

**Gas exchange rates for *Chaptalia texana* (silver-puff, Asteraceae)
An herbaceous understory species**

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ABSTRACT

Chaptalia texana Greene (silver-puff) is found in parts of southwestern North America including central and western Texas, southern New Mexico, and Mexico. We examined the local density distribution of *C. texana* to determine its habitat preference. We found *C. texana* below the canopy of *Juniperus-Quercus* (juniper-oak) mottes or woodlands, and not in adjacent C₄ grasslands. *Chaptalia texana* density was highly variable with 0-15 plants/m² below the woodland canopy and none in adjacent C₄ grassland. We examined its gas exchange rates to see if it was a habitat specialist. Maximum gas exchange rates ($A_{max} \pm SD$) of leaves of *C. texana* growing below the canopy were 19.24 ± 1.23 $\mu\text{mol}\cdot\text{CO}_2/\text{m}^2/\text{s}$ at mid-day open area light levels (photosynthetically flux density [PFD] = 2098 ± 41 $\mu\text{mol}/\text{m}^2/\text{s}$). This was 3.91 times higher than its sub-canopy mid-day ambient CO₂ uptake rate at sub-canopy mid-day light levels (PFD = 545 ± 86 $\mu\text{mol}/\text{m}^2/\text{s}$). Rates of other measured physiological characteristics of *C. texana* plants in shade as compared to rates of known shade plants were high. Mean light intensities (10:00-17:00 hr) below the canopy were approximately 20% of the full sun light levels, and were 1.46 times higher than *C. texana* light saturation. Gas exchange rates for this species at sub-canopy light levels were similar to other understory or shade species, while gas exchange rates for this species at open gap or grassland light levels were similar to other open grassland or sun species. This species seems best described as photosynthetically facultative; however results do not explain why *C. texana* plants were not found in the open grasslands. Published on-line www.phytologia.org *Phytologia* 97(1): 32-44 (Jan 2, 2015). ISSN 030319430.

KEY WORDS: Photosynthesis, CO₂ uptake, woodlands, savannas, shade leaves, light levels, understory, canopy, *Chaptalia*, silver-puff.

Many arid and semi-arid grassland communities have undergone encroachment by woody plants and are now some type of woodland or savanna (Begon et al. 2006; Reynolds et al. 2007; Bond 2008; Van Auken 2009). Savannas have woodland and grassland phases with plant species usually restricted to one phase or the other, but reasons for the restrictions are not clear. Transformations of grasslands have taken place throughout the world (Van Auken and McKinley 2008; Maze 2009) involving encroachment or invasion of a few woody species with as many as 10% of the herbaceous grassland species being true invaders (Van Auken 2009). Included are many of the woodland and grassland communities of the central Texas Edwards Plateau which vary from east to west along a rainfall gradient (more arid in the west, Van Auken and McKinley 2008; Van Auken and Smeins 2008).

Chaptalia texana Greene (silver-puff, Asteraceae) is an herbaceous, perennial, rosette plant reported from the woodland phase of some central Texas savanna communities (Correll and Johnston 1979; Enquist 1987; USDA 2009; Harms 2011). It seems to be an understory species found below the canopy of some of these woodlands (personal observation) but reasons for its occurrence below the

canopy are undetermined. Physiological differences between plants native to open, full-sun habitats as compared to those found in shady, understory communities are fairly well known (Begon et al. 2006; Valladares and Niinemets 2008; Smith and Smith 2012). Typical shade species have low maximum photosynthetic rates (A_{max} values $< 7.0 \mu\text{mol}\cdot\text{CO}_2/\text{m}^2/\text{s}$), low light saturation, light compensation, dark respiration rates, conductance, and transpiration compared to sun adapted species that have A_{max} values $> 15.0 \mu\text{mol}\cdot\text{CO}_2/\text{m}^2/\text{s}$ and other physiological characteristics that are high (Begon et al. 2006; Valladares and Niinemets 2008; Smith and Smith 2012). In addition, most if not all understory or shade plants are C_3 plants, many with one layer of horizontal leaves, large leaf surface area, thinner leaf blades, and more chlorophyll per mass but less per unit area (Begon et al. 2006; Valladares and Niinemets 2008; Smith and Smith 2012). *Chaptalia texana* has some of these morphological characteristics including one layer of horizontal leaves and large leaf blades (personal observation).

No reports have been found that consider gas exchange rates for any species of *Chaptalia*. No ecological studies have been identified that might assist in ascertaining why *Chaptalia* species are found in shaded canopy environments. In addition the successional status, disturbance requirements, densities, or resource requirements of any species of *Chaptalia* are not known. However, one study of the southeastern coastal plain longleaf and slash pine forests in Georgia examined successional herbaceous species changes after fire and reported the presence of *C. tomentosa* after prescribed winter fires with cover reductions by about half eight years after the fire (Lemon 1949). In addition, there are some reports of related *Chaptalia* species in grazed grasslands in South America, suggesting that frequent disturbances such as fire, clipping or herbivory of adjacent species promoted *Chaptalia* density (Fidelis et al. 2010; Joiner et al. 2011).

Gas exchange rates of some central Texas savanna community species have been examined. One true understory species (*Carex planostachys*) had low gas exchange rates (Wayne and Van Auken 2009). A series of C_4 grasses (sun species) from open habitats in this same area had high gas exchange rates at high light levels and much lower rates at low light levels, apparently preventing them from occurring below the canopy (Wayne and Van Auken 2012). *Sophora secundiflora* (leguminosae, Texas mountain laurel, a shrub), four asteraceae (one herbaceous perennial *Verbesina virginica* and three sub-shrubs *Simsia calva*, *Wedelia texana*, and *Brickellia cylindracea*), and a Malvaceae sub-shrub (*Malvaviscus arboreus* var. *drummondii*) all had intermediate levels of gas exchange and were considered facultative species and all were found below the woodland canopy, at the canopy edge and sometimes in open areas (Furuya and Van Auken 2009; Gagliardi and Van Auken 2009; Furuya and Van Auken 2010; Van Auken and Bush 2011).

The purposes of this study were to measure the density of *C. texana* below the canopy of *Juniperus ashei-Quercus virginiana* var. *fusiformis* woodlands and adjacent open savanna grasslands. In addition, we measured ambient light levels in the open and below the canopy on clear and cloudy days. Gas exchange rates of leaves at ambient light levels and light response curves of *C. texana* plants growing below the canopy were also measured. Based on the habitat where *C. texana* is reported to occur, we hypothesized that it was a shade species. We also hypothesized that it would have low gas exchange rates including low maximum photosynthetic rates, low light saturation, light compensation, and low dark respiration, conductance, and transpiration compared to sun adapted species.

Study Species

Approximately 60 species of *Chaptalia* are found in the southern United States, Mexico, the Caribbean, and South America (Flora of North America 2003). Our study species, *Chaptalia texana*, is reported from south-western Texas, south-central New Mexico, and most of Mexico. It is a native, herbaceous, perennial that grows as a rosette of basal leaves with scapose, monocephalous stems (single flowering head or inflorescence) (Nesom 1995). Consequently, it is similar to other species of *Chaptalia*. The flowering scapes can be 13-34 cm tall at anthesis and become longer in fruit. Leaves are obovate to

ovate or elliptical and relatively thick with dense, gray-white pubescence below and dark green and glabrescent above (Enquist 1987; Nesom 1995). It is reported from thin, rocky, limestone soils and mostly from oak, pine-oak and juniper-oak woodlands (Enquist 1987; Nesom 1995; Harms 2011). It potentially flowers year round, but mainly when temperatures and rainfall are moderate. Achenes (one seeded fruits) start to germinate soon after maturation with 100% germination at 25°C in low light 16 days after the start of incubation, with slight innate seed dormancy (Van Auken 2013).

Chaptalia texana and *C. nutans* L. have sometimes been considered conspecific (Correll and Johnston 1979; Nesom 1995). Recently, it was suggested that there were two species of *Chaptalia* in central Texas including *C. texana* and *C. carduacea* Green (Harms 2011). Ranges of these species overlap in central Texas. They appear to be ecologically separated with *C. texana* being found more inland, northern and usually higher in elevation. *Chaptalia carduacea* appears to have morphological, phenological and behavioral differences from *C. texana*. Another species, *C. tomentosa* Vent., is found in east Texas, east to Florida and then north into North Carolina usually on sandy soils.

Study Site

The field site for the current study was on the southern edge of the Edwards Plateau just south of the Balcones Escarpment in northern Bexar County, central Texas. This area is rough, well-drained, with elevations increasing abruptly from approximately 200 m above mean sea level (AMSL) to 500 to 700 m AMSL. The area was a *Juniperus-Quercus* savanna with mottes (clumps) of *Juniperus*, *Quercus*, and other woody species with gaps or patches of grasses and other herbaceous species (Correll and Johnston 1979; Van Auken and McKinley 2008; Furuya and Van Auken 2009). All *C. texana* plants in the present field study were found in this area (approximately 29°68' N and 98°50' W).

Most of the subsurface of the study area is Cretaceous limestone, and soils are usually shallow on slopes and deep in broad valleys and flats (Taylor et al. 1962; NRCS 2006). Soils are dark colored, calcareous with usually neutral or slightly basic pH. They are clayey-skeletal, smectitic, thermic lithic calciustolls, mostly Crawford Series that are stony clay in texture, shallow to moderately deep over hard limestone with a zero to 3% slope (NRCS 2006). The soils have a non-calcareous clay surface layer which is 20-22 cm thick and a calcareous subsurface which is approximately 66 cm thick (Taylor et al. 1962).

Area climate has a mean annual temperature of 20°C with monthly means ranging from 9.6°C in January to 29.4°C in July (NOAA 2004). Mean annual precipitation is 78.7 cm, highly variable, bimodal, with peaks occurring in May and September (10.7 cm and 8.7 cm, respectively), with little summer rainfall and high evaporation. Light levels are higher in gaps or patches compared to below the woodland canopy, with seasonal significant differences in surface soil temperature and soil moisture (Wayne and Van Auken 2004; Van Auken and Bush 2011).

Area Vegetation

Juniperus-Quercus savanna was present throughout the area and is representative of savanna and woodlands in this region (Van Auken and McKinley 2008). Over all, dominant woody species in the study area were *J. ashei* (Ashe juniper) and *Q. virginiana* var. *fusiformis* (plateau live oak) with various subdominants including *Diospyros texana* (Texas persimmon), *Sophora secundiflora* (Texas mountain laurel), *Berberis trifoliata* (agarita), *Rhus virens* (evergreen sumac) and others. The major herbaceous species below the canopy was *Carex planostachys* (cedar sedge) (Wayne and Van Auken 2008), but *Malvaviscus arboreus* (wax mallow or Turk's cap) and *Pinaropappus roseus* (white rock lettuce) were also present (Van Auken and Bush 2011).

Gaps or sparsely vegetated intercanopy patches are interconnected within these woodland communities (Van Auken 2000) and various C₄ grasses and a mixture of herbaceous annuals were common. In the gaps one can find the grasses *Aristida longiseta* (red three-awn), *Bouteloua curtipendula*

(side-oats grama), *Bothriochloa laguroides* ssp. *torreyana* (silver bluestem), and *B. ischaemum* var. *songarica* (King Ranch bluestem). Some of the major herbaceous annuals included *Chaetopappa bellidifolia* (dwarf white aster), *Evax prolifera* (rabbit-tobacco), *Croton monanthogynus* (prairie-tea), *Spermolepis inermis* (scale weed), *Centaurium texense* (Lady Bird's centaury), and *Galium virgatum* (southwest bedstraw) (Van Auken 2000).

METHODS

Chaptalia Density

Four *C. texana* sub-canopy populations were identified associated with or adjacent to the grassland phase of the savanna. The density of *C. texana* within each population was counted per quadrat (m^2). Mean density of *C. texana* for each savanna community type (grassland and woodland) was calculated. We report the area of each population (canopy area), the number of *C. texana* plants counted and the density (plants/ m^2) of each population.

Transects were used and consisted of 20 contiguous 1 m^2 quadrats. Measurements in the adjacent grassland phase were parallel to the *C. texana* population below the canopy and were approximately five meters from the canopy edge. The number of transects in each community type was 6 to 16 and dependent on the size of the population sampled. Seven hundred twenty total quadrats were sampled within the woodland and the same number in the grassland.

Light Levels

Photosynthetic flux density (PFD) was measured below the woodland canopy and in the open grassland. We measured PFD below the canopy in the approximate center of one population of *C. texana* and in the adjacent grassland. We used Spectrum Watchdogs (Spectrum Technologies, Plainfield, Illinois) to measure the PFD every 30 minutes over 24 hour periods from 20 April - 30 April 2012. We placed three sensors in an open grassland phase and three under the canopy. We calculated the mean PFD at each 30 minute interval using each replication (3) over 11 days. However, there were six days with full sun and three cloudy, springtime days that were grouped and are reported separately. In addition to the 24 hour light cycle, we present daily mean light levels over all daylight hours and mean midday light levels for 9 hours, 3.5 hours, and 2 hours for each community type.

Gas Exchange Measurements

Light response curves--CO₂ uptake was measured and then plotted as a function of PFD or light level for leaves of *C. texana*. Gas exchange parameters were measured on 22 April 2012 from fully expanded, basal, rosette leaves from what appeared to be mature *C. texana* plants. Leaves from five replications (individuals) were measured. Because variance was small, increasing the sample size would not change the mean values (Mendenhall and Beaver 1994). Plants that were used for making measurements were randomly selected. The average PFD outside of the chamber during the gas exchange measurements for *C. texana* was $243 \pm 42 \mu\text{mol}/m^2/s$ and the soil was at field capacity. Measurements were made on leaves within ± 3 hours of solar noon with a LI-COR[®] 6400 infrared gas analyzer (LI-COR Environmental, Lincoln, Nebraska). The irradiances used were generated by the LI-COR[®] LED red-blue light source using the auto light curve program. The CO₂ concentration was 400 $\mu\text{mol}/\text{mol}$ and the flow rate was 400 $\mu\text{mol}/s$. The LI-COR[®] 6400 was operated at approximately ambient temperature (25°C), relative humidity (35 – 57%), and was calibrated prior to making measurements. Response measurements were recorded after two-three minutes (stable total coefficient of variation =1%). Light response curves were started at a PFD of 2000 $\mu\text{mol}/m^2/s$ and then decreased to 1800, 1500, 1200, 900, 600, 300, 100, 75, 50, 25, 10, and 0 $\mu\text{mol}/m^2/s$.

Measurements included net photosynthesis, stomatal conductance, and transpiration, which were measured over 13 light levels (see above). A one-way ANOVA was used to determine if net photosynthesis, stomatal conductance, and transpiration were significantly different over the PFD's tested (Sall et al. 2001). The Shapiro-Wilks test was used to test for normal distributions and Bartlett's Test was

used to test for homogeneity of variances. If unequal variances were detected, data were log transformed prior to analyses.

Data presented in the figures were taken directly from the LI-COR[®]6400. Tabular results were adjusted for each replication (plant) and fitted to the model of Prioul and Chartier (Prioul and Chartier 1977) using the PC software package Photosyn Assistant (Dundee Scientific, Dundee, Scotland). Fitted data included A_{\max} (maximum photosynthesis)($\mu\text{mol}\cdot\text{CO}_2/\text{m}^2/\text{s}$), PFD at A_{\max} ($\mu\text{mol}/\text{m}^2/\text{s}$), transpiration at A_{\max} ($\mu\text{mol}\cdot\text{H}_2\text{O}/\text{m}^2/\text{s}$), conductance at A_{\max} ($\text{mmol}\cdot\text{H}_2\text{O}/\text{m}^2/\text{s}$), light saturation point ($\mu\text{mol}/\text{m}^2/\text{s}$), dark respiration ($\mu\text{mol}\cdot\text{CO}_2/\text{m}^2/\text{s}$), light compensation point ($\mu\text{mol}/\text{m}^2/\text{s}$), and the quantum yield efficiency ($\mu\text{mol}\cdot\text{CO}_2/\mu\text{mol}$ quanta). Values were calculated for each replicate and then averaged. The highest net photosynthesis rate was the A_{\max} . The PFD when the slope of the initial rate line reached the A_{\max} was light saturating photosynthesis. The gas exchange rate at a PFD of zero $\mu\text{mol}/\text{m}^2/\text{s}$ (y-intercept of the line for the initial rate) was dark respiration. The light compensation point was calculated as the PFD when the photosynthetic rate was zero $\mu\text{mol}\cdot\text{CO}_2/\text{m}^2/\text{s}$ (x-intercept of the line for the initial rate). The quantum yield efficiency was determined by using the dark value and increasing PFDs until the regression coefficient of the slope decreased. An alpha value of 0.05 was used for all tests. Tukey-Kramer HSDs were used to detect significant differences between gas exchange rates at each PFD (Sall et al. 2001).

Ambient CO₂ uptake--CO₂ uptake and other gas exchange parameters (see above) were also made at ambient light, temperature, and humidity levels in the field below the canopy with the soil at field capacity. Measurements were made \pm 2 hr. of solar noon on a clear sunny day (30 April 2012). We used the clear window (2 X 3 cm) for making these measurements and leaf material covered the entire surface area of the window. Ten replicate plants from the same population as above were measured with five replicate measurements per leaf or plant (total=50). Measurements were averaged to get mean and standard deviations for all parameters and compared with the gas exchange rates at specific light levels of the light response curves previously measured.

RESULTS

Size and density of four *Chaptalia texana* populations were examined (Table 1). All *C. texana* plants found were below the canopy of *Juniperus-Quercus* woodlands with no *C. texana* plants found in the adjacent C₄ grassland phase of the savanna. Mean area (\pm SD) occupied by the populations was $175 \pm 84 \text{ m}^2$. The mean number of *C. texana* plants in the populations was 97 ± 41 and they had a mean density of $0.57 \pm 0.05 \text{ plants}/\text{m}^2$. In the community with the greatest number of plants (Fig. 1), the distribution of *C. texana* appears to be clumped or non-random with density varying from zero to 15 plants/ m^2 .

Light levels were highest in the open grassland on clear, sunny, spring days versus cloudy days (Fig. 2, Table 2), and reduced below the *Juniperus-Quercus* canopy. Light levels in the open over the whole diurnal period on a sunny spring day were $1129 \pm 659 \mu\text{mol}/\text{m}^2/\text{s}$ and were reduced 52–63% to $651 \pm 360 \mu\text{mol}/\text{m}^2/\text{s}$ on cloudy days. Over the diurnal period, mean light levels increased to a maximum of approximately $2100 \mu\text{mol}/\text{m}^2/\text{s}$ on clear, spring days near 1400 hr. (Fig. 2A, Table 2). Below the canopy, light levels were quite variable and reduced to 20-26% on sunny days relative to adjacent open areas (Table 2). On cloudy, spring days, light levels in the open were more variable (Fig. 2B, Table 2), reaching high or low values more quickly and remaining at these values for shorter times. Light levels below the canopy on cloudy days were reduced to about the same percentage as on clear, sunny days, but actual light levels were between approximately 200 and 300 $\mu\text{mol}/\text{m}^2/\text{s}$ during the brightest part of the day.

The mean CO₂ uptake for the photosynthetic light response curve for leaves of plants grown in shade was significantly different over the light levels measured (one-way ANOVA, $F=107.7$, $P < 0.0001$; Fig. 3). At PFD's between 300-2000 $\mu\text{mol}/\text{m}^2/\text{s}$ uptake rates were fairly constant, with few significant differences and many of the rates overlapping. At the highest light level tested, the A_{\max} was $19.24 \pm 1.23 \mu\text{mol}\cdot\text{CO}_2/\text{m}^2/\text{s}$ (Table 3). At light levels (PFD's) below approximately 300 $\mu\text{mol}/\text{m}^2/\text{s}$ there was a rapid decline in the photosynthetic rates with few significant differences (Fig. 3).

Dark respiration (R_d) for *C. texana* was $1.18 \pm 0.16 \mu\text{mol}\cdot\text{CO}_2/\text{m}^2/\text{s}$ (Table 3) and the quantum yield efficiency or the initial slope was $0.081 \pm 0.004 \mu\text{mol}\cdot\text{CO}_2/\mu\text{mol quanta}$. Mean light saturation (L_{sat}) for *C. texana* was $254 \pm 22 \mu\text{mol}/\text{m}^2/\text{s}$ and the light compensation point (L_{cp}) was $15 \pm 2 \mu\text{mol}/\text{m}^2/\text{s}$ (Table 3).

Mean stomatal conductance (g_{leaf}) was significantly different over the light levels examined (one-way ANOVA, $F=12.9$, $P < 0.001$). Significant differences in stomatal conductance were at the highest and lowest light levels tested. The lowest rate, $0.082 \text{ mol}\cdot\text{H}_2\text{O}/\text{m}^2/\text{s}$, was at the zero light level. Stomatal conductance was highest at $0.379 \text{ mmol}\cdot\text{H}_2\text{O}/\text{m}^2/\text{s}$ at the highest light level tested, the A_{max} (Table 3). Transpiration rates were also significantly different over the light levels measured (one-way ANOVA, $F=12.5$, $P = 0.001$). However, differences were significant only at the highest and the lowest light level tested. Lowest transpiration was $2.201 \text{ mmol}\cdot\text{H}_2\text{O}/\text{m}^2/\text{s}$ at zero PFD and the highest value was $6.902 \pm 0.828 \text{ mmol}\cdot\text{H}_2\text{O}/\text{m}^2/\text{s}$ at the A_{max} ($2000 \mu\text{mol}/\text{m}^2/\text{s}$) (Table 3).

Ambient CO_2 uptake was also measured in the field on leaves of *C. texana* growing below the *Juniperus-Quercus* canopy. Mean CO_2 uptake rates were $4.92 \pm 0.72 \mu\text{mol}\cdot\text{CO}_2/\text{m}^2/\text{s}$ at ambient light levels of $143 \pm 50 \mu\text{mol}/\text{m}^2/\text{s}$. Carbon dioxide uptake rates were similar to those measured for the light response curves at the ambient light level (Fig. 3). Relativity humidity and air temperature at the time of measurement (1000-1400 hrs.) were $33.6 \pm 3.1\%$ and $32.4 \pm 1.9^\circ\text{C}$ (30 April 2012, Table 4). Conductance and transpiration at ambient PFD were $0.086 \pm 0.026 \text{ mol}\cdot\text{H}_2\text{O}/\text{m}^2/\text{s}$ and $2.394 \pm 0.566 \text{ mmol}\cdot\text{H}_2\text{O}/\text{m}^2/\text{s}$.

DISCUSSION

Herbaceous species found below forest canopies typically have gas exchange rates that are low and if exposed to light levels characteristic of open grassland communities, their gas exchange rates do not usually increase greatly (Zangerl and Bazzaz 1983; Hättenschwiler and Körner 1996; Hirose and Bazzaz 1998; Hull 2002)(see Table 3 for comparisons). However, species from central Texas savannas have mixed responses to light levels. *Carex planostachys*, a drought tolerant sedge found mainly below the *Juniperus-Quercus* canopy had low gas exchange rates similar to true forest understory shade species (Wayne and Van Auken 2012). A series of C_4 grasses (sun species) from open habitats in this same area had high gas exchange rates at high light levels (Wayne and Van Auken 2012). A leguminosae, shrub, four asteraceae and all malvaceae sub-shrubs had intermediate levels of gas exchange and were considered facultative species found below the canopy, at the canopy edge and sometimes in open areas (Furuya and Van Auken 2009; Gagliardi and Van Auken 2009; Furuya and Van Auken 2010; Van Auken and Bush 2011). These species were able to modify their gas exchange rates depending on the light levels where they were growing.

Chaptalia texana was found in low light environments below the canopy of *Juniperus-Quercus* woodlands in Central Texas savannas, not in open grasslands. Gas exchange rates for *C. texana* below the canopy at low light levels were equivalent or a little higher than rates measured for true understory species and rates measured for *C. texana* in light response curves at the same light levels (Table 4, Fig. 3). These rates should make *C. texana* a good competitor with other understory species in this same understory environment. Interestingly, gas exchange rates for *C. texana* at higher light levels were typical of species of open not understory habitats (Begon et al. 2006) (see Table 3). Other photosynthetic parameters, including light saturation, light compensation, dark respiration, conductance, and transpiration, were high as well (see Table 3). These responses are not consistent with findings for shade plants, but for sun plants or intermediate or facultative species (Boardman 1977; Hull 2002; Larcher 2003; Givnish et al. 2004; Begon et al. 2006; Valladares and Niinemets 2008). The parameters measured for shade adapted leaves of *C. texana* at elevated light levels suggest that this species is not a true understory species but a facultative species, one capable of growth in high light environments like disturbances in open grasslands.

In general, true understory species or shade species have much lower A_{max} values and photosynthetic rates than the rates reported for *C. texana* in the current study (see Table 3). No *C. texana* plants were found in full sun, consequently we do not know if they could acclimate to a variable light environment as reported for other species (Hull 2002; Valladares and Niinemets 2008).

Dark respiration of shade leaves of *C. texana* ($1.18 \pm 0.16 \mu\text{mol}\cdot\text{CO}_2/\text{m}^2/\text{s}$) was about 33% of values for sun-adapted species (Hamerlynck and Knapp 1994)(Table 3). This rate for *C. texana* is about 50% higher than the R_d of leaves of shade adapted species (Hirose and Bazzaz 1998; Hull 2002). Dark respiration for shade-adapted species is typically low due to their lower metabolism (Bjorkman 1968; Bazzaz and Carlson 1982). *Polygonum pensylvanicum* grown at $200 \mu\text{mol}/\text{m}^2/\text{s}$ had a respiration rate of $\sim 0.5 \mu\text{mol}\cdot\text{CO}_2/\text{m}^2/\text{s}$, while the rate for its sun leaves was twice as high (Bazzaz and Carlson 1982).

Other gas exchange values reported in this study for *C. texana* are similar to those reported for sun plants or sun leaves from the literature (Table 3). For example, the quantum yield efficiency reported here was $0.081 \pm 0.004 \mu\text{mol}\cdot\text{CO}_2/\mu\text{mol}$ quanta, for shade leaves which is 37% higher than values reported for other shade species ($0.035 - 0.052 \mu\text{mol}\cdot\text{CO}_2/\mu\text{mol}$ quanta) (Hirose et al. 1997). This may be a rapid response to light flecks below the canopy (Fig. 2), but this is speculation at this time. Stomatal conductance and transpiration reported for *C. texana* in the current study were similar to other studies and indicate open stomates; however, many factors affect the levels of these parameters including temperature and soil water content (Wieland and Bazzaz 1975; Zangerl and Bazzaz 1984; Yun and Taylor 1986; Munger et al. 1987a; Munger et al. 1987b; Stafford 1989).

The high gas exchange rates and A_{max} values reported for light response curves of shade leaves of *C. texana* present a conundrum. The reason being that all of the plants we found were below the *Juniperus-Quercus* canopy and all had high A_{max} values when leaves were exposed to high light levels. We never found plants of this species or associated species in open grasslands. Descriptions of this species suggest it is a canopy adapted species (Correll and Johnston 1979; Enquist 1987; Nesom 1995; Flora of North America 2003). Earlier work suggests that the various species of *Chaptalia* are found below *Quercus* or *Pinus-Quercus* woodlands or savannas (Nesom 1984; 1995; Flora of North America 2003) and *Juniperus-Quercus* woodlands and savannas (Harms 2011). In parts of the range of the genus *Chaptalia*, some species or individuals of all species of *Chaptalia* may establish and grow in low density grasslands outside of the woodland canopy. However, all of the *C. texana* plants that we found were below the *Juniperus-Quercus* woodland canopy.

When a species is found in a given habitat, it can tolerate or requires the environmental conditions present in that habitat. Conditions where it is found may be optimal for its growth and survival. However, sorting out the characteristics or factors that determine why a species is present in a given habitat and not in other habitats is challenging (Begon et al. 2006; Smith and Smith 2012). We believe that while *C. texana* is usually found growing in shade, gas exchange characteristics are not the factor controlling its apparent habitat preference. We would like to further evaluate the drought tolerance of this species to determine if it is restricted to areas below the canopy because it cannot compete with the drought tolerant C_4 grasses growing in the open. Another environmental factor or a combination of factors may limit the growth of *C. texana* to shaded understory habitats including possible photo-inhibition of leaf pigments or overheating of leaves (Begon et al. 2006). Similar patterns have been reported for other species, but restrictions were caused by herbivory (Louda and Rodman 1996; Maron and Crone 2006; Leonard and Van Auken 2013).

Soil water may be a resource limiting *C. texana* because of water use by more drought tolerant C_4 grasses, which seems to keep *C. texana* restricted to canopy habitats where these grasses cannot grow and compete because of low light levels and their high light requirements (Wayne and Van Auken 2009) or

because of higher soil water levels below the canopy available to *C. texana* or because of some combination of the two factors.

ACKNOWLEDGEMENTS

We thank Kelly Jo Stephens for help with preparation of various parts of the manuscript. Ms. Vonnie Jackson, Mr. Tristan Cofer and Dr. David D. Diamond reviewed an earlier version of this paper and offered many helpful suggestions.

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Table 1. Mean area (\pm one standard deviation) of the four *C. texana* populations studied, the mean number of plants counted per population and the density of plants/m² in the populations. Measurements were below woodland canopies and in adjacent open grasslands.

	Mean Area of population (m ²)	Number of plants	Density (plants/m ²)
Woodland	175 \pm 84	97 \pm 41	0.57 \pm 0.05
Grassland	---*	---	---

* --- no plants were found

Table 2. Mean \pm one standard deviation of the photosynthetic-flux density (PFD, $\mu\text{mol}/\text{m}^2/\text{s}$) at various time intervals measured in the open or below the woodland canopy and percent values of light levels reaching the *C. texana* plants at those times and light conditions.

Time	Sunny day			Cloudy day		
	Open	Below canopy	%	Open	Below canopy	%
All Daylight Hours	1129 \pm 659	222 \pm 195	20	651 \pm 360	138 \pm 80	21
10:00-17:00	1857 \pm 269	371 \pm 238	20	968 \pm 261	210 \pm 66	22
12:15-15:45	1982 \pm 153	464 \pm 297	23	1129 \pm 214	260 \pm 64	23
12:45-14:45	2098 \pm 41	545 \pm 86	26	1102 \pm 190	288 \pm 95	26

Table 3. Physiological measurements of *C. texana* leaves taken from light response curves (means \pm one standard deviation, SD). Plants were growing below a *Juniperus-Quercus* woodland canopy. Ranges of gas exchange rates for a number of sun and shade species are also presented.

Parameter	Sun species-range	Shade species-range	<i>Chaptalia</i>
A_{max} – Max. gas exchange ($\mu\text{mol}\cdot\text{CO}_2/\text{m}^2/\text{s}$)	15.0-34.6*	3.5-7.0*	19.24 \pm 1.23**
Photosyn. flux density at A_{max} ($\mu\text{mol}/\text{m}^2/\text{s}$)	1300-2000	700-1300	2000 \pm 0.0
R_d - Dark Respiration ($\mu\text{mol}\cdot\text{CO}_2/\text{m}^2/\text{s}$)	2.4-3.0	0.29-1.00	1.18 \pm 0.16
Q_e - Initial slope-quantum yield	0.059-0.090	0.070-0.090	0.081 \pm 0.004
L_{sat} - Mean light saturation ($\mu\text{mol}/\text{m}^2/\text{s}$)	326-1000	114-262	254 \pm 22
L_{cp} - Light compensation point ($\mu\text{mol}/\text{m}^2/\text{s}$)	13-61	3-21	15 \pm 2
g_{leaf} – Conductance ($\text{mol}\cdot\text{H}_2\text{O}/\text{m}^2/\text{s}$) at A_{max}	-	-	0.379 \pm 0.077
Conductance range (mean)	0.13-0.60	0.05-0.36	0.082-0.379
E_{leaf} – Transpiration ($\text{mmol}\cdot\text{H}_2\text{O}/\text{m}^2/\text{s}$) at A_{max}	-	-	6.902 \pm 0.828
Transpiration range (mean)	7.1-12.1	0.9-3.9	2.201-6.902

*From Van Auken and Bush 2009, Hull 2002, Wayne and Van Auken 2012, Valladares and Niinemets 2008; **Mean \pm one SD

Table 4. Gas exchange and physical measurements (means ± one SD) for leaves of *C. texana* plants made in the field. Measurements were made on 30 April 2012, a clear day, between 1100 and 1300 hours. The clear window chamber was used with ambient light levels.

Parameter	<i>Chaptalia texana</i>
CO ₂ uptake at ambient light level (μmol·CO ₂ /m ² /s)	4.92 ± 0.72
Ambient Photosynthetic-flux density PFD (μmol/m ² /s)	143 ± 50
Relative Humidity (%)	33.6 ± 3.1
Air Temperature (°C)	32.4 ± 1.9
Leaf Temperature (°C)	30.6 ± 0.7
<i>g</i> _{leaf} — Conductance (mol·H ₂ O/m ² /s) at Ambient PFD	0.086 ± 0.026
<i>E</i> _{leaf} — Transpiration (mmol·H ₂ O/m ² /s) at Ambient PFD	2.394 ± 0.568

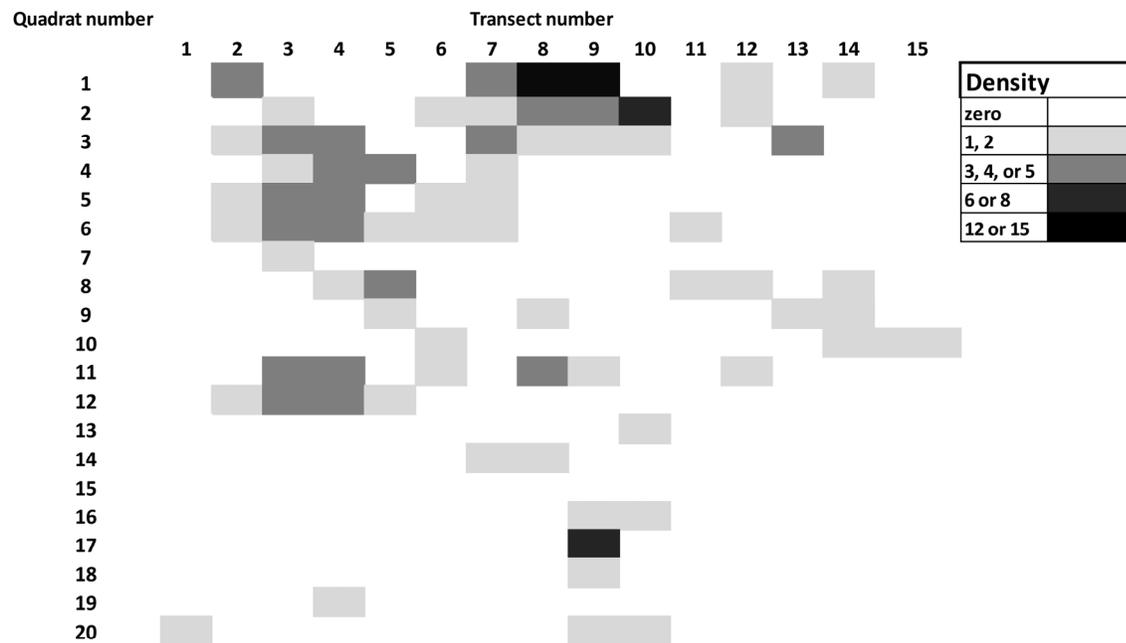


Figure. 1. Example distribution and density of the largest population of *C. texana* plants found growing below a *Juniperus-Quercus* woodland in central Texas. Blocks represent one meter square. Density ranged from zero plants/m² (white or clear blocks) to 12-15 plants/m² (black blocks). Plants appear to be clumped in distribution, but the reason was not investigated.

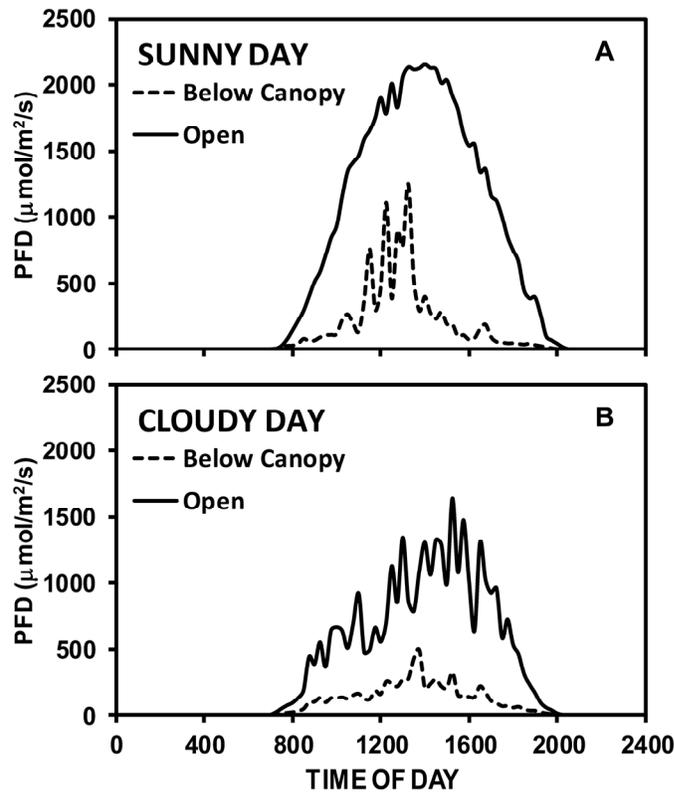


Figure 2. Mean diurnal light levels (PFD = Photosynthetic Flux Density, $\mu\text{M}/\text{m}^2/\text{s}$) are shown for an open grassland or glade (solid line) and below a *Juniperus-Quercus* woodland canopy (dashed line) for a clear spring day (A) and an overcast, cloudy spring day (B).

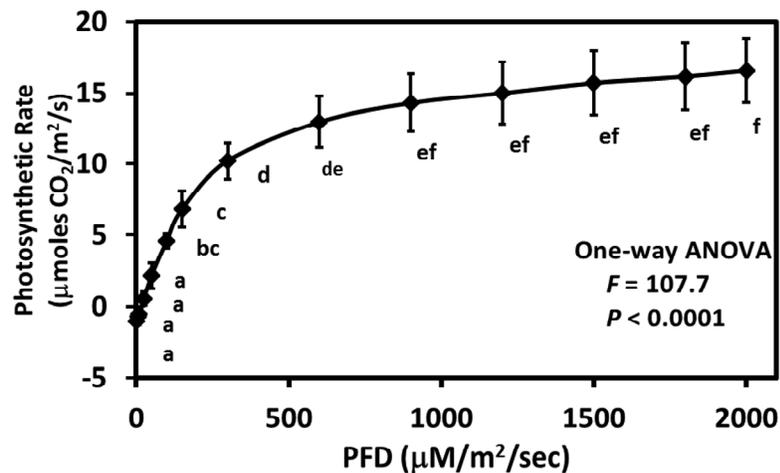


Figure 3. Gas exchange rates (photosynthetic rates, CO_2 uptake) for leaves of *C. texana* growing below a *Juniperus-Quercus* woodland canopy as a function of light levels or photosynthetic flux density (PFD, $\mu\text{M}/\text{m}^2/\text{s}$). There were significant differences in photosynthetic rates at different light levels (one-way ANOVA, $P < 0.0001$). Error bars represent \pm one standard deviation of the mean. Same letters between light levels indicate no significant differences between light levels (Tukey-Kramer HSD, $P > 0.05$).