

**Do Gas Exchange Rates of *Phaseolus texensis* (Boerne Bean, Leguminosae)
Reflect its Potential Niche?**

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ABSTRACT

Gas exchange rates were measured to examine potential niche requirements of *Phaseolus texensis* Delgado-Salinas and Carr (Boerne Bean, Leguminosae = Fabaceae) a rare species found in the Edwards Plateau physiographic region of Central Texas. Plants were found below a *Juniperus ashei*/*Quercus fusiformis* (Ashe juniper/live oak) canopy at a light level of $169 \pm 28 \mu\text{mol}/\text{m}^2/\text{s}$ (mean \pm se). Light response curves were generated using photosynthetic rates of leaflets from plants below the tree canopy in shade. Gas exchange rates were measured at light levels from 0-2000 $\mu\text{mol}/\text{m}^2/\text{s}$. A number of photosynthetic parameters were calculated and then compared. The maximum photosynthetic rate (A_{max}) was $5.99 \pm 0.17 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ for leaflets of sub-canopy plants. Light saturation was $158 \pm 42 \mu\text{mol}/\text{m}^2/\text{s}$. Light levels below the canopy where plants were found was 7% higher than the light saturation point of *P. texensis*, which means the plants were fixing carbon at their highest level even in the low light, shaded, sub-canopy environment. At A_{max} , the light compensation point was $0.102 \pm 0.099 \mu\text{mol}/\text{m}^2/\text{s}$ for sub-canopy plants and dark respiration was $0.235 \pm 0.227 \mu\text{mol}/\text{m}^2/\text{s}$. *Phaseolus texensis* exhibits photosynthetic characteristics equivalent to other shade plants which seem to be part of the reason it can persist in the understory of relatively open, but low light understory environments in isolated Central Texas woodland communities. *Published on-line* www.phytologia.org *Phytologia* 102(3): 162-171 (Sep 21, 2020). ISSN 030319430.

KEY WORDS: light levels; CO₂ uptake; photosynthetic rates; shade plants; sun plants; edge plants; light saturation; light compensation; respiration.

Understanding environmental factors controlling growth and recruitment of herbaceous and woody species in woodland communities is challenging, even though many papers have examined the topic (see Baker et al. 2005). This is especially true for populations of relic, endemic, threatened, and rare species (Falk et al. 1996; Poole et al 2007; Nelson Dickerson and Van Auken 2016). There are approximately 5,500 species of plants known in Texas (Correll and Johnston 1970) with 314 endemic or only occurring in Texas (Carr 2019). Of these, 75 or 23.5% occur in the central Texas Edwards Plateau Physiographic Region. Many of these endemic species are rare and some are endangered and include both woody and herbaceous species (Correll and Johnston 1970; Poole et al 2007; Van Auken 2018; Carr 2019).

The species examined in the present study, *Phaseolus texensis* Delgado-Salinas and Carr (Boerne Bean, Fabaceae = Leguminosae) is a relatively newly described species endemic in central Texas (Delgado and Carr 2007). It has been found in the southeastern part of the Edwards Plateau Physiographic Region, in juniper live oak-woodlands, (Van Auken 2018).

There have been several new herbaceous species recently described from central Texas including two legumes (Delgado-Salinas and Carr 2007; Holmes and Singhurst 2008), one carrot or parsley (Apiaceae = Umbelliferae, Keith 2012), and one mustard (Brassicaceae, Turner 2012). Although the morphological characteristics of these species including flowers, fruits, leaves, and stems have been

described along with general descriptions of where they have been found, little is written about their physiological or ecological characteristics. *Phaseolus texensis* is considered endemic in Texas, found in rocky canyons of the eastern and southern part of the Edwards Plateau physiographic region of central Texas (Delgado-Salinas and Carr 2007). Although molecular phylogenetic analyses have been completed, no physiographic studies have been identified.

A plant's photosynthetic parameters affect its inherent growth rate and thus its biomass (Givnish et al, 2004; Begon et al. 2006; Valladares and Niinemets 2008; Keddy 2017). Consequently, understanding a plant's photosynthetic characteristics can help explain how a plant is adapted to environmental stress (Crowley 1997). Nevertheless, until now, there have been no studies that we could find concerning photosynthetic rates or growth rates of *Phaseolus texensis*. Photosynthetic rates have been measured for a number of the species occurring in the central Texas Edwards Plateau Physiographic Region (Van Auken and Bush 2015). Some have high photosynthetic rates suggesting they are sun species (Boeck and Van Auken 2017) and others have low photosynthetic rates indicating they are shade adapted understory species (Wayne and Van Auken 2012). While another group has photosynthetic rates that lie in-between sun and shade plants, this group may be highly variable and comprise many edge species (Van Auken and Bush 2011) or they are potentially juveniles of overstory species starting growth in the understory with the potential to reach the overstory.

Usually, if a plant is found below another plant or is in the understory it is probably a sciophyte (shade) plant, however, many tree species start their growth in the understory and then grow into the overstory. An example would be *Celtis laevigata*, a late successional dominant species, which is found under the canopy of dominant early successional species (Bush and Van Auken 1986; Van Auken and Bush 2013). Although, sometimes plants grow in the shade not because they cannot grow in the sun, but because competition from heliophytes (sun plants) is high and the heliophytes restrict them to the understory. Similar distribution patterns have been described for other species, but the distributions have been caused by differential herbivory in high light versus low light or shady environmental conditions (Louda and Rodman 1996; Marion and Crone 2006; Leonard and Van Auken 2013). It is possible that *P. texensis* leaf pigments are photo-oxidized at high light levels or overheating of the leaves occurs (Begon et al. 2006). It seems *Phaseolus texensis* grows in the understory of various species, but the reason is unknown. It could be that it is a sciophyte and the C₄ grasses out compete it in the open for sunlight or for some other resource.

PURPOSES

The purposes of the present study were to examine the light response of leaves of *Phaseolus texensis* growing in the understory of a *Juniperus ashei*/*Quercus fusiformis* (Ashe juniper/live oak) canopy and to compare gas exchange rates at various light levels to determine if photosynthetic rates represent a heliophyte, sciophyte, or intermediate level species.

MATERIALS AND METHODS

STUDY AREA-The plants examined were located below a *Juniperus ashei*/*Quercus fusiformis* canopy or overstory, on private property, near Boerne, Texas (98.6808W-29.6977N); approximately 48 km (30 miles) north of San Antonio, Texas. The field site was near the southern edge of the Edwards Plateau just north of the Balcones Escarpment in central Texas. Soils in this area are in the Crawford Series. They are stony clay in texture, and are shallow to moderately deep over hard limestone with a zero to three percent slope (USDA NRCS Accessed 2017). Soils have a non-calcareous clay surface layer which is 20-22 cm thick and a subsurface layer which contains limestone which is approximately 66 cm thick (Mollisols over limestone bedrock, SCS 1977).

The area 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 2018). Mean annual precipitation is 78.7 cm, bimodal, with peaks occurring in May and September (10.7 cm and 8.7 cm, respectively), with little summer rainfall, high evaporation and high variability.

Vegetation in the area where *P. texensis* has been found consists of *Juniperus-Quercus* savanna or woodland, representative of savanna and woodlands found throughout this region, but higher in woody plant density than woodland communities farther to the west (Van Auken et al. 1979; Van Auken et al. 1980; Smeins and Merrill 1988). *Juniperus ashei* (Ashe juniper) and *Quercus fusiformis* (plateau live oak) are dominant woody species with subdominants including *Diospyros texana* (Texas persimmon) and *Sophora secundiflora* (mountain laurel). Interspersed in the woodlands are sparsely vegetated intercanopy patches or gaps (Van Auken 2000). The major herbaceous species below the canopy is usually *Carex planostachys* (cedar sedge)(Wayne and Van Auken 2008). *Aristida longiseta* (red three-awn), *Bouteloua curtipendula* (side-oats grama), *Bothriochloa laguroides* ssp. *torreyana* (silver bluestem), *B. ischaemum* var. *songarica* (King Ranch bluestem), various other C₄ grasses, and a variety of herbaceous annuals are common in the gaps. Light levels are higher in the gaps compared to woodland (Boeck and Van Auken 2017) which is also true for soil temperature (Wayne and Van Auken 2004).

GAS EXCHANGE-A Li-Cor 6400 portable photosynthetic meter was used to measure gas exchange of individual leaflets as a function of light level or photosynthetic-flux density (PFD). Measurements were made with plants fully leafed out in March and April 2020, within \pm three hours of solar noon using a gas flow rate of 400 $\mu\text{mol/s}$ and a CO₂ concentration of 400 $\mu\text{mol/mol}$ at PFDs of 0, 5, 10, 25, 50, 75, 100, 200, 400, 600, 800, 1000, 1200, 1600, 1800 and 2000 $\mu\text{mol/m}^2/\text{s}$. Each leaflet used covered the entire chamber.

Leaflets from six plants growing below a *Juniperus ashei/Quercus fusiformis* canopy were selected and measured separately. Leaves were fully expanded on the growing vine (stem) and not newly expanded leaves. One undamaged leaflet was selected on each tri-foliolate leaf for measurements. Plants in the shaded canopy understory were at light levels of 169 $\mu\text{mol/m}^2/\text{s}$ with a range from < 5 to 431 $\mu\text{mol/m}^2/\text{s}$.

Maximum photosynthesis, A_{max} ($\mu\text{mol CO}_2/\text{m}^2/\text{s}$) was calculated. Photosynthetic-flux density PFD at A_{max} ($\mu\text{mol/m}^2/\text{s}$), transpiration at A_{max} ($\mu\text{mol H}_2\text{O}/\text{m}^2/\text{s}$), conductance at A_{max} ($\text{mmol H}_2\text{O}/\text{m}^2/\text{s}$), light saturation point ($\mu\text{mol/m}^2/\text{s}$), dark respiration ($\mu\text{mol CO}_2/\text{m}^2/\text{s}$), light compensation point ($\mu\text{mol/m}^2/\text{s}$), and the quantum yield efficiency ($\mu\text{mol CO}_2/ \mu\text{mol quanta}$) for each replicate was determined and then means for leaves of each treatment were calculated. Data for each replication (leaflet) was fit to the model of Prioul and Chartier (Prioul and Chartier 1977) using the PC software package Photosyn Assistant (Dundee Scientific, Dundee, Scotland). A_{max} represented the highest net photosynthesis rate. Light saturating photosynthesis depicted 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 $\mu\text{mol/m}^2/\text{s}$ (y-intercept of the line for the initial rate). The light compensation point was calculated as the PFD when the photosynthetic rate was 0 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ (x-intercept of the line for the initial rate). The quantum yield efficiency was calculated using the dark value and increasing PFDs until the regression coefficient of the slope decreased.

Light response curves were generated for each leaflet. Assumptions for parametric statistics were not met, therefore the Kruskal-Wallis Test (rank sum) was used to determine if differences occurred between photosynthesis, conductance, or transpiration (Hajek 1969; SAS Institute Inc. 2017). An alpha value of 0.05 was used throughout.

RESULTS

The mean photosynthetic light response curve for *Phaseolus texensis* grown in the understory of a *Juniperus ashei/Quercus fusiformis* canopy at a light level of $169 \pm 28 \mu\text{mol}/\text{m}^2/\text{s}$ is presented (Figure 1A). The function is a positive polynomial function reaching a plateau or steady state as light levels increased. The mean photosynthetic rate for the leaflets of *P. texensis* was $3.29 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ ranging from -0.235 to $5.475 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ over the 16 light levels measured. There were significant differences in photosynthetic rates between at least two of the light levels (Kruskal-Wallis Test, $P = < 0.0001$). Conductance and transpiration as a function of light level are shown in Figure 1B and 1C. The transpiration rate for leaflets decreased from $0.54 \text{ mmol H}_2\text{O}/\text{m}^2/\text{s}$ at the lowest light level examined to $0.31 \text{ mmol H}_2\text{O}/\text{m}^2/\text{s}$ at a PFD of $50 \mu\text{mol}/\text{m}^2/\text{s}$ and then increased to $0.92 \text{ mmol H}_2\text{O}/\text{m}^2/\text{s}$ at an approximate PFD of $1000 \mu\text{mol}/\text{m}^2/\text{s}$. There were only slight additional differences as light levels were increased to the maximum level tested (Figure 1C). Mean stomatal conductance followed a very similar trend (Figure 1B). There were significant differences in conductance or transpiration rates between at least two of the light levels (Kruskal-Wallis Test, $P = 0.0006$ and $P = 0.0003$, respectively).

Mean maximum photosynthetic rate (A_{max}) for leaflets of *P. texensis* was estimated at $5.99 \pm 0.17 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ (Table 1). The quantum yield efficiency or initial slope (ϕ or IS) for leaflets of *P. texensis* was $0.039 \pm 0.006 \mu\text{mol CO}_2/\mu\text{mol quanta}$ (Table 1). The light compensation point (L_{cp}) was $0.102 \pm 0.011 \mu\text{mol}/\text{m}^2/\text{s}$, the light saturation point (L_{sp}) was $155 \pm 19 \mu\text{mol}/\text{m}^2/\text{s}$ and dark respiration (R_d) was $0.235 \pm 0.135 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ (Table 1).

DISCUSSION

Species that are present below closed forest canopies generally have photosynthetic rates (A_{max}) that are low compared to species in the open (Zangerl and Bazzaz 1983; Hättenschwiler and Körner 1996; Hirose and Bazzaz 1998; Hull 2002). When understory plants are exposed to higher light levels more distinctive of open grassland communities or disturbed areas, gas exchange rates do not generally increase. Species from the Edwards Plateau region in central Texas savannas have responses to light levels that have been difficult to predict, probably because of recent community changes such as species encroachment or habitat manipulation.

Comparison of *Phaseolus texensis* A_{max} rate with the A_{max} of C_4 grasses in open habitats confirmed that the C_4 grasses such as *Bouteloua curtipendula* had A_{max} rates 5.26 times higher than *P. texensis* (Wayne and Van Auken 2012) (see Table 1). An open habitat herbaceous species (*Heliotropium tenellium*) had A_{max} rates that were 5.83 times higher than *P. texensis* (Table 1). Other species included a leguminosae shrub, as well as four asteraceae and a malvaceae sub-shrubs; all had intermediate photosynthetic rates and were thought to be facultative species able to grow below a canopy, at the canopy edge and sometimes in the open (Furuya and Van Auken 2009; Gagliardia and Van Auken 2009; Furuya and Van Auken 2010; Van Auken and Bush 2011). Photosynthetic rates of these species were modified by the light levels they were exposed to, but they never had A_{max} values as high as the C_4 grasses found in associated open high light habitats.

Phaseolus texensis is apparently “restricted to the eastern and southern part of the Edwards Plateau of Texas at elevations from 200 to 600 m” (Delgado-Salinas and Carr 2007). They list specific locations where it has been found and more recent sites can be observed by searching Boerne Bean (Boerne Bean 2020). Small populations have been noted in various mixed central Texas woodlands usually on limestone cliffs or outcrops and in some places along intermittent creeks (Delgado-Salinas and Carr 2007). The environments where this species has been reported appear to be low light environments below the canopy of *Juniperus-Quercus* woodlands in Central Texas savannas and not in open grasslands.

Gas exchange rates for *P. texensis* below the canopy at low light levels, (just above the light saturation point, L_{sat}) were equivalent or within the range of rates measured for true understory species (Table 1). These rates should make *P. texensis* a good competitor with other understory species in this same understory environment. Interestingly, gas exchange rates for *P. texensis* at higher light levels were within the range of other typical shade or understory species (Begon et al. 2006). Other photosynthetic parameters, including light saturation, light compensation, dark respiration, conductance, and transpiration, were within the range of values for understory or shade adapted species (Table 1). These responses are consistent with findings for shade plants, but close to values reported for facultative species (Hull 2002; Larcher 2003; Givnish et al. 2004; Valladares and Niinemets 2008; Van Auken and Bush 2015). The parameters measured for shade adapted leaves of *P. texensis* at elevated light levels did not increase significantly, suggesting that *P. texensis* is a true understory species capable of growth in low to medium light environments, but not in high light environments such as open grasslands.

In general, true understory species or shade species from eastern North American deciduous forest have A_{max} values and photosynthetic rates comparable to rates reported for *P. texensis* in the current study. No *P. texensis* 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 and Niinemets 2008).

The dark respiration rate of shade leaves of *P. texensis* growing below a *Juniperus ashei/Quercus fusiformis* canopy at light levels of $169 \pm 28 \mu\text{mol}/\text{m}^2/\text{s}$ was $0.235 \pm 0.135 \mu\text{molCO}_2/\text{m}^2/\text{s}$ or about 20% of values for other species growing in the same habitat type (Hirose and Bazzaz 1998; Hull 2002; Van Auken and Bush 2015). Dark respiration for shade-adapted species is typically low due to their lower metabolism (Bjorkman 1968; Bazzaz and Carlson 1982). The respiration rate of *Polygonum pennsylvanicum* a wetland plant grown in low light was $\sim 0.5 \mu\text{mol}\cdot\text{CO}_2/\text{m}^2/\text{s}$, whereas the rate for its leaves in full sun was twice as high (Bazzaz and Carlson 1982).

Other gas exchange values reported for *P. texensis* are within the range or lower than values reported for similar shade adapted plants. For example, the quantum yield efficiency reported here was $0.039 \pm 0.006 \mu\text{mol}\cdot\text{CO}_2/\mu\text{mol quanta}$, for shade leaves which is in the range of 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, but this is speculation at this time. Stomatal conductance and transpiration reported for *P. texensis* 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).

We never found plants of this species in open grasslands. Descriptions of this species suggest it is shade adapted (Delgado-Salinas and Carr 2007; Boerne Bean 2020). In parts of the range of the genus *Phaseolus*, some species or individuals of various species may establish and grow in low density grasslands outside of or at the edge of woodland canopies. However, all of the *P. texensis* plants that we found were below the *Juniperus-Quercus* woodland canopy.

A species found in a given habitat can tolerate or requires the conditions present in that habitat where conditions may be most favorable for its growth and survival. Nonetheless, sorting out the characteristics and levels of that or those factors can be taxing (Smith and Smith 2012; Keddy 2017). We believe that while *P. texensis* is usually found growing in shade, gas exchange characteristics may not be the only factor controlling its apparent habitat preference. The drought tolerance of this species should be compared with the drought tolerant C_4 grasses growing in the open. Another environmental factor or a combination of factors may limit the growth of *P. texensis* to shaded understory habitats including possible photo-inhibition of leaf pigments or overheating of leaves (Begon et al. 2006). Similar patterns

of distribution have been reported for other species, but restrictions were caused by differential herbivory (Louda and Rodman 1996; Maron and Crone 2006; Leonard and Van Auken 2013).

Water may be a resource limiting *P. texensis* to sub canopy positions because of greater water use efficiency by more drought tolerant C₄ grasses in open areas. This factor may keep *P. texana* restricted to canopy habitats where the C₄ grasses cannot grow because of low light levels and the high light requirements of the C₄ grasses (Wayne and Van Auken 2009). Possibly, higher soil water levels below the canopy might be available to *P. texensis* rather than to other species in this understory environment. Survival of deep rooted woody species seems to be key to their survival during extreme drought conditions, with shallow rooted woody species like *Juniperus ashei* suffering higher mortality (Johnson et al. 2018). Unfortunately, root growth and depth of penetration is unknown at this time for *P. texensis*.

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Table 1. Comparison of mean \pm one se for the maximum net photosynthetic rates (A_{max}), light level (PFD) at the A_{max} , and other photosynthetic parameters for *Phaseolus texensis*, an additional shade plant and two known sun plants from central Texas are presented. Leaflets growing on *P. texensis* plants found in the understory of a *Juniperus ashei*/*Quercus fusiformis* canopy at a light level of $169 \pm 28 \mu\text{mol}/\text{m}^2/\text{s}$ are presented.

Parameter	<i>Phaseolus texensis</i> *	<i>Carex planostachys</i> **	<i>Heliotropium tenellium</i> ***	<i>Bouteloua curtipendula</i> ****
A_{max} -max. photo. rate	5.99 ± 0.17	4.9 ± 0.3	34.96 ± 4.43	31.6 ± 0.5
Light Level at A_{max}	1000	500	2000	1633
L_{sat} - Light saturation	155 ± 19	151 ± 16	591 ± 122	630 ± 78
L_{cp} - Light comp. point	0.102 ± 0.011	4 ± 2	38 ± 3	58 ± 10
R_d - Dark respiration	0.235 ± 0.135	0.4 ± 0.0	2.63 ± 0.38	3.0 ± 0.1
IS - Initial slope	0.039 ± 0.006		0.07 ± 0.01	
g_s - Stomatal cond.	0.06818	0.07 ± 0.01	0.44 ± 0.08	0.25 ± 0.01

*This study

**Wayne and Van Auken (2012)

***Boeck and Van Auken (2017)

****Wayne and Van Auken (2012)

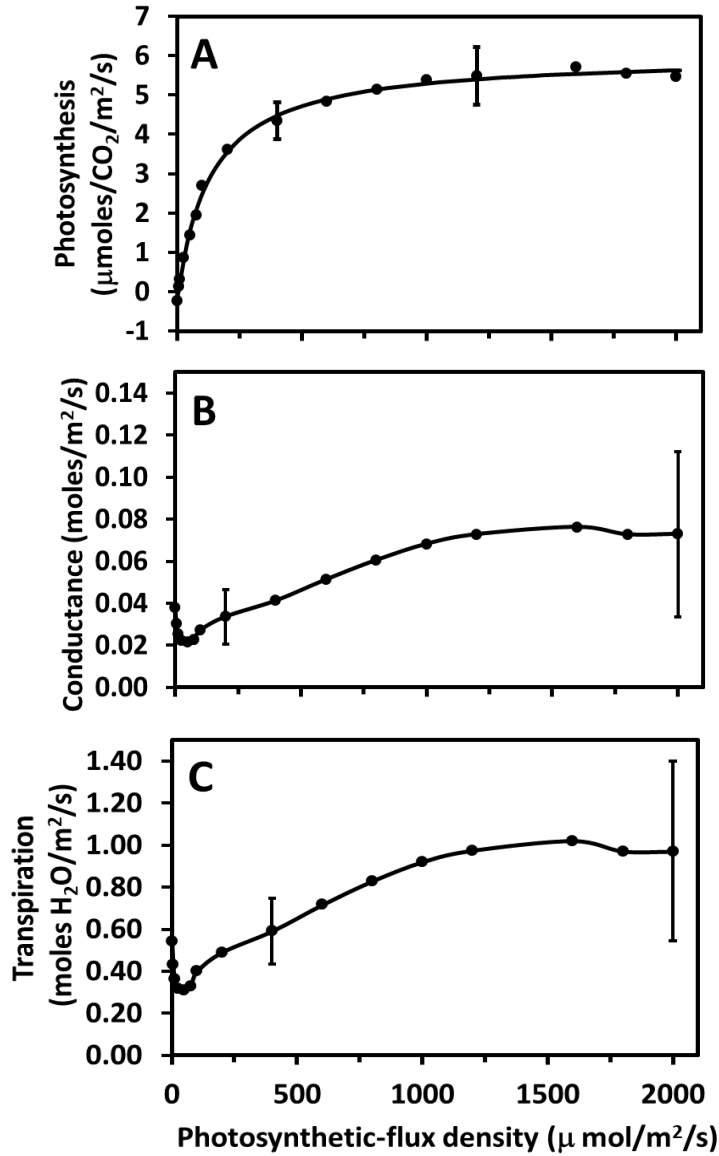


Figure 1. A) Mean photosynthetic light response curve, B) conductance, and C) transpiration for *Phaseolus texensis* measured from 0.0 $\mu\text{mol}/\text{m}^2/\text{sec}$ to 2000 $\mu\text{mol}/\text{m}^2/\text{sec}$. Standard error bars are examples. Plants were in the understory of a *Juniperus ashei/Quercus fusiformis* canopy at a light level of $169 \pm 28 \mu\text{mol}/\text{m}^2/\text{s}$ (mean \pm se). Measurements were made on April 13 and April 14, 2020.