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STAND DENSITY EFFECTS ON BIOMASS ALLOCATION PATTERNS AND SUBSEQUENT SOIL NITROGEN DEMAND

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Abstract—Growth and yield data from a loblolly pine plantation in southeastern Louisiana were obtained yearly from 1993 to 1996 on numbered trees within two stands initially planted on a 1.22- by 1.22-meter spacing, and two stands planted on a 2.44- by 2.44-meter spacing. Using allometric equations derived from a 1994 on-site destructive harvest, cited nitrogen concentrations of various tree tissues, and accounting for foliar nitrogen retranslocation, stand growth and soil nitrogen demands were determined.

Results showed that production of all aboveground tissues increased as stand density index (SDI) increased. Annual soil nitrogen demand increased with SDI primarily as a result of an increase in nitrogen-rich foliage on the denser sites. Belowground production, as estimated from minirhizotron censuses, also increased as SDI and aboveground nitrogen demands increased. More fine-root production per unit aboveground nitrogen demand was observed on less fertile plots. Stemwood production per unit leaf biomass decreased with increasing SDI, and is assumed to be the result of a greater percentage of total net primary production being partitioned to fine-root production in the denser plots.

The results of this study suggest that the density of forest stands may influence nutrient demands from the soil and subsequent belowground productivity through differential aboveground biomass allocation patterns and tissue nitrogen concentrations.

INTRODUCTION

The underlying mechanisms of plant biomass partitioning are of great importance to the study of forest productivity. As gains are made in understanding the fundamental principles of photosynthate allocation to various tree components, the potential exists to manipulate forest stands to increase the production of merchantable wood despite constant site productivity, thereby increasing economic return for forest landowners.

The ultimate objective for production foresters is to maximize allocation of photosynthate to merchantable stemwood. Strides have been made in improving yield through various silvicultural practices. In many agricultural crops, enhanced yields have resulted primarily from a shift in carbon allocation to harvestable parts, rather than an actual gain in total productivity (Evans 1976).

The mechanisms for aboveground productivity and tissue carbon allocation are becoming more readily understood. Knowledge of belowground productivity patterns, however, lags far behind that of aboveground productivity. If enhancing productivity of merchantable aboveground tree components includes reallocation of available photosynthate from unharvestable belowground sinks, then the study of carbon allocation in the whole forest stand, both above- and belowground, is necessary. The objective of this preliminary study was to determine if there is evidence that different aboveground stand structures resulting from varying stand densities influence soil nutrient demand and subsequent belowground productivity.

CARBON ALLOCATION PATTERNS

Stand density is a factor that has significant influence on stand carbon allocation. Stand density is known to influence tree crown morphology (Dean and Baldwin 1996a), which influences carbon allocation among stems, foliage, and branches (Ford 1982). These relations are complicated because both stand structure and productivity are associated with differences in age and site quality (Assmann 1970). However, Dean and Baldwin (1996b) have shown that stand density index (SDI), a measure of growing stock that includes quadratic mean diameter and trees per hectare (Reineke 1933), may be predicted solely from foliage density, mean live crown ratio, and canopy depth.

There is a positive relationship between stand density and stand foliage production. For a stand of a given stand density, the amount of foliage in a closed canopy stand is a function of the site quality. However, an increase in stand density has been shown to increase leaf area index (LAI) in loblolly stands (Dean and Baldwin 1996a). Stand density has also been shown to positively influence yearly needle fall, a measure of foliage production, in other pine stands (Gholz and others 1985, Gresham 1982).

There is also a positive relationship between stand density and stand stemwood production that is related to changes in canopy structure. Canopy structure is the result of many simultaneous processes including light penetration, height growth, crown lifting, and intercrown abrasion (Dean and Long 1992). After the onset of competition at crown closure, foliage is driven to the top of the canopy as a result of the natural pruning of lower branches (Mar:Mohler 1947). Wind action on the crown of a tree creates a bending stress on the stem, and as the crown midpoint becomes higher, coupled with an increase in the amount of foliage associated with increasing stand density (Dean and Baldwin 1996a), there is an increased load placed on the stem (Dean and Long 1986). Bending of the stem also

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increases the resistance to flow of water in the stem so that more sapwood is needed to transport the same amount of water to the foliage (Dean 1991). Therefore, as stand density and the subsequent physical load on the stem is increased, the carbon sink strength of the stem increases.

The amount of stand branchwood produced, however, is negatively related to stand density. Trees in sparser stands have deeper and wider canopies than do those in denser stands (Dean and Baldwin 1996a) and, therefore, must allocate a greater percentage of total net primary production (TNPP) toward the production and maintenance of branches to support the equilibrium level of foliage. In summary, then, as stand density increases, stand foliage and stemwood biomass production increase, while stand branchwood production decreases.

Another major sink for carbohydrates is production of the fine-root system. Indeed fine root production has been estimated to consume 30-70 percent of TNPP (Santantonio 1989) and has been shown to be inversely related to nutrient and water availability (Gower and others 1992).

On sites of equal nutrition, the belowground proportion of TNPP should correlate with the aboveground demand for nutrients and water according to the functional balance equation (Davidson 1969), which states that as aboveground nutrient demands increase, fine-root production will increase to meet that demand. Nutrient demands will vary during ontogeny (Imsande and Touraine 1994) with the greatest demands being placed on the nutrient reserves of a site during the early stages of stand development when the stand is approaching maximum leaf area (Switzer and others 1968). All else being equal, though, stands with a higher aboveground nutrient demand should allocate more carbon to belowground productivity to meet that demand and maintain a functional balance.

Switzer and others (1968) found that the nitrogen concentration of foliar, branch, and stemwood tissue to be 1.08 percent, 0.23 percent and 0.06 percent nitrogen, respectively, in 18-year-old loblolly pine trees, exhibiting little change with stand age. Foliar nitrogen concentration was 18 times greater than that of stemwood, representing the greatest portion of a stands nutrient requirements, averaging 80 percent for all nutrients (Switzer and Nelson 1972). Because stand density influences the proportion of different aboveground tree tissues in a stand and those tissues vary in nitrogen concentration, stand density should also affect nutrient uptake and subsequent belowground biomass production if a functional balance exists. This preliminary study investigated the above hypothesis to determine if evidence existed to warrant a conclusive study.

METHODS

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 temperature of 12.5 °C and 25.5 °C, respectively. Soil there is a Ruston series fine-loamy, siliceous, thermic typic paleudult.

Four 25x25-m plots were established after a 1981 clearcut and planted with loblolly pine (*Pinus taeda* L.) seedlings, two on a 1.22x1.22-m spacing, and two on a 2.44x2.44-m spacing. Prior to data collection, understory vegetation on the plots was felled and drug off-site. Then plots were treated with the herbicide imazapyr to reduce variability from interspecific competition. To minimize edge effects, measurements were restricted to an inner 20x20-m plot.

Each tree in each plot was numbered and measured for outside bark d.b.h., total height, and height to the base of the live crown before the 1993, 1994, 1995, and 1996 growing seasons. Allometric equations were derived from an onsite destructive harvest in November 1994, when leaf area consisted primarily of foliage produced in the previous growing season, and served to give estimates of biomass for each of the aboveground tissue types and leaf area. Annual stand-level, aboveground production for each tissue type in each plot was calculated as the difference in biomass (as determined from the allometric equations) between two measurement periods. Trees that died between measurement periods were assumed to contribute no growth to stand-level production.

Nitrogen concentrations of each of the aboveground tissue types were taken from values cited by Switzer and others (1968), in which the foliar, branch, and stem nitrogen concentrations were 1.08 percent, 0.23 percent, and 0.06 percent nitrogen, respectively. Foliar retranslocated nitrogen that was assumed to be available for a single growing season was estimated to be 58 percent of the total nitrogen located in foliage that senesced the previous fall (Birk and Vitousek 1986). Stand-level nitrogen demand of the soil for a growing season in each plot was then calculated as the sum of the production of each tissue type for that growing season, multiplied by the nitrogen concentration of each tissue type, and then subtracting the estimate of nitrogen retranslocation.

Belowground root production was estimated by two minirhizotron censuses taken in the summer of 1996. For each of 10, clear PVC tubes placed randomly within each plot, fine roots that intersected one of three transects were counted and summed to give a total number of fine-root intersections per tube.

Since differences in stand age and fertility affect relations between production and leaf area (Gholz and others 1986, Waring and Schlesinger 1985), analysis was limited to plots of identical age and similar site quality (Smith and Long 1989). However, data were blocked into two sites as a result of a fertility gradient across the study area. Both sites 1 and 2 included a 1.22x1.22-m spacing plot and a 2.44x2.44-m spacing plot, but unpublished data show site 1 to have a greater nitrogen availability.

RESULTS AND DISCUSSION

Results, using a 3 year mean of the 1993, 1994, and 1995 growing seasons, showed that as SDI increased, total aboveground production increased (fig. 1). As predicted, on both sites, as SDI increased, foliage and stemwood

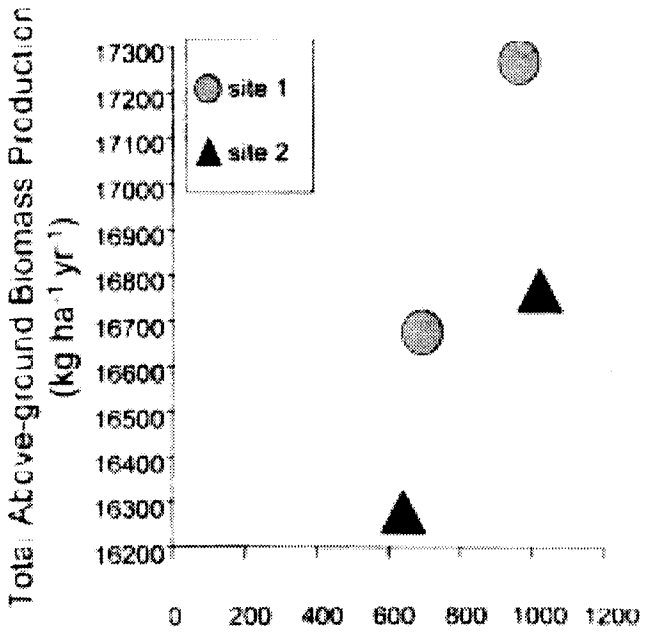

Figure 1—Total stand level aboveground biomass production as a function of stand density index.

production increased while branchwood production decreased. It was also found that the more fertile site 1 plots produced more aboveground biomass in all tissue types than the less-fertile site 2 plots.

As SDI increased, soil nitrogen demands also increased (fig. 2), primarily as a result of increased production of nitrogen-rich foliage on the denser plots. Indeed, over 85 percent of the total annual nitrogen demand in each plot was attributed to foliage. Again, the more fertile site 1 plots had a greater aboveground nitrogen demand.

Belowground fine-root intersections increased as SDI and aboveground nitrogen demands increased (fig. 3), giving support for a functional balance. Also, a greater number of root intersections per unit of nitrogen demand were recorded on the less-fertile site 2, suggesting that on these plots, a greater percentage of TNPP was allocated to fine-root production to meet aboveground demands.

Although total annual stemwood production and stemwood production per unit of leaf area increased with increasing SDI, as has been shown in previous studies (Long and Smith 1990, Smith and Long 1989), stemwood production per unit leaf biomass decreased with increasing SDI (fig. 4). This is assumed to be the result of a greater percentage of TNPP being partitioned to fine-root production in the denser stands. Santantonio (1989) has shown that a strong, negative relationship exists between fine-root and stemwood production in closed canopy stands. Although there is a greater amount of foliage biomass produced in the denser plots, it appears that foliage there is less efficient at producing photosynthate, perhaps as a result of an increase in self-shading caused by increased foliar density, a characteristic of denser stands (Dean and Baldwin 1996a).

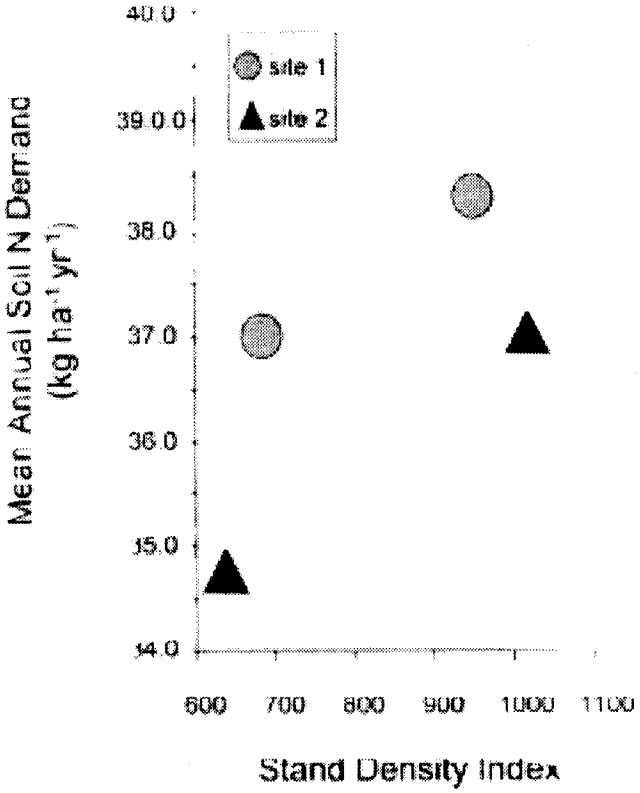

Figure 2—Stand level aboveground nitrogen demands as a function of stand density index.

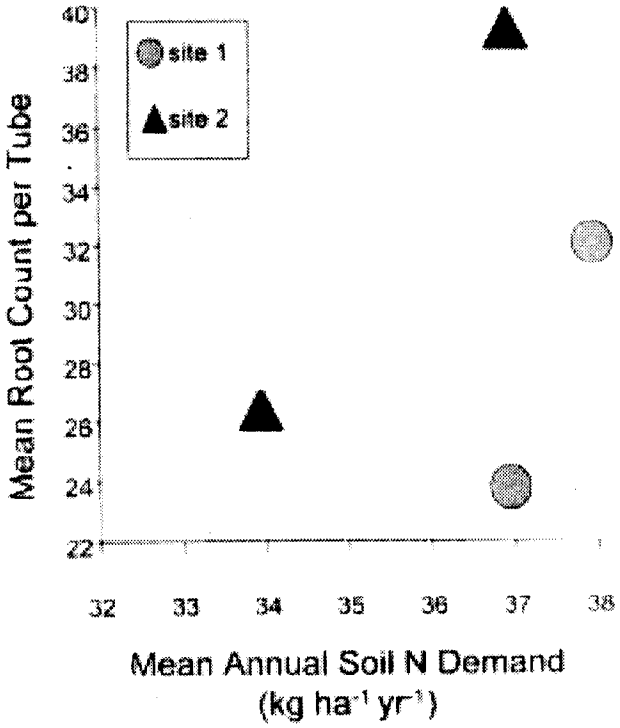

Figure 3—Mean number of root intersections counted as a function of aboveground nitrogen demand.

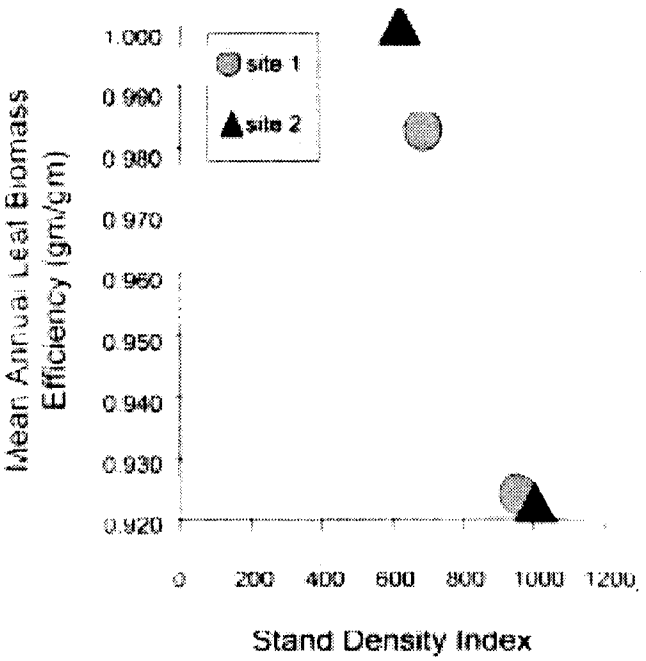

Figure 4—Mean stemwood produced per unit of leaf biomass as a function of stand density index.

One means of reallocating carbon from unharvestable belowground sinks to harvestable aboveground stemwood, then, may be by increasing foliar efficiency through various silvicultural means. For example, foliage does not contribute to stemwood production until maintenance respiration requirements of supporting branches are met (Ford 1975). Foliage in the shaded lower crown, then, would contribute little to production as a result of lowered photosynthetic rates and increased branch maintenance, yet would retain a carbon cost associated with production of fine-root biomass to meet foliar nutrient requirements. By pruning lower branches, a forester may lose little in production, but gain significant amounts of carbon that would have been allocated to fine-root production that supported the low efficiency foliage, thereby gaining in net carbon that could be used for stemwood production.

CONCLUSIONS

Results showed that as stand density increases, changes in aboveground carbon allocation increases both nitrogen demand and belowground productivity to meet that demand. Also, more belowground production is needed on less fertile sites to meet similar demands, decreasing photosynthate that could potentially be used in aboveground production. Therefore, more photosynthate may be available to aboveground sinks as sites become more fertile (through fertilization) or as foliage become more efficient.

The lack of plots in this preliminary study limited statistical analysis, but did provide insightful data. Therefore, a more conclusive study is in progress that will have greater statistical power and include analysis with additional stand densities and species.

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