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PRODUCTION PHYSIOLOGY OF THREE NATIVE ORNAMENTAL SHRUBS INTERCROPPED IN A YOUNG LONGLEAF PINE PLANTATION

Donald L. Hagan[1], Shibu Jose[1], Mack Thetford[2], and Kimberly Bohn[3]

[1]School of Forest Resources & Conservation, University of Florida, Gainesville, FL USA 32611
[2]Department of Environmental Horticulture, University of Florida, Milton, FL, USA 32583
[3]School of Forest Resources & Conservation, University of Florida, Milton, FL, USA 32583
Contact: donhagan@ufl.edu

Abstract: The production of woody floral products – the fresh or dried stems that are used for decorative purposes – may be an attractive option for southeastern landowners looking to generate income from small landholdings. Since many shrubs native to the understory of the longleaf pine ecosystem have market potential, one possibility is the intercropping of select species in the between-row spacing of young longleaf pine plantations. The objective of this study was to evaluate how competition affects the physiology, and thus the productivity of American beautyberry (*Callicarpa americana* L.), wax myrtle (*Morella cerifera* (L.) Small) and inkberry (*Ilex glabra* (L.) A.Gray) when intercropped in a longleaf pine (*Pinus palustris* Mill.) plantation in the southeastern United States. The effect of competition was assessed via comparisons of mortality, biomass, light transmittance, gas exchange and soil moisture between intercropping and monoculture (treeless) treatments. Overall, shrubs in the intercropping treatment performed worse than those in the monoculture, with higher mortality, and reductions in biomass of 75.5%, 50.6 %, and 68.7% for *C. americana*, *M. cerifera* and *I. glabra*, respectively. Root-shoot ratios for all species were significantly higher and soil moisture during dry periods was significantly lower in the intercropping treatment. Light transmittance below the pine canopy was high (57.7%) and *I. glabra* was the only species that exhibited reduced photosynthesis due to shading. These results suggest that the effect of shading is minimal and belowground competition is likely the most important determinant of productivity in this system.

Keywords: Intercropping, longleaf pine, ornamentals, woody florals, competition, physiology

INTRODUCTION

The interest in alternative cropping practices such as intercropping has been increasing in the United States over the years. However, the knowledge base required for the proper design and implementation of such systems is limited (Vandermeer 1992, Jose and Gordon 2008). This is due to the fact that the science and practice of temperate intercropping is relatively new, and that these systems, with their potential for interspecific interactions, are much more complex than conventional monocultures (Garrett and Buck 1997; Gillespie et al. 2000).

The productivity of a mixed-species cropping system is ultimately determined by the type and extent of interactions that occur within it (Zhang et al. 2003, Jose et al. 2006). In the broadest sense, these interactions can be classified as either competitive or facilitative, and divided into two main categories: aboveground and belowground (Ong et al. 1991; Schroth 1999; Jose et al.

2004). Paramount among aboveground interactions is shading (Boardman 1977), which, depending on the degree of canopy closure, the shade tolerance of the understory crop, and interactions with below-canopy microclimate, can have either a competitive or facilitative effect (Chirko et al. 1996; Jose et al. 2004). The typical leaf-level response to shading is a reduction in photosynthesis – the degree of which being inversely related to the plant's level of shade tolerance – but this reduction in CO_2 uptake may be offset by increased photosynthetic efficiency at lower light levels. Plants also acclimate to reduced light conditions through increases in specific leaf area or by an increase in carbon allocation to aboveground tissues (Chapin et al. 2002). The ability to quantify the relationship between shading and plant productivity is key to selecting the species that are best adapted to reduced-light conditions and for developing an understanding of how best to manage mixed-species system.

Resource limitations that arise due to belowground competition can result in an adjustment of carbon allocation patterns to favor root development over shoot development. The ratio of root biomass to shoot biomass is, therefore, a helpful diagnostic tool for determining whether aboveground or belowground competition is most prevalent in a given system (Chapin et al. 2002). Competition for water can cause loss of turgor and induce stomatal closure (Kho 2007). This reduces photosynthesis, resulting in decreased carbon uptake. Competition for water can also affect the mobility and thus the availability of soil nutrients (Baldwin 1975), which can further hinder photosynthesis and growth. Tissue analyses, particularly those that assess foliar nitrogen and chlorophyll concentrations, are effective means of quantifying plant nutritional status (Porro et al. 2000; Netto et al. 2005). As such, they are also useful in assessments of belowground interspecific competition in mixed-species systems (Caton et al. 2003). Instantaneous gas exchange measurements correlated with environmental parameters such as soil moisture can also be good indicators of belowground competition in a system (Miller and Pallardy 2001), but have not been extensively employed in field studies.

The inherent complexity of intercropping systems makes them more analogous to natural ecosystems than to conventional cropping systems. The most sustainable and productive intercropping systems, therefore, are often those that are modeled after native plant communities (Ewel 1999). Since many shrubs native to the understory of the longleaf pine (*Pinus palustris* Mill.) ecosystem have market potential as woody floral products, one exciting possibility is the intercropping of select species in the between-row spacing of young longleaf pine plantations. Such a system would provide yearly income, which would supplement the long-term returns from longleaf pine timber sales. The development of a longleaf pine-native woody ornamental intercropping system, however, is dependent upon an understanding of how the trees and shrubs interact in the context of a managed, mixed-species setting. Thus, the overall objective of this study was to evaluate how above and belowground competition would affect the productivity of three native shrub species: American beautyberry (*Callicarpa americana* L.) (Verbenaceae), wax myrtle (*Morella cerifera* (L.) Small) (Myricaceae), and inkberry (*Ilex glabra* (L.) A.Gray) (Aquifoliaceae) in such a system. The three specific objectives were:

1. Determine how PAR transmittance and soil water content vary in monoculture and intercropping systems.
2. Determine growth and biomass allocation patterns of the three shrub species with respect to shading and belowground competition from longleaf pine trees.

3. Quantify the effect of above and belowground competition on leaf-level physiological processes for the three shrub species.

Species native to the understory of the longleaf pine ecosystem were chosen for this study. It was hypothesized, therefore, that all would be well adapted to the shaded conditions of an intercropping system. Reductions in growth and yield, if observed, would likely be due to belowground competition with longleaf pine.

MATERIALS AND METHODS

Study Site and Experimental Design

This study was conducted on a private 15-year-old longleaf pine plantation in Santa Rosa County, Florida, USA (30°37' N, 87°2' W). The climate of the region is classified as temperate, with mild winters and hot, humid summers. Mean annual precipitation is 1645 mm. The soil is an ultisol and classified as a Fuquay sand (loamy, kaolinitic, thermic Arenic Plinthic Kandiudult), nutrient poor, deep, well-drained sand over loamy marine or fluviomarine deposits.

Trees in the study site were uniformly spaced, with approximately 3 meters between rows and 1.5 meters between stems within the row, a typical pre-thinning planting density for southern pines. Approximately 10% mortality, however, had occurred over the course of the 15 years due to hurricanes and pine beetles. At the initiation of the study (December 2005), mean tree height was approximately 6.1 meters and mean diameter at breast height (DBH) was 8.3 cm. Basal area was estimated at 12.6 m^2 ha^{-1}. Canopy coverage was estimated at 35% using canopy photographs.

In December 2005, containerized native woody ornamental shrubs were incorporated into the existing between-row spacing of the site, and as an equivalently spaced monoculture treatment in an adjacent open field. Selected species were American beautyberry (*Callicarpa americana*), wax myrtle (*Morella cerifera*), and inkberry (*Ilex glabra*). These species have not been extensively domesticated, but each produces an attractive stem that was identified as potentially marketable by local florists. *C. americana* produces long (up to 1 m) unbranched stems with clusters of purple berries at the base of each petiole. *M. cerifera* produces straight or crooked stems with small fragrant drupes and deep green foliage. *I. glabra* produces long (up to 1 m) sometimes branched stems with deep green foliage and black drupes (on female plants). Shrubs were given a year for proper establishment with dead or dying shrubs being replaced in the winter of 2006, prior to the initiation of the study.

The effect of intercropping on shrub productivity in this system was assessed via comparisons with the monoculture treatment. The trial was laid out as a split-plot completely randomized design with treatment (monoculture or intercropped) as the whole plot factor and shrub species as the split-plot factor. There were four replications, each consisting of six subplots (one for each species by treatment combination) with eight shrubs each. Subplots were 2 alleys wide (or equivalent distance in the monoculture) with shrubs planted in two rows of four at a spacing of 3 meters. As a control, four subplots of the same dimensions were established in the plantation and not planted with shrubs.

Fertilizer Application and Plot Maintenance

To simulate the effect of a slow-release fertilizer, three applications of ammonium sulfate fertilizer $(NH_4)_2SO_4$ (21% N) each at a rate of 146.5 kg N ha^{-1} were uniformly hand applied at approximately 60 day intervals in a circular area of 325 cm^2 at the base of each shrub. The first application was on 21 March 2007, shortly after bud swelling and leaf emergence were first observed. Pesticide and herbicide application, along with manual weed removal, were conducted as needed throughout the growing season. Plots were non-irrigated, but supplemental water was uniformly provided to all shrubs when at least 20% showed signs of extreme drought stress. This occurred on three occasions during a particularly dry period from mid May to early June 2007.

Light Transmittance and Soil Water Content

Two Hobo® quantum sensors, wired to Micro Station data loggers (Onset Computer Corporation, Bourne, MA, USA) were installed at a height of 105 cm above ground level in each of the two experimental treatments (intercropping or monoculture). Automated measurements of photosynthetically active radiation (PAR) were taken at 30 minute intervals from May 2007 until October 2007.

Soil water potential (kPa) measurements were taken in conjunction with gas exchange measurements using tensiometers (Soil Measurement Systems, Tucson, Arizona, USA), set at depths of 20 and 50 cm at 20 cm from the base of one shrub (or shrubless control) per subplot. Biweekly measurements were taken from May 2007 until October 2007. Volumetric soil water content was measured using a 12 cm electronic time domain reflectometry (TDR) probe (Campbell Scientific Inc. Logan, UT, USA). Readings were taken for each shrub at three distances in the intercropping treatment (at the base of the tree, midway between tree and alley center and at alley center), and equivalent distances in monoculture plots. Measurements were taken at monthly intervals, beginning shortly after leaf emergence in early April and continuing until shrubs were harvested at the end of the growing season.

Biomass, Chlorophyll and Leaf Area Sampling

In order to shed light on the physiological processes that affect growth and yield in this system, two shrubs per species-plot combination (48 total) were selected for destructive harvesting in October 2007. For these shrubs, 20 leaves were randomly selected and analyzed for chlorophyll concentration with a hand-held SPAD-502 meter (Minolta Corp., Japan). Stem subsamples from each of the four cardinal directions were then harvested and separated into stem and leaf and (when applicable) fruit components. The remaining aboveground biomass was then harvested and all samples were transported to the lab where they were separately weighed. In the lab, subsample leaf area was determined on fresh leaves using a LICOR Li-3100C leaf area meter (Lincoln, Nebraska, USA).

Belowground biomass of the same 48 shrubs was harvested later. For this, a hole with a 70 cm radius centered on each shrub was excavated and roots were separated from those of non-target

species in the field on the basis of texture and color. Further separation was done in the lab, where roots were washed with water over a 1 mm mesh screen to remove soil and debris. All tissues were dried separately at 70°C for 48 hours. Specific leaf area (SLA) was determined by dividing LA by dry leaf weight. The ratio of leaf area to subsample biomass (g) was multiplied by the aboveground dry biomass of the respective shrub to obtain an estimate of whole plant LA. Dry weights were used to determine root:shoot biomass ratio for each shrub.

Pine Root Length Density

Soil cores (8 x 90 cm) were taken in control (shrubless) plots at 40, 80 and 120 cm from a tree, divided into 30 cm sections and sifted to separate pine roots from soil. Root length was determined by using the line intercept method described by Tennant (1975) and divided by soil core volume to determine root length density (RLD). Sampling was conducted after the growing season ended (November 2007) to prevent interference with water and nutrient uptake.

Gas Exchange Measurements

A LICOR 6400 (Lincoln, Nebraska, USA) infrared gas analyzer (IRGA) was used to create photosynthetic light response curves during the peak of the growing season (July 2007). These were done using the internal LED light source at 8 pre-set levels of descending PAR (1600, 1000, 700, 400, 100, 50, 25 and 0 μmol cm^2 sec^{-1}) on 6 plants per species by treatment combination. The IRGA was operated at a flow rate of 400 μmol CO_2 s^{-1} and set to control chamber CO_2 concentration at 380 ppm. An effort was made to maintain chamber humidity as close as possible to ambient levels. Measurements were taken over a 4 day period during which several rainfall events maintained soil moisture at or near field capacity. This, it was assumed, would ensure that water stress would not be a major determinant of photosynthesis, thereby helping to isolate light level as the variable of interest. Curves were fit using a nonlinear Mitscherlich model, as described by Peek et al. (2002).

The LICOR 6400 was also used to measure net photosynthesis (A) (μmol CO_2 m^{-2} s^{-1}) and stomatal conductance (g) (mm m^{-2} s^{-1}) of two shrubs per species-plot combination (48 total). Measurements were taken twice monthly on clear days between 1000 and 1300 hrs, beginning with the full expansion of new leaves in late May 2007 and continuing until the latter part of the growing season in September 2007. No measurements were taken within 48 hours of any significant rainfall event. The same plants were used for each set of measurements in a repeated measures design. The IRGA was operated in a survey mode with a transparent 0.785 cm^2 arabidopsis chamber, a flow rate of 400 μmol CO_2 s^{-1} and with reference CO_2 set at 400 ppm.

Tree Growth

Diameter at breast height (DBH) was measured in February of 2006, 2007 and 2008 on all trees in the intercropping plots to monitor annual incremental growth.

Data Analysis

SPAD units were converted to chlorophyll concentration (μg Chl cm^{-2}) as described by Markwell et al. (1995). Data for biomass, root length density, specific leaf area and chlorophyll concentration were analyzed using a two-way analysis of variance (ANOVA) procedure using PROC GLM in SAS 9.1 (SAS Institute, Cary, NC, USA). Time-integrated measurements (gas exchange, soil moisture and PAR) were analyzed with a repeated-measures ANOVA using the PROC MIXED procedure in SAS 9.1. With the exception of RLD, all analyses were conducted within the framework of a split-plot, completely randomized experimental design. Specifically, treatment effects (intercropping vs. monoculture) were compared for each shrub species for each variable of interest. Log transformations were performed when necessary to improve data normality. Differences between means were considered significant at $\alpha < 0.05$ and Tukey's HSD post hoc test was used for pairwise comparisons.

RESULTS

Light Transmittance and Soil Water Content

Overall, PAR transmittance below the pine canopy averaged 57.7% over the 6 month time period from May to October 2007. The highest transmittance levels (64.8 and 62.0%) were observed in June and July, respectively. Values for other months were significantly lower, with August being the lowest at 52.4% (Figure 1). Significant variability was observed on a daily time scale, with periods of near 100% transmittance alternating with periods where transmittance was greatly reduced by shading (Figure 2).
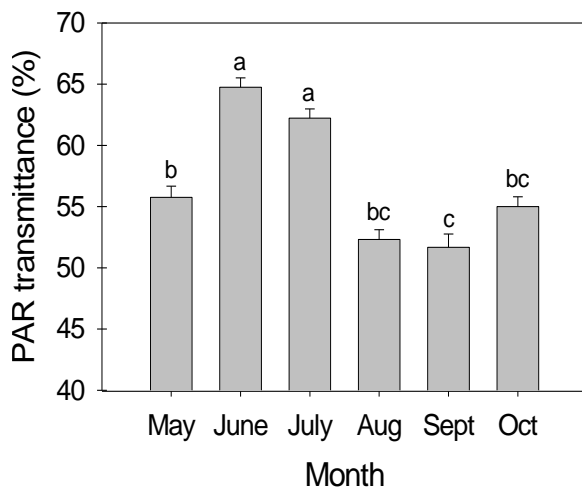

Figure 1. Mean transmittance (by month) of photosynthetically active radiation (PAR). Means with different lowercase letters are significantly different at $\alpha < 0.05$.
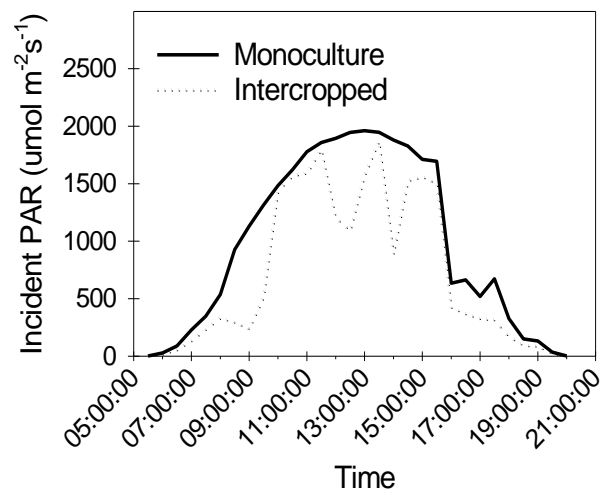
Figure 2. Typical patterns of incident PAR over the course of a cloud-free day in June 2007.

Soil water potential varied by date ($P < 0.0001$) and depth ($P < 0.0001$) and there was a significant treatment by depth interaction ($P = 0.0165$). At 20 cm, soil moisture was generally lower in the intercropping treatment, with the difference becoming statistically significant in late

August. At 50 cm, soil moisture was significantly higher in the intercropping treatment in late June and in early September (Figure 3). Volumetric water content showed significant variation by date ($P < 0.0001$) and distance from shrub base ($P < 0.0001$) and there was an interaction between treatment and distance ($P < 0.0001$) (Figure 4).
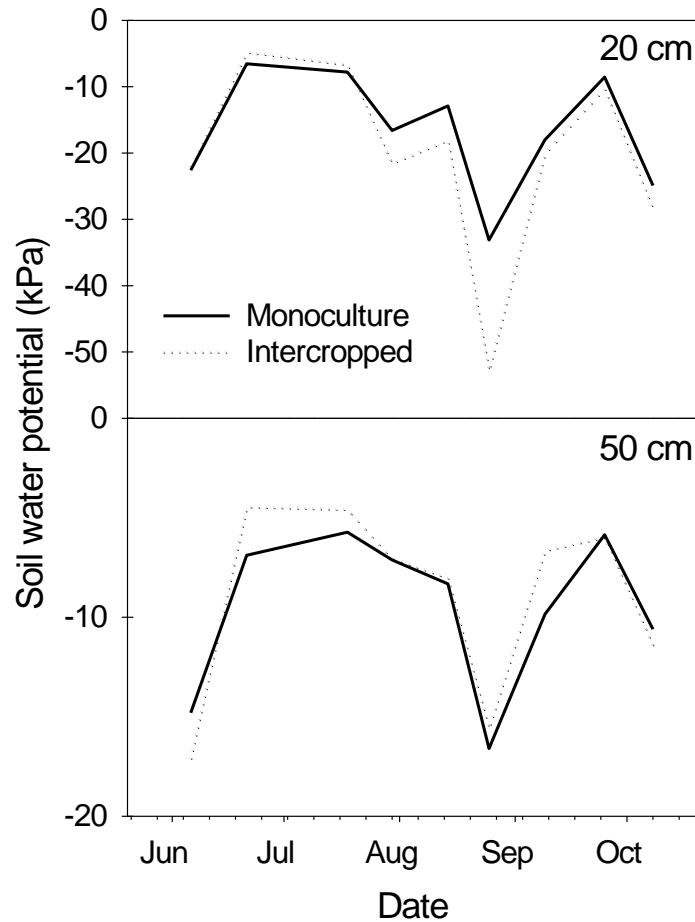

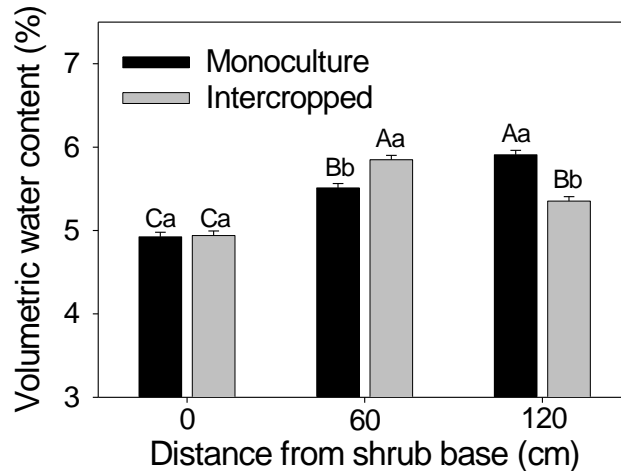Figure 3. Soil water potential (kPa) at 20 cm (top) and 50 cm (bottom).

Figure 4. Mean (March to October) volumetric water content (%) at 0, 60 and 120 cm from shrub base. Within-treatment means with different uppercase letters are statistically different at $\alpha < 0.05$. Between-treatment means (by distance) with different lowercase letters are statistically different at $\alpha < 0.05$.

Survival, Growth and Biomass Allocation Patterns

Mortality was higher for all shrub species in the intercropping treatment, particularly so for *C. americana* (Table 1). Growth was also affected, with reductions in biomass in the intercropping treatment of 75.5% ($P = 0.0030$), 50.6 % ($P = 0.0200$), and 68.7% ($P = 0.0012$) for *C. americana*, *M. cerifera* and *I. glabra*, respectively. Differences in biomass allocation patterns were also observed, with root:shoot ratios being higher by 14% for *C. americana* ($P < 0.0001$), 6% for *M. cerifera* ($P = 0.0020$), and 11% for *I. glabra* ($P < 0.0001$) in the intercropping treatment (Figure 5).

Table 1. Survival (%) by species * treatment combination

Species	Treatment[1]	
	MC	IC
C. americana	97	53
M. cerifera	94	81
I. glabra	78	75

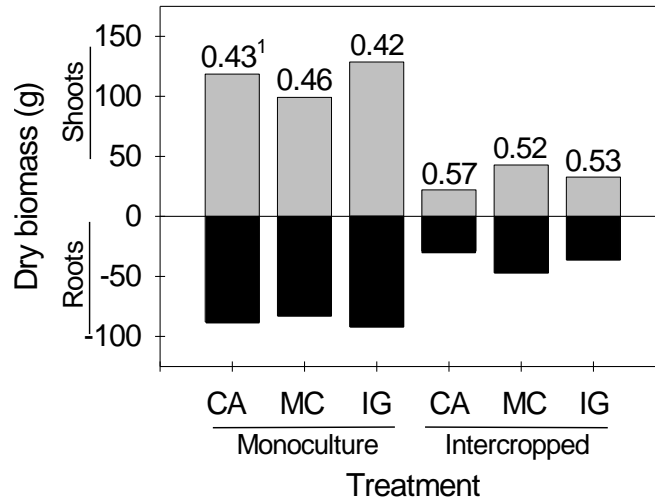[1]MC = monoculture, IC = intercropped

Figure 5. Above and belowground biomass for *C. americana* (CA), *M. cerifera* (MC) and *I. glabra* (IG). [1]Numbers above bars represent root:shoot ratios.

Overall, leaf area was higher in the monoculture, with reductions of 81.4% ($P = 0.0136$) and 78.3% ($P = 0.0022$) observed in the intercropping treatment for *C. americana* and *I. glabra*, respectively. SLA was significantly higher for all species in the intercropping treatment. Observed differences were 18.0% for *C. americana* ($P = 0.0303$), 14.2% for *M. cerifera* ($P = 0.0021$) and 12.4% for *I. glabra* ($P = 0.0449$). Chlorophyll concentrations were 42.6% lower for *C. americana* in the intercropping treatment ($P = 0.0114$), but there were no treatment effects for *M. cerifera* or *I. glabra* (Table 2).

Table 2. Mean leaf area, specific leaf area (SLA) and chlorophyll concentration (Chl).

Species	Treatment	Leaf area (cm^2)	SLA (cm^2 g-1)	Chl (μg Chl cm^2)
C. americana	Monoculture	4896.9	82.9±4.0	14.9±1.1
C. americana	Intercropped	908.2	101.2±4.8	8.2±1.3
		(0.0136)[1,2]	(0.0303)	(0.0114)
M. cerifera	Monoculture	1806.3	59.7 ±1.3	13.7±0.9
M. cerifera	Intercropped	898.8	68.1 ±1.2	13.3±0.8
		(0.1106)	(0.0021)	(0.8576)
I. glabra	Monoculture	3125.3	62.5±2.6	32.4±2.6
I. glabra	Intercropped	676.9	70.3±2.3	28.0±2.3
		(0.0022)	(0.0449)	(0.2462)

[1]*P*-values given in parentheses. [2]Leaf area *P*-values determined from log transformed data

Root length density for longleaf pine varied by distance in the alleyway ($P = 0.01$) and depth ($P < 0.0001$). Values decreased with increasing depth, and were highest (at all depths) at 120 cm

from the trees – a distance which coincides with the middle of the alley (Figure 6). In total, 81.1% of longleaf pine fine roots were confined to the uppermost 30 cm of the soil profile.
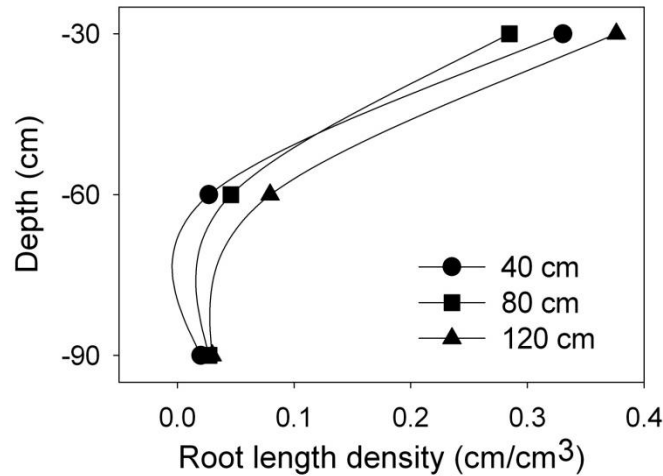

Figure 6. Mean root length density (RLD) for longleaf pine at three distances from a tree (40, 80 and 120 cm) and at three depths (30, 60 and 90 cm).

Photosynthesis and Stomatal Conductance

With soil moisture at field capacity, treatment differences in light saturated photosynthesis (A_{max}) were not observed for *C. americana* or *M. cerifera*. A significant reduction in A_{max}, however, was observed for *I. glabra* in the intercropping compared to the monoculture treatment. Quantum yield (A_{qe}) and light compensation point (LCP) values did not differ between species or treatments (Table 3 and Figure 7). Survey measurements of net photosynthesis showed significant variability by species ($P < 0.0001$), treatment ($P = 0.0042$) and date ($P < 0.0001$), and there were significant species*treatment and species*treatment*date interactions ($P = 0.0218$ and 0.0014, respectively) (Figure 8). Both *M. cerifera* and *I. glabra* had positive relationships between stomatal conductance and soil water potential (Figure 9).

Table 3. Parameter estimates from the photosynthesis model: light saturated photosynthesis (A_{max}), quantum yield (A_{qe}), and light compensation point (LCP). Means and standard errors.

Species	Treatment	A_{max}	A_{qe}	LCP
C. americana	Monoculture	15.76±0.42	32.78±3.04	38.87±4.84
C. americana	Intercropped	12.43±0.35	39.64±4.37	37.24±4.94
		(0.0681)[1]	(0.7717)	(0.9223)
M. cerifera	Monoculture	17.27±0.44	34.66±3.21	35.82±4.63
M. cerifera	Intercropped	13.79±0.39	31.97±3.03	48.42±5.03
		(0.0626)	(0.7531)	(0.4516)
I. glabra	Monoculture	17.70±0.63	29.40±3.57	27.92±7.07
I. glabra	Intercropped	11.77±0.44	34.72±4.71	35.47±6.78
		(0.0028)	(0.8604)	(0.7125)

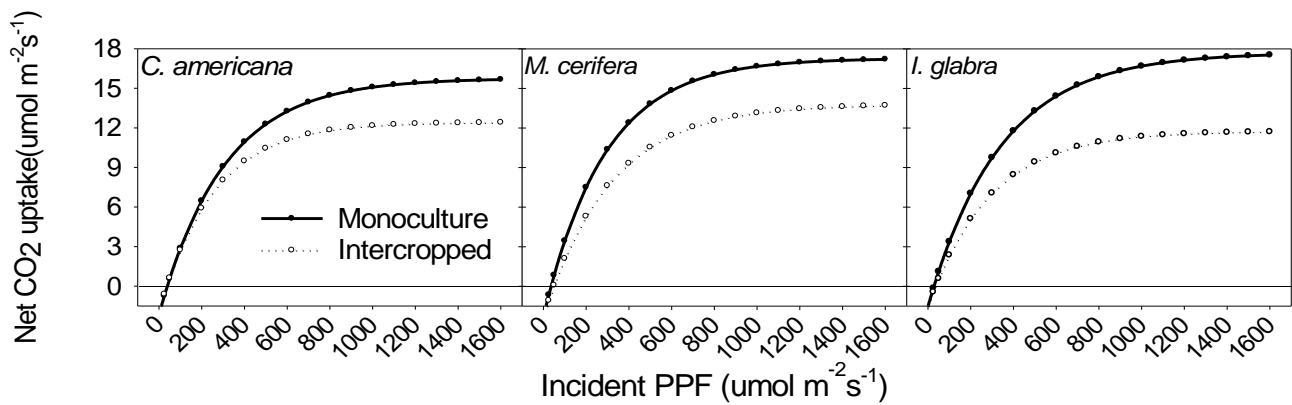[1]*P*-values given in parentheses.

Figure 7. Photosynthetic light response curves fitted using parameter estimates (Table 3).
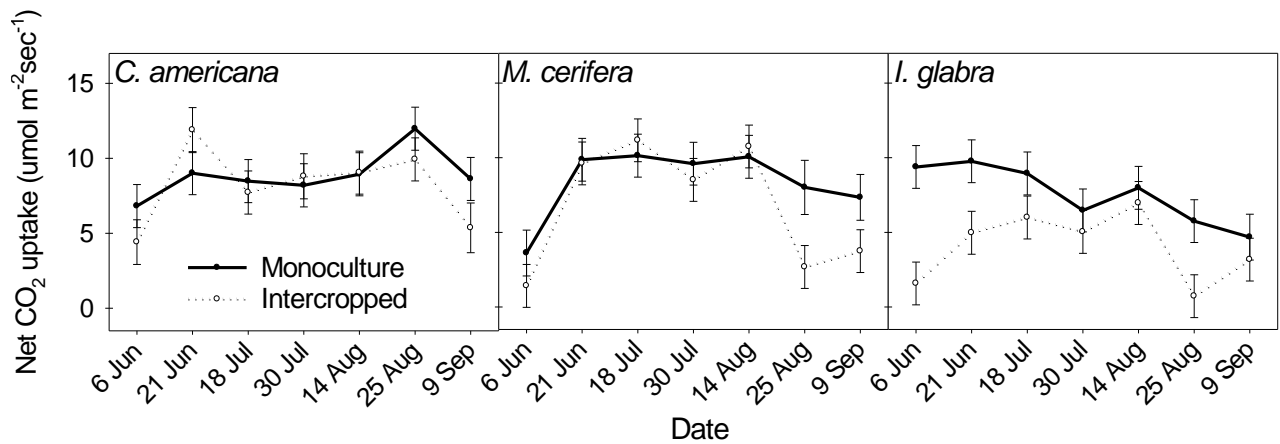

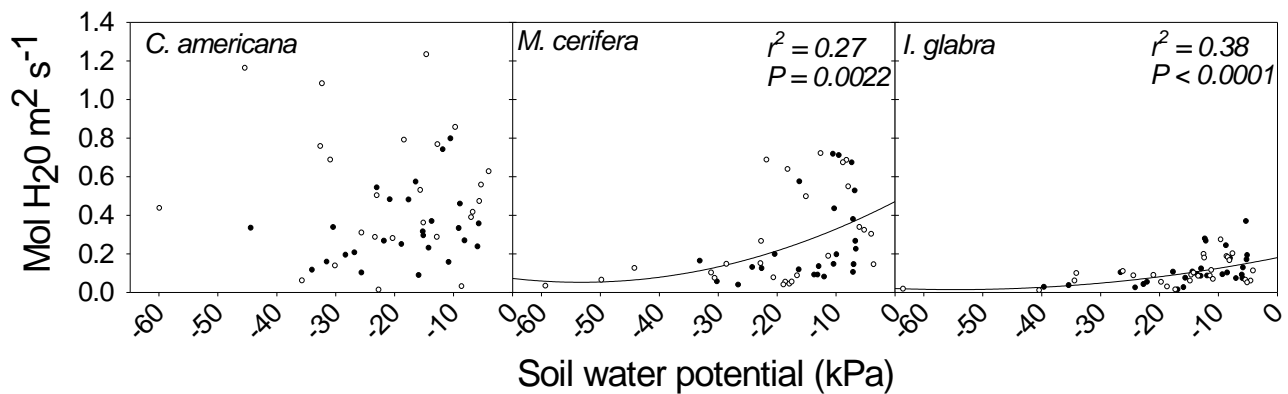Figure 8. Treatment comparisons (by species) of biweekly incident photosynthesis measurements.

Figure 9. Relationship between soil water potential (kPa) and stomatal conductance (mol H_2O m^{-2} s^{-1}) for the three species.

Tree Growth and Mortality

Annual increment for longleaf pines in the study plots was 0.24 cm in 2006 and -0.01 cm in 2007. Species (shrub) effects were not observed between species or between species and control. There was no mortality in 2006 and 2% mortality in 2007 (7 trees).

DISCUSSION

Contrary to our hypothesis that shade-tolerant native understory species would perform well under longleaf pine trees, we observed increased mortality and reduced growth for all three shrub species in the intercropping system. Apparently, competition with longleaf pine was a major determinant of shrub productivity in this treatment (Jose et al. 2006). Despite supplemental fertilization, annual incremental growth of longleaf pine also decreased substantially, suggesting that intraspecific competition was a major stressor on the trees. This competition may have been magnified by water stress, as total rainfall for March – September 2007, at 55.2 cm, was only 47.1% of the 44 year average (NOAA National Climate Data Center).

While instantaneous gas exchange measurements at the leaf level do not adequately account for the factors (e.g. carbon allocation patterns, temporal variability in CO_2 uptake, *etc*.) that affect plant growth and mortality (Givnish 1988), they are useful for comparing instantaneous rates of CO_2 uptake under different field conditions. The typical photosynthetic response of plants grown under reduced light conditions is a reduction of light saturated photosynthesis (A_{max}) and light compensation point (LCP) and an increase in quantum yield (A_{qe}). For light demanding plants, the reduction in A_{max} can be substantial and result in significant decreases in carbon uptake. This is particularly true for plants with the C_4 photosynthetic pathway, which have a near linear relationship between photosynthetic rates and PAR interception. C_3 plants, however, typically reach A_{max} at 25-50% of full sunlight – a characteristic which presumably makes them better adapted to reduced-light conditions (Jose et al. 2004). For shade-tolerant or shade demanding C_3 plants, reductions in A_{max} are often minimal (compared to plants grown in full sun) and may be compensated for, in terms of carbon uptake, by the decreased LCP, increased A_{qe} and an increase in photosynthesis per unit leaf mass (Bazzaz 1979; Poorter and Evans 1998; Niinemets et al. 1999).

Observed patterns of PAR transmittance were comparable to those recorded in longleaf pine forests. Light transmittance estimates reported by Battaglia et al. (2003), for example were between 40 and 78%, with variability on a daily time scale largely attributed to the irregular canopy structure of the overstory. We observed an average transmittance of 57.7% in the intercropping treatment, with similar daily variability. As C_3 plants native to the partial shade of the longleaf pine ecosystem, *C. americana*, *M. cerifera* and *I. glabra* were assumed to be well-adapted to these conditions. Photosynthetic curves created for *C. americana* and *M. cerifera* under field capacity largely supported this assumption, as neither species had a statistically significant reduction in A_{max} in the intercropping treatment. There was, however, a significant reduction in A_{max} for *I. glabra*, suggesting a lower level of shade tolerance for this species. It should be emphasized, however, that all species had higher specific leaf area in the intercropping treatment – a typical response to shading (Chapin et al. 2002). Furthermore, observed differences in total leaf area indicate that light capture, and thus whole plant carbon uptake, was

reduced for all species (Givnish 1988). Quantum yield and light compensation point did not vary between treatments. Ambient photosynthetic rates for all species were consistently lower than their respective A_{max} values. This is not unusual, as A_{max} is a *potential* maximum level that is rarely attained due to resource limitations and/or environmental constraints (Bazzaz 1996).

The fact that all species allocated a greater % of carbon to roots than to shoots supports the argument that shading was not a major determinant of productivity in the intercropping treatment (Chapin et al. 2002). Belowground competitive vectors, therefore, are likely more responsible for the observed differences between treatments. Studies have shown that longleaf pine, once established, develops an extensive shallow lateral root system, often extending well beyond the area covered by the canopy (Heyward 1933; Brockway and Outcalt 1998). Since resource uptake is strongly correlated to root length density (van Noordwijk and Lusiana 1996; Green and Clothier 2002), this can result in significant intra- and interspecific competition in the comparatively nutrient-rich but often water-deprived upper soil horizons (Callaway and Walker 1997).

The proportion of longleaf pine fine roots in the upper 30 cm of soil of this system was more than double than that reported by Jose et al. (2006) – a difference that is likely due to age, spacing or soil characteristics. A highly uneven fine root distribution such as this indicates the presence of a shallow zone of very intense competition and a deeper zone where resources, particularly water, are underexploited. An intercropped shrub with a deeper root system would likely be able to exploit this niche and coexist favorably with longleaf pine. The shrub species chosen for this study, however, appear to have lacked such belowground complementarity. The lack of complementarity was likely magnified by the fact that the highest fine root length density for the pines was in the middle of the alley, presumably where the root systems of trees from the two adjacent rows overlapped.

Water stress can affect photosynthesis by inducing stomatal closure (Farquhar and Sharkey 1982), which in turn may inhibit gas exchange (Bennett and Sinclair 1998). It can also inhibit cell expansion and differentiation (Hsiao 1973), resulting in reduced growth. Since stomatal conductance for *M. cerifera* and *I. glabra* (two faculative wetland species) decreased with decreasing soil moisture, and soil moisture at 20 cm was generally lower in the intercropping treatmment, it is possible that water stress was partially responsible for the observed treatment differences. In temperate agroforestry systems, mixed-species plantings, and natural longleaf pine forests, competition for water appears to be the rule, rather than the exception (Miller and Pallardy 2001; Harrington et al. 2003; Wanvestraut et al. 2004; Jose et al. 2006). This competition further magnifies the stresses created by drought, possibly requiring management interventions (i.e., irrigation, trenching, or "root barriers") to minimize deleterious effects on the growth and yield of component species (Harrington et al. 2003; Wanvestraut et al. 2004; Zamora et al. 2008). Tree removal, however, was probably not necessary, given the openness of the canopy and the fact that the basal area was only 55% of the recommended level for a first thinning (12.6 vs. 22.9 m^2 ha^{-1}).

There was no evidence to suggest that the productivity of *C. americana*, an upland species, was affected by treatment-induced water stress. Nonetheless, high mortality and reduced growth in the intercropping treatment suggest that *C. americana* is, indeed, adversely affected by

competition from longleaf pine. Reduced chlorophyll content, while apparently having little effect on photosynthesis, could be evidence of interspecific competition for nitrogen. A companion fertilization study using labeled ^{15}N ammonium sulfate (Hagan et al. in review) further supports this notion, as foliar nitrogen was 28.9% lower and percent nitrogen derived from fertilizer was 50.8% higher in the intercropping treatment for this species (no such treatment differences were observed for *M. cerifera* or *I. glabra*). Nitrogen is an integral component of chlorophyll (Chappelle et al. 1984) and is essential for the synthesis of amino acids, enzymes and proteins (Sugiharto et al. 1990). While nitrogen deficiency may or may not affect photosynthetic capacity at the leaf level, it can slow the rate of leaf expansion, as well as limit leaf area and number (Ciompi et al. 1996). Nitrogen-based amino acids also serve as important overwinter reserves (Chapin et al. 1990). Competition for nitrogen would therefore have a deleterious effect on growth and yield particularly for a deciduous species such as *C. americana* which likely has a high early-season nitrogen demand.

CONCLUSIONS

It is clear, based on the results of this study, that the effective management of competition is essential to the viability of a longleaf pine/native woody ornamental intercropping system. Ideally this could be done in a manner that minimizes the deleterious effects of competition while retaining a high basal area. Irrigation, trenching or the installation of root barriers have also proven effective at reducing belowground competition (Harrington et al. 2003; Wanvestraut et al. 2004; Zamora et al. 2008) and should be considered in future studies. Future studies should also address the effect of other belowground interspecific processes (e.g. phosphorus competition) on shrub productivity.

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