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Drought Tolerance and Recovery of the Sedge *Carex planostachys* (Cyperaceae) from Central Texas Woodlands

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Abstract

Carex planostachys Kunze (Cyperaceae, Cedar sedge) is an herbaceous species in a genus commonly inhabiting mesic or hydric habitats. *Carex planostachys* is found in arid and semi-arid *Juniperus* woodlands. Arid conditions impose survival challenges to plants in dry areas. Some plants have plasticity responses to soil water content and continued normal though reduced functions through droughts, but most herbaceous plants do not survive. Limited previous studies have suggested *C. planostachys* is tolerant of drought. Physiological responses of *C. planostachys* from *Juniperus* woodlands was examined is this study to determine how long plants could survive without water and if they are capable of recovery from very negative water potentials beyond what is considered the permanent wilting point for most herbaceous plants. Plants were placed in pots in partial shade in this experiment. Water loss from the soil with plants was an inverse 2nd order polynomial function with soil water decreasing from 32% to 8% by day 28 of the study. Leaf water potential was also an inverse 2nd order polynomial function but did not decline significantly until 14 days without watering. Leaf water potential was −10.0 MPa after 35 days without watering. Non-watered plants $A_{net,}$ (photosynthetic rate) was significantly lower compared to the water treatment by day 21 as was stomatal conductance and transpiration. When non-watered plants were watered after 21, 28 or 35 days, full recovery of physiological responses occurred within 7 days. The length of time that *C. planostachys* was able to withstand drought was greater than the annual trends in lack of precipitation during springtime in this area. *Carex planostachys* can photosynthesize at water stress between −8 and −10 MPa. *Carex planostachys* drought and shade tolerance enables it to occupy an understory niche devoid of other herbaceous plants.

Keywords

CO_2 Uptake, Conductance, Gas Exchange, Photosynthesis, Respiration, Transpiration, Water Stress, Water Potential.

1. Introduction

In areas of the arid and semi-arid southwestern United States, *Juniperus* woodlands and savannas are major vegetation types [1]-[3]. As rainfall increases communities change from desert to semiarid grasslands to savanna, to biphasic savannas then to woodland; these woodlands or forests are usually at higher elevations [4] [5]. Many reports suggest that understory herbaceous ground cover is absent in the woodland phase of these communities because of the presence of juveniles of various *Juniperus* species [6]-[8]. The loss of grass ground cover below the *Juniperus* canopy is attributed to decreases in light availability or soil moisture or a combination of both [9]-[11]. The reduction in light that occurs at ground level is attributed to attenuation of light by the evergreen canopy [12] [13]. The reduction in soil water is a modification of the microclimate attributed to the canopy presence, through interception of rainfall or use by the canopy species [11] [13]. Soil water is also related to the frequency of rainfall, amount of rainfall, its distribution through the year and soil depth [11]-[15]. In the study area in central Texas annual rainfall is 72.4 cm/y but is biphasic with 10.7 cm in May and 8.7 cm in September and little or none in June, July and August [3]. The rainfall during the present study is shown in mm/day (**Figure 1**) with three weeks during the mid-part of the study with no rainfall. However, plants were covered with a plastic tarp to keep natural rainfall from the study plants.

The central Texas Edwards Plateau is a biphasic savanna community of *J. ashei/Quercus virginiana* woodlands and inter-canopy grasslands or gaps 8. There is a rainfall gradient across the region, with more rainfall in the east and decreasing in the west [2] [3] [23]. Grass cover may be high in the open grasslands and low below the woodland canopy; but in some areas the understory cover is high and dominated by a single species, *Carex planostachys* Kunze (Cyperaceae, Cedar sedge) (**Figure 2**) [2] [23] [24]. In some areas below the woodland canopy, cover of *C. planostachys* is ca. 43 % and marginally higher at the canopy edge [25].

In several respects, the presence of *C. planostachys* in the xeric *J. ashei* woodlands is a paradox. During summer, soil water is below the permanent wilting point of most plants [14] [23]-[26]. Sedges are usually associated with riparian woodlands, grasslands or marshes and swamps, and may occur at high latitude or altitude where cooler, wetter conditions are more common [27]. Sedges are not usually considered drought tolerant, though some drought can be endured. Sedges are usually associated with wetlands that may have periodic short-term fluctuations in the water level and have a minimum water stress of −4.0 MPa [28]. The only species having physiological responses comparable to *C. planostachys* in

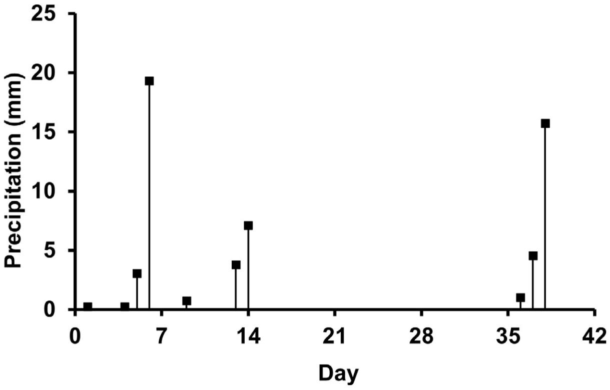

Figure 1. Daily precipitation (mm) reported from March 14 through May 4, 2007. Data was obtained from the San Antonio International Airport, National Oceanic and Atmospheric Administration weather service, San Antonio, TX.

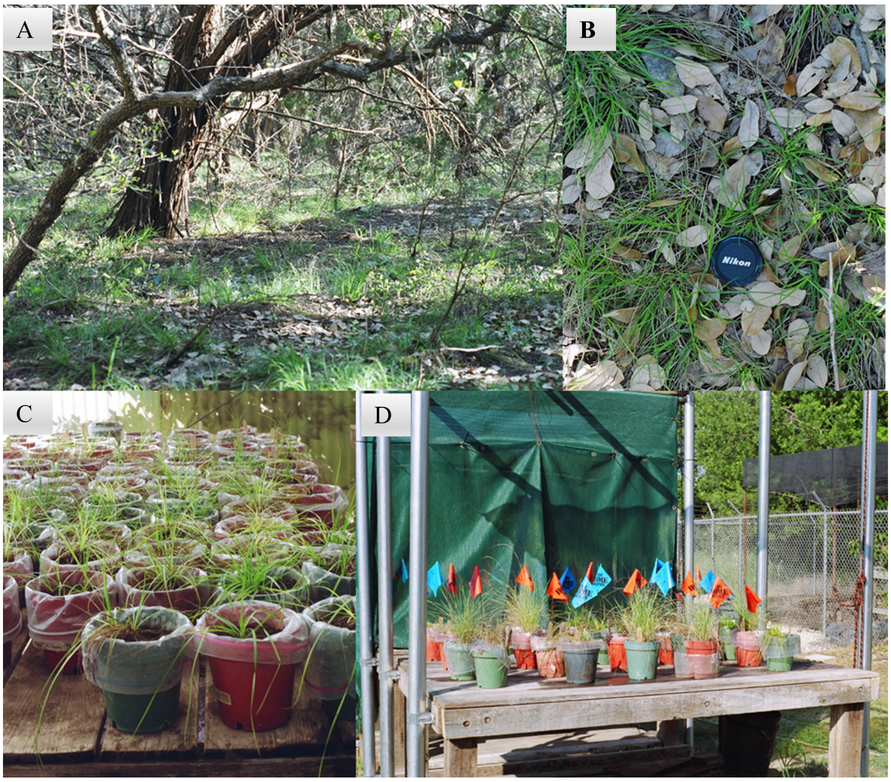

Figure 2. *Carex planostachys* below a *Juniperus ashei* woodland canopy (A) and close-up of sedge in the field (B). Plants were harvested from a nearby site and transplanted into pots and allowed several months to establish (C). Light levels in the greenhouse were similar levels below the *J. ashei* canopy. Pots were transferred to a bench outside the greenhouse (D) and given a month to acclimate. The bench in the foreground were plants to be used in a transplant study. The covered bench in the background was the bench used for this study.

these Central Texas plant systems is *J. ashei* witch is a tree [41].

Complex environmental gradients, caused by a variety of biotic and abiotic factors affect plant photosynthetic activity, growth, survival and a species' distribution [14] [15]. Both light levels and soil water availability will simultaneously affect photosynthetic activity and transpirational water loss [24]-[28]. Consequently, these two elements are coupled and both bring about modifications in levels of plant carbon gain. Levels of light and soil water interact and are not independently controlling the presence of *C. planostachys* in *Juniperus* woodlands and associated gaps [29]. However, the ability to survive lack of water or droughts has not been independently tested for this species.

Extended or prolonged drought will place greater survival risk on plants because of reduced photosynthate produced to meet metabolic needs [14] [15] [26] [30]. *Carex planostachys* is known to tolerate summer drought and can survive water stress below −9.0 MPa while sustaining physiological activity [29]. During early spring growth when the inflorescence is present, photosynthetic rates of ca. 7.5 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ have been measured [29]. During summer drought when leaf water potential is low, the carbon gain for *C. planostachys* is sufficient only to meet respiratory demands. In addition, despite the low water potential values reached, *C. planostachys* recovers rapidly following small precipitation events (personal observation). *Carex planostachys* has been shown to maintain conductance and carbon uptake during water limitations, but at reduced levels [24] [28].

Herbivory has been studied in these *Juniperus/Quercus* woodlands [23] but mainly for the woody species. What has been shown is a lack of recruitment of juveniles of almost all of the woody species into the canopies of these woodlands [3]. Unfortunately, recruitment of *C. planostachys* has not been examined.

One purpose of this study was to examine the effect of withholding water (forced drought) on *C. planostachys* physiologic responses. In addition, the recovery of *C. planostachys* physiologic responses to drought were examined. The light response characteristics of *C. planostachys* to variation in water availability were also measured.

2. Methods

Experimental set-up

This study was conducted with potted plants but as an our-door or garden type study. *Carex planostachys* plants were carefully excavated from a research site in Eisenhower Municipal Park, in San Antonio, TX (**Figure 2(A)** and **Figure 2(B)**). Plants were separated into units each with 3 to 4 ramets, with rhizomes and roots trimmed to 15 cm. Plants were transplanted into 15 cm wide × 15 cm deep plastic bag lined pots filled with ca. 1400 g of a sieved, air-dried Patrick series soil obtained on the University of Texas at San Antonio campus, within a *J. ashei* woodland - grassland matrix. *Carex planostachys* occurs widely in this area [31]. Pots were watered with 500 ml of deionized water and 150 ml of a 25% Miracle Gro® fertilizer solution. Plants were grown in an air-cooled greenhouse for two months and monitored every two to three days to maintain soil at field capacity. There were two additional applications of fertilizer solution. Pots with less than three surviving ramets were removed.

In February 2006, plants were transferred out of the greenhouse to a table covered with 75% shade cloth (**Figure 2(C)** and **Figure 2(D)**) and clear plastic (rainfall excluder). On March 13, 2006, all pots were given a final 150 ml of fertilizer solution. Individual numbered pots were randomly assigned to blocks and treatment groups of supplemental water or no supplemental water using the SAS procedure Proc Plan. Each block (n = 6) consisted of 10 pots, with five pots in each water treatment (n = 2, watered or not watered). Each week during the study, all pots were randomly rearranged on the table. Pots in the watered treatment were checked every three days for a damp surface and watered as needed.

Physiological measurements

The study was initiated on March 14, 2006 (= day 0) and continued through May 4 (= day 42) with planned measurements at weekly intervals. Measurements included soil moisture, leaf water potential, net leaf photosynthesis, stomatal conductance and transpiration. Volumetric soil moisture (%) was determined using a Trime-FM (Mesa Systems Company, Medfield, MA) portable moisture meter with probes 80 cm in length. Leaf xylem water potential was measured in megapascals (MPa) using a Scholander type pressure chamber (PMS Model 1000, PMS Instrument Company, Albany, OR). A single leaf was used for each measurement.

Photosynthetic measurements were made with a LiCor 6400 (Lincoln, NE) portable photosynthetic meter with an attached Red-Blue LED light source. Measurements were made between 1000 and 1200 hours, at saturating light, 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$, and saturating CO_2, 390 $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$. Temperature and humidity were held constant for all plants measured on a single date, with the ambient levels established prior to the first leaf measurement. Three to four leaves were carefully placed across the cuvette and then the cuvette was closed. Photosynthetic measurements were recorded after a stable coefficient of variation ≤ 3% was reached, ca 2 to 3 minutes. Recorded values were net photosynthesis (A_{net}, $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$), stomatal conductance (g, $mol\ H_2O \cdot m^{-2} \cdot s^{-1}$) and transpiration (E, $mmol\ H_2O \cdot m^{-2} s^{-1}$). After day 28, leaf curling prevented conducting photosynthetic measurements on plants in the no water treatment.

After a significant decline in leaf water potential was detected at 21 days, a recovery experiment was initiated. A single block was randomly selected from among blocks previously sampled. Pots of that block in the drought treatment were watered with ca. 500 ml of deionized water. In addition, pots were checked for a damp surface every three days. Pots in the recovery group were measured the subsequent day and at the same time as watered and drought treatments on subsequent weeks. Two additional recovery experiments were initiated on days 28 and 35, following the procedure described. Concerning the recovery experiment commencing on day 35, leaves were tightly curled on days 36 and 42; thus, no measurements were made on these days. In addition, no measurements were made beyond day 42 (May 4) because an unexpected storm gust overturned the bench with plants, resulting in termination of the study.

Light response curves

Steady-state gas-exchange photosynthetic light response curves (A_{net} vs. PAR) were conducted on day 21 (drought pots), day 22 (recovery pots) and day 23 (watered pots) to estimate the maximum photosynthetic rate (A_{max}), the light saturation point ($\mathrm{L_{sp}}$), the quantum yield, the light compensation point ($\mathrm{L_{cp}}$) and the dark respiration rate (R_{d}). Three pots were randomly selected from each treatment group. Plants were dark adapted for 30 minutes prior to conducting a response curve. Response curves were conducted within two hours prior to solar noon. Three to four mature intact leaves were selected from a plant and placed into the cuvette of a LiCor 6400 portable photosynthetic meter. Both the cuvette and plant were covered with shade cloth to exclude external light. Light levels were provided with an integrated red-blue LED light source attached to the cuvette. Chamber temperature and humidity were controlled at initial ambient levels. Cuvette CO_2 was saturating at 390 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$. The loaded cuvette was allowed to equilibrate prior to initiating the response curve to a stable dark respiration rate. Response curves were initiated at high light levels (PPF = 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$) to photoactivate rubisco [32] and after a steady state was achieved light levels were ramped down to 1400, 1200, 1000, 800, 600, 400, 200, 100, 75, 50, 25,10, 5 and 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$. A stable coefficient of variation (< 0.3%) was obtained at each level before data logging, ca. 3 - 5 min.

Statistical analysis

The statistical design of the first part of the study, comparing the effect of drought on *C. planostachys* was conducted as a factorial study, inclusive of days 0 through 28. Statistical Analysis Software [33] was used to test for differences in dependent factors between treatment groups with ANOVA in a mixed model design [34]. Treatment and day were fixed effects and plant pot was a random effect. The slice procedure was used to test for within treatment differences and within days treatment effects. Least square means with a Bonferroni correction were used to determine where significant differences occurred in multi-way paired comparisons.

In the recovery experiment, data were analyzed in a longitudinal mixed model study to account for repeated measures [34] [35] to test the effect of treatment on *C. planostachys* from day-21 through day-42. Treatments were inclusive of water, drought and recovery. The recovery treatment was at two levels, the first introduced into the model on day-21 and the second on day-28. Since only one day lapsed between the droughted pot and the recovered pot, data were grouped by week to simplify analysis. The slice procedure was used to test for within treatment temporal effects and within week treatment effects. Least square means with a Bonferroni's correction were used to determine where significant differences occurred in multi-way paired comparisons.

The maximum photosynthetic rate (A_{max}) was calculated from the five highest asymptotic values and the quantum yield equation was derived by regressing the gas-exchange rate from 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPF upward until the regression coefficient of the slope decreased [36]. Light saturation ($\mathrm{L_{sp}}$) for each position was calculated at 90% A_{max} [36]. $\mathrm{L_{cp}}$ was calculated from the quantum yield equation by setting the photosynthetic rate = 0 $\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. R_d was calculated by averaging the net photosynthetic rate for each plant/position at PPF = 0 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Differences in light saturation between treatments were determined with ANOVA. To test for treatment differences between light response curves, non-linear analysis was used [37] [38] to account for repeated measures and generated estimated parameter means, standard error and covariance matrix of the response variables (R_d, L_{cp}, A_{max}). Photosynthetic response data was fit with an empirical non-rectangular hyperbola function $A = A_{max}\ \text{X}\ [1 - (1 - R_d/A_{max})^{(1\text{-PPF/Lcp})}]$ to model the nonlinear response of carbon uptake to change in PPF [36]. To test for differences across treatments, the Wald test for equality of variance was used on the estimated covariance parameters.

3. Results

Rainfall data during the study period is presented (**Figure 1**). Rainfall continued (although slightly) until day 14 of the study and stopped until day 36. No rain for more than three weeks. Soil moisture (**Figure 3**) varied significantly temporally ($F = 9.99$, $P \leq 0.0001$) and across treatments ($F = 239.53$, $P \leq 0.0001$), along with a significant interaction ($F = 22.68$, $P \leq 0.0001$). There was a slight significant variation in the water treatment ($F = 3.52$, $P < 0.05$), ranging from 29.2 ± 2.3 % (±SE) to 37.1 ± 1.6 %. The drought treatment varied significantly ($F = 29.15$, $P \leq 0.0001$), decreasing from 32.1 ± 1.6 % (day 0) to 7.1 ± 0.7 % (day 28). The least square means, paired comparisons, indicated that the first significant decline in soil moisture for the drought treatment occurred on day 7 and after day 14. Beyond day 14 no further significant declines in soil water were detected. The slice procedure indicated that significant differences between the water and drought treatments occurred on day 7 and all days after (note **** in figure). A recovery test was initiated on day

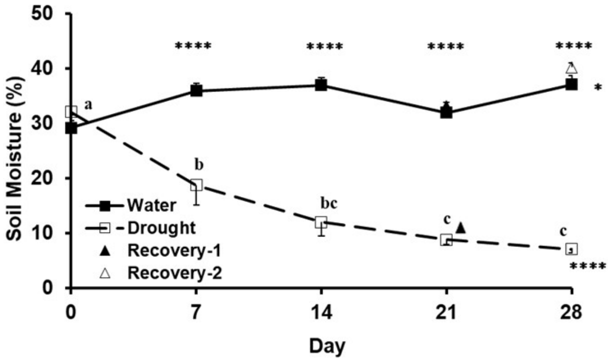

Figure 3. Percent soil moisture measured during the drought study using a time domain reflectometer (Trime-FM, Mesa Systems Company, Medfield, MA). Presented is watered and drought treatments from day 0 through day 28. Upper or lower standard error bars are included. Measurements for recovery tests are also included (Recovery one ▲, recovery two △). Symbols at the terminus of a line indicate significant differences within a treatment across days (*$P > 0.05$). Symbols above treatment days (**** is $P \leq 0.0001$) indicate significant differences between treatments within that day. Different lower-case letters indicate significant differences among the drought treatment days.

21 (recovery 1) and an additional recovery test commenced on day 22 (recovery 2). These were followed with measurements on day 28, 35 and 42. Soil moisture (**Figure 3**, individual symbols on graph) in the first recovery test (recovery 1) increased significantly from the drought treatment ($P \leq 0.0001$) but was not significantly different from the water treatment ($P > 0.05$). Soil moisture on day 21 ranged from 8.9 ± 0.8 % (drought) and after watering increased to 33.2 ± 0.7 % (recovery 1) and was not significantly different from the watered treatment on day 28 (31.9 ± 0.8 %). The second recovery test (recovery 2), started on day 21 soil water increased significantly over the drought treatment ($P < 0.001$) and was slightly higher than the watered treatment ($P < 0.05$). Soil moisture was 7.1 ± 0.7% in the drought treatment and significantly different at 40.2 ± 0.8 % in recovery 2 but not significantly different at 37.1 ± 1.6% from the watered treatment (**Figure 3**).

Leaf water potential ($\Psi_{\text{leaf,}}$ **Figure 4**) varied significantly temporally ($F = 9.56$, $P \leq 0.0001$) and across treatments ($F = 46.65$, $P \leq 0.0001$), along with a significant interaction ($F = 12.69$, $P \leq 0.0001$). In the watered treatment, Ψ_{leaf} fluctuated non-significantly from −1.7 ± 0.4 MPa (day 0) to −0.5 ± 0.1 MPa (day 35). The drought treatment varied significantly temporally ($F = 21.70$, $P \leq 0.0001$), with Ψ_{leaf} ranging from −1.6 ± 0.3 MPa on day 0 to −6.9 ± 1.6 MPa on day 28. No significant declines were observed in the drought treatment until day14, that was significantly different from day 7 and 21. There were no differences between day 21 and day 28. Leaf water potential was measured on day 35, but the values observed exceeded equipment limitations and were estimated at ≤ −10 MPa. However, significant differences were estimated between day 28 and day 35. There were significant differences between the watered and non-watered treatments on days 21, 28 and 35 (**Figure 4**).

Net leaf photosynthesis (**Figure 5(A)**) varied significantly by treatment ($F = 18.67$, $P \leq 0.0001$), along with a significant interaction ($F = 3.61$, $P < 0.05$). The

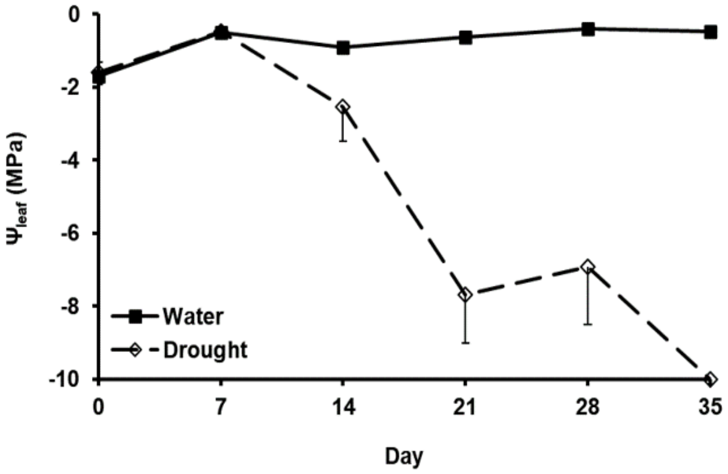

Figure 4. Leaf water potential (Ψ - MPa) for watered and drought treatments from day 0 through day 35. Upper or lower standard error bars are included.

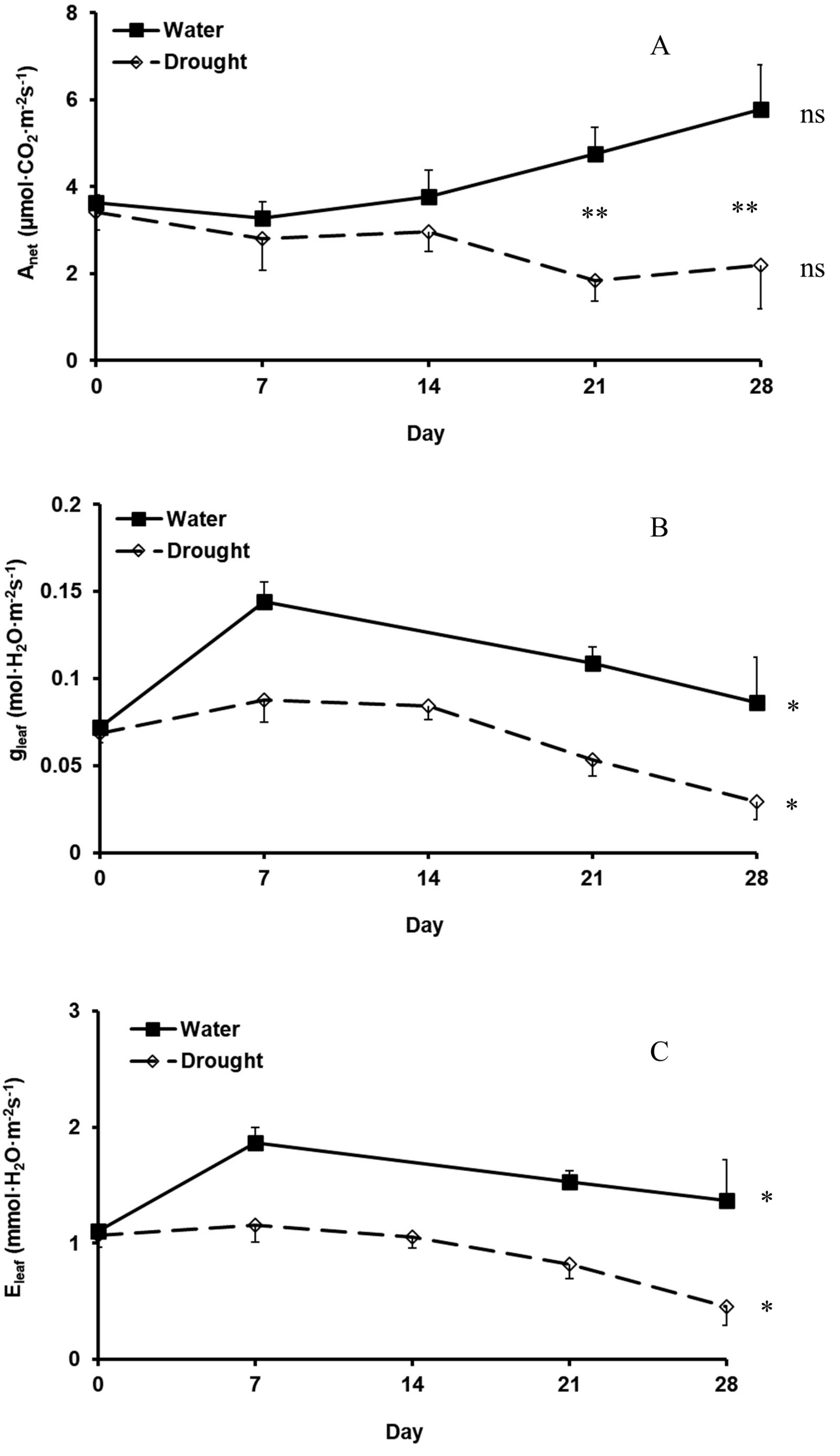

Figure 5. (A) *Carex planostachys* leaf photosynthesis (A_{net}), (B) stomatal conductance (g_{leaf}) and (C) transpiration (E). Lines for water and drought treatments from day 0 through day 28 are indicated in each figure. Upper or lower standard error bars are included. Symbols at the terminus of a line indicate significant differences occurred within a treatment across days. The number of * indicate significant differences in the treatments: * is $P > 0.05$, ** is $P < 0.01$, **** is $P \le 0.0001$ and ns = not significant.

watered treatment ranged from 3.6 ± 0.2 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (day 0) to 5.8 ± 1.0 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (day 28) and the drought treatment ranged from 3.4 ± 0.4 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (day 0) to 2.2 ± 1.0 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (day 28). Neither the water treatment nor the drought treatment was temporally significantly, but the slice procedure indicated a significant departure in A_{net} between treatments on day 21 and day 28.

Values for both stomatal conductance (**Figure 5(B)**) and transpiration (**Figure 5(C)**) followed the same statistical trends. For leaf conductance, there was a significant temporal effect ($F = 5.68$, $P < 0.001$), treatment effect ($F = 21.56$, $P \leq 0.0001$) and interaction ($F = 3.47$, $P < 0.05$). Conductance values in the watered treatment varied significantly ($F = 4.63$, $P < 0.01$), but the fluctuation was small (**Figure 5B**), ranging from 0.07 ± 0.00 mol $H_2O \cdot m^{-2} \cdot s^{-1}$ (day 0) to 0.08 ± 0.02 mol $H_2O \cdot m^{-2} \cdot s^{-1}$ (day 28). The drought treatment had a gradual, but significant decline ($F = 4.52$, $P < 0.01$), ranging from 0.07 ± 0.01 mol $H_2O \cdot m^{-2} \cdot s^{-1}$ (day 0) to 0.03 ± 0.01 mol $H_2O \cdot m^{-2} \cdot s^{-1}$ (day 28); however, the paired comparisons did not detect any differences.

For leaf transpiration (**Figure 5(C)**), there was a significant temporal effect ($F = 3.96$, $P < 0.05$), treatment effect ($F = 20.41$, $P \leq 0.0001$) and interaction ($F = 4.51$, $P < 0.01$). Leaf transpiration (**Figure 5(C)**) had a similar profile to that of leaf conductance. The watered treatment varied significantly, ($F = 3.97$, $P < 0.01$), ranging from 1.1 ± 0.1 mmol $H_2O \cdot m^{-2} s^{-1}$ (day 0) to 1.4 ± 0.3 mmol $H_2O \cdot m^{-2} s^{-1}$ (day 28). The drought treatment varied significantly ($F = 3.57$, $P < 0.05$), ranging from 1.1 ± 0.1 mmol $H_2O \cdot m^{-2} s^{-1}$ (day 0) to 0.5 ± 0.2 mmol $H_2O \cdot m^{-2} s^{-1}$ (day 28), but the paired comparisons did not show any significant differences.

Leaf water potential varied during the recovery experiment (**Figure 6(A)**) through day 42, with a significant treatment effect ($F = 7.38$, $P < 0.01$). Recovery 1 ranged from −4.3 ± 2.3 MPa (day 21) to −0.5 ± 0.0 MPa (day 28), while recovery 2 ranged from −2.6 ± 0.2 MPa (day 28) to −0.6 ± 0.1 MPa (day 35). The Ψ_{leaf} in the water treatment ranged from −0.6 ± 0.1 MPa (day 21) to −0.5 ± 0.1 MPa (day 42). Between treatments (within days), there were significant differences in leaf water potential on days 21 and 28, afterwards no differences were observed.

For net photosynthetic rates (**Figure 6(B)**) there was a significant treatment effect ($F = 3.51$, $P < 0.05$) and a borderline temporal effect ($F = 2.94$, $P = 0.053$). Recovery 1 photosynthesis was borderline significant ($F = 2.88$, $P = 0.54$) and ranged from 2.3 ± 0.3 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (day 21) to 4.9 ± 1.1 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (day 42). Recovery 2 varied significantly ($F = 4.80$, $P < 0.05$) and ranged from 1.7 ± 0.6 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (day 28) to 7.7 ± 1.2 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (day 42). The water treatment ranged from 4.8 ± 0.6 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (day 21) to 5.5 ± 1.2 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (day 42). The between treatment (within day) effects were significant on day 21 and 28 only, the start of the experiment.

Stomatal conductance (**Figure 6(C)**) had a significant temporal effect ($F = 62.20$, $P \leq 0.0001$), treatment effect ($F = 102.90$, $P \leq 0.0001$) and interaction ($F = 47.28$, $P \leq 0.0001$). A significant difference was observed in recovery 1 ($F = 158.82$, $P \leq 0.0001$) and ranged from 0.06 ± 0.01 mol $H_2O \cdot m^{-2} \cdot s^{-1}$ (day 21) to 0.18 ± 0.04 mol $H_2O \cdot m^{-2} \cdot s^{-1}$

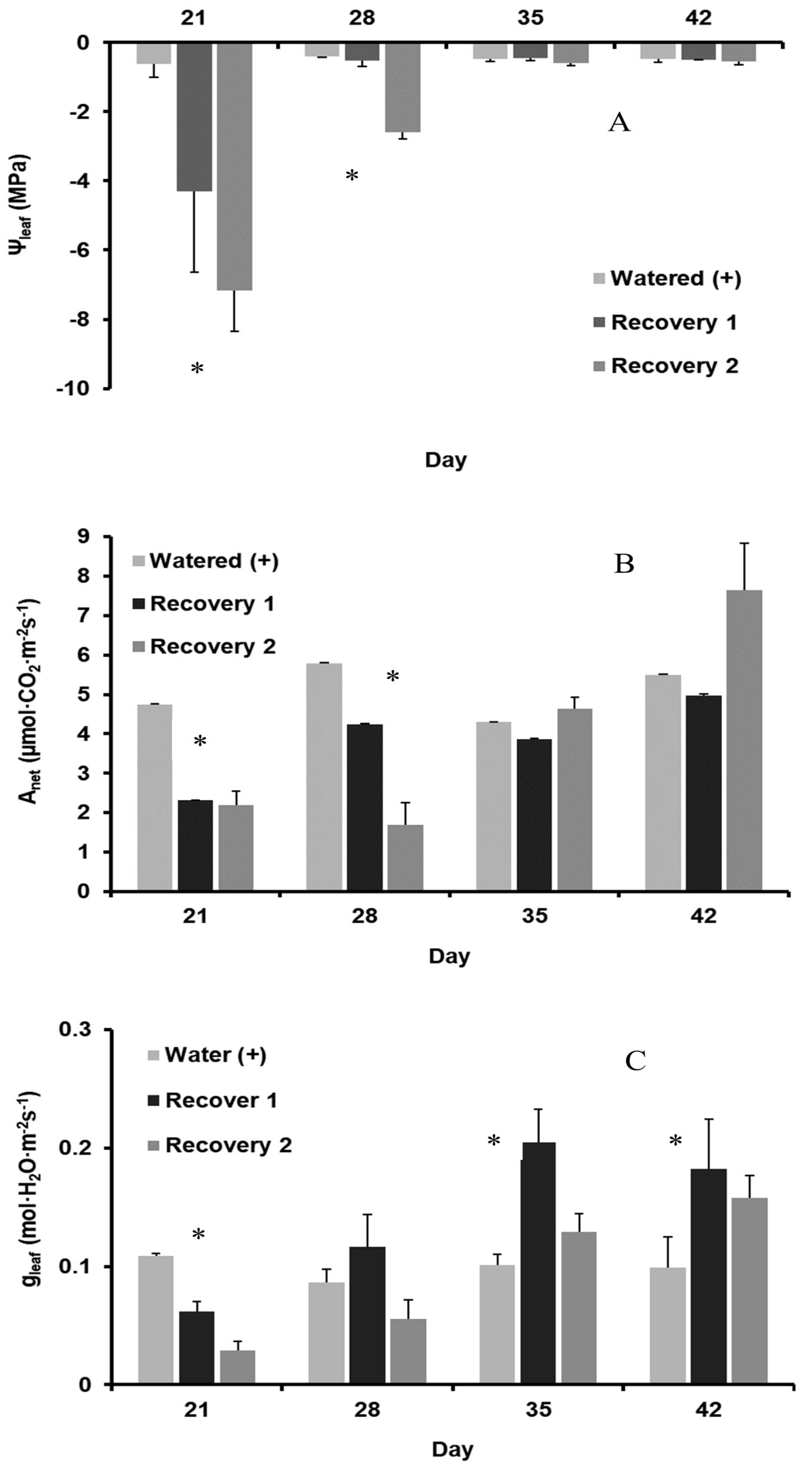

Figure 6. Presented is a test for recovery from drought stress for *Carex planostachys* (A) leaf water potential (Ψ_{leaf}), (B) maximum photosynthetic rate (A_{net}), and (C) stomatal conductance (g_{leaf}), comparing the effects of watered, droughted and recover treatments from day-21 through day-42. There were two recovery treatments started, the first on day 21 and the second on day 22. Recovery 1 was measured on days 21, 28, 35 and 42. Recovery 2 measurements (pre-recovery day 21 presented) was measured on days 28, 35, and 42. Upper or lower standard error bars are included. Symbols (*) indicate significant differences exist between treatments within days.

(day 42). Recovery 2 varied significantly ($F = 4.80$, $P < 0.05$) and ranged from 0.06 ± 0.02 mol $H_2O \cdot m^{-2} \cdot s^{-1}$ (day 28) to 0.16 ± 0.02 mol $H_2O \cdot m^{-2} \cdot s^{-1}$ (day 42). In the continuous watered treatment, conductance ranged from 0.11 ± 0.03 mol $H_2O \cdot m^{-2} \cdot s^{-1}$ (day 21) to 0.10 ± 0.02 mol $H_2O \cdot m^{-2} \cdot s^{-1}$ (day 42) and was not significant. Significant differences were detected between treatments within all days except day 28.

Leaf transpiration (not shown, but very similar to stomatal conductance) also had a significant temporal effect ($F = 9.67$, $P < 0.001$), treatment effect ($F = 3.11$, $P < 0.05$) and interaction ($F = 8.17$, $P \leq 0.0001$). Transpiration for recovery 1 varied significantly ($F = 24.73$, $P \leq 0.0001$) and ranged from 0.9 ± 0.1 mmol $H_2O \cdot m^{-2}s^{-1}$ (day 21) to 2.4 ± 0.5 mmol $H_2O \cdot m^{-2}s^{-1}$ (day 42), Recovery 2 ranged from 0.9 ± 0.3 mmol $H_2O \cdot m^{-2}s^{-1}$ (day 28) to 2.2 ± 0.2 mmol $H_2O \cdot m^{-2}s^{-1}$ (day 42). Transpiration in the water treatment ranged from 1.5 ± 0.3 mmol $H_2O \cdot m^{-2}s^{-1}$ (day 21) to 1.4 ± 0.2 mmol $H_2O \cdot m^{-2}s^{-1}$ (day 42), but not significantly. Significant differences in transpiration were detected between treatments (within day) for all days except day 28.

Results from the light response curves (**Table 1**, **Figure 7**) indicated the watered treatment had the highest maximum photosynthetic rate, followed by the recovery treatment with the lowest value in the drought treatment. The highest photosynthetic rate 3.2 ± 0.3 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ was in the water treatment and lowest in the drought treatment at 1.5 ± 0.3 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (**Table 1**). The Wald test ($P < 0.05$) indicated that the watered treatment maximum photosynthetic rate was significantly different from the other treatments that were not different from each other. The light compensation point was highest in the drought treatment and lowest in the watered treatment and all treatments were significantly different from each other (Wald test, $P < 0.05$, **Table 1**). Dark respiration was higher in the watered and recovery treatments and lower in the drought treatment, but only the water treatment was significantly different (Wald test, $P < 0.05$, **Table 1**). Light saturation did not vary significantly between treatments ($F = 1.30$, $P > 0.05$), but was highest in the watered treatment and lowest in the drought treatment.

Table 1. Actual values from light response curve (±*SE*) for *C. planostachys* at three levels of treatment, watered, droughted, and recover. Response curves and recovery measurements were initiated on day-21 or day-22. Physiologic parameters presented are maximum photosynthetic rate (A_{max}, μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$), light compensation point (L_{cp}, $\mu mol \cdot m^{-2} \cdot s^{-1}$), dark respiration rate (R_d, μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) and light saturation point (L_{sp}, $\mu mol \cdot m^{-2} \cdot s^{-1}$). Different letters adjacent to mean values indicate significant differences exist for that parameter determined by the Wald test ($P < 0.05$).

	A_{max}	L_{cp}	R_d	L_{sp}
Water	$3.2 \pm 0.3_a$	$6.0 \pm 2.8_c$	$-0.7 \pm 0.1_a$	$81 \pm 12_a$
Drought	$1.5 \pm 0.3_b$	$27.6 \pm 14.5_a$	$-0.6 \pm 0.1_b$	$40 \pm 25_a$
Recovery	$2.3 \pm 0.2_b$	$15.8 \pm 8.0_b$	$-0.7 \pm 0.2_b$	$68 \pm 15_a$

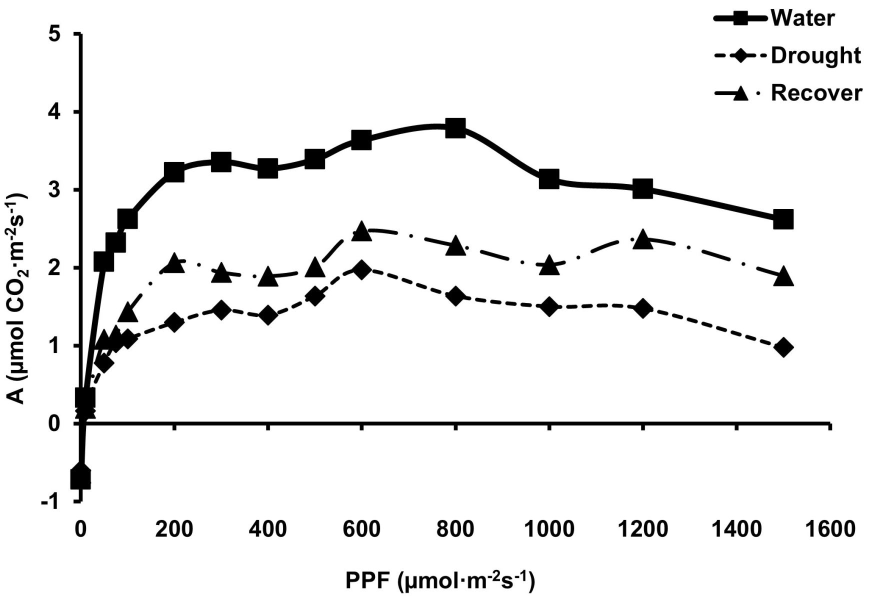

Figure 7. Mean light response curves for CO_2 uptake (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) to incremental change in light from 1500 μmol·$m^{-2} \cdot s^{-1}$ to light extinction comparing watered and droughted plants on day 21 and the influence of watering on the droughted cohort after 24 hours.

4. Discussion

The declines in soil moisture in this study were rapid and consistent with a previous drought study in this area, where the greatest declines occurred in the first two week of the study [13]. Lack of water defines arid or semi-arid environments and the plant species found in these areas [15] [18] [30] [39] [40]. Two factors that appear responsible for the reduction in soil moisture are soil surface evaporation and leaf transpiration [14] [41]-[43]. Most striking during this study was the extreme water stress reached by *C. planostachys*. The reported limitation in Ψ_{leaf} for most grasses and trees is −2.75 MPa and −3.70 MPa, respectively [14] [44]. Plants exceeding their capacity to extract water from the soil, reach the permanent wilting point where a loss of hydraulic conductance occurs, resulting in loss of leaves or the whole plant depending on the severity of tissue cavitation [43] [45]. Studies of prairie systems rarely report grass experiencing drought conditions trending below −3.00 MPa and the change in Ψ_{leaf} closely tracked the change in soil water potential [43] [46]-[49]. The grass response to drought is senescence of aboveground tissue and/or induced dormancy.

At high water stress, *C. planostachys* did not appear to reach a permanent wilting point, as evidenced by rapid recovery of physiological responses, and it had a higher ability to resist desiccation than most herbaceous species. In addition, the Ψ_{leaf} values that *C. planostachys* reached were similar to a few xeric woody species that are reported to have an extreme tolerance to loss of hydraulic conductance [45] [50] [51]. This would include *J. ashei* seedling which co-occur in the understory of these woodlands [42] [52]. The only observable response that *C. planostachys* elicits when water stress exceeds −7.00 MPa is leaf curling, a possibly protective mechanism to conserve water loss. Leaf curling is a reported leaf level response to conserve water loss by providing a secondary boundary layer to water loss [43] [53] [54]. The decline in *C. planostachys* Ψ_{leaf} was not as rapid as expected for most herbaceous perennials. It required at least two weeks for a significant decline to occur. It is common for drought tolerant plants to maintain a high and stable Ψ_{leaf} despite precipitous declines in soil water. Two previous studies on *C. planostachys*, also observed that Ψ_{leaf} did not decline significantly until well after most water had been depleted from the soil [31] [52]. A similar response to water stress was observed for *J. ashei* seedlings [31] [42].

The mechanism that allows *C. planostachys* to resist loss of hydraulic conductance is not known. Stomatal conductance is often considered a critical regulator in transpirational loss of water, as a means to retard water stress [45] [54] [55]. However, this does not appear to be a functional trait for *C. planostachys*. Examination of leaf stomatal conductance and transpiration indicated that the drought treatment did cause changes in water loss but there was no indication of stomatal closure. There were differences in stomatal conductance between water and drought treatments. Leaf wilting, as indicated previously, provided some protective benefit toward catastrophic loss in hydraulic conductance, but also stomatal regulation or change in solute concentration may be important in turgor maintenance [43] [45] [54].

During drought-induced stress, the response of many herbaceous species is a reduction in photosynthetic rates, which mostly are related to changes in Ψ_{leaf}. Rapid declines in the C_4 grass *Andropogon gerardii* photosynthesis (50 % - 80 %) followed reductions in Ψ_{leaf} of 2 or 3 MPa [46]. The principal cause for reductions of the physiologic processes were considered related to water limitation in shallow soils [48], which is also true in central Texas [16]. An additional study demonstrated a similar response with reductions in photosynthesis by ca. 80 % over two weeks [56]. While the decrease in the photosynthetic response of the drought tolerant C_4 grass *A. gerardii* is rapid, occurring in a few days, the response for *C. planostachys* is much slower, requiring up to three weeks. *Carex planostachys* in the field showed a delayed response of change in photosynthetic rates to drought after ca. 60 days [31]. The cause for a delayed photosynthetic response is unknown. But, in the absence of a decline in conductance suggests stomatal closure is not occurring. A more probable cause is that during severe stress, a late-drought response, limiting photosynthesis, is associated with a biochemical response occurring with decreased metabolic activity [43] [57] [66]. Thus, a reduction in photosynthesis may be a protective response due to increased photorespiration [43] [57].

The response curve parameters suggest that *C. planostachys* is a shade tolerant plant having a low compensation point, dark respiration and saturates at low light levels [24] [25] [58]-[62]. These values are comparable to other shade tolerant, herbaceous plants, that occur beneath a canopy [14] [36] [60]. During both drought and recovery, *C. planostachys* demonstrated a plastic response in its photosynthetic parameters to change in light levels. A plastic response is critical toward a plants survival in habitat that experience change in environmental stress [25] [63]-[65]. *Carex planostachys* demonstrated the expected downward trend in the maximum photosynthetic rate and saturation rate, while the light compensation point increased. These responses are likely due to non-stomatal limitations to reduce heat related damage that could occur with loss of transpirational cooling or an attribute of shunting light energy. Several studies have demonstrated that the increase observed in the saturation rate could result from a photorespiratory effect to promote dissipation of excess light energy [65]-[67]. During stomatal closure or reduced aperture size, photorespiration acts as a mechanism to maintain a higher intercellular CO_2 concentration, thus preventing damage to the photosystem. Photorespiratory shunting of excess light from the photosystem during drought stress can dissipate from 70 to 90 % of the light absorbed by the leaf, thus serving as a thermal protective mechanism [43]. Following rehydration, preservation of the photosystem permits a rapid recovery from stress following stomatal opening.

The rate of *C. planostachys* recovery in its photosynthetic process following long-term water stress was rapid. Following rehydration of plants after 21 days of drought, an increase in photosynthetic gain was observed in 24 hours and within one week appeared fully recovered. In the second recovery experiment following day 28 of drought recovery did not begin in the first 24 hours, but plants appeared fully recovered by the next week. Daily measurements were not made until the week after rehydration, so it is unclear if full recovery could have occurred sooner. Photosynthesis decreased slightly over the course of the drought treatment; however, the effect, whether a result of a decreasing stomatal aperture or alteration of metabolic activity was not permanent, as evidenced by physiologic recovery. If a photoinhibition response, such as photorespiration, was responsible for the downward regulation in photosynthesis, this could explain the rapid recovery observed. It is rare, even under severe drought stress for permanent photoinhibition to occur [65]. Maintenance of a functional photosystem would allow for CO_2 uptake to occur when stress negatively affecting photosynthesis is reduced. If conductance for *C. planostachys* is coupled to photosynthesis and not soil water, this could in part explain rapid recovery. For recovery in plants to occur when conductance is coupled to soil water, then a signaling system must first be initiated from the roots to override stomatal closure [68]. However, if conductance is coupled to photosynthesis through increases in light levels, then CO_2 uptake could begin rapidly after rehydration without a lag. Water is considered a primary factor influencing growth, particularly in arid systems and can have a negative impact on CO_2 uptake. Few studies have examined the recovery of photosynthesis following rehydration after drought. One study though demonstrated that the drought tolerant *Larrea tridentata* has rapid recovery, which initiates within one day, accompanied by recovery in leaf water status [69]. Within three days, rehydrated *L. tridentata* demonstrated a significant increase in photosynthetic gain.

5. Conclusion

Carex planostachys is found in arid and semi-arid upland *Juniperus/Quercus* woodlands. In this experiment plants were placed in pots in partial shade. Water loss was from 32% to 8% by day 28. Leaf water potential declined to −10.0 MPa after 35 days without watering. Non-watered plant $A_{net,}$ (photosynthetic rate), stomatal conductance and transpiration were significantly lower than the water treatment by day 21. Recovery of physiological responses to values similar to continuously watered plants occurred within 7 days of watering. *Carex planostachys* was able to withstand drought greater than the annual spring trends in lack of precipitation in this area. *Carex planostachys* can photosynthesize at water stress between −8 and −10 MPa and drought and shade tolerance enable it to occupy the understory of these woodlands.

Conflicts of Interest

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

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