

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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ARTICLE INFO

Keywords:

Pinus taeda
Water use efficiency
Nitrogen
Growth
Silviculture

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 × 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, semiactive, thermic Aquic Endoaquult	39	36	46	27.7
Escambia, AL	PUCP	Orangeburg	Fine-loamy, kaolinitic, thermic Typic Kandiuults	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 ¹³C/¹²C 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

time of planting: bedding was employed in the LCP installations while tillage was employed in the PUCP installations. Fall banded chemical site preparation was employed in the LCP installations while broadcast chemical site preparation was employed in the PUCP installations.

Each installation was arranged as a split-plot design with silvicultural management intensity as the whole-plot factor and planting density as the sub-plot factor. There were two management intensities: a low intensity (LI) and a high intensity (HI). Compared to the LI treatment, the HI treatment received more fertilizer and vegetative competition control. The LI treatment received a fertilization regime of 651 kg ha⁻¹ 10-10-10 NPK at planting and 224 kg ha⁻¹ N and 28 kg ha⁻¹ P before the 8th and 12th growth season while the HI treatment received the same fertilization at planting in addition to 673 kg ha⁻¹ 10-10-10 NPK and micronutrients and 131 kg ha⁻¹ NH₄NO₃ in spring of the 3rd growing season, 131 kg ha⁻¹ NH₄NO₃ in spring of the 4th growing season, 336 kg ha⁻¹ NH₄NO₃ in spring of the 6th growing season, and finally 224 kg ha⁻¹ N and 28 kg ha⁻¹ P in the 8th, 10th, 12th and 14th growing seasons. In total, the LI treatment received 513.1 kg ha⁻¹ N, 121.1 kg ha⁻¹ P, and 65.1 kg ha⁻¹ K while the HI treatment received 1,237.7 kg ha⁻¹ N, 244.4 kg ha⁻¹ P, and 132.4 kg ha⁻¹ K. The LI treatment received a banded herbicide application to control herbaceous competitors during the first growth year while HI treatment received periodic herbicide applications as needed to eliminate competing vegetation throughout the study. The HI treatment in the LCP received tip moth control while the HI in the PUCP did not. Within each management intensity there were six sub-plots of planting densities at 741, 1483, 2224, 2965, 3706 and 4448 trees ha⁻¹ at each installation. Two seedlings were planted at each spot, if both were alive at the beginning of the second year then the smaller of the two was removed. Measurements in this study were conducted on planting densities ranging from 1483 to 4448 trees ha⁻¹.

2.2. Current annual increment (CAI)

After the 15th and 16th growing seasons for the LCP installation and after the 12th and 15th growing seasons in the PUCP, tree measurements were taken in the dormant season. All trees were measured for diameter at breast height (DBH). Total height (H) and height to live crown were measured on every other tree. Total heights of trees not measured for height were estimated from the model $\ln(H) = b_0 + b_1 DBH^{-1}$ separately fitted for height measured trees at each measurement in each plot. The average dominant height is defined as the average height of trees with diameter (DBH) larger than the average DBH of the stand, and the SI was calculated for each installation based on the average dominant height of the LI plot with the planting density of 1483 trees/ha. Total outside bark volumes were estimated using the individual-tree volume equation developed by Pienaar et al. (1987). Tree stem wood, branch and foliage biomass and tree total above-ground biomass were estimated using the additive tree biomass equations developed by Zhao et al. (2015).

The annual increment of stand volume, stem wood biomass, branch biomass, foliage biomass, and stand total above-ground biomass were calculated for the LCP plots from the trees that were alive at both ages 15 and 16 and for the PUCP plots from the trees that were alive at both ages 12 and 15. That is, the CAIs for the LCP plots used in the following analysis are the annual increments from age 15 to age 16, while the CAIs for the PUCP plots are the average annual increments from age 12 to age 15. Notably, in the case of foliar CAI, these values represent the net change in foliar biomass as new needles are grown and old needles are lost each year.

2.3. IPAR, $\delta^{13}C$, foliar N concentration and content

IPAR was determined by subtracting the amount of photosynthetically active radiation measured inside each plot (management intensity \times planting density \times installation combination) from nearby

measurements taken outside each plot in full sunlight. Photosynthetically active radiation was measured beneath the canopy inside each plot with a ceptometer (SunScan Canopy Analysis type SS1, Delta-T Devices Ltd., Cambridge, UK) and recorded on a hand-held computer (Allegro Field PC, Juniper Systems, Logan, UT, USA). Photosynthetically active radiation outside of each plot was continuously measured with a stationary pyranometer (Sunshine Sensor type BF2 Delta-T Devices Ltd., Cambridge, UK) and recorded on a data logger (CR23X, Campbell Scientific, Logan, UT, USA) at 10-s intervals. Plot measurements were conducted along four transects: two lengthwise transects that were parallel to the tree rows and two diagonal transects that moved between the rows from corner to corner. All measurements were taken within the interior of each plot with an approximant 8 m buffer, which was not measured, surrounding the plot perimeter. Approximately 60 measurements were taken inside each plot. Measurements for the determination of IPAR in LCP installations were conducted five times, at approximately six-week intervals, between February to October 2012. Measurements for the determination of IPAR in the PUCP installations were conducted 4 times, in approximately evenly spaced intervals, from May to September during 2013 or 2014. Measurements were not taken in the LI treatments at the Escambia County, AL, installation due to dense understory vegetation. The Hancock County, GA, installation was unexpectedly harvested early in the summer of 2013. The only data that we have for this site is from May 2013. All measurements were conducted between 11:00–15:00 h, when zenith angle was between 10° and 30° under sunny, cloud-free, conditions as described in Will et al. (2001). The grand mean for each plot across all measurement dates was used for analyses.

The $\delta^{13}C$ and N were determined from a bulk sample of needles harvested from four trees that were felled in each plot. Of the selected trees, two had an above average diameter at breast height (DBH), one had an average DBH, and one had a below average DBH. Sampling was performed in the dormant season of 2011/2012 in the LCP installations (at age 16 years) and in the dormant season of 2012/2013 on the PUCP installations (at age 15 years). Needle $\delta^{13}C$ and foliar N concentration are affected by tree height and canopy location (Gebauer and Schulze, 1991; Prasolova et al., 2001), thus stratified sampling was conducted on the bottom, middle, and top crown sections. Each sample consisted of 5–10 fascicles. Fascicles in each sample were dried at 65 °C to a constant mass, then finely ground and analyzed for $\delta^{13}C$ and N by mass spectrometry at the Stable Isotope and Soil Biology Laboratory, Odum School of Ecology, University of Georgia, Athens, GA, USA, per the methodology described in Farquhar and Richards (1984). Plot values were determined by averaging the sample values of each canopy level. Foliar N content was calculated by multiplying foliar biomass by the average percent foliar N concentration.

2.4. Statistical analyses

The effects of management intensity, planting density and site index and their interactions were studied on CAI growth indices, IPAR, $\delta^{13}C$, foliar N concentration and content with an analysis of covariance (ANCOVA) using a mixed model (Littell et al., 1996). Differences among treatment means were evaluated using Fisher's Least Significant Differences (LSD) test. Management intensity and planting density were treated as independent categorical variables and SI was treated as a continuous independent variable. CAI growth indices, IPAR, $\delta^{13}C$, foliar N concentration and N content were treated as independent variables. The effects of IPAR, $\delta^{13}C$, foliar N concentration, foliar N concentration, and their interactions on CAI growth indices were further studied; however, IPAR, $\delta^{13}C$, foliar N were subsequently treated as independent variables. In the latter analysis, installation was equivalent to replicate and thus installation and installation \times management intensity were treated as random effects. All other factors were treated as fixed effects unless otherwise specified. Due to the high correlation between foliar N concentration and foliar N content ($R^2 = 0.4188$, $p < 0.0001$), the

Table 2

P-values for density, site index (SI, in meters at a base age of 25 yrs) and their interactions on current annual increment (CAI) of loblolly pine growth indices, carbon isotope composition ($\delta^{13}\text{C}$), intercepted photosynthetically active radiation (IPAR), foliar N concentration and foliar N content in mid-rotation stands. Significant differences ($p < 0.05$) are shown in bold.

Effect	CAI stem volume ($\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$)	CAI stem wood ($\text{Mg ha}^{-1} \text{yr}^{-1}$)	CAI branch ($\text{Mg ha}^{-1} \text{yr}^{-1}$)	CAI foliage ($\text{Mg ha}^{-1} \text{yr}^{-1}$)	CAI total above ground ($\text{Mg ha}^{-1} \text{yr}^{-1}$)	$\delta^{13}\text{C}$	Foliar N concentration (kg ha^{-1})	Foliar N content (g kg^{-1})	IPAR (%)
Manage	0.0027	0.4508	0.8733	0.9508	0.0008	0.4508	0.0003	0.0032	0.6612
Planting density	0.8781	0.5574	0.9818	0.9433	0.7941	0.5574	0.7946	0.3461	0.0151
SI	< 0.0001	< 0.0001	0.1095	0.6204	< 0.0001	< 0.0001	0.1463	0.5447	0.5896
Manage \times planting density	0.4804	0.4583	0.9035	0.9893	0.2954	0.7566	0.9044	0.9538	0.9078
SI \times manage	0.0020	0.1670	0.5195	0.6833	0.0007	0.1670	0.2730	0.0076	0.0827
SI \times planting density	0.2807	0.3575	0.8000	0.8555	0.2003	0.3575	0.6724	0.9826	0.3605
SI \times manage \times planting density	0.9792	0.9722	0.4788	0.7527	0.9718	0.9734	0.9811	0.9997	0.9236

effects of foliar N content, foliar N concentration, and their interactions with other independent variables, on CAI growth indices were tested separately. A Type-1 error rate of 0.05 was used for all analyses. Figures were prepared with SigmaPlot graphing software (version 11.0, SysStat Software, San Jose, CA, USA).

3. Results

3.1. Effects of management intensity, planting density and SI

The CAI of stem volume and total above-ground biomass were both affected by management intensity, SI, and their interaction, while CAI of stem wood biomass was only affected by SI (Table 2). There were no significant effects on the CAI of branch or the CAI of foliage biomass. The positive relationships between SI and CAI of stem volume and total above-ground biomass (Fig. 1) indicate that a greater amount of stand volume or biomass accumulated on installations with higher SI values. The significant SI \times management interaction observed for CAI of stem volume (Fig. 1A) and total above-ground biomass (Fig. 1B) indicates that stands on low SI sites, under the LI treatment, exhibited less growth than stands on low SI stands in the HI treatment. Planting density did not affect the CAI growth indices in this study.

The $\delta^{13}\text{C}$ values were significantly and negatively affected by SI (Table 2, Fig. 2A). Foliar N content was significantly affected by management intensity, and management intensity \times SI interaction (Table 2). For stands under the LI treatment, stand foliar N content was significantly and positively related to the SI; for stands under the HI treatment, the relationship between foliar N content and SI was not significant (Fig. 2B).

Foliar N concentration was affected by silvicultural management intensity (Table 2) with higher concentrations in stands under the HI treatment than under the LI treatment (19.1 vs 16.9 g kg^{-1}). IPAR was significantly affected by planting density only with values being significantly lower at 1483 tree ha^{-1} and 2224 trees ha^{-1} than at 2965 trees ha^{-1} or 4448 trees ha^{-1} (Table 3).

3.2. Relationships between IPAR, $\delta^{13}\text{C}$, foliar N content, foliar N concentration and CAI indices

Among the physiological measurements, only $\delta^{13}\text{C}$ was related to the CAI growth indices (Tables 4 and 5). No significant interactions were found among the physiological measurements. Significant negative relationships were found for CAI of stem volume (Fig. 3A), stem wood biomass (Fig. 3B) and total above-ground biomass (Fig. 3E) but not branch biomass (Fig. 3C) nor foliar biomass (Fig. 3D).

4. Discussion

The correlations between $\delta^{13}\text{C}$, SI, and CAI growth during mid-

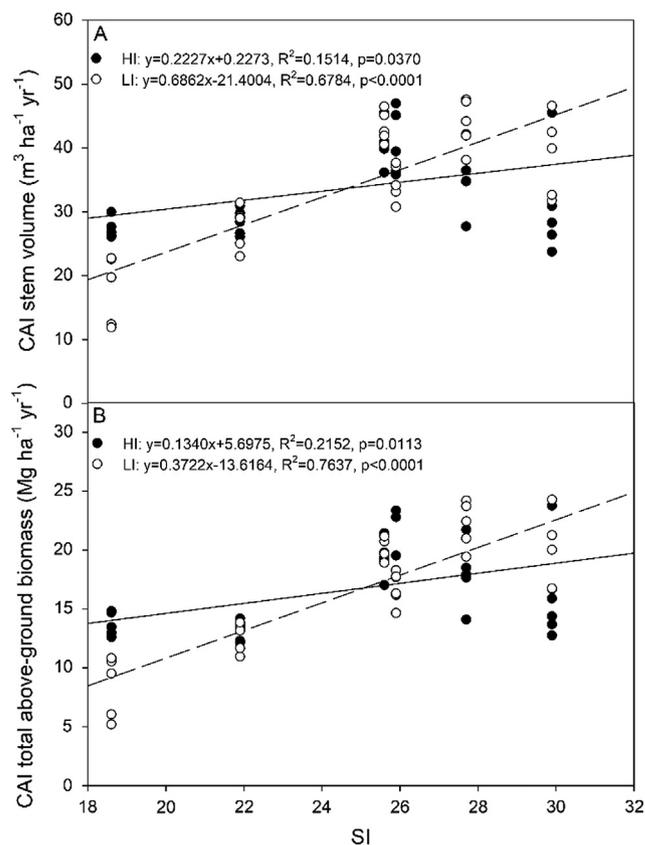


Fig. 1. The relationships between loblolly pine Site Index (SI in meters at a base age of 25 yrs) and Current Annual Increment (CAI) of stem volume (A), and CAI of above-ground biomass (B) in mid-rotation stands. High (HI) and low (LI) silvicultural intensities are represented by filled and unfilled symbols, and solid and slashed lines, respectively.

rotation indicate that water, and access to water, were a major contributor to CAI and SI in this study. The lower $\delta^{13}\text{C}$ observed at higher SI sites suggest a lower water use efficiency and thus greater moisture availability. The relationship between SI and $\delta^{13}\text{C}$ observed in this study could indicate that SI may be improved by increased soil moisture or factors that improve access to soil moisture such as higher soil hydraulic conductivity. We therefore hypothesize that high SI sites have greater access to soil moisture, resulting in lower $\delta^{13}\text{C}$ values and higher CAI growth in mid-rotation stands. Contrary to our second hypothesis, the findings here indicate that moisture availability may have been the greatest limiting factor to stand growth, when compared to nitrogen (inferred from foliar N concentration and content) or light (inferred from IPAR) availability; however, our results are not

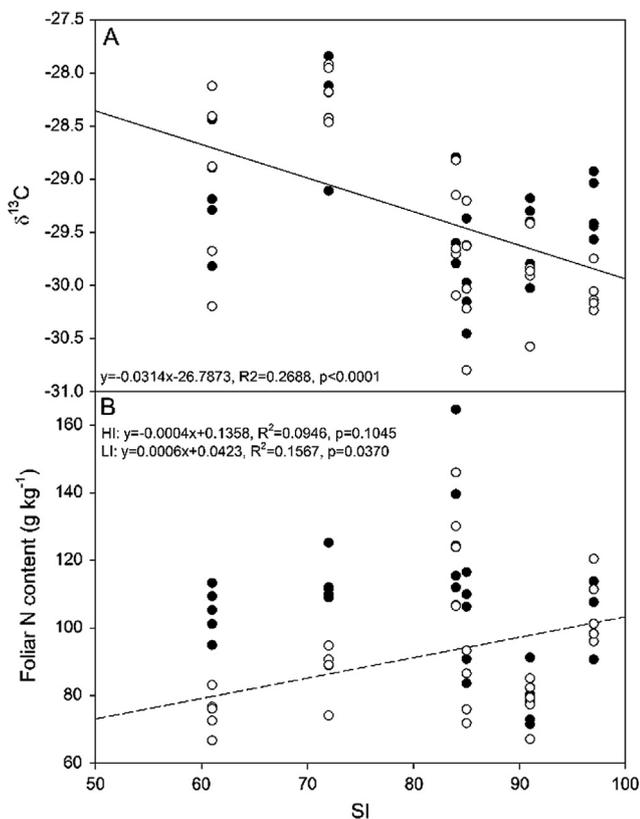


Fig. 2. The relationships between loblolly pine site index (SI, in meters at a base age of 25 yrs) and carbon isotope composition ($\delta^{13}\text{C}$) (A), and foliar N content under both low and high silvicultural intensities (B) in mid-rotation stands. High (HI) and low (LI) silvicultural intensities are represented by filled and unfilled symbols. The relationships between SI and $\delta^{13}\text{C}$ (A) did not differ between silviculture intensities and is thus represented as a single set of regression parameters.

consistent with the numerous fertilization and irrigation studies in loblolly pine which demonstrates that nutrient availability, not water availability, is a better predictor of stand growth (Jokela et al., 2004; Coyle et al., 2008; Campoe et al., 2013; Coyle et al., 2016). For example, a 2 × 2 nutrient and soil moisture factorial experiment on 8-year-old loblolly pine stands found that stem growth volume increased 21% with fertilization compared to 9% with just irrigation after four years of treatment (Albaugh et al., 1998). In the same stands, after 9 years of treatment, stem volume increased by 100% in the fertilization treatment and just 25% in the irrigation treatment (Albaugh et al.,

2004). In the present study, however, nutrients were likely not limiting due to a large amount of fertilization. The findings reported here instead suggest that soil moisture (water) may become the major limiting factor in mid-rotation stand growth when nutrients are not limiting.

The $\delta^{13}\text{C}$ values observed in this study are similar to those previously observed in loblolly pine seedlings (Ingwers et al., 2017) and saplings (Ingwers et al., 2016) as well as four-year-old loblolly pine trees (Samuelson et al., 2014) and 15-year old loblolly pine stands (Choi et al., 2005). Negative correlations between $\delta^{13}\text{C}$ and growth were also observed in seedling-stage loblolly pine clones (Ingwers et al., 2017). Negative correlations were found in the present study between $\delta^{13}\text{C}$ and CAI of stem volume, stem wood biomass, and total above-ground biomass, but not increment growth of foliage or branches; potentially indicating that $\delta^{13}\text{C}$ may be a good metric to predict wood biomass formation but not foliage or branch biomass accumulation.

The lack of correlation between CAI and foliar N content and concentration was somewhat unexpected. A strong linear relationship was found between canopy nitrogen content and annual stem volume increment in 4-year-old loblolly pine stands (Will et al., 2005). Mean foliar nitrogen concentration in this study was all above the 1.20% threshold that has been previously found to be limiting for growth in loblolly pine (Albaugh et al., 2010), thus, nitrogen may not have been limiting to growth in either of the management intensity treatments. Recent work in loblolly pine has shown that fertilization increases stem volume production (Maggard et al., 2017) and water use efficiency (Maggard et al., 2016). Jokela et al. (2004) also found that soil nutrient availability rather than site water balance is the major drivers of stand productivity (Jokela et al., 2004). Our results, however, do not validate or invalidate these findings and instead suggest that water availability becomes limiting when there are no nutrient limitations.

Observed differences in foliar N concentration between management intensities were likely due to differences in nitrogen inputs between the two treatments. These findings differ from a previous culture × density study, conducted on 13-year-old stands, which found no differences in foliar N concentration between management intensities (Akers et al., 2013). Nor was foliar N concentration affected by planting density in two-year-old loblolly pine stands (Will et al., 2001). Somewhat consistent with the present findings, a study in 12-year old loblolly pine plantations also found significant differences in whole tree above-ground N content between culture intensities; however, it also found differences in planting densities (Zhao et al., 2014).

It is also possible that the effects of management intensities on foliar N varied across years. A study comparing the combined and independent effects of fertilization and through-fall reduction across years in seven-year-old loblolly pine stands found significant differences in foliar N content between fertilization treatments in some, but not all, years (Maggard et al., 2017). Although foliar N differed between

Table 3

Mean (SE) values for current annual increment (CAI) of loblolly pine growth indices and physiological attributes including carbon isotope composition ($\delta^{13}\text{C}$), foliar N concentration, foliar N content, and intercepted photosynthetically active radiation (IPAR), in mid-rotation stands by main effects of silvicultural intensity and planting density. Letters denote significant differences among treatments at $\alpha = 0.05$.

Attribute	Silvicultural intensity		Planting density (tree planted ha ⁻¹)				
	Low	High	1483	2224	2965	3706	4448
<i>Increment growth</i>							
CAI stem volume (m ³ ha ⁻¹ year ⁻¹)	34.5 (2.0)	33.7 (1.3)	35.2 (3.3)	32.2 (3.3)	34.5 (2.5)	33.5 (2.5)	34.9 (1.9)
CAI stem wood biomass (Mg ha ⁻¹ yr ⁻¹)	14.7 (1.0)	14.7 (0.7)	15.6 (1.7)	14.1 (1.6)	14.7 (1.2)	14.2 (1.2)	14.7 (1.0)
CAI branch biomass (Mg ha ⁻¹ yr ⁻¹)	1.03 (0.08)	1.05 (0.07)	1.07 (0.16)	1.04 (0.11)	1.08 (0.09)	1.00 (0.14)	1.01 (0.11)
CAI foliage biomass (Mg ha ⁻¹ yr ⁻¹)	0.08 (0.04)	0.08 (0.03)	0.05 (0.05)	0.08 (0.06)	0.11 (0.04)	0.08 (0.06)	0.08 (0.06)
CAI Total above ground biomass (Mg ha ⁻¹ yr ⁻¹)	16.7 (1.0)	16.6 (0.7)	17.6 (1.8)	16.0 (1.6)	16.8 (1.3)	16.2 (1.2)	16.8 (0.9)
<i>Physiological attributes</i>							
$\delta^{13}\text{C}$	-29.4 (0.2)	-29.3 (0.1)	-29.2 (0.2)	-29.2 (0.3)	-29.4 (0.2)	-29.3 (0.2)	-29.6 (0.2)
Nitrogen concentration (g kg ⁻¹)	16.9 ^b (< 0.1)	19.1 ^a (< 0.1)	17.5 (0.1)	18.3 (0.1)	18.6 (0.1)	18.1 (0.1)	17.7 (0.1)
Nitrogen content (kg ha ⁻¹)	92.8 ^b (3.7)	103.3 ^a (9.6)	99.7 (6.4)	103.2 (7.3)	102.5 (5.1)	94.8 (4.3)	90.8 (4.0)
IPAR (%)	83.7 (0.9)	82.8 (1.0)	80.3 ^b (1.88)	81.9 ^a (1.7)	83.7 ^a (1.3)	83.69 ^{ab} (1.3)	85.1 ^a (0.4)

Table 4

P-values for the effects of carbon isotope composition ($\delta^{13}\text{C}$), intercepted photosynthetically active radiation (IPAR), foliar N concentration and their interactions on the current annual increment (CAI) of different loblolly pine growth indices in mid-rotation stands. Significant differences ($p < 0.05$) are shown in bold.

	CAI stem volume (m^3 $\text{ha}^{-1} \text{yr}^{-1}$)	CAI stem wood (Mg $\text{ha}^{-1} \text{yr}^{-1}$)	CAI branch (Mg ha^{-1} yr^{-1})	CAI foliage (Mg ha^{-1} yr^{-1})	CAI total above-ground (Mg $\text{ha}^{-1} \text{yr}^{-1}$)
$\delta^{13}\text{C}$	0.0002	0.0002	0.0195	0.0724	< 0.0001
IPAR	0.7982	0.7480	0.7586	0.7914	0.7055
Foliar N concentration	0.3987	0.9872	0.7986	0.8213	0.9288
$\delta^{13}\text{C} \times \text{IPAR}$	0.1095	0.0763	0.1233	0.0635	0.1280
$\delta^{13}\text{C} \times \text{foliar N concentration}$	0.7061	0.8184	0.9877	0.8428	0.8137
IPAR \times foliar N concentration	0.2286	0.1758	0.3612	0.9226	0.1654
$\delta^{13}\text{C} \times \text{IPAR} \times \text{foliar N concentration}$	0.8600	0.6922	0.0721	0.2111	0.6082

management intensities, it is unclear if these differences affected photosynthetic capacity. Fertilization and management intensity has been shown to affect (Maier et al., 2002) and not affect gas exchange (Samuelson, 1998; Munger et al., 2003; Gough et al., 2004; Yáñez et al., 2017) in different loblolly pine studies.

The steeper relationship (slope) observed between SI and CAI of both stem volume and total above-ground biomass in the LI treatment relative to the HI treatment may indicate that different silvicultural strategies should be applied on low and high SI sites. Stands on low SI sites may benefit more from silvicultural inputs compared to stands on high SI sites. In a similar finding, a recent meta-analysis conducted on loblolly pine culture \times density studies demonstrated that high levels of silvicultural inputs resulted in greater gain in productivity in low SI sites compared to high SI sites (Zhao et al., 2016). The significant positive relationship between foliar N content and SI in the LI treatment may be indicative of increased nitrogen acquisition or more available nitrogen at higher site indices.

Contrary to our third hypothesis, and consistent with previous studies, planting density significantly affected IPAR. Previous work in loblolly pine, at the same planting densities, or even in some cases the same stands at earlier ages, have also shown that planting density affects IPAR (Will et al., 2005; Akers et al., 2013). For example, in four-year-old loblolly pine stands, IPAR was found to significantly increase from 740 tree ha^{-1} to 4440 tree ha^{-1} (Will et al., 2005). A study in 13-year-old loblolly pine stands also found that IPAR increased with planting density; however, significant differences were only found between the two lowest planting densities (740 tree ha^{-1} and 1483 tree ha^{-1}) and three of the higher planting densities (2224 tree ha^{-1} , 3706 tree ha^{-1} , 4448 tree ha^{-1}) (Akers et al., 2013). The IPAR results from the present study, which ranged from 1483 tree ha^{-1} to 4448 tree ha^{-1} , were similar to Akers et al. (2013) in that significant differences were only found between two of the lower planting densities (1483 tree ha^{-1} and 2224 tree ha^{-1}) and two of the higher planting densities (2965 tree ha^{-1} and 4448 tree ha^{-1}). The IPAR values from the 15 and 16-year old stands reported here, and those reported from 13-year-old stands (Akers et al., 2013), were higher than those reported from the same planting densities (and in some cases the same stands) in four-year-old stands (Will et al., 2005). The reduction in IPAR with increased stand age is likely due to increased canopy closure with age.

Table 5

P-values for the effects of carbon isotope composition ($\delta^{13}\text{C}$), intercepted photosynthetically active radiation (IPAR), foliar N concentration and their interactions on the current annual increment (CAI) of different loblolly pine growth indices in mid-rotation stands. Significant differences ($p < 0.05$) are shown in bold.

	CAI stem volume (m^3 $\text{ha}^{-1} \text{yr}^{-1}$)	CAI stem wood (Mg ha^{-1} yr^{-1})	CAI branch (Mg ha^{-1} yr^{-1})	CAI foliage (Mg ha^{-1} yr^{-1})	CAI total above-ground (Mg ha^{-1} yr^{-1})
$\delta^{13}\text{C}$	0.0002	< 0.0001	0.0099	0.0692	< 0.0001
IPAR	0.7909	0.5340	0.8997	0.5977	0.4749
Foliar N content	0.1404	0.0511	0.5516	0.3515	0.0697
$\delta^{13}\text{C} \times \text{IPAR}$	0.4797	0.1378	0.2187	0.1553	0.2094
$\delta^{13}\text{C} \times \text{foliar N content}$	0.2180	0.8243	0.4950	0.2146	0.6481
IPAR \times foliar N content	0.4282	0.2763	0.1516	0.7231	0.4593
$\delta^{13}\text{C} \times \text{IPAR} \times \text{foliar N content}$	0.4176	0.3201	0.1387	0.2968	0.2773

In the present study, IPAR did not significantly affect CAI as was observed in previous studies. These results are surprising as positive correlations between above-ground net productivity and IPAR have been previously observed in two-year-old (Will et al., 2001), four-year-old (Will et al., 2005), six-year-old (Allen et al., 2005), nine-year-old (Campoe et al., 2013), and 13-year-old (Akers et al., 2013) loblolly pine stands. A meta-analysis of eight different tree species (including loblolly pine) further found significant relationships between absorbed PAR and biomass accumulation (Albaugh et al., 2016). Canopy closure, in the present study, may have made IPAR a less informative metric than in other studies. The findings reported here, relative to similar culture \times density studies in mostly younger stands, suggest that stand growth limitations may shift from light limitations to soil moisture limitations after canopy closure.

5. Conclusion

The findings in the present study highlight the potential value of $\delta^{13}\text{C}$ as a metric for predicting stand growth and suggest that access to water may be a major limitation of mid-rotation stand growth in stands that are not nutrient limited. The IPAR, a well-known informative metric for young stands, may have been less informative in the more mature stands in the present study due to canopy closure. Nitrogen did not appear to be limiting due to multiple fertilizations prior to the study. The $\delta^{13}\text{C}$ significantly impacted SI and CAI of stem volume, stem wood and total above-ground biomass. Differences in foliar N concentration were found between management intensities, while differences in both foliar N content and IPAR were found among planting densities. The relationships between SI, $\delta^{13}\text{C}$, and CAI may be useful in predicting or estimating one metric from another. The results suggest that water, and access to water, becomes the greatest limiting factor to growth in mid-rotations stands that are not nutrient limited.

Acknowledgements

We thank Dr. Mary Anne McGuire, Dr. Doug Aubrey, Madison Akers and Dr. Josef Urban for their technical expertise and or assistance with field measurements. We further thank the Plantation Management Research Cooperative (PMRC) at the University of Georgia, for

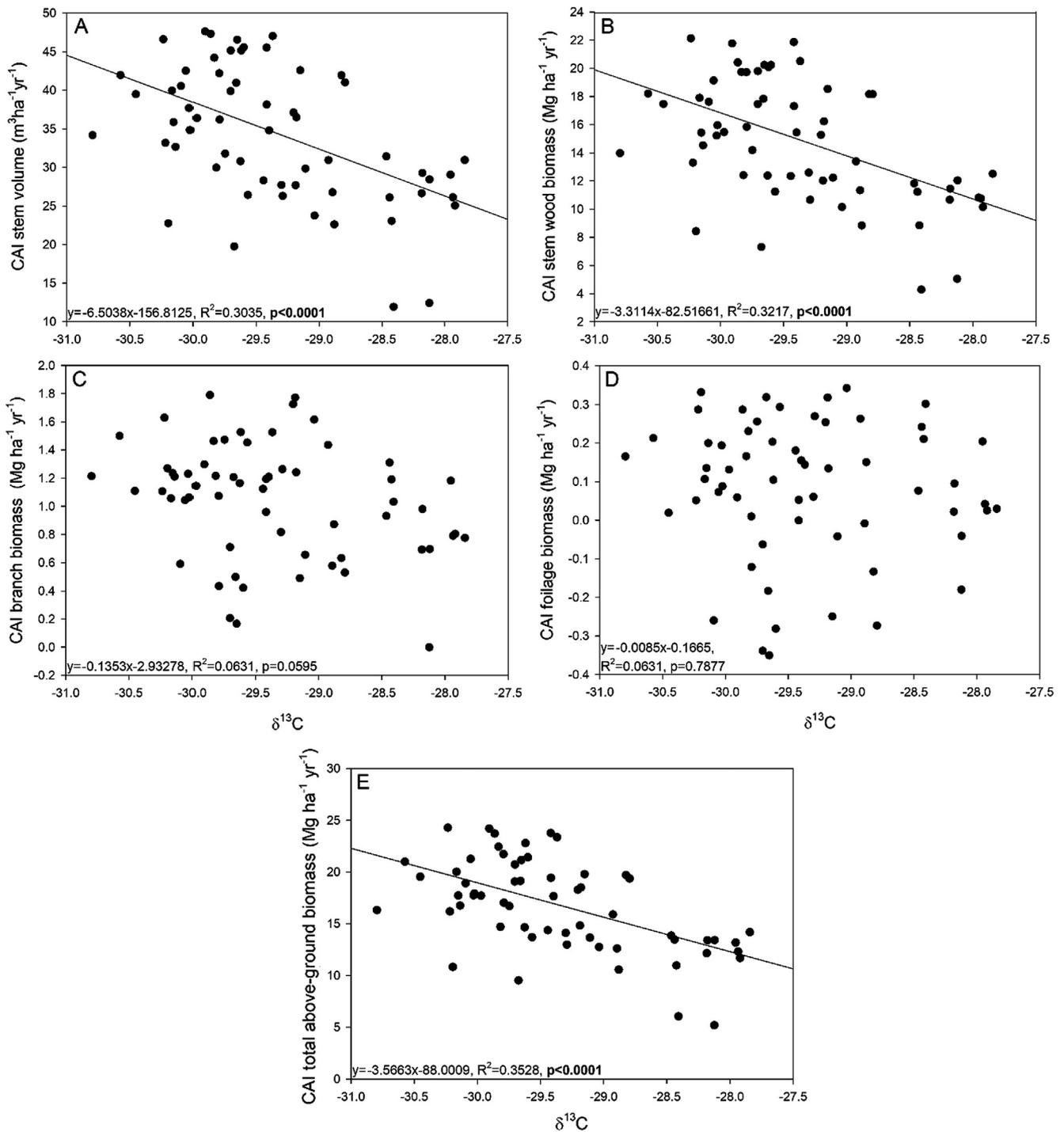


Fig. 3. Relationships between carbon isotope composition ($\delta^{13}\text{C}$) and loblolly pine current annual increment (CAI) of stem volume (A, measured outside of bark), stem wood (B), bark (C), branch (D), foliage (needle) (E), and total above-ground (F) biomass. The relationships were significant except those with CAI of branch and foliage biomass.

establishing and maintaining the research installations used in this study.

Funding

This work was supported by the USDA National Institute of Food and Agriculture (Grant No. 2011-67009-30065, 2011).

Conflict of interests

The authors declare no conflict of interest.

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