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PHOTOSYNTHESIS OF INDIAN WOODOATS IN CENTRAL TEXAS WOODLANDS

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Abstract.–Measurements of photosynthetic rates were made on leaves of *Chasmanthium latifolium* (Michx.) Yates, Indian woodoats (Poaceae ⁄ Gramineae–Grass family). Plants were in the understory of *Juniperus ashei/Quercus fusiformis* (Ashe juniper/live oak) woodlands in central Texas. Density was low for *C. latifolium* in the woodlands where it was found. External light level (PFD, photosynthetic-flux density) at midday in the open, above the canopy, on a cloudless day was 1897 ± 21 µmol/m^2/s (mean ± *SE*). Below the canopy, light level was 203 ± 28 µmol/m^2/s. Leaves were exposed to light levels from zero to 2000 µmol/m^2/s using a Li Cor 6400 photosynthetic meter. Photosynthetic rates were measured and used to generate light response curves. Leaf maximum photosynthetic rate (A_{max}) was 12.92 ± 0.50 µmol CO_2/m^2/s. Dark respiration was 0.08 ± 0.09 µmol CO_2/m^2/s. Light saturation was 1027 ± 42 µmol/m^2/s or 54% of the midday maximum light level. The light compensation point was 6 ± 2 µmol/m^2/s or 0.32% of the midday light level in the open, above the canopy. Thus, *C. latifolium* had a positive carbon uptake at very low light levels below canopies where it is usually found. *Chasmanthium latifolium* was able to fix carbon at light levels almost 10 times lower than some C_4 grasses. Light levels below the canopy were 80% below the light saturation point of *C. latifolium*, which means the plants were fixing carbon at less than their A_{max}. However, for part of the day, if plants were in light gaps, gas exchange rates would be near the maximum rates measured.

Keywords: CO_2 uptake, edge plants, light compensation, light levels, light saturation, photosynthetic rates, shade plants, sub canopy plants, respiration

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Texas has been divided into ten major plant zones (Correll & Johnston 1979). These “zones” are not plant communities and have been called vegetation regions or biomes, which is not correct (Van Auken 2018). They are physiographic regions described by physical geography or geomorphology. Hill (1892) first called Central Texas the Edwards Plateau and the name has been widely adopted (Gould 1975a;

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1975b; Correll & Johnston 1979; Amos & Gehlbach 1988; Van Auken 2018). Some have suggested this is too simple an approach and have divided the area into four smaller but more specific areas that are not plant community types either (LBJ School of Public Affairs 1978; Riskind & Diamond 1988). More recently, the ecological regions of Texas, and more specifically the vegetation of Texas, has been mapped (Elliott et al. 2014), however, there are many plants, especially those with lower densities that are not well delineated.

Plants in woodlands or forests, similar to those in central Texas, can be separated vertically into overstory, understory and plants in-between. In addition, there is horizontal separation, those growing in the open high light and those growing below a canopy in low light as well as those growing at the edge. Species present below closed forest or woodland canopies generally have photosynthetic rates that are low compared to species in the open (Zangerl & Bazzaz 1983; Hättenschwiler & Körner 1996; Hirose & Bazzaz 1998; Hull 2002). If true understory plants are exposed to high light levels more characteristic of open grassland communities or disturbed habitats, gas exchange rates do not generally increase very much (Larcher 2003; Keddy 2017). Edge or intermediate plants can increase carbon fixation dramatically (Boardman 1977; Larcher 2003; Keddy 2017). Many species in central Texas savannas have responses to light levels that have been difficult to predict, possibly because of recent community changes including encroachment or habitat manipulation.

In central and eastern Texas, as well as much of southeastern North America *Chasmanthium latifolium* (Michy.) Yates (Indian woodoats or woodland oats, Poaceae/Gramineae), a grass species, is found below woodland or forest canopies (USDA NCRS 2021). Sometimes this species is found in uplands but more commonly in riparian forest washes, creeks, streams and on rivers banks (Brown & Smith 1974). This species is morphologically very similar to *Uniola paniculata* L. (Figure 1). Early on, both species were placed in the genus *Uniola* (Holm 1891a; 1891b). In 1966 the nine species of *Uniola*, which seemed to separate into two habitat types, were placed into three

Figure 1. The C_3 grass *Chasmanthium latifolium* (Michx.) Yates, Indian woodoats (formerly *Uniola latifolia* Michx.) - UNLA3. Figure from Hitchcock (1950).

genera, *Chasmanthium* (five species), *Uniola* (two species) and *Leptochloöpsis* (two species) (Yates 1966a; 1966b; 1966c).

The two habitat types were (1) the wet woodlands and forests of southeastern North America and (2) the dry coastal habitats of eastern North America, Central America and northwestern South America. The *Chasmanthium* species in the relatively wet or damp forest or woodland habitats were in low light understories. Three of the species of *Uniola* and *Leptochloöpsis* were costal sand dunes species growing in high light. The western limits of the *Chasmanthium* species in Texas were below the woodland and riparian forest canopies in central Texas (USDA NCRS 2021). However, *Chasmanthium latifolium* does occur very sporadically in New Mexico and Arizona in some riparian communities, but the other *Chasmanthium* species are farther east.

The species in these two habitats seem to be different photosynthetic types based on leaf anatomy (Yates 1966a; 1966b; 1966c) and $^{13}C/^{12}C$ ratios (Smith & Brown 1973). These characteristics for *Uniola* and *Leptochloöpsis* suggest the C_4 photosynthetic pathway. For the *Chasmanthium* species the characteristics suggest the C_3 photosynthetic pathway (Smith & Brown 1973; Cerling et al. 1997; Ehleringer & Sandquist 2015; Keddy 2017). Plants with C_4 photosynthesis have high rates of carbon fixation at high light levels (full sun) while plants with C_3 photosynthesis usually have lower rates of carbon fixation at high light levels (Boardman 1977; Larcher 2003; Keddy 2017; Poorter et al. 2019). In addition, C_3 plants usually have a positive carbon fixation rate at low light levels, higher than that of C_4 plants (Wayne & Van Auken 2009; 2011). There is usually some overlap at the high and low light levels depending on the species and other factors can influence carbon fixation rates including temperature, CO_2 level, humidity, soil water and soil nutrient levels (Boardman 1977; Larcher 2003; Keddy 2017; Poorter et al. 2019).

Uniola paniculata (sea oats) has high rates of photosynthesis like other C_4 species (Valero-Aracama et al. 2006) and a number of conservation and reclamation studies have been completed with this and related species (Gormally & Donovan 2011; Gormally et al. 2013). However, the same is not true for the C_3 understory *Chasmanthium* species. *Chasmanthium latifolium* is found in low light riparian woodlands and forests in eastern and central Texas (Gould 1975a; 1975b; Correll & Johnston 1979; USDA NCRS 2021). I have not identified any studies of the photosynthetic rates of any of the species of *Chasmanthium* in Texas or elsewhere.

The present study examined the light response of leaves of *Chasmanthium latifolium* in the understory of a *Juniperus ashei/Quercus fusiformis* (Ashe juniper/live oak) canopy. Gas exchange rates were measured to decide if its understory presence is related to its gas exchange or photosynthetic properties.

MATERIALS & METHODS

Site description.—Plants studied were below a *Juniperus ashei/Quercus fusiformis* canopy on private property (98.681W, -29.698 N) approximately 48 km north of San Antonio, Texas, near the southern edge of the Edwards Plateau just north of the Balcones Escarpment. Soils were Crawford Series, stony clay, shallow over hard limestone, zero to three percent slope, non-calcareous clay about 20–22 cm thick with limestone below (Mollisol over limestone bedrock, USDA NRCS 2017).

Annual mean temperature was 20°C with monthly means from 9.6°–29.4°C (1981-2020, NOAA 2020). Precipitation was 78.7 cm/yr, bimodal, with peaks in May and September (10.7 cm and 8.7 cm, respectively,1981-2020, NOAA 2020), with little summer rain, high evaporation and high variability.

Area vegetation was *Juniperus*-*Quercus* savanna or woodland, but higher in woody plant density than communities farther west (Van Auken et al. 1979; Van Auken et al. 1980; Van Auken et al. 1981; Smeins & Merrill 1988). Woody species were *Juniperus ashei* (Ashe juniper) and *Quercus fusiformis* (plateau live oak), *Diospyros texana* (Texas persimmon) and *Dermatophyllum secundiflorum* (Texas mountain laurel). *Chasmanthium latifolium* was present at low density usually in areas that were not grazed (USDA NCRS 2021).

Interspersed in the woodlands were sparsely vegetated inter-canopy patches or gaps (Van Auken 2000). Herbaceous vegetation below the canopy was mostly *Carex planostachys* (cedar sedge, Wayne & Van Auken 2008). The gap species included *Aristida longiseta* (red threeawn), *Bouteloua curtipendula* (side-oats grama), *Bothriochloa laguroides* ssp. *torreyana* (silver bluestem), *B. ischaemum* var. *songarica* (King Ranch bluestem), various other C_4 grasses, and a variety of herbaceous annuals (Correll & Johnston 1979; Enquist 1987). Light levels and soil temperatures were higher in the gaps than the associated woodland (Wayne & Van Auken 2004; Boeck & Van Auken 2017).

Gas exchange.—A Li-Cor 6400 portable photosynthetic meter was used to measure gas exchange and light levels. Photosynthetic-flux density (PFD) was the fixed variable. Plants were fully leafed out in April 2020 when leaves were measured (± three h of solar noon). Gas flow was 400 µmol/s and the CO_2 concentration was 400 µmol/mol with PFDs as follows: 0, 5, 10, 25, 50, 75, 100, 200, 400, 600, 800, 1000, 1200, 1600, 1800 and 2000 µmol/m^2/s. Measurements were started at the highest light level then recorded after two-three minutes when the coefficient or variation stabilized at < 1%, at which point the PDF was reduced to 1800 and measurements continued through the sequence indicated above. Three separate leaves from adjacent plants (20–30 cm above the soil surface) were placed next to each other across the narrow width of the chamber so they covered the entire surface of the chamber. This represented one of five replicates measured (Van Auken et al. 2020). Temperature and relatively humidity were set at 16ºC and 34 % respectively.

Fully expanded leaves on plants below a *Juniperus ashei/Quercus fusiformis* canopy were measured on a clear, cloudless day (April 16, 2020). Understory light level was 203 ± 28 µmol/m^2/s (mean ± *SE*) and range was 29 to 335 µmol/m^2/s. Light levels at or above the canopy were 1897 ± 21 µmol/m^2/s.

Calculated or measured gas exchange values were as follows: maximum photosynthetic rate (A_{max} = µmol CO_2/m^2/s), photosynthetic-flux density PFD at A_{max} (µmol/m^2/s), transpiration at A_{max} (µmol H_2O/m^2/s), conductance at A_{max} (mmol H_2O/m^2/s), light saturation point (µmol/m^2/s), dark respiration (µmol CO_2/m^2/s), light compensation point (µmol/m^2/s), and the quantum yield efficiency (µmol CO_2/ µmol quanta). Data for each replicate measurement was fit to the model of Prioul & Chartier (1977) using the PC software package Photosyn Assistant (Dundee Scientific, Dundee, Scotland).

$A_{\max}$ was the highest net photosynthetic rate. Light saturating photosynthesis was the PFD when the slope of the initial rate line reached the $A_{\max}$. Dark respiration was the gas exchange rate at a PFD of 0 µmol/m^2/s (y-intercept of the line for the initial rate). The light compensation point was the PFD when the photosynthetic rate was 0 µmol CO_2/m^2/s (x-intercept of the line for the initial rate). The quantum yield efficiency was the dark value and increasing PFDs until the regression coefficient decreased.

Light response curves were generated for each replicate. Assumptions for parametric statistics were met (Shapiro Wilk test for normal distribution and Bartlett test for equal variance (Sall et al. 2007)). A one-way *ANOVA* was completed for the variables followed by the Tukey Kramer HSD to determine if differences occurred at various PFD levels (Sall et al. 2007). An alpha value of 0.05 was used.

RESULTS

Presented first is a photosynthetic light response curve for *Chasmanthium latifolium* growing in the understory of a *Juniperus ashei/Quercus fusiformis* canopy in central Texas at a light level of 203 ± 28 µmol/m^2/s (mean ± *SE*) (Figure 2). Results appear to be a polynomial function with a high R^2 value (0.997). Mean photosynthetic rates reached a plateau as light levels increased. Each black dot is the mean of five replications. The p value for the one-way *ANOVA* was <0.0001. The mean photosynthetic rate for the leaves of *C. latifolium* was 5.48 ± 1.30 µmol CO_2/m^2/s ranging from -0.34 to 12.92 µmol CO_2/m^2/s over the 16 light levels measured. Negative values at lower light levels indicate respiration was greater than CO_2 uptake. Significant differences in photosynthetic rates (Tukey Kramer HSD, $p<0.05$) were detected between several of the light levels but there was considerable overlap between measurements (Figure 2). Light levels with the same letter (above or below the mean) are not significantly different (Tukey Kramer HSD, $p>0.05$). There were no significant

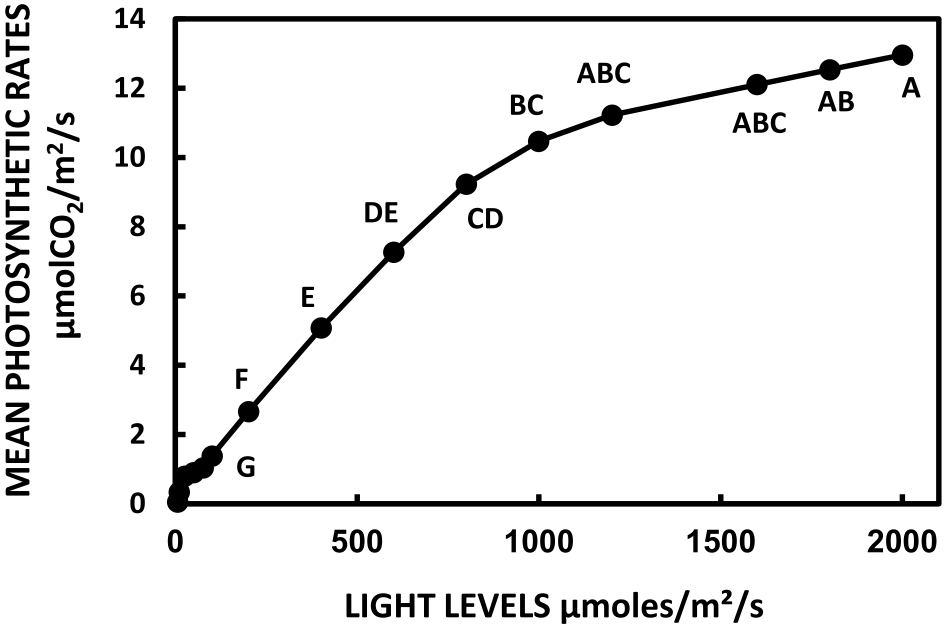

Figure 2. Mean photosynthetic rates for *Chasmanthium latifolium* measured at light levels from zero to 2000 µmol/m^2/s. Each black dot is a mean of five replicates at a given light level. The mean range of photosynthetic rates was from -0.34 to 12.95 molCO$_2$ m^2/s (the lowest measurements were negative or indicate respiration was greater than photosynthesis). Standard error at 2000 µmol/m^2/s was 2.01µmol CO$_2$/m^2/s. Plot is best represented by a 2nd order polynomial function with a high R^2 value (0.997). The p value for the one-way *ANOVA* was <0.0001. Light levels with the same letter (above or below) are not significantly different (p>0.05 Tukey Kramer HSD). Plants were in the understory of a *Juniperus ashei/Quercus fusiformis* canopy at a light level of 203 ± 28 µmol/m^2/s (mean ± *SE*). Measurements were made on April 16, 2020.

differences between light levels of 1200 and 2000 µmol/m^2/s nor between 0 and 100 (Figure 2). Care has to be used to see difference among other light levels because of data overlap. It should be noted that photosynthetic levels were positive but low even at 5 µmol/m^2/s.

Both transpiration and conductance were measured as a function of light level and are shown sequentially (Figures 3 and 4). These rates were measured at the same time photosynthetic rates were measures on the same replicates. Plot results are best represented by polynomial

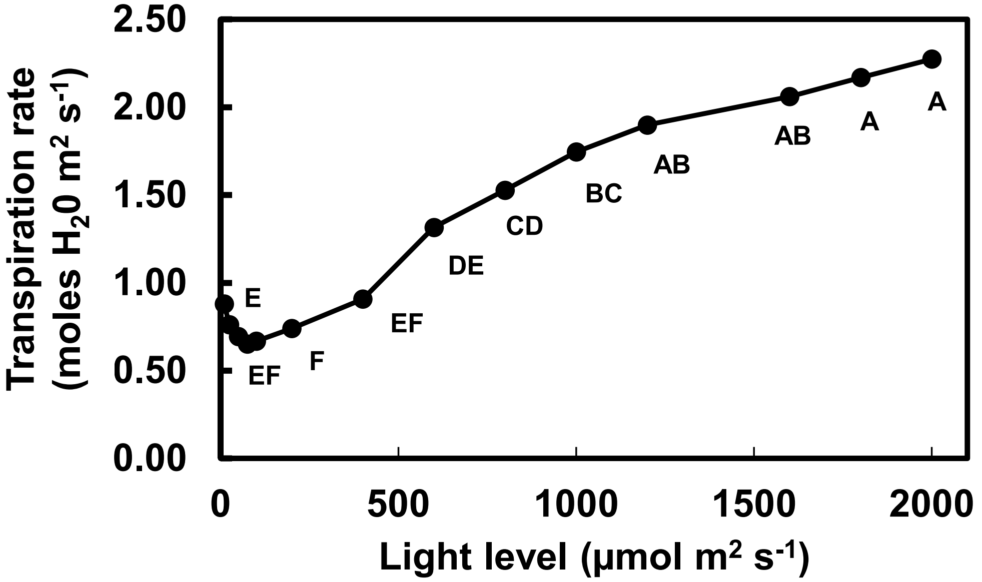

Figure 3. Mean transpiration rates for *Chasmanthium latifolium* measured at light levels from 0 µmol/m^2/s to 2000 µmol/m^2/s. Each black dot is a mean of five replicates at a given light level. Range was from 0.652 to 2.266 molH_2O m^2/s. Standard error at 2000 µmol/m^2/s was 0.145 mol H_20/m^2/s. Plot is best represented by a 3rd order polynomial function (with a high R^2 value (0.946). The *p* value for the one-way *ANOVA* was <0.0001. Light levels with the same letter (above or below) are not significantly different ($p>0.05$ Tukey Kramer HSD). Plants were in the understory of a *Juniperus ashei/Quercus fusiformis* canopy at a light level of 203 ± 28 µmol/m^2/s (mean ± *SE*). Measurements were made on April 16, 2020.

functions with high R^2 values (>0.95). *ANOVA* results were very highly significant for both transpiration and conductance rates (p<0.0001) Transpiration rates decreased from a mean high of 2.266 µmol H_2O/m^2/s at the highest light level to 0.652 µmol H_2O/m^2/s at a light level of 75 µmol/m^2/s. From there the transpiration rate increased as the light level approached zero with no significant differences in values. There were no significant differences in transpiration rates between 2000 and 1200 µmol/m^2/s or between 0 and 600, but they were some significant differences between 600 and 1200 µmol/m^2/s (Tukey-Kramer HST, $p < 0.0001$). Mean stomatal conductance followed a similar trend but water loss is much lower (Figures 3 and 4). Values indicated stomates were open and functioning.

The mean maximum photosynthetic rate (A_{max}) for leaves of *C. latifolium* was estimated at 13.92 ± 0.50 µmol $CO_2/m^2/s$ (Table 1). The quantum yield efficiency or initial slope (ϕ or IS) for leaves of *C. latifolium* was 0.013 ± 0.001 µmol CO_2/µmol quanta (Table 1). The light compensation point (L_{cp}) was 6 ± 2 µmol/m^2/s, the light saturation point (L_{sp}) was 1027 ± 42 µmol /m^2/s and dark respiration (R_d) was 0.08 ± 0.09 µmol $CO_2/m^2/s$ (Table 1). Stomatal conductance at the A_{max} was 0.155 ± 0.017 and the transpiration rate at the A_{max} *was* 2.266 ± 0.042 (Table 1).

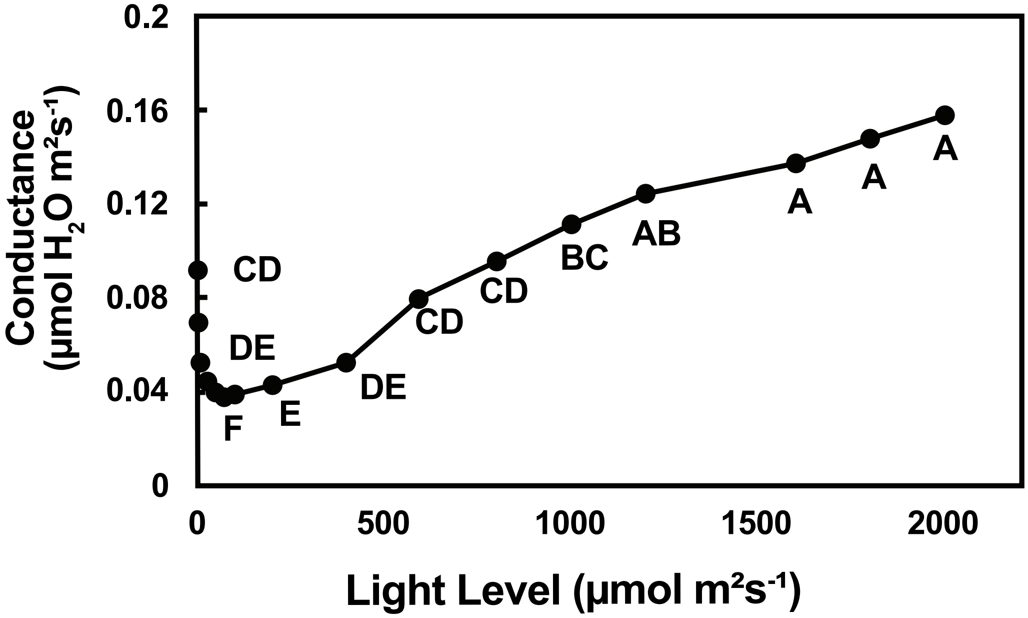

Figure 4. Mean stomatal conductance rates for *Chasmanthium latifolium* measured at light levels from 0 µmol/m^2/s to 2000 µmol/m^2/s. Each black dot is a mean of five replicates at a given light level. Range was from 0.039 to 0.155 µmol H_2O m^2/s. Standard error at 2000 µmol/m^2/s was 0.245 µmol $H_20/m^2/s$. Plot is best represented by a 3rd order polynomial function (with a high R^2 value (0.946). The *p* value for the one-way *ANOVA* was <0.0001. Light levels with the same letter (above or below) are not significantly different (*p*> 0.05 Tukey Kramer HSD). Plants were in the understory of a *Juniperus ashei/Quercus fusiformis* canopy at a light level of 203 ± 28 µmol/m^2/s (mean ± *SE*). Measurements were made on April 16, 2020.

Table 1. Comparison of mean ± *SE* for maximum net photosynthetic rates (A_{max}), light level (PFD) at the A_{max}, and other photosynthetic parameters for *Chasmanthium latifolium* (Michx.) Yates Inian woodoats and *Carex planostachys* (a shade plant) and two known sun plants (one Boraginaceae and one Gramineae) from central Texas are presented. *Chasmanthium latifolium* plants were in the understory of a *Juniperus ashei/Quercus fusiformis* canopy at a light level of 203 ± 111 µmol/m^2/s.

Parameter	*Chasmanthium latifolium* *	*Carex planostachys***	*Heliotropium tenellium****	*Boutaloua curtipendula***
A_{max}-max. photo. rate	12.92 ± 0.50	4.9 ± 0.3	34.96 ± 4.43	31.6 ± 0.5
Light Level at A_{max}	2000	318 ± 49	2000	1633 ± 98
L_{sat} - Light saturation	1027 ± 42	151 ± 43	591 ± 122	630 ± 78
L_{cp} - Light comp. point	6 ± 2	4 ± 2	38 ± 3	58 ± 10
R_d - Dark respiration	0.08 ± 0.09	0.4 ± 0.0	2.63 ± 0.38	3.0 ± 0.1
IS - Initial slope	0.013 ± 0.001		0.07 ± 0.01	
g_{leaf} - Stomatal cond. at A_{max}	0.155 ± 0.17	0.07 ± 0.01	0.44 ± 0.08	0.25 ± 0.01
E_{leaf}–Transpiration at A_{max}	2.266 ± 0.042			

*This study adj.3/6/2021****
**Wayne and Van Auken (2009)
***Boeck and Van Auken (2017)

point (L_{sp}) was 1027 ± 42 µmol /m^2/s and dark respiration (R_d) was 0.08 ± 0.09 µmol CO$_2$/m^2/s (Table 1). Stomatal conductance at the A_{max} was 0.034 ± 0.017 and the transpiration rate at the A_{max} *was* 2.265 ± 0.042 (Table 1).

DISCUSSION

When the A_{max} rate of *Chasmanthium latifolium* was compared with the A_{max} of a C$_4$ grass such as *Bouteloua curtipendula* from a high light habitat, the C$_4$ grass had an A_{max} rate 2.3 times higher than *C. latifolium* (Wayne & Van Auken 2011) (Figure 5). When photosynthesis was compared at low light levels (shade, 100 µmol/m^2/s) values of the two species were very similar, but at 10 µmol/m^2/s photosynthetic rates for

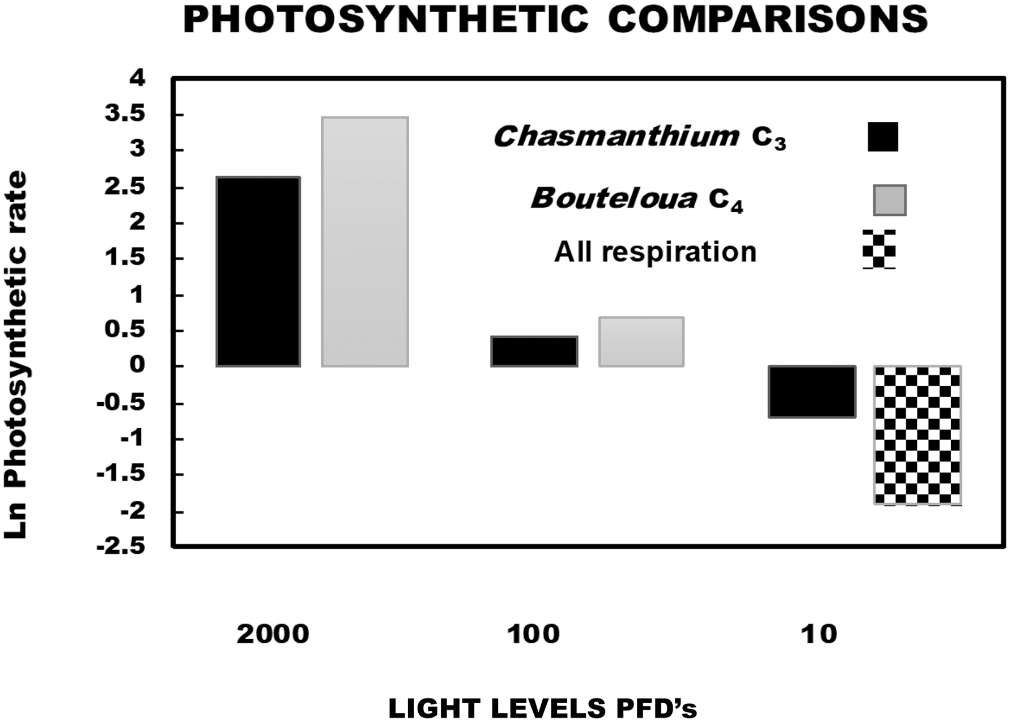

Figure 5. Comparison of the log of photosynthetic rates for *Chasmanthium latifolium* a C_3 grass and *Bouteloua curtipendula* a C_4 grass found in Texas in the same general area as *C. latifolium.* The *y*-axis is the log of the photosynthesis or respiration rate at three light levels, the *x*-axis at full sun to partial shade to full shade. In high light the C_4 grass has the highest photosynthetic rate but in low light the C_3 grass still has a positive photosynthetic rate but the gas exchange rate for the C_4 grass is all respiration, carbon dioxide release not uptake.

C. latifolium were low but positive (Figure 5). For *B. curtipendula* carbon uptake at this light level was negative, that is, only respiration was occurring. While CO_2 uptake for *C. latifolium* was low, it was still positive.

The A_{max} of *C. latifolium* was 2.8 times higher than that of *Carex planostachys,* a known woodland understory species (Table 1). An open habitat member of the borage family (*Heliotropium tenellum*) had an A_{max} rate 2.5 times higher than *C. latifolium* (Table 1). Six facultative species had intermediate photosynthetic rates and were thought to be canopy edge species (Furuya & Van Auken 2009; Gagliardia & Van Auken 2009; Furuya & Van Auken 2010; Van Auken & Bush 2011). Photosynthetic rates of these species were modified by the light levels they were exposed to, but usually had A_{max} values less than the C_4 grasses. The A_{max} of *C. latifolium* was lower or approximately equal to the A_{max} of these species. Populations of *C. latifolium* have been noted in various mixed central Texas riparian woodlands usually along intermittent creeks. The environments where this species has been observed are low light environments below the canopy of riparian woodlands in Central Texas and not in open grasslands.

Interestingly, gas exchange rates for *C. latifolium* at higher light levels were within the range of other intermediate photosynthetic species including most C_3 species (Boardman 1977; Larcher 2003; Begon et al. 2006). Other photosynthetic parameters, including light saturation, light compensation, dark respiration, conductance, and transpiration, were within the range of values for many C_3 species (Table 1). These responses are consistent with findings for some shade plants, but closer to values reported for facultative species (Boardman 1977; Hull 2002; Larcher 2003; Givnish et al. 2004; Valladares & Niinemets 2008; Van Auken & Bush 2015). The parameters measured for shade adapted leaves of *C. latifolium* at elevated light levels increased but suggested that *C. latifolium* can grow in the understory and is more of an intermediates light level species capable of growth in low to medium light environments. Also suggested is that it will not usually be found in high light environments such as open grasslands. No *C. latifolium* plants were found in full sun, consequently we do not know if they could acclimate to a variable light environment as seen for example in light gaps such as reported for other species (Hull 2002; Valladares & Niinemets 2008).

Respiration rate of leaves of *C. latifolium* growing in shade below a *Juniperus ashei/Quercus fusiformis* canopy was estimated at 0.08 ± 0.09 $\mu molCO_2/m^2/s$ or about 12% of values for other species growing in similar habitats (Hirose & Bazzaz 1998; Hull 2002; Van Auken & Bush 2015). Dark respiration for shade-adapted species is normally low due to lower metabolic rates (Bjorkman 1968; Bazzaz & Carlson 1982). Respiration of *Polygonum pensylvanicum,* a wetland plant grown in low light, was about 0.5 $\mu mol \cdot CO_2/m^2/s$, whereas the rate for its leaves in full sun was twice as high (Bazzaz & Carlson 1982).

Grunstra & Van Auken (2015) measured dark respiration at various temperatures for other species in this area and did not find significant differences. Other gas exchange values reported for *C. latifolium* are within the range or lower than values reported for similar intermediate light requiring or edge adapted species.

Where a species is found is determined by conditions present in that habitat and the response of the species to those conditions. However, unraveling the specific characteristics and levels of the factors present is challenging (Smith & Smith 2015; Keddy 2017). I believe that *C. latifolium* usually grows in shade, and gas exchange characteristics indicate that is its habitat preference which is where the C_4 grasses cannot grow because of higher light requirements (Wayne & Van Auken 2011). However, photo-inhibition of leaf pigments or overheating of leaves (Begon et al. 2006) or shallow roots (Johnson et al. 2018) could be problematic and comparable patterns of distribution of other species were caused by differential herbivory (Louda & Rodman 1996; Maron & Crone 2006; Leonard & Van Auken 2013). As a personal observation, *C. latifolium* is occasionally used in some high light plantings where it seems to do well, however, if high light competitors are present it will likely be overgrown and replaced.

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