Comparative Gas Exchange of *Ulmus crassifolia* (Cedar Elm, Ulmaceae) and *Ungnadia speciosa* (Mexican Buckey, Sapindaceae) at Ambient and Elevated Levels of Light, CO₂ and Temperature

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Abstract

Ulmus crassifolia Nutt. (Cedar elm, Ulmaceae) is a tree found in central and east Texas, northern Mexico, east to Florida, and north to southern Missouri and Oklahoma. *Ungnadia speciosa* Endl. (Mexican-buckeye, Sapindaceae) is a shrub or small tree found in woodlands and savannas of central and western Texas, southern New Mexico and northern Mexico. In central Texas, both species are found in *Juniperus ashei/Quercus virginiana* woodlands or savannas or also at low density in inter-canopy grassland gaps or patches. Environmental conditions in this area are stressful because of shallow soils, high summer temperatures, and inconsistent low rainfall. Currently, both species have a low density in these areas, and *Ulmus crassifolia* is usually a tree, while *Ungnadia speciosa* is a woody understory shrub. This study suggests *U. crassifolia* and *U. speciosa* are tolerant or intermediate species, with juveniles starting in shade. 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 for both species, but not when temperatures were elevated. Stomatal conductance decreased when the CO₂ concentration doubled, but there were few effects from elevated temperature. These findings suggest that *U. speciosa* and *U. crassifolia* should be more common and imply that they will have a higher density in a future high CO₂ environment.

Keywords

Light Response, Gas Exchange, Photosynthesis, Respiration, Water Use Efficiency

1. Introduction

Plant communities around the world have changed many times historically and will continue changing in the future [1] [2]. Woodlands and savannas in central Texas are composed of communities with various densities of *Juniperus ashei* Buch. and *Quercus virginiana* Mill. (Ashe juniper and hill country live oak) [3] [4] [5] [6] [7]. These central Texas *Juniperus* woodlands are an example of Juniperus woodlands from all over the world (7) but contain specific species and sometimes species with very limited distributions (4). The structure of these communities in a future high-CO_2 and high-temperature world is unknown. There are various understory woody species in these communities 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) [3] [5] [6] [7] [8]. Most of the understory species have received little ecological or environmental study.

We have not found anything in the literature regarding the current level of atmospheric CO_2 if it is in limited supply or excess in these central Texas *Juniperus* woodlands. In some plant communities, CO_2 concentration has been shown to be limiting and increasing levels promoted higher photosynthetic uptake and growth in the species present (8). However, we have not seen any work showing the effects of elevated CO_2, temperature and light levels in any *Juniperus* woodland communities, which is the focus of the present study and work presented.

Woodlands with various *Juniperus* species are found in many parts of North America, with elevation, climate and species composition varying [6]-[18]. In North America, these woodlands are found from the Atlantic to the Pacific coasts through the Great Plains to the low and mid-elevations of the mountains of the western United States, Canada and Mexico [14] [19] [20] [21] [22] [23]. In past times, in central and western North America, they were more commonly along canyon walls or steep slopes protected from fire or where there was not enough fuel for a fire [24] [25] [26].

Juniperus communities today are widespread and have been treated by many as stable communities [6] [11] [13] [14] [17] [18] [21] [22] [23] [24]. However, various studies of encroachment have suggested they are pioneer successional communities leading to various forests [6] [27] [28]. Over time, the area covered and species composition of these communities will continue to transform, but their future composition and structure are unknown [29] [30] [31] [32].

In the past 15,000 - 20,000 years, changes in the composition and distribution of plant communities have been mainly due to climate warming and glacial retreat [33]. More recently, in the past 200 - 500 years, changes in many North American plant communities were caused by the introduction of large populations of domestic ungulates, with constant grass herbivory and decreased fire

frequency [34] [35] [36] [37]. Conditions resulted in the formation of *Juniperus/Quercus* savannas and woodlands in many places. Other environmental conditions appeared secondary [7] [38]-[44]. Future community composition will most likely be influenced by elevated atmospheric CO_2 and temperature [33].

Canopy density can be highly variable in *Juniperus* communities, with a canopy cover of 40% to 90% [3] [6] [45]. Most of these communities have open patches with shallow soils populated by juvenile woody species, some grasses and other herbaceous species [46]-[51]. There are many low-density woody species in these communities, but it is unknown if some could become part of the canopy in the future.

In the future, these woodlands may remain dominated by a few species or the *Juniperus* species may be replaced by other species from below the canopy, changing to another community type. The pattern is controlled by the interaction of species, surface light, soil resources, herbivory, and fire [6] [27] [28] [31] [52] [53]. Due to modifications of climactic variables, the structure of many of these woodlands will change, and the composition of the future communities is unknown. These changing factors include atmospheric CO_2 and temperature, which are expected to continue increasing into the foreseeable future [33]. These central Texas *Juniperus* woodlands are an example of *Juniperus* woodlands that are present across the globe, but species here are different and some are quite rare [5]. Ecological success or competitive success of the low-density species found in these woodlands has never been examined [7].

We hypothesize that the central Texas *Juniperus/Quercus* plant communities are changing. In addition, we theorize that certain understory species will become future canopy species. We envision that atmospheric CO_2 and temperature will be the driving forces. In the present study, we tested the short-term gas exchange response of *Ungnadia speciosa* and *Ulmus crassifolia,* two low-density and low-biomass understory species, to ambient and increased levels of light, CO_2, and temperature to project their future community composition.

2. Materials and Methods

The study site is in central Texas and is part of the University of Texas at San Antonio campus. Topography is rolling with slopes between 4.5˚ and 13.5˚ [54] and soils are clayey-skeletal, smectitic, thermic lithic calciustolls [55] in the Tarrant association with surface horizons between 0 and 25 cm thick [54]. The subsurface is heavily fractured limestone over limestone bedrock. Climate is subtropical-subhumid [56] with a mean annual temperature of 20˚C and ranges between 9.6˚C in January and 29.4˚C in July [57]. Precipitation is 78.7 cm/yr and bimodal, with peaks in May (10.7 cm) and September (8.7 cm) [57]. Precipitation is highly variable with very little reported in June and July with peaks in May and September. No domestic livestock were present in the study area for the past 75 years. There are large areas of *Juniperus ashei*/*Quercus virginiana* woodlands or savannas on former grassland sites which is considered represent-

ative of similar communities found in this region [3].

Plants in the understory of mature relatively undisturbed *J. ashei/Q. virginiana* woodland communities were randomly selected for study. Mean structure of the communities was determined but limited information about structure is presented here (see [8] [58]). All trees were identified, counted and measured. Concise but succinct information about community structure is presented below. Gas exchange measurements were made in the summer of 2007. Three plants were randomly selected for gas exchange responses at both ambient and elevated levels of CO_2 and temperature. Mature, non-damaged leaves were selected at breast height (approximately 137 cm above the soil surface) on each plant. Steady state photosynthetic light response curves (A_{net} vs. PAR) were completed [60]. Photosynthetic response curves were measured on fully expanded leaves at mid-day (1000 - 1400 hrs) when relative humidity had stabilized [60]. Replicates were one fully expanded leaf per plant that was placed into the cuvette of a portable photosynthetic meter (LICOR® LI-6400). A leaf covered the entire chamber (2 × 3 cm) and was attached to the plant. Measurements made and recorded were: A_{net} (net photosynthesis = μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$), C_i (intercellular [CO_2] = μmol $CO_2 \cdot mol \cdot air^{-1}$), T_{leaf} (chamber leaf temperature = ˚C), T_{air} (air temperature outside the chamber = ˚C), PAR (photosynthetic active radiation = μmol·m^{-2}·s^{-1}), g (stomatal conductance = mol·H_2O·m^{-2}·s^{-1}) and E (transpiration = mmol·H_2O·m^{-2}s^{-1}).

The chamber was used to mimic varying degrees of environmental modifications. The light level, CO_2 concentration, and temperature were manipulated. Relative humidity was kept at 30% - 40% and the gas flow rate was set at 400 μmol/s. Coefficient of variation stabilized (<1%) before recording and moving to the next setting. Light levels started at 1800 μmol·m^{-2}·s^{-1} and decreased to 1600, 1400, 1200, 1000, 800, 600, 400, 200, 100, 75, 50, 25, 10, 5 and finally 0 μmol·m^{-2}·s^{-1}. Light curves and CO_2 response curves were measured for different combinations of the leaf chamber CO_2 and temperature environments.

The leaf chamber was set at 2007 CO_2 levels (390 μL·L^{-1}) and a 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 CO_2 constant while raising the chamber temperature to 40˚C and then to 45˚C. Next, the leaf chamber CO_2 was raised to 1.5 times the 2007 CO_2 levels to 585 μL·L^{-1}. Light curves were completed at a temperature of 35˚C, 40˚C and 45˚C. This process was then repeated with the leaf chamber CO_2 level set at twice the ambient level at 780 μL·L^{-1}. Lastly, CO_2 response curves were measured at a canopy shade light level (700 μmol·m^{-2}·s^{-1}). Measurements were made at 35˚C, 40˚C and 45˚C.

Microsoft Excel© and JMP© IN 5.1 were used for data organization and analysis. The JMP© IN 5.1 software measured significant differences using a repeated measures MANOVA on the photosynthetic rate curves, intercellular CO_2 concentrations, stomatal conductance and transpiration using the light level, PAR,

as the repeat variable [61]. 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 $P \leq 0.05$. Normality was checked with the Shapiro-Wilk W test and homogeneity of variance with Bartlett's test and log transformed as necessary. A standard least squared ANOVA was used to detect significant differences in each curve at each CO_2 concentration and temperature combination. However, this is a curve to curve comparison and individual CO_2 uptake was not compared at individual light levels on each plant and each replication.

Other measurements were derived from Excel® plots of the LICOR® LI-6400 measurements. These included 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 quantum yield ($\Phi$) was the linear initial slope 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_{sp}) 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 [61].

3. Results

Before gas exchange measurements were started, structure of the communities was examined [8]. Communities were simple with two major overstory species, but all the trees were identified, counted and measured. *Juniperus ashei* and *Quercus virginiana* were present in every community examined (Relative Occurrence = 100%). Relative *J. ashei* canopy density of was 61% ± 12% (mean ± standard deviation). Relative *Q. virginiana* canopy density of was 36% ± 6%. Low density community species included *Diospyros texana* (Texas persimmon), *Celtis laevigata* (sugarberry or hackberry), *Ulmus crassifolia* (cedar elm), *Prosopis glandulosa* (mesquite), *Sophora secundiflora* (Texas mountain laurel) and *Ungnadia speciosa* (Mexican buckeye) with relative densities of 0.06% - 1.8%. The two species examined in this study had low relative occurrence, low density and low relative density. *Ulmus crassifolia* relative occurrence was 38% with density and relative density at 175 plants/ha and 0.5% respectively. Relative occurrence of *U. speciosa* was 25% with density and relative density at 15 plants/ha and 0.06%, respectively.

Comparisons of light curve results examining the main effects of CO_2 concentration and temperature were made for both species. Interactions were not significant and removed from the models (Table 1). For *Ulmus crassifolia,* there were no significant temperature effects on photosynthetic rates, conduction or

internal [CO_2] concentrations (Table 1 upper). Temperature only had a significant effect on the transpiration rate and water use efficiency (WUE). For CO_2 there were significant effects on response variables including photosynthetic rate, stomatal conductance, intercellular CO_2 concentration, and WUE. Transpiration rate was not significantly affected by CO_2 (Table 1 upper). For *Ungnadia speciosa,* there were no significant temperature effects (repeated measures MANOVAs Table 1 lower). However, CO_2 had significant effects on photosynthetic rates, conduction, internal [CO_2] levels, and WUE (Table 1 lower). The CO_2 had no significant effect on the transpiration rate.

The mean curves of the photosynthetic rates for *U. crassifolia* are shown by temperature and CO_2 effects (Figure 1(a) and Figure 1(c)). Photosynthetic rates compared by temperature were not significantly different (MANOVA, *P* = 0.1873) (Figure 1(a)). However, photosynthetic rates increased to a plateau of approximately 7.4 - 8.9 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ as light levels increased. The comparisons by CO_2 concentration were statistically significant between the curves (repeated measures MANOVA, *P* = 0.0002) (Figure 1(c)). The curves increased as the light levels increased and as the CO_2 concentration increased. The ambient (390 μL·L^{-1}) or low CO_2 concentration was significantly different from both the middle (585 μL·L^{-1}) and the high (780 μL·L^{-1}) CO_2 concentration (*P* = 0.0033 and *P* = 0.0009). Between the ambient CO_2 concentration (390 μL·L^{-1}) and the middle CO_2 concentration the plateau photosynthetic rate increased approximately 27% from 5.9 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ to 8.1 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ while between the low and the high CO_2 concentration the plateau rate increased approximately 45% to 10.8 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (Figure 1(c)).

The mean curves of the photosynthetic rates for *U. speciosa* are shown by temperature and CO_2 effects (Figure 1(b) and Figure 1(d)). Photosynthetic rates compared by temperature were not significantly different (MANOVA, *P* = 0.8856) (Figure 1(b)). Rates reached a plateau of approximately 8.5 μmol

Table 1. Table includes *P*-values for repeated measures MANOVAs of gas exchange measurements for *Ulmus crassifolia* (upper) and *Ungnadia speciosa* (lower) comparing the main effects of temperature and CO_2 at 16 light levels (interactions were not significant and removed from the models). Data is from three replicates at three CO_2 concentrations (390, 585 and 780 μL·L^{-1}) and three temperatures (35°C, 40°C and 45°C). Bold entries are significant.

P-values for *Ulmus crassifolia*					
Main effects	Photo. Rate	Conduction	[CO_2]	Transpir.	WUE
Temperature	0.1873	0.6053	0.6309	**0.0275**	**0.0004**
CO_2	**<0.0002**	**0.0374**	**<0.0001**	0.0763	**<0.0001**

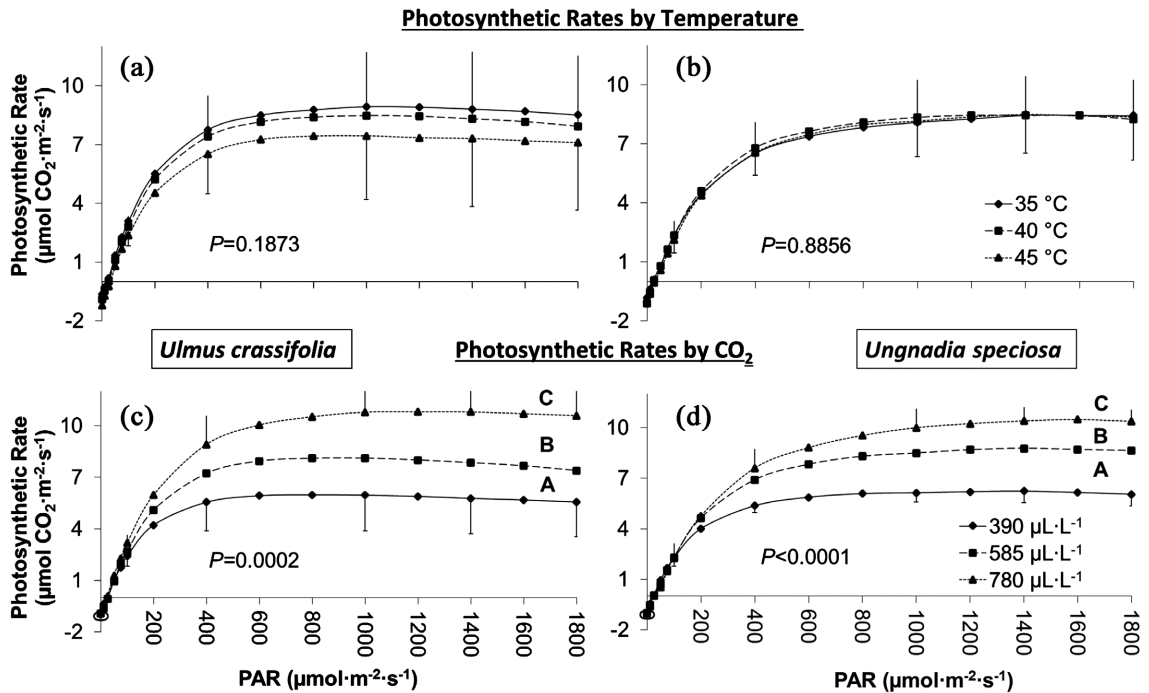| *P*-values for *Ungnadia speciosa*					
Main effects	Photo. Rate	*Conduction*	[CO_2]	Transpir.	WUE
Temperature	0.8856	0.9565	0.9503	0.1469	0.1465
CO_2	**<0.0001**	**0.0479**	**<0.0001**	0.2371	**0.0002**

Photosynthetic Rates by Temperature

Figure 1. Presented are repeated measures MANOVA curves for treatments of main effects on photosynthetic rates for *Ulmus crassifolia* displayed by temperature (a) and CO_2 concentration (c) and *Ungnadia speciosa* displayed by temperature (b) and CO_2 concentration (d). *P*-values are shown from the repeated measures MANOVAs. No letters or like letters at the end of the curves indicate no significant difference. There were three concentrations of CO_2 (390, 585 and 780 $\mu L \cdot L^{-1}$) and three temperatures (35˚C, 40˚C and 45˚C). Error bars are shown indicating standard deviation with the open end (|) for the upper most curve and the bar end (⊤) for the lower curve.

$CO_2 \cdot m^{-2} \cdot s^{-1}$. The comparisons by CO_2 concentration were statistically significant between the curves (repeated measures MANOVA, $P < 0.0001$) (Figure 1(d)). The curves increased as the light levels increased and as the CO_2 concentration increased. Each level of CO_2 concentration was significantly different from the other. The approximate photosynthetic rate at the plateau and lower CO_2 concentration was 6.2 $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$ and then increased to 8.7% or 29% and 10.4 or 40% $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$ at the highest level of CO_2 used.

The mean curves of the water use efficiency (WUE) for *U. crassifolia* are shown by temperature and CO_2 effects (Figure 2(a) and Figure 2(c)). Water use efficiency was significantly different when compared by temperature (MANOVA, $P = 0.0004$) (Figure 2(a)). Water use efficiency values decreased from a plateau of approximately 4.0 $mmol \cdot mol^{-1}$ to approximately 2.4 $mmol \cdot mol^{-1}$ as temperature increased or by a total of 40%. The comparisons by CO_2 concentration were also statistically significant between the curves (repeated measures MANOVA, $P < 0.0001$) (Figure 2(c)). The curves generally increased as the light levels increased and as the CO_2 concentration increased. At the ambient (390 $\mu L \cdot L^{-1}$) or low CO_2 concentration the WUE value was lowest at approximately 1.9 $mmol \cdot mol^{-1}$ (Figure 2(c)). At the highest CO_2 concentration, the WUE value increased approximately 57% to a value of approximately 4.4 $mmol \cdot mol^{-1}$.
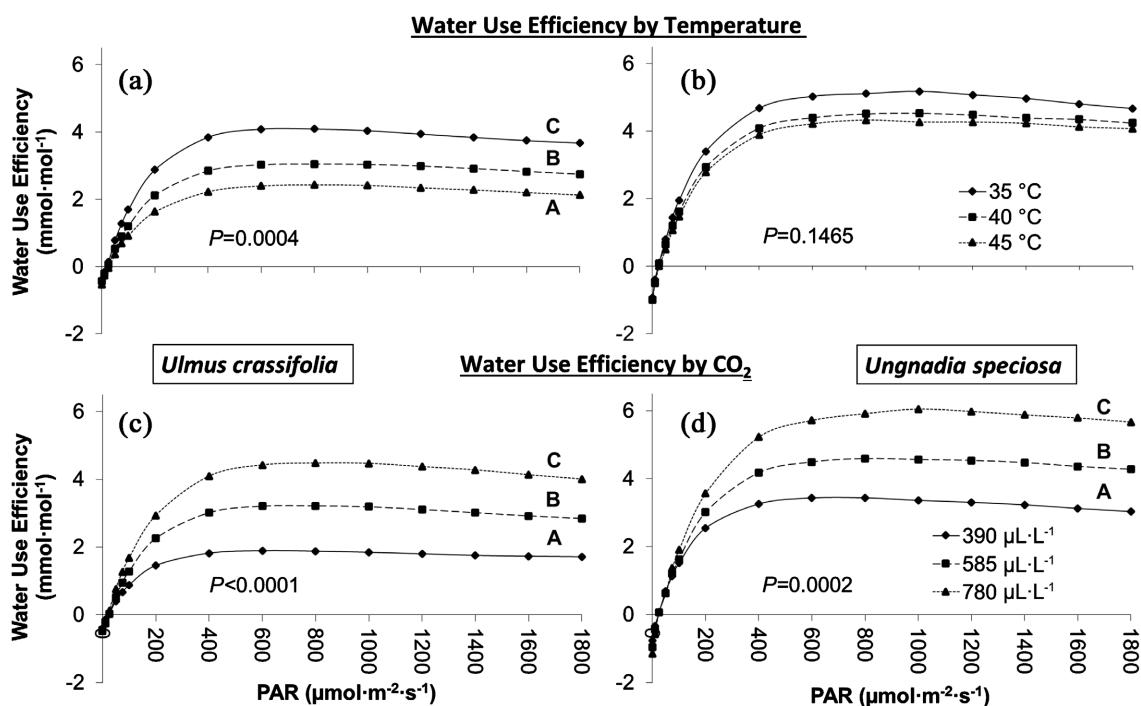
Figure 2. Presented are repeated measures MANOVA curves of main effects on water use efficiency for *Ulmus crassifolia* displayed by temperature (a) and CO_2 concentration (c) and *Ungnadia speciosa* displayed by temperature (b) and CO_2 concentration (d). *P*-values are shown from the repeated measures MANOVAs. No letters or like letters at the end of the curves indicate no significant difference. There were three concentrations of CO_2 (390, 585 and 780 $\mu L \cdot L^{-1}$) and three temperatures (35˚C, 40˚C and 45˚C).

The mean curves of the water use efficiency (WUE) for *U. speciosa* are shown by temperature and CO_2 effects (**Figure 2(b)** and **Figure 2(d)**). Water use efficiency was not significantly different when compared by temperature (MANOVA, *P* = 0.1465) (**Figure 2(b)**). The water use efficiency value was approximately 4.2 - 5.1 mmol·mol^{-1}. There were statistically significant differences between CO_2 treatments (repeated measures MANOVA, *P* = 0.0002) (**Figure 2(d)**). The curves generally increased as the light levels increased and as the CO_2 concentration increased. At the ambient (390 $\mu L \cdot L^{-1}$) or low CO_2 concentration the WUE value was the lowest around approximately 3.4 mmol·mol^{-1} while increasing approximately 42% to a value of 5.9 mmol·mol^{-1} at the highest CO_2 concentration (**Figure 2(d)**).

Measured light curve parameters including photosynthetic maximum (A_{max}), light saturation point (L_{sp}), light compensation point (L_{cp}), dark respiration (R_d) and quantum yield (Φ) were compared with the standard least squared ANOVA (**Table 2**). Temperature and CO_2 concentration were main effects for both species and each of the comparisons. The interactions were not significant and removed from the model.

For *U. crassifolia*, the maximum photosynthetic rate (A_{max}) did not change with temperature (*P* = 0.4399) while it did increase significantly with CO_2 concentration (*P* = 0.0006) (**Table 2**). Tukey comparisons of the CO_2 effect showed significant differences between the ambient CO_2, 5.93 $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$, and

Table 2. Factors measured and *P*-values for Standard Least Squared ANOVAs for measured light curve parameters for *Ulmus crassifolia* and *Ungnadia speciosa*. Data is from three replicates at three CO_2 concentrations of (390, 585 and 780 $\mu L \cdot L^{-1}$) and three temperatures (35˚C, 40˚C and 45˚C). Interactions were not significant and removed from the models. Bold entries are significant at 0.05 or less. Same upper-case or lower-case letters following measurements within a column for a species indicate treatment was not significantly different (TUKEY comparisons *P* > 0.05).

SPECIES & TREATMENT	FACTORS AND MEASUREMENT LEVELS				
	A_{max}	L_{spt}	L_{cp}	R_d	Ø
CO_2 *Ulmus*					
CO_2 390	5.93A	205A	24.8A	0.79A	0.033A
CO_2 585	8.10AB	246AB	25.8A	0.93A	0.037A
CO_2 780	10.85B	286B	21.4A	0.87A	0.041B
SIG.	***P* = 0.0006**	***P* = 0.0376**	*P* = 0.4380	*P* = 0.5431	***P* = 0.0002**
TEMP. *Ulmus*					
35˚C	8.93a	251a	17.4a	0.65a	0.037a
40˚C	8.45a	245a	23.3ab	0.86ab	0.037a
45˚C	7.50a	242a	31.4b	1.09b	0.035a
SIG.	*P* = 0.4399	*P* = 0.9569	***P* = 0.0015**	***P* = 0.0066**	*P* = 0.2824
CO_2 *Ungnadia*					
CO_2 390	6.22A	231A	25.1A	0.79A	0.032A
CO_2 585	8.73AB	328AB	28.2A	0.88A	0.031A
CO_2 780	10.48B	385B	30.6A	0.93A	0.032A
SIG.	***P* = 0.0001**	***P* = 0.0051**	*P* = 0.3754	P = 0.5521	*P* = 0.9823
TEMP. *Ungnadia*					
35˚C	8.45a	323a	24.1a	0.72a	0.031a
40˚C	8.47a	303a	28.0a	0.89a	0.033a
45˚C	8.51a	318a	31.8a	0.95a	0.031a
SIG.	*P* = 0.9812	P = 0.9812	*P* = 0.1539	P = 0.1539	*P* = 0.8765

high CO_2 concentration, 10.05 $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$ for an A_{max} increase of approximately 41%. A similar response was measured for *U. speciosa,* it's maximum photosynthetic rate (A_{max}) did not change with temperature ($P = 0.9812$) while it did increase significantly with CO_2 concentration ($P = 0.0001$). Tukey comparisons of the CO_2 effect showed significant differences between the ambient CO_2, 6.22 $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$, and high CO_2 concentration, 10.48 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ for an A_{max} increase of approximately 41%.

For *U. crassifolia*, the light saturation point (L_{sp}) did not change significantly with temperature ($P = 0.9569$) (Table 2). A significant difference was found between the values for the ambient CO_2 L_{sp} at 205 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and high CO_2 L_{sp} at

286 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for a 28% increase. *Ungnadia speciosa* also showed a similar L_{sp} response. It showed no significantly different change with temperature ($P = 0.9812$) but was significantly different by CO_2 (Table 2). For *U. speciosa* a significant difference was found between the ambient CO_2 L_{sp} at 231 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and high CO_2 L_{sp} at 385 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for a 40% increase.

For *U. crassifolia*, the light compensation point (L_{cp}) showed a significant difference by temperature but not by CO_2 concentration ($P = 0.0015$ and $P = 0.4380$) (Table 2). The 35°C L_{cp} (17.4 $\mu mol \cdot m^{-2} \cdot s^{-1}$) was significantly different from the 45°C L_{cp} (31.4 $\mu mol \cdot m^{-2} \cdot s^{-1}$) for a 45% increase. For *U. speciosa* there were no significant differences in the light compensation point (L_{cp}) at any CO_2 concentration or as the temperature increased ($P = 0.1539$ and $P = 0.5521$).

For *U. crassifolia*, the dark respiration rate (R_d) showed a significant difference by temperature but not by CO_2 concentration ($P = 0.0066$ and $P = 0.5431$) (Table 2). The 35°C R_d (0.65 $\mu mol \ CO_2 \cdot m^{-2} \cdot s^{-1}$) was significantly different from the 45°C R_d (1.09 $\mu mol \ CO_2 \cdot m^{-2} \cdot s^{-1}$) for a 40% increase. For *U. speciosa* the dark respiration rate (R_d) did not show a significant different between CO_2 concentration or temperature level ($P = 0.1539$ and $P = 0.5521$).

For *U. crassifolia*, the quantum yield (Φ) showed a significant difference by CO_2 concentration ($P = 0.0002$) (Table 2). The high CO_2 Φ (0.041 $\mu mol \ CO_2 \cdot m^{-2} \cdot s^{-1}/\mu mol \cdot m^{-2} \cdot s^{-1}$) was significantly different from both the ambient CO_2 Φ (0.033 $\mu mol \ CO_2 \cdot m^{-2} \cdot s^{-1}/\mu mol \cdot m^{-2} \cdot s^{-1}$) and medium CO_2 Φ (0.037 $\mu mol \ CO_2 \cdot m^{-2} \cdot s^{-1}/\mu mol \cdot m^{-2} \cdot s^{-1}$). For *U. speciosa* the quantum yield (Φ) did not differ significantly with temperature or CO_2 treatment ($P = 0.8754$ or $P = 0.9823$).

The CO_2 response curves for *U. crassifolia* were measured at light levels that were held constant at approximately 700 $\mu mol \cdot m^{-2} \cdot s^{-1}$ as a function of the three temperature (35°C, 40°C and 45°C) and were found to be not significantly different ($P = 0.5777$) (Figure 3(a)). At CO_2 concentration of about 800 $\mu L \cdot L^{-1}$, the photosynthetic rates reached a plateau of approximately 10 $\mu mol \ CO_2 \cdot m^{-2} \cdot s^{-1}$. None of the repeated measures MANOVAs performed on the photosynthetic response, intercellular CO_2 concentration, stomatal conductance and transpiration were significantly different by temperature and are not presented ($P > 0.05$ for all). When the WUE by CO_2 was examined for *U. crassifolia* the repeated measures MANOVA of the response to temperature with increasing CO_2 levels was not significantly different ($P = 0.5447$) (Figure 3(c)). The curves plateaued around 800 - 1000 $\mu L \cdot L^{-1}$ of CO_2 with approximate values of 2.8 - 3.6 mmol $H_2O \cdot mol \ CO_2^{-1}$.

The *U. speciosa* CO_2 response curves measured at light levels that were held constant at approximate 700 $\mu mol \cdot m^{-2} \cdot s^{-1}$ as a function of the three temperatures (35, 40 and 45°C) and were found to be not significantly different ($P = 0.7542$) (Figure 3(b)). Photosynthetic rates increased as CO_2 increased up to a plateau starting at about 800 $\mu L \cdot L^{-1}$ of approximately 8.5 - 9.5 $\mu mol \ CO_2 \cdot m^{-2} \cdot s^{-1}$. None of the repeated measures MANOVAs performed on the photosynthetic response, intercellular CO_2 concentration, stomatal conductance and transpiration were significantly different by temperature and are not presented ($P > 0.05$ for all).
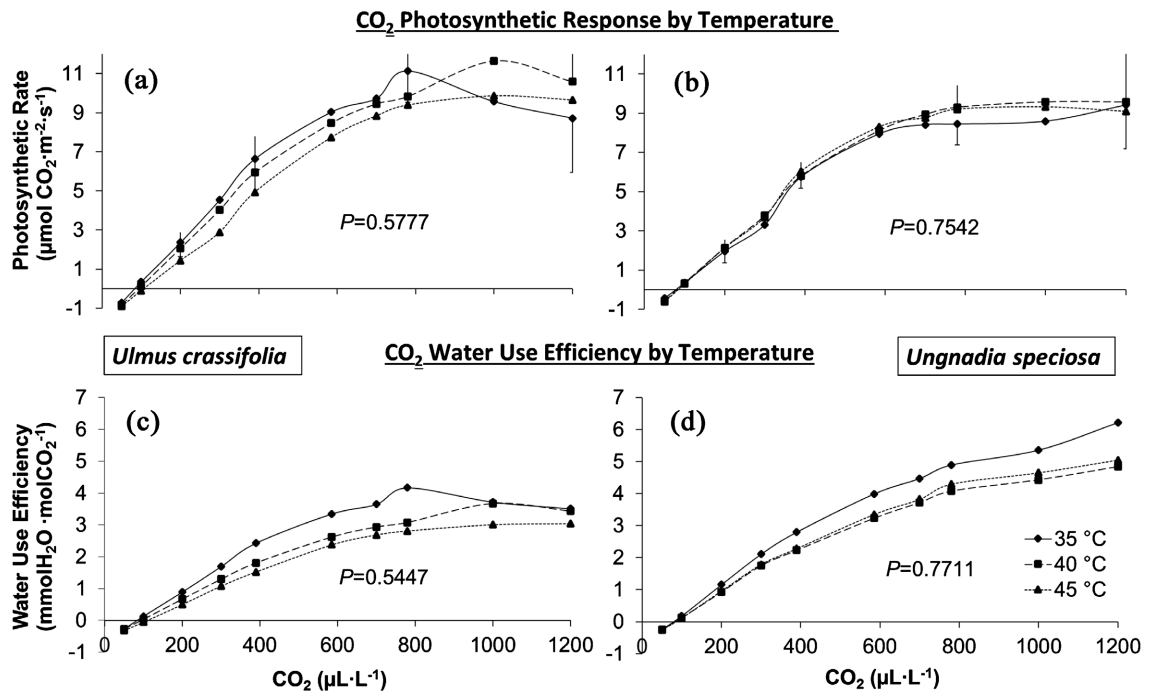
Figure 3. Photosynthetic response curves for increasing CO_2 levels for *Ulmus crassifolia* and *Ungnadia speciosa* ((a) and (b), respectively) and water use efficiency curves ((c) and (d), respectively) at a light level of 700 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and three temperatures (35°C, 40°C and 45°C). Each curve was plotted from a mean of three replicates. *P*-values are shown from the repeated measures MANOVAs. Error bars are shown indicating standard deviation with the open end (|) for the upper most curve and the bar end (⊤) for the lower curve.

When the WUE by CO_2 was examined for *U. speciosa* the repeated measures MANOVA of the response to temperature and with increasing CO_2 levels was not significant ($P = 0.7711$). The curves started to plateau around 8000 $\mu L \cdot L^{-1}$ at approximately 4.2 mmol $H_2O \cdot mol\ CO_2^{-1}$ at until a peak value of 6.2 mmol $H_2O \cdot mol\ CO_2^{-1}$ was reached at the 1200 $\mu L \cdot L^{-1}$ of CO_2 (**Figure 3(d)**).

4. Discussion

Increasing atmospheric CO_2 concentration and temperature are expected to continue into the future [1] [2] and their potential effects on forests, woodlands and other plant communities are not well understood. This is not the first time the world has experienced high levels of atmospheric CO_2 and concomitant higher temperatures [1] [2]. At the end of the Cretaceous period, approximately 60 million years ago, there was a huge release of carbon into the Earth's atmosphere [2] [62]. The atmospheric CO_2 level was approximately 1500 ppm and did not decline to lower levels for approximately 1000 years [2]. Before the last glaciation, about 125,000 years before the present, the atmospheric CO_2 level was about 280 ppm and the mean temperature was 2°C above the present [63]. Then the CO_2 levels dropped to 230 ppm and the temperature dropped by 6°C, with both rebounding to higher levels today [63]. These levels of CO_2 and associated higher temperatures resulted in changes in the plants and animals present and a change in the communities as well. Changes in plant communities will happen

in the future as carbon dioxide levels and temperatures increase, but how the plants and animals will change is uncertain.

Considering our results and comparisons with values for other species [8] [9] [64] [65], both *U. crassifolia* and *U. speciosa* appear to be shade-adapted or intermediate species [59] [66] [67]. Both *U. crassifolia* and *U. speciosa* have relatively lower A_{max} values when compared with other central Texas woodland species [8]. *Ulmus crassifolia* has a low relative A_{max} value under ambient CO_2 conditions, while it increased more than other species at the high CO_2 concentration. This would suggest that this species starts as a shade-tolerant species but would appear to become relatively less shade tolerant as the CO_2 concentration increases. This is similarly expressed by *U. speciosa*. Both *U. crassifolia* and *U. speciosa* had lower L_{cp} values, which would also reinforce their classification as relatively shade-tolerant species. *Ulmus crassifolia* did show an increase in L_{cp} with increased temperature, which may indicate an increase in future shade intolerance. *Ungnadia speciosa* had low Φ values, indicating it also has other shade-tolerant characteristics.

Ulmus crassifolia showed an increasing transpiration response to increasing temperature but did not respond to the elevated CO_2. This suggests that *U. crassifolia* may be more susceptible to the predicted increased temperatures. *Ulmus crassifolia* showed a decrease in water use efficiency from increasing temperature, but at the same time, an increase in water use efficiency from increasing CO_2 concentration. *Ungnadia speciosa* showed an increase in water use efficiency as the CO_2 concentration increased with no temperature response. This will most likely allow the species to be more drought resistant in the future climate.

Not only is the modification to the overall water use efficiency of note, but it may be important that for all species, the water use efficiency closely mimicked the light curves. As the light level decreased, the water use efficiency decreased. This is due to the photosynthetic responses decreasing in the low light environment while the transpiration rate only decreased slightly over the lower light levels. This shows that at lower light levels, these species can not properly regulate water loss. This may be the reason why understory seedlings suffer high mortalities [28]. Shade-tolerant species may be better able to moderate this disconnected water use efficiency at lower light levels, thereby increasing their survival. However, this does not explain the low density of these species in these woodland communities or the lack of them in the grassland gaps and patches.

Something else that has changed radically in these central Texas woodlands is the density of large native herbivores, which has increased dramatically [68]. These increases over the past hundred years have happened in many other areas of North America, causing plant community structure and composition changes [69]-[76]. Certain plant species in the study area are susceptible to herbivory and seem to require exclosures to maintain future populations [5] [77] [78] [79] [80] [81]. This is similar to what has been reported for various *Quercus* and other woody species in many North American forests [69] [74] [77]. Although the herbivory of *U. crassifolia* and *U. speciosa* was not examined directly in this current

study, there is a high possibility that browsing may have a similar effect on the population structure and distribution of these species in the future.

The responses to light level suggest that *U. crassifolia and U. speciosa* are similar to other restricted eastern North American low-density shade-tolerant and herbivory susceptible plants [16]. The canopy position of these plants and their low relative density may be caused by the high density of other woody shrubs that could afford some protection from the herbivores (probably white-tailed deer), masking their presence and position [78].

Juniperus woodlands seem to be successional communities [82]. In the eastern North American deciduous forests, *Juniperus* plants are often found in gaps, blow downs or on shallow soil in glades [6]. 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 [37]. In central Texas, *Juniperus ashei* establishes on hillsides and in former grasslands on shallow soil [49]. *Juniperus* woodlands in many parts of the world are probably caused by a number of factors, with constant high levels of grass herbivory and a reduction of grassland fire frequency being dominant [37] [82].

Grasslands are favored when biomass and fire frequency are high, while woody plants, like various species of *Juniperus,* and many species of nitrogen-fixing legumes, are favored when fire frequency is low or nonexistent [83] [84]. The structure of many grasslands and savannas has changed and the direction of community succession has been altered because of new conditions controlling their structure and composition [32] [83] [84] [85] [86].

The new higher atmospheric CO_2 and temperature conditions in the woodlands, plus browsing by native herbivores, are causing community change. Community changes in woodlands are hard to detect, but conditions will be modified in the future [33]. These new conditions will allow some species to expand their density, while other species will decline. The result will be changes in community composition and structure. The current study species, *U. crassifolia and U. speciosa,* found in these central Texas *Juniperus/Quercus* communities are expected to change in density and basal area. This study suggests that they will gain competitive advantages over other community species with increased atmospheric CO_2 levels and light 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 species in many areas of central Texas [78]. This difficulty in the establishment has been shown for various woody species, possibly in conjunction with competition for water with C_4 southern grasses [65] [72]-[77] [87]. These complications mean predicting future plant community changes will be a demanding task.

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Conflicts of Interest

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