



Relationships among growth, $\delta^{13}\text{C}$, foliar nitrogen concentration, foliar nitrogen content and intercepted radiation at different cultural intensities, planting densities and site indices reveal the importance of water use efficiency in mid-rotation loblolly pine stands

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ABSTRACT

Carbon isotope composition ($\delta^{13}\text{C}$), intercepted photosynthetically active radiation (IPAR), foliar nitrogen (N) content and foliar N concentration are all factors related to stand growth and productivity. The relationships between these attributes and growth were studied in 15 and 16-year-old loblolly pine (*Pinus taeda* L.) stands at planting densities ranging from 1483 to 4448 tree ha⁻¹ grown under two silvicultural management intensities, both having different fertilization inputs. Measurements were conducted on six sites in the lower and upper coastal plains of Florida, Georgia and Alabama at site indices (SI) (base age 25 years) ranging from 18.6 to 29.6 m. The effects of planting density, cultural intensity and SI on the aforementioned attributes were studied. Correlations between $\delta^{13}\text{C}$, foliar N concentration, foliar N content, IPAR and current annual increment (CAI) of stem volume, stem wood biomass, branch biomass, foliage biomass and total above-ground biomass were also studied. We hypothesized that foliar N would be a better predictor of growth than either $\delta^{13}\text{C}$ or IPAR, and that IPAR would be the same across planting densities due to canopy closure.

The results indicated that CAI of stem volume, stem wood biomass and total above-ground biomass were affected by SI or the interaction between SI and management intensity. The significant relationships between SI and CAI growth indices were all positive indicating greater growth at greater site indices. A negative correlation was found between $\delta^{13}\text{C}$, a surrogate for water use efficiency, and SI, meaning stands had lower water use efficiencies at sites with higher SI values. Foliar N concentration and content were both affected by silvicultural intensity, while IPAR was only affected by planting density. Among the physiological parameters, $\delta^{13}\text{C}$ was the only parameter significantly correlated with the CAI indices. Significant negative correlations were found between CAI of stem volume, stem wood biomass, total above-ground biomass and $\delta^{13}\text{C}$. These results indicated that moisture availability affected growth of the highly fertilized mature stands in this study. The findings reported here, when compared to similar studies in younger stands, suggest that growth limitations shifted from light availability to soil moisture availability in older stands when nitrogen was not limiting.

1. Introduction

Loblolly pine (*Pinus taeda* L.) is an extensively planted species of major economic and ecological importance in the southeastern USA (Schultz, 1997). In addition to providing wood and pulp based products, loblolly pine has the potential of providing biomass feedstock for bioenergy, biomaterial, and carbon sequestration markets (Zhao et al., 2014). Factors related to the improvement of loblolly pine growth and productivity are therefore of major interest.

Planting density, site index, and management intensity, which

includes site preparation, fertilization, weed control and genetically improved trees, can affect stand growth and productivity (Allen et al., 1990; Colbert et al., 1990; Fox et al., 2007; Zhao et al., 2014). Numerous studies have documented the combined and independent positive effects of weed control and fertilization on stand productivity (Colbert et al., 1990; Jokela and Martin, 2000; Adegbedi et al., 2002; Zhao et al., 2011a; Zhao et al., 2011b). The implementation of intensive management techniques has resulted in stand productivity increasing from 2 to 20 m³ ha⁻¹ yr⁻¹ over the last 50 years (Fox et al., 2007). Fertilization is particularly important, as many sites in the southeastern

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Table 1

Location and attributes of the loblolly pine culture \times density installations used in this study. Data summarized from Zhao and Kane (2014) for Lower Coastal Plain (LCP) installations and Wang et al. (2014) for Piedmont and Upper Coastal Plain (PUCP) installations.

County, state	Physiographic region	Soil series [*]	Soil Taxonomy	Mean basal area m ² ha ^{-1**}	Minimum basal area m ² ha ^{-1**}	Maximum basal area m ² ha ^{-1**}	Site Index (m) ***
Baker, FL	LCP	Sapelo	Sandy, siliceous, thermic Ultic Alaquod	44	36	50	29.6
Nassau, FL	LCP	Ocilla	Loamy, siliceous, subactive, thermic aquic Arenic Paleudult	37	24	47	18.6
Nassau, FL	LCP	Yemassee – Eunola	Fine-loamy, siliceous, semiaactive, thermic Aquic Endoaquult	39	36	46	27.7
Escambia, AL	PUCP	Orangeburg	Fine-loamy, kaolinitic, thermic Typic Kandiodults	43	38	48	25.9
Hancock, GA	PUCP	Bonifay/Cowarts	Loamy, siliceous, subactive, thermic grossarenic plinthic Paleudults	42	31	47	21.9
Harolson, GA	PUCP	Grover	Fine-loamy, micaceous, thermic Typic Hapludults	53	49	57	25.6

* Soil information provided by the USDA-NRCS Soil Survey Division.

** Calculated at age 15 across silvicultural intensities and planting densities.

*** Site index was calculated in terms of average dominant height of plots with operational culture and 1483 trees ha⁻¹ planting density at a base age of 25 years.

USA are both N and P deficient. For example, a one-time application of 224 kg ha⁻¹ N and 25 kg ha⁻¹ P resulted in an average growth increase of 30% (3.5 m³ ha⁻¹ yr⁻¹) over an 8-year period (Fox et al., 2006).

In three and four-year-old loblolly pine stands, stem biomass has been shown to increase with increased planting density (Burkes et al., 2003; Will et al., 2005). Interactions between planting density, management intensity and base site quality (site index) in stand productivity have also been observed (Zhao et al., 2016). For example, high levels of silvicultural inputs increase productivity more at low quality sites compared to high quality sites. A better understanding of the physiological factors that drive growth and productivity at different planting densities, management intensities, and site qualities, and how these factors change as stands mature, could be helpful to further increase loblolly pine stand productivity.

In four-year-old loblolly pine stands planted at densities from 740 to 4440 trees ha⁻¹, annual intercepted photosynthetically active radiation (IPAR), a measurement of photosynthetic energy capture by the canopy (Gallo and Daughtry, 1986), was correlated with current annual increment (CAI) of stem volume across all planting densities, and was a better predictor of growth than leaf area index or total canopy nitrogen content (Will et al., 2005). In four 12-year-old stands that were part of the same study, a significant relationship was found between IPAR and CAI, but variability was much higher (Akers et al. 2013). IPAR has been correlated to aboveground growth in young stands in different irrigation and fertilization regimes (Dalla-Tea and Jokela, 1991; Allen et al., 2005), among loblolly pine families (McCrary and Jokela, 1998; Chmura and Tjoelker, 2008), and in a rainfall-exclusion study (Samuelson et al., 2014).

Will et al. (2005) found a weaker correlation between foliar nitrogen (N) content and CAI of stem volume than that of IPAR and growth in young loblolly pine stands. Foliar N content has been further shown to be related to photosynthetic capacity in Douglas-fir (*Pseudotsuga menziesii*) (Mitchell and Hinckley, 1993); however, in loblolly pine, an increased N content was not found to coincide with differences in light-saturated photosynthesis (Munger et al., 2003). When foliar N concentration and content were assessed in a silvicultural intensity and planting density, it was determined that both factors were affected by silvicultural intensity while planting density only affected foliar N content (Akers et al., 2013).

Carbon isotope composition ($\delta^{13}\text{C}$), a measurement of the $^{13}\text{C}/^{12}\text{C}$ ratio, is considered a time integrative surrogate for water use efficiency (Farquhar et al., 1982; Farquhar and Richards, 1984; Farquhar et al., 1989; Condon et al., 2004). Water use efficiency and $\delta^{13}\text{C}$ are positively correlated with higher $\delta^{13}\text{C}$ values coinciding with higher water use efficiency values (Condon et al., 2002). In a greenhouse study, a

negative correlation was found between $\delta^{13}\text{C}$ and biomass accumulation in loblolly pine (Ingwers et al., 2017). Contrary to Ingwers et al. (2017), positive correlations have been reported between $\delta^{13}\text{C}$ and tree height (negative relationship between $\Delta^{13}\text{C}$, the inverse of $\delta^{13}\text{C}$, and height) in *Picea mariana* (Flanagan and Johnsen, 1995; Johnsen et al., 1999), and *P. elliotti* Engelman var. *elliotti* x *P. caribaea* hybrids (Xu et al., 2000; Prasolova et al., 2003). Water use efficiency has been shown to increase in even moderate soil moisture stress conditions (Peuke et al., 2006; Li and Liu, 2016). Strong treatment effects have further been found when the effects of soil moisture availability were studied on water use efficiency, measured from $\delta^{13}\text{C}$, in loblolly pine seedlings (Ingwers et al., 2017). A better understanding of the relationship between $\delta^{13}\text{C}$ and CAI of growth indices in field-grown loblolly pine may improve stand management techniques and allow for the development of $\delta^{13}\text{C}$ as a potential metric for genotypic screening, selection, and selective deployment.

There were three objectives in this study. The first objective was to determine how planting density, silvicultural intensity and site index (SI) affects $\delta^{13}\text{C}$, IPAR, foliar N content, and foliar N concentration. The second objective was to determine how $\delta^{13}\text{C}$, foliar N, and IPAR correlated to CAI growth indices, and the third objective was to further evaluate if growth factors in the mid-rotations stands in this study were different from those in previous studies conducted on younger stands. We hypothesized that: (1) planting density, silvicultural intensity and SI would affect CAI, $\delta^{13}\text{C}$, foliar N concentration and foliar N content, (2) that foliar N content would have a stronger relationship with the CAI of stem volume, stem wood, branch, foliage and above-ground biomass than IPAR or $\delta^{13}\text{C}$ and (3) that IPAR would be the same across planting densities due to canopy closure.

2. Methods

2.1. Study installations and treatments

Six loblolly pine research installations were used in this study, three in the Lower Coastal Plain (LCP) in Florida and three were in the Piedmont and Upper Coastal Plain (PUCP) in Georgia and Alabama (Table 1). Detailed information on establishment and management can be found in Zhao et al. (2014) for LCP installations and Wang et al. (2014) for PUCP installations. All six installations were maintained by the Plantation Management Research Cooperative (PMRC) of the University of Georgia. The LCP installations were established in 1995/1996. The PUCP installations were established in 1997/1998. The soils and depth to the water table of LCP and PUCP installations differed, which was reflected in some differences in management activities at the

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