COMPARISON OF GROWTH EFFICIENCY OF MATURE LONGLEAF AND SLASH PINE TREES

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Abstract—Variation in aboveground biomass partitioning (between the stem, branches, and foliage) of mature trees is a key determinant of growth potential. Investment of photosynthate in crown components generally results in greater overall biomass production of longer duration. The increased production of crown components may be an investment in longterm aboveground production and can result in increased growth efficiency (defined as biomass increment per unit leaf area). This study was initiated to compare the relationships of crown structure to aboveground allocation and stemwood growth for mature planted slash pine (*Pinus elliottii* Engelm.) and naturally regenerated longleaf pine (*P. palustris* Mill.) trees. Total tree height, diameter at breast height, height to base of the live crown, and bark thickness were measured and increment cores taken from longleaf and slash pine trees of similar ages growing on similar sites. These data were used with allometric equations, developed previously for each species from destructive sampling procedures at these sites, to predict projected leaf area and 5-year stem biomass production. Growth efficiency for trees was calculated as 5-year stemwood biomass increment per unit projected leaf area. Average (per tree) stem biomass production was not statistically different between longleaf pine and slash pine, nor were average projected leaf areas. Average growth efficiency of longleaf pine was significantly greater than that of slash pine ($P < 0.10$); graphical examination of individual tree data, however, did not indicate strong or significant differences in growth efficiency between species when comparing trees of equal size. These findings suggest that greater investment in crown structural components by longleaf pine may, at the stand-level, help to maintain stemwood production over a longer lifespan relative to slash pine, but individual tree results are less clear.

INTRODUCTION

Crown structure, characterized by the size (biomass or surface area) and distribution of individual crown elements (i.e., branches, shoots, and foliage), is a key variable in forest ecological studies. Crown structure is functionally related to tree growth through its inherent relation to radiation interception and gas exchange (Jarvis and Leverenz 1983, Stenberg and others 1994, Teskey and others 1994). It also strongly affects sub-canopy plant diversity by modifying light quantity and quality, thereby affecting understory species composition (Kimmins 1997).

Biomass and surface area equations have been used to determine dry weight allocation patterns, which in turn have been related to productivity. Research has shown that dry matter allocation to foliage, branches, and stemwood is variable and affected by several factors including tree age, species, and climatic conditions (Gholz and Cropper 1991, Gower and others 1994, Teskey and others 1994). Many, and perhaps most, of these studies, however, have investigated the effects of these factors on dry weight partitioning in young trees, with far fewer studies looking at allocation patterns in mature trees. For example, little is known about how mature trees allocate carbon or how the relationship between crown structure and stemwood growth varies with age for different tree species.

One species comparison of interest is that between longleaf pine (*Pinus palustris* Mill.) and slash pine (*P. elliottii* Engelm.) because of the large overlap in their habitat distributions and because they are often found growing on the same sites. It is generally accepted that slash pine grows more quickly (and probably with greater efficiency) at young ages, but longleaf pine produces more cumulative growth at older ages and over longer time periods (Boyer 1990, Lohrey and Kossuth 1990); i.e., growth rates decline in slash pine at ages greater than 25-30 years whereas longleaf pine growth rates are maintained or may increase for many more years. This presumption has not been rigorously tested for older trees, however, largely due to the lack of older slash pine stands and few comparable stands of longleaf and slash pine growing on similar soils. An additional factor is that slash pine is shorter-lived, generally not exceeding 100-200 years in age (Hebb and Clewell 1976), whereas longleaf pine can live to be as old as 500 years (Landers and others 1995). Thus, the same chronological ages may represent different physiological ages for the two species.

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Table 1—Average stand structural characteristics for the sampled longleaf and slash pine stands

	Longleaf pine	Slash pine
Density (trees/ha)	135	107
DBH (cm)	37.4	41.7
Height (m)	24.1	27.2
Basal area (m^2/ha)	13.3	14.8

In an earlier, unpublished biomass comparison study of longleaf pine and slash pine, we developed allometric equations for predicting stem biomass production and projected leaf area for both species at these sites. That study indicated that mature (60-75 year old) planted slash pine and naturally regenerated longleaf pine exhibited strong differences in aboveground allocation between foliage, branches, and stemwood. The objective of this study was to use the allometric equations developed in the previous study in conjunction with recent growth measurements to examine how patterns of allocation affect growth efficiency in mature longleaf pine and slash pine stands growing on similar sites.

METHODS

Site Descriptions

This study was conducted at the Joseph W. Jones Ecological Research Center located in Baker County, Georgia (31° 13'N, 84° 29'W). Two specific sites were sampled: a 52 hectare stand dominated by naturally regenerated longleaf pine (average age of 73 years), and a 77 hectare slash pine stand planted in 1938. Both sites are located on well-drained upland and fluvial terraces, and the soils are Typic and Arenic Hapludults, with loamy sands over sandy loams to sandy clay loams. The soil moisture regime is similar at the two sites. The slash pine stand was thinned periodically and is relatively open, although a small component of younger, naturally occurring slash pine and *Quercus* species occupies the under- and mid-stories. The longleaf pine stand has also had some harvest entries, though less frequently than the slash pine, and contains multiple age classes of longleaf pine. The understory of the longleaf pine stand is dominated by grasses with some hardwoods maintained in a shrubby state through the use of frequent prescribed fire. Stand structural characteristics are summarized in table 1.

Biomass Sampling

Longleaf pine biomass was sampled in 1996 through the destructive sampling of 23 trees representing the range of tree diameters in the stand. Common biomass sampling techniques were employed, including the measurement of stem diameter and collection of disks at fixed points along the stem, measurement of all branch diameters and lengths, measurement of total green weight of the stem, branches and foliage in the field, and the collection of subsamples from each component to determine fresh weight:dry weight ratios. In addition, projected leaf area per unit dry weight of foliage was determined in the laboratory. Sixteen slash pine trees were sampled in 1998 using comparable field and laboratory methodologies. These data were used to develop allometric prediction equations for each species to predict individual tree stem, branch and foliage biomass and projected leaf area from easily measured parameters.

Growth Measurements and Calculations

Six 0.5 hectare plots were established for sampling biomass increment and growth efficiency, with 3 plots in each stand type (longleaf and slash pine). At each plot all trees greater than 15 centimeter dbh were sampled for a total of approximately 50-65 trees per plot. Total tree height, diameter at breast height, height to the base of the live crown, and bark thickness were measured. In addition, two increment cores were extracted at right angles from every tree and measured for 5-year radial increment.

Using these data and the previously developed allometric equations, aboveground biomass allocation and projected leaf area were predicted for each tree, and a 5-year stem biomass increment calculated using the radial increment measurements. Growth efficiency was calculated for each tree as the 5-year stem biomass increment divided by the projected leaf area.

Statistical Analyses

T-tests were conducted to determine if differences in stem biomass production, projected leaf area and overall growth efficiency existed between species, with statistical significance set at a = 0.10. Also, linear regressions were developed for the transformed individual tree data and the slopes of the relationships compared for the two species.

RESULTS

The average aboveground biomass allocation, as predicted from the allometric equations, differed considerably between species as shown in figure 1. Longleaf pine had more than double the percentage allocation to crown components in comparison to slash pine, and this same doubling effect also held true for the individual crown components (branches and foliage). In other words, for equal size trees, slash pine allocated significantly more biomass increment to the stem than did longleaf pine.

Table 2—Comparison of average per tree values calculated for projected leaf area, stem biomass increment and stem growth efficiency for longleaf and slash pine. Statistical comparisons were conducted using T-tests

	Longleaf Pine	Slash Pine	P>T
Projected leaf area (m^2)	100.5	93.2	0.14
Stem biomass increment(kg)	53.4	52.7	0.78
Growth efficiency (kg/m^2)	0.64	0.58	0.07

When comparing average tree-level values (table 2) we found that projected leaf area and 5-year stem biomass increment did not differ statistically between species. Average growth efficiency was significantly greater for longleaf pine (table 2), indicating that, on average, longleaf pine produced more stem biomass per unit of projected leaf area than slash pine. Yet when the individual tree data for stem increment and growth efficiency were plotted versus projected leaf area (figure 2), no clear species differences were apparent. Linear regressions of log-transformed data for growth efficiency as a function of projected leaf area produced significantly different slopes (results not shown). Given the relationship shown in figure 2, however, we did not think this result was biologically significant but instead was likely only the result of examining dissimilar ranges of data for the two species. Figure 3 indicates that the species do segregate based upon stand-influenced structural characteristics, as indicated by the index of modified crown ratio (defined as live crown length divided by (height - 1.3 meters)).

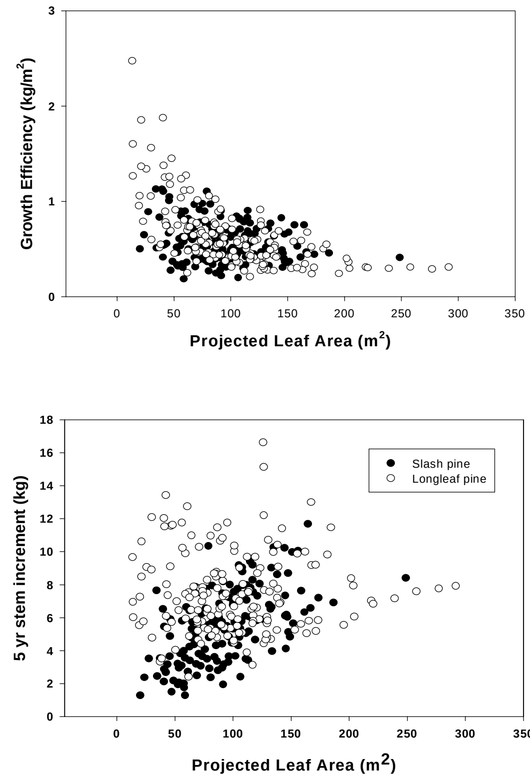

Figure 2—Relationship between 5-year stem biomass increment (top) and stem growth efficiency (bottom) and projected leaf area for all sampled trees.

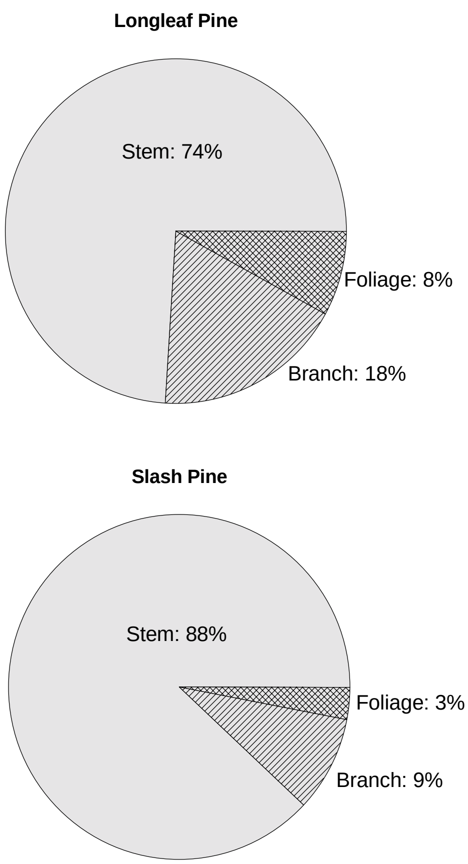

Figure 1—Average aboveground biomass distribution (by percent) for longleaf pine (top) and slash pine (bottom).

DISCUSSION

Studies of resource allocation in other species suggest that stemwood accumulation relative to branches and foliage increases with age, stand density and site quality (Binkley 1983, Espinosa Bancalari and Perry 1987, Fogel and Hunt 1983, Keyes and Grier 1981, Turner and Long 1975). Younger or more open stands, or stands growing on poor sites, tend to have a relatively higher proportion of biomass in foliage and branches (e.g., Binkley 1983), whereas older or denser stands invest relatively less in crowns (e.g., Espinosa Bancalari and Perry 1987 for density).

It is clear from figure 1 that the two species, though of similar age and growing on comparable sites, allocate aboveground growth quite differently. This result was not surprising given the known differences in growth patterns and the visually distinct crown forms of the two species. What was surprising, however, is that these different patterns of allocation did not lead to significant differences in per tree projected leaf area or stem biomass increment for the 5-year period measured.

The lack of clear differences in stem increment between species was contrary to the results we expected given the ages of the trees in this study. Plantation grown 60-year-old slash pine are likely at a more advanced physiological age

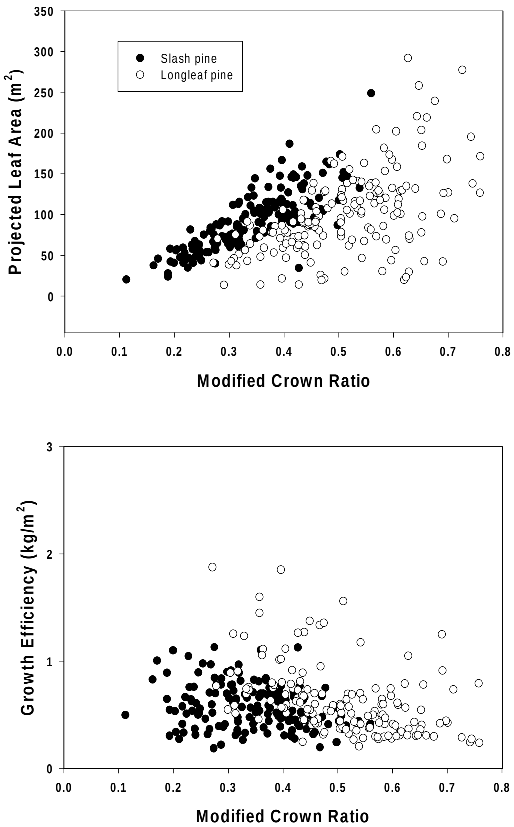

Figure 3—Influence of stand and tree structure, as indicated by a modified crown ratio (live crown length divided by (total tree height - 1.3)), on per tree projected leaf area (top) and stem growth efficiency (bottom).

than 73-year-old (on average) longleaf pine in a natural stand. We therefore expected that production in slash pine would have declined and the longleaf pine would, on average, have higher production. Past stand management must be taken into account, however. The slash pine stand was thinned for a research study subsequent to the biomass sampling but prior to the plot sampling for growth predictions. Thus, the slash pine results presented here are from the residual trees (not marked for removal) and represent the best growing individuals in the stand, as was documented in a companion study from the same area (McConville and others 1999). In this instance, then, we actually compared the "best" slash pine trees with randomly selected trees from the longleaf pine stand (i.e., not those selected for good growth). This fact could have an effect on the results presented.

The results for growth efficiency were also not quite as we expected a priori. Growth efficiency was higher on average for longleaf pine (table 2). But, upon examining results for individual trees (figure 2), any differences in the average values appear to be due to disparities in the range of data included in the sample rather than to true biological differences between the species. The form of the relationship between growth efficiency and leaf area found in figure 2 is typical of those found for other shade intolerant species where light is not a limiting factor (Roberts and others 1993). The negative exponential form of the relationship can be attributed to variation in structural characteristics of the canopy (Roberts and others 1993); figs. 1 and 3 indicate that there are some differences in canopy structure for the two species, and these differences may in part explain the observed small differences in growth efficiency between slash and longleaf pine.

The discussion so far has focused on results for individual trees. When comparing stem growth at the stand-level, however, the relatively small differences measured for individual trees may become more significant. That is, the longleaf pine stand had higher tree densities (table 1); thus, if these trees had the same or slightly higher average stem increment or growth efficiency, then the total, stand-level production of longleaf pine will be greater than for slash pine. It is important not to push this line of reasoning too far, however, because the results represent only a single case study.

CONCLUSIONS

Despite expectations, in this study the stem biomass increment and projected leaf area of mature longleaf and slash pine did not differ significantly even though there are clear differences in the allocation of aboveground biomass. Also, the statistical differences in average growth efficiency were not apparent when data from all individual trees were examined. The lack of clear differentiation between species is probably attributable to past stand history and management, but this factor should be investigated more closely through additional studies.

In short, individual trees of the two species with similar chronological ages and grown on comparable sites do not appear to produce greatly different stem biomass for a given tree size. There may, however, be some disparities in stand-level production, at least as indicated by the results of this one study. For longterm planning purposes an additional consideration is the known difference in longevity for the two species, which could affect how long each species can be expected to maintain adequate stand stocking over long rotations.

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