

GENERAL SESSION PAPERS

Evaluation of Native Legume Growth and Phenology under Shaded Conditions for Restoration of Longleaf Pine-Wiregrass Ecosystem

S. E. Cathey¹, T. R. Sinclair,^{1*} L. R. Boring²

ABSTRACT

In fire-maintained longleaf pine- (*Pinus palustris*) wiregrass (*Aristida stricta*) ecosystem, nitrogen-fixing legumes are important for replacing nitrogen lost from frequent prescribed burns. Restoration and maintenance of the ecosystem, including the wildlife habitat it provides, depends on a legume population that sustains nitrogen input to the system. The objectives of this study were to obtain information about the growth under unshaded and shaded conditions of eight native legumes that are candidates for introduction into the longleaf pine-wiregrass ecosystem. Measurements were made throughout the season on plant phenology and development, and final accumulated shoot and root mass at the end of the season. Observations were also reported on nodule number and morphology for each species. The legume species included represented all three major subfamilies of *Leguminosae* and two distinctly different growth forms: vining/spreading and erect herbs. Biomass accumulation was not significantly reduced by shade for any of the species. Although stem elongation responses to shade were only significant for three species, *Clitoria mariana*, *Crotalaria rotundifolia*, and *Lespedeza hirta*, a general pattern of vining/spreading under shaded conditions was evident. *Mimosa quadrivalvis* (L.) had the greatest mass accumulation, and was among those species with the highest root-to-shoot ratio. Nodules varied among species from spheroid to elongate to coralloid.

Keywords: Legume growth, Native legumes, Plant phenology, Shade tolerance.

INTRODUCTION

The variably shaded and frequently burned environment of the longleaf pine- (*Pinus palustris* Mill.) wiregrass (*Aristida stricta* Michx.) ecosystem supports many species of native herbaceous legumes. These legumes constitute more than 10 percent of the vascular species in longleaf pine savannas and occur in high densities across a great range of site conditions (Hains et al. 1999). As a group, these native legume species are fire tolerant, adaptable to infertile and droughty soils, valuable as wildlife food, and may be significant fixers of atmospheric N₂ (Hains et al. 1999; Hendricks and Boring 1999; Hiers et al. 2003). Although these are understory species, their shade tolerance has not been explored. N₂-fixing legumes are generally assumed to be shade intolerant species due to the high energetic cost of nodule production, maintenance, and N₂ fixation (Vitousek et al. 2002).

Since 1998, reforestation initiatives on public and private lands in southeastern United States have resulted in planting of approximately 283,000 ha of former agricultural fields, harvested pulpwood plantations and otherwise fire-suppressed land back into longleaf pine stands. About 48,000 ha of marginal coastal plain farmland in Georgia alone are being planted to pine-wiregrass vegetation as part of the USDA Conservation Reserve Program (Coffey and Kirkman 2004). Groundcover restoration is critical to recovery of soil organic matter and N-availability on these sites (Markewitz et al. 2002). Although the longleaf pine overstory has been successfully established, there is a great need to better determine the compatibility of legume groundcover species to shaded light conditions so that suitable species may be integrated into habitat restoration projects.

This study was designed to observe the effects of two light conditions on growth responses of eight species of legumes native to the longleaf pine-wiregrass ecosystem over a growing season. An unshaded treatment as well as a shade treatment resulting in about half normal irradiance on the plants was included. The half irradiance treatment is approximately that anticipated following a thinning tree harvest when legumes would be added to the restoration stand. Battaglia et al. (2003) and Pecot et al. (2005) reported that a full canopy still averages 40 % light penetration. The specific objectives of this research were: (1) to make observations of phenological development and nodule morphology for each species; and (2) to document the influence of shading on growth habits and biomass accumulation. Shoot, root and nodule mass accumulation as well as shoot elongation were measured to document the response to light. A companion study focused on measuring N₂-fixation responses of these species (Cathey et al., 2009).

MATERIALS AND METHODS

Plants

Young plants of eight species of native legumes were grown outdoors in Gainesville, Florida (82° 20' W, 29° 38' N) between April and November of 2004. Four letter abbreviations as listed in Table 1 are used in this paper to identify each species. One-half of the plants from each species were grown in the sun and one-half in a shade-cloth enclosure that excluded approximately 50% ambient

S.E. Cathey and *T.R. Sinclair, Agronomy Dept., Univ. of Florida, Gainesville, FL 33611-0965; L.R. Boring, Joseph W. Jones Ecological Research Center at Ichauway, Rte. 2, Box 2324, Newton, GA 39870, USA

*Corresponding author (trsinc@ufl.edu). Contribution published in *Soil Crop Sci. Soc. Florida Proc.* 67:1-9 (2008).

Table 1. Descriptions of native legumes used in the current study.

Species [†]	Code [‡]	Common Name
Subfamily Papilionoideae		
<i>Centrosema virginianum</i> (L.) Benth.	CEVI	Spurred Butterfly Pea
<i>Clitoria mariana</i> (L.)	CLMA	Butterfly Pea
<i>Crotalaria rotundifolia</i> J.F. Gmel.	CRRO	Rabbitbells
<i>Lespedeza hirta</i> (L.) Hornem.	LEHI	Hairy Lespedeza
<i>Orbexillum lupinellus</i> (Michx.) Isley	ORLU	Piedmont Leatherroot
<i>Tephrosia virginiana</i> (L.) Pers.	TEVI	Goats Rue
Subfamily: Caesalpinioideae		
<i>Chamaecrista nictitans</i> (L.) Moench	CHNI	Sensitive/Partridge Pea
Subfamily: Mimosoideae		
<i>Mimosa quadrivalvis</i> (L.)	MIQU	Sensitive Briar

[†]Nomenclature follows Wunderlin and Hansen (2003).

[‡]Codes listed will be used to refer to species names throughout the text.

light. Difference in photosynthetically active radiation (PAR) between light treatments was determined using a Li-Cor Quantum Sensor, LI-185A. Measurements were taken on a clear day, 19 March 2004, at approximately 13:00 Eastern Standard Time. Three readings each were taken under the shade cloth and in open sun adjacent to the potted plants. The PAR in the shaded area ($753 \pm 82 \mu\text{mol s}^{-1}\text{m}^{-2}$) was 56 percent of full sun ($1340 \pm 51 \mu\text{mol s}^{-1}\text{m}^{-2}$).

The seedlings for all species, except *Chamaecrista nictitans* (CHNI), were initially propagated at the Joseph W. Jones Ecological Research Center (JWJERC) from seed. Seeds were collected throughout the native woodland on the 12,500 ha Ichauway reserve, located in Baker County, Georgia, USA (31°19'N and 80°20'W). Seeds were scarified by physical abrasion and then sown in June/July 2003 into an organic-mix soil. Plug flats were used to contain the soil and they were kept in a greenhouse over the following winter. Seeds for the annual CHNI were obtained from the forage breeding lab, Agronomy Department, University of Florida. These seeds were collected along the roadside in Gainesville, FL. Seeds for CHNI were scarified with sand paper and then germinated on moist filter paper.

The small seedlings from JWJERC were transferred when 7 months-old into cylindrical polyvinyl chloride (PVC) pots, 35 cm x 86 cm² surface area, or similar sized plastic pots (35cm tall x 80 cm² surface area). The CHNI seedlings were planted directly into the PVC and plastic pots on 21 April. The PVC pots were also used to assess N₂-fixation using the acetylene reduction assay in a companion study (Cathey et al., 2009). The plastic pots were used to increase the number of specimens in the study. Since the two pots were of similar shape and volume, measurement and harvest data were treated as a single set. A total of six PVC pots and 14 plastic pots were planted for each species in the experiment. One half of each set of pots was grown in the shade enclosure and the other half was grown unshaded adjacent to the enclosure. Transplanting was completed on 11 February 2004.

All plants in the study were inoculated by introducing native soil as the top layer of soil in the pots. Top soil was

collected at two sites at the Jones Center: a fine-loamy, kaolinitic, thermic Typic Kandiodult (Orangeburg Series), and a loamy, kaolinitic, thermic Arenic Kandiodult (Wagram Series) site. Soils were dug from the top 0 to 20 cm of the soil profile in areas with thriving and diverse legume populations. A mixture of equal parts of each native soil type was used as the bacteria inoculation source. The pots had been previously filled with a commercial topsoil (Walmart Corp.) to within 6 cm from the top, then 2 cm of native soil was added to the surface of all pots. Plants were transplanted into the pots, and additional topsoil was used to cover the roots as needed.

Water was applied to each pot by drip-irrigation every 12 hours (5:00 and 17:00 EST) using a battery-operated timer (Rainbird). The amount of the irrigation was adjusted as needed throughout the experiment to prevent excessive watering during periods of heavy rainfall. Gainesville experienced hurricane activity around 14 August and 3 September 2004. Some plants experienced leaf loss due to wind, and LEHI, which was moved indoors, suffered some water-deficit stress.

Measurements

Stem length was measured for all plants on a weekly basis as the distance from the soil surface to the furthest point on the plant. Representative stem length of vining plants such as MIQU, CEVI, and CLMA was considered to be the length of the longest stem. Each of these vines was measured until the date when the branches became too tangled for a measurement to be plausible.

Cumulative leaf production was measured by counting the number of leaflets on each plant on a weekly basis. This method was continued throughout the experiment for CLMA, LEHI, and TEVI. However, due to the very large number of leaflets on CEVI, MIQU, CRRO and ORLU, plant vigor was estimated by measuring the width of the plant. The width of CEVI and MIQU was determined by measuring the lengths of the two longest stems and adding them together. Widths of CRRO and ORLU were determined as the width of the plant at the widest point, leaf tip to leaf tip. Width measurements were taken using a measuring tape or ruler.

The presence of flowers and fruits was noted weekly. Phenological phase were defined as: 1) more than 50% of the plants of each species had flowers 2) more than 50% of the plants had flowers and fruit, and 3) more than 50% of the plants had fruit only.

At the conclusion of the experiment, all plants were destructively harvested to obtain both above- and below-ground mass. Roots and nodules were washed free of soil. Nodules were removed from the roots, counted and the diameter of each spherical nodule recorded. Elongated nodules were measured across the longest axis. All tissues were dried to constant weight at 80°C and weighed.

Means were compared with analysis of variance using the General Linear Models procedure of SAS (SAS Institute, 2003). Species and light treatments were used as main effects. Where means differed ($p < 0.05$), Duncan's multiple comparison post-test was used to compare means. Patterns of stem elongation were analyzed using a non-linear regression model (third-order polynomial), followed by an analysis of slope using the derivative (dh/dt). The slope (dh/dt) of the curve at selected points was calculated and compared using ANOVA to test for species and treatment effects. Student's t-test ($\alpha=0.05$) was used to test for differences in mean stem length, number of leaves and plant vigor (measured as plant width) response to light treatments within a species. Non-linear regression and t-tests were performed using Prism (GraphPad Prism, 1996).

RESULTS

Phenological Development

Shade- and sun-grown plants reached reproductive maturity at approximately the same time. The weekly observations of phenological phases did not allow sufficient resolution to determine treatment effects on flowering and fruit initiation, thus data for the two light treatments within a species were combined. All species examined in this study were late spring and summer-flowering and fruiting except for LEHI, which is considered to be fall flowering and did not begin to flower until around 24 September. MIQU was the first of the species to flower (28 May; Fig. 1) and to produce fruit (30 June), followed by CRRO, CLMA, CEVI, and LEHI, respectively.

Flowering and fruiting continued throughout the season for MIQU, CRRO and CEVI (Fig. 1). The lack of a narrow time frame for flowering and fruiting indicates that these species follow an opportunistic fruit production strategy. Both flowers and fruits were present on MIQU, CRRO and CEVI from the first fruiting until the end of the experiment. In contrast, CLMA, which stopped flowering around 14 September, had a much more determinant flowering and fruiting pattern. Flowers and fruits were only concurrently present for approximately 30 days on CLMA before fruit production ceased and the plant

returned to a vegetative state. TEVI did not flower during this experiment. ORLU flowered for the shortest duration of any of the species in this study, only 20 days, but no fruits were detected.

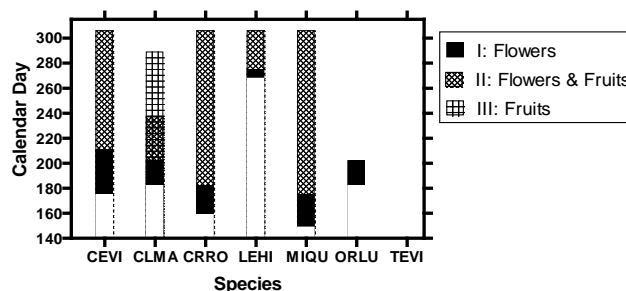


Figure 1. Phenological stages of species over time. Bars represent the time at which over one-half of specimens for a species had reached the prescribed phenological phase, such as the onset of flowering. †TEVI did not flower during the experiment.

Plant Development

Although these legume species were quite different in structure and life history, they could be categorized into two general morphological types, a vining/spreading herb or an erect herb. The vining/spreading species were CEVI, CLMA, CRRO and MIQU and the erect herbs are LEHI, ORLU, CHNI, and TEVI

Out of the 20 individual plants of each species, an average of 10 survived, ranging from 8 (CHNI and CLMA, each) to 16 (LEHI) individuals remaining. There were sufficient plants for six of the eight species to make statistical comparisons of growth variables. Species MIQU and CEVI were not included in the statistical analysis of the development data.

Overall, stem elongation (stem length) patterns of all species showed rapid increase in stem elongation toward the beginning of the season, with the exception of CRRO, and LEHI. Growth curves were fitted to a third order polynomial (Fig. 2; Table 2). Stem elongation rates for all species were greatest around 14 May, followed by decline as the season progressed, with the exception of LEHI, which had its strongest elongation rate during the middle portion of the season, between 29 June and 19 August (Table 3). CHNI, CRRO and LEHI underwent a slight decline by the final measurement before harvest, 22 October.

Stem elongation rates of CRRO, LEHI, ORLU and TEVI diverged among treatments on 19 August and 22 October (Table 3). Stem length was also statistically different (unpaired t test, $p < 0.05$) at dates within the range that elongation rate diverged for CLMA, CRRO, and LEHI (Fig. 2). For CLMA, stem elongation rates in the shade were approximately twice that of sun-grown plants across all calculated dates. Slopes and stem lengths for CHNI were very similar for both sun and shade-grown plants throughout the growing season.

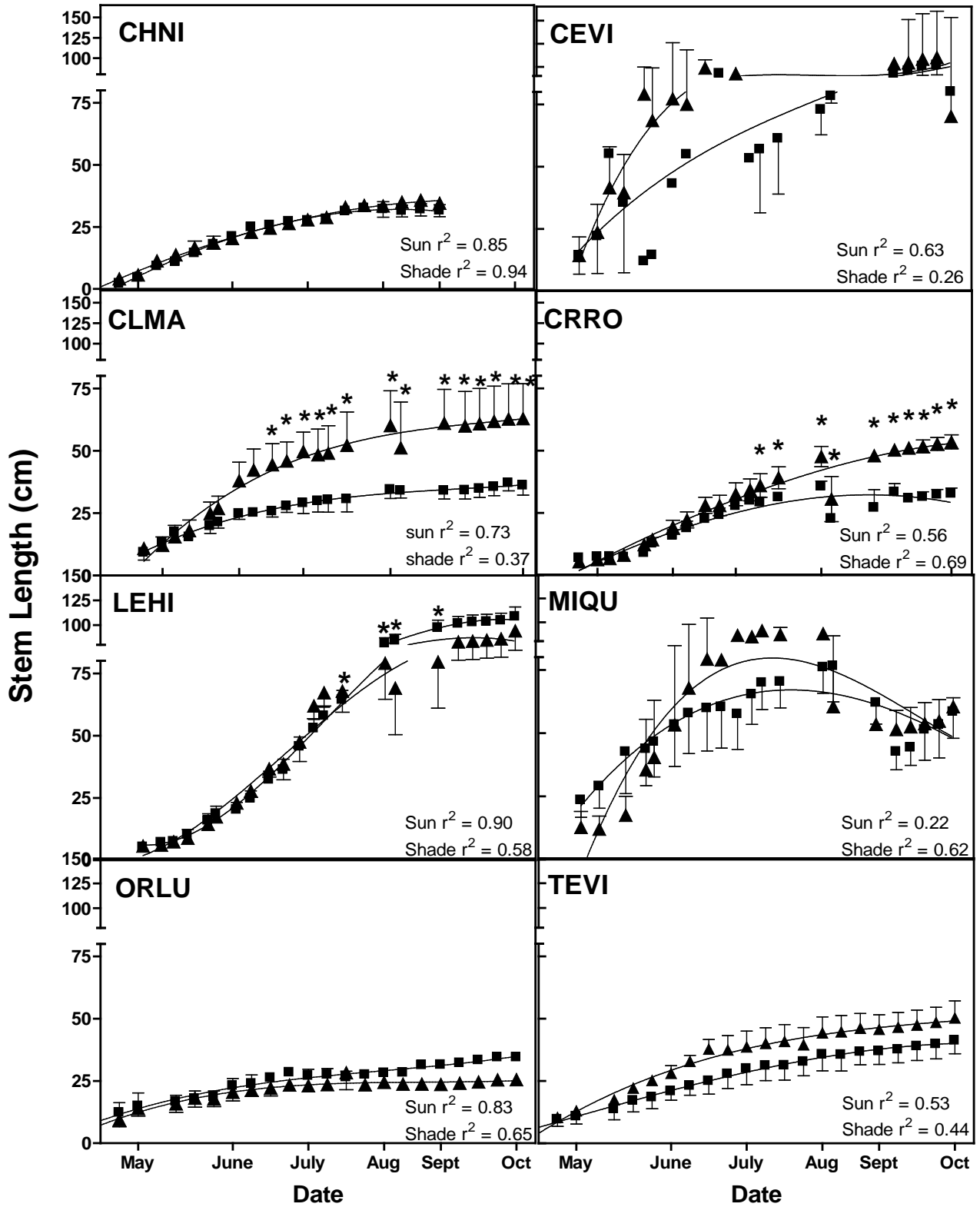


Figure 2. Stem elongation. Values are means \pm SE. ■ represents plants grown in the sun, and▲ represents plants grown under the shade treatment. Goodness of fit values (r^2 , $\alpha=0.05$) are given for each curve that was fitted with a third-order polynomial.

Table 2. Regression equations for stem elongation curves of the form $y = A + Bx + Cx^2 + Dx^3$.

Species	Light	Equation Coefficients [†]			
		A	B	C	D
CHNI	Sun	-107.0 ± 32.3	1.4 ± 0.5	-0.004 ± -0.002	-3.8x10 ⁻⁶ ± 5.2x10 ⁻⁶
CHNI	Shade	-63.2 ± 28.2	0.7 ± 0.5	-0.001 ± 0.002	-5.2x10 ⁻⁷ ± 4.5x10 ⁻⁶
CLMA	Sun	-71.0 ± 37.3	1.1 ± 0.6	-0.003 ± 0.002	4.8x10 ⁻⁶ ± 4.8x10 ⁻⁶
CLMA	Shade	-155.6 ± 129.7	2.1 ± 2.1	-0.007 ± 0.010	8.5x10 ⁻⁶ ± 1.7x10 ⁻⁵
CRRO	Sun	-48.5 ± 44.6	0.5 ± 0.7	-8.05x10 ⁻⁵ ± 0.003	-2.3x10 ⁻⁶ ± 6.0x10 ⁻⁶
CRRO	Shade	-50.5 ± 51.6	0.5 ± 0.8	-9.77x10 ⁻⁵ ± 0.004	-1.3x10 ⁻⁶ ± 7.0x10 ⁻⁶
LEHI	Sun	186.0 ± 60.9	3.6 ± 1.0	0.02 ± 0.004	-3.7x10 ⁻⁵ ± 8.1x10 ⁻⁶
LEHI	Shade	80.9 ± 120.1	2.1 ± 2.0	0.01 ± 0.01	-2.8x10 ⁻⁵ ± 1.7x10 ⁻⁵
ORLU	Sun	-69.9 ± 26.7	1.2 ± 0.4	-0.004 ± 0.002	7.1x10 ⁻⁶ ± 3.5x10 ⁻⁶
ORLU	Shade	-76.8 ± 29.5	1.3 ± 0.4	-0.005 ± 0.002	7.3x10 ⁻⁶ ± 3.9x10 ⁻⁶
TEVI	Sun	-48.1 ± 59.0	0.7 ± 0.9	-0.001 ± 0.004	1.0x10 ⁻⁶ ± 7.8x10 ⁻⁶
TEVI	Shade	-120.4 ± 66.1	1.7 ± 1.1	-0.006 ± 0.005	7.9x10 ⁻⁶ ± 8.7x10 ⁻⁶

[†]Coefficients shown are mean values ± SE.

Table 3. Slopes calculated from the derivative of the non-linear regression equations given in Table 2 at the mean for each coefficient.

Species	Light	dh/dt on date (2004)			
		14 May	29 June	19 Aug.	22 Oct.
CHNI	Sun	0.462	0.213	0.018	-0.141
CHNI	Shade	0.384	0.232	0.070	-0.145
CLMA	Sun	0.319	-0.160	-0.455	-0.790
CLMA	Shade	0.677	0.350	0.148	0.080
CRRO	Sun	0.346	0.233	0.081	-0.157
CRRO	Shade	0.399	0.329	0.237	0.094
LEHI	Sun	0.294	0.799	0.749	-0.120
LEHI	Shade	0.497	0.721	0.520	-0.346
ORLU	Sun	0.263	0.106	0.569	0.151
ORLU	Shade	0.260	0.073	-0.003	0.061
TEVI	Sun	0.311	0.208	0.119	0.292
TEVI	Shade	0.500	0.239	0.095	0.087

Most species reached maximum stem length around 9 or 22 October. However, maximum stem length was observed earlier in CHNI (15 August) and MIQU and ORLU (1 July to 5 September). CHNI and MIQU experienced a slight decline in measured height after peaking due to stem breakage. There were differences in maximum stem length among species as determined by analysis of variance ($p < 0.001$), and treatment effect was not significant due to the amount of variation between individual plants. Without regard to treatment, LEHI and CEVI had the longest stems, followed by MIQU, CLMA, TEVI, CRRO, CHNI, and ORLU, respectively (Table 4).

Leaf accumulation trends for CEVI, CRRO (after 15 June), and TEVI showed that plants grown in the shade tended to have more leaves on a given date than those grown in the sun. Due to large variability among individual plants, this pattern was only significant on a few

Table 4. Maximum plant heights by species, regardless of treatment.

Species	Day	Max. Height (cm) [†]	n
CEVI	289 (15 October)	53.2 ± 27.6 a [‡]	5
LEHI	296 (22 October)	102.0 ± 10.1 a	11
MIQU	225 (12 August)	81.3 ± 9.5 ab	6
CLMA	293 (19 October)	53.2 ± 9.7 bc	8
TEVI	296 (22 October)	46.6 ± 4.6 c	10
CRRO	283 (9 October)	44.5 ± 4.1 c	9
CHNI	228 (15 August)	33.6 ± 1.3 c	9
ORLU	249 (5 October)	31.4 ± 3.3 c	4

[†]Values are means ± SE.

[‡]Different letters indicate significant differences ($\alpha = 0.05$) Duncan's post-test).

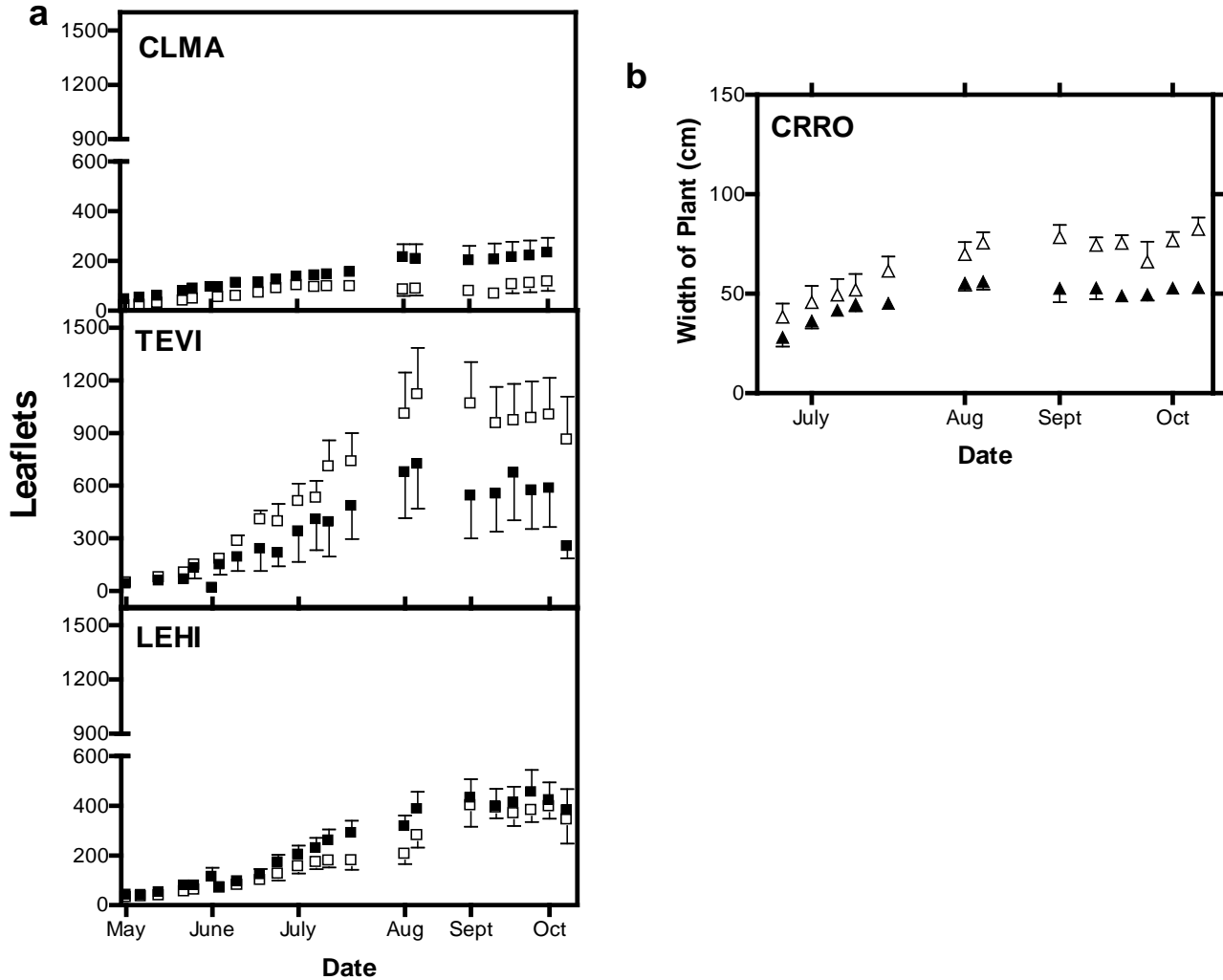


Figure 3. Leaflet counts and plant widths of sun and shade grown plants. Values shown are means \pm SE. The open symbols are shaded plants and the solid symbols are unshaded. a) Leaflet counts for CLMA, TEVI and LEHI plants grown in sun and shade. b) Width of CRRO plants grown in sun and shade.

dates for CRRO during the season (Fig. 3b). CLMA, CRRO (before 15 June), and LEHI leaf accumulation patterns revealed the opposite effect; more leaves were added on those plants grown in the sun than those in the shade. Again, due to large variability between individual plants, this effect was only significant for CLMA and LEHI on a few dates across the season (Fig. 3a). ORLU, MIQU, and CHNI did not show distinct patterns with regard to leaf accumulation over the season, and no statistical differences according to treatment were found on any dates.

Nodule Morphology

Inoculation with a mixture of native soils resulted in nodule development in all species. Nodule morphology differed among species. CEVI, CLMA, CHNI, LEHI, and ORLU all had spheroid nodules varying from 1 mm to nearly 10 mm in diameter (Table 5). CRRO and MIQU had coralloid nodules from >2 mm to <10 mm in length.

Table 5. Descriptions of nodule morphology and size with respect to light environment.

Species	Shape	Nodules	
		Size: Sun	Size: Shade
Subfamily Papilionoideae			
CEVI	Spheroid	+++ (2)	++ (5)
CLMA	Spheroid	+++ (2)	+++ (5)
CRRO	Coralloid	++++ (8)	+++ (8)
LEHI	Spheroid	+++ (7)	++++ (6)
ORLU	Spheroid	+++ (3)	++ (2)
TEVI	Elongated	++++ (4)	++++ (7)
Subfamily: Caesalpiinoideae			
CHNI	Spheroid	-- (4)	++++ (3)
Subfamily: Mimosoideae			
MIQU	Spheroid	++++ (4)	++++ (2)

[†]Nodule sizes represent an average of ratings given to each individual nodule: --, no nodules; +, <1mm; ++, 1-2mm; +++, <2 to ≤6mm; +++++, >6mm to 10mm.

[‡]Number of plants examined to estimate nodule size is given in parentheses.

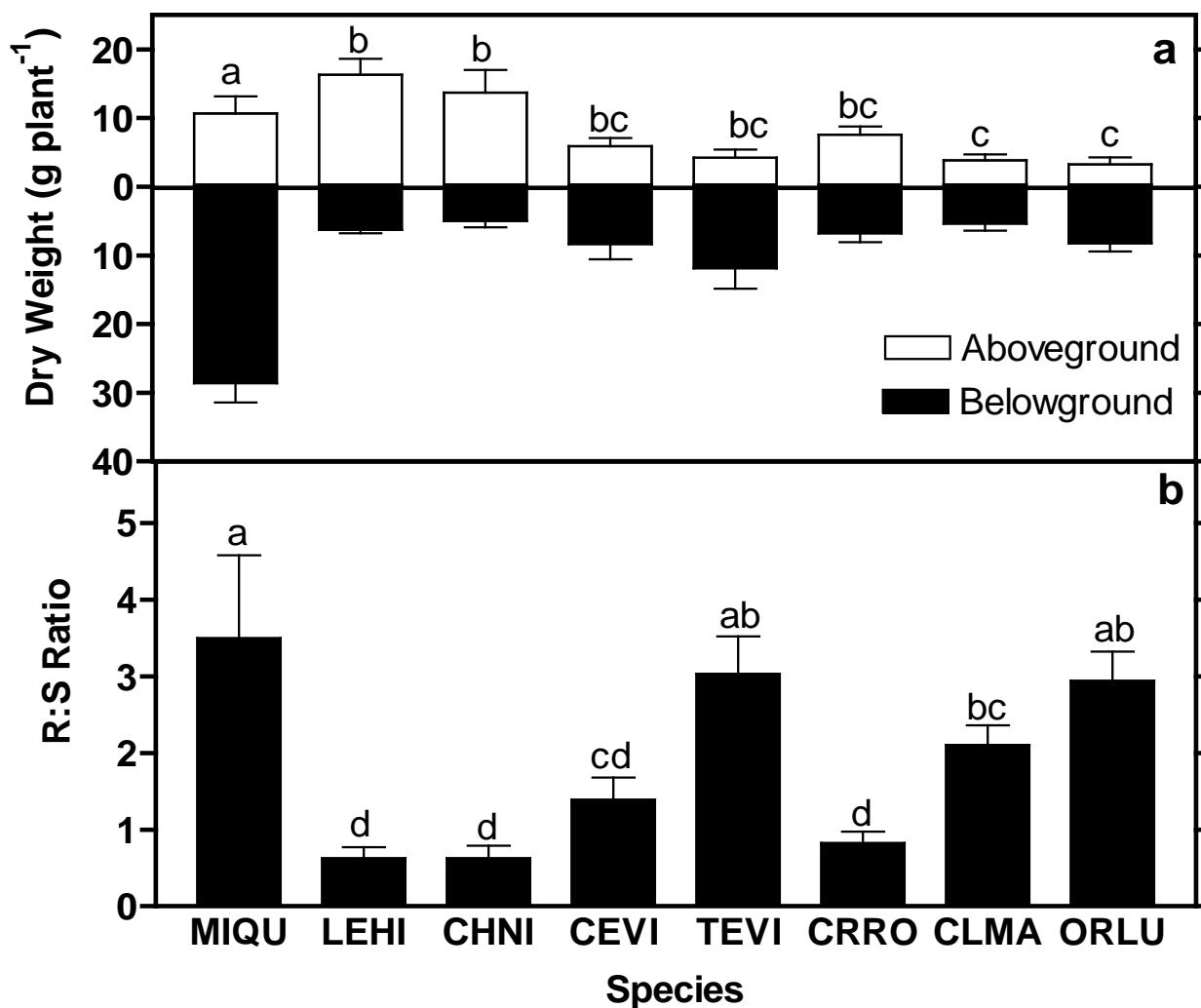


Figure 4. (a) Aboveground and belowground harvested biomass. Different letters represent significantly different total biomass (aboveground + belowground) values, and alphabetical order designates order of total biomass values, greatest to least (Duncan's post-test, $\alpha = 0.05$). (b) Root to shoot ratio of harvested biomass. Different letters represent significantly different root-to-shoot ratios (Duncan's post-test, $\alpha = 0.05$). For the entire figure, values shown are means \pm SE and data are composited by species because light treatment effect is not significant.

Coralloid nodules have a central branching point from which they randomly bifurcate, with occasional twice-bifurcation. TEVI nodules were elongate, cylindrical and often bifurcated. The length of TEVI nodules averaged >6 mm to 10 mm, although the largest nodules were >10-mm long.

Plant Growth

Mass accumulation was not significantly affected by light treatment for total mass, aboveground accumulation, or belowground accumulation, therefore, the data were pooled for the two light treatments. MIQU accumulated the largest total amount of mass over the season (Fig. 4a). There were no statistical differences among the remainder of the species except that CHNI and LEHI had greater mass than CLMA and ORLU.

Root-to-shoot ratios (R/S) showed no significant shade-treatment effect, but species effect was highly significant ($p < 0.001$). MIQU, TEVI, and ORLU had the greatest relative allocation of mass belowground (R/S>3, Fig. 4b). CLMA had twice as much allocation belowground versus aboveground (R/S>2). CEVI and CRRO had a balanced allocation pattern (R/S ~ 1). CHNI and LEHI favored aboveground accumulation (R/S < 1).

DISCUSSION

Plant Development

Native legumes in this study represented all three major sub-families of *Fabaceae*, as well as vining/spreading and erect forb growth forms. The life histories of these species represented a variety of strategies for overcoming shade, frequent fire and drought

conditions. However, of the forty native legume species that grow extensively across the Ichauway reserve, only two are annual species: *Chamaecrista fasciculata* and *C. nictitans* (CHNI; Hains et al. 1999). Perennial growth form is common in many frequently-burned ecosystems (Knapp et al. 1998; Morgan 1999; Jacobs and Schloeder 2002) and is an effective adaptation to the frequently-burned longleaf pine ecosystem.

The effect of shading on stem lengths of CLMA, CRRO, and LEHI was significant after 15 June (Fig. 2). Shaded plants of CRRO and CLMA plants had significantly longer stems than the sun-grown plants at the end of the growing season. CRRO, which is a prostrate spreading plant, and CLMA, which is semi-erect to vining, both grow below and amongst or on the bunchgrasses of the native woodland, thus, their tolerance of shade is not surprising. LEHI, a tall semi-woody species, showed a more favorable growth response to sun than shade during the last weeks of the growing season (Fig. 2). In the woodland, LEHI quickly outgrows the surrounding grasses and avoids mutual shading in the understory more easily than the smaller-stature species.

CHNI and TEVI, which showed no significant responses to shading, attain the same height as commonly found for the surrounding grasses in the native woodland. The effects of shading on the two large vines, CEVI and MIQU, were not well defined in this study due to their poor survival in this experiment, and difficulties of measuring vines that intertwine and break easily. However, even if these vines have reduced shade tolerance, they still have the ability to climb over neighboring plants and to grow into light gaps in the woodland in order to reach more direct light than smaller species, such as ORLU.

Nodule Development

Nodule morphology descriptions for species in this study (Table 2) were similar to the variations described by Sprent (2000) where species were grouped by subfamily and tribe. MIQU fits the indeterminate nodule shape of the Mimosoideae subfamily. Of the species of the Caesalpineoideae subfamily, only the genus *Chaemecrista* is known to be nodulated in the temperate regions, and the nodules have an indeterminate morphology. Nodules of CHNI were coralloid and frequently-branched.

Species belonging to the large subfamily Papilionoideae occur in various tribes. Species from this study, CLMA and CEVI, of the tribe Phaseoleae, all had desmoidoid, spheroid nodules and bear lenticels on their surface. This spheroid nodule type is also common to the tribe Desmodieae, represented in this study by LEHI. Two species of Papilionoideae from this study had indeterminate nodules, CRRO (tribe Crotalarieae) and TEVI (tribe Millettieae), and nodules from each of these

species matched the forms typical of the appropriate tribes (Table 2, Sprent 2000).

Growth

The 56% shading treatment in this study did not have a significant impact on total biomass (Fig. 4a), or R/S allocation patterns (Fig. 4b) on these eight native legumes. There were, however, substantial differences among species in both the total accumulated mass and the R/S partitioning. In particular, MIQU had the greatest mass accumulation and was among the species that partitioned the greatest fraction of the mass to the roots. The R/S for MIQU and TEVI was greater than 3 indicating a heavy investment in root growth.

Many of the species had a R/S ratio that was greater than one. In an ecosystem that is frequently-burned and prone to frequent drought, significant allocation to belowground biomass is a positive survival adaptation (Knapp et al. 1998). Those perennial species that can re-sprout quickly from nitrogen and carbohydrate reserves in the roots have a temporal and light-accessibility advantage over neighbors. MIQU plants excavated in the field had taproots exceeding 2 m long (personal observation). Plants that have greater R/S ratios and deep, branching root systems are also likely to be better at enduring droughty conditions (Kramer and Kozlowski 1979; Knapp et al. 1998), such as those that develop quickly in the coarse-sandy soils present in much of the longleaf-wiregrass ecosystem (Hains et al. 1999). For a legume, an extensive root surface area also provides increased opportunity for rhizobial colonization.

CONCLUSIONS

It is clear in this study that legume species cannot be assigned common characteristics of development and growth. For the limited group of legumes in this study there was a substantial range in growth form, reproductive phenology, and seasonal growth cycle. The results of this study showed examples of legumes from this temperate climate with shade tolerance at the level imposed in this study similar to the observations of legumes in the tropics (Sprent 1999). Some species exhibited greater stem elongation with shading (Fig. 2), but none of the species in this study demonstrated decreased mass accumulation in response to the decreased light level (56% of ambient) treatment. Although a more heavily shaded treatment might have provided a greater effect upon several species, the light environment to which plants were exposed in this experiment is roughly the irradiance in the understory of a longleaf pine canopy especially following a thinning harvest. *Mimosa quadrivalvis* (L.) proved to have both rapid plant development and the greatest mass growth among the tested legumes indicating it to be a prime candidate for use in restoration of the longleaf pine – wiregrass ecosystem.

ACKNOWLEDGMENTS

This research was funded through a cooperative agreement between the Joseph W. Jones Ecological Research Center, the Robert W. Woodruff Foundation, and the University of Florida College of Natural Resources and Environment and is approved for publication as Journal Series No. 65.

REFERENCES

- Battaglia, M.A., R.F. Mitchell, P.P. Mou, and S.D. Pecot. 2003. Light transmittance estimates in a longleaf pine woodland. *Forest Sci.* 49:752-762.
- Cathey, S.E., L.R. Boring, and T.R. Sinclair. 2009. Assessment of N₂ fixation capability of native legumes from the longleaf-wiregrass ecosystem. *Environ. Exp. Botany* (In Press).
- Coffey, K.L. And L.K. Kirkman. 2004. Native ground cover partners: reestablishing native ground cover in longleaf pine savannas. *Ecol. Restor.* 22:288-289.
- GraphPad Prism, Inc. 1996. GraphPad Prism, release 2.01. San Diego, California, USA.
- Hains, M.J., R.J. Mitchell, B.J. Palik, L.R. Boring, and D.H. Gjerstad. 1999. Distribution of native legumes (Leguminosae) in frequently burned longleaf pine (Pinaceae)-wiregrass (Poaceae) ecosystems. *Am. J. Bot.* 86:1606-1614.
- Hendricks, J.J. and L.R. Boring. 1999. N₂-fixation by native legumes in burned pine ecosystems of the southeastern United States. *For. Ecol. Manage.* 113:167-177.
- Hiers, J.K., R.J. Mitchell, L.R. Boring, J.J. Hendricks, and R. Wyatt. 2003. Legumes native to longleaf pine savannas exhibit capacity for high N₂-fixation rates and negligible impacts due to timing of fire. *New Phytol.* 157:327-338.
- Jacobs, M.J. and C.A. Schloeder. 2002. Fire frequency and species associations in perennial grasslands of south-west Ethiopia. *Afr. J. Ecol.* 40:1-9.
- Knapp, A.K., J.M. Briggs, D.C. Hartnett, and S.L. Collins (eds). 1998. *Grassland Dynamics: Long-term Ecological Research in Tallgrass Prairie*. Oxford University Press, New York.
- Kramer, P.J., and T.T. Kozlowski. 1979. *Physiology of Woody Plants*. Academic Press, New York.
- Markewitz, D., F. Sartori, and C. Craft. 2002. Soil change and carbon storage in longleaf pine stands planted on marginal agricultural lands. *Ecol. Appl.* 12:1276-1285.
- Morgan, J.W. 1999. Defining grassland fire events and the response of perennial plants to annual fire in temperate grasslands of south-eastern Australia. *Plant Ecol.* 144:127-144.
- Pecot, S.D., S.B. Horsley, M.A. Battaglia, and R.J. Mitchell. 2005. The influence of canopy, sky conditions, and solar angle on light quality in a longleaf pine woodland. *Can. J. Forest Res.* 35:1356-1366.
- SAS Institute, Inc. 2003. *SAS/STAT and Base SAS*, Release 9.1.3. Cary, North Carolina, USA.
- Sprent, J.I. 1999. Nitrogen fixation and growth of non-crop legume species in diverse environments. *Perspect. Plant Ecol. Evol. Syst.* 2:149-162.
- Sprent, J.I. 2000. Nodulation as a taxonomic tool. In Herendeen, P.S. And Bruneau, A. [eds.], *Advances in Legume Systematics*, Part 9, 21-44. Royal Botanical Gardens, Kew, London.
- Vitousek, P.M., K. Cassman, C. Cleveland, T. Crews, C.B. Field, N.B. Grimm, R.W. Howarth, R. Marino, L. Martinelli, E.B. Rastetter, and J.I. Sprent, J.I. 2002. Towards and ecological understanding of biological nitrogen fixation. *Biogeochemistry* 57:1-45.
- Wunderlin, R.P. and B.F. Hansen. 2003. *Guide to the Vascular Plants of Florida*, 2nd ed. University Press of Florida, Gainesville