

**DIFFERENCES IN GAS EXCHANGE RATES PROVIDE  
INSIGHT INTO THE DISTRIBUTION OF C<sub>3</sub> SEDGES AND  
C<sub>4</sub> GRASSES IN CENTRAL TEXAS SAVANNAS**

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**ABSTRACT**

The Edwards Plateau of central Texas is mainly a savanna community with *Juniperus ashei-Quercus virginiana* woodlands and C<sub>4</sub> grasslands. C<sub>4</sub> grasses are common in the open grasslands but not below the woodland canopy while some C<sub>3</sub> sedges are found below the canopies and at the canopy edges. This study measured and compared gas exchange rates of these C<sub>3</sub> sedges and C<sub>4</sub> grasses to look for potential causes in distribution differences. In general, the response variables were 4 to 6.5 times higher for the grasses in high light while the sedges had higher values than the grasses in low light. The C<sub>4</sub> grass, *Bouteloua curtipendula* had the highest overall responses, while the C<sub>3</sub> sedge, *Carex planostachys* below the canopy had lowest values. Grasses had high A<sub>max</sub> values (maximum photosynthetic rates), light saturation and respiration rates, suggesting they are sun species. The sedges had low values similar to shade species. Light levels appear to affect the distribution of both groups of plants but in different ways. Light attenuation seems to promote the sedges below the canopy and at the same time excluding grasses from the canopy habitat, while the reverse seems to be true in open grassland habitats. *Phytologia* 94(1): 71-90 (April 2, 2012).

**KEY WORDS:** C<sub>3</sub> sedges, C<sub>4</sub> grasses, savanna, gas exchange, photosynthesis, CO<sub>2</sub> uptake, woodlands, light response curves, *Juniperus-Quercus* woodlands, central Texas, sw North America

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Complex gradients of abiotic and biotic factors or combinations occur throughout the World, including the central Texas Edwards Plateau, and these gradients determine the kind of communities and species that are present (Begon, Townsend, and Harper, 2006). This area of central Texas consists of savannas that are biphasic communities and have been difficult to study (House et al., 2003). Usually the grassland or gap phase is studied separately from the woodland phase (Van Auken, 2000; Van Auken and McKinley, 2008). In some central Texas woodland phase *Juniperus* communities, a drought tolerant sedge (*Carex planostachys* - cedar sedge, Cyperaceae) is found in the understory with high density, cover and dry mass (Wayne and Van Auken, 2008; 2010). Causes for differences in *C. planostachys* distribution, cover, and biomass seem to be related to the reduced light levels and enhanced soil moisture below the *Juniperus* canopy. This is unlike a majority of sedges that occur in cool and/or wet environments usually at higher latitudes and altitudes (Ball, 1990). Other sedges including *Carex tetrastachya* and *C. perdentata* are also reported in the Edwards Plateau region (Correll and Johnston, 1979). They seem to occur below the canopies of several deciduous tree species early in spring after bud break when canopy leaves are still emerging and light levels are less attenuated, but in deeper soils similar to some eastern deciduous forest understory species (Hull, 2002).

Physiological differences between plants native to open, full sun habitats compared to those found in shady, understory communities are fairly well known (Begon, Townsend, and Harper, 2006; Valladares and Niinemets, 2008). There are many papers concerning the  $C_4$  grasses that occur in Texas full sun, grasslands and prairies and the grasslands of central North America (Gould, 1975; Correll and Johnston, 1979; Van Auken, Bush, and Diamond, 1994; Knapp and Medina, 1999; McCarron and Knapp, 2001). Most of these  $C_4$  grasses seem to be sun species, but there are few papers about their gas exchange rates being suppressed at low light levels (McCarron and Knapp, 2001). Also, there is little information about their performance in the shade of woodland canopies specifically at low light levels (see Wayne and Van Auken 2009) and no published studies that we could find comparing the  $C_3$  sedges and the  $C_4$  grasses found in these communities.

Gas exchange rates reported for species found in sun or shade in these savanna ecosystems seem mixed. Rates for *Abutilon theophrasti* including  $A_{\max}$  (maximum photosynthesis) and dark respiration ( $R_d$ ) were high indicating a sun species (Van Auken and Bush, 2011). Similar measurements for *Malvavicus arborius*, *Verbesina virginica*, *Sophora secundiflora* and others were intermediate and suggest they could grow in full sun, shade or transitional light habitats (Furuya and Van Auken, 2009; Furuya and Van Auken, 2010; Gagliardi and Van Auken, 2010; Van Auken and Bush, 2011). Light compensation ( $L_{cp}$ ), light saturation ( $L_{sat}$ ), conduction ( $g_{leaf}$ ), and transpiration (E) measurements all suggest that these species are either sun plants or intermediate sun species. One apparent high density but unusual understory species found in this area is *Carex planostachys* which has gas exchange rates that are similar to those reported for understory eastern deciduous forest species (Hull, 2002).

The purpose of this study was to measure and compare gas exchange rates of three  $C_3$  sedges including *Carex planostachys*, *C. tetrastachya*, and *C. perdentata* that occur mostly below canopies in central Texas woodlands with four  $C_4$  grasses including *Aristida purpurea*, *Bouteloua curtipendula*, *Bothriochloa laguroides*, and *B. ischaemum* that occur in the open gaps or grassland phase in this same area to see if gas exchange rates could help explain their distributions.

## METHODS AND MATERIALS

Study site - The central Texas Edwards Plateau is a biphasic savanna community (Correll and Johnston, 1979; Van Auken, Ford, and Allen, 1981; Van Auken and McKinley, 2008; Furuya and Van Auken, 2009). The major vegetation type is *Juniperus-Quercus* savanna and is representative of savannas and woodlands found throughout this region. However, there are more woodlands with higher woody plant density, and smaller and fewer gaps in the east compared to savanna communities farther to the west (Van Auken and Smeins, 2008). This study was conducted on the southern edge of the Edwards Plateau near the University of Texas at San Antonio in Bexar County (29°34'53"N, 98°37'49"W). Soils at the study site vary, but in general are characterized as gentle to rolling, clayey-skeletal, smectitic, thermic

lithic calciustolls in the Tarrant association or moderately deep, dark-colored, nearly level alluvial soils in the Lewisville series (Taylor, Hailey, and Richmond, 1962; NRCS, 2006). Tarrant soils ranged from 0 to 25 cm in depth and the Lewisville soils were up to ca. 61 cm in depth. Regional climate is classified as sub-tropical – sub-humid with a mean annual temperature of 20 °C (Arbingast et al., 1976). Monthly mean temperature ranges from 9.6 °C in January to 29.4 °C in July (NOAA, 2004). Annual precipitation in the study area is 78.7 cm, bimodal, with peaks occurring in May and September with monthly means of 10.7 cm and 8.7 cm, respectively.

Vegetation on the shallow upland soil in the wooded habitat is dominated by *J. ashei* Buchh. (ashe juniper) and *Quercus virginiana* Mill. (live oak=*Q. fusiformis*) (Van Auken and Smeins, 2008) and representative species in the open grassland are *Aristida purpurea* Nutt. var. *longiseta* (Steud.) Vasey (Red three-awn), *Bouteloua curtipendula* (Michx.) Torr. (side-oats grama), *Bothriochloa laguroides* (de Candolle) Herter var. *torreyana* (von Steudel) Allred and Gould (silver bluestem), *Bothriochloa ischaemum* (L.) Keng var. *songarica* (Rupr.) Celerier and Harlan (KR or King Ranch bluestem), various other C<sub>4</sub> grasses and a variety of herbaceous annuals (Terletzky and Van Auken, 1996; Dibbs, Lipscomb, and O'Kennon, 1999; Barnes et al., 2000). *Carex planostachys* Kunze (cedar sedge) occurs mainly in wooded habitats in this area but occasionally in open grasslands (Wayne and Van Auken, 2008, 2009, 2010). In addition, in shaded deciduous woodland with deeper soils, two other sedges occur, *C. perdentata* S. D. Jones (sand sedge) and *C. tetrastachya* Scheele (britton sedge) (Ball, Reznicek, and Murray, 2003). The dominant woody species in these woodlands with deeper soil are *Q. virginiana*, *Ulmus crassifolia* Nutt. (cedar elm), *Celtis laevigata* Willd. (Texas sugarberry) and *Prosopis glandulosa* Torr. (honey mesquite).

Sampling procedures - Photosynthetic response curves were carried out on three randomly selected plants for each species, using mature, fully elongated leaves. Measurements were made when plant growth was most active, late March 2006 for the sedges and mid-July 2006 for the grasses. Previous observations verified that *C. perdentata* and *C. tetrastachya* were dormant by mid-April. Before making any measurements, all plants were watered to ensure full hydration (Peek et

al., 2002). Response curves for *C. planostachys* were made for plants below a *J. ashei* canopy and in the open grassland. Response curves for the other two sedges were made below a deciduous canopy prior to full leaf expansion of the canopy species. Response curves for all of the C<sub>4</sub> grasses were made in a gap between *J. ashei* canopy woodlands.

Gas-exchange measurements - Steady-state gas-exchange response curves as a function of light levels (photosynthetic active radiation, PAR,  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) were completed to determine the maximum photosynthetic rate ( $A_{\text{max}}$ ,  $\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), the light saturation point ( $L_{\text{sp}}$ ,  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), the quantum yield, the light compensation point ( $L_{\text{cp}}$ ,  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), the dark respiration rate ( $R_{\text{d}}$ ,  $\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) and stomatal conductance ( $g_{\text{leaf}}$ ,  $\text{mol H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ). Photosynthetic active radiation was measured using an integrated external quantum sensor, LiCor<sup>®</sup> LI-170 (Lincoln, NE). Plants were dark adapted for 30 minutes prior to making measurements for the response curves. Response curves were conducted within two hours prior to solar noon. Three to four intact, fully elongated, mature leaves were selected on a plant and placed on the surface of the cuvette of a LiCor<sup>®</sup> 6400 portable photosynthetic meter with the adaxial surface up, prior to closing the chamber. Both the cuvette and plant were covered with shade cloth to exclude external light. Leaf width was measured and total leaf area was calculated from the parallel portion of the leaves in the chamber. Gas-exchange measurements were standardized to a constant leaf area based on measurements for each sample.

Light levels were provided with an integrated red-blue LED light source attached to the cuvette. Chamber temperature and humidity were controlled at initial ambient levels. Cuvette CO<sub>2</sub> was maintained at 390  $\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . The loaded cuvette was allowed to equilibrate prior to inducting the response curve. Response curves were initiated at high light levels to ensure stomatal opening and photoactivated Rubisco (Givnish, Montgomery, and Goldstein, 2004). After a steady state was achieved light levels were ramped down in 17 or 18 steps to 0  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . Sedges reached a steady state rapidly, < 1 minute, but grasses required up to 10 minutes for full induction. A stable coefficient of variation (< 0.3 %) was obtained at each level before data logging, ca. 2–3 min. Response curves were initiated at 1500  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for the sedges and 2000  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for the grasses.

Natural log transformations were made on the averaged fitted data for CO<sub>2</sub> uptake for each species to better understand the species response as a function of light level. Comparisons were made between all of the sedges and all of the grasses.

Data Analysis - To compensate for within position differences between plant responses,  $A_{\max}$  was averaged across the five highest asymptotic gas-exchange values ( $A_{\text{net}}$ ) for each plant replication (Hull, 2002). Photosynthetic response data was fit with an empirical non-rectangular hyperbola function  $A = A_{\max} \times [1 - (1 - R_d/A_{\max})^{(1-PPF/L_{cp})}]$  to model the nonlinear response of carbon uptake to change in light level (Bond et al., 1999). The quantum yield equation was derived by regressing the gas-exchange rate  $A_{\text{net}}$  from 0  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  PAR upward until the regression coefficient of the slope decreased (Hull, 2002).  $L_{\text{sp}}$  for each replication was calculated from the regression of the initial linear portion of the response curve and was in agreement with the derived value of 90 %  $A_{\max}$  (Bond et al., 1999).  $L_{\text{cp}}$  was calculated from the quantum yield equation by setting  $A_{\text{net}} = 0 \mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ .  $R_d$  was calculated by averaging the  $A_{\text{net}}$  rate for each plant replication at PAR = 0  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . The non-linear analysis described by Peek et al. (2002) was used to account for repeated measures. To test for differences within functional groups, grass or sedge, the Wald test for equality of variance was used on the estimated covariance parameters.  $A_{\max}$  and  $g_{\max}$  (raw data) were also evaluated for statistical differences with a repeated measures ANOVA and contrast statements to determine where differences occurred.  $L_{\text{sp}}$  and  $R_d$  were treated as stationary points and evaluated for statistical differences with ANOVA and linear regression (SAS, 2005). Comparisons between species  $A_{\max}$ ,  $L_{\text{sp}}$ , and  $R_d$  were conducted by testing for differences using ANOVA. Means separation tests were used when significant differences were detected.

## RESULTS

C<sub>3</sub> sedge comparisons - Ambient light levels in March were high in habitats without a *Juniperus* canopy ( $1165 \pm 484 \mu\text{mol m}^{-2}\cdot\text{s}^{-1}$ , mean  $\pm$  SE) and reduced under a *Juniperus* canopy ( $318 \pm 132 \mu\text{mol m}^{-2}\cdot\text{s}^{-1}$ ). Light levels below the leafless deciduous canopy were higher than light levels below a *Juniperus* canopy (Table 1).  $A_{\max}$  values (Table 1, Fig. 1a) ranged from a low of  $4.9 \pm 0.3 \mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for

*C. planostachys* below the *Juniperus* canopy to a high of  $9.0 \pm 0.8$   $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  for *C. tetrastachya* below the canopy. The ANOVA

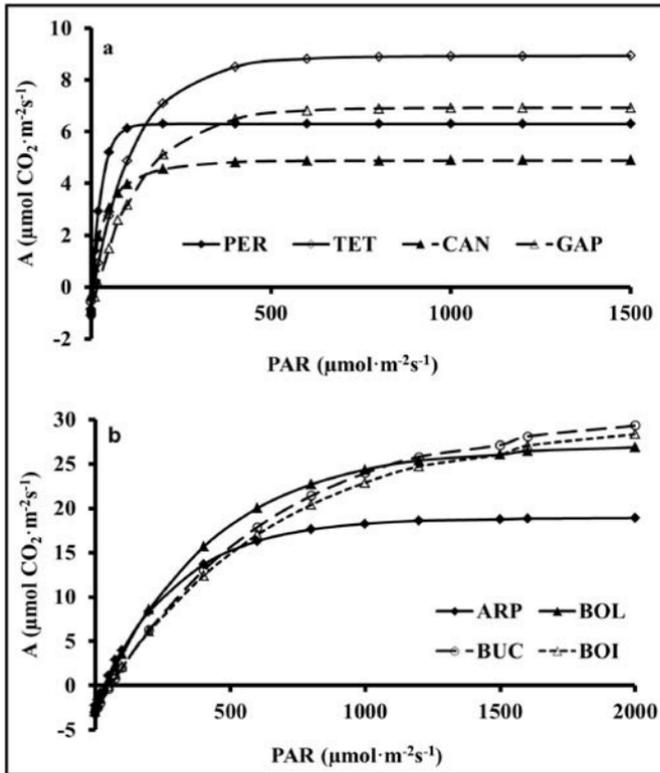


Figure 1. Mean light response curves for CO<sub>2</sub> uptake to incremental change in light levels for a) C<sub>3</sub> sedges *C. planostachys* below the *J. ashei* canopy (CAN) and intercanopy gap (GAP) and *C. perdentata* (PER) and *C. tetrastachya* (TET) below a leafless deciduous woodland canopy, and b) for the C<sub>4</sub> grasses in the grassland *A. purpurea* (ARL), *B. laguroides* (BOL), *B. ischaemum* (BOI) and *B. curtipendula* (BUC). Response curves were fitted to a non-rectangular hyperbola function. Measurements were made during active growth, March (sedges) and July (grasses) 2006, on fully expanded leaves. Standard error bars are not presented because they were smaller than the symbols used.

Table 1. Mean response parameters for C<sub>3</sub> sedges and C<sub>4</sub> grasses derived from light response curves for plants occurring in contrasting light environments. Means ( $\pm SE$ ) are ambient photosynthetically active radiation (PAR), maximum photosynthetic rate ( $A_{max}$ ), light compensation point ( $L_{cp}$ ), dark respiration ( $R_d$ ), light saturation ( $L_{sp}$ ), and maximum rate of stomatal conductance ( $g_{max}$ ). A repeated measure ANOVA with p-1 contrasts was used to detect significant differences within columns and *P*-values are provided. Means with different letters within a column are significantly different.

Sedge Species	PAR	$A_{max}$	$L_{cp}$	$R_d$	$L_{sp}$	$g_{max}$
<i>C. planostachys</i> Gap *	1165 $\pm 484$	7.0 $\pm 0.9$ <b>b</b>	17 $\pm 3$	1.0 $\pm 0.2$	151 $\pm 16$	0.12 $\pm 0.01$ <b>a</b>
<i>C. planostachys</i> Canopy *	318 $\pm 132$	4.9 $\pm 0.3$ <b>c</b>	4 $\pm 2$	0.4 $\pm 0.0$	151 $\pm 43$	0.07 $\pm 0.01$ <b>c</b>
<i>C. tetrastachya</i>	1322 $\pm 199$	9.0 $\pm 0.8$ <b>a</b>	7 $\pm 2$	0.6 $\pm 0.1$	187 $\pm 24$	0.09 $\pm 0.01$ <b>b</b>
<i>C. perdentata</i>	800 $\pm 152$	5.8 $\pm 1.7$ <b>b</b>	3 $\pm 1$	0.9 $\pm 0.1$	114 $\pm 42$	0.08 $\pm 0.00$ <b>bc</b>
Col. <i>P</i>		****		ns	ns	****
Grass Species	PAR	$A_{max}$	$L_{cp}$	$R_d$	$L_{sp}$	$g_{max}$
<i>A. purpurea</i>	1576 $\pm 14$	19.2 $\pm 0.5$ <b>c</b>	33 $\pm 4$	2.3 $\pm 0.5$	428 $\pm 31$	0.23 $\pm 0.02$ <b>b</b>
<i>B. laguroides</i>	1619 $\pm 26$	28.0 $\pm 1.1$ <b>b</b>	42 $\pm 2$	2.9 $\pm 0.3$	561 $\pm 100$	0.36 $\pm 0.70$ <b>a</b>
<i>B. ischaemum</i>	1662 $\pm 82$	30.0 $\pm 1.4$ <b>ab</b>	52 $\pm 15$	2.5 $\pm 0.3$	732 $\pm 13$	0.17 $\pm 0.01$ <b>c</b>
<i>B. curtipendula</i>	1633 $\pm 98$	31.6 $\pm 0.5$ <b>a</b>	58 $\pm 10$	3.0 $\pm 0.1$	630 $\pm 78$	0.25 $\pm 0.01$ <b>b</b>
Col. <i>P</i>		****		ns	ns	**

\* From Wayne and Van Auken 2009. \*\* =  $P < 0.05$ , \*\*\*\* =  $P < 0.0001$ , ns = not significant.

with repeated measures to test for differences in  $A_{\max}$  was significant ( $F = 22.86$ ,  $P < 0.0001$ ), and with the exception of the *C. planostachys* in the gap and *C. perdentata* below the canopy, all paired comparisons were significantly different (Table 1).  $L_{cp}$  was lowest for *C. perdentata* at  $3 \pm 1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and highest for *C. planostachys* in the gap at  $17 \pm 3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , but statistical differences were not detected (Table 1, Fig. 1a). The  $R_d$  was smallest for *C. planostachys* below the canopy at  $0.4 \pm 0.0 \mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and highest for *C. planostachys* in the gaps at  $1.0 \pm 0.2 \mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (Table 1, Fig. 1a) but not significantly different ( $F = 4.03$ ,  $P > 0.05$ ). The  $L_{sp}$  also did not vary significantly (ANOVA,  $F = 0.81$ ,  $P > 0.05$ ), but  $L_{sp}$  values ranged from  $114 \pm 42 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for *C. perdentata* to  $187 \pm 24 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for *C. tetrastachya* (Table 1). The repeated measures ANOVA indicated that  $g_{\max}$  varied significantly ( $F = 8.89$ ,  $P \leq 0.0001$ ), but values did not differ greatly (Table 1, Fig. 2a). At light extinction ( $0 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  PPF), conductance did not vary across any of the species of *Carex* examined ( $F = 0.81$ ,  $P > 0.05$ , Fig 2b), with values ranging from  $0.08 \pm 0.00 \text{ mol H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (*C. perdentata*) to  $0.12 \pm 01 \text{ mol H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (*C. planostachys* in the gaps).

$C_4$  grass comparisons - Ambient light levels were high and consistent across all measurements (Table 1). The repeated measures ANOVA indicated significant differences in  $A_{\max}$  between the  $C_4$  grasses ( $F = 35.73$ ,  $P < 0.0001$ , Table 1, Fig. 1b).  $A_{\max}$  ranged from  $19.2 \pm 0.5 \mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for *A. purpurea* to  $31.6 \pm 0.5 \mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for *B. curtipendula*. The repeated measures ANOVA indicated no significant differences for the  $L_{cp}$ . However, it was lowest for *A. purpurea* at  $33 \pm 4 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and highest for *B. curtipendula* at  $58 \pm 10 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . The repeated measures ANOVA indicated no significant differences between  $R_d$  for the grasses, but was smallest for *A. purpurea* at  $2.3 \pm 0.5 \mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and highest for *B. curtipendula* at  $3.0 \pm 0.1 \mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (Table 1, Fig. 1b). The  $L_{sp}$  did not vary significantly between grasses (ANOVA,  $F = 3.78$ ,  $P > 0.05$ ), but ranged from  $428 \pm 31$  to  $732 \pm 11 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . There were significant differences in stomatal conductance (ANOVA,  $F = 3.33$ ,  $P < 0.05$ ), lowest for *B.*

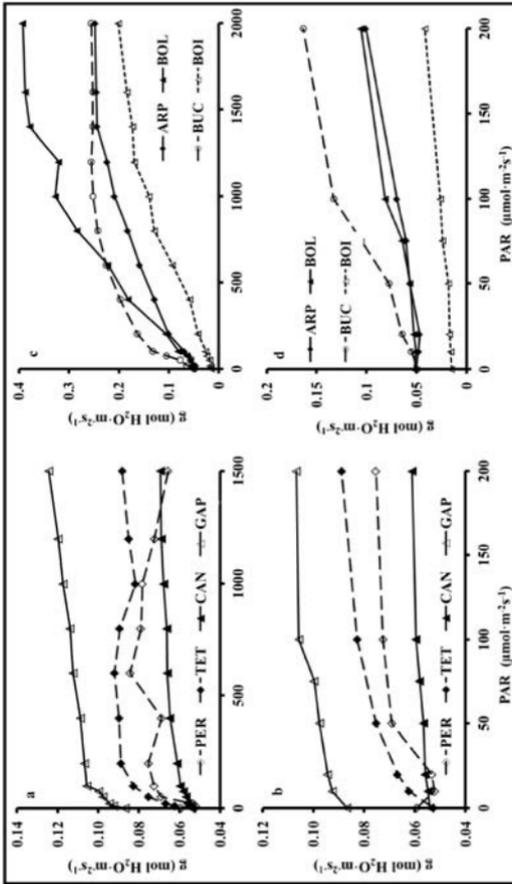


Figure 2. Mean stomatal conductance response curves ( $\text{mol H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) to the incremental change in light intensity for  $\text{C}_3$  sedges from a) 0-1500 PAR and b) a magnified view from 0-200 PAR and for  $\text{C}_4$  grasses from c) 0-2000 PAR and d) a magnified view from 0-200 PAR. Abbreviations are as in Fig. 1. Measurements were made during active growth on fully expanded leaves in March 2006 for sedges and in July 2006 for grasses. Standard error bars are not presented because they were smaller than the symbols used.

*ischaemum* at  $0.17 \pm 0.01 \text{ mol H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and highest for *B. laguroides* at  $0.36 \pm 0.07 \text{ mol H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (Table 1, Fig. 2c). The paired comparisons indicated that there were significant differences between all species except *A. purpurea* and *B. curtispindula*. At light extinction ( $0 \text{ }\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  PPF) conductance did not vary across grass species ( $F = 0.95, P > 0.05$ , Fig. 2d), ranging from a low of  $0.02 \pm 0.00 \text{ mol H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for *B. ischaemum* to ca.  $0.05 \text{ mol H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for the other grasses.

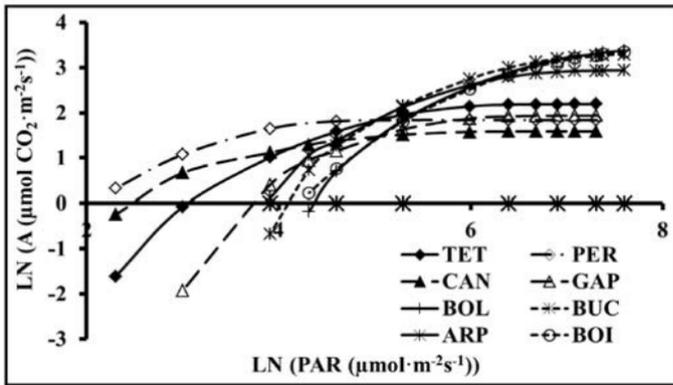


Figure 3. Natural log transformations of axes from the fitted response curves presented for the  $C_3$  sedges and the  $C_4$  grasses in Fig. 1. Asterisks on x-axis (from left to right) indicate light levels of 50, 100, 200, 500, 1000, 1500 and 2000  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , respectively. Positions where curves intersect suggest adaptive crossover.

Comparison of species performance - At high light, above approximately  $400 \text{ }\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (ln 6, Fig. 3) to  $1500 - 2000 \text{ }\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (ln 8, Fig. 3), the grasses had higher  $\text{CO}_2$  uptake (between approximately 20 and  $35 \text{ }\mu\text{molCO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), while the rate for the sedges was much lower (approximately  $4 - 9 \text{ }\mu\text{molCO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ).  $\text{CO}_2$  uptake was approximately equal for the grasses and sedges between a PAR of 100 and  $200 \text{ }\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (Fig. 3,  $\ln \geq 5$  but  $< 6$ ). When light levels were reduced to  $50 - 100 \text{ }\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ,  $\text{CO}_2$  uptake for the grasses was very low, at or below their  $\text{CO}_2$  uptake rate at their light compensation point, but the sedges had positive  $\text{CO}_2$  uptake rates between approximately 2 and  $6 \text{ }\mu\text{molCO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (Fig. 3,  $\ln \leq 5$ ). The

sedges continued to fix CO<sub>2</sub> until they reached their L<sub>cp</sub> at between 20 and 100 μmol·m<sup>-2</sup>·s<sup>-1</sup>.

## DISCUSSION

Theory suggests that plants occurring in habitat with a woodland or forest overstorey are shade tolerant plants or shade plants and have low rates of CO<sub>2</sub> uptake, low light compensation and saturation, along with a low dark respiration rate; while shade intolerant plants or sun plants have considerably higher rates (Björkman et al., 1972; Givnish, 1988; Valladares and Niinemets, 2008). The photosynthetic response profiles for the C<sub>3</sub> *Carex* species we studied were considerably lower than the response profiles for the C<sub>4</sub> grass species examined when light levels exceeded ca. 200 μmol·m<sup>-2</sup>·s<sup>-1</sup>, which is what is reported for sun and shade species from other areas.

The photosynthetic rates for the C<sub>4</sub> grasses examined were consistent with values reported for C<sub>4</sub> grass in water-limited northern prairie (Knapp, 1993; Turner, Kneisler, and Knapp, 1995; McCarron and Knapp, 2001; Fay et al., 2002). The photosynthetic rates for the C<sub>3</sub> sedges were similar to values reported for sedges in water stressed environments (Busch, 2001; Wayne and Van Auken, 2009). For both *C. perdentata* and *C. tetrastachya* the time of year seemed to be important for their growth and gas exchange responses, but was not examined in this study. Herbaceous annuals found in the understory of deciduous woodlands or forests are usually physiologically active at times when the solar track is low and there is an absence of canopy leaves, resulting in an environment suitable for the growth of shade tolerant herbaceous species (Baldocchi et al., 1984; Hull, 2002; Muth and Bazzaz, 2002). *Carex planostachys*, in central Texas woodlands, is physiologically active throughout the year below the evergreen canopy, but gas exchange is reduced during the hottest and driest time of year (Wayne and Van Auken, 2004, 2009). Although there are many sedge that occur in open habitats, these habitats are in higher latitudes or altitude and are cooler and wetter, reducing the negative impacts of water stress on photosynthesis (Busch, 2001). Thus, from a light tolerance perspective, the sedges studied were tolerant of low light, or shade species, while the grasses were shade intolerant or sun species.

Stomatal responses – Both light and soil water are required for carbon uptake and plant growth. Most plants have a stomatal response coupled to water availability or elevated rates of transpiration, which triggers a stomatal response to regulate aperture size (Chaves, Maroco, and Pereira, 2003; Osborne et al., 2003; Tuzet, Perrier, and Leuning, 2003). Like *C. perdentata*, the decline in conductance at elevated light levels for *C. tetrastachya* suggests there is a stomatal limitation regulating the photosynthetic response. In addition, the stomatal response observed at low light levels suggests that *C. tetrastachya* is coupled more strongly to light levels, but at higher light levels it uncouples. Some plants, such as *C. planostachys*, have conductance rates that appear fully coupled to the photosynthetic process or light availability rather than water induced stress (Wayne and Van Auken, 2009). This phenomenon may change with time of year, increasing daily temperatures and the severity of drought (Ogle and Reynolds, 2002). In the present study, *C. planostachys* did not appear to have any stomatal limitation regulating photosynthesis. The overall benefit of stomatal regulation maintaining water status comes at a cost of reduced carbon gain (Percy, 2000; Chaves, Maroco, and Pereira, 2003).

The C<sub>4</sub> grasses investigated had substantially higher rates of conductance at PAR > 100  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and stabilized approaching 1500  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , except for *Bothriochloa ischaemum*. The conductance values were also consistent with values reported for C<sub>4</sub> grasses in northern prairies (Knapp, 1993). There was marginal evidence that *A. purpurea* conductance was coupled to soil moisture like *C. perdentata* (see Fig. 2b and d). Assuming stability when light was at higher levels, a benefit of a reduced or stable conductance, and corresponding transpiration, is a water conserving response identified for grasses as a means to limit plant water stress (Knapp, 1993; Chaves, Maroco, and Pereira, 2003; Lecain et al., 2003), this also appears to be true for *C. perdentata* and *C. tetrastachya*.

Species performance - Differences in response profiles between species are attributed to factors related to natural selection for a habitat type, usually high light or low light (Percy, 2000; Hull, 2002). It could be assumed there is an ecological or competitive advantage particular in the habitat that a species occupies, to have optimal photosynthesis and carbon-uptake in that habitat. In oak savanna in southern Wisconsin, C<sub>4</sub> grasses, having high light

requirements, are ideally suited for survival in open areas lacking a woody canopy. Sedges and C<sub>3</sub> grasses with reduced light requirements are more often found in shaded habitats and appear to be shade tolerant (Leach and Givnish, 1999). Sedges such as *C. planostachys*, *C. perdentata* and *C. tetrastachya*, with tolerance to low light, appear better suited to habitats that have a woody canopy to reduce light levels. Comparisons of response profiles among species in the present study (see Fig. 3), demonstrated interesting trends that suggest the C<sub>3</sub> sedges and C<sub>4</sub> grasses should occur in distinct ecological habitats, which seems to be true. Grasses perform better at high light and appear to be photosynthetically suited to open areas or gaps with high light levels. At lower light levels, ca. 200  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  or lower, the rate of grass CO<sub>2</sub> uptake decreased rapidly. Below 200  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , the shade tolerant C<sub>3</sub> sedges have the higher CO<sub>2</sub> uptake rates and probably higher growth rates; thus they seem better suited to habitats where canopy structure attenuates incoming light. When light levels reached substantially low values, ca. 50  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , *C. perdentata* has the highest performance. Similar responses were observed in northern grasslands where canopy shade from taller grass plants modified the microclimate for plants nearer the soil, promoting cost savings in photosynthetic rates resulting from reduced stress (Turner and Knapp, 1996). *Carex perdentata* with a low compensation point may have rapid photosynthetic induction to maximize photosynthetic gain in light-flecks in the reduced light environment, however, this is not known.

*Carex planostachys* is tolerant of low light levels and severe aridity, and occurs on the shallow soils common to many central Texas *Juniperus* woodlands. The light response characteristics of *C. perdentata* and *C. tetrastachya* suggest they should also be able to fix carbon and grow below a *Juniperus* canopy as well; however, their tolerance to drought is probably low but currently unknown. For the C<sub>4</sub> grasses, soil depth, texture and organic content are factors that have an important role in explaining differences in their growth in semi-arid and arid habitats through their influence on plant water stress (Turner, Kneisler, and Knapp, 1995; Leach and Givnish, 1999; Weiher et al., 2004; Rosenthal, Ludwig, and Donovan, 2005). However, in the present study, light levels were critical.

The light compensation points, along with light saturation levels, and respiration rates are strong predictors of species distribution

in various habitats (Givnish, Montgomery, and Goldstein, 2004; Begon, Townsend, and Harper, 2006; Valladares and Niinemets, 2008), with many species being tolerant of either high or low light levels. Canopy overstory appeared to be an important influencing factor on *Carex* plant responses and thus distribution. Other factors including soil depth and the soil water holding capacity are probably also important in determining where the *Carex* species studied are found at least in central Texas. In arid or semiarid savanna systems, it is more likely that any sedges that are present would occur below a woody canopy that reduces light levels (Leach and Givnish, 1999) or at times of the year when temperatures are cooler and water stress is reduced (Knapp, 1993; Knapp et al., 1993). The dominance of C<sub>4</sub> grasses in the gaps is likely related to the higher light levels, temperatures, and increased aridity that occur in this habitat (Paruelo and Lauenroth, 1996). The C<sub>4</sub> grasses should also be capable of survival at the canopy edge where light levels are intermediate and equivalent to their saturation point (Leach and Givnish, 1999; Wayne and Van Auken, 2009). Most grasses though are inhibited in areas that have a woody canopy (Peltzer and Köchy, 2001) probably due to reduced light levels (Naumburg, De Wald, and Kolb, 2001).

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#### LITERATURE CITED

- Arbingast, S. A., L. G. Kennamer, J. R. Buchanan, W. L. Hezlep, L. T. Ellis, T. G. Jordan, C. T. Granger, et al. 1976. Atlas of Texas. 5<sup>th</sup> ed. University of Texas, Austin.
- Baldocchi, D. D., D. R. Matt, B. A. Hutchison, and R. T. McMillen. 1984. Solar radiation within an oak-hickory forest: an evaluation of the extinction coefficients for several radiation components during fully-leafed and leafless periods. *Agricultural and Forest Meteorology* 32: 307-322.

- Ball, P. W. 1990. Some aspects of the phytogeography of *Carex*. *Canadian Journal of Botany* 68: 1462-1472.
- Ball, P. W., A. A. Reznicek, and D. F. Murray. 2003. Flora of North America North of Mexico. Oxford University Press, New York and Oxford.
- Barnes, P. W., S. Liang, K. E. Jessup, L. E. Ruiseco, P. L. Phillips, and S. J. Reagan. 2000. Soils, topography and vegetation of the Freeman Ranch. Department of Biology, Southwest Texas State University, San Marcos, Texas, US.
- Begon, M., C. R. Townsend, and J. L. Harper. 2006. Ecology: from individuals to ecosystems. Blackwell Publishing, Malden, MA.
- Björkman, O., N. K. Boardman, J. M. Anderson, S. W. Thorne, D. J. Goodchild, and N. A. Pylotis. 1972. Effect of light intensity during growth of *Artiplex patula* on the capacity of photosynthetic reactions, chloroplast components and structure. *Carnegie Institute Washington Year Book* 71: 115-135.
- Bond, B. J., B. T. Farnsworth, R. A. Coulombe, and W. E. Winner. 1999. Foliage physiology and biochemistry in response to light gradients in conifers with varying shade tolerance. *Oecologia* 120: 183-192.
- Busch, J. 2001. Characteristic values of key ecophysiological parameters in the genus *Carex*. *Flora* 196: 405-430.
- Chaves, M. M., J. P. Maroco, and J. S. Pereira. 2003. Understanding plant responses to drought - from genes to whole plant. *Functional Plant Biology* 30: 239-264.
- Correll, D. S., and M. C. Johnston. 1979. Manual of the vascular plants of Texas. Texas Research Foundation, Renner, Texas.
- Dibbs, G. M., B. L. Lipscomb, and R. J. O'Kennon. 1999. *Shinners & Mahler's* Illustrated Flora of North Central Texas. Center for Environmental Studies and Department of Biology, Austin College, Sherman, Texas, and Botanical Research Institute of Texas (BRIT), Fort Worth, Texas.
- Fay, P. A., J. D. Carlise, B. T. Danner, M. S. Lett, J. K. McCarron, C. Stewart, A. K. Knapp, et al. 2002. Altered rainfall patterns, gas exchange, and growth in grasses and forbs. *International Journal of Plant Sciences* 163: 549-557.
- Furuya, M., and O. W. Van Auken. 2009. Gas exchange rates of sun and shade leaves of *Sophora secundiflora*. *Texas Journal of Science* 61: 243-258.

- Furuya, M., and O. W. Van Auken. 2010. Gas exchange rates of three sub-shrubs of central Texas savannas. *Madrono* 57: 170-179.
- Gagliardi, J. W., and O. W. Van Auken. 2010. Distribution of *Verbena virginica* (Asteraceae, frost weed) in central Texas and possible causes. *Texas Journal of Science* 62: 163-182.
- Givnish, T. J. 1988. Adaptation to sun and shade: a whole-plant perspective. *Australian Journal of Plant Physiology* 15: 63-92.
- Givnish, T. J., R. A. Montgomery, and G. Goldstein. 2004. Adaptive radiation of photosynthetic physiology in the Hawaiian Lobeliads: light regimes, static-light responses, and whole-plant compensation points. *American Journal of Botany* 91: 228-246.
- Gould, F. W. 1975. Texas plants – A checklist and ecological summary. Texas Agricultural Experimental Station, College Station, TX.
- House, J. I., S. Archer, D. D. Breshears, and R. J. Scholes. 2003. Conundrums in mixed woody-herbaceous plant systems. *Journal of Biogeography* 30: 1763-1778.
- Hull, J. C. 2002. Photosynthetic induction dynamics to sunflecks of four deciduous forest understory herbs with different phenologies. *International Journal of Plant Sciences* 163: 913-924.
- Knapp, A. K. 1993. Gas exchange dynamics in C<sub>3</sub> and C<sub>4</sub> grasses: consequences of differences in stomatal conductance. *Ecology* 74: 113-123.
- Knapp, A. K., and E. Medina. 1999. Successes of C<sub>4</sub> photosynthesis in the field: lessons from communities dominated by C<sub>4</sub> plants. In R. Sage AND R. Monson [eds.], *The Biology of C<sub>4</sub> Plants*, 251-283. Academic Press, New York.
- Knapp, A. K., J. T. Fahnestock, S. P. Hamburg, L. B. Statland, T. R. Seastedt, and D. S. Schimel. 1993. Landscape patterns in soil-plant water relations and primary production in tallgrass prairie. *Ecology* 74: 549-560.
- Leach, M. K., and T. J. Givnish. 1999. Gradients in the composition, structure, and diversity of remnant oak savannas in southern Wisconsin. *Ecological Monographs* 69: 353-374.
- Lecain, D. R., J. A. Morgan, A. R. Mosier, and J. A. Nelson. 2003. Soil and plant water relations determine photosynthetic responses of C<sub>3</sub> and C<sub>4</sub> grasses in a semi-arid ecosystem under elevated CO<sub>2</sub>. *Annals of Botany* 92: 41-52.

- McCarron, J. K., and A. K. Knapp. 2001. C<sub>3</sub> woody plant expansion in a C<sub>4</sub> grassland: are grasses and shrubs functionally distinct. *American Journal of Botany* 88: 1818-1823.
- Muth, C. C., and F. A. Bazzaz. 2002. Tree canopy displacement at forest gap edges. *Canadian Journal of Forest Research* 32: 247-254.
- Naumburg, E., L. E. De Wald, and T. E. Kolb. 2001. Shade responses of five grasses native to southwestern U.S. *Pinus ponderosa* forests. *Canadian Journal of Botany* 79: 1001-1009.
- NOAA. 2004. Meteorological Data. National Oceanic and Atmospheric Administration, Asheville, North Carolina, USA.
- NRCS. 2006. Web Soil Surveys. Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture.
- Ogle, K., and J. F. Reynolds. 2002. Desert dogma revisited: coupling of stomatal conductance and photosynthesis in the desert shrub, *Larrea tridentata*. *Plant, Cell and Environment* 25: 909-921.
- Osborne, B., K. Black, G. Lanigan, M. Perka, and G. Clabby. 2003. Survival on the exposed limestone pavement in the Burren: photosynthesis and water relations of three co-occurring plant species. *Biology and Environment: Proceedings of the Royal Irish Academy* 103B: 125-137.
- Paruelo, J. M., and W. K. Lauenroth. 1996. Relative abundance of plant functional types in grasslands and shrublands of North America. *Ecological Applications* 6: 1212-1224.
- Pearcy, R. W. 2000. Acclimation to sun and shade. In A. S. Raghavendra [ed.], *Photosynthesis: A Comprehensive Treatise*, 250-263. Cambridge University Press, Cambridge.
- Peek, M. S., E. Russek-Cohen, D. A. Wait, and I. N. Forseth. 2002. Physiological response curve analysis using nonlinear mixed models. *Oecologia* 132: 175-180.
- Peltzer, D. A., and M. Köchy. 2001. Competitive effects of grasses and woody plants in mixed-grass prairie. *Journal of Ecology* 89: 519-527.
- Rosenthal, D. M., F. Ludwig, and L. A. Donovan. 2005. Plant responses to an edaphic gradient across an active sand dune/desert boundary in the great basin. *International Journal of Plant Sciences* 166: 247-255.
- SAS. 2005. SAS/STAT 9.1 User's Guide SAS Publishing, Cary, North Carolina.

- Taylor, F. B., R. B. Hailey, and D. L. Richmond. 1962. Soil survey of Bexar County, Texas. United States Department of Agriculture. Soil Conservation Service, Washington D. C.
- Terletzky, P. A., and O. W. Van Auken. 1996. Comparison of cedar glades and associated woodlands of the southern Edwards Plateau. *Texas Journal of Science* 48: 55-67.
- Turner, C. L., and A. K. Knapp. 1996. Responses of a C<sub>4</sub> grass and three C<sub>3</sub> forbs to variation in nitrogen and light in tallgrass prairie. *Ecology* 77: 1738-1749.
- Turner, C. L., J. R. Kneisler, and A. K. Knapp. 1995. Comparative gas exchange and nitrogen responses of the dominant C<sub>4</sub> grass *Andropogon gerardii* and five C<sub>3</sub> forbs to fire and topographic position in a tallgrass prairie during a wet year. *International Journal of Plant Sciences* 156: 216-226.
- Tuzet, A., A. Perrier, and R. Leuning. 2003. A coupled model of stomatal conductance, photosynthesis and transpiration. *Plant, Cell and Environment* 26: 1097-1116.
- Valladares, F., and U. Niinemets. 2008. Shade tolerance, a key plant feature on complex nature and consequences. *Annual Review of Ecology and Systematics* 39: 237-257.
- Van Auken, O. W. 2000. Shrub invasion of North American semiarid grasslands. *Annual Review of Ecology and Systematics* 31: 197-215.
- Van Auken, O. W., and D. C. McKinley. 2008. Structure and composition of *Juniperus* communities and factors that control them. In O. W. Van Auken [ed.], *Western North American Juniperus communities: a dynamic vegetation type*, vol. 196, 19-47. Springer, New York.
- Van Auken, O. W., and F. E. Smeins. 2008. Western North American *Juniperus* communities: patterns and causes of distribution and abundance. In O. W. Van Auken [ed.], *Western North American Juniperus communities: a dynamic vegetation type*, vol. 196, Ecological Series, 3-18. Springer, New York.
- Van Auken, O. W., and J. K. Bush. 2011. Photosynthetic rates of two species of Malvaceae, *Malvaviscus arboreus* var. *Drummondii* (wax mallow) and *Abutilion theophrasti* (velvetleaf). *Southwestern Naturalist* 56: 325-332.

- Van Auken, O. W., A. L. Ford, and J. L. Allen. 1981. An ecological comparison of upland deciduous forests of central Texas. *American Journal of Botany* 68: 1249-1256.
- Van Auken, O. W., J. K. Bush, and D. D. Diamond. 1994. Changes in growth of two C<sub>4</sub> grasses (*Schizachyrium scoparium* and *Paspalum plicatulum*) in monoculture and mixture: influence of soil depth. *American Journal of Botany* 81: 15-20.
- Wayne, E. R., and O. W. Van Auken. 2004. Spatial and temporal abiotic changes along a canopy to intercanopy gradient in central Texas *Juniperus ashei* woodlands. *Texas Journal of Science* 56: 35-54.
- Wayne, E. R., and O. W. Van Auken. 2008. Comparisons of the understory vegetation of *Juniperus* woodlands. In O. W. Van Auken [ed.], *Western North American Juniperus communities: a dynamic vegetation type*, vol. 196, Ecological Studies, 93-110. Springer, New York.
- Wayne, E. R., and O. W. Van Auken. 2009. Light responses of *Carex planostachys* from various microsites in a *Juniperus* community. *Journal of Arid Environments* 73: 435-443.
- Wayne, E. R., and O. W. Van Auken. 2010. Herbaceous understory cover and biomass of *Carex planostachys* in *Juniperus ashei* woodlands of central Texas. *The Southwestern Naturalist* 55: 434-469.
- Weihner, E., S. Forbes, T. Schauwecker, and J. B. Grace. 2004. Multivariate control of plant species richness and community biomass in blackland prairie. *Oikos* 106: 151-157.