FAMILY DIFFERENCES IN ABOVEGROUND BIOMASS ALLOCATION IN LOBLOLLY PINE

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Abstract — The proportion of tree growth allocated to stemwood is an important economic component of growth efficiency. Differences in growth efficiency between species, or between families within species, may therefore be related to how growth is proportionally allocated between the stem and other aboveground biomass components. This study examines genetically related differences in aboveground biomass allocation in loblolly pine. I destructively sampled 58 trees from seven families selected to represent differences in growth rate (fast vs. slow) and crown size(large vs. small). The 15-year-old trees were all planted on the same site at the same spacing. Relative allocation to stem, foliage, and branch wood, and the ratio of foliage biomass to total crown biomass, were examined as a function of the logarithm of DBH. Large-crowned trees, compared to small-crowned trees of similar DBH, differed significantly in percent of total aboveground biomass allocated to the stem and to branch wood. Small-crowned families generally allocated proportionally less biomass to branch wood and more to the stem across the range of tree sizes examined. Relative allocation to foliage biomass did not differ, although lower allocation to branch biomass in small-crowned trees resulted in a significantly greater ratio of foliage to total crown biomass. Comparing trees from fast- and slow-growing families, only relative allocation to foliage differed significantly, although a strong interaction between DBH and growth characteristic made interpretation of the relationship difficult. These results suggest that families do differ in relative aboveground allocation, but these differences may not be related to family differences in stemwood productivity.

INTRODUCTION

A primary emphasis in silviculture is the management and control of tree growth. Total tree growth is a function of how much foliage is contained in the crown, the average photosynthetic rate of that foliage, and the efficiency in which the tree converts fixed carbohydrates into biomass. Of commercial importance is how much of that biomass, or growth, is converted to stemwood. Thus, how biomass is allocated within the tree plays an important role in forest productivity. Being able to manipulate growth allocation is one way that forest production can be improved. Allocation patterns in trees have been shown to vary with tree age, nutrient or water availability, and with stand density under which the tree develops.

Genetics also influence the proportion of growth allocated to useable portion of the plant, or harvest index (Dickmann 1985). Several analyses have suggested that genotypes promoting narrow, sparsely branched crowns lend themselves to greater growth efficiency (stem growth per unit leaf area)(Kärki and Tigerstedt 1985, Kuuluvainen 1988). However, studies specifically examining genetic differences in allocation patterns in trees, including examinations of southern pines, have had mixed results.

Seedling studies have often suggested genetic differences in allocation patterns. Li and others (1991), working with 1st-year seedlings of 23 loblolly pine families, found family differences in relative biomass allocation between root and shoot and between needles and stem. Bongarten and Teskey (1987) compared growth partitioning among 1-yr-old loblolly pine seedlings from seven seedlots of diverse geographic origin and found seedlot differences in relative allocation between root, stem, and foliage. However, these differences were not strongly related to differences in productivity. It is also not clear whether allocation differences observed in seedlings will be maintained in older stands.

Studies on older trees have been more equivocal, not always showing clear differences in allocation patterns. Pope (1979) examined 11-yr-old trees from four loblolly pine families, all selected for fast growth. The families differed in total production, but not in relative allocation patterns. Conversely, Matthews and others (1975) found family differences in the proportional distribution of woody biomass to the stems in 8-yr-old Virginia pine. Cannell and others (1983) reported that clones displaying sparse branching of both Sitka spruce and lodgepole pine were more efficient stemwood producers.

Commercial agriculture has exploited genetic differences in growth allocation to greatly increase crop yields. Forestry, however, while making some gains, has yet to take full advantage of these opportunities; and in fact has yet to establish a conclusive correlation between genetic differences in growth allocation and productivity. My objectives in this study were to determine if genetic differences in aboveground carbon partitioning could be observed in 15-year-old loblolly pine. If genetic differences were observed, I wanted to determine if these differences were related to family differences in productivity.

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Table 1—Genetic characteristics and size distribution of 58 destructively sampled 15-year-old loblolly pine

Type				D. B. H.(cm)		Height (m)	
Family	n	Growth	Crown	Mean	Range	Mean	Range
NC1	8	Fast	Small	18.7	14.7-22.1	17.5	16.0-18.8
NC8	8	Fast	Small	19.8	15.8-23.5	17.2	15.4-18.5
NC4	9	Fast	Large	18.8	12.6-24.3	16.7	14.0-18.0
NC3	8	Slow	Small	19.2	12.4-23.3	16.4	13.8-18.0
NC6	8	Slow	Small	17.2	14.5-19.4	16.7	16.0-18.0
NC2	9	Slow	Large	20.1	15.8-25.3	16.2	14.4-17.5
NC5	8	Slow	Large	18.1	11.6-22.5	16.6	13.8-18.0
ALL	58			18.9	11.6-25.3	16.7	13.8-18.8

METHODS

This study was conducted on Mississippi State University's John Starr Memorial Forest located in Winston County, MS (33°16'N, 88°52W). The soils on this interior flatwood site are a Glossic Fragiudult (Prentiss loam) with a fragipan at a depth of approximately 0.5 to 0.8 m. Average annual temperature is ca. 17.2°, and average annual precipitation is ca. 1375 mm. Site index at base age 25 for loblolly pine is approximately 23 m.

Fifty-eight 15-year-old loblolly pine trees were destructively sampled in August 1999. The trees were open-pollinated progenies of seven North Carolina families selected from an industrial tree improvement program. Families were selected to represent combinations of fast vs. slow growth rate, and large vs. small crowns. The trees were all from a single block that had been planted in family rows on a 1.5m x 3.0m spacing. Trees ranged in size from 11.6 cm to 25.3 cm DBH (table 1). An eighth family and an unimproved check were excluded from this analysis because they were planted as border rows. A more complete description of the families is provided by Land and others (1991).

Height and DBH of each tree was measured before felling. After felling, each tree was separated into aboveground biomass components – stem (including bark), branches, and foliage with subtending twigs. Each component was weighed fresh in the field, and a subsample was weighed fresh and retained for further analysis. In the laboratory, subsamples were dried at 80°C to a constant weight and weighed to determine a fresh weight:dry weight ratio. Foliage was removed from twigs to determine a foliage weight:wood weight ratio. Using these ratios, a total dry weight for stemwood, branchwood, and foliage was determined for each tree.

Analysis to determine genetic differences in relative aboveground biomass allocation was based on the relationship between percent allocation to each biomass component and stem DBH. This accounted for the changes in biomass allocation that occur as trees get larger. Log-transformed values of DBH were used to account for the nonlinear nature of the relationships. Standard analysis of covariance procedures were employed to test for genetic differences, using the GLM procedure in SAS. Significance was accepted at a P-value ≤ 0.10.

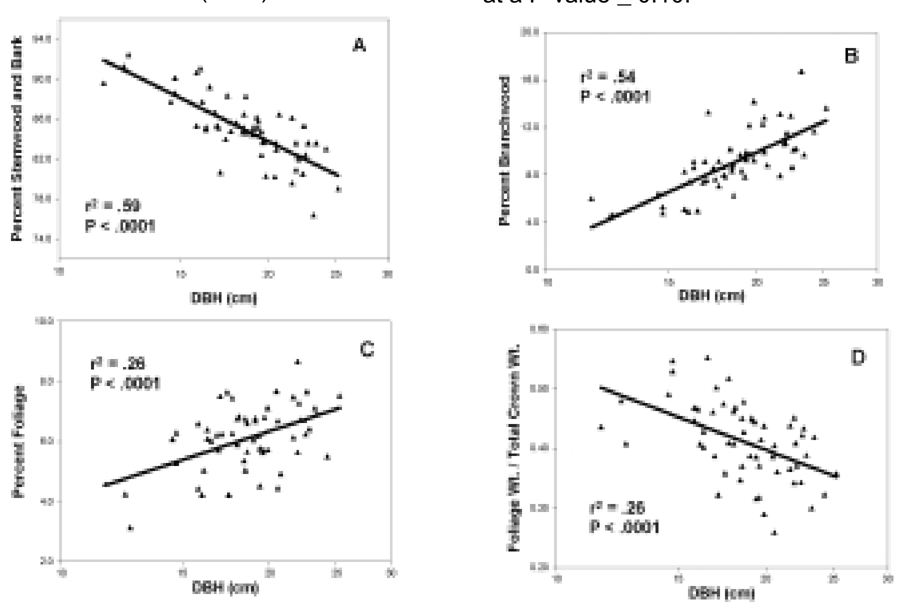

Figure 1 –- Log-linear relationships between stem DBH and percent of aboveground biomass allocated to (A) Stemwood and Bark, (B) Branchwood, and (C) Foliage. (D) shows the relationship between DBH and the ratio of foliage weight to total crown weight

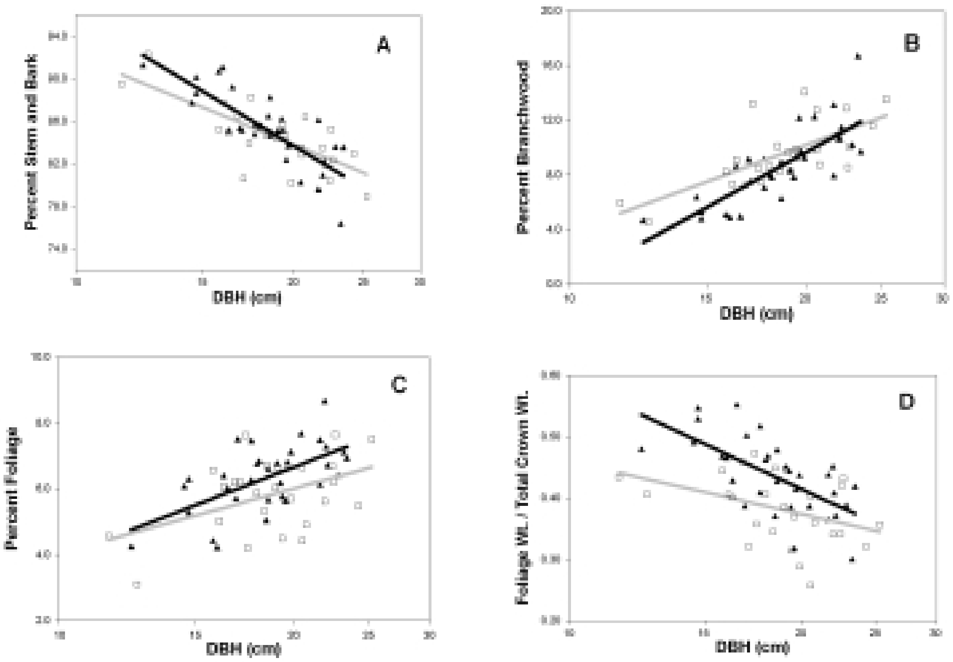

Figure 2 — Comparison of relative biomass allocation patterns between trees from small-crowned families (black triangles, black line) and trees from large-crowned families (gray squares, gray line). Differences in allocation to Stem (A) and Branchwood (B) are statistically significant. Differences in allocation to Foliage (C) are not significant. Differences in Foliage Ratio (D) are statistically significant.

RESULTS

The relationships between relative allocation to each of the biomass components and the logarithm of DBH across all 58 trees were all highly significant. Relative allocation to stemwood decreased as trees got larger (figure 1A), while allocation to both branches and foliage (figure 1B & 1C) increased with tree size. In addition, the ratio of foliage weight to total crown weight decreased as trees got larger (figure 1D). This foliage ratio has been used to help explain the decrease in leaf area efficiency (stem growth / LA) that has often been observed as mean crown size (leaf area per tree) increases (Roberts and Long 1992).

Reduced allocation to the stem and increased allocation to the crown as trees get larger is a common observation that illustrates the influence of normal developmental processes. Considerable variation exists in these relationships, however. Some of this variation might be explained by family differences in allocation patterns. However, when family was

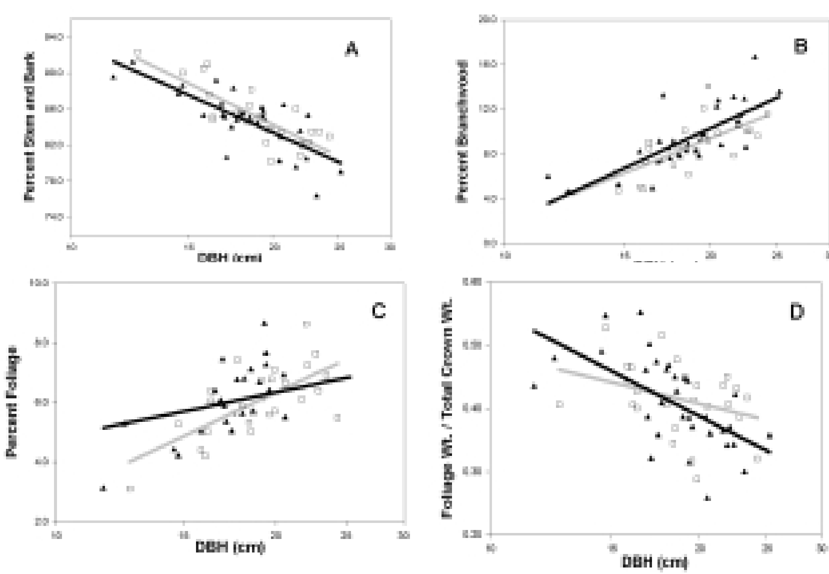

Figure 3 — Comparison of relative biomass allocation patterns between trees from fast growing families (gray squares, gray line) and trees from slow growing families (black triangles, black line). Differences in allocation to Stem (A) and Branchwood (B) are not statistically significant. Differences in allocation to Foliage (C) are statistically significant. Differences in Foliage Ratio (D) are not statistically significant.

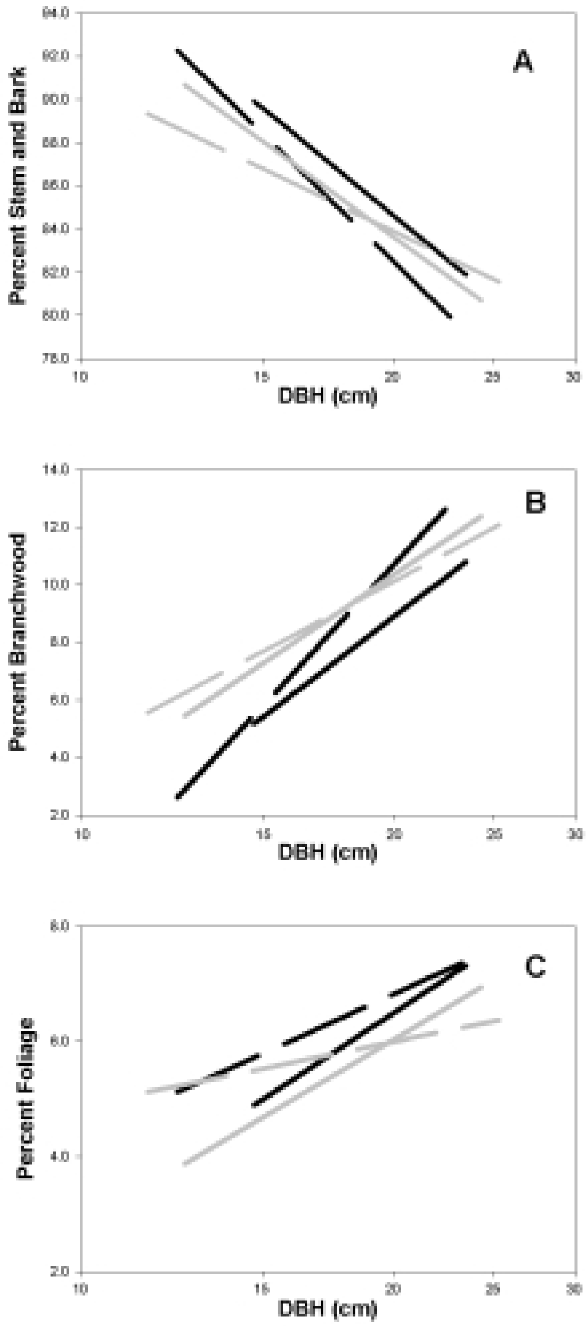

Figure 4 — Comparison of relative biomass allocation patterns between tree “types” representing combinations of crown size and growth rate. Solid black line = fast growing, small crown. Solid gray line = fast growing, large crown. Dashed black line = slow growing, small crown. Dashed gray line = slow growing, large crown. Type is statistically significant in explaining percent allocation to Stem (A). Differences in allocation to Branchwood (B) and to Foliage (C) are not statistically significant.

included as a covariate in the analysis, it was not significant suggesting that the variability in these relationships could not be explained by individual families.

The trees were separated into two groups of families that had been selected for differences in crown size, and the allocation relationships between these two groups were compared. Relative allocation to the stem differed significantly between the two groups. The slope adjusted mean percent allocation to stemwood was greater for small crowned families than for large crowned families (P = .08)(figure 2A), although there was a significant interaction (P = .08) between growth rate and log DBH.

Relative allocation to branchwood also differed significantly between the two groups. As might be expected, allocation to branches was greater for large crowned families than for small crowned families(P = .08)(figure 2B). The interaction term was again significant (P = .10), although when plotted on non-transformed axes, the curves appear to be coming together at higher DBH. This might indicate that the differences in allocation to branches are becoming less as the trees get larger.

Relative allocation to foliage was not significantly different between large and small crowned families (P = .53); although mean allocation to foliage was slightly higher for small crowned families (figure 2C). Due to differences in relative allocation to branches, foliage ratio did differ significantly between the two groups (P = .07). Families selected for small crowns had a higher ratio of foliage to total crown weight (figure 2D). Again, this could be an indication of greater leaf area efficiency for small crowned families.

The trees were next separated into two groups of families based on differences in inherent growth rate, and the allocation patterns of families selected for fast growth rate were compared to those selected for relatively slower growth rates. Relative allocation to the stem was not significantly different between the two groups (P = .62), although on average, fast growing families allocated slightly more to stem (figure 3A). Relative allocation to branches was also not significant (P = .66), but again, on average, fast growing families put slightly less into branches (figure 3B). There was a significant difference in the slope adjusted mean for relative allocation to foliage (P = .06), although, somewhat counter intuitively, slow growing families appear to allocate slightly more to foliage (fiigure 3C). However, a significant interaction between the growth term and *log* DBH (P = .06) made this difficult to interpret. Foliage ratio was not significantly different between the groups of fast growing versus slow growing families (figure 3D).

The families were lastly grouped based on combinations of crown size (large vs. small) and growth rate (fast vs. slow), and allocation patterns were compared between the four genetic “types.” Type was statistically significant in explaining variation in relative allocation to stem (P = .09), however, the significant interaction (P = .09) makes it difficult to separate the various types in any meaningful way. It is interesting to note, however, that the fast growing/small crowned families generally allocated proportionally more biomass to the stem than the other types (figure 4A) across the range of trees examined.

Genetic type had a P-value of .11 in explaining relative branch allocation, with a P-value of .12 for the interaction between type and dbh. Again, the fast growing/small crowned families separated themselves somewhat from the other types, allocating relatively less biomass to branchwood (figure 4B). Type was not significant in explaining allocation to foliage (P = .30), although relative allocation to foliage was again slightly lower for fast/large compared to fast/small (figure 4C).

DISCUSSION

This study is somewhat unique in that the genetic selections included not just families that differed in growth rate, but also families that presumably had inherent differences in allocation patterns, i.e., large vs. small crowns. As expected, there were differences in patterns of biomass partitioning related to selected differences in crown size. For a given tree dbh, families selected for small crowns allocated slightly more to the stem and slightly less to branches. Also, while not statistically significant, small crown families on average allocated slightly more to foliage. Small crowned families also tended to have significantly higher foliage ratios, which could be an indirect indicator of greater leaf area efficiency for small crowned trees. Comparisons among families selected for differences in growth rate showed only relative allocation to foliage differed significantly; and even then, the strong interaction makes interpretation difficult.

This study was limited in the range of tree sizes sampled; although to a certain extent that was a positive in this study. All of the trees developed on the same site, at the same spacing, and under essentially the same competitive environment, thus minimizing some of the developmentally influenced differences in growth allocation.

The results from this study provide support that there are genetic differences in aboveground allocation patterns in loblolly pine. This showed up primarily as differences in allocation between the stem and branches. The data do not statistically support the contention that faster growing families preferentially allocate more of their aboveground growth to the stem and less to the crown. However, while not statistically significant, mean values do suggest the possibility of greater relative allocation to stem in fast growing trees.

The results of this analysis agree with the conclusion of Bongarten and Teskey (1987) that genetic differences in dry matter partitioning do exist in loblolly pine, but that these differences are likely only partially responsible for observed differences in productivity. Other physiological and structural differences between families are sure to have major influences on growth and growth efficiency.

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