EFFECTS OF AS&/E-GROUND BIOMASS ALLOCATION ON SOIL NITROGEN DEMAND AND BELOW-GROUND PRODUCTIVITY: THE INFLUENCE OF STAND DENSITY'

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Abstract-Two stands in a loblolly pine (*Pinus taeda* L.) plantation were established in southeastern Louisiana in 1981 at three initial planting densities (1.2 x 1.2 m, 2.4 x 2.4 m, and 3.6 x 3.6 m). Height, height to the base of the live crown, and DBH measurements taken in consecutive years, coupled with allometric equations, yielded estimates of annual stand level foliage, branchwood, and stemwood biomass increment in each plot. Stemwood, branchwood, first-year foliage, second-year foliage, and litter tissues were obtained in each plot and analyzed for nitrogen concentration, and were used to provide estimates of annual foliar nitrogen retranslocation and above-ground nitrogen demands. Also, estimates of relative fine-root production for two collection periods were obtained in each plot by the coring method. Results indicated that stand density influenced stand-level partitioning to various above-ground component types. As partitioning patterns changed at different levels of stand density, the subsequent demand for nitrogen needed to produce the various components also changed. Changes in above-ground nitrogen demand were subsequently reflected in corresponding changes in fine-root biomass.

INTRODUCTION

Stand density exerts a strong influence on above-ground biomass allocation patterns in conifer stands, primarily through its effects on tree crowns (Dean and Baldwin 1996a). The initial number of seedlings that are planted after a stand replacing harvest have an effect on subsequent crown development and biomass allocation patterns; e.g., stands with greater initial numbers generally have less branchwood biomass as a result of a more limited space for lateral expansion of the branches as the stand ages.

Stand density influences crown development after canopy closure through its influence on foliage amount and distribution. There is a positive relationship in loblolly pine (*Pinus taeda* L.) stands between leaf area index (leaf area per unit ground area, LAI) and stand density (Dean and Baldwin 1996a). Likewise, stand density influences the distribution of the foliage; as stand density increases, the fraction of photosynthetically transmitted radiation through the crown decreases exponentially (Smith 1991), leading to a decline in the rate of photosynthesis per unit leaf mass (Korol and others 1995). With time, branches lowest in the canopy may experience a net carbon loss and self-prune, leading to a stand with a lowered canopy depth and live-crown ratio. Indeed, Dean and Baldwin (1996b) have shown that Reineke's stand density index (SDI) can be predicted solely from foliage density (leaf area per unit crown volume), mean live crown ratio, and canopy depth in loblolly pine stands. The net result is that as stand density increases, trees develop higher, more compact crowns. The compact crowns of high density stands then result in an increased mechanical load placed on the stem that subsequently induces increased stemwood production (Dean and Baldwin 1996a).

The above-ground biomass allocation patterns that result from stand density may affect below-ground production. Each of the above-ground components vary in nitrogen concentration (Switzer and others 1968). As the ratio of above-ground components changes with varying stand densities, the stand-level nitrogen needed to produce these components should then also change. The functional balance hypothesis states that as above-ground demands of a limiting factor (here, nitrogen) increase, below-ground production will increase proportionally to meet that demand (Davidson 1969).

The present study investigated the functional-balance hypothesis as it applies to stands of loblolly pine. Specifically, the two objectives of this preliminary study were to (1) determine if the above-ground stand structures that result from varying stand densities influence soil nitrogen demand, and (2) determine if any changes that occurred in the soil nitrogen demand were reflected in changes in below-ground production.

METHODS

Site

The study site was located on the Lee Memorial Forest in southeast Louisiana. The site annually receives 1620 mm precipitation and has a mean low and high temperatures of 12.5 °C and 25.5 °C, respectively. Soil is a Ruston series tine-loamy, siliceous, thermic typic Paleudult.

Data were blocked into two sites as a result of a slight fertility gradient across the study area. At each site, loblolly pine seedlings were planted in 25 x 25 m plots established after a 1981 clearcut at spacings of 1.22 x 1.22 m, 2.44 x 2.44 m, and 3.66 x 3.66 m for a total of six plots.

Prior to data collection, understory woody vegetation on the plots was eliminated by felling with a chainsaw. Residual stumps were treated with herbicide to minimize sprouting and thereby reduce variability from interspecific competition. Measurements were restricted to an inner 20 x 20 m plot to minimize edge effects.

Above-Ground Biomass Allocation

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. Using these measurements, standing first-year foliage, second-year foliage, stemwood, and branchwood dry weights for each tree for each year were calculated using allometric equations produced by Baldwin (1987) and Baldwin and others (1997). Stand-level stemwood and branchwood increments in each plot during 1997 were estimated by summing the differences in standing biomass for each component on each tree between the end of the 1996 and 1997 growing seasons and expanding to a per-hectare basis. Stand-level foliage increment in each plot during 1997 was estimated by summing first-year foliage for each tree in each respective plot in the 1997 growing season and expanding to a per-hectare basis. Trees that died during the 1997 growing season were assumed to have the same dimensions as at the end of the 1996 growing season, and therefore biomass increment was limited on these trees to first-year foliage.

Above-Ground Nutrient Demand
First-year foliage, second-year foliage, and branchwood samples were obtained in mid-September 1997 by shooting a mid-canopy branch from four trees in each plot with a 12-gauge shotgun, using #4 shot. Branches were selected so as to minimize damage to the residual canopy. Stemwood samples were obtained by coring four trees in each plot at breast height during the first week of December 1997. Senesced foliage samples were obtained during the first week of December 1997 during litter fall; four 1 -square meter litter traps were placed in each plot, and foliage that fell into the litter traps were collected one week later. Each component type was separated and bulked by plot, oven-dried, ground, and mixed. Each mixed sample then had three sub-samples analyzed for nitrogen concentration by the Louisiana State University Plant Analysis Laboratory. The amount of stand-level nitrogen in each component type was estimated by multiplying the standing biomass in each component by its nitrogen concentration and expanding to a per-hectare basis.

Retranslocated nitrogen in the foliage was estimated in each plot as the sum of (1) the amount of standing nitrogen in 1996 first-year foliage minus the amount of standing nitrogen in 1997 second-year foliage, plus (2) the amount of standing nitrogen in 1996 second-year foliage minus the amount of standing nitrogen in 1996 senesced foliage (product of the 1996 second-year foliage mass and the nitrogen concentration of senesced foliage).

Yearly estimates of nitrogen demand from the soil were then calculated as the per-hectare increment of each component type for the 1997 growing season times the nitrogen concentration of its respective component type minus the estimate of 1997 nitrogen retranslocation.

Below-Ground Production
A measure of relative below-ground fine-root production was estimated by sequential coring. Twenty soil cores were obtained in each plot during both July and October 1997 by driving a 5-cm diameter steel tube into the soil to a 30-cm depth. The soil cores were bulked by plot and placed into a device that washed soil through a mesh screen, leaving residual organic material. Pine roots <1 mm were extracted from the organic matter, oven dried, and weighed. Weights from both collection periods were summed by plot and scaled to stand level to provide an index of relative fine-root production.

RESULTS AND DISCUSSION
Nitrogen Demand
Stand density influenced above-ground biomass partitioning (fig. 1). Biomass allocation to the branchwood component decreased with increasing stand density as expected, while foliage and stemwood increment both increased from the low density plots to the mid-density plots, then decreased as stand density increased. Although the stand-level foliage and stemwood increment pattern was the same on both sites, it was not expected. Dean and Baldwin (1996a) found that as SDI increased in loblolly pine stands, LAI increased. Likewise, Dicus and Dean (1998) found a similar pattern on the same sites considered in the present study during 1993-1995, although the lowest values of SDI were not considered then. Long (1985) has argued against a decrease in stand-level stemwood production at the upper levels of stand density. He contended that because stand-level stemwood production was directly correlated with LAI, and LAI continued to increase up to the upper boundaries of stand density, stand-level stemwood increment should then also increase up to the upper boundaries of stand density. However, the present study shows that stand-level stemwood increment indeed appears to be correlated with foliage biomass, but unlike previous studies (Dean and Baldwin 1996a, Dicus and Dean 1998), foliage biomass decreased at the upper levels of stand density.

As expected, the nitrogen concentrations of the tree components varied, with first-year foliage having the highest concentration and stemwood having the lowest concentration (table 1). When N concentrations were combined with the increment for each respective component, total N needed for 1997 production was calculated. Of note, even though foliage increment amounted to less than half that of stemwood increment, about 70 percent of the total N found in new above-ground biomass production was found in the foliage, a result of its high N concentration. Plot values of the demand for N from the soil were calculated after N retranslocation was accounted for (fig. 2).

At both sites, above-ground, stand-level N demand increased from the low- to mid-density plots then decreased in the high-density plots (fig. 2). This pattern appears to likely result from changes in the high-N foliage with stand density. The resulting pattern at both sites indicate that stand density influenced N demand in the stands through its effect on above-ground partitioning to different components, each of which varied in N concentration.

The measure of fine-root biomass also varied with changes in stand density (fig. 1) and followed a pattern similar to N demand (fig. 2). Of most interest, as above-ground N demand increased, fine-root production increased (fig. 3). Nadelhoffer and Raich (1992) found that production of fine-roots was correlated with above-ground production. Here, fine-root production appears to be correlated to the above-ground demand of a limiting nutrient, and therefore gives some support to the functional balance hypothesis. It must be noted, however, that soil P may be more limiting to tree production than N on the study site, and will be analyzed in a future paper.
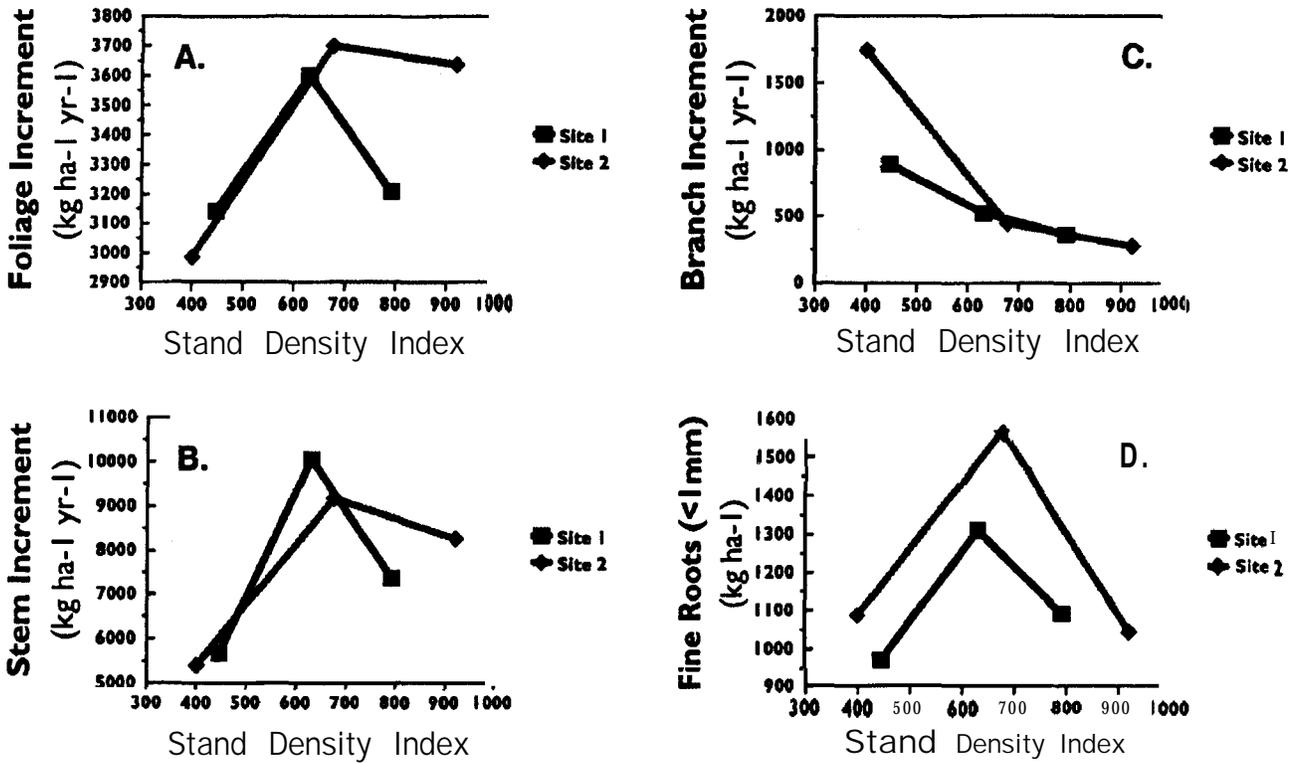
Figure I-Annual stand level biomass increments of loblolly pine (*Pinus taeda* L.) (A) foliage, (B) stemwood, and (C) branchwood as related to Reineke's stand density index. (D) Loblolly pine fine-roots (<1 mm) collected in two sampling periods as related to Reineke's stand density index.

Table I--Mean nitrogen concentrations of various loblolly pine (*Pinus taeda* L.) components in low, mid, and high density plots

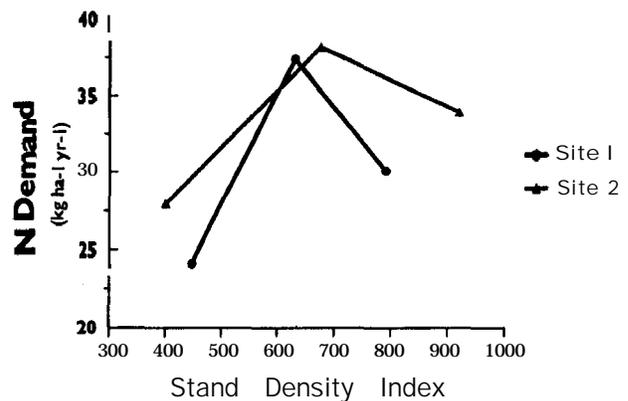|	N concentration		
Component	Low	Mid	High
	Percent		
Foliage (year-I)	1.05	1.18	1.12
Foliage (year-2)	.93	1.02	1.08
Foliage (senesced)	.48	.56	.59
Branchwood	.40	.39	.40
Stemwood	.15	.19	.16

Figure 2—Annual stand level nitrogen demand in a loblolly pine (*Pinus taeda* L.) plantation as related to Reineke's stand density index.

CONCLUSION

Stand density appears to affect below-ground biomass production through changes in above-ground N demand, Stand density influenced biomass partitioning to the above-ground components of foliage, stemwood, and branchwood, each of which varied in N concentration. The changes in above-ground partitioning, coupled with varying N concentrations in those components, resulted in changes in above-ground N demand. Differences in above-ground N demand were somewhat related to differences in below-ground biomass production of fine-roots to meet the above-ground needs. The functional balance hypothesis is supported, but additional analyses are necessary because the present study is preliminary in nature. Fine-root turnover, which may have a significant effect on estimates of fine-root production (Vogt 1991), was not considered; this, however, is addressed in an ongoing study on the Lee Memorial Forest. In addition, another site and species is being investigated there. Also, actual estimates of N and P mineralization and uptake are being investigated.
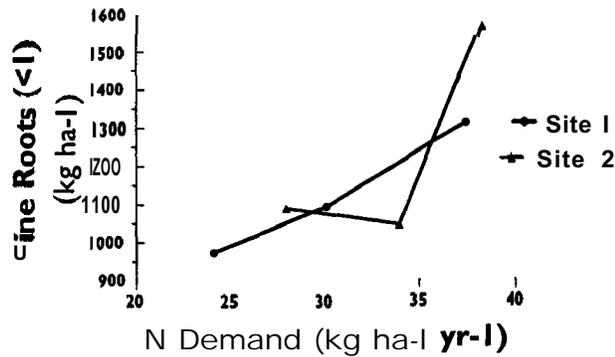
Figure 3—Stand level fine-root biomass as related to annual nitrogen demand in a loblolly pine (*Pinus taeda* L.) plantation.

The analysis of these parameters will provide greater statistical power that may provide more conclusive evidence for the functional balance hypothesis.

ACKNOWLEDGMENTS

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