88.3</td>
</tr>
<tr>
<td>S(_S)I(_M)</td>
<td>97.8</td>
<td>6.2</td>
<td>7.1</td>
<td>101.2</td>
</tr>
<tr>
<td>S(_S)I(_N)</td>
<td>113.1</td>
<td>5.2</td>
<td>7.2</td>
<td>125.4</td>
</tr>
</tbody>
</table>

\(^1\)Root MSE 10.9 1.3 0.6 12.6

<table>
<thead>
<tr>
<th>P-values for effect</th>
<th>Stem(_B)</th>
<th>Branch(_B)</th>
<th>Foliage(_B)</th>
<th>Total(_B)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Block</td>
<td>0.015</td>
<td>0.110</td>
<td>0.064</td>
<td>0.018</td>
</tr>
<tr>
<td>S</td>
<td>0.013</td>
<td>&lt;0.001</td>
<td>0.732</td>
<td>0.059</td>
</tr>
<tr>
<td>I</td>
<td>0.271</td>
<td>0.004</td>
<td>0.665</td>
<td>0.599</td>
</tr>
<tr>
<td>S(_x)I</td>
<td>0.031</td>
<td>0.017</td>
<td>0.632</td>
<td>0.032</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>P-values for contrasts</th>
<th>Stem(_B)</th>
<th>Branch(_B)</th>
<th>Foliage(_B)</th>
<th>Total(_B)</th>
</tr>
</thead>
<tbody>
<tr>
<td>S(_L) vs. S(_S) in I(_M)</td>
<td>0.633</td>
<td>&lt;0.001</td>
<td>0.765</td>
<td></td>
</tr>
<tr>
<td>S(_L) vs. S(_S) in I(_N)</td>
<td>0.004</td>
<td>0.038</td>
<td>0.011</td>
<td></td>
</tr>
<tr>
<td>I(_M) vs. I(_N) in S(_L)</td>
<td>0.304</td>
<td>0.001</td>
<td>0.168</td>
<td></td>
</tr>
<tr>
<td>I(_M) vs. I(_N) in S(_S)</td>
<td>0.030</td>
<td>0.381</td>
<td>0.057</td>
<td></td>
</tr>
</tbody>
</table>

\(^1\)Treatment levels for the Species (S) variable are denoted by L (loblolly pine) or S (slash pine).

Treatment levels for the Initial spacing (I) variable are denoted by M (medium-spaced, 2.44x2.44 m spacing) or N (narrowly spaced, 1.22x1.22 m).

\(^2\)Mean square error.
wet sites (Shiver et al. 2000). Loblolly pine had significantly greater branch wood mass at both initial spacings. Loblolly pine branch wood was also apparently more sensitive to initial spacing than slash pine as branch wood mass in loblolly pine, but not slash pine, was significantly reduced in narrowly spaced stands compared to medium-spaced stands. The effect of species on total aboveground biomass was apparently dependent on initial spacing. While total aboveground biomass did not vary between species in the medium-spaced stands, increased slash pine stem wood and decreased loblolly pine branch wood caused greater total aboveground biomass in slash pine in the narrowly spaced stands.

In both species, less than 20% of standing aboveground biomass was located in crown components (foliage + branch wood). With time, this percentage is expected to decrease as stem wood biomass continues to increase while foliage mass reaches a maximum and slowly declines (Switzer et al. 1968, Gholz and Fischer 1982). Loblolly pine accumulated a greater proportion of total aboveground biomass in crown components than slash pine (Figure 3.1a). Species differences in relative allocation are apparently manifested early in stand development as the same trend was documented in 4-year-old loblolly and slash pine plantations (Colbert et al. 1990). Initial spacing also affected the percentage of total aboveground biomass accumulated into crown components (Figure 3.1b). The reduced percentage of biomass accumulated in crown components in narrowly spaced stands compared to medium-spaced stands is likely the result of more limited space for lateral branch expansion in the narrowly spaced stands.
Figure 3.1. Mean percentage of biomass, N, and P located in the crown by species (a) and initial spacings (b) in 16-year-old unthinned stands of loblolly and slash pine near Flanklinton, LA, USA (n=12). Stands were planted on an initial spacing of 2.4 X 2.4 m (medium-spaced) and 1.2 X 1.2 m (narrow spaced).

N and P concentrations varied widely by component with the greatest concentrations in first-year foliage followed by second-year foliage, branch wood, and stem wood (Table 3.2). Although stem wood N concentration did not significantly vary between species, loblolly pine had greater N concentrations than slash pine in all crown components. Phosphorus concentrations in all components were considerably lower than N-concentrations. Unlike N, stem wood P concentration was significantly greater in slash pine than loblolly pine and branch wood P concentration was unrelated to species. Like N, however, P concentrations in both first- and second-year foliage were greater in loblolly pine.

Both species and initial spacing affected the distribution of N into the various components and also total N accumulation (Table 3.3). The range of total aboveground N in these 16-year-old loblolly and slash pine stands was considerably higher than the 180 kg ha\(^{-1}\) reported for 13-year-old loblolly pine (Larsen et al. 1976), the 140 kg ha\(^{-1}\) reported for 15-year-old loblolly pine (Switzer and Nelson 1972), and the 148 kg ha\(^{-1}\) and 185 kg ha\(^{-1}\) reported for 19-year-old red pine and jack pine, respectively (Alban 1988). Loblolly pine accumulated more N in both foliage and branch wood than slash pine. Slash pine accumulated more N in stem wood in the narrowly spaced stands but not in medium-spaced stands. Species differences in N accumulated in the various components was related to differences in both the amount of dry matter accumulated in a component and the nutrient concentration of the
Table 3.2. Mean values and results from analyses of variance for N concentration (%) in stem wood ($f_{N,S}$), branch wood ($f_{N,B}$), first-year foliage ($f_{N,F1}$), and second-year foliage ($f_{N,F2}$) and for P concentration (%) in stem wood ($f_{P,S}$), branch wood ($f_{P,B}$), first-year foliage ($f_{P,F1}$), and second-year foliage ($f_{P,F2}$) in relation to species and initial spacing. Data are from unthinned 16-year-old stands of loblolly and slash pine near Franklinton, LA, USA.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>$f_{N,S}$</th>
<th>$f_{N,B}$</th>
<th>$f_{N,F1}$</th>
<th>$f_{N,F2}$</th>
<th>$f_{P,S}$</th>
<th>$f_{P,B}$</th>
<th>$f_{P,F1}$</th>
<th>$f_{P,F2}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S_{L,M}$</td>
<td>0.18</td>
<td>0.39</td>
<td>1.16</td>
<td>1.00</td>
<td>0.0038</td>
<td>0.0248</td>
<td>0.0746</td>
<td>0.0592</td>
</tr>
<tr>
<td>$S_{L,N}$</td>
<td>0.16</td>
<td>0.40</td>
<td>1.14</td>
<td>1.01</td>
<td>0.0036</td>
<td>0.0260</td>
<td>0.0717</td>
<td>0.0544</td>
</tr>
<tr>
<td>$S_{S,M}$</td>
<td>0.18</td>
<td>0.36</td>
<td>0.93</td>
<td>0.84</td>
<td>0.0048</td>
<td>0.0255</td>
<td>0.0643</td>
<td>0.0452</td>
</tr>
<tr>
<td>$S_{S,N}$</td>
<td>0.18</td>
<td>0.36</td>
<td>0.92</td>
<td>0.78</td>
<td>0.0043</td>
<td>0.0229</td>
<td>0.0590</td>
<td>0.0461</td>
</tr>
<tr>
<td><strong>Root MSE</strong></td>
<td>0.02</td>
<td>0.02</td>
<td>0.09</td>
<td>0.07</td>
<td>0.0004</td>
<td>0.0033</td>
<td>0.0044</td>
<td>0.0046</td>
</tr>
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</table>

P-values for effect

<table>
<thead>
<tr>
<th>Block</th>
<th>0.418</th>
<th>0.086</th>
<th>0.870</th>
<th>0.347</th>
<th>0.653</th>
<th>0.086</th>
<th>0.089</th>
<th>0.192</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S$</td>
<td>0.457</td>
<td>0.068</td>
<td>0.004</td>
<td>0.004</td>
<td>0.015</td>
<td>0.542</td>
<td>0.004</td>
<td>0.006</td>
</tr>
<tr>
<td>$I$</td>
<td>0.335</td>
<td>0.734</td>
<td>0.762</td>
<td>0.584</td>
<td>0.196</td>
<td>0.713</td>
<td>0.158</td>
<td>0.492</td>
</tr>
<tr>
<td>$S_{xI}$</td>
<td>0.512</td>
<td>0.778</td>
<td>0.944</td>
<td>0.466</td>
<td>0.626</td>
<td>0.351</td>
<td>0.655</td>
<td>0.325</td>
</tr>
</tbody>
</table>

1Treatment levels for the Species (S) variable are denoted by L (loblolly pine) or S (slash pine). Treatment levels for the Initial spacing (I) variable are denoted by M (medium-spaced, 2.44x2.44 m spacing) or N (narrowly spaced, 1.22x1.22 m).

2Mean square error.
Table 3.3. Mean values and results from analyses of variance for N accumulated (kg ha⁻¹) in stem wood (StemN), branch wood (BranchN), foliage (FoliageN), and total aboveground components (stem wood + foliage + branch wood, TotalN) in relation to species and initial spacing. Data are from unthinned 16-year-old stands of loblolly and slash pine near Franklinton, LA, USA.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>StemN</th>
<th>BranchN</th>
<th>FoliageN</th>
<th>TotalN</th>
</tr>
</thead>
<tbody>
<tr>
<td>S₁I₅</td>
<td>148</td>
<td>54</td>
<td>78</td>
<td>279</td>
</tr>
<tr>
<td>S₁I₆</td>
<td>121</td>
<td>32</td>
<td>74</td>
<td>226</td>
</tr>
<tr>
<td>S₅I₅</td>
<td>161</td>
<td>22</td>
<td>63</td>
<td>246</td>
</tr>
<tr>
<td>S₅I₆</td>
<td>202</td>
<td>19</td>
<td>61</td>
<td>282</td>
</tr>
</tbody>
</table>

2 Root MSE

<table>
<thead>
<tr>
<th>P-values for effect</th>
<th>StemN</th>
<th>BranchN</th>
<th>FoliageN</th>
<th>TotalN</th>
</tr>
</thead>
<tbody>
<tr>
<td>Block</td>
<td>0.154</td>
<td>0.038</td>
<td>0.046</td>
<td>0.057</td>
</tr>
<tr>
<td>S</td>
<td>0.014</td>
<td>&lt;0.001</td>
<td>0.003</td>
<td>0.483</td>
</tr>
<tr>
<td>I</td>
<td>0.617</td>
<td>0.010</td>
<td>0.310</td>
<td>0.590</td>
</tr>
<tr>
<td>SxI</td>
<td>0.046</td>
<td>0.002</td>
<td>0.694</td>
<td>0.027</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>P-values for contrasts</th>
<th>StemN</th>
<th>BranchN</th>
<th>FoliageN</th>
<th>TotalN</th>
</tr>
</thead>
<tbody>
<tr>
<td>S₁ vs. S₅ in I₅</td>
<td>0.530</td>
<td>&lt;0.001</td>
<td></td>
<td>0.175</td>
</tr>
<tr>
<td>S₁ vs. S₅ in I₆</td>
<td>0.006</td>
<td>0.010</td>
<td></td>
<td>0.041</td>
</tr>
<tr>
<td>I₅ vs. I₆ in S₁</td>
<td>0.212</td>
<td>&lt;0.001</td>
<td></td>
<td>0.049</td>
</tr>
<tr>
<td>I₅ vs. I₆ in S₅</td>
<td>0.076</td>
<td>0.340</td>
<td></td>
<td>0.147</td>
</tr>
</tbody>
</table>

1 Treatment levels for the Species (S) variable are denoted by L (loblolly pine) or S (slash pine). Treatment levels for the Initial spacing (I) variable are denoted by M (medium-spaced, 2.44x2.44 m spacing) or N (narrowly spaced, 1.22x1.22 m).

2 Mean square error.
component. For example, loblolly pine accumulated more N in foliage than slash pine as a result of greater foliar N concentrations in loblolly pine while slash pine accumulated more N in stem wood than loblolly pine in the narrowly spaced stands as a result of greater stem wood mass in slash pine at that initial spacing. The effect of initial spacing on N accumulation varied by species. Compared to medium-spaced stands, there was less N accumulated in loblolly pine branch wood but more N accumulated in slash pine stem wood in narrowly spaced stands. Species differences in total N accumulation was dependent on initial spacing. While total aboveground N did not vary between species in the medium-spaced stands, an increase in slash pine stem wood N and a decrease in loblolly pine branch wood N in the narrowly spaced stands caused greater total aboveground N in slash pine at that initial spacing.

Noteworthy, the greater total N accumulation by slash pine in narrowly spaced stands occurred even though N mineralization rates were lower under slash pine stands (Chapter 2). Efficiency at foliar retranslocation partially explains these seemingly conflicting observations. Slash pine litter concentration (from Chapter 2) was 58% less than first-year foliage N concentration compared to only a 51% difference in loblolly pine indicating that slash pine foliage retranslocates a significantly greater percentage (P=0.040) of N throughout its lifespan than loblolly pine foliage. These results are consistent with other studies that showed a negative correlation between soil nutrient availability and foliar retranslocation (Flanagan and VanCleve 1983, Boerner 1984, Birk and Vitousek 1986, Dalla-Tea and Jokela 1994). It is not clear whether slash pine would maintain a higher efficiency of internal N recycling than loblolly pine under
greater N availability. While loblolly pine had greater stem wood production than slash pine in a number of studies (Cole 1975, Shoulders 1976, Haines et al. 1981, Shiver et al. 2000), a greater relative allocation to stemwood and a greater efficiency of N retranslocation by slash pine enabled it to maintain similar levels of stem wood production as loblolly pine on this site even though there was less available soil N.

P accumulation varied by species in all individual components (Table 3.4). Unlike total aboveground N, the range of total aboveground P in these stands was considerably lower than the 15.8 kg ha\(^{-1}\) reported in loblolly pine (Switzer et al. 1972) and the 16.7 kg ha\(^{-1}\) and 19.5 kg ha\(^{-1}\) reported for red pine and jack pine, respectively (Alban 1988). Slash pine accumulated significantly more P in stem wood but loblolly pine accumulated significantly more P in both branch wood and foliage which led to a net result of no species differences in total aboveground P. The solitary effect of initial spacing was to reduce the amount of P accumulated in loblolly pine branch wood in narrowly spaced stands compared to medium-spaced stands. P accumulation was much lower than N accumulation as a result of lower P concentrations.

The crown was an important sink for both N and P. For example, while less than 20% of total loblolly pine biomass was located in crown components across both initial spacings, 47% of total N and 72% of total P was located in the crown as a result of high N and P concentrations of crown components compared to stem wood N and P concentrations; these percentages are similar to those reported for red pine and jack pine (Alban 1988). The distribution of N and P into the crown varied by species. Loblolly pine accumulated a significantly greater percentage of total aboveground N
Table 3.4. Mean values and results from analyses of variance for P accumulated (kg ha\(^{-1}\)) in stem wood (Stem\(_P\)), branch wood (Branch\(_P\)), foliage (Foliage\(_P\)), and total aboveground components (stem wood + foliage + branch wood, Total\(_P\)) in relation to species and initial spacing. Data are from unthinned 16-year-old stands of loblolly and slash pine near Franklinton, LA, USA.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Stem(_P)</th>
<th>Branch(_P)</th>
<th>Foliage(_P)</th>
<th>Total(_P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>S(_L)I(_M)</td>
<td>3.2</td>
<td>3.5</td>
<td>4.9</td>
<td>11.6</td>
</tr>
<tr>
<td>S(_L)I(_N)</td>
<td>2.7</td>
<td>2.1</td>
<td>4.4</td>
<td>9.2</td>
</tr>
<tr>
<td>S(_S)I(_M)</td>
<td>4.3</td>
<td>1.6</td>
<td>4.0</td>
<td>9.9</td>
</tr>
<tr>
<td>S(_S)I(_N)</td>
<td>4.9</td>
<td>1.2</td>
<td>3.8</td>
<td>9.9</td>
</tr>
</tbody>
</table>

2 Root MSE

<table>
<thead>
<tr>
<th>P-values for effect</th>
</tr>
</thead>
<tbody>
<tr>
<td>Block</td>
</tr>
<tr>
<td>S</td>
</tr>
<tr>
<td>I</td>
</tr>
<tr>
<td>SxI</td>
</tr>
</tbody>
</table>

P-values for contrasts

| S\(_L\) vs. S\(_S\) in I\(_M\) | 0.010 |
| S\(_L\) vs. S\(_S\) in I\(_N\) | 0.020 |
| I\(_M\) vs. I\(_N\) in S\(_L\) | 0.010 |
| I\(_M\) vs. I\(_N\) in S\(_S\) | 0.230 |

1 Treatment levels for the Species (S) variable are denoted by L (loblolly pine) or S (slash pine).

Treatment levels for the Initial spacing (P) variable are denoted by M (medium-spaced, 2.44x2.44 m spacing) or N (narrowly spaced, 1.22x1.22 m).

2 Mean square error.
and P in crown components than slash pine (Figure 3.1a) due to a greater percentage of total aboveground biomass allocated to the crown and also greater N and P concentrations in loblolly pine crown components. Absolute N and P accumulated in the crown was also greater in loblolly pine than slash pine (P<0.001 and P=0.006, respectively).

Initial spacing also affected the distribution of N and P into the crown. The percentage of total aboveground P, but not N, accumulated in the crown was significantly greater in medium-spaced stands compared to narrowly spaced stands (Figure 3.1b). Narrower initial spacing led to a decrease in absolute crown N in loblolly but not slash pine (P=0.012 and P=0.478, respectively). Narrower spacing also led to a decrease in absolute crown P in both species (P=0.052).

3.3.2 Current Stand Density Effects

In loblolly pine stands, no N or P concentrations of any component was significantly related to stand density (all P>0.18). Thus, all patterns of N and P accumulation with stand density were strongly influenced by biomass allocation. The effect of current stand density on N accumulation in each component is illustrated in Figure 3.2. Data are grouped by the block in which they were collected. Blocks are for replication purposes and represent a perceived fertility gradient from a high in Block 1 to a low in Block 3. The typical pattern of N in stem wood was an increase with stand density from the widely spaced stands to the medium-spaced stands followed by a decrease with stand density to the narrowly spaced stands (Figure 3.2a). The decrease in stem N on the narrowly spaced stands was unexpected as stand level
Figure 3.2. Nitrogen accumulated in stem wood (kg ha\(^{-1}\)) (a), branch wood (kg ha\(^{-1}\)) (b), and foliage (kg ha\(^{-1}\)) (c) in stands at varying levels of Reineke's stand density index (SDI). Data are from 16-year-old unthinned loblolly pine stands near Flanklinton, LA, USA.
stem wood production generally continues to increase with stand density (Long 1985, Dean and Baldwin 1996). It is likely that trees in the narrowly spaced stands were of lower vigor than trees in medium-spaced stands and therefore could not compete as efficiently for limited resources thereby limiting production in narrowly spaced stands. As evidence, 1.53% of stand volume was lost to mortality during the 1997 growing season in the narrowly spaced stands compared to 0.09% and 0.02% lost in the medium- and widely spaced stands, respectively. The continuing decrease of N accumulated in branch wood (Figure 3.2b) was predicted and can be explained by reduced area for crown expansion with increasing stand density (Assman 1970, Jack and Long 1991). Generally, N in foliage continued to increase with stand density although the increase in the narrowly spaced stands was relatively small with one block even showing a decrease (Figure 3.2c). It was predicted that N accumulated in foliage would continue to increase with stand density as there is a linear increase in leaf area with increasing stand density in loblolly pine (Dean and Baldwin 1996). And indeed, there was a significant linear relationship between N accumulated in foliage and stand density (P=0.036, R²=0.49). Total N increased with stand density from the widely spaced stands to the medium-spaced stands followed by a decrease with stand density to the narrowly spaced stands (Figure 3.3a). This pattern is most similar to N accumulated in stem wood because the increase in foliage N with stand density was offset by a corresponding decrease in branch wood N.

Relationships of loblolly pine P accumulation with stand density were similar to N which was expected considering that both N and P accumulation were most
Figure 3.3. Total aboveground N (kg ha\(^{-1}\)) (a) and P (kg ha\(^{-1}\)) (b) in stands at varying levels of Reineke's stand density index (SDI). Data are from 16-year-old unthinned loblolly pine stands near Flanklinton, LA, USA.
influenced by biomass accumulation patterns. As with N, the typical pattern of P in stem wood was an increase with stand density from the widely spaced stands to the medium-spaced stands followed by a decrease with stand density to the narrowly spaced stands (Figure 3.4a). P in branch wood decreased with stand density (Figure 3.4b). And P in foliage exhibited a positive and linear relationship with stand density (P=0.053, R^2=0.43). Total P continued to decrease with stand density in Block-1 and was nearly constant at all stand densities in Blocks 2 and 3 (Figure 3.3b). As with total N, the pattern of total P was most similar to P accumulated in stem wood.

Current stand density also influenced the distribution of N and P into the crown. The percentage of total N and P that was accumulated in the crown decreased linearly with stand density (Figure 3.5). As stand density increased, crowns became more restricted thereby limiting the percentage of total N and P accumulated there.

3.3.3 Management Implications

The results of this study suggest that the choice of species made at stand establishment can have long-term effects on site nutrient management. Slash pine accumulated more N than loblolly pine in higher density stands where loblolly pine crowns were restricted. This greater N utilization by slash pine could suggest that fertilization may be more effective in slash pine because of greater N demand. However, loblolly pine foliage had a greater N concentration than slash pine and thus requires more N to produce photosynthetic material. Also, loblolly pine has lower efficiency at foliar retranslocation and thus requires more N from the soil for biomass
Figure 3.4. Phosphorus accumulated in stem wood (kg ha\(^{-1}\)) (a), branch wood (kg ha\(^{-1}\)) (b), and foliage (kg ha\(^{-1}\)) (c) in stands at varying levels of Reineke's stand density index (SDI). Data are from 16-year-old unthinned loblolly pine stands near Flanklinton, LA, USA.
Figure 3.5. Percent of total aboveground N (a) and P (b) located in crown components in stands at varying levels of Reineke's stand density index (SDI). Data are from 16-year-old unthinned loblolly pine stands near Flanklinton, LA, USA. Lines are least squares fit (n=9).
production. In addition, slash pine allocates a greater percentage of N to stemwood than loblolly pine (Figure 3.1), effectively restricting the nutrient from recycling. Therefore, the effectiveness and longevity of fertilization may actually be less in slash pine stands compared to loblolly pine, an outcome confirmed by Jokela et. al (2000).

Initial spacing and stand density can also have implications for site nutrient management. For example, the period of greatest N demand from the soil is early in stand development just before canopy closure when N-rich foliage is the primary sink for aboveground N (Smith et al. 1971, Miller 1995). Because trees grow independent of stand density until canopy closure (Long and Smith 1984), denser stands will accumulate foliage (and nutrients) more rapidly than wider spaced stands (Long and Turner 1975) thus creating a greater demand from the soil for nutrients. Therefore, fertilization early in stand development may be most effective in narrower spaced stands.

Harvest intensity may also have varying effects on nutrient removal dependent on species and stand density. Evidence presented in this study suggests that additional nutrient losses from the harvesting of tree crowns would be greater in loblolly pine stands compared to slash pine as a result of greater biomass in loblolly pine crown components and greater N and P concentrations of those components. Compared to a conventional stem-only harvest, a whole-tree harvest in the medium- and narrowly spaced loblolly pine stands examined in this study would on average increase biomass by only 23% but would increase N loss by 88% and P loss by 253%. The percentages of additional loss by whole-tree harvesting would be reduced in higher density stands.
Thus, compared to a stem-only harvest, a whole-tree harvest would have the greatest effect in lower density loblolly pine stands and the least effect in high density slash pine stands.

3.4. Conclusions

Species and stand density affected both the accumulation and distribution of biomass, N, and P. Species differences in total N accumulation was dependent on initial spacing. At wider initial spacings, where crowns constituted a greater percentage of total aboveground biomass, loblolly pine accumulated more N than slash pine because of greater N and P concentrations in loblolly pine crown components and greater biomass production of those components; however, at narrower initial spacings where crown biomass was restricted slash pine had greater N accumulation. There were no species differences in total P accumulation at either initial spacings; greater foliage P by loblolly pine was offset by greater stem wood P by slash pine. A large proportion of nutrients were partitioned to the crown because of the relatively high nutrient concentrations in crown components. Although the crown components averaged less than 20% of total biomass in stands of loblolly and slash pine, 40-60% of total accumulated N and 60-80% of total accumulated P were found in the crown. Loblolly pine generally accumulated more N and P in the crown than slash pine.

Current stand density had variable results on biomass and nutrient accumulation. With increasing stand density, stemwood N and P increased from widely spaced stands to medium-spaced stands then decreased to narrowly spaced stands, branchwood N and P continued to decrease, and foliage N and P continued to
increase. Total N and P was similar to stemwood N and P. In addition, with increasing stand density, the fraction of total biomass, N, and P partitioned to the crown decreased.
CHAPTER 4

THE RELATIONSHIP OF NUTRIENT DEMAND AND FINE ROOT PRODUCTION IN STANDS OF LOBLOLLY AND SLASH PINE AT VARYING STAND DENSITIES

4.1. Introduction

The underlying mechanisms of biomass allocation are fundamental to the study of forest productivity. A better understanding of biomass allocation will aid in the prediction of environmental effects on growth and may serve to increase yield, an important objective of production foresters. In many agricultural crops, enhanced yield results primarily by maximizing allocation of photosynthate to harvestable parts rather than an actual gain in total net primary production, TNPP (Evans 1976). Belowground production has been estimated to account for 30-70% of TNPP in forests (Santantonio 1989), and therefore the potential exists to increase the yield of merchantable stem wood by decreasing the proportion of TNPP allocated to roots (Cannell 1985). For example, Linder and Axelsson (1982) found that the combined treatments of fertilization and irrigation in 20-year-old *Pinus sylvestris* doubled yield, but only 40% of the gain in stem production was explained by an increase in TNPP; the remaining 60% was explained by a reduction in relative allocation to fine roots.

While the mechanisms that control aboveground allocation are becoming clearer, belowground allocation is less understood as a result of the difficult nature of obtaining belowground data and various techniques of estimating belowground production that often do not produce consistent trends. Waring and Pitman (1985) were one of the first to propose whole-tree allocation priorities in forest stands;
however, they did not provide data to support their rankings of allocation priority. One modeling approach to explain allocation to fine roots was forwarded by Davidson (1969) who hypothesized that a functional balance existed between the size and activity of the photosynthetic system (shoots) and the size and activity of the nutrient acquisition system (roots) of plants. In general, the functional balance hypothesis states that photosynthate is allocated to foliage production when there is a shortage of carbon, and conversely, photosynthate is allocated to fine roots when nutrients are limiting.

This functional balance has been expressed by the relationship

$$\frac{W_s}{W_r} = \frac{a_r f_r}{a_s f_n}$$

where $W_s$ is mass of the photosynthetic shoot, $W_r$ is mass of the nutrient and water acquiring roots, $a_r$ is specific activity of roots (e.g., N uptake per unit root mass), $a_s$ is the specific activity of the shoot (C assimilated per unit shoot mass), and $f_r$ and $f_n$ are the fractions of dry matter consisting of carbon and N, respectively. Eq. [4.1] is a mass balance equation developed to describe root to shoot ratios in simple annuals. Due to the complexity of forest systems, however, complications arise when eq. [4.1] is applied to trees. For example, eq. [4.1] was designed to explain standing biomass in annuals, but trees are perennial and continually accumulate biomass while turning over foliage and fine roots. Also, the majority of aboveground tree biomass is nonphotosynthetic and trees conserve nutrients by foliar retranslocation. Because these differences are not taken into account, eq. [4.1] is not appropriate for use in making quantitative predictions about biomass allocation in forest systems.

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The functional balance hypothesis does, however, provide a framework in which general predictions can be made. For example, it suggests that if specific root activity is increased (e.g., by increased nutrition), then relative production of fine roots will decrease. This was first confirmed in forest stands by Keyes and Grier (1981) who showed in 40-year *Pseudotsuga menziesii* stands that even though TNPP was slightly greater on the "good" site compared to the "poor" site, root production was three times less on the good site.

Of interest to this study, the functional balance hypothesis also suggests that fine root production may be linked to demands for a limiting nutrient. It predicts that, with all else being equal, if the amount of a limiting nutrient needed for new production is increased, then fine root production should also increase to meet that demand. To test this relationship, a range of demands for a limiting nutrient is needed.

Species differences often have varying nutrient demands. Two commercially important species in the southeastern United States are loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.). These closely related species vary in biomass allocation patterns with loblolly pine generally accumulating more biomass in crown components than slash pine (Colbert et al. 1990, Chapter 3). The N and P concentrations of foliage, branch wood, and stem wood also vary between species (Chapter 3). Thus, differences in biomass allocation patterns and component nutrient concentrations between these species likely result in varying amounts of nutrients needed for annual aboveground production.
Another factor that exerts a strong influence on aboveground biomass allocation patterns and subsequent nutrient demands in conifer stands is stand density. For example, with increasing stand density, branch-wood mass generally decreases as a result of more limited space for lateral expansion of the branches (Jack and Long 1991) while leaf area index increases (Dean and Baldwin 1996). Because the various aboveground components vary in nutrient concentration, stand density will also likely affect the total amount of nutrients needed for aboveground production.

Not all nutrients used in the production of new biomass are acquired directly from the soil. Existing nutrients in foliage are often translocated before senescence, thereby conserving nutrients and providing a significant source of nutrients for new growth, especially in older trees (Miller 1995). For example, retranslocated N constitutes 40-50% of N required for new foliage production in Pinus radiata (Crane and Banks 1992). As a result of this internal recycling of nutrients, the demand from the soil for nutrients in new growth is reduced and must be taken into account.

This study was conducted to evaluate the validity of the functional balance hypothesis so as to provide a potential mechanism for fine root production in southern pine forests. Annual fine root production in loblolly and slash pine was compared with the demand and uptake of N and P, two commonly limiting nutrients in soils of the southeastern United States. In order to provide a range of N and P demands, aboveground biomass allocation and subsequent N and P demand and uptake were examined in stands of varying stand densities. The specific objectives of this study were to (1) determine whether apparent N and P demand and uptake and also fine-root
production varied in stands of loblolly and slash pine, (2) determine whether apparent N and P demand and uptake and also fine-root production changed with stand density, and (3) determine if fine-root production varied with apparent N and P demand and uptake.

4.2. Methods

4.2.1. Site Description

The study was conducted on the Lee Memorial Forest in southeast Louisiana in a species and spacing trial planted in 1981 on a site that was previously used as a Christmas tree plantation. Data are from pure, unthinned stands of loblolly or slash pine planted at spacings of 1.2 x 1.2 m (narrowly spaced), 2.4 x 2.4 m (medium-spaced), and 3.7 x 3.7 m (widely spaced). Each species and spacing combination was replicated three times in contiguous blocks that represented a perceived fertility gradient. Data were not collected in widely spaced slash pine stands as a result of unacceptable mortality of planted trees and subsequent invasion of loblolly pine volunteers. The physical characteristics of the study site and attributes of the plots at the time of measurement are described in Chapter 2.

4.2.2. Aboveground Apparent N and P Demand

Aboveground biomass was estimated with regression equations. Each tree in each plot was numbered and measured for outside bark diameter at breast height (DBH, 1.37 m), total height and height to the base of the live crown after the 1996, 1997, and 1998 growing seasons. Using these measurements, standing first-year foliage, second-year foliage, stem wood, and branch wood mass for each loblolly pine
tree were estimated with equations developed by Baldwin (1987) and Baldwin et al. (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, estimated total foliage on each slash pine tree was multiplied by the mean percentage of total loblolly pine foliage that consisted of first-year foliage, 0.5362, to obtain an estimate of first-year foliage. Second-year foliage on slash pine trees was the residual of total foliage minus first-year foliage. The assumption that the percentage of first-year to second-year foliage in slash pine stands was the same as in loblolly pine stands was not tested; however, both loblolly and slash pine foliage live for two years before senescence, and a value near 50% of total foliage that consisted of a given year seems reasonable.

Annual stand-level foliage increment in each plot for each year was estimated by summing first-year foliage on each tree in each plot for each year and expanding the plot sum to a per-hectare basis. Annual stem wood and branch wood increments on each tree were calculated by subtracting the previous-year standing biomass in each respective component from current-year standing biomass. Per-tree biomass increment for each respective component was summed by plot and expanded to a per-hectare basis. Trees that died during a growing season were assumed to have the same dimensions as at the end of the previous year, and therefore biomass increment was limited on these trees to first-year foliage. Periodic mean annual increment by biomass component is the mean stand-level biomass increment for each respective component in 1997 and 1998.
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 increment in each component in each plot by its corresponding nutrient concentration. The procedures for determining the N and P concentration of needle litter and each of the aboveground components were described in Chapters 2 and 3, respectively. 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 by the equation

\[ \text{[4.2]} \quad R_{N,P} = (F_{1,i} - F_{2,i+1}) + (F_{2,i} - L_i) \]

where \( R_{N,P} \) is kg ha\(^{-1}\) of N or P supplied by foliar retranslocation for a given year, \( F_{1,i} \) is kg ha\(^{-1}\) of N or P in first-year foliage measured in the previous year, \( F_{2,i+1} \) is kg ha\(^{-1}\) of N or P in second-year foliage measured in the current year, \( F_{2,i} \) is kg ha\(^{-1}\) of N or P in second-year foliage measured in the previous year, and \( L_i \) is kg ha\(^{-1}\) of N or P in needle litter measured in the previous year. Apparent N and P demand was the difference between N and P used for new biomass production and \( R_{N,P} \).

4.2.3. Soil N and P Uptake

Stand-level soil N and P uptake was estimated by a sequential coring technique modified from Raison et al. (1987) that compared nutrient content in ambient soil with nutrient content in soil where root uptake was prevented. N and P uptake was estimated over two time periods: from July 1997 to January 1998 and from January...
1998 to September 1998. At the beginning of each time period, twenty 5-cm diameter PVC tubes were vertically inserted 30 cm into the ground in each plot to impose a barrier to root uptake. Two holes were drilled in each tube at ground-level to drain standing water in the tube that could result in denitrification and anaerobic mineralization. At the end of each measurement period, soil within the tubes was collected, combined by horizon (A and B) and plot, and mixed into a composite sample (roots-excluded samples). Also at the end of each sampling period, soil was collected adjacent to each tube, combined by horizon and plot, and mixed into a composite sample (ambient-soil samples). Three replicates were taken from each composite sample to account for imperfect mixing of the soil and were transported to the laboratory to be analyzed for extractable N and P. All soil replicates were stored in the laboratory in refrigeration at approximately 2°C for less than 24 hours before they were placed in extracting solution.

Mineral N was extracted from a 10-g subsample taken from each replicate with 100 ml of 2 N KCl. A paired 10 g subsample of soil was dried at 105°C for 24 hours to determine dry weight. The soil-KCl mixture was mechanically agitated for one hour, allowed to settle for 30 minutes, filtered with No. 42 ashless filter paper, and stored in refrigeration until analyzed. Extracts were analyzed for total N concentration (NH₄⁺ plus NO₃⁻; weight basis) with an NH₄⁺ analyzer (Alltech 320 Conductivity Detector) and converted to a dry weight basis using the weight of dried subsamples. The mineral-N content of each composite sample is the mean of the three replicate measurements of mineral-N content. Mineral N in each horizon in each plot (kg ha⁻¹ to
30 cm) was calculated by multiplying the N content in each composite sample by the appropriate values of bulk density and horizon depth. The procedures for measuring bulk density and horizon depth were described in Chapter 2.

Mineral P was extracted from a 5-g subsample taken from each soil replicate with 50 ml of Mehlich-3 solution. The soil and solution were mechanically agitated for one hour, allowed to settle for 30 minutes, filtered with No. 42 ashless filter paper, and stored in refrigeration until analyzed. Extracts were analyzed for total P concentration (weight basis) colorimetrically (Hewlett Packard HP 8453 UV-visible Spectrophotometer) and converted to a dry weight basis using the weight of dried subsamples. The P content of each composite sample is the mean of the three replicate measurements of P. Mineral P (kg ha\(^{-1}\)) in each horizon in each plot was calculated by multiplying the P content in each composite sample by the respective values of bulk density and horizon depth.

\[ \text{N and P uptake (kg ha}\,^{-1}\,\text{to 30 cm), } \text{U}_{\text{N,P}} \text{, during each time period in each plot was calculated as} \]

\[ [4.3] \text{U}_{\text{N,P}} = (E_{i+1} - A_{i+1})_{A-\text{horizon}} + (E_{i+1} - A_{i+1})_{B-\text{horizon}} \]

where \( E_{i+1} \) is the N or P content (kg ha\(^{-1}\) to 30 cm) in roots-excluded soil collected at the end of a time period, \( A_{i+1} \) is the N or P content (kg ha\(^{-1}\) to 30 cm) in ambient-soil collected at the end of a time period, and A- and B-horizon are horizon designations. Total N and P uptake from July 1997 to September 1998 (A and B horizon to 30 cm) in each plot is the sum of N and P uptake from both measurement periods.

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4.2.4. Belowground Production

Belowground net primary production was calculated with a compartment-flow model modified from Santantonio and Grace (1987) that included periodic measurements of standing live and dead roots and of root decay. This approach used calculations of root decay rate, stand-level root decomposition, and stand-level root mortality to calculate stand-level root production. To obtain samples of standing live and dead roots, twenty soil cores, 5-cm in diameter and 30-cm deep, were collected five times in each plot at approximately 3-month intervals between July 1997 and July 1998. Soil cores were bulked by plot, transported to the laboratory, and stored at approximately 2°C until processing. Within one week of collection, soil cores were placed in a device that mechanically washed mineral soil through a 40-mesh screen leaving residual organic matter. Pine roots were extracted from the residual organic matter and separated into live and dead classes based on visual and mechanical properties (Santantonio and Herman 1985, Vogt and Persson 1991). Pine roots were further separated into <1 mm, 1-5 mm, and >5 mm diameter classes (fine, medium, and coarse roots, respectively), oven-dried, and weighed.

Root decomposition was measured by following the decay of loblolly pine roots. As a result of similar fine root anatomy, decomposition rates of loblolly and slash pines were assumed to be equivalent. Pine roots <5 mm were excavated and separated from soil in a loblolly pine stand near the study site in July 1997. The roots were air-dried for 48 hours in the laboratory, separated into <1 mm and 1-5 mm diameter classes (fine and medium roots, respectively), and then 5 g of air-dried roots
were placed by diameter class into nylon mesh bags (cf. McClaugherty et al. 1982, 1984). Four root-filled bags of each diameter class were buried to a depth of 15 cm in each of four plot quadrants in the wide and narrowly spaced loblolly pine plots in Blocks 1 and 3. These plots were chosen because they represented the extremes of initial spacing and a perceived fertility gradient. When standing live and dead root samples were collected, one root-filled bag of each size class in each quadrant was extracted from the soil, transported to the laboratory, air-dried for 48 hours, and then root mass within the bag was weighed.

Residual root mass (g) at any time after burial, $W_{\text{res}}$, was modeled by least squares nonlinear regression (Proc NLIn, Statistical Analysis System Version 6.12, SAS Institute Inc., Cary, NC, USA) with the general model

$$W_{\text{res}} = 5 - (a/b) + a/(T_b + b)$$

where $a$ and $b$ are regression constants, and $T_b$ is time in days since burial.

The effects of block, diameter class, and initial spacing on residual root mass were analyzed with reduced and full models. The full model for diameter class was

$$W_{\text{res}} = 5 - [(a/b) + a/(T_b + b)] \cdot D1 - [(a/b) + a/(T_b + b)] \cdot D2$$

where $a$ and $b$ are regression constants, $T_b$ is time in days since burial, $D1$ is a dummy variable where $D1=1$ if diameter class was $<1$ mm and $D1=0$ if diameter class was 1-5 mm, and $D2$ is a dummy variable where $D2=0$ if diameter class was $<1$ mm and $D2=1$ if diameter class was 1-5 mm. Full models for block and initial spacing were of the same form. Diameter class ($P<0.001$) and block ($P<0.001$), but not initial spacing ($P=0.396$), were significant factors in root decomposition. Fine root decay was
initially rapid but then began to slow (Figure 4.1), which is a typical pattern (Fogel and Hunt 1979, Berg 1981, McClaugherty et al. 1984, King et al. 1997).

The absence of decomposition bags in Block 2 necessitated a quantitative measure of block to predict $W_{res}$ there. Measures of N and P mineralization, needle litter N and P concentration, and vertical flux of soil N from data in Chapter 2, as well as site index (base age 50, SI) were each evaluated as quantitative measures of block. Stepwise regression led to models that used SI as a quantitative measure of block to estimate fine and medium root $W_{res}$ at any time in Block 2 (Figure 4.1). The nonlinear models explained 98.4% and 98.5% of the variation in fine and medium root decomposition, respectively. SI provided the best fit of examined variables likely because it best incorporates all aspects of a site, including nutrient content, texture, water holding capacity, and others.

A decay coefficient, $k$, was calculated for each sampling interval for each block and diameter class combination by

$$ [4.6] \quad k = -\frac{\ln(W_{res, t+i})-\ln(W_{res, t})}{T_s} $$

where $W_{res, t+i}$ is residual root mass at the end of a sampling period, $W_{res, t}$ is residual root mass at the beginning of a sampling period, and $T_s$ is number of days within the interval.

Decomposition of roots (kg ha$^{-1}$) for each sampling interval in each plot for each diameter class, $D_r$, was calculated as

$$ [4.7] \quad D_r = W_{d, t+i} \cdot [1 - \exp(-k \cdot T_s)] $$

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Figure 4.1. Residual mass (g) of loblolly pine fine roots (<1 mm) (a) and medium roots (1-5 mm) (b) through time after burial. Solid lines represent residual root weight modeled by least squares nonlinear regression from data collected in Blocks 1 and 3. Dashed line represents residual root mass in Block 2 as estimated for fine roots by the equation $M_{res} = 5 - \left[ (-3596.65 + 66.52 \cdot SI)/(-8.56 + 15.91 \cdot SI) \right]$
\[ + \left( -3596.65 + 66.52 \cdot SI \right)/(T_b + (-855.59 + 15.91 \cdot SI)) \]
where $M_{res}$ is residual root weight, SI is site index (base age 50), and $T_b$ is number of days buried. Residual root mass for medium roots in Block 2 are estimated by the equation $M_{res} = 5 - [(15.04 \cdot SI)/(3.81 \cdot SI)) + 15.04 \cdot SI/(T_b + (3.812 \cdot SI))].$
where $W_{d, t=i}$ is mass of dead roots (kg ha$^{-1}$) collected at the beginning of an interval for a particular block by diameter class combination (Santantonio and Grace 1987).

Mortality of roots (kg ha$^{-1}$) for each sampling interval in each plot for each diameter class, $M_r$, was calculated as

$$[4.8] \quad M_r = W_{d, t=i+1} - W_{d, t=i} + D_r$$

where $W_{d, t=i+1}$ is mass of dead roots (kg ha$^{-1}$) collected at the end of an interval for a particular block by diameter class combination (Santantonio and Grace 1987).

Finally, production of roots (kg ha$^{-1}$) for each sampling interval in each plot for each diameter class, $P_r$, was calculated as

$$[4.9] \quad P_r = W_{l, t=i+1} - W_{l, t=i} + M_r$$

where $W_{l, t=i+1}$ is mass of live roots (kg ha$^{-1}$) in a diameter class collected at the end of an interval and $W_{l, t=i}$ is mass of live roots (kg ha$^{-1}$) in a diameter class collected at the beginning of an interval (Santantonio and Grace 1987).

### 4.2.5. Statistical Analysis

Separate methods were used in the analyses of species and initial spacing effects and of current stand density effects. Species and initial spacing effects on individual variables were analyzed in a randomized complete block by analysis of variance with a general linear model procedure (Statistical Analysis System, SAS Institute Inc., Cary, NC, USA). This approach examined the discreet variables to investigate the long-term effects of treatments made at stand establishment. Because of the missing cell caused by unacceptable mortality in the widely spaced slash pine
stands, analyses of species and initial spacing effects were limited to the medium and narrowly spaced stands, where initial spacings were common for both species.

The effects of current stand density on individual variables were analyzed by linear regression (Statistical Analysis System, SAS Institute Inc., Cary, NC, USA). Reineke's stand density index (SDI) was used to quantify current stand density and was calculated with the equation

\[ 4.10 \quad SDI = TPH \cdot (D_q/25)^{1.6} \]

where \( D_q \) is quadratic mean diameter (cm) and TPH is the number of trees per hectare (Daniel and Sterba 1980). The regression approach examined the continuous variable to elucidate a relationship between current stand conditions and N and P accumulation. Analyses of slash pine would be limited to only two clusters of points (medium- and narrowly spaced stands) thereby making all relationships suspect. Therefore, only loblolly pine stands were used in the analyses of current stand density effects.

Because of the large amount of variability inherent in forest stands, the critical value of \( \alpha \) for significant effects was set at 0.10. Detailed methods of species and initial spacing analyses and of current density analyses are described in Chapter 2.

The effects of both apparent nutrient demand and also nutrient uptake on fine-root production was also analyzed by linear regression. If the slope of the regression was significantly different than zero (\( \alpha=0.10 \)), then it was concluded that nutrient demand influenced fine-root production, thus supporting the functional balance hypothesis.
4.3. Results and Discussion

4.3.1 Species and Initial Spacing Effects on N and P

Loblolly pine allocated more N to new aboveground biomass than slash pine in the medium-spaced stands (Table 4.1), even though total annual aboveground biomass production did not vary between species (P=0.362). The greater total N by loblolly pine was due primarily to greater N content in loblolly pine foliage caused by greater foliar N concentrations (Chapter 3). In the narrowly spaced stands, however, total N in new aboveground biomass did not vary between species; this was the result of loblolly pine, but not slash pine, significantly reducing total N in new aboveground biomass with narrower spacing. Thus, species differences in total aboveground N allocation were dependent on initial spacing. Absolute retranslocation of N was greater in loblolly pine than slash pine and greater in medium-spaced stands than narrowly spaced stands; however, the percentage of total N supplied by retranslocation did not significantly differ by species or initial spacing, averaging 42% of the N needed for new production. This indicates that while there may be differences between loblolly and slash pine in N needed for production of new biomass, the apparent aboveground demand for N from the soil did not differ between species and remained relatively constant.

Although total P in new production was greater in loblolly pine than slash pine at both spacings, the difference was not significant (Table 4.2). Loblolly pine allocated significantly more P to foliage but significantly less P to stem wood than slash pine. Retranslocation supplied a greater percentage of total P in new biomass than N in new

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Table 4.1. Mean values and results from analyses of variance for periodic annual N allocation (kg ha⁻¹ yr⁻¹, 1997 and 1998) to stem wood (StemN), branch wood (BranchN), and foliage (FoliageN), and also total N in new production (TotalN), annual N supplied by foliar retranslocation (R_N), and apparent aboveground N demand from soil (D_N) in relation to species and initial spacing. Number in parentheses represents percentages of TotalN supplied by R_N. Data are from unthinned stands of loblolly and slash pine planted in 1981 near Franklinton, LA, USA.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>StemN</th>
<th>BranchN</th>
<th>FoliageN</th>
<th>TotalN</th>
<th>R_N</th>
<th>D_N</th>
</tr>
</thead>
<tbody>
<tr>
<td>S_L I_M</td>
<td>17.0</td>
<td>2.4</td>
<td>47.8</td>
<td>67.1</td>
<td>29.0 (43.1)</td>
<td>38.1</td>
</tr>
<tr>
<td>S_L I_N</td>
<td>10.1</td>
<td>1.2</td>
<td>41.8</td>
<td>53.2</td>
<td>22.9 (43.2)</td>
<td>30.2</td>
</tr>
<tr>
<td>S_S I_M</td>
<td>17.1</td>
<td>1.6</td>
<td>36.6</td>
<td>55.3</td>
<td>22.7 (41.4)</td>
<td>32.6</td>
</tr>
<tr>
<td>S_S I_N</td>
<td>15.0</td>
<td>1.0</td>
<td>36.3</td>
<td>52.3</td>
<td>20.5 (39.7)</td>
<td>31.9</td>
</tr>
<tr>
<td>²Root MSE</td>
<td>2.6</td>
<td>0.6</td>
<td>3.3</td>
<td>4.4</td>
<td>2.7 (4.8)</td>
<td>4.2</td>
</tr>
</tbody>
</table>

P values for effect

| Block    | 0.286  | 0.347  | 0.097 | 0.277 | 0.062 (0.159) | 0.427 |
| S        | 0.151  | 0.228  | 0.004 | 0.046 | 0.030 (0.379) | 0.456 |
| I        | 0.026  | 0.044  | 0.153 | 0.015 | 0.036 (0.781) | 0.124 |
| S x I    | 0.172  | 0.445  | 0.184 | 0.071 | 0.266 (0.760) | 0.187 |

P values for contrasts

| S_L vs. S_S in I_M | 0.016 |
| S_L vs. S_S in I_N | 0.829 |
| I_M vs. I_N in S_L | 0.008 |
| I_M vs. I_N in S_S | 0.431 |

¹Treatment levels for the Species (S) variable are denoted by L (loblolly pine) or S (slash pine). Treatment levels for the Initial spacing (I) variable are denoted by M (medium-spaced, 2.4 x 2.4 m spacing) or N (narrowly spaced, 1.2 x 1.2 m).

²Mean square error.
Table 4.2. Mean values and results from analyses of variance for periodic annual aboveground P allocation (kg ha\(^{-1}\) yr\(^{-1}\), 1997 and 1998) to stem wood (Stem\(_{p}\)), branch wood (Branch\(_{p}\)), and foliage (Foliage\(_{p}\)), and also total P (Total\(_{p}\)), annual P supplied by foliar retranslocation (R\(_{p}\)), and apparent aboveground P demand from soil (D\(_{p}\)) in relation to species and initial spacing. Number in parentheses represents percentages of Total\(_{p}\) supplied by R\(_{p}\). Data are from unthinned stands of loblolly and slash pine planted in 1981 near Franklinton, LA, USA.

<table>
<thead>
<tr>
<th></th>
<th>Stem(_{p})</th>
<th>Branch(_{p})</th>
<th>Foliage(_{p})</th>
<th>Total(_{p})</th>
<th>R(_{p})</th>
<th>D(_{p})</th>
</tr>
</thead>
<tbody>
<tr>
<td>(^1)Treatment</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S(_{I})M</td>
<td>0.36</td>
<td>0.15</td>
<td>3.12</td>
<td>3.64</td>
<td>2.27 (61.7)</td>
<td>1.36</td>
</tr>
<tr>
<td>S(_{I})N</td>
<td>0.22</td>
<td>0.08</td>
<td>2.65</td>
<td>2.96</td>
<td>1.77 (60.0)</td>
<td>1.19</td>
</tr>
<tr>
<td>S(_{S})M</td>
<td>0.45</td>
<td>0.11</td>
<td>2.53</td>
<td>3.10</td>
<td>1.93 (62.7)</td>
<td>1.16</td>
</tr>
<tr>
<td>S(_{S})N</td>
<td>0.36</td>
<td>0.06</td>
<td>2.32</td>
<td>2.75</td>
<td>1.66 (60.7)</td>
<td>1.09</td>
</tr>
<tr>
<td>(^2)Root MSE</td>
<td>0.07</td>
<td>0.05</td>
<td>0.38</td>
<td>0.43</td>
<td>0.33 (4.1)</td>
<td>0.20</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>P values for effect</th>
<th>Stem(_{p})</th>
<th>Branch(_{p})</th>
<th>Foliage(_{p})</th>
<th>Total(_{p})</th>
<th>R(_{p})</th>
<th>D(_{p})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Block</td>
<td>0.862</td>
<td>0.454</td>
<td>0.071</td>
<td>0.098</td>
<td>0.080 (0.372)</td>
<td>0.571</td>
</tr>
<tr>
<td>S</td>
<td>0.032</td>
<td>0.284</td>
<td>0.080</td>
<td>0.183</td>
<td>0.279 (0.738)</td>
<td>0.245</td>
</tr>
<tr>
<td>I</td>
<td>0.036</td>
<td>0.057</td>
<td>0.173</td>
<td>0.084</td>
<td>0.083 (0.467)</td>
<td>0.327</td>
</tr>
<tr>
<td>SxI</td>
<td>0.638</td>
<td>0.763</td>
<td>0.557</td>
<td>0.531</td>
<td>0.568 (0.970)</td>
<td>0.673</td>
</tr>
</tbody>
</table>

\(^1\)Treatment levels for the Species (S) variable are denoted by L (loblolly pine) or S (slash pine). Treatment levels for the Initial spacing (I) variable are denoted by M (medium-spaced, 2.4 x 2.4 m spacing) or N (narrowly spaced, 1.2 x 1.2 m).

\(^2\)Mean square error.
biomass (61% and 42%, respectively). The larger percentage of P supplied by retranslocation is possibly related to the extremely low levels of P in the soils of the Gulf Coastal Plain which are often below the levels of detectability. The high levels of P retranslocation may be necessary for new production because the majority of pine ecosystem P is located in aboveground biomass (Gholz et al. 1985). Like N, the percentages of total P supplied by retranslocation did not significantly differ between species or initial spacing which indicated that the apparent demand for P from the soil did not vary between species and remained relatively constant.

Loblolly pine stands had significantly greater N and P uptake (as calculated from soil measurements) than slash pine (Table 4.3). Initial spacing did not significantly affect either N or P uptake from the soil. The greater uptake of N and P in loblolly pine stands conflict with the results of apparent N and P demand. One possible explanation is that loblolly pine had greater N and P allocated to root production than slash pine. While production of fine roots did not significantly differ between species in these stands (Table 4.4), it is possible that loblolly pine had greater fine root N and P concentrations than slash pine, which is conceivable considering that loblolly pine had greater N and P concentrations in first-year foliage, second-year foliage, and branch wood than slash pine (Chapter 3).

4.3.2 Current Stand Density Effects on N and P

The effect of current stand density on total N accumulation is illustrated in Figure 4.2. Data are grouped by the block in which they were collected. Blocks are for replication purposes and represent a perceived fertility gradient from a high in
Table 4.3. Mean values and results from analyses of variance for total soil N uptake (kg ha\(^{-1}\) yr\(^{-1}\), \(U_{PN}\)) and total soil P uptake (kg ha\(^{-1}\) yr\(^{-1}\), \(U_{PP}\)) to 30 cm that occurred from July 1997 to September 1998 in relation to species and initial spacing. Data are from unthinned stands of loblolly and slash pine planted in 1981 near Franklinton, LA, USA.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>(U_{PN})</th>
<th>(U_{PP})</th>
</tr>
</thead>
<tbody>
<tr>
<td>SLIM</td>
<td>21.1</td>
<td>0.36</td>
</tr>
<tr>
<td>SLIN</td>
<td>20.4</td>
<td>0.10</td>
</tr>
<tr>
<td>SSM</td>
<td>8.7</td>
<td>-0.10</td>
</tr>
<tr>
<td>SSIN</td>
<td>14.4</td>
<td>-0.20</td>
</tr>
<tr>
<td>2 Root MSE</td>
<td>6.7</td>
<td>0.20</td>
</tr>
</tbody>
</table>

P values for effect

<table>
<thead>
<tr>
<th>Factor</th>
<th>(U_{PN})</th>
<th>(U_{PP})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Block</td>
<td>0.061</td>
<td>0.451</td>
</tr>
<tr>
<td>S</td>
<td>0.054</td>
<td>0.015</td>
</tr>
<tr>
<td>I</td>
<td>0.548</td>
<td>0.156</td>
</tr>
<tr>
<td>SxI</td>
<td>0.444</td>
<td>0.503</td>
</tr>
</tbody>
</table>

\(^1\)Treatment levels for the Species (S) variable are denoted by L (loblolly pine) or S (slash pine). Treatment levels for the Initial spacing (I) variable are denoted by M (medium-spaced, 2.4 x 2.4 m spacing) or N (narrowly spaced, 1.2 x 1.2 m).

\(^2\)Mean square error.
Table 4.4. Mean values (kg ha\(^{-1}\)) and results from analyses of variance for standing weights (mean of five measurement periods) of live (\(W_l\)), dead (\(W_d\)), and total fine roots (\(W_t\)), and also fine root decomposition (kg ha\(^{-1}\), \(D_r\)), mortality (kg ha\(^{-1}\), \(M_r\)), and production (kg ha\(^{-1}\), \(P_r\)) from June 1997 through July 1998 in relation to species and initial spacing. Numbers in parentheses are proportion of TNPP allocated to fine roots. Data are for roots <1 mm diameter collected to 30 cm in unthinned stands of loblolly and slash pine planted in 1981 near Franklinton, LA, USA.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>(W_l)</th>
<th>(W_d)</th>
<th>(W_t)</th>
<th>(D_r)</th>
<th>(M_r)</th>
<th>(P_r)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(S_lI_M)</td>
<td>514</td>
<td>337</td>
<td>852</td>
<td>270</td>
<td>408</td>
<td>625 (4.1)</td>
</tr>
<tr>
<td>(S_lI_N)</td>
<td>474</td>
<td>288</td>
<td>762</td>
<td>238</td>
<td>394</td>
<td>535 (4.9)</td>
</tr>
<tr>
<td>(S_sI_M)</td>
<td>464</td>
<td>305</td>
<td>769</td>
<td>221</td>
<td>365</td>
<td>410 (2.9)</td>
</tr>
<tr>
<td>(S_sI_N)</td>
<td>450</td>
<td>287</td>
<td>737</td>
<td>244</td>
<td>341</td>
<td>581 (4.7)</td>
</tr>
</tbody>
</table>

Root MSE: 165 141.7 190 44 98 234 (2.0)

P-values for effect

<table>
<thead>
<tr>
<th>Block</th>
<th>(W_l)</th>
<th>(W_d)</th>
<th>(W_t)</th>
<th>(D_r)</th>
<th>(M_r)</th>
<th>(P_r)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.025</td>
<td>0.010</td>
<td>&lt;0.001</td>
<td>0.010</td>
<td>0.042</td>
<td>0.192</td>
<td>(0.188)</td>
</tr>
<tr>
<td>0.383</td>
<td>0.654</td>
<td>0.276</td>
<td>0.436</td>
<td>0.429</td>
<td>0.554</td>
<td>(0.541)</td>
</tr>
<tr>
<td>0.527</td>
<td>0.358</td>
<td>0.284</td>
<td>0.856</td>
<td>0.752</td>
<td>0.773</td>
<td>(0.305)</td>
</tr>
<tr>
<td>0.766</td>
<td>0.668</td>
<td>0.563</td>
<td>0.329</td>
<td>0.925</td>
<td>0.373</td>
<td>(0.692)</td>
</tr>
</tbody>
</table>

1^Treatment levels for the Species (S) variable are denoted by L (loblolly pine) or S (slash pine). Treatment levels for the Initial spacing (I) variable are denoted by M (medium-spaced, 2.4 x 2.4 m spacing) or N (narrowly spaced, 1.2 x 1.2 m).

2^Mean square error.
Figure 4.2. Mean N in annual aboveground production (kg ha\textsuperscript{-1} yr\textsuperscript{-1}, 1997 and 1998) (a), mean N supplied by foliar retranslocation (kg ha\textsuperscript{-1} yr\textsuperscript{-1}, 1997 and 1998) (b), and mean apparent N demand from soil (kg ha\textsuperscript{-1} yr\textsuperscript{-1}, 1997 and 1998) (c) at varying levels of Reineke's stand density index (SDI). Data are from unthinned stands of loblolly pine planted in three blocks in 1981 near Franklinton, LA, USA.
Block 1 to a low in Block 3. Total N in new biomass increased from the widely spaced stands to the medium-spaced stands followed by a decrease with stand density to the narrowly spaced stands (Figure 4.2a). This pattern was similar to allocation of N to foliage and stem wood (not shown) which is not surprising given that stem wood and foliage accounted for 95% of N in new biomass. A decline in foliage and stemwood N at the highest densities was unexpected given that stand density is positively correlated with stand-level production of stemwood (Long 1985) and foliage (Dean and Baldwin 1996). The decline in stem wood and foliage N at the highest stand densities may be related to a sustained drought that occurred throughout length of the study that caused intense intraspecific competition for water, particularly in the narrowly spaced stands, thus limiting production there. As evidence for greater competition, the narrowly spaced stands had a significantly greater percentage of total volume lost each year to mortality than medium and widely spaced stands (1.18%, 0.08%, and 0.03% per year, respectively). N supplied by foliar retranslocation exhibited the same trend as total N in new biomass in two of three blocks (Figure 4.2b). Apparent N demand followed the same trend in all blocks; however, the difference between values of SDI appeared more subtle than N in new biomass (Figure 4.2c). Although apparent N demand was slightly greater at medium-levels of SDI, retranslocation of N appears to have caused relatively constant apparent aboveground N demands from the soil at all levels of SDI. P in new biomass showed similar patterns as N in new biomass; after retranslocation was accounted for, there was little difference in apparent P demand at the varying levels of SDI (Figure 4.3).
Figure 4.3. Mean P in annual aboveground production (kg ha\(^{-1}\) yr\(^{-1}\), 1997 and 1998) (a), mean P supplied by foliar retranslocation (kg ha\(^{-1}\) yr\(^{-1}\), 1997 and 1998) (b), and apparent P demand from soil (kg ha\(^{-1}\) yr\(^{-1}\), 1997 and 1998) (c) at varying levels of Reineke's stand density index (SDI). Data are from unthinned stands of loblolly pine planted in three blocks in 1981 near Franklinton, LA, USA.
Actual soil N uptake increased with stand density from the widely spaced stands to the medium-spaced stands, but unlike apparent N demand continued to increase with stand density to the narrowly spaced stands in two of the three blocks (Figure 4.4a) resulting in a significant linear relationship between N uptake and stand density ($P=0.008$, $R^2=0.66$). Actual P uptake was expected to be similar to the pattern of N uptake. However, Blocks 2 and 3 showed the characteristic spike in the medium-spaced stands, but unlike N, P uptake decreased with increasing stand density to the narrowly spaced stands (Figure 4.4b). The reversed pattern in Block 1 is somewhat of an anomaly.

Results of actual N uptake conflicted with apparent N demand. A comparison of apparent N demand and N uptake as measures of N utilization in loblolly pine showed no significant linear relationship (Figure 4.5a). Both estimations, however, may be realistic given that apparent N demand does not account for an N cost associated with root production. Actual N uptake values were lower than apparent N demand values in 8 of 9 loblolly pine stands including one negative value that is unrealistic, indicating that N uptake may be underestimated. While N uptake may be underestimated, relative patterns between treatments were considered realistic.

P uptake was significantly and linearly related to apparent P demand (Figure 4.5b). It is not clear why there was a significant linear relationship between apparent P demand and P uptake, but not between apparent N demand and N uptake. P uptake over the 14-month period was negative in three stands, which is unrealistic. Like N, P
Figure 4.4. Total uptake of N (kg ha⁻¹) (a) and P (kg ha⁻¹) (b) to 30 cm that occurred from July 1997 to September 1989 as related to Reineke's stand density index (SDI). Data are from unthinned stands of loblolly pine planted in three blocks in 1981 near Franklinton, LA, USA.
Figure 4.5. N uptake as a function of apparent N demand (a), and P uptake as a function of apparent P demand in stands of loblolly pine (b). Uptake is the total uptake of each respective nutrient to 30 cm that occurred from 1997 to September 1998. Apparent nutrient demand is the mean N or P in total annual aboveground production minus N or P supplied by foliar retranslocation (kg ha\(^{-1}\) yr\(^{-1}\), 1997 and 1998). Data are from unthinned stands of loblolly pine planted in three blocks in 1981 near Franklinton, LA, USA.
uptake was underestimated, but relative patterns between treatments were considered realistic.

4.3.3 Root Production

Neither species nor initial spacing significantly affected the mean mass of standing live, dead, or total fine roots (<1mm diameter; Table 4.4). Nor did they significantly affect the decomposition, mortality, or production of fine roots. Fine root mortality averaged 70% of production across both species and initial spacing which indicated that fine root turnover was similar to production which has previously been shown in loblolly pine (Harris et al. 1977). These results indicate that the residence times of fine roots are a little over 1 year which is consistent with Gholz et al. (1986) who showed a residence time of 1.5 years for slash pine roots <1 mm diameter.

The percentage of TNPP allocated to fine roots averaged 3-5% of TNPP and did not vary by species or initial spacing (Table 4.4). The percentage here is considerably lower than the 20-70% reported in other studies (Harris et al. 1977, Grier et al. 1981, Ägren et al. 1980, Santantonio 1989, Gower et al. 1992). While lack of a standard method of estimating root production may partially explain the discrepancy, fine root production is likely underestimated here. Undoubtedly, some root mass passed through the 40-mesh screens that were used to separate organic matter from mineral soil; also, it is likely that not all fine root biomass was extracted from residual organic matter. However, the greatest contributor to the underestimation of fine root production was likely due to sampling only to 30 cm. Most fine roots occur in the upper 15 cm of a forest soil where water and nutrient availability, aeration, soil
strength, and temperature are most favorable for production (Pritchett 1979, Vogt et al.
1983, Gholz et al. 1986, Van Rees and Comerford 1986); however, the severe drought
that occurred during the study likely shifted fine root production deeper in the soil to
attain water (Ludovici and Morris 1996, López et al. 1998). Casual observation in
minirhizotrons that were located on four of the loblolly pine plots in this study revealed
that roots were often located below 30 cm. Although absolute fine root production
may be underestimated in this study, relative patterns of fine root production between
treatments are considered realistic.

While there were species by initial spacing interactions for standing live and
total medium roots (1-5 mm diameter) and also for medium root production (Table
4.5), there was no clear pattern. For example, loblolly pine had significantly greater
standing medium roots than slash pine in the medium-spaced stands, but the trend was
reversed in the narrowly spaced stands. Medium root production was negative in 3 of
4 treatments with considerable variability between plots. Santantonio and Santantonio
(1987) showed that in stands of Pinus radiata, only roots <1 mm have seasonal cycles
of growth, death, and replacement, which may explain the extremely variable
production values for medium roots. Standing coarse roots (>5 mm diameter) also had
no clear pattern and was extremely variable (Table 4.6).

There were no clear relationships between stand density and live or total
standing roots in any diameter class. Nor was fine root production clearly related to
stand density (Figure 4.6). Fine root production appeared to have a positive, linear
relationship with stand density in Blocks 1 and 3; however, fine root production
Table 4.5. Mean values (kg ha\(^{-1}\)) and results from analyses of variance for standing weights (mean of five measurement periods) of live (\(W_l\)), dead (\(W_d\)), and total medium roots (\(W_t\)), and also medium root decomposition (\(D_r\)), mortality (\(M_r\)), and production (\(P_r\)) from June 1997 through July 1998 in relation to species and initial spacing. Data are for roots 1-5 mm diameter collected to 30 cm in unthinned stands of loblolly and slash pine planted in 1981 near Franklinton, LA, USA.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>(W_l)</th>
<th>(W_d)</th>
<th>(W_t)</th>
<th>(D_r)</th>
<th>(M_r)</th>
<th>(P_r)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(S_LI_M)</td>
<td>1,218</td>
<td>113</td>
<td>1,331</td>
<td>79</td>
<td>122</td>
<td>-65</td>
</tr>
<tr>
<td>(S_LI_N)</td>
<td>1,440</td>
<td>92</td>
<td>1,533</td>
<td>73</td>
<td>53</td>
<td>-20</td>
</tr>
<tr>
<td>(S_SI_M)</td>
<td>1,525</td>
<td>129</td>
<td>1,654</td>
<td>43</td>
<td>130</td>
<td>-453</td>
</tr>
<tr>
<td>(S_SI_N)</td>
<td>1,183</td>
<td>81</td>
<td>1,264</td>
<td>73</td>
<td>178</td>
<td>420</td>
</tr>
</tbody>
</table>

2 Root MSE

<table>
<thead>
<tr>
<th>Block</th>
<th>0.178</th>
<th>0.519</th>
<th>0.139</th>
<th>0.514</th>
<th>0.699</th>
<th>0.921</th>
</tr>
</thead>
<tbody>
<tr>
<td>(S)</td>
<td>0.789</td>
<td>0.900</td>
<td>0.778</td>
<td>0.212</td>
<td>0.156</td>
<td>0.885</td>
</tr>
<tr>
<td>(I)</td>
<td>0.525</td>
<td>0.038</td>
<td>0.327</td>
<td>0.367</td>
<td>0.797</td>
<td>0.040</td>
</tr>
<tr>
<td>(SxI)</td>
<td>0.004</td>
<td>0.404</td>
<td>0.003</td>
<td>0.193</td>
<td>0.202</td>
<td>0.057</td>
</tr>
</tbody>
</table>

P-values for contrasts

| \(S_L\) vs. \(S_S\) in \(I_M\) | 0.023 | 0.020 | 0.170 |
| \(S_L\) vs. \(S_S\) in \(I_N\) | 0.056 | 0.052 | 0.127 |
| \(I_M\) vs. \(I_N\) in \(S_L\) | 0.097 | 0.142 | 0.864 |
| \(I_M\) vs. \(I_N\) in \(S_S\) | 0.056 | 0.006 | 0.013 |

\(^1\) Treatment levels for the Species (\(S\)) variable are denoted by \(L\) (loblolly pine) or \(S\) (slash pine).

\(^2\) Mean square error.
Table 4.6. Mean values (kg ha\(^{-1}\)) and results from analyses of variance for standing weights (mean of five measurement periods) of live (\(W_i\)), dead (\(W_d\)), and total coarse roots (\(W_t\)) from June 1997 through July 1998 in relation to species and initial spacing. Data are for roots >5 mm diameter collected to 30 cm in unthinned stands of loblolly and slash pine planted in 1981 near Franklinton, LA, USA.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>(W_i)</th>
<th>(W_d)</th>
<th>(W_t)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(S_L I_M)</td>
<td>3,327</td>
<td>265</td>
<td>3,592</td>
</tr>
<tr>
<td>(S_L I_N)</td>
<td>2,604</td>
<td>142</td>
<td>2,746</td>
</tr>
<tr>
<td>(S_S I_M)</td>
<td>2,464</td>
<td>135</td>
<td>2,599</td>
</tr>
<tr>
<td>(S_S I_N)</td>
<td>4,451</td>
<td>96</td>
<td>4,547</td>
</tr>
<tr>
<td>Root MSE</td>
<td>2,426</td>
<td>428</td>
<td>2,487</td>
</tr>
</tbody>
</table>

P-values for effect

| Block | 0.134 | 0.541 | 0.144 |
| S | 0.436 | 0.432 | 0.532 |
| I | 0.317 | 0.468 | 0.395 |
| SxI | 0.035 | 0.703 | 0.034 |

P-values for contrasts

| \(S_L\) vs. \(S_S\) in \(I_M\) | 0.334 | 0.279 |
| \(S_L\) vs. \(S_S\) in \(I_N\) | 0.042 | 0.052 |
| \(I_M\) vs. \(I_N\) in \(S_L\) | 0.418 | 0.356 |
| \(I_M\) vs. \(I_N\) in \(S_S\) | 0.029 | 0.036 |

1 Treatment levels for the Species (S) variable are denoted by L (loblolly pine) or S (slash pine).
2 Treatment levels for the Initial spacing (I) variable are denoted by M (medium-spaced, 2.4 x 2.4 m spacing) or N (narrowly spaced, 1.2 x 1.2 m).
3 Mean square error.
Figure 4.6. Loblolly pine fine root (<1mm) production (kg ha\(^{-1}\)) from June 1997 through July 1998 at varying levels of Reineke's stand density index (SDI). Data are from unthinned stands of loblolly pine planted in 1981 near Franklinton, LA, USA.
decreased with increasing stand density in the narrowly spaced stands in Block 2. Root
decay rate was not directly measured in Block 2, and therefore the pattern of fine root
production there may be unrealistic. However, the predicted rate of root decay in
Block 2 was within the range modeled for Blocks 1 and 3 (Figure 4.1) and thus, the
pattern of fine root production in Block 2 is likely correct.

While stand density did not appear to directly affect fine root production, it
may have indirectly affected fine root production through its influence on aboveground
structure and subsequent nutrient demands. Stand density influenced biomass
allocation to the various aboveground components and because each of the
aboveground components varied in N and P concentration, the apparent demand and
uptake of N and P also changed with stand density. According to the functional
balance hypothesis, fine root production should correspond with changes in
aboveground nutrient demands so as to meet the varying demands.

Indeed, there was a positive, linear relationship between fine root production
and both apparent aboveground N demand and N uptake in the loblolly pine stands
(Figure 4.7). This relationship exists even though retranslocation appeared to
substantially lower the range of apparent N demand. There was no significant
relationship between fine root production and apparent P demand or P uptake (P=0.489
and P=0.197, respectively) indicating aboveground production in these stands was
most limited by N. As the aboveground demand for N increased, belowground
production of fine roots apparently increased to meet those demands. So then, the
effect of stand density on fine root production in loblolly pine is apparently indirect:
Figure 4.7. Loblolly pine fine root (<1 mm) production (kg ha\(^{-1}\) to 30 cm) from June 1997 through July 1998 as related to mean apparent aboveground N demand (kg ha\(^{-1}\) yr\(^{-1}\), 1997 and 1998) (a) and N uptake (kg ha\(^{-1}\) to 30 cm) from June 1997 through July 1998 (b). Data are from unthinned stands of loblolly pine planted in 1981 near Franklinton, LA, USA.
stand density influenced aboveground biomass allocation and subsequent demands for N, and fine root production adjusted to meet those varying demands. These results therefore support the functional balance hypothesis.

It is not implied that trees have the ability to purposely signal belowground meristems whenever there is additional growing space available aboveground. Rather, there seems to be a negative feedback loop between fine root and aboveground production where fine root production is limited by photosynthate from the foliage and foliage production in limited by nutrients from the roots. As trees are limited by both light and soil resources, to get one there must be a tradeoff of taking less of another (Tilman 1988).

There was no evidence to support the functional balance hypothesis in slash pine stands (Figure 4.8). Fine root production in slash pine was negatively and linearly related to apparent N demand, opposite of that predicted by the functional balance hypothesis, and was not related to N uptake (P=0.527). Nor was fine root production in slash pine related to either apparent P demand or P uptake (P=0.105 and P=0.334, respectively). There was less confidence in the results for slash pine than loblolly pine. Lack of widely spaced slash pine plots limited the range of apparent N and P demand and uptake to test the functional balance hypothesis. And there were multiple assumptions made regarding slash pine stands including the assumptions that the proportion of first-year to second-year foliage and also root decay rates were equivalent to loblolly pine. However, it is also possible that fine root production is simply not related to nutrient demands in slash pine, but is controlled by other factors.
Figure 4.8. Slash pine fine root (<1mm) production (kg ha\(^{-1}\) to 30 cm) from June 1997 through July 1998 as related to mean apparent aboveground N demand (kg ha\(^{-1}\) yr\(^{-1}\), 1997 and 1998) (a) and N uptake (kg ha\(^{-1}\) to 30 cm) from June 1997 through July 1998 (b). Data are from unthinned stands of slash pine planted in 1981 near Franklinton, LA, USA.
Genotype has been shown elsewhere to affect the functional balance between shoot mass and root mass. For example, two species of *Carex* that characteristically lived in nutrient-poor sites had a higher proportion of photosynthate allocated to belowground production compared to two very similar species that grew in nutrient-rich sites, even when the nutrient level was held constant (Aerts et al. 1992). Similarly, seedlings of loblolly pine from east Texas (low rainfall) produced a greater number of roots than seedlings from other parts of its range (higher rainfall) when put into a common site that was not limited by water (Van Buijtenin et al. 1976).

The results of this study suggest that, at least in loblolly pine, there is potential to increase aboveground yield by reducing the proportion of TNPP allocated to belowground sinks. One method of decreasing belowground allocation is to ameliorate site quality by fertilization and irrigation (Linder and Axelsson 1982, Beets and Whitehead 1996, Albaugh et al. 1998, King et al. 1999). On areas of equal site quality, increased yields may be realized by minimizing nutrient demand and uptake for a given TNPP. As shown, one potential silvicultural method of manipulating nutrient demand and uptake is through the control of stand density.

4.4 Conclusions

Species differences in total N allocation was dependent on initial spacing. Loblolly pine had greater total N in new production than slash pine in medium-spaced stands; however, loblolly pine, but not slash pine, total N was reduced in narrowly spaced stands resulting in no species differences at that initial spacing. Absolute N
retranslocation was also greater in loblolly pine leading to no significant differences between species in apparent N demand. Although loblolly pine had greater foliar P content, slash pine had a greater stemwood P content which led to no species differences in total P in new production. Absolute P retranslocation and apparent P demand also did not vary between species. Both actual N uptake and P uptake was greater in loblolly pine, conflicting with results of apparent N and P demand; the differences may result because the estimation of apparent nutrient demand did not account for the N and P cost of fine root production.

In loblolly pine stands, apparent N and P demand increased with stand density from the widely spaced stands to the medium-spaced stands then decreased with stand density to the narrowly spaced stands; the reduced apparent N and P demand in the narrowly stands may be related to reduced biomass production caused by drought-induced stress. Retranslocation seemed to minimize differences in apparent N and P demand between stand densities. Actual N uptake was positively and linearly related to stand density; P uptake was not related to stand density. Apparent P demand, but not N demand, was significantly related with actual uptake.

Fine root production did not significantly differ between loblolly and slash pine. The proportion of TNPP allocated to fine roots was lower than that reported in other studies and may be related to a sustained drought that potentially forced roots below the maximum sampling depth. Stand density appeared to have indirectly affected fine root dynamics by its effect on aboveground structure. Stand density influenced aboveground biomass allocation and subsequent N demand and uptake.
which was positively and linearly related to fine root production in the loblolly pine stands. Thus, evidence supported the functional balance hypothesis in loblolly pine stands. However, in the slash pine stands, fine root production was negatively related to apparent N demand and unrelated to N uptake; thus there was no evidence to support the functional balance hypothesis in the slash pine stands.
CHAPTER 5
CONCLUSIONS

This study examined aboveground biomass allocation and its subsequent effect on various aspects of nutrient dynamics. Further, the relationship of nutrient demand, as influenced by biomass allocation, and root production was investigated. The study was conducted in stands of loblolly pine and slash pine, two commercially important species in the southeast United States that are commonly limited by N and P. Based on this research, the following conclusions are offered.

Choice of species at stand establishment and the level of current stand density affect rates of N and P mineralization, likely through changes in litter quality and quantity. N mineralization was significantly greater in loblolly pine stands than slash pine, corresponding with greater needle litter N concentration in loblolly pine. Both N and P mineralization increased in the loblolly pine stands with increasing stand density, but this increase does not appear related to needle litter N and P concentration. Instead, increased litter production with increasing stand density apparently led to greater N and P input and subsequent N and P mineralization. Stand volume production was positively correlated with N mineralization, but not P mineralization. The species and density of a stand apparently produces secondary effects on soil productivity through its effects on litter quality and quantity.

Species and stand density affected the distribution of standing aboveground biomass, N, and P. Species differences in total standing N was dependent on initial spacing. At wider initial spacings, where crowns constituted a greater percentage of
total aboveground biomass, loblolly pine accumulated more N than slash pine because of greater N concentrations in loblolly pine crown components and greater biomass production of those components; however, at narrower initial spacings where crown biomass was restricted slash pine had greater standing N. There were no species differences in total standing P at either initial spacings; greater foliage P by loblolly pine was offset by greater stem wood P by slash pine. A large proportion of standing N and P was located in the crown because of the relatively high nutrient concentrations in crown components. Loblolly pine generally had more standing N and P in the crown than slash pine. Current stand density had variable results on standing biomass, N, and P. With increasing stand density, stemwood N and P increased from widely spaced stands to medium-spaced stands then decreased to narrowly spaced stands, branchwood N and P continued to decrease, and foliage N and P continued to increase. Total N and P exhibited a pattern similar to stemwood N and P. In addition, with increasing stand density, the fraction of total standing biomass, N, and P in the crown decreased.

Like standing N, species differences in total annual N allocation was dependent on initial spacing. Loblolly pine had greater total N in new production than slash pine in medium-spaced stands; however, loblolly pine, but not slash pine, total N was reduced in narrowly spaced stands resulting in no species differences in annual N allocation at that initial spacing. Absolute N retranslocation was also greater in loblolly pine leading to no differences between species in apparent N demand. Although loblolly pine had greater foliar P content, slash pine had a greater stemwood

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P content which led to no species differences in total P in new production. Absolute P retranslocation and apparent P demand also did not vary between species. Both actual N uptake and P uptake was greater in loblolly pine, conflicting with results of apparent N and P demand; the differences may result because the estimation of apparent nutrient demand did not account for the N and P cost of fine root production.

Again like standing N, apparent annual N and P demand in loblolly pine stands increased with stand density from the widely spaced stands to the medium-spaced stands then decreased with stand density to the narrowly spaced stands. Retranslocation seemed to minimize differences in apparent N and P demand between stand densities. Actual N uptake was positively and linearly related to stand density; P uptake was not related to stand density.

Fine root production did not significantly vary between loblolly and slash pine. The proportion of TNPP allocated to fine roots was lower than that reported in other studies and may be related to a sustained drought that potentially forced roots below the maximum sampling depth. Stand density appeared to have indirectly affected fine root dynamics by its effect on aboveground structure. Stand density influenced annual aboveground biomass allocation and subsequent N demand and uptake which was positively and linearly related to fine root production in the loblolly pine stands. Thus, evidence supported the functional balance hypothesis in loblolly pine stands.

However, in the slash pine stands, fine root production was negatively related to apparent N demand and unrelated to N uptake; thus there was no evidence to support the functional balance hypothesis in the slash pine stands.
LITERATURE CITED


Christopher Ashley Dicus was born May 28, 1970, in Little Rock, Arkansas, to Terri and Jesse Dicus. He attended high school in Hot Springs, Arkansas. He graduated high school with honors in 1988 and enrolled in forestry at Louisiana Tech University in Ruston, Louisiana. While at Louisiana Tech, he served as president of the Delta Chi fraternity and the Association of Southern Forestry Clubs Conclave. He graduated *Summa Cum Laude* in 1992 with a bachelor of science in Forestry (wildlife option). Dicus entered Utah State University in 1992 and earned a master of science degree in Forestry in 1995 under the direction of Dr. Michael Jenkins. While at Utah State, he served as a Senator in the Utah State University Graduate Student Senate and Graduate Student Representative on the Utah State College of Natural Resources Dean's Council. His thesis was titled "Post-fire Succession and Disturbance Interactions on an Intermountain Subalpine Spruce-fir Forest". Dicus began a doctoral studies program as a Lucius Gilbert Fellow at Louisiana State University in 1995 under the direction of Dr. Thomas J. Dean. At LSU, he served as president of the Xi Sigma Pi Forestry Honor Society. His current research addresses above- and belowground biomass allocation and nutrient dynamics in stands of loblolly and slash pine. He is scheduled to complete his doctoral program in December 2000.

DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Christopher Ashley Dicus

Major Field: Forestry

Title of Dissertation: The Relationship of Biomass Allocation and Nutrient Dynamics in Loblolly and Slash Pine Forests

Date of Examination: 8-1-00

Approved:

[Signatures]

Dean of the Graduate School

EXAMINING COMMITTEE:

[Signatures]

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