Switchgrass growth and pine–switchgrass interactions in established intercropping systems

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Abstract

Intercropping switchgrass (Panicum virgatum L.) with loblolly pine (Pinus taeda L.) has been proposed for producing bioenergy feedstock in the southeastern United States. This study investigated switchgrass growth and pine–switchgrass interactions at two established experimental fields (7-year-old Lenoir site and 5-year-old Carteret site) located on the coastal plain of eastern United States. Position effects (edge and center of switchgrass alley in intercropping plots) and treatment effects (intercropping vs. grass-only) on aboveground switchgrass growth were evaluated. Interspecific interactions with respect to capturing resources (light, soil water, and nitrogen) were investigated by measuring photosynthetically active radiation (PAR) above grass canopy, soil moisture, and soil mineral nitrogen contents. Switchgrass growth was significantly (P = 0.001) affected by treatments in Lenoir and by position (P < 0.0001) in both study sites. Relative to the center, PAR above grass canopy at edge in both sites was about 48% less during the growing season. Soil water content during the growing season at the edge of grass alley was significantly (P = 0.0001) lower by 23% than at the center in Lenoir, while no significant (P = 0.42) difference was observed in Carteret, in spite of more grass growth at center at both sites. Soil mineral nitrogen content at the center of intercropping plots in Lenoir (no fertilization during 2015) was significantly (P < 0.07) lower than at the edge during the peak of growing season (June, July, and August), but not during early and late parts of growing season (May, September, and November). Position effects on soil water and mineral nitrogen were less evident under conditions with higher external inputs (rainfall and fertilization) and lower plant uptake during nongrowing seasons. Results from this study contributed to a better understanding of above- and belowground pine–switchgrass interactions which is necessary to properly manage this new cultivation system for bioenergy production in the southeastern United States.

Keywords: agroforestry, competition, grass growth, interspecific interactions, loblolly pine, switchgrass

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Introduction

Bioenergy derived from dedicated perennial grasses (e.g., switchgrass, Miscanthus) has potential to assist future energy security worldwide (Mclaughlin & Kszos, 2005; Heaton et al., 2008; Schmer et al., 2008; Dale et al., 2014). These perennial grasses can grow on marginal lands and require relatively fewer inputs (e.g., fertilizer) and considerably less intensive management (e.g., soil disturbance and tillage) compared to grain-based biofuels (Tilman et al., 2006; Schmer et al., 2008). Given the vast area of pine plantations in the southern United States, they have recently been proposed as a new source of bioenergy feedstock by intercropping switchgrass (Panicum virgatum L.) between rows of loblolly pine (Pinus taeda L.) in managed plantations (Albaugh et al., 2012; Blazier et al., 2012; Susaeta et al., 2012). This system takes advantage of the wide space between managed pine rows during the initial growing stage of the pine stand. The productivity and longevity of this cultivation system is primarily influenced by tree-grass interactions and competition for resources (i.e., light, water, and nutrients) (Susaeta et al., 2012; Tian et al., 2015). Information of these interactions is a prerequisite for properly managing this new cultivation system to maximize grass biomass productivity and minimize detrimental impacts on tree growth and productivity.

Many studies on traditional agroforestry systems have reported a decline of the yield of understory species as woody plants continue to grow (Singh et al., 1989; Jose et al., 2004; Li et al., 2008). Switchgrass yield was lower when mixed with other nonwoody species than in monocultures (Wang et al., 2010). Only a few
field studies have investigated growth and yield of switchgrass grown between pine trees in the United States (Albaugh et al., 2012, 2014b; Blazier et al., 2012; Krapfl et al., 2015). Some studies showed that switchgrass growth and leaf-level gas exchange (CO₂ and H₂O) were not affected by adjacent trees in the intercropping system during the first two years after planting (Albaugh et al., 2012, 2014b). Moreover, Blazier et al. (2012) found that the intercropping treatment produced even greater switchgrass biomass yields in the juvenile stand than the grass-only treatment in a field study conducted in northwest Louisiana, USA. Similarly, another alley-cropping study conducted in Minnesota reported that switchgrass growth was not affected by adjacent poplar hybrid ‘NM6’ (Populus maximeovitzii x P. nigra) and willow cultivar ‘Fish Creek’ (Salix purpurea) during the first two years following establishment (Gamble et al., 2014). These previous field findings suggest that tree-grass intercropping can be a viable source for producing biomass during the early rotation period prior to tree canopy closure. However, as all of these studies suggested, development of a tree canopy and root systems could induce interspecies competition for resources (light, water, and nutrients) and ultimately impose negative impacts on switchgrass growth. Based on findings from a greenhouse study and considering typical pine leaf area-to-age relationships, switchgrass productivity in a switchgrass–loblolly pine system in southeastern United States was projected to be significantly reduced between 6 and 8 years after establishment (Albaugh et al., 2014a). A negative effect on the biomass yield of switchgrass was observed in a midrotation (~13 year old) loblolly pine plantation in northwest Louisiana, USA (Blazier et al., 2012). Further, a recent field study conducted in eastern North Carolina showed that switchgrass growth was negatively affected by adjacent trees six years after establishment (Tian et al., 2015). Results of these studies confirmed that switchgrass growth would be eventually limited by tree growth, similar to many other silvopasture systems (Benavides et al., 2009).

Interspecies interactions in agroforestry are complex and occur both below- and aboveground (Ong et al., 1991; Schroth, 1998; Jose et al., 2004; Malezieux et al., 2009). Aboveground interactions typically involve microclimate variation (e.g., reducing temperature and wind speed) and shading effects on understory species (Jose et al., 2004). Belowground interactions generally occur when roots of multiple species simultaneously exploit resources (water and nutrients) from shared soil space (Schroth, 1998). These interactions can pose positive, nil, and negative impacts on understory species depending on their likelihood, intensity, and nature. Changes in microclimate conditions and some belowground interactions (e.g., hydraulic lift) in intercropping systems could benefit growth of understory species in traditional agroforestry systems (Lin et al., 1998; Jose et al., 2004; Tsonkova et al., 2012). Blazier et al. (2012) observed greater ground coverage of switchgrass in loblolly pine alleys than in open conditions, which was possibly due to the reduced heat stress under the tree canopy shade. On the other hand, competition for resources (light, water, nutrients) poses negative impacts on plant growth in agroforestry. The intensity of competition is subject to many site-specific factors, including tree size (age), root characteristics, physiological properties, and management practices. These factors, especially tree size (canopy and root) development with time, explain the distinct findings of tree impacts on switchgrass growth from several sites in the United States (Albaugh et al., 2012, 2014b; Blazier et al., 2012; Gamble et al., 2014; Tian et al., 2015). However, studies have seldom investigated the possible interspecific interactions and competition for resources that could negatively affect switchgrass growth in tree-switchgrass intercropping systems.

The objectives of this study were to (i) further evaluate the effects of pine trees on switchgrass growth to validate the hypothesis that switchgrass growth will be more negatively affected as trees grow larger, and (ii) investigate above- and belowground interactions for resources between pine trees and switchgrass to explore potential constraints suppressing switchgrass growth in intercropping system. The study was carried out at two established pine–switchgrass intercropping fields located in the coastal plain of North Carolina, United States.

Materials and methods

Description of study sites

Field measurements were conducted at two pine–switchgrass intercropping sites located in Lenoir and Carteret counties on the Coastal Plain of North Carolina, United States (Fig. 1a, b). Lenoir (35°15′N, 77°27′W) (Fig. 1c) and Carteret (34°48′N, 76°42′W) (Fig. 1d) were established to investigate sustainability and productivity of loblolly pine–switchgrass intercropping systems to produce saw timber and bioenergy feedstocks using a widespread traditional land use system in the southeastern United States. Both experimental sites are owned and operationally managed by Weyerhaeuser NR Company.

Soil in Lenoir site was characterized as either Pantego (fine, loamy, siliceous, semiactive, thermic Umbric Paleaquults) or Rains (fine, loamy, siliceous, semiactive, thermic Typic Paleaquults) soil series. The mean bulk density and mean porosity in the top 10 cm were 1.17 g cm⁻³ and 0.5 cm³ cm⁻³, respectively (Cacho et al., 2015). A network of 1.0–1.2-m-deep parallel open ditches was dug at approximate spacing of 100 m in the early 1970s to improve trafficability and provide

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desirable soil water conditions for tree growth. Long-term mean annual precipitation and temperature were 1252 mm and 16.5 °C, respectively (Albaugh et al., 2012). Experimental treatments including switchgrass monoculture (SWITCH) and pine–switchgrass intercropping (PSWITCH) were established as a randomized complete block design (Albaugh et al., 2012). The preexisting 34-year-old loblolly pine stand was harvested in September 2008. After site preparation, loblolly pine seedlings were planted during winter of 2008 at about 1100 stems ha$^{-1}$. The pine rows were spaced 6.1 m apart and oriented in the northeast–southwest direction (Fig. 1c). Switchgrass (Alamo cultivar) was planted in June 2009 in 3-m-wide alleys with edges approximately 1.5 m away from the rows of pine trees (Cacho et al., 2015). Switchgrass in both treatments have received the same management practices. The switchgrass received coated urea Arborite® fertilizer (65.6 kg N ha$^{-1}$, 6.6 kg P ha$^{-1}$ and 0.2 kg K ha$^{-1}$) during 2010, 2012, and 2014. Leaf area index (LAI) of pine trees measured using AccuPAR LP-80 (Decagon Devices, Inc., Pullman, WA, USA) was about 3.7 m$^2$ m$^{-2}$ in June 2015, and tree height was about 7.5 m (unpublished data). Detailed descriptions of the study site, experimental design, site preparation, and treatments can be found elsewhere (Albaugh et al., 2012, 2014b; Cacho et al., 2015; Tian et al., 2015).

Carteret site was also artificially drained by four 1.2-m-deep parallel lateral ditches dug at 100 m spacing. The poorly drained soil (Deloss fine sandy loam, fine-loamy, mixed, semi-active, Thermic Typic Umbraults) has a mean bulk density of 1.25 g cm$^{-3}$ and mean porosity of 0.36 cm$^3$ cm$^{-3}$ in the top 10 cm. Long-term mean annual precipitation and temperature were 1517 mm and 16.4 °C, respectively (Amatya & Skaggs, 2011). This study site was initiated in early 1980s to study the hydrology and water quality in the artificially drained pine plantations (Amatya et al., 1996, 2003; Amatya & Skaggs, 2011; Tian et al., 2012, 2013). PSWITCH was established after clearcutting a 35-year-old loblolly pine stand (about 25 ha) in spring of 2009. Information about site preparation for planting switchgrass is described in detail by Muwamba et al. (2015). Pine seedlings were planted at a density of 1087 trees ha$^{-1}$ in January 2010 after standard site preparation. Tree rows were oriented in the east–west direction (Fig. 1d). Switchgrass (Alamo cultivar) was initially planted during August 2011 and replanted in April 2012 because of low germination rate. After planting, switchgrass was fertilized using Weyerhaeuser’s coated urea Arborite® fertilizer once per year during late spring at the same rate as Lenoir site. As of July 2015, measured LAI and tree height of pine trees were 3.9 m$^2$ m$^{-2}$ and 7.6 m, respectively (unpublished data).

**Grass sampling and laboratory processing**

Destructive samples of switchgrass were collected through the growing season (May to November) of 2015 to determine aboveground biomass productivity and its seasonal pattern (growth curve). To evaluate effects of pine trees on switchgrass in PSWITCH, we collected grass samples at two positions from both study sites: one at the center (CENTER) and one at the edge (EDGE) of the switchgrass alley between two adjacent tree beds. For Lenoir, two transects between tree rows were randomly selected during each sampling time at each study plot, which provided eight samples (four at CENTER and four at EDGE). We applied pseudoduplicated experimental design in Carteret by dividing the study site into front and back sampling plots (Fig. 1d). A total of six samples (three at EDGE and...
three at CENTER) were collected from each sampling plot during each sampling time, which yielded 12 samples per treatment per sampling time. For SWITCH in Lenoir, four samples were randomly collected from each plot at individual sampling times.

Sampling area was restricted by a 1 m x 1 m quadrat made of PVC. Switchgrass shoots were cut at about 10 cm from the ground surface using hedge shears. Samples were placed inside paper bags and transported to the laboratory for further processing. In the laboratory, other herbaceous plants (relatively small) were removed from collected samples before weighing to determine total fresh weight of switchgrass per square meter. A 200- to 250-g subsample was taken from each biomass sample to determine water content by oven-drying at 70 °C for 48 h. Total dry biomass per square meter was calculated based on the total fresh weight and measured water content. Detailed procedures of field sampling and laboratory processing can be found in Tian et al. (2015).

Measurements of soil water content, photosynthetically active radiation (PAR), and soil mineral nitrogen content

As several studies from agroforestry systems have demonstrated that water competition between tree and crop typically occurs at the very top soil layers (Livesley et al., 2004; Gao et al., 2013; Sudmeyer & Hall, 2015), volumetric soil water content (θsv, cm) was measured only at 5 cm deep throughout July to December 2015. Two soil water content probes (Decagon Devices, Inc.) were installed in the intercropped treatments at the EDGE (1.5 m away from the tree row) and CENTER (3 m away from the tree row) (Fig. 1c, d). At the same spots, PAR was measured at EDGE and CENTER using a HOBO PAR Smart Sensor S-LIA-M003 placed above the top of switchgrass canopy to measure light available for switchgrass growth. Continuous soil moisture data and PAR were each recorded for 1 min and averaged at 15-min intervals using a HOBO U30 NRC data logger (Onset Computer Corporation, Bourne, MA, USA).

Composted soil samples were collected at depths 0–15 and 15–30 cm from the study sites using a hand auger (2 cm radius). At the beginning of sampling, two sampling subplot sets were set up for PSWITCH at Lenoir (Fig. 1c) and for both front and back (approximately 200-m apart) at Carteret (Fig. 1d). Two sampling transects were set up for SWITCH in Lenoir to represent the average site condition (Fig. 1c). Soil samples were collected from six sampling points located approximately 20 m apart in subplots or along sampling transects at each sampling time (Fig. 1c, d). At each sampling point, samples were collected from both EDGE and CENTER in PSWITCH. Six samples from each subplot/transect were put into a plastic bag. At each sampling time, we collected four soil samples (two for each depth) from EDGE and CENTER at each study plot, which yielded 16 samples in total from PSWITCH at both sites. All soil samples were transported to the laboratory in an iced cooler for subsequent analysis. Soil samples were passed through 2-mm sieve after removing woody debris, roots, and stones. A K2SO4 solution was used for chemical extraction of sieved samples. Extracted solution was analyzed for ammonium nitrogen and nitrate nitrogen concentrations using AA3 air-segmented continuous flow system analyzer (SEAL Analytical, Ltd., Mequon, WI, USA). The sum of ammonium nitrogen and nitrate nitrogen represented total mineral nitrogen.

Light-response curve

We measured light-response curves (LRC) using two portable photosynthesis systems (LI-6400, LI-COR, Inc., Lincoln, NE, USA) equipped with a standard 6 cm2 area cuvette. Six fully developed and healthy leaves from the upper third of plants were selected from grasses growing at both EDGE and CENTER. During measurements, the two systems were rotationally used on leaves at EDGE and CENTER to eliminate possible equipment artifacts. For each leaf, gas exchange measurements were made in a sequence at 9 light levels starting at saturation as follows: 2000, 1500, 1000, 500, 200, 100, 50, 20, and 0 μmol m−2 s−1. The CO2 reference was maintained at a constant concentration of 400 μmol mol−1, while temperature and humidity were maintained at ambient conditions characterized by mean temperature of 25.4 °C and mean humidity of 72%. Humidity inside the chamber was monitored during measurements to ensure it was high enough (above 50%) to provide accurate measurements. Measurements of LRC were taken when the leaf was fully induced at that irradiance level. Leaf measurements were carried out between 9:30 AM and 1:30 PM, in coordination with timing of maximum gas exchange rates not impacted by afternoon partial stomatal closure. Each curve took approximately 30–40 min, prohibiting us to obtain a larger number of samples.

The response of leaf assimilation rate (A, μmol m−2 s−1) to light was modeled using the rectangular hyperbolic light-response curve model [Equation 1 (Lobo et al., 2013)].

\[
A = \frac{A_{\text{max}}}{I} - R_d
\]

where I is the apparent quantum yield (i.e., the initial slope of the light-response curve [μmol (CO2) mmol−1 (photons)])], I is measured photosynthetic photon flux density [μmol (photon) m−2 s−1], Amax is the maximum leaf-level CO2 uptake rate [μmol (CO2) m−2 s−1] at light saturation, and Rd is dark respiration rate [μmol (CO2) m−2 s−1]. The equation was fitted by least squares minimization using a published Microsoft Excel tool (Lobo et al., 2013). In addition to Equation 1 parameters, several other variables were also estimated to explore differences in light response of leaves at EDGE and CENTER: Icomp = light compensation point [μmol (photon) m−2 s−1], Imax = light saturation point beyond which there is no significant change in A [μmol (photon) m−2 s−1], A(Imax) = maximum photosynthetic rate obtained at I = Imax [μmol (CO2) m−2 s−1].

Statistical analysis

An analysis of variance (ANOVA) was performed to test for treatment and position effects on grass growth, physiology, and soil mineral nitrogen content. The statistical analysis was carried out using SAS 9.4 mixed procedures (PROC MIXED) (SAS Institute Inc., Cary, NC, USA).
The variance components covariance (VCC) structure was used to take into account varying residual variances for each time of measurement. Readers are referred to Tian et al. (2015) for details of statistical analyses for treatment and location effects on switchgrass growth. For comparing treatment effects on soil mineral nitrogen in Lenoir, treatment (PSWITCH vs. SWITCH), we considered time of measurement, depth, and associated interactions (treatment by time of measurement, treatment by depth, time of measurement by depth, and treatment by time of measurement by depth) to be fixed effects, while block, block × treatment, and block × treatment × depth to be random effects. Similarly, to determine tree impacts on soil mineral nitrogen within PSWITCH in both sites, we considered position (EDGE and CENTER), time of measurement, depth and corresponding interactions (position by time of measurement, position by depth, time of measurement by depth, and position by time of measurement by depth) to be fixed effects. Location (front and back), location by depth of measurement interaction were considered to be random effects. Paired Student’s $t$-test was used to investigate effects of position on PAR and soil water content by assuming a normal distribution of these continuous measurements. The following conventions were used to define the significance of statistical tests: nonsignificant when $P > 0.1$, marginally significant when $0.05 < P \leq 0.1$, and significant when $P \leq 0.05$.

**Results**

**Biomass accumulation during the growing season of 2015**

From May to November of the 2015 growing season, aboveground biomass of switchgrass increased from $92 \pm 22$ to $524 \pm 130$ g m$^{-2}$ at EDGE, and from $131 \pm 38$ to $840 \pm 140$ g m$^{-2}$ at CENTER in Lenoir (Fig. 2a). Similarly, aboveground switchgrass biomass increased from $84 \pm 9$ g m$^{-2}$ to $460 \pm 90$ g m$^{-2}$ at EDGE, and from $117 \pm 25$ to $732 \pm 115$ g m$^{-2}$ at CENTER in Carteret (Fig. 2b). Switchgrass growth and biomass accumulation primarily occurred during May through July. By the end of the growing season, switchgrass at EDGE produced about 37% less ($P < 0.001$) biomass than grass at CENTER in both Lenoir and Carteret. Aboveground biomass accumulation during the growing season in both sites was significantly affected by position ($P < 0.001$), time ($P < 0.001$), and position–time interaction ($P < 0.02$) (Table 1). Aboveground biomass accumulation of switchgrass for SWITCH and PSWITCH treatments in Lenoir was also compared (Fig. 2a). Aboveground biomass of switchgrass in PSWITCH increased from $112 \pm 36$ to $682 \pm 210$ g m$^{-2}$ and from $124 \pm 40$ to $927 \pm 187$ g m$^{-2}$ for SWITCH. Switchgrass in SWITCH produced about 36% more ($P = 0.002$) biomass than in PSWITCH. Aboveground biomass accumulation was significantly affected

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### Table 1

Type 3 tests of fixed effects results ($P > F$) from the mixed model analysis of variance (ANOVA) for aboveground biomass under different treatments (SWITCH and PSWITCH), and between two positions (CENTER and EDGE) in PSWITCH at Lenoir and Carteret

| Effect         | Lenoir | Carteret |
|----------------|--------|----------|
| Treatment      |       |          |
|                | df   | $F$   | $P > F$ | $F$       | $P > F$ |
| Treatment      | 1    | 24.9  | 0.001  |          |          |
| Time           | 5    | 117.9 | <0.001 |          |          |
| Treatment × Time| 5   | 5.0   | 0.002  |          |          |
| Position       | 1    | 44.4  | <0.001 | 83.6     | <0.0001 |
| Time           | 5    | 50.2  | 0.0001 | 170.1    | <0.0001 |
| Position × Time| 5   | 2.2   | 0.02   | 11.6     | <0.0001 |

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by time \((P < 0.001)\), treatment \((P = 0.001)\), and treatment–time interaction \((P = 0.002)\) (Table 1). It is worth noting that grass growth in SWITCH and CENTER in PSWITCH was not statistically different \((P > 0.4)\).

Effects of pine trees on PAR above grass canopy

To investigate tree shading effects on PAR level above grass canopy, we compared PAR measurements between treatments and between positions. According to paired t-test, tree canopy significantly \((P < 0.001)\) reduced PAR level above grass canopy by approximately 58\% over the study period when compared to grass at SWITCH in Lenoir (Fig. 3a–c). As expected, switchgrass at CENTER continuously received significantly \((P < 0.003)\) higher PAR than grass at EDGE for both Lenoir (Fig. 3d–f) and Carteret (Fig. 3g–i). The relationships of PAR above grass canopy between treatments (Fig. 3b) and between positions were linear for both sites (Fig. 3d, h), while the relationship between treatments was relatively weak based on the coefficients of determination. The ratio of PAR above grass canopy in PSWITCH to SWITCH ranged from 0.15 to 0.63 and declined from July to December (Fig. 3c). In Lenoir, daily mean PAR at the EDGE was about 52 ± 9\% of that at CENTER and the ratio was relatively constant over the study period (Fig. 3f). In Carteret, however, the ratio of PAR at EDGE to PAR at CENTER was about 29 ± 11\% during July to middle September and increased to 65 ± 24\% afterward (Fig. 3i).

The shape of the light-response curves of photosynthesis (Fig. 4) shows that switchgrass grown at EDGE tended to display slightly higher assimilation rates under low light levels, but had lower assimilation rates under higher light levels. Maximum gross photosynthesis rate of grass grown at CENTER was higher by 15\% \((P = 0.04)\) than grass at EDGE (Table 2). Conversely, apparent quantum yield of grass grown at CENTER was lower by 28.5\% \((P = 0.04)\) than grass at EDGE. The dark respiration of grass grown at EDGE was significantly \((P = 0.03)\) higher than that at CENTER. Light
saturation point of grass grown at CENTER was higher by 40% ($P = 0.03$) than grass at EDGE. Meanwhile, light compensation point and maximum net photosynthetic rate of grass grown at CENTER and at the EDGE were not significantly different ($P > 0.12$).

Soil water content difference between EDGE and CENTER

Lenoir depicted high temporal dynamics of soil water content at a depth of 5 cm ($\theta_5$ cm$^{-3}$) (Fig. 5a). At the EDGE, $\theta_5$ cm ranged from 0.07 to 0.51 cm$^{-3}$ with a mean of 0.23 cm$^{-3}$, while at the CENTER, it ranged from 0.18 to 0.45 cm$^{-3}$ with a mean of 0.29 cm$^{-3}$. The differences in $\theta_5$ cm between the CENTER and EDGE at Lenoir was statistically significant ($P = 0.0001$) with CENTER having consistently higher values. In addition, the average difference between $\theta_5$ cm at the EDGE and CENTER in Lenoir evidently decreased from 0.09 cm$^{-3}$ during peak growing season (July and August) to 0.02 cm$^{-3}$ during postgrowing season. Carteret showed relatively small temporal variations of $\theta_5$ cm changing from 0.11 to 0.28 cm$^{-3}$ with a mean of 0.2 cm$^{-3}$ at the EDGE and from 0.09 to 0.31 cm$^{-3}$ with a mean of 0.2 cm$^{-3}$ at the CENTER. Further, differences in $\theta_5$ cm between the EDGE and CENTER in Carteret were not significant ($P = 0.42$). The relationship between $\theta_5$ cm at the EDGE and CENTER was linear with coefficient of determination of 0.9 for both Lenoir (Fig. 5c) and Carteret (Fig. 5b).

Monthly changes of soil mineral nitrogen content

Large temporal variations were observed for soil mineral nitrogen content from both 0 to 15 cm ($[N]_{15}$ cm) and 15–30 cm ($[N]_{30}$ cm) in both sites (Fig. 6). In Lenoir, $[N]_{15}$ cm at EDGE increased from 6.2 mg kg$^{-1}$ soil in early May to 9.2 mg kg$^{-1}$ soil in mid-June and then decreased steadily to 3.5 mg kg$^{-1}$ soil by November. In contrast, $[N]_{15}$ cm at CENTER continuously decreased from 6.6 mg kg$^{-1}$ soil to 3.6 mg kg$^{-1}$ soil by November with a slight increase during August. Soil mineral nitrogen content at 30 cm at EDGE and CENTER showed

### Table 2  Photosynthetic parameters (fitted and calculated) of light response curves of switchgrass located at EDGE and CENTER in Lenoir, bold P values highlight significant difference of photosynthetic parameters for leaves at EDGE and CENTER

| Parameters | Edge       | Center     | P value (df = 5) |
|------------|------------|------------|-----------------|
| $A_{\text{gmax}}$ | 15.3 ± 2.9 | 17.6 ± 2.9 | 0.04            |
| $\alpha$   | 0.09 ± 0.02| 0.07 ± 0.01| 0.04            |
| $R_d$      | 0.5 ± 0.4  | 0.8 ± 0.2  | 0.03            |
| $I_{\text{comp}}$ | 7.2 ± 3.1 | 7.7 ± 2.4  | 0.13            |
| $I_{\text{max}}$ | 706 ± 183 | 991 ± 290  | 0.03            |
| $A_{(\text{max})}$ | 14.8 ± 2.9 | 16.9 ± 2.9 | 0.12            |

$A_{\text{gmax}}$ = maximum gross photosynthesis rate [mmol (CO$_2$) m$^{-2}$ s$^{-1}$], $\alpha$ = apparent quantum yield at $I = 0$ [mmol (CO$_2$) mmol$^{-1}$ (photon)], $R_d$ = dark respiration rate [mmol (CO$_2$) m$^{-2}$ s$^{-1}$], $I_{\text{comp}}$ = light compensation point [mmol (photon) m$^{-2}$ s$^{-1}$], $I_{\text{max}}$ = light saturation point beyond which there is no significant change in net assimilation [mmol (photon) m$^{-2}$ s$^{-1}$], $A_{(\text{max})}$ = maximum net photosynthetic rate obtained at $I = I_{\text{max}}$ [mmol (CO$_2$) m$^{-2}$ s$^{-1}$]; Values are means (± STD), $n = 6$.

![Fig. 5](https://i.imgur.com/3.png) Comparison between soil moisture content of top 5 cm ($\theta_5$ cm$^{-3}$) at edge and center of the intercropped grass bed in Lenoir (a) and Carteret (b) from July to December in 2015. Inset figures depicts the relationship between $\theta_5$ cm at the EDGE and CENTER in Lenoir (c) and Carteret (d).
similar temporal variations as \([N]_{15}\) cm (Fig. 6b), but was significantly \((P = 0.0002)\) lower (Table 3). Soil mineral nitrogen content was significantly affected by position \((P < 0.0001)\), depth \((P < 0.0001)\), and time \((P < 0.0001)\), but not by their interactions \((P > 0.5)\), except position \(\times\) time \((P = 0.009)\). The pairwise comparison showed that \([N]_{15}\) cm and \([N]_{30}\) cm at EDGE were significantly \((P < 0.1)\) higher than those at CENTER from June to August, but not significantly different \((P > 0.5)\) in early May or during late growing season (September and November, Table 4).

Temporal variations of \([N]_{15}\) cm and \([N]_{30}\) cm in Carteret were not as evident as in Lenoir except for the sudden increase in June immediately after fertilizer application (Fig. 6c, d). The fertilization increased \([N]_{15}\) cm from 11.5 mg kg\(^{-1}\) soil to 28.2 mg kg\(^{-1}\) soil at EDGE and from 7.2 mg kg\(^{-1}\) soil to 24.7 mg kg\(^{-1}\) soil at CENTER, and increased \([N]_{30}\) cm from 4.8 mg kg\(^{-1}\) soil to 12.5 mg kg\(^{-1}\) soil at EDGE and from 4.6 mg kg\(^{-1}\) soil to 11.2 mg kg\(^{-1}\) soil at CENTER. Soil mineral nitrogen content was significantly affected by depth \((P = 0.02)\), time \((P < 0.0001)\), and their interactions \((P < 0.0001)\), but not by position \((P = 0.28)\) or its interactions with other factors \((P > 0.2)\). The pairwise comparison suggested that the \([N]\) was significantly \((P < 0.02)\) affected by depth through the study period, but not by position \((P > 0.11)\).

Soil mineral nitrogen content at 15 cm at PSWITCH increased from 6.4 mg kg\(^{-1}\) soil in early May to 7.6 mg kg\(^{-1}\) soil in mid-June, then steadily decreased to 3.6 mg kg\(^{-1}\) soil by November (Fig. 7). Soil mineral nitrogen content at 15 cm at SWITCH depicted similar seasonal changes, but its magnitudes were consistently lower than PSWITCH (Fig. 7). At PSWITCH, \([N]_{15}\) cm was about 21% higher than at SWITCH from May to July, and about two times higher during August and September, but decreased to 42% by November. Temporal variations of \([N]_{30}\) cm for both SWITCH and PSWITCH were very similar to \([N]_{15}\) cm. Although differences in \([N]_{30}\) cm between treatments were smaller than for \([N]_{15}\) cm, the larger differences between treatments occurred during August and September for both depths.

Soil mineral nitrogen content was not significantly affected by treatment \((P = 0.39)\), but pairwise comparison suggested that treatment impacts were marginally significant \((P = 0.09)\) on August 6 (Table 4). In SWITCH, the effect of depth on \([N]\) was not significant \((P > 0.16)\). In PSWITCH, the effect of depth on \([N]\) was marginally significant \((P < 0.1)\) on May 5 and September 13, and significant \((P = 0.01)\) on November 12.
Discussion

Tree growth intensified negative effects on grass growth

Tree size/age in terms of canopy and root characteristics (e.g., canopy size and shape, rooting depth, root length, and plasticity) is a critical factor in determining the intensity of tree-crop interactions in agroforestry systems (Ong et al., 1991; Schroth, 1998; Jose et al., 2004; Benavides et al., 2009; Blazier et al., 2012). For example, an alley-cropping study conducted in the Midwestern United States showed that yields of corn grown in rows adjacent to black walnut (Juglans nigra L.) or red oak (Quercus rubra L.) declined by more than 50% as trees grew bigger 10 years after establishment (Gillespie et al., 2000). Therefore, we expected pine–switchgrass interactions to quickly evolve with stand development of pine–switchgrass intercropping system because of the rapid juvenile growth of loblolly pine.

Table 3 Type 3 tests of fixed effects results ($P > F$) from the mixed model analysis of variance (ANOVA) for soil mineral nitrogen content under different treatments (SWITCH and PSWITCH), and at two positions (CENTER and EDGE) in PSWITCH at Lenoir and Carteret

| df | Lenoir | Carteret |
|----|--------|----------|
| Treatment | 1 | $P = 0.39$ | $P = 0.93$ |
| Time | 5 | $P < 0.0001$ | $P < 0.0001$ |
| Depth | 1 | $P = 0.12$ | $P = 0.93$ |
| Treatment × Time | 5 | $P = 0.067$ | $P = 0.93$ |
| Treatment × Depth | 1 | $P = 0.12$ | $P = 0.93$ |
| Treatment × Time × Depth | 5 | $P = 0.93$ | $P = 0.93$ |
| Time | 5 | $P < 0.0001$ | $P < 0.0001$ |
| Position | 1 | $P = 0.0002$ | $P = 0.28$ |
| Depth | 1 | $P = 0.0002$ | $P = 0.28$ |
| Position × Depth | 1 | $P = 0.55$ | $P = 0.24$ |
| Position × Time | 5 | $P = 0.009$ | $P = 0.55$ |
| Depth × Time | 5 | $P = 0.7$ | $P < 0.0001$ |
| Position × Depth × Time | 5 | $P = 0.88$ | $P = 0.93$ |

Table 4 Pairwise comparison results ($P > F$) using the Tukey-Kramer adjustment method for effects of multiple factors on soil mineral nitrogen content in Lenoir (treatment, position, and depth) and Carteret (position, and depth), significant factors at individual day are highlighted by bold values

| Date | Lenoir | Carteret |
|------|--------|----------|
|      | Position | Treatment | Depth (PSWITCH) | Depth (SWITCH) | Position | Depth |
| 5-May | 0.99 | 0.94 | 0.09 | 0.91 | 0.31 | 0.02 |
| 13-Jun | 0.002 | 0.91 | 0.33 | 0.16 | 0.22 | <0.0001 |
| 9-Jul | 0.01 | 0.57 | 0.41 | 0.73 | 0.11 | 0.004 |
| 6-Aug | 0.07 | 0.09 | 0.33 | 0.83 | 0.17 | 0.007 |
| 13-Sep | 0.50 | 0.16 | 0.09 | 0.57 | 0.26 | 0.005 |
| 12-Nov | 0.95 | 0.52 | 0.01 | 0.17 | 0.41 | 0.07 |

Previous studies in Lenoir showed that biomass yields and leaf-level gas exchange rates of switchgrass were not affected by adjacent trees during the first three years after site establishment (Albaugh et al., 2012, 2014b). In contrast, a more recent study at the same site demonstrated that switchgrass growth was negatively affected by six-year-old pine trees (Tian et al., 2015), suggesting tree–grass competition in the intercropping system has intensified from early stages. Our measurements of biomass yields during two consecutive years supported the hypothesis that tree–grass interactions will intensify toward canopy closure for this system (Table 5). Compared to yield measurements during 2014 (Tian et al., 2015), grass yield in 2015 reduced by 13% at EDGE and remained comparable at CENTER at Lenoir, while reduced by 21% and 9% at EDGE and CENTER, respectively, at Carteret. The ratio of biomass yield at EDGE to CENTER decreased by approximately 10% at both sites. This finding can be explained by the fast growth of loblolly pines with tree height and LAI increasing, respectively, by 0.5 m and 0.4 m² m⁻² in Lenoir and by 0.9 m and 0.6 m² m⁻² in Carteret. The magnified differences in biomass yields between EDGE and CENTER from 2014 to 2015 in both sites suggested that the system is highly dynamic and switchgrass growth has been increasingly suppressed by adjacent trees at the current stage.

Light is a dominant factor affecting grass growth in the intercropping system

Others have reported that shade from adjacent trees is a critical factor limiting switchgrass growth in pine–switchgrass intercropping systems (Blazier et al., 2012; Albaugh et al., 2014a; Tian et al., 2015). Tian et al. (2015) reported significant position impacts on PAR between tree rows based on two day measurements in early summer and late fall. Continuous measurements in this study showed that PAR availability was significantly reduced by adjacent trees during the growing...
season at both study sites (Fig. 3). Compared to Lenoir, Carteret had abundant soil resources with approximately twice the amount of precipitation (unpublished data) and soil mineral nitrogen availability (Fig. 6) during the 2015 growing season. However, PSWITCH in Lenoir produced 15% higher biomass than Carteret did (Fig. 2), which is in consistent with about 18% higher mean PAR above switchgrass canopy in Lenoir (Fig. 3). This comparison demonstrated that light availability was the dominant factor that affected switchgrass growth in the intercropping system at current stage of development.

We observed different seasonal changes of PAR under tree canopy in Lenoir and Carteret. Variation of PAR with time and their magnitudes at different locations varied somewhat between the two sites. Specifically, PAR measured during July at CENTER of Lenoir was almost 1.5 times higher than PAR measured at CENTER of Carteret (Fig. 3e, h). The decline in PAR measured at CENTER of Carteret was much steeper than the decline in PAR measured at CENTER of Lenoir (Fig. 3e, h). Higher reduction of PAR in Carteret was mainly attributed to its larger tree size, while we attributed the different seasonal variation of the ratio of PAR at EDGE to CENTER at the two sites mainly to their different tree row orientations (Fig. 1d). Impact of tree row orientation on the reduction of PAR level in agroforestry system has also been reported by other studies (Jackson & Palmer, 1972; Dufour et al., 2013).

A reduction in PAR level may not lead to a proportional decrease in biomass growth because of compensatory responses of plant morphological and physiological properties to tree shade. Tian et al. (2015) reported tree shade induced morphological changes of switchgrass with higher specific leaf area and taller height observed at PSWITCH compared to SWITCH. This study found that switchgrass grown at the EDGE had significant lower maximum gross photosynthetic rate and light saturation point, but higher apparent quantum yield (Table 2). Observed physiological changes of grass due to shading are different from findings by Albaugh et al. (2014b) who reported no effects of distance from trees on gas exchange variables of switchgrass. This is likely because tree size has almost doubled in terms of LAI and height since the

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**Table 5** Comparison of biomass productivity (mean ± SE, kg m⁻² yr⁻¹) at different positions (EDGE and CENTER) at Lenoir and Carteret in 2014 and 2015. Biomass yield data of 2014 were obtained from (Tian et al., 2015). Bold values of the bottom are ratios between grass yield at EDGE and CENTER during both years.

|        | Lenoir* |            | Carteret† |            |
|--------|---------|------------|-----------|------------|
|        | 2014    | 2015       | 2014      | 2015       |
| EDGE   | 598 ± 58| 523 ± 65   | 577 ± 98  | 459 ± 37   |
| CENTER | 843 ± 70| 839 ± 70   | 800 ± 121 | 732 ± 47   |
| PSWITCH| 722 ± 80| 681 ± 74   | 689 ± 81  | 595 ± 50   |
| EDGE/CENTER | 0.71   | 0.62       | 0.72      | 0.63       |

*Tree plant date: December 2008, grass plat date: June of 2009 in Lenoir.
†Tree plant date: January 2010, grass plat date: August of 2011 in Carteret.
field measurements of Albaugh et al. (2014a,b). Similar physiological responses to shading have also been observed for other C4 plants (Kephart et al., 1992; Cruz, 1997).

Belowground tree–grass interactions

Belowground tree–grass interaction and associated competition for soil resources (i.e., water, nitrogen) is another well-recognized factor that may limit understory species growth, but is much less studied (Ong et al., 1991; Schroth, 1998; Jose et al., 2004; Malezieux et al., 2009). Belowground interaction is affected by several biotic and abiotic factors such as soil resources availability, root characteristics, climatic conditions, and phenology (Ong et al., 1991; Jose et al., 2004) and could result in various outcomes in terms of understory growth. Some studies have observed favorable soil water conditions for understory growth in agroforestry because of hydraulic lift by trees (Emerman & Dawson, 1996; Hirota et al., 2004), while many others have reported crop yield reduction due to competition for water (Gillespie et al., 2000; Jose et al., 2000a; Miller & Pallardy, 2001; Livesley et al., 2004; Everson et al., 2009; Sudmeyer & Hall, 2015). Roots of pine trees and switchgrass could share some soil space despite the presence of 1.5-m-wide buffer between the switchgrass alley and tree row. This is supported by evidence showing surficial fine roots of a loblolly pine plantation at midrotation stage can reach as much as 5.8 m laterally (Johnsen et al., 2005). In the absence of belowground interspecific interactions for soil water at the tree–grass interface, we expected \( \theta_5 \) cm at EDGE to be higher than at CENTER because of less grass growing at EDGE (Fig. 2). However, field observations showed significantly lower \( \theta_5 \) cm at EDGE compared to CENTER in Lenoir (Fig. 5a) and no significant difference was found for Carteret (Fig. 5b). This finding is comparable to several published studies in agroforestry fields (Livesley et al., 2004; Gao et al., 2013; Sudmeyer & Hall, 2015). These results suggest possible competition because both tree and grass took up soil water at the interface in both sites, while the intensity of interaction was higher in Lenoir. The relatively less intense tree–grass interaction and competition for water in Carteret was most likely due to higher precipitation occurring at that site during July through October (1065 mm), compared to only 484 mm in Lenoir for the same period. This inference is consistent with the phenomena that competition for resources among species increases with resource scarcity and declines when resources are abundant. Lastly, it is worthy to note that the difference between \( \theta_5 \) cm at EDGE and at CENTER in both sites may also have been partially caused by spatial differences in rainfall interception. Nevertheless, we believe such a contribution was minimal because the soil water measurements at EDGE was at the edge of tree canopy (about 2.1 m in radius).

Crop yield reduction due to competition for nutrients is less commonly reported (Campbell et al., 1994; Jose et al., 2000b), because application of fertilizer at conventional agronomic levels is a common practice in most agroforestry systems (Jose et al., 2004). Position was found to be an important factor affecting soil [N] in Lenoir (not fertilized in 2015), but not in Carteret (fertilized in 2015). This contrasting finding between two study sites was mainly caused by fertilizer application, which significantly reduced the spatial difference of [N] at EDGE and CENTER in Carteret. For Lenoir, position effects on soil [N] were only significant from June to August (Table 4). Temporal changes of difference in soil [N] between CENTER and EDGE (Fig. 6) coincided with seasonal switchgrass biomass increments (Fig. 2). Fast growth of switchgrass from May to July primarily contributed to the more evident differences in [N] at EDGE and CENTER during these periods. The difference quickly decreased after August when switchgrass began to senesce, while loblolly pine was still growing. As expected, due to different assimilation metabolism (C3 vs. C4), this finding suggests that there is a difference in phenology between switchgrass and loblolly pine with respect to nitrogen uptake and underground interspecific interactions in terms of soil nitrogen uptake at the tree–grass interface. This inference was also supported by the seasonal changes in difference of [N] between SWITCH and PSWITCH in Lenoir (Fig. 7). Other studies have also reported that trees effectively reduced soil mineral nitrogen in agroforestry systems during autumn (Jose et al., 2000b; Palma et al., 2007; Andrianarisoa et al., 2015).

Implications and recommendations

Results of this study verified that loblolly pine negatively affected switchgrass growth in intercropping systems (Fig. 2 and Table 5) five to seven years after establishment in the coastal area of southeastern United States. Switchgrass growth in 2015 was increasingly suppressed due to loblolly pine tree growth (Table 5) when compared to 2014 measurements (Tian et al., 2015). This finding suggested rapidly intensified interspecific competition for resources at current stand age. Tree shade, which is function of tree row orientation and tree canopy size, was found in this study to be a critical constraint for switchgrass growth in intercropping systems (Figs 3 and 4). As tree canopy approaches closure, production of intercropped switchgrass in these studied sites may only be possible for one or two more years if no further management practices are applied (e.g.,
pruning, thinning). It is worth noting that reported grass yields in this study may not be suitable for estimating overall site productivity, because our sampling strategies were mainly intended to evaluate the tree effects on switchgrass growth, rather than quantifying overall biomass yield. More studies are also necessary to evaluate possible intercropping impacts on pine tree growth because timber production is the primary goal of this cultural system. Previous studies found that switchgrass exerted considerable competitive pressures on loblolly pine seedlings (Krapfl et al., 2015) resulting in reduction in biomass yield of loblolly pine in intercropping systems (Haile et al., 2016), although tree–grass combined biomass yield was evidently enhanced in intercropping systems (Susaea et al., 2012; Haile et al., 2016).

Distinct soil water and mineral nitrogen contents at EDGE and CENTER of the grass bed (Fig. 5) suggested that pine and switchgrass shared the same soil domain at their interface. However, it is unknown if interspecific competitions for soil resources were occurring. We surmise that competitions for water in both study sites are unlikely given the high precipitation and poorly drained soil. Larger difference of soil mineral nitrogen during peak grass growing season suggested that asynchronous nitrogen uptake between loblolly pine and switchgrass occurred, which could partly alleviate interspecific competition for soil nitrogen. Observed rapid decline of soil nitrogen availability at CENTER (Fig. 6) and in SWITCH (Fig. 7) during the peak grass growing season is consistent with findings from another study (Minick et al., 2014) and has important implications for long-term soil nitrogen availability if switchgrass production and removal without supplemental fertilization continues in these forests. Dedicated field measurements on temporal and spatial distribution of roots, isotope tracer studies, or root exclusion studies are necessary to advance our understanding of belowground interspecific interactions.

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