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Crown structure and biomass allocation patterns modulate aboveground productivity in young loblolly pine and slash pine

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Abstract

Crown architecture affects tree growth through control of leaf area and its display for effective light capture and photosynthesis. It may be important to quantify crown traits for effective use of intensive silvicultural practices to improve tree growth in forest plantations. We examined growth and crown characteristics in two families of loblolly pine (*Pinus taeda* L.) with contrasting growth—superior and average, and one slash pine (*Pinus elliottii* Engelm.) family, growing at three experimental sites in the West Gulf Coastal Plain of Texas and Louisiana, USA. The families were subjected to two contrasting silvicultural treatments—repeated fertilization and control of competing vegetation (high intensity), and control (low intensity). Families differed in height and diameter growth after the second growing period in the field, and high intensity treatment in general increased tree growth, although family ranks and silvicultural effects were dependent on the experimental site. The families differed in crown and needle traits, and biomass partitioning patterns. Aboveground biomass accumulation was related to crown structure among families, but biomass partitioning was independent of the crown traits. Cultural treatment generally had no effect on crown properties or aboveground biomass partitioning. Slash pine produced significantly smaller crowns than loblolly pine at a given tree size, but was capable of maintaining larger needle area and producing more bole-wood biomass for a given crown volume. Tree growth was highly correlated with accumulated foliage area, but bole-wood production per unit leaf area (growth efficiency) was similar for both pine species. The superior loblolly pine family had the largest number of flushes and a different crown shape than two other families that most likely led to better light-capture and greater carbon assimilation, as this family also produced the greatest aboveground biomass.

Keywords: Leaf area; Crown volume; Growth efficiency; Fertilization; *Pinus taeda*; *Pinus elliottii*

1. Introduction

Tree growth reflects the interdependence of physiological processes, biomass allocation patterns and growth rates as influenced by the inherent genetic background of the individuals and the environment in which the individuals are grown. Spatial and temporal integration of these processes determines stand-level production, expressed either as accumulated carbon, biomass, or wood production (Will et al., 2001; Chapin et al., 2002; Martin et al., 2005).

In the Southeastern United States, loblolly pine and slash pine are the main softwood timber species. The natural geographic range of slash pine is smaller than that of loblolly pine, but both species are widely planted throughout the South. Genetic variability lies at the basis of tree breeding programs aimed at increasing forest productivity and providing a sustainable supply of timber products (McKeand et al., 2003). Although practically all seedlings of both species planted in commercial forest plantations in the region come from genetically improved sources (McKeand et al., 2003), the potential remains to increase productivity through the use of best-performing genotypes. However, the deployment of genetically improved planting material should be coupled with appropriate silvicultural practices to obtain the best possible returns from resources invested in the establishment and maintenance of forest sites.

Loblolly and slash pine differ in aboveground biomass productivity and in growth response to intensive silvicultural treatments (Colbert et al., 1990; Jokela and Martin, 2000; Xiao et al., 2003a; Martin and Jokela, 2004b). Also genotypes within both species differ in growth and biomass accumulation (McCrady and Jokela, 1996, 1998; Lopez-Upton et al., 2000;

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Roberts, 2002; McKeand et al., 2006; Roth et al., 2007), but the exact causes of this variability remain unknown.

Although growth differences in plants may result from variation in rates of carbon gain, the published results regarding differences in leaf-level net photosynthesis between loblolly and slash pine are mixed. Will et al. (2001) found no significant differences in leaf-level photosynthesis rates between slash and loblolly pine. In contrast, McGarvey et al. (2004) reported about 14% higher leaf-level area-based photosynthetic rates for slash than for loblolly pine; however, when integrated for the whole tree, total canopy photosynthesis was slightly higher for loblolly than for slash pine. Consequently, differences in productivity between loblolly and slash pine have been proposed to arise largely from variation in accumulated leaf area, rather than from different leaf-level photosynthetic rates (Will et al., 2001; McGarvey et al., 2004).

The lack of obvious between-species differences in leaf-level photosynthesis and the close link of tree productivity with leaf area imply that species-or genotype-specific differences in crown structure and leaf biomass allocation patterns might modify tree growth and productivity. The spatial distribution of leaf area and biomass within a crown might control light interception and influence net CO_2 exchange rates at the whole tree and stand levels (Wang and Jarvis, 1990). Different leaf area or leaf biomass distributions within crowns have been reported among families of loblolly pine (McCrady and Jokela, 1996, 1998) and between loblolly and slash pine (Xiao et al., 2003a). Fertilization only or applied with thinning had no effect on vertical leaf area distribution in loblolly pine stands 9–14 years of age (Vose, 1988; Gillespie et al., 1994). A positive relationship of aboveground growth and leaf area index (LAI—m^2 leaf area m^{-2} ground area) has been reported in 4–18-year-old stands of both loblolly and slash pine, independent of management intensity (McCrady and Jokela, 1998; Jokela and Martin, 2000; Borders et al., 2004; Martin and Jokela, 2004a; Samuelson et al., 2004; Will et al., 2005), suggesting that the development and maintenance of leaf area in a forest plantation is an important determinant of productivity. However, little is known about family- or species-specific responses to various silvicultural practices in terms of crown structure and its consequences for biomass productivity.

Currently most industrially managed forest plantations in the South utilize intensive treatments to alleviate nutrient and water limitations (Allen et al., 2005). The most common practices include fertilization and control of competing vegetation. Results from seven long-term experiments summarized by Jokela et al. (2004) confirm the effectiveness of these treatments in enhancing stem-wood biomass production in loblolly pine; they are also successful in slash pine plantations (Jokela and Martin, 2000; Martin and Jokela, 2004b) However, as suggested by Xiao et al. (2003b), nutrient demands for growth might be dependent on the genotype of these species. Therefore, it is important to examine both the effect of silvicultural practices and their interactions with species and/or genotype on growth performance in forest plantations.

In this paper we investigate variability in aboveground biomass accumulation in selected families of loblolly and slash pine growing in replicated experiments under two contrasting silvicultural intensities in the West Gulf Coastal Plain area in Texas and Louisiana. Our specific objectives were to (i) determine relative differences in accumulated aboveground biomass; (ii) establish whether and how crown characteristics are linked to differences in productivity and biomass allocation patterns in the examined families; (iii) determine how the above-mentioned relationships are affected by silvicultural management intensity.

2. Material and methods

2.1. Experimental sites

The West Gulf series of the PPINES (Pine Productivity Interactions on Experimental Sites) experiment consists of three sites: Kirbyville, Texas (30°35′N, 93°59′W); DeRidder, Louisiana (30°51′N, 93°21′W); and Bogalusa, Louisiana (30°52′N, 89°51′W). The study is a part of the Forest Biology Research Cooperative coordinated by the University of Florida. The Bogalusa site is located in the East Gulf Coastal Plain area and two other sites are located in the West Gulf Coastal Plain, but together are hereafter referred to as West Gulf Coastal Plain sites. Hot and humid summers and mild winters characterize the climate of this region (Table 1). The sites differ in their soil drainage classification and texture in the surface and sub-surface layers. The Kirbyville site is a moderately well drained site, DeRidder is a somewhat poorly drained site and Bogalusa is a poorly drained site. Both DeRidder and Bogalusa have a silt loam surface and sub-surface soil texture, while Kirbyville has a fine sandy loam surface soil and sandy clay loam sub-surface soil.

The experiment was established using a split-plot design. Two contrasting silvicultural treatments—control (C) and high intensity (HI) were assigned as a main-plot factor. Both treatments at all three sites were sprayed with Arsenal®

Table 1
Long-term (1971–2000) mean values of climatic data[a] for each of three experimental sites in the West Gulf Coastal Plain area

Site	Temperature (°C)			Precipitation sum (mm)
	Average	Maximum	Minimum	
Bogalusa, LA				
Annual	19.2	25.4	12.9	1627
January	9.6	15.7	3.5	157
July	27.8	33.4	22.1	144
DeRidder, LA				
Annual	19.3	25.3	14.4	1560
January	9.3	15.2	3.3	160
July	27.8	32.7	22.9	133
Kirbyville, TX[b]				
Annual	19.2	25.1	13.2	1399
January	9.3	15.1	3.5	149
July	27.7	33.4	22.0	94

[a] From the nearest recording station, NOAA, National Oceanic and Atmospheric Administration.
[b] Town Bluff Dam, Texas.