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Gas Exchange Rates of Texas Persimmon (*Diospyros texana*) in Central Texas Woodlands

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Abstract

Diospyros texana (Texas persimmon) is a secondary species in most *Juniperus ashei/Quercus fusiformis* woodlands in central Texas. It has high density, but plants are mostly in the community understory. Light response curves at ambient and elevated levels of CO_2 and temperature were measured for *D. texana*. The A_{net} (photosynthetic rate) increased significantly as both light level and CO_2 levels increased but not temperature. The A_{max} (maximum photosynthetic rate) of *D. texana* in full sun at elevated levels of CO_2 was increased for all treatments. Stomatal conductance increased with levels of CO_2 but only if the interaction was removed from the model. Intercellular levels of CO_2 increased with both temperature and CO_2 treatments as did water use efficiency (WUE). Furthermore, light saturation (L_{sat}) increased with CO_2 treatments and light compensation (L_{cp}) increased with temperature. The dark respiration (R_d) increased with both temperature and CO_2 treatments. Markov population models suggested *D. texana* populations would remain ecologically similar in the future. However, sub-canopy light levels and herbivory should be considered when examining population projections. For example, *Juniperus ashei* juveniles are not recruited into any canopy unless there are high light levels. Herbivory reduces the success of *Quercus* juveniles from reaching the canopy. These factors do not seem to be a problem for *D. texana* juveniles which would allow them to reach the canopy without need of a high light gap and are not prevented by herbivory. Thus, *Juniperus/Quercus* woodlands will change in the future to woodlands with *D. texana* a more common species.

Keywords

Replacement Dynamics, Ecological Succession, CO_2 Concentrations, Temperature Levels, Photosynthetic Rates, Drought Tolerance, Herbivory, Species Replacement, Encroachment, Juniper

1. Introduction

Diospyros texana is a small tree or shrub in the Ebenaceae family with about 500 species in the family [1] [2], and three genera but only one genus *Diospyros* is found in Texas with two species. *Diospyros texana* (Texas persimmon) has been found in most *Juniperus ashei/Quercus fusiformis* woodlands in central Texas [3]. Except it is usually not a major species in these woodlands, it has high density, but most plants are in the community understory and seemingly not recruited into the overstory [3]. Although one study showed *D. texana* as a high density overstory and understory species [4], however, reasons for its high density in the overstory in this one study were not clear. Soils in this community were deeper than in other studies, but the soils were still limestone soils and reasons for the high overstory density were undefined.

Plant communities throughout the World, including Texas, range from various grasslands to savannas, woodlands and forests [5] [6] [7] [8] with some woodlands and forests being evergreen or deciduous. These communities including those in central Texas, have changed since the late Pleistocene (120,000 years ago) when the climate was much cooler [9] [10]. Major warming and glacier retreat began in the early Holocene (15,000 - 20,000 years ago) and continue today [11]. More recently, from about 400 - 500 years ago through the present, plant communities changed more rapidly and changes were associated with the arrival of European settlers and their animals [12]. Estimates suggest that nearly 60 million ha of grasslands in the southwestern part of the United States have been planted or encroached by various woody species and converted into savannas, shrub lands or woodlands [7] [13] [14]. However, most of these changes are not well documented and the suggested area altered is larger than the projected area of all of these former grasslands together [15] [16].

The major woody species in central Texas woodlands today are *Juniperus ashei* Buchh. (Ashe's juniper) and *Quercus fusiformis* Small (Texas live oak) [1] [17] [18]. *Juniperus* communities have expanded dramatically with juvenile encroachment into many grasslands at the expense of grass community cover and biomass [19] [20] [21]. As woody plant density increased, their biomass increased as the biomass of the C_4 grasses decreased [22]. In addition, the biomass of a shade tolerant sedge (*Carex planostachys*) increased below the woodland canopy as conditions changed [23] [24]. Thus, the sunlight level in the understory of these communities seems to be important in determining their structure. However, the structure of these woodland communities in a high CO_2 and temperature world is not known and is hard to predict.

Juniperus communities are found from the east coast of North America to the Pacific Ocean in the west [25] [26]. *Juniperus* communities of eastern North America are considered successional, but believed to be permanent in the mountains of the southwestern United States and central Texas. Factors that control structure of plant communities are not always easily recognized and the species composition of the future communities are hard to predict because of the long life of the woody species present [6] [8] [27] [28]. The ideas of community change are not new, in 1863 Thoreau recognized that pine communities were replaced in time by hardwood deciduous trees [29]. But, once forest communities develop, succession is hard to follow. The process seems to slow late in succession and the end or climax community, if there is one, is hard to define or see [30] [31] [32].

Most of central and western Texas was considered prairie or grassland in the past [5] but more recently was divided into physiographic regions (described by physical geography or geomorphology conditions). The central Texas area is a large physiographic region called The Edwards Plateau [1] [33] [34] and has been treated as a single unit by many authors [1] [18] [33] [35] [36] [37]. However, there are a variety of plant communities with many endemic species in this diverse region [18] [34] [38]. Some have suggested this is too simplistic an approach and does not address the various plant communities in the area [3] [18] [19] [21] [34] [38] [39] [40].

In the past, we hypothesized that the *Juniperus/Quercus* (juniper/live oak) woodlands would change in a future high CO_2 and high temperature world [18] [41] [42] [43]. Many of these *Juniperus* communities appear successional based on observations and gas exchange measurements. We propose that in the future *D. texana* may become a dominant species in some of these communities based on its ecological characteristics and work presented in the current study.

2. Materials and Methods

Field population from three areas in central Texas including Eisenhower Park, Lost Maples State Natural Area and The University of Texas San Antonio West campus were examined [41] [42] [43] [44]. Areas were similar in soil type, precipitation, temperature, plant communities and last known time of domestic grazing. Approximate locations are 98˚34'26”W-29˚37'19”N, 99˚34'59"W-29˚49'11"N and 98˚34'27"W-29˚37'19"N. Slopes are between 4.5˚ and 13.5˚ [45] and soils are clayey-skeletal, smectitic, thermic lithic calciustolls [46] in the Tarrant association and surface is usually between 0 and 25 cm thick [45]. Subsurface is heavily fractured limestone over limestone bedrock. Climate is subtropical – sub humid [47]. Mean annual temperature is 20˚C and precipitation is 78.7 - 89.1 cm with peaks in May (10.7 cm) and September (8.7 cm) [48]. Precipitation is highly variable, usually none or very little in June and July. The areas studied are similar to large areas of *Juniperus ashei* / *Quercus fusiformis* woodlands or savannas on former grassland that are present throughout this region [3] [17] [18].

Transects were contiguous, side by side, 5 by 5 m quadrats, 50 m in length and 20 quadrats per transect. All canopy trees and understory woody plants were identified, counted and measured. 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 as well as relative values were calculated from these measurements and sample adequacy was confirmed [49]. Literature was reviewed and consulted for ecological values of *Diospyros texana* Scheele (Texas persimmon, Ebenaceae, ebony family, [21]).

Gas exchange measurements were made on plants found on the West Campus of the University of Texas San Antonio in the summer of 2007. Three plants of each species were selected for measurement of physiological light responses levels at both ambient levels and elevated levels of CO_2 and temperature. Steady state photosynthetic light response curves (A_{net} vs. PAR) were then completed [41] [42] [43] [50]. Fully expanded leaves were used for photosynthetic response curves which were measured at mid-day (1000 - 1400 hours) when relative humidity had stabilized [51]. A fully expanded leaf per plant served as a replicate and was used in the cuvette of a portable photosynthetic meter (LICOR$^{®}$ LI-6400). Leaves covered the entire chamber (2 × 3 cm). The measurements that were made and recorded for each plant were: A_{net} (net photosynthesis = μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$), C_i (intercellular [CO_2] = μmol $CO_2 \cdot \text{mol} \cdot \text{air}^{-1}$), T_{leaf} (chamber leaf temperature = ˚C), T_{air} (air temperature outside the chamber = ˚C), PAR (photosynthetic active radiation = $\mu\text{mol} \cdot m^{-2} \cdot s^{-1}$), *g* (stomatal conductance = $\text{mol} \cdot H_2O \cdot m^{-2} \cdot s^{-1}$) and *E* (transpiration = $\text{mmol} \cdot H_2O \cdot m^{-2} \cdot s^{-1}$).

The leaf chamber was used to mimic various environmental conditions including light level, CO_2 concentration, and temperature. Relative humidity was maintained at 30% - 40% and the gas flow rate was 400 μmol/s. Stable coefficients of variation (<1%) were obtained for each measurement before recording and moving to the next setting. Light levels were instigated at 1800 $\mu\text{mol} \cdot m^{-2} \cdot s^{-1}$ and decreased to 1600, 1400, 1200, 1000, 800, 600, 400, 200, 100, 75, 50, 25, 10, 5 and finally 0 $\mu\text{mol} \cdot m^{-2} \cdot s^{-1}$. The photosynthetic light curves and CO_2 response curves were measured for different combinations of the leaf chamber [CO_2] and temperature conditions.

For [CO_2] measurements, the leaf chamber was first set at ambient levels (390 $\mu L \cdot L^{-1}$). Next, maintaining the ambient CO_2 level, a light curve was completed starting at 1800 $\mu\text{mol} \cdot m^{-2} \cdot s^{-1}$ and proceeding to 0 $\mu\text{mol} \cdot m^{-2} \cdot s^{-1}$ while the chamber temperature of 35˚C was maintained. This temperature was the mean high temperatures for San Antonio during the months of June, July and August. Light curves were repeated with the ambient CO_2 constant while raising the chamber temperature to 40˚C and then to 45˚C. Chamber CO_2 was next raised to 585 $\mu L \cdot L^{-1}$. Photosynthetic light curves were carried out at a temperature of 35, 40 and 45˚C. The third CO_2 manipulation raised the leaf chamber CO_2 level to 780 $\mu L \cdot L^{-1}$. Photosynthetic light curves were measured for the three temperature conditions as above. Finally, CO_2 response curves were measured at canopy shade levels (700 $\mu\text{mol} \cdot m^{-2} \cdot s^{-1}$) and at 35˚C, 40˚C and 45˚C.

Microsoft Excel© and JMP© IN 5.1 were used for data organization and analysis. JMP© IN 5.1 software was used to show significant differences using a repeated measures MANOVA on the curves for the photosynthetic rate, intercellular CO_2 concentration, stomatal conductance and transpiration using the light level as the repeat variable [52]. Water use efficiency (WUE) was the photosynthetic rate divided by the transpiration rate and also analyzed using a repeated measures MANOVA. Significance levels were $P \leq 0.05$. Normality was checked with the Shapiro-Wilk W test and homogeneity of variance with Bartlett's test and when necessary data was log transformed. A standard least squared ANOVA was used to show significant differences in the characteristics for each light response curve at each different CO_2 concentration and temperature combination examined. ANOVAs for most light response characteristics were significant ($P \leq 0.05$).

Characteristics examined were 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 $\mu mol \cdot m^{-2} \cdot s^{-1}$. 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 $A_{net} = 0$ $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$ 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 CO_2 concentration and temperature effects. Tukey-Kramer HSD multiple comparison tests were used to determine differences between pair wise comparisons [52].

3. Results

Ten *Juniperus* woodlands were sampled in central Texas and *D. texana* was present in the overstory of one of these communities (Table 1). The mean density of *D. texana* in that community was 16 plants/ha with the mean density of all overstory plants being 1164 plants/ha. Relative density was <1% and the relative basal area was <1%. *Juniperus* density in this same community was 715 ± 342 plants/ha and relative density of the *Juniperus* plants was 61%. Overall, there were seven overstory species in these communities (Table 1). In the understory (Table 2), *D. texana* was found in every community with an overall mean density

Table 1. Overstory species and mean ecological values for the ten communities sampled.

OVERSTORY SPECIES	% occurrence	MEAN DENSITY PLANTS/HA	SD	% DENSITY	Avg Basal area cm²/plant	Basal area m²/ha	% BASAL AREA
Juniperus ashei	100	715	±342	61	17.2	22.6	52
Quercus fusiformis	100	404	±223	35	4.4	18.8	43
Celtis laevigata	9	15	±42	1	2.8	0.3	1
Ulmus crassifolia	18	13	±28	1	0.1	<0.1	<1
Calia secundifora	18	11	±36	1	0.8	0.2	0
Diospyros texana	9	4	±12	0	6.5	1.5	3
Prosopis glandulosa	9	4	±12	0	1.2	<0.1	<1
		1164				43.4	100

of 440 ± 344 plants/ha. Relative density was 1% out of a total understory density of 38,136 ± 16,255 plants/ha. The four high density woody understory species in descending order were *Quercus fusiformis*, *Juniperus ashei*, *Mahonia trifoliolata* (agarita) and *Calia secundifora* (*formerly Sophora secundifora Texas mountain laurel). Quercus fusiformis and Juniperus ashei* made up 93% of the relative density of understory woody plants (**Table 2**).

Results of the repeated measures MANOVA of the light response curves including the main effects of temperature and [CO_2] as well as their interactions are displayed (**Table 3**, upper part). In this analysis the main effect of temperature was significant for intercellular [CO_2], transpiration rate and water use efficiency. The main effect of [CO_2] was significant for the photosynthetic rate, intercellular [CO_2] and water use efficiency (WEU). The interactions for the model including photosynthetic rate, stomatal conductance, transpiration rate and water use efficiency were not significant at the 0.05 level. Consequently, the interactions that were not significant were removed and the repeated measures MANOVAs were rerun with only the main effects (**Table 3**, lower part). Without the interaction terms, when temperature was the main effect, intercellular [CO_2], transpiration rate and water use efficiency were significant at the 0.05 level (**Table 3** lower). Examining [CO_2] as a main effect, the photosynthetic rate, stomatal conductance, intercellular CO_2 and water use efficiency were significant.

The mean repeated measures MANOVA curves of the photosynthetic rates are shown below by temperature and [CO_2] effects (**Figure 1**). The photosynthetic rates by temperature were not significantly different ($P = 0.7016$) (**Figure 1(a)**). However, as light levels increased, the photosynthetic rates increased to about 9 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$. The comparisons by [$CO_2$] were statistical difference

Table 2. Understory species and mean ecological values for the ten communities sampled.

UNDERSTORY SPECIES	% occur	MEAN DEN PLANTS/HA	SD	% DENSITY
Quercus fusiformis	100	22,891	±16,356	60
Juniperus ashei	100	12,445	±6500	33
Mahonia trifoliolata	100	1356	±1132	4
Calia secundifora	100	596	±453	2
Diospyros texana	100	440	±344	1
Juglans microcarpa	36	124	±320	<1
Celtis laevigata	45	104	±182	<1
Prosopis glandulosa	45	49	±64	<1
Eysenhardtia texana	27	33	±64	<1
Ungnadia speciosa	18	11	±24	<1
Garrya ovata	9	11	±36	<1
TOTAL		38,136	±16,255	99

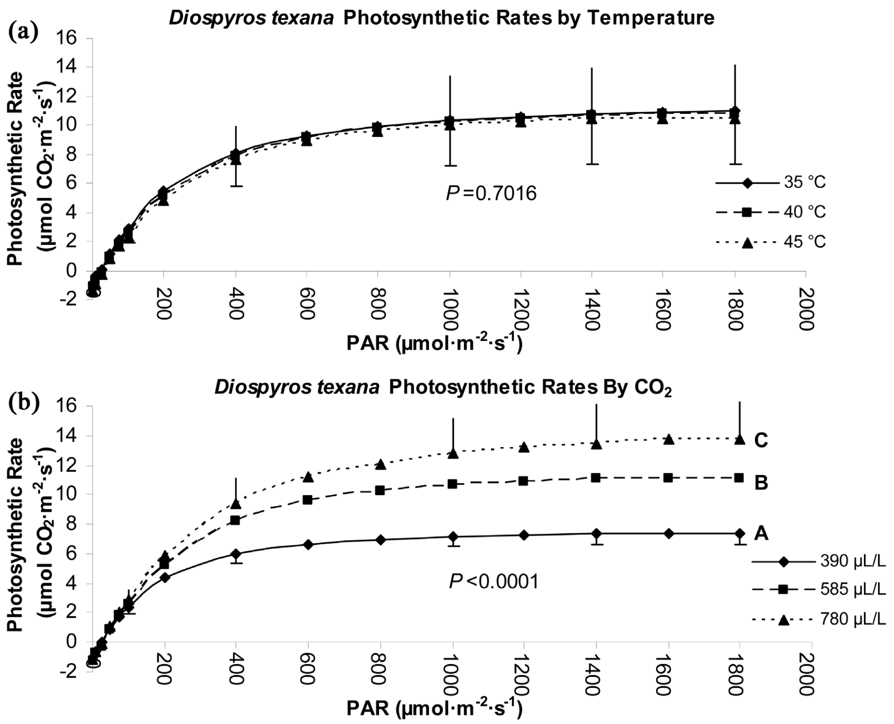

Figure 1. Mean repeated measures MANOVA for light response curves of the photosynthetic rates for *Diospyros texana* displayed by temperature (a) and CO_2 (b) treatment for main effects only. P-values are shown from the repeated measures MANOVA for the main effects (Temperature and CO_2). Like letters or no letters at the end of the curves indicate no significant difference. Data is from three replicates at three concentrations of CO_2 (390, 585 and 780 μL/L) and three temperatures (35˚C, 40˚C and 45˚C). Representative error bars are shown indicating standard deviation with the open end (|) for the upper curve and the bar end (┬) for the bottom curve.

(P < 0.0001) (**Figure 1(b)**). All of the curves increased as the light levels increased and they also increased as the [CO_2] increased. Generally, there was a greater difference (≈ 34% increase, P = 0.0001) between the ambient (390 μL/L) or low [CO_2] and the middle concentration (585 μL/L) compared to the difference between the middle concentration (585 μL/L) and the high [CO_2] (780 μL/L, ≈ 18% increase, P = 0.0498), but all were significantly different from each other.

The mean repeated measures MANOVA for the light response curves of the intercellular [CO_2] by temperature and [CO_2] effects were significant but differences were small (P = 0.0232, figures not shown). The 35˚C and 40˚C curves and the 40˚C and 45˚C were not significantly different (P = 0.0948 and P = 0.1455). The 35˚C and 45˚C curves were significantly different (P = 0.0163). The comparison by [CO_2] was also statistically different (P < 0.0001). The curves increased as the [CO_2] increased and show fairly uniform increases in maximum value between the low to middle [CO_2] of approximately 35% and the middle to high [CO_2] of approximately 24% (P < 0.0001 for both).

The mean repeated measures MANOVA for light response curves of the stomatal conductance are presented by temperature (**Figure 2(a)**) and CO_2 effects

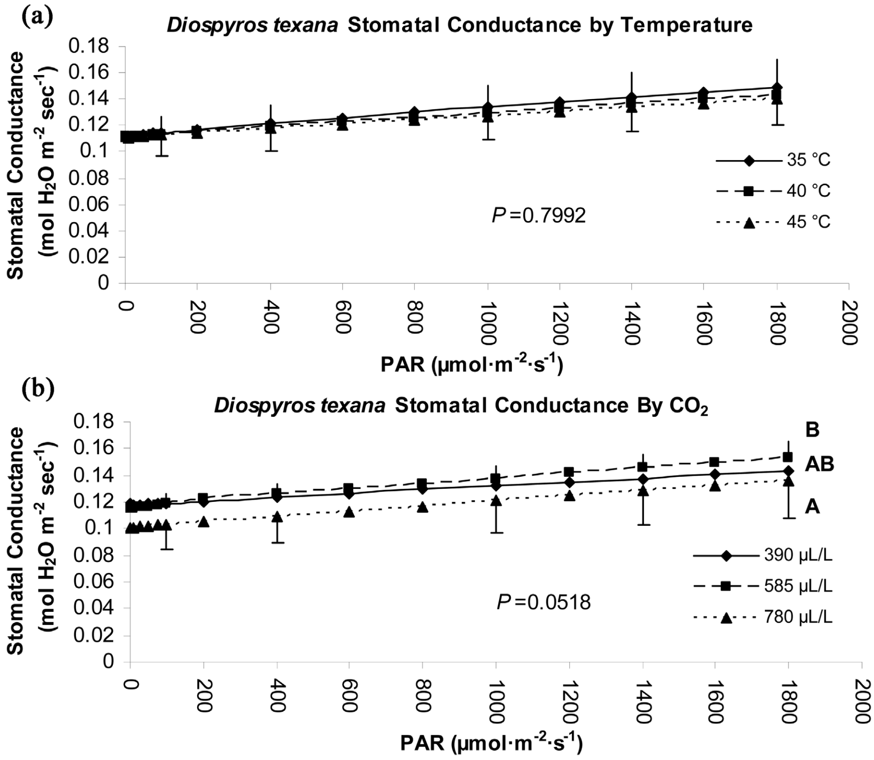

Figure 2. Mean repeated measures MANOVA light response curves of the stomatal conductance for *Diospyros texana* displayed by temperature (a) and CO_2 (b) treatments for main effects only. *P*-values are shown from the repeated measures MANOVA for the main effects (Temperature and CO_2). Like letters at the end of the curves indicate no significant difference. Data is from three replicates at three concentrations of CO_2 (390, 585 and 780 μL/L) and three temperatures (35˚C, 40˚C and 45˚C). Representative error bars are shown indicating standard deviation with the open end (|) for the upper curve and the bar end (┬) for the lowest curve.

(**Figure 2(b)**). The stomatal conductance by temperature curves were not statistical different ($P = 0.7992$) (**Figure 2(a)**). The comparison by [CO_2] was borderline significant ($P = 0.0518$) (**Figure 2(b)**). As the [CO_2] increased the stomatal conductance decreased. The ambient (390 μL/L) [CO_2] curve was not significantly different from either the middle (585 μL/L) or the high (780 μL/L) [CO_2] curve ($P = 0.4635$ and $P = 0.1040$, but the middle and high [CO_2] curves were significantly different from each other ($P = 0.0493$, **Figure 2(b)**).

The mean repeated measures MANOVA curves of the transpiration rates are shown by temperature and [CO_2] effects (**Figure 3**). The transpiration rates by temperature were significantly different ($P < 0.0001$) (**Figure 3(a)**). As the temperature increased through both of the five degree increments the transpiration rates increased uniformly by approximately 22% ($P < 0.0001$). The transpiration rate comparisons by [CO_2] were not significantly different ($P = 0.1425$) (**Figure 3(b)**), although all three curves increased as light levels increased.

The mean repeated measures MANOVA for light response curves of the calculated water use efficiencies are displayed by temperature and [CO_2] (**Figure 4**). Water use efficiency significantly increased from zero up to approximately

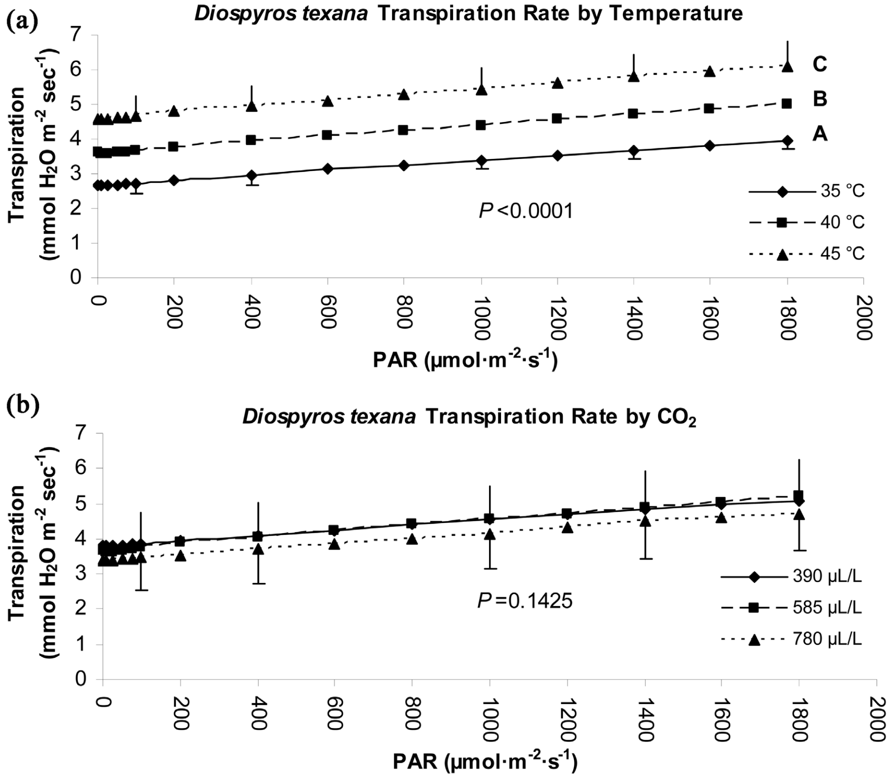

Figure 3. Mean repeated measures MANOVA for light response curves of the transpiration rates for *Diospyros texana* displayed by temperature (a) and CO_2 (b) for main effects only. *P*-values are shown from the repeated measures MANOVA for the main effects (Temperature and CO_2). Data is from three replicates at three concentrations of CO_2 (390, 585 and 780 μL/L) and three temperatures (35˚C, 40˚C and 45˚C). Representative error bars are shown indicating standard deviation with the open end (|) for the upper curve and the bar end (┬) for the lower curve.

800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and then decreased as light levels continued to increase. As the temperature increased from 35˚C to 45˚C the water use efficiency decreased ($P < 0.0001$) (**Figure 4(a)**). The 35˚C curve was significantly different from the 40˚C curve which was significantly different from the 45˚C curve. Overall, at the high temperature, water use efficiency decreased by approximately 55%. Water use efficiency was also significantly affected by [CO_2] ($P < 0.0001$) (**Figure 4(b)**). As the [CO_2] increased the water use efficiency increased. The water use efficiency showed a significant increase from the ambient [CO_2] to the middle [CO_2] (≈ 33%) and a further significant increase to the high [CO_2] for a value 23% higher with an overall increase of 56% (**Figure 4(b)**).

The standard least squared ANOVA results for the light curve parameters measured including photosynthetic maximum (A_{max}), light saturation point (L_{sp}), light compensation point (L_{cp}), dark respiration (R_d) and initial slope (*IS*) are shown below (**Table 4** upper part). The comparisons of A_{max}, L_{sp} and R_d by [CO_2] were significant, in addition, L_{cp} and R_d by temperature were also significant. However, comparisons of all of the interactions were not significant. Since the interactions were not significant the standard least squared ANOVAs were

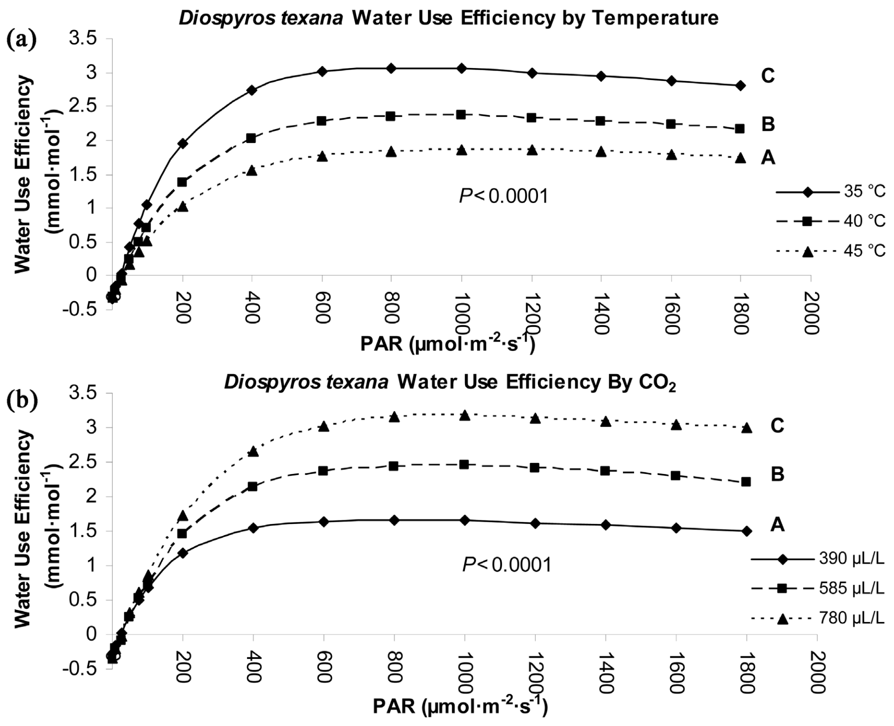

Figure 4. Mean repeated measures MANOVA curves of the water use efficiency for *Diospyros texana* displayed by temperature (a) and CO_2 (b) effects for main effects only. *P*-values are shown from the repeated measures MANOVA for the main effects (Temperature and CO_2). Data is from three replicates at three concentrations of CO_2 (390, 585 and 780 μL/L) and three temperatures (35˚C, 40˚C and 45˚C).

Table 3. Table of *P*-values for repeated measures MANOVA for *Diospyros texana* light response curves including the main effects (Temperature and CO_2) and their interaction (upper part of table). Because the interactions were not significant, they were removed and the analysis was redone (lower part of table). Data is from three replicates at three concentrations of CO_2 (390, 585 and 780 μL/L) and three temperatures (35, 40 and 45˚C). Bolded measurements were significant at $P < 0.05$.

	Photosynthetic Rate	Stomatal Conductance	Intercellular CO_2	Transpiration Rate	WUE
With Interaction					
Temperature	0.7473	0.8105	0.0092	<0.0001	<0.0001
CO_2	<0.0001	0.0653	<0.0001	0.1895	<0.0001
Interaction	0.9989	0.6262	0.0442	0.9263	0.8018
Without Interaction					
Temperature	0.7016	0.7992	0.0232	<0.0001	<0.0001
CO_2	<0.0001	0.0518	<0.0001	0.1425	<0.0001

rerun with only the main effects (Table 4 lower part). Without the interaction term, the same comparisons of A_{max}, L_{sp} and R_d by [CO_2] and the comparison of L_{cp} and R_d by temperature were also found to be significant (Table 4 lower part).

The maximum photosynthetic rate (A_{max}) did not change with temperature (*P*

= 0.8993) while it did increase significantly with [CO_2] ($P < 0.0001$) (**Table 4**). Temperature had little effect on the mean A_{max} with values of 10.80, 10.66 and 10.40 $\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$ with a standard error of approximately 0.62. Tukey comparisons of the [CO_2] effect showed significant differences between each concentration. The [CO_2] increased the A_{max} from 7.29 $\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$ for the ambient [CO_2] to 10.98 $\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$ for the middle [CO_2] and to 13.59 $\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$ for the high [CO_2]. This was an A_{max} increase of approximately 34% from the low to medium [CO_2] and another 19% increase from medium to high [CO_2] giving an overall increase of approximately 46%. The interaction term was not significant ($P = 0.9997$). The A_{max} nid not change with temperature treatment but as the [CO_2] increased the A_{max} increased, but not temperature dependently.

The light saturation point (L_{sp}) was not significantly different by temperature ($P = 0.6289$). The mean L_{sp} for the three temperatures tested were 310.8, 317.2 and 302.6 $\mu mol \cdot m^{-2} \cdot s^{-1}$ with a standard error of 10.6 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The [$CO_2$] had a significant effect on L_{sp} ($P < 0.0001$). The Tukey comparisons showed significant differences between the mean ambient [CO_2] L_{sp} (237.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and the middle [$CO_2$] L_{sp} (322.3 $\mu mol \cdot m^{-2} \cdot s^{-1}$) as well as a significant difference between the middle and the high [CO_2] L_{sp} (370.8 $\mu mol \cdot m^{-2} \cdot s^{-1}$). A significant difference was demonstrated between the low and the high [CO_2] when the L_{sp} increased by approximately 36%. The interaction term was not significant ($P = 0.8489$). The L_{sp} did not change as the temperature and [CO_2] increased.

The light compensation point (L_{cp}) showed a significant difference by temperature but not [CO_2] ($P = 0.0033$ and $P = 0.2467$). The 35˚C L_{cp} (22.0 $\mu mol \cdot m^{-2} \cdot s^{-1}$) was significantly different than both the 40˚C L_{cp} (30.0 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and the 45˚C L_{cp} (33.3 $\mu mol \cdot m^{-2} \cdot s^{-1}$), but not between the 40 and 45˚C L_{cp}. The [CO_2] did not show a trend with L_{cp} (26.8, 31.4 and 27.0 $\mu mol \cdot m^{-2} \cdot s^{-1} \pm 2.1$ $\mu mol \cdot m^{-2} \cdot s^{-1}$) with increasing [$CO_2$] (390, 585 and 780 µL/L respectively) ($P = 0.2467$). In addition, the interaction term was not significant ($P = 0.9674$).

Table 4. Table of P-values for Standard Least Squared ANOVAs for *Diospyros texana* photosynthetic characteristics including the main effects (Temperature and CO_2) and their interaction (upper part). Analysis was also rerun after the interaction term was removed (lower part). Data is from three replicates at three concentrations of CO_2 (390, 585 and 780 µL/L) and three temperatures (35˚C, 40˚C and 45˚C).

	A_{max}	L_{sp}	L_{cp}	R_d	IS
With Interaction					
Temperature	0.9166	0.6655	0.0083	0.0002	0.9344
CO_2	<0.0001	<0.0001	0.3082	0.0222	0.3196
Temp × CO_2	0.9997	0.8489	0.9674	0.9767	0.9830
Without Interaction					
Temperature	0.8993	0.6289	0.0033	<0.0001	0.9220
CO_2	<0.0001	<0.0001	0.2467	0.0104	0.2548

The dark respiration rate (R_d) increased significantly (0.81, 1.06 and 1.26 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ ± 0.054 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) as the temperature increased from 35, 40 and 45˚C respectively ($P < 0.0001$). The effect of CO_2 concentration was also significant ($P = 0.0104$). The ambient R_d (0.92 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) was significantly different from the medium [CO_2] at an R_d rate of 1.17 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ while the effect of the high [CO_2] on the R_d rate (1.04 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) was not significantly different from either the ambient or medium [CO_2]. The interaction term was not significant ($P = 0.9767$) while the R_d increased with temperature the response to [CO_2] was independent of temperature.

The temperature increases did not have a statistically significant effect on the *IS* (0.038, 0.037 and 0.038 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$/μmol·$m^{-2} \cdot s^{-1}$ ($P = 0.9220$) and the variation was small. As with temperature, an elevated CO_2 concentration did not have a significant effect on the *IS* (0.035, 0.038 and 0.040 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$/μmol·$m^{-2} \cdot s^{-1}$) ($P = 0.2548$). The interaction term was not significant either ($P = 0.9830$).

When light levels for *D. texana* were held constant at 700 μmol·$m^{-2} \cdot s^{-1}$ and the [CO_2] varied from 50 μL/L to 1200 μL/L with three temperatures tested (35˚C, 40˚C and 45˚C), there was not a significant effect of temperature on the photosynthetic response ($P = 0.9961$) (**Figure 5(a)**). The curves showing photosynthetic rate exhibit a fairly linear increase from the [CO_2] of 50 μL/L to 1200 μL/L. The maximum photosynthetic rate was approximately 13 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (**Figure 5(a)**). The CO_2 intercellular CO_2 response curves by temperature were not significantly different ($P = 0.2408$) and showed little variation from each other (**Figure 5(b)**). The intercellular CO_2 response curves show a fairly linear trend which increases from a low of approximately 60 μmol CO_2·mol·air^{-1} to a high of approximately 900 μmol CO_2·mol·air^{-1}. The intercellular [CO_2] was always lower than the external [CO_2].

The stomatal conductance and transpiration curves showed similar responses to changes in [CO_2] (**Figure 5(c)** and **Figure 5(d)**). The stomatal conductance curves were very similar in value for all three temperatures ($P = 0.4507$). The stomatal conductance had a linear relationship and maintained values of approximately 0.12 mol H_2O $m^{-2} \cdot s^{-1}$ over the entire range of [CO_2] tested (**Figure 5(c)**). Stomatal conductance did not respond to [CO_2] changes but decreased as the temperature increased but not significantly ($P = 0.4507$).

The transpiration rate was significantly difference by temperature ($P = 0.0392$) (**Figure 5(d)**). The 35˚C transpiration rate (3.0 mmolH_2O $m^{-2} \cdot s^{-1}$) was significantly different than the 45˚C transpiration rate (4.7 mmolH_2O $m^{-2} \cdot s^{-1}$), but the 40˚C transpiration rate (3.9 mmolH_2O $m^{-2} \cdot s^{-1}$) was not different from either the 35˚C or the 45˚C transpiration rates and there was little variation.

The repeated measures MANOVA of the calculated photosynthetic rate as a function of [CO_2] for water use efficiency was significant by temperature ($P = 0.0321$) (**Figure 6**). The curves increased from a low of approximately -0.24 mmol·mol^{-1} at 50 μLCO_2/L air to a high value of approximately 4.2 mmol·mol^{-1} at 1200 μLCO_2 /L air. The 40˚C curve was not significantly different from either

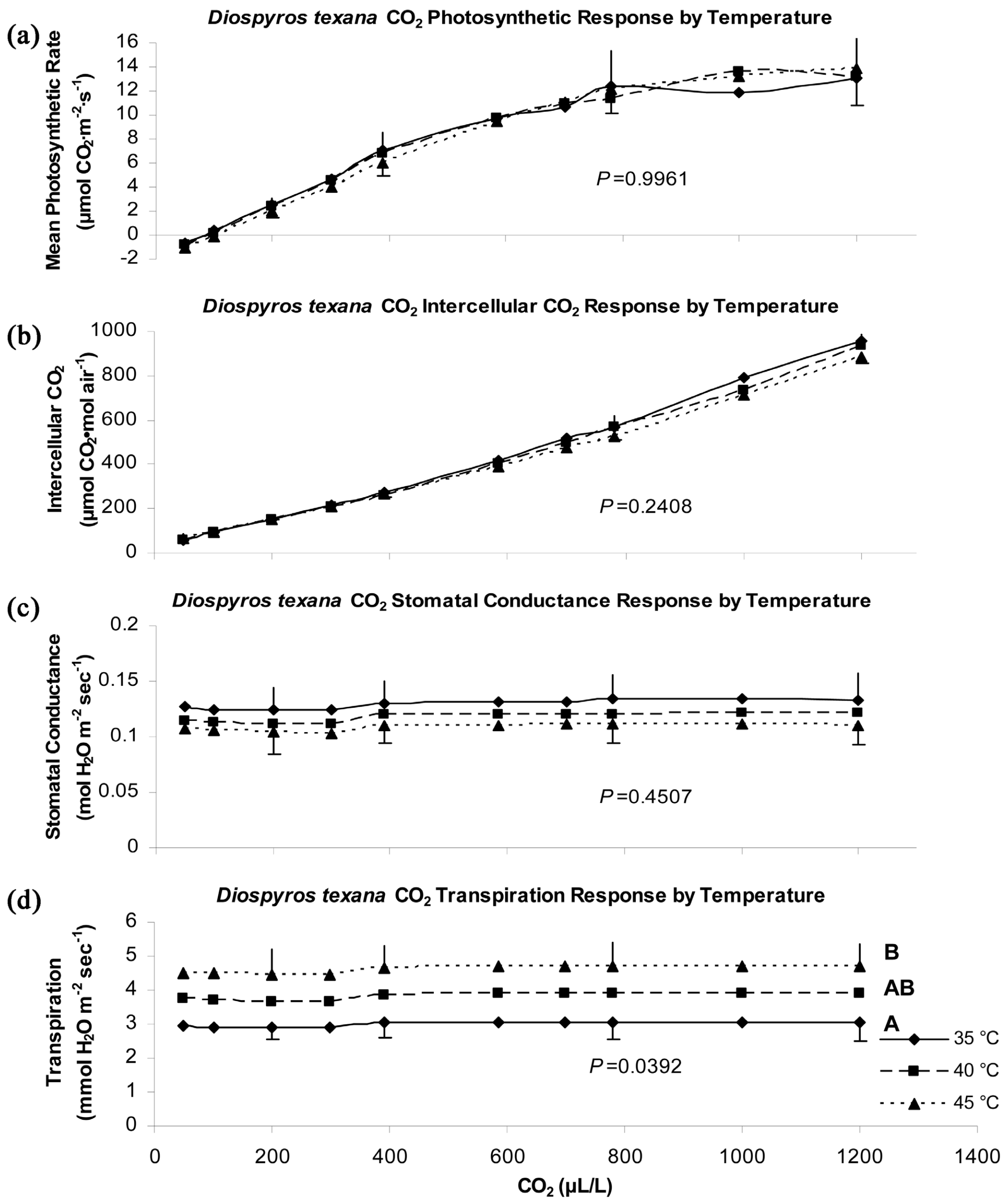

Figure 5. Repeated measures CO_2 response curves for three replicates of *Diospyros texana* at a light level of and three temperatures (35˚C, 40˚C and 45˚C). Representative error bars are shown indicating standard deviation with the open end (|) for the upper curve and the bar end (┬) for the lower most curve. Like letters at the end of the curves indicate no significant difference.

the 35˚C or the 45˚C curves. The 35˚C curve was significantly different from the 45˚C curve (Figure 6).

4. Discussion

One species in the *Ebenaceae family*, *Diospyros texana* is found in central Texas. It is present in various mixed woodlands from central Texas west to New Mexico and south into northern Mexico. It is considered part of the "brush problem" that exists in former Texas grasslands and many other areas because of

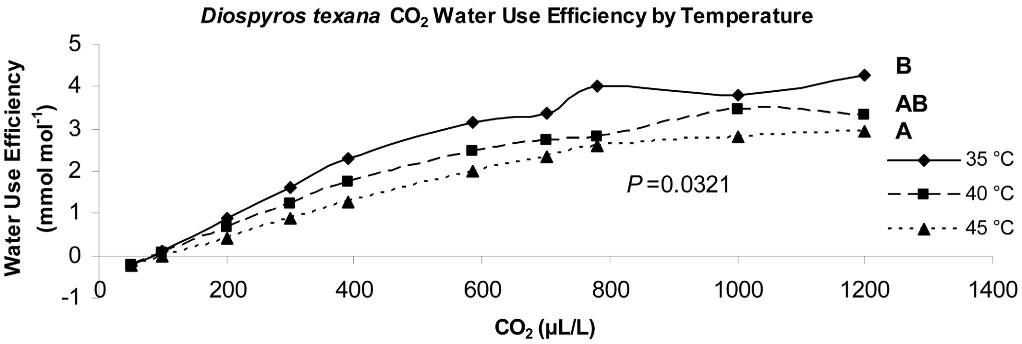

Figure 6. Repeated measures CO_2 response curves of the calculated water use efficiency for three replicates of *Diospyros texana* at a light level of 700 μmol·m^{-2}·s^{-1} and three temperatures (35˚C, 40˚C and 45˚C). Like letters at the end of the curves indicate no significant difference.

overgrazing and lack of fire [12] [53]. It is a fairly common species in central Texas riparian communities and upland woodland communities [3] [34] [54]. It occurs with *Quercus virginiana* (live oak), *Celtis laevigata* (hackberry or sugarberry), *Carya illinoensis* (pecan), *Ulmus crassifolia* (cedar elm) and a few other species in riparian woodlands. In uplands it is found with *J. ashei* (ashe juniper), *Q. fusiformis* (live oal), *C. laevigata* (hackberry or sugarberry), *U. crassifolia* (cedar elm), *Calia secundifora* (Texas mountain laurel) and others [3]. Many species of mammals and some birds use *D. texana* fruit as a source of food but foliage is only browsed lightly [53]. In addition, juveniles have been reported as being shade tolerant [55].

In the present study, we examined ambient and elevated light levels, atmospheric CO_2 levels and associated higher temperatures on *D. texana* gas exchange responses. Our interest was to measure gas exchange rates and to demonstrate that *D. texana* could exist in the understory shade of various species at ambient and elevated levels of light, CO_2 and temperature. Measurements will be compared with other studies [24] [41] [42] [43] [56]. The current study demonstrates that *D. texana* is a species that can grow in both canopy shade and full sun [50] [57].

Species that grow well in full sun have a high maximum photosynthetic rate (A_{max}), light saturation point (L_{sp}), light compensation point (L_{cp}) and dark respiration rates (R_d). *Diospyros texana* has a relatively high A_{max} value at ambient and at elevated CO_2 levels, increasing by 52% (13.5 μmolCO_2 · m^{-2} · s^{-1}) from ambient to the highest level of CO_2 tested (780 μL·L^{-1}). In addition, the L_{sp}, L_{cp}, and R_d, were high which indicates *D. texana* it is more of a sun species but not a shade intolerant species and it will remain so in an elevated CO_2 world. Even In shade A_{net} did not change with temperature. *Diospyros texana* A_{max} values were not altered significantly with elevated temperature but did increase significantly when CO_2 levels were increased. In shade the A_{net} only increased slightly. The light saturation point (L_{sp}) did not change significantly with temperature but did increase significantly with elevated levels of CO_2 which tracks the values of the A_{max}. The light compensation was not significantly affected by elevated levels of

CO_2 but almost doubled at the highest temperature *D. texana* leaves were exposed to. This was due to increased metabolism at the higher exposure temperature [8] [57].

In spite of having reasonably high photosynthetic rates at low or high levels of light and CO_2, *D. texana* was not recruited into a canopy of *J. ashei* or other species [3]. The reason for lack of recruitment does not appear related to gas exchange rates. However, over the past century, there has been a large increase in the overall number of large native herbivores (Odocoileus virginianus Zimmerman [white-tailed deer]) in central Texas [58] [59]. Increases in the number of large herbivores have been linked to alterations to the local plant community composition all over the world [59]-[68]. Almost all woody species in the study area are susceptible to juvenile herbivory and populations seem to have a minimal number or no juveniles for recruiting except for *J. ashei [3]*. This lack of recruitment has been demonstrated for most *Quercus sp*. and other species in woodlands throughout North America [4] [7] [59] [60] [62] and does not seem to be caused by low or altered gas exchange rates.

Juniperus woodlands appear to be successional communities [3] [5] [8] [40] [67] [68] [69]. In the eastern North American deciduous forests, *Juniperus* plants are often found in gaps, blow downs or on shallow soil in glades [70]. In western North America, *Juniperus* tends to occur above the desert communities and above the arid or semiarid grasslands, but usually below the higher-elevation pine, spruce, or fir forests [5] [7] [67]. In central Texas, *J. ashei* establishes on hillsides and in over grazed, former grasslands on shallow soil [71] [21].

Over the past century, plant communities have been changed through the increased browsing pressure from large herbivores as well as the suppression of grassland fires [3]. In the future this will be further complicated by the increasing air temperatures and CO_2 concentrations [8] [11] [72] [73] [74] [75]. Some species will be able to take advantage of the new conditions and expand their numbers, while other species lose competitive advantage and decline in number potentially resulting in different and new dominant species and community structure. We expect these central Texas *Juniperus/Quercus* woodlands will be affected by future shifts in atmospheric CO_2 concentration and temperatures, and *D. texana* will become a more important species in these communities.

5. Conclusion

Based off our study results, we believe *J. ashei* will gain some competitive advantages in the higher light levels of the open woodland canopy gaps with higher future CO_2 concentrations which should allow it to encroach and better able to establish in those former grassland areas. But below the canopy in the lower light levels, *J. ashei* will not maintain the same advantages, which means it possibly will be replaced by other more shade tolerant species such as *D. texana*. Studying community dynamics and predicting future community composition has always been a challenging mission but with the added complications of forecasted environmental changes this has become an even more enigmatic puzzle to tease apart.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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