

Photosynthetic characteristics of *Garrya ovata* Benth. (Lindheimer's silktassle, Garryaceae) at ambient and elevated levels of light, CO₂ and temperature

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ABSTRACT

Garrya ovata Benth. (Lindheimer's silktassle) is a shrub or small tree found in woodlands and savannas of the central Texas Edwards Plateau region. Plant communities where *G. ovata* occurs are mainly *Juniperus ashei*/*Quercus virginiana* woodlands or savannas with intercanopy grassland gaps or patches. These communities are found in stressful environments of shallow soils, high summer temperatures, and inconsistent low rainfall. Currently, *G. ovata* is a low density, woody understory species in these communities. Although *G. ovata* was only found in the understory, this study suggests it is more of a sun or edge species and not truly a shade or understory species. Maximum photosynthetic rate (A_{max}), dark respiration (R_d), intercellular CO₂, light saturation (L_{sp}) and water use efficiency significantly increased when light levels and CO₂ concentrations were elevated but not when temperatures were elevated. Stomatal conductance decreased when the CO₂ concentration doubled but was little affected by elevated temperature. These findings suggest that *G. ovata* should be more common in central Texas *Juniperus/Quercus* woodlands or savannas as well as in associated gaps or grasslands today and imply that it will have a higher density in these communities in a future high CO₂ environment. However, they do not explain why it has a low density in these communities today. Published on-line www.phytologia.org *Phytologia* 97(2): 103-119 (April 1, 2015). ISSN 030319430.

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Today the major canopy species in central Texas woodlands and savannas are *Juniperus ashei* Buchh. and *Quercus virginiana* Mill. (Ash juniper and hill country live oak)(Van Auken et al. 1981; Van Auken 1988; Van Auken and McKinley 2008). The potential composition and structure of these communities in a predicted future high CO₂ world is unknown. There are various understory woody species in these communities that could be canopy species today that may become canopy species in the future including *Garrya ovata* Benth. (Lindheimer's silktassle), *Diospyros texana* Scheele (Texas persimmon), *Rhus virens* Gray (evergreen sumac), *Sophora secundiflora* (Ort.) DC (Texas mountain laurel), several species of *Quercus* (L., oaks) and a few other Leguminosae (Juss., legumes)(Van Auken et al. 1981; Van Auken 1988; Van Auken and McKinley 2008). Most of these understory species including *Garrya ovata* have received little ecological or environmental study.

Juniperus woodlands occur in many parts of the northern hemisphere varying in elevation, climate and species composition (Wells 1965; Gould 1969; Blackburn and Tueller 1970; Correll and Johnston 1970; Little 1971; Baskin and Baskin 1986, 1988; West 1988; Dick-Pettie 1993; Van Auken and McKinley 2008). In North America they are found from the east coast through the Great Plains to the low

and mid-elevations of the mountains of the western United States, Canada and Mexico (Little 1971; Johnson and Alexander 1974; Elias 1980; Hora 1981;). In the past, in central and western North America, they occurred along canyon walls, steep slopes or other areas that were protected from fire (Bray 1904; Foster 1917; Smeins 1980).

Today, these *Juniperus* communities are extensive and have been treated as stable communities by most (Bray 1904; Gould 1969; Little 1971; Correll and Johnston 1970; Hora 1981; West 1988; Dick-Pettie 1993; Van Auken and McKinley 2008). However, various studies of encroachment and invasion have suggested that these are pioneer or intermediate communities that may lead to the development of forests or other types of woodlands (Jackson and Van Auken 1997; Van Auken et al. 2004; Van Auken and McKinley 2005). Over time, area covered and the species composition of these communities has apparently changed and will continue to transform, but their future composition and structure is unknown (Miller and Wigand 1994; Miller et al. 2000).

Changes in density, species composition and community distribution in the past 15-20,000 years have been due to climate warming and glacial retreat (NCA 2014). More recently, the past 200-300 years, changes have been attributed to the introduction of large populations of domestic ungulates causing high levels of constant grass herbivory which reduced the grass competitive ability and biomass and caused a decrease in fire frequency because of lack of fuel (Archer et al. 1995; Bush and Van Auken 1995; Van Auken and Bush 1997; Van Auken 2000b). These more recent conditions of decreased grass biomass and fire frequency have led to the formation of *Juniperus/Quercus* savannas and woodlands. Other factors such as soil moisture, shading, and seed dispersal seem secondary (Breshears et al. 1997, 1998; Martens et al. 2000, 2001; Joy and Young 2002; Wayne and Van Auken 2002, 2004). Conditions that may be more important for future community change include elevated atmospheric CO₂ concentration and temperature (NCA 2014).

Many *Juniperus* woodland communities including those in central Texas tend to be fairly open with gaps or open patches with shallow soils populated by grass and other herbaceous species (Quarterman 1950; Baskin and Baskin 1978, Quarterman et al. 1993; Terletsky and Van Auken 1996; Baskin and Baskin 2000; Van Auken 2000a). Canopy density can be high and canopy cover is 40 to 90% (Van Auken et al. 1981; Smeins and Merrill 1988; Van Auken and McKinley 2008). There are many very low density woody species in these communities but most are shrubby and it is unknown if some or most will or could become part of the woodland canopy in the future.

Many consider the entry of new woody species into these former grasslands, savannas or woodlands as encroachment or invasion (Van Auken 2000b; Van Auken and McKinley 2008; Van Auken 2009). However, it appears that community succession is the process governing replacement dynamics as this conversion from grassland to woodland continues. In the future, these *Juniperus/Quercus* woodlands may remain simple communities dominated by a few species or the *Juniperus* species may be replaced by other species from within or below the canopy or from elsewhere to progress to another successional stage or community type. This pattern is controlled by the interaction of the adult canopy species, surface light levels, soil moisture and nutrients, herbivory and fire (Jackson and Van Auken 1997; Batchelor and Fowler 2004; McKinley and Van Auken 2004; Van Auken et al. 2004; Van Auken and McKinley 2005). Due to modifications of these factors through time, the structure of many of these woodlands will probably change, but the direction of the changes and the future composition of the communities are unknown. Other environmental factors are changing and will continue to change in the future as well. These other factors include levels of atmospheric CO₂ and temperature which have been increasing and are expected to continue increasing into the foreseeable future (NCA. 2014).

We hypothesize that the *Juniperus/Quercus* communities in central Texas will change in the future. We further hypothesize that new understory species will be introduced and some of the current

understory species will become part of the canopy and may become dominant overstory or canopy species in the future. We hypothesize that elevated levels of atmospheric CO₂ and temperature will be the driving forces for these changes. In the present study, we have examined current *Juniperus/Quercus* community composition and structure specifically as it relates to *Garrya ovata*. We have also examined the short term response of *G. ovata* to ambient and elevated levels of light, CO₂ and temperature.

METHODS

Study sites were located in central Texas in Eisenhower Park, Lost Maples State Natural Area and a remote part of the University of Texas at San Antonio campus. Each area has slight variations in soil type, precipitation, temperature, plant communities previously observed, as well as length of time since last known exposure to grazing. Eisenhower Park is a 128 ha San Antonio city park in northern Bexar County, Texas (98°34'26"W, 29°37'19"N). Topography is rolling with slopes between 4.5° and 13.5° (Taylor et al.1962) and soils are clayey-skeletal, smectitic, thermic lithic calciustolls (USDA 2000) in the Tarrant association with surface horizons between 0 and 25 cm thick (Taylor et al.1966). The subsurface is heavily fractured limestone over limestone bedrock. Local climate is subtropical – subhumid (Arbingast et al.1976). Mean annual temperature for the area is 20 °C and ranges between monthly means of 9.6 °C in January and 29.4 °C in July (NOAA 2001). Mean annual precipitation is 78.7 cm and bimodal with peaks in May (10.7 cm) and September (8.7 cm) (NOAA 2001). Monthly precipitation is highly variable with usually very little reported in June and July. Eisenhower Park is a natural area with no domestic livestock for the past 55 years. The Park is composed of large areas of *Juniperus ashei/Quercus virginiana* woodlands or savannas on former grassland sites and is considered representative of similar communities found in this region (Van Auken et al.1981).

Lost Maples State Natural Area is in Bandera and Real counties, Texas (99°34'59"W, 29°49'11"N). The Park is 880 ha, located approximately 8 km north of Vanderpool, Texas on the Sabinal River with elevation from 550 to 686 m. Climate is similar to Eisenhower Park with a mean annual temperature of 20°C and mean annual precipitation of 89.1 cm with peaks in May and September (NOAA 2001). Uplands and slopes are dominated by similar *Juniperus/Quercus* savannas and woodlands. The third study site was located in a remote, undeveloped area on the west campus of the University of Texas at San Antonio. This area has similar topography, soils, climate and species as the other two sites.

Plant surveys and population estimations were completed to determine the community structure and population characteristics and to identify the woody species present at the Eisenhower and Lost Maples locations in both the canopy and understory. Mature relatively undisturbed *J. ashei/Q.virginiana* woodland communities were selected for study. Transects were established in each study area in a contiguous woodland with eight transects in Eisenhower City Park and three transects in Lost Maples State Natural Area.

Each transect consisted of contiguous, side by side, 5 by 5 m quadrats. Transects were 50 m in length for a total of 20 quadrats per transect. Sampling included all canopy trees and understory woody plants. Basal circumferences of all woody plants were measured at the soil surface and converted to basal areas. Total density, species density, total basal area and species basal area were calculated from these measurements. Sample adequacy was confirmed using density stabilization curves with all samples being adequate (Van Auken et al. 2005).

Gas exchange measurements were made at the University of Texas at San Antonio field site in the summer of 2007. Three *Garrya ovata* plants were selected for measurement of physiological responses at both ambient levels and elevated levels of CO₂ and temperature. Steady state photosynthetic light response curves (A_{net} vs. PAR) were completed (Van Auken and Bush 2009). Photosynthetic response

curves were measured on fully expanded leaves at mid-day (1000 – 1400 hours) when relative humidity had stabilized (Turner and Knapp 1996). One fully expanded leaf per plant served as a replicate and was placed into the cuvette of a portable photosynthetic meter (LICOR[®] LI-6400). Each leaf covered the entire chamber (2 x 3 cm). Measurements made and recorded for each plant were: A_{net} (net photosynthesis = $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), C_i (intercellular $[\text{CO}_2] = \mu\text{mol CO}_2 \cdot \text{mol air}^{-1}$), T_{leaf} (chamber leaf temperature = °C), T_{air} (air temperature outside the chamber = °C), PAR (photosynthetic active radiation = $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), g (stomatal conductance = $\text{mol} \cdot \text{H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) and E (transpiration = $\text{mmol} \cdot \text{H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$).

The leaf chamber was used to mimic varying degrees of environmental change. This was accomplished through systematic manipulations of the light level, CO_2 concentration, and temperature. The leaf chamber's relative humidity was maintained at 30 - 40% and the gas flow rate was set at $400 \mu\text{mol s}^{-1}$. A stable coefficient of variation (< 1%) was obtained for each measurement before recording and moving to the next programmed setting. Light levels were begun at $1800 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ and decreased to 1600, 1400, 1200, 1000, 800, 600, 400, 200, 100, 75, 50, 25, 10, 5 and finally $0 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Both photosynthetic light curves as well as CO_2 response curves were measured for several different combinations of the leaf chamber $[\text{CO}_2]$ and temperature conditions.

The leaf chamber $[\text{CO}_2]$ was first set at current ambient levels ($390 \mu\text{L} \cdot \text{L}^{-1}$). While maintaining ambient CO_2 , a light curve was completed starting at $1800 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ and moving downwards to $0 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ while maintaining a chamber temperature of 35°C . This temperature was chosen based on the mean high temperatures for San Antonio during the summer months of June, July and August. Light curves were repeated holding the ambient $[\text{CO}_2]$ constant while raising the chamber temperature to 40°C and then to 45°C .

The leaf chamber CO_2 was then raised to 1.5 times the current atmospheric CO_2 level to $585 \mu\text{L} \cdot \text{L}^{-1}$. Photosynthetic light curves were carried out at a temperature of 35°C , 40°C and 45°C . The final CO_2 manipulation raised the leaf chamber CO_2 level to twice the current atmospheric level to $780 \mu\text{L} \cdot \text{L}^{-1}$. Photosynthetic light curves were again measured for the three temperature conditions using the same procedure as above. Finally, CO_2 response curves were measured at a light level approximating canopy shade ($700 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$). This was first completed at 35°C and then at 40°C and 45°C as described for the light curves.

Both Microsoft Excel[®] and JMP[®] IN 5.1 were used for data organization and analysis. The JMP[®] IN 5.1 software was used to determine significant differences using a repeated measures MANOVA on the curves of the photosynthetic rate, intercellular CO_2 concentration, stomatal conductance and transpiration using the light level, PAR, as the repeat variable (Sall et al. 2011). Water use efficiency was calculated by dividing the photosynthetic rate by the transpiration rate and also analyzed using a repeated measures MANOVA. Significance levels for all tests were $P \leq 0.05$. All data were checked for normality with the Shapiro-Wilk W test and homogeneity of variance with Bartlett's test and when necessary log transformed. A standard least squared ANOVA was used to determine significant differences in each light response curve at each different CO_2 concentration and temperature combination examined. All ANOVAs for light response curves were significant ($P \leq 0.05$).

Additional characteristics were determined including the maximum photosynthetic rate (A_{max}) which was the highest A_{net} measured for each replicate or a mean of the highest A_{net} values that were not significantly different. The dark respiration rate (R_d) was the gas exchange rate at PAR = $0 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. The initial slope (IS) or initial response, also known as the quantum yield (Φ) was the linear relationship calculated using the dark values and A_{net} at increasing PAR until the regression coefficient of the slope decreased. The light compensation point (L_{cp}) was calculated as the PAR when $A_{\text{net}} = 0 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ using the linear regression of the initial response. The light saturation point (L_{sat}) was the light level when the initial slope reached A_{max} . A standard least squared ANOVA was used to determine significant

differences for the CO₂ concentration and temperature effects. Tukey-Kramer HSD multiple comparison tests were used to determine differences between pair wise comparisons (Sall et al. 2011).

RESULTS

All canopy trees were identified and counted and the communities were simple with two major overstory species. Relative canopy density of *Juniperus ashei* was $61 \pm 12\%$ (mean \pm standard deviation). Relative canopy density of *Quercus virginiana* was $36 \pm 6\%$. Other canopy species found in one or two stands were *Diospyros texana* (Texas persimmon), *Celtis laevigata* (sugarberry or hackberry), *Ulmus crasifolia* (cedar elm), *Prosopis glandulosa* (mesquite) and *Sophora secundiflora* (Texas mountain laurel) with relative densities of 0.4 – 1.8%. *Garrya ovata* was not present in the canopy, it was present in the understory of 10/11 stands examined with a relative density of $0.12 \pm 0.04\%$ and density of 120 plants/ha.

Light curve results of the main effects of CO₂ concentration and temperature were compared. Response variables including photosynthetic rate, stomatal conductance, dark respiration rate, intercellular CO₂ concentration and water use efficiency were significant only for CO₂ concentration and not temperature. Interactions were not significant and removed from the model (Table 1).

Main effects	Photo.Rate	Conduction	Resp.	[CO ₂]	Transpir.	WUE
Temperature	0.9425	0.5153	0.3346	0.5427	0.2331	0.2143
[CO ₂]	<0.0001	0.0038	0.0314	<0.0001	0.1376	0.0014

Table 1. Table includes *P*-values for repeated measures MANOVAs of gas exchange measurements for *Garrya ovata* comparing the main effects of temperature and CO₂ at 16 light levels (interactions were not significant and removed from the models). Data is from three replicates at three concentrations of CO₂ (390, 585 and 780 $\mu\text{L}\cdot\text{L}^{-1}$) and three temperatures (35, 40 and 45 °C). Bold entries are significant.

The mean curves of the photosynthetic rates are shown by temperature and CO₂ effects (Figure 1A and 1B). Photosynthetic rates compared by temperature were not significantly different (MANOVA, $P = 0.9364$) (Figure 1A). However, photosynthetic rates increased to a plateau of approximately 9 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ as light levels increased. The comparisons by CO₂ concentration were statistically different between the curves (repeated measures MANOVA, $P = 0.0010$) (Figure 1B). The curves increased as the light levels increased and as the CO₂ concentration increased. The ambient (390 $\mu\text{L}\cdot\text{L}^{-1}$) or low CO₂ concentration was significantly different from both the middle (585 $\mu\text{L}\cdot\text{L}^{-1}$) and the high (780 $\mu\text{L}\cdot\text{L}^{-1}$) CO₂ concentration ($P = 0.0033$ and $P = 0.0009$). The middle (585 $\mu\text{L}\cdot\text{L}^{-1}$) and the high (780 $\mu\text{L}\cdot\text{L}^{-1}$) CO₂ concentration were not significantly different from each other ($P = 0.4582$). Between the ambient CO₂ concentration (390 $\mu\text{L}\cdot\text{L}^{-1}$) and the middle CO₂ concentration the highest photosynthetic rate increased approximately 35% while between the middle and the high CO₂ concentration the rate increased 11% for a total increase of 46% (Figure 1B).

Transpiration rate was not affected by increasing temperature or CO₂ level as light levels were increased ($P = 0.2331$ and 0.1376 respectively). Stomatal conductance was not affected by increasing temperatures as light levels changed ($P = 0.5153$). Stomatal conductance did differ significantly by CO₂ level but differences were small and are not presented ($P = 0.0038$).

The mean curves of the calculated water use efficiencies are displayed by temperature and CO₂ concentration (Figure 2A and 2B). Water use efficiency did not differ significantly by temperature ($P = 0.2143$) (Figure 2A), but did differ significantly by CO₂ level ($P = 0.0014$) (Figure 2B). As light levels and the CO₂ concentration increased the water use efficiency increased. The water use efficiency at ambient CO₂ did not show a significant increase compared to the middle CO₂ concentration (17%) but did

increase significantly compared to the high CO₂ concentration for a total increase of approximately 37% (Figure 2B).

Measured light curve parameters including photosynthetic maximum (A_{\max}), light saturation point (L_{sp}), light compensation point (L_{cp}), dark respiration (R_{d}) and initial slope (IS) were compared with the standard least squared ANOVA (Table 2). Temperature and CO₂ concentration were main effects. For each of the comparisons the interactions were not significant and removed from the model. None of the temperature comparisons were significant (Table 2). The A_{\max} , L_{sp} and R_{d} were found to be significant by CO₂ concentration with no other CO₂ comparisons being significant (Table 2).

Main effects	A_{\max}	L_{sp}	L_{cp}	R_{d}	IS
Temperature	0.9425	0.5734	0.6895	0.3346	0.8541
CO ₂ concentration	<0.0001	<0.0001	0.0897	0.0314	0.9268

Table 2: Table of P -values for Standard Least Squared ANOVAs for measured light curve parameters for *Garrya ovata* including the main effects of temperature and CO₂ (interactions were not significant and removed from the models). Data is from three replicates at three concentrations of CO₂ (390, 585 and 780 $\mu\text{L}\cdot\text{L}^{-1}$) and three temperatures (35, 40 and 45 °C). Bold entries are significant.

The maximum photosynthetic rate (A_{\max}) did not change with temperature ($P = 0.9425$) while it did increase significantly with CO₂ concentration ($P < 0.0001$) (Table 2; Figure 3). Temperature had little effect on the mean A_{\max} with values of 9.94 , 10.15 and $10.25 \pm 0.64 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \text{s}^{-1}$. Tukey comparisons of the CO₂ effect showed significant differences between the ambient CO₂ concentration and both the middle and high CO₂ concentrations (Figure 3). The A_{\max} increased from $7.06 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \text{s}^{-1}$ for the ambient CO₂ concentration to $10.90 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \text{s}^{-1}$ for the middle CO₂ concentration and again to $12.38 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \text{s}^{-1}$ for the high CO₂ concentration. This was an A_{\max} increase of approximately 35% from the low to medium CO₂ concentration and another 12% increase from medium to high CO₂ concentration giving an overall increase of approximately 47%. The interaction term was not significant ($P = 0.9975$). The interaction plot of A_{\max} did not show a trend for temperature at any CO₂ concentration (Figure 3).

The light saturation point (L_{sp}) did not change significantly with temperature ($P = 0.5734$) (Table 2; Figure 4). The mean L_{sp} for the three temperatures were 375.0 , 341.7 and $348.4 \pm 23.4 \mu\text{mol}\cdot\text{m}^{-2} \text{s}^{-1}$ (Figure 4). [CO₂] had a significant effect on L_{sp} ($P < 0.0001$) (Figure 4). A significant difference was found between values for the ambient CO₂ L_{sp} ($245.6 \mu\text{mol}\cdot\text{m}^{-2} \text{s}^{-1}$) and both the medium CO₂ L_{sp} ($374.3 \mu\text{mol}\cdot\text{m}^{-2} \text{s}^{-1}$) and high CO₂ L_{sp} ($445.1 \mu\text{mol}\cdot\text{m}^{-2} \text{s}^{-1}$). The Tukey comparisons showed no significant differences for L_{sp} between the middle and the high CO₂ concentrations (Figure 4). The interaction term was not significant ($P = 0.7757$). The interaction graph for L_{sp} did not show a trend for temperature at any CO₂ concentration (Figure 4). Light saturation increased approximately 59% from ambient to high CO₂.

There were no significant difference for the light compensation point (L_{cp}) values (25.4 , 25.5 and $29.0 \pm 3.4 \mu\text{mol}\cdot\text{m}^{-2} \text{s}^{-1}$) as the temperature increased (35, 40 and 45 °C respectively) ($P = 0.6895$). The light compensation point increased slightly as the CO₂ concentration increased (21.3 , 26.3 and $32.3 \mu\text{mol}\cdot\text{m}^{-2} \text{s}^{-1}$) but this trend was marginal ($P = 0.0897$). The interaction term was not significant ($P = 0.9460$), thus the interaction graph for L_{cp} did not show a trend for temperature at any CO₂ concentration.

For the dark respiration rate (R_{d}) there was a non-significant trend of increasing values (0.72 , 0.78 and $0.89 \pm 0.079 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \text{s}^{-1}$) as the temperature increased from 35 to 40 and 45 °C respectively ($P = 0.3346$) (Figure 5). The trend for CO₂ concentration was significant. The R_{d} at the ambient CO₂ concentration ($0.63 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \text{s}^{-1}$) was significantly different from the R_{d} at the high CO₂

concentration ($0.95 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \text{s}^{-1}$) while the medium $\text{CO}_2 R_d$ ($0.80 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \text{s}^{-1}$) was not significantly different from either the ambient or the high $\text{CO}_2 R_d$ (Figure 5). The interaction term was not significant ($P = 0.9856$) and when removed from the model results did not change. The R_d increased approximately 34% from ambient to high CO_2 .

The IS did not differ significantly with temperature or CO_2 concentration and results are not presented. There were no statistical difference as temperature changed but IS values were 0.031, 0.034 and $0.033 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \text{s}^{-1} / \mu\text{mol} \cdot \text{m}^{-2} \text{s}^{-1}$ ($P = 0.8541$). CO_2 concentration did not have a significant effect on the IS and values were 0.033, 0.033 and $0.031 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \text{s}^{-1} / \mu\text{mol} \cdot \text{m}^{-2} \text{s}^{-1}$ ($P = 0.9268$). The interaction term was not significant ($P = 0.9835$) and removed from the model and the results did not change.

When light levels were held constant at sub canopy levels ($700 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) gas exchange rates increased with CO_2 concentrations but the response to elevated temperatures were not significant and differences were small (Figure 6). CO_2 uptake increased as the CO_2 concentration increased but there was no significant difference ($P > 0.05$) between temperature treatments (35, 40 and 45°C). The highest CO_2 concentrations tested (1000 and $1200 \mu\text{L} \cdot \text{L}^{-1}$) had higher amounts of variation around the mean than the lower levels. Once the CO_2 concentration reached 585 - $700 \mu\text{L} \cdot \text{L}^{-1}$, the photosynthetic rates reached a plateau of approximately $10 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \text{s}^{-1}$.

None of the repeated measures MANOVAs performed on the photosynthetic response, intercellular CO_2 concentration, stomatal conductance and transpiration were significantly different by temperature ($P > 0.05$ for all). Both CO_2 uptake and intercellular CO_2 concentration increase with increasing CO_2 concentration but not to changing temperature. The stomatal conductance and transpiration curves mimicked each other seemingly following the same overall trend (not presented).

Temperature had little effect on the overall CO_2 photosynthetic response curves ($P = 0.8672$). The curves exhibit a fairly linear relationship from the low CO_2 concentration ($50 \mu\text{L} \cdot \text{L}^{-1}$) to approximately $600 \mu\text{L} \cdot \text{L}^{-1}$. Once the CO_2 concentration reached 585 - $700 \mu\text{L} \cdot \text{L}^{-1}$ the photosynthetic rates reached a plateau of approximately $10 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \text{s}^{-1}$.

The repeated measures MANOVA of the water use efficiency response to temperature was not significant ($P = 0.4885$). The curves increased from a low of approximately $-0.15 \text{mmol H}_2\text{O} \cdot \text{mol CO}_2^{-1}$ at $50 \mu\text{L} \cdot \text{L}^{-1}$ to a plateau of approximately $3.2 \text{mmol H}_2\text{O} \cdot \text{mol CO}_2^{-1}$ at $585 \mu\text{L} \cdot \text{L}^{-1}$ which was maintained until a peak value of $4.2 \text{mmol H}_2\text{O} \cdot \text{mol CO}_2^{-1}$ was reached at the $1000 \mu\text{L} \cdot \text{L}^{-1}$ of CO_2 (Figure 7).

DISCUSSION

Based on our results and comparisons with literature values with other species (Hull 2002; Wayne and Van Auken 2012), *Garrya ovata* appears to be a sun adapted species (Valladares and Niinemets 2008; Van Auken and Bush 2009). Our experiments showed increased CO_2 uptake at higher light levels (Figure 1). In addition, increasing atmospheric CO_2 caused increased plant CO_2 uptake especially at higher light levels (Figure 1) also suggesting that *G. ovata* is a sun plant. This does not explain the low density of *G. ovata* found below the canopy of these woodland communities or the lack of *G. ovata* in the grassland gaps and patches. Density of large native herbivores have increased dramatically in central Texas over the past few decades as well as in many other areas of North America causing community structural and composition changes (Anderson and Loucks 1979; Doughty 1983; Augustine and Frelich 1998; Russel et al. 2001; Cadenasso et al. 2002; Abrams 2003; Krueger et al. 2009; Kain et al. 2011; Abrams and Johnson 2012). Plant species in the study areas have been shown to be susceptible to herbivory and require exclosures to maintain populations (Van Auken 1988, 1993; Leonard and Van Auken 2013). This is similar to what is happening to *Quercus* sp. and a number of other woody species in

many North American forests (Anderson and Loucks 1979; Abrams 2003; Abrams and Johnson 2012). Although herbivory of *G. ovata* was not directly examined in this study there is a high potential for herbivory (browsing) to have a major effect on the population structure and distribution of this species.

The light level responses found in this study suggest that *G. ovata* is similar to other geographically restricted eastern North American low density species reported to be shade intolerant and susceptible to herbivory (Baskin and Baskin 1988). The response of *G. ovata* to canopy position (open grassland or below a canopy) is probably dependent on the presence of herbivores and *G. ovata*'s current low relative density is caused by a high density of large native herbivores (probably white tailed deer). Presence of some *G. ovata* plants below the canopy maybe because of the presence of the high levels of other woody shrubs below the canopy that could afford some level of protection from the herbivores, masking their presence and position similar to what has been reported for other species (Leonard and Van Auken 2013).

These central Texas *Juniperus* woodlands seem to be successional communities (Van Auken 2009). In the eastern North American deciduous forests *Juniperus* plants are often found in forest gaps or blow downs or on shallow soil in glades (Van Auken and McKinley 2008). In western North America *Juniperus* tend to occur above the desert communities and above the arid or semiarid grasslands, but usually below the higher elevation pine, spruce or fir forests (Van Auken 2000b). In central Texas *Juniperus ashei* establishes on hillsides and in former grasslands usually on shallow soil (Terletzky and Van Auken 1996). The presence of *Juniperus* woodlands in central Texas and many other parts of the world today has probably been caused by a number of factors with constant high levels of domestic grass herbivory and a concomitant reduction of grassland fire frequency being paramount (Van Auken 2000B, 2009).

Grass plants and grasslands are favored when grassland biomass and fire frequency are relatively high while woody plants, like various species of *Juniperus*, and many species of nitrogen fixing legumes, like *Prosopis*, *Senegalia* and *Vachellia* (formerly *Acacia*), are favored when fire frequency is low or nonexistent (Bond 2008; Van Auken and Bush 2013). Apparently the composition of many grasslands and savannas has changed and the direction of community succession has changed because of a new set of conditions controlling the structure and composition of these communities (Begon et al. 2006; Bond 2008; Smith and Smith 2012; Van Auken and Bush 2013).

These new, recent conditions in the grasslands which include high and constant levels of herbivory by domestic animals resulting in low levels of light, fluffy fuel and a concomitant reduction in fire frequency have resulted in woody plant establishment. In the woodlands, browsing by native herbivores is causing community change. These conditions will be further modified in the future by higher levels of atmospheric CO₂ and higher temperatures (NCA 2014). These new conditions will allow some species to expand their aerial cover and increase their density, while other species will decline. The result will be changes in community composition and structure. A species in these central Texas *Juniperus/Quercus* communities expected to change in density and basal area is *G. ovata*. It has a high gas exchange rate which we have shown to increase with increased light levels and increased atmospheric CO₂ levels. But, there seems to be a factor or factors that we have not examined or accounted for which is natural herbivory or browsing by white-tailed deer (*Odocoileus virginianus*). This species has been shown to cause establishment difficulties for herbaceous species in many areas of central Texas (Leonard and VanAuken 2013). This difficulty in establishment has also been shown for many woody species possibly in conjunction with competition for water with C₄ southern grasses (Van Auken 1993; Russel et al. 2001; Cadenasso et al. 2002; Krueger et al. 2009; Kain et al. 2011). However, predicting future plant community changes and rates of species change will be an arduous task.

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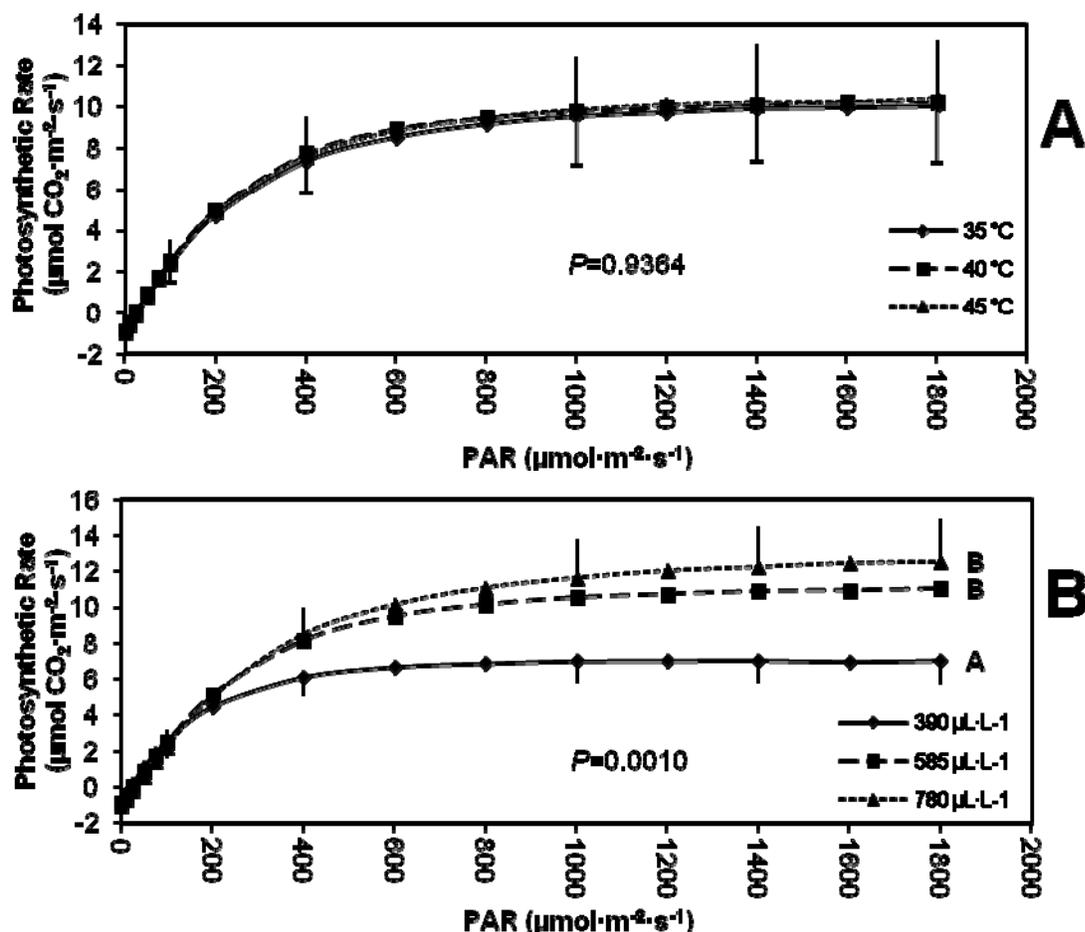


Figure 1: Mean repeated measures MANOVA curves of the photosynthetic rates for *Garrya ovata* displayed by temperature (A) and CO₂ concentration (B) treatment for main effects only. *P*-values are shown from the repeated measures MANOVA for the main effects (Temperature and CO₂). Like letters at the end of the curves indicate no significant difference. Data is from three replicates at three concentrations of CO₂ (390, 585 and 780 μL·L⁻¹) and three temperatures (35, 40 and 45 °C). Representative error bars are shown indicating standard deviations.

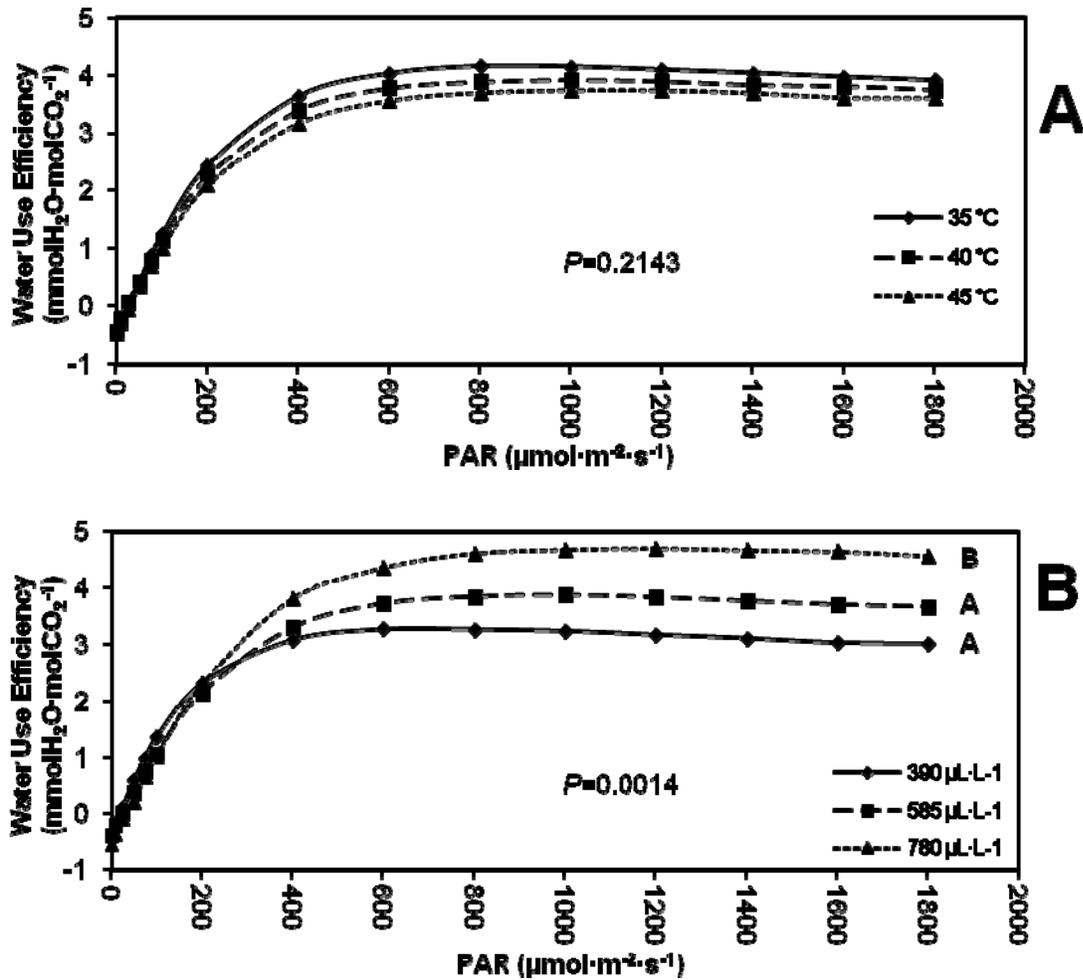


Figure 2: Mean repeated measures MANOVA curves of the water use efficiency for *Garrya ovata* displayed by temperature (A) and CO₂ (B) treatment for main effects only. *P*-values are shown from the repeated measures MANOVA for the main effects (Temperature and CO₂). Data is from three replicates at three concentrations of CO₂ (390, 585 and 780 µL·L⁻¹) and three temperatures (35, 40 and 45 °C).

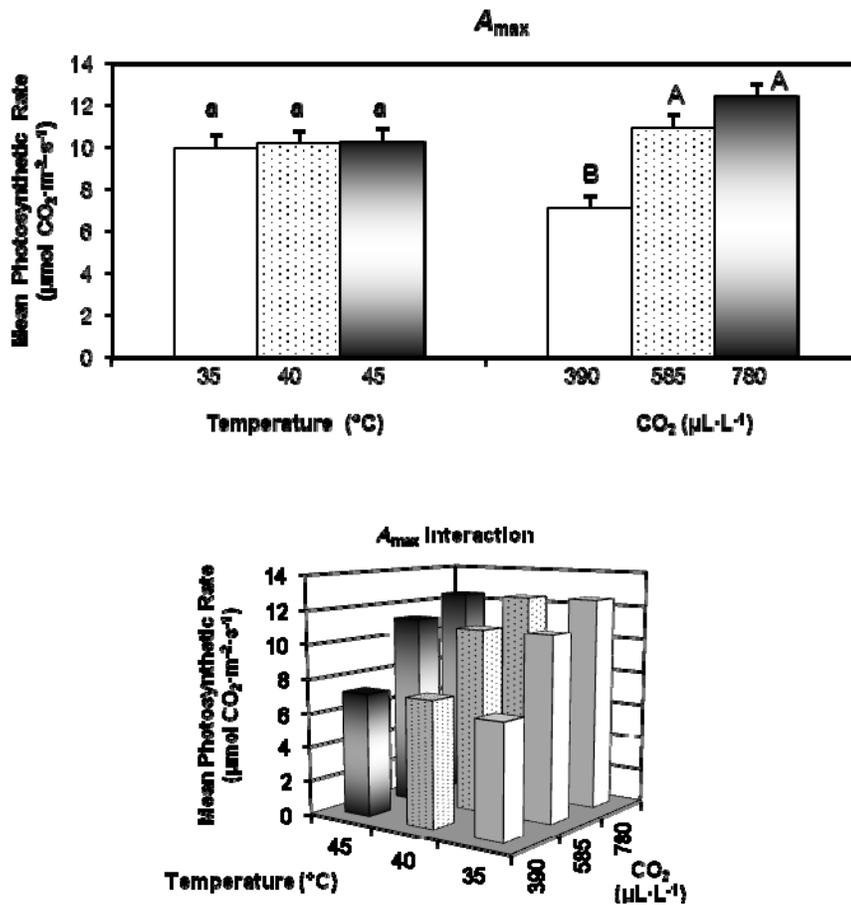


Figure 3: Standard least squared ANOVA results for the *Garrya ovata* A_{max} comparisons. Temperature and CO_2 graphs are for main effects only with the Tukey comparisons labeled. Temperature and the interaction are not significant ($P = 0.9425$ and $P = 0.9975$) while the CO_2 concentration is significant ($P < 0.0001$). Like letters from the Tukey comparisons indicate no significant difference between the means. Data is from three replicates at three levels of CO_2 (390, 585 and $780 \mu\text{L} \cdot \text{L}^{-1}$) and three temperatures (35, 40 and 45°C).

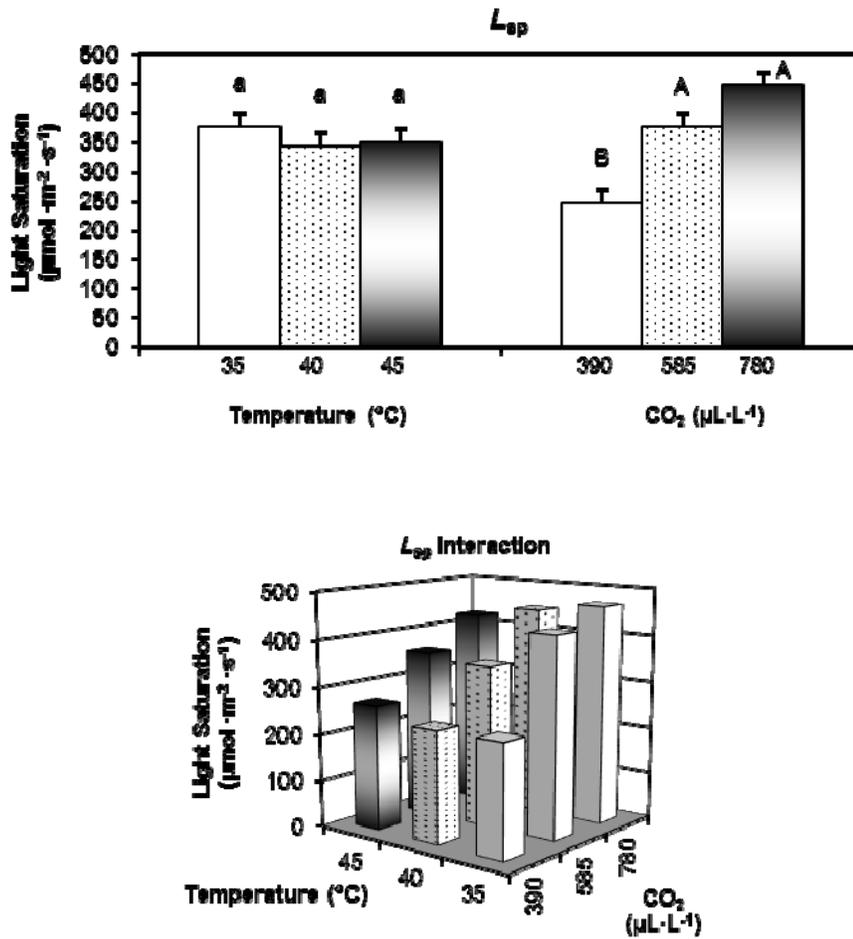


Figure 4: Standard least squared ANOVA results for the *Garrya ovata* L_{sp} comparisons. Temperature and CO_2 graphs are for main effects only with the Tukey comparisons labeled. Temperature and the interaction are not significant ($P = 0.5734$ and $P = 0.7757$) while the CO_2 concentration is significant ($P < 0.0001$). Like letters from the Tukey comparisons indicate no significant difference between the means. Data is from three replicates at three concentrations of CO_2 (390, 585 and $780 \mu\text{L}\cdot\text{L}^{-1}$) and three temperatures (35, 40 and $45 ^{\circ}\text{C}$).

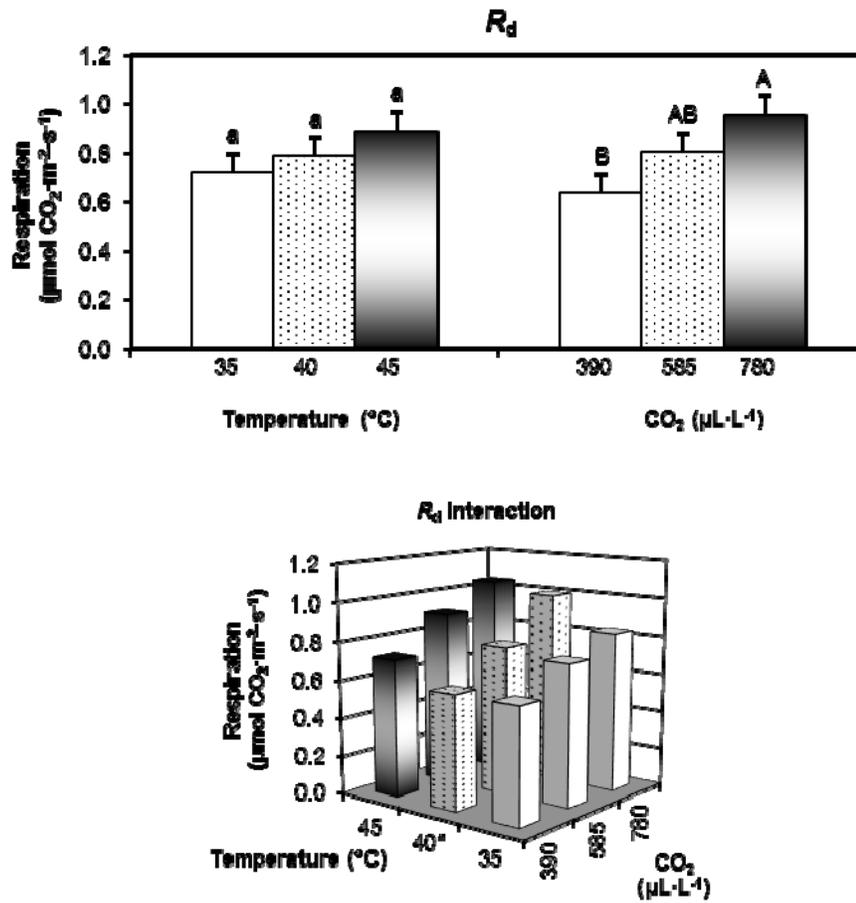


Figure 5: Standard least squared ANOVA results for the *Garrya ovata* R_d comparisons. Temperature and CO_2 graphs are for main effects only with the Tukey comparisons labeled. Temperature and the interaction were not significant ($P = 0.3346$ and $P = 0.9856$). The CO_2 concentrations were significantly different ($P = 0.0314$). Like letters from the Tukey comparisons indicate no significant difference between the means. Data is from three replicates at three concentrations of CO_2 (390, 585 and $780 \mu\text{L}\cdot\text{L}^{-1}$) and three temperatures (35, 40 and $45 ^{\circ}\text{C}$).

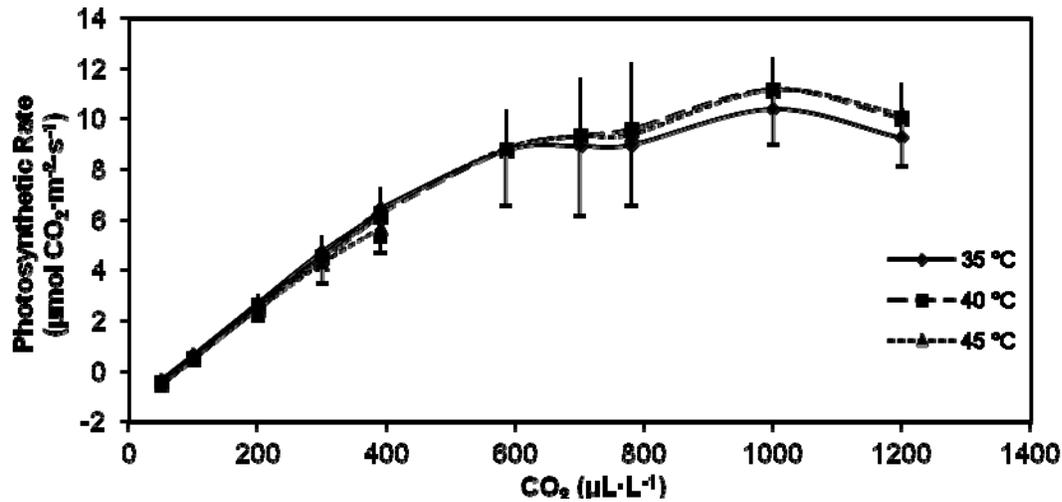


Figure 6: CO₂ response curves for *Garrya ovata* at a light level of 700 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and three temperatures (35, 40 and 45 °C). The repeated measures MANOVA of the calculated CO₂ response was not significant by temperature ($P = 0.8854$). A standard least squared ANOVA was used to determine significant differences in each light response curve for each temperature. All three ANOVAs were significant ($P \leq 0.05$). Each curve was plotted from a mean of three replicates. Error bars are shown indicating standard deviation with the open end (|) for the upper most curve and the bar end (⊥) for the lower curve.

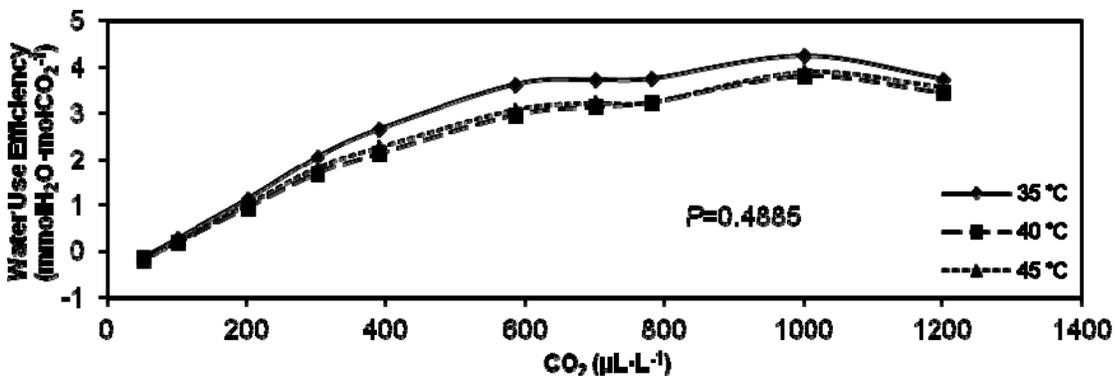


Figure 7: Repeated measures CO₂ response curves of the water use efficiency for three replicates of *Garrya ovata* at a light level of 700 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and three temperatures (35, 40 and 45 °C). Temperature was not significant ($P = 0.4885$). A standard least squared ANOVA was used to determine significant differences in each light response curve for each temperature. All three ANOVAs were significant ($P \leq 0.05$). Each curve was plotted from a mean of three replicates. Error bars are shown indicating standard deviation with the open end (|) for the upper most curve and the bar end (⊥) for the lower curve.