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Effects of flooding on photosynthesis and root respiration in Saltcedar (tamarix ramosissima), an invasive riparian shrub

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EFFECTS OF FLOODING ON PHOTOSYNTHESIS AND ROOT RESPIRATION IN SALTCEDAR (*TAMARIX RAMOSISSIMA*), AN INVASIVE RIPARIAN SHRUB

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ABSTRACT

The introduced shrub *Tamarix ramosissima* Lebed. invades riparian zones, but loses competitiveness under flooding. This was tested in *Tamarix ramosissima* by examining responses to flooding by soil type in a greenhouse setting. A field study examined responses of *Tamarix ramosissima* and other species to natural flooding. Leaf level photosynthesis rates, stomatal conductance, transpiration, and root alcohol dehydrogenase (ADH) activity were measured weekly to assess oxygen stress. In the field, stomatal conductance, leaf water potential, transpiration, canopy cover, and $\delta^{13}C$ were measured as responses to soil water potential, soil moisture, Julian date, relative humidity, and water depth. In the greenhouse study, flooding affected *Tamarix ramosissima* initially. Photosynthesis rates within flooded plants ranged from 7.5 to 14 μmol CO_2 m^{-2} s^{-1} during the first two weeks, but increased to 26.9 to 27 μmol CO_2 m^{-2} s^{-1} by the fourth week. As flooding progressed, photosynthesis rates increased as plants became acclimated. Lower photosynthesis rates at the onset of flooding could account for the susceptibility of *Tamarix ramosissima* to flooding. Soil type had no effect on photosynthesis rates or on root ADH activity. Root ADH activity was higher in flooded plants compared to drained plants, indicating oxygen stress in flooded plants. The ability of *Tamarix ramosissima* to acclimate to flooding within four weeks indicated metabolic acclimation. In the field study, *Tamarix ramosissima* had lower stomatal conductance and leaf water potential compared to *Populus deltoides* Bartr. and *Phragmites australis* (Cav.) Trin. ex Steud at -1.4 MPa and 1.5 mmol H_2O m^{-2} s^{-1}. Lower leaf water potential and stomatal conductance in the field can also account for loss of competitiveness of *Tamarix ramosissima* under flooding. *Typha angustifolia* L. had the highest canopy cover

compared to *Tamarix ramosissima*, *Melilotus officinalis* (L.) Lam., *Baccharis salicina* Torr. & A. Gray, and *Saccharum ravennae* (L.) L. Differences in canopy cover indicated *Typha angustifolia* was more tolerant of flooding compared to *Tamarix ramosissima*. Nonetheless, *T. ramosissima* is more flooding tolerant than previously realized. Differences in physiological responses for *Tamarix ramosissima* could become important for ecological or management concerns with this species.

Key words: *Tamarix ramosissima* Lebed., flooding, root alcohol dehydrogenase, photosynthesis, $\delta^{13}C$, plant water potential, canopy cover

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PREFACE

The thesis is written in the style of Journal of Arid Environments. This is the journal to which the thesis will be submitted shortly after its defense.

1. INTRODUCTION

There is a growing concern worldwide with invasive species. A species is considered invasive when it establishes a new range in which it proliferates, spreads, and persists, doing harm to the environment (Mack et al., 2000). It is estimated that 400 of 958 species on the U.S. Endangered Species list are due to competition with or predation by invasive species (Pimentel et al., 2005). Invasive species are not only harmful to flora and fauna, but are also costly. It was recently estimated that invasive species cost the United States $120 billion per year in environmental damages and losses (Pimentel et al., 2005), but it is difficult to estimate the total impact of these species.

Riparian systems are especially vulnerable to invasion by exotic species due to several factors. Each year, riparian systems undergo disturbances such as floods, droughts, and fires that can open areas to invasion (Naiman and Décamps, 1997). Effects of invasive species in these areas include changes in habitat structure, biodiversity, nutrient cycling, and food webs (Zedler and Kercher, 2004). Riparian areas are important for preservation because these ecosystems act as habitat for many species, function as filtration between land and water, and are migratory corridors for many organisms (Nilsson and Berggren, 2000).

Vegetation within riparian zones is determined by several factors, including regional climate, other species, hydrology, and disturbance (Richardson et al., 2007). Along riparian zones in the western United States, disturbance regimes have been altered due to impoundments (Busch and Smith, 1995), water retention developments, and groundwater mining (Hancock, 2002). Consequences of altered flood regimes include increased sedimentation from adjacent land use (Richardson et al., 2007), narrowing of

channels and reduction in overbank flooding (Shafroth et al., 2002). These alterations can enhance invasion by introduced species. Riparian zones aid in dispersal of propagules by currents and seasonal receding floodwaters (Naiman and Décamps, 1997). Additionally, riparian hydrology often causes fluctuations in water levels, destroying vegetation that cannot tolerate drought or high water levels (Richardson et al., 2007). These fluctuations release resources and introduce new areas in which invasive genera can establish. One such genus in the southwestern United States that takes advantage of hydrologic fluctuations is *Tamarix* L.

Eight species of *Tamarix* were brought to the United States in the 1800s for erosion control, shade, ornamentation, and wind breaks (DiTomaso, 1998). Many of these species escaped cultivation, and by the 1920s had invaded 4,000 ha of riparian systems in the southwestern United States (Neill, 1985). By the late 1980s, these species were estimated to have overtaken 600,000 ha of riparian and wetland systems (DiTomaso, 1998). More recent estimates suggest these species are expanding 18,000 ha per year (Gaskin and Schaal, 2002).

One species of *Tamarix* is especially problematic in the west. *Tamarix ramosissima* Lebed. (saltcedar) displaces native tree genera of willow (*Salix* L.), cottonwood (*Populus* L.) (Frasier and Johnsen, 1991; DiTomaso, 1998), and mesquite (*Prosopis* L.) (Cleverly et al., 1997). *Tamarix ramosissima* also changes the ecological functions of invaded areas. For example, *T. ramosissima* has reduced nesting habitat for bird species such as the least tern (*Sternula antillarum*) in the Great Plains and for the Yumma clapper rail (*Rallus longirostris yumanensis*) in the Colorado River Valley

(DeLoach et al., 2000). Many insects have also lost habitat, which provide a food source for birds (Ohmart et al., 1988). *Tamarix ramosissima* not only impacts animal species in invaded areas, but also alters ecosystem structure. For instance, *Tamarix ramosissima* narrows waterways, causing subsequent flooding (Busch and Smith, 1995).

During drought, *T. ramosissima* has several competitive advantages over native riparian tree species. *Tamarix ramosissima* has greater control over stomatal conductance compared to native species, which limits water loss (Anderson, 1982). It is less susceptible to cavitation of xylem elements during water stress compared to native species (Glenn and Nagler, 2005). *Tamarix ramosissima* can physiologically withstand lower water potentials (Devitt et al., 1997), and it is phreatophytic, which allows it to reach ground water more readily (Brotherson and Field, 1987).

In field conditions, *Tamarix ramosissima* can survive 5,000 ppm salts in soil, which is double the concentration that willows and cottonwoods can tolerate (Busch and Smith, 1995). The main reason *T. ramosissima* can survive in high saline conditions is because it can accumulate salts within its tissues (Maryam et al., 1995). In a field study by Tomar et al. (2003), *Tamarix articulate* Vahl. grew better in saline conditions compared to 31 other different species tested.

Under flooded conditions, the competitive advantage of *Tamarix ramosissima* is unclear. In one study by Vandersande et al. (2001), adult *T. ramossisima* lost their competitive advantage, stopped growing, and dislodged after 70 days of flooding. However, another study showed that *T. ramosissima* can withstand flooding up to 70 days (Brotherson and Field, 1987).

Seedlings of *Tamarix ramosissima* have been out competed during flooding in several studies. For example, Gladwin and Roelle (1998) showed *T. ramosissima* seedlings died under 25 days of flooding, whereas *Populus deltoides* Bartr. seedlings survived. In a study by Sher et al. (2000), *P. deltoides* seedlings were able to outcompete *T. ramosissima* under flooding. The Sher et al. (2000) study highlighted that one possible mechanism for *P. deltoides* seedlings outcompeting *T. ramosissima* was that *P. deltoides* was able to increase above and below ground biomass more. However, Sprenger et al. (2001) reported *P. deltoides* seedlings were outcompeted by *T. ramosissima* seedlings under 30 days of flooding. In a study by Tallent-Halsell and Walker (2002), *T. ramosissima* was able to grow more rapidly than *Salix goodingii* Ball. under saturated conditions in gravel and sand soil types, but both species did not survive complete inundation. It has also been observed that *T. ramosissima* and native species can establish in the same area under flooding in gravel if species occupy different flood zones (Roelle et al., 2001). In most cases, *T. ramosissima* is less tolerant of flooding compared to native riparian tree species. Although there has been extensive work regarding survival and competition of *T. ramosissima* during flooding, the mechanisms that make *T. ramosissima* less competitive under flooding are unclear. None of these studies examined physiological responses of *T. ramosissima* to flooding.

One explanation for loss of competitiveness of *Tamarix ramosissima* under flooding could be increased oxygen stress during flooding, indicating a sensitivity to waterlogged sediments. Water displaces oxygen in flooded soils, owing to low solubility

and slow diffusion (Blom and Voesenek, 1996). Any remaining oxygen will be consumed by plants and microorganisms, resulting in anaerobic conditions (Pezeshki, 2001).

Under oxygen-poor conditions such as flooding, anaerobic respiration occurs. The enzyme that helps regulate anaerobic respiration in plants is alcohol dehydrogenase (ADH) (Kimmerer, 1987). ADH plays an important role within alcohol fermentation in flooded plants. When there is no oxygen present, NADH cannot be oxidized in oxidative phosphorylation (Liao and Lin, 2001). This causes the plant to carry out alcohol fermentation, where ADH helps to convert acetaldehyde into ethanol by oxidizing NADH (Kimmerer, 1987). This allows glycolysis to continue, meeting some of the metabolic energy needs of the plant. Accordingly, oxygen stress is one potential explanation for decreased performance of *T. ramosissima* under flooding. This is measurable by increased ADH activities in roots.

Decreases in photosynthesis could also explain why *Tamarix ramosissima* is less competitive under flooding. In some plants, flooding causes photosynthesis rates to decrease (Pezeshki, 2001). This can occur within hours of flooding (Kozlowski, 1997). As a stress response, stomata typically close during flooding (Kozlowski, 1984), potentially lowering photosynthesis and gas exchange rates of the plant (Pezeshki, 2001). Any treatment reducing photosynthesis would be expected to decrease growth and performance of a plant.

Stomatal closure decreases intake of atmospheric CO_2. Whole leaf stomatal regulation can be measured through the analysis of leaf $\delta^{13}C$. In C_3 plants, the enzyme Rubisco discriminates against ^{13}C during photosynthesis (Rounick and Winterbourn,

1986). Isotopic discrimination of carbon can change due to stomatal closure. For C_3 plants, $\delta^{13}C$ values increase with stomatal closure. A decrease in CO_2 within leaf tissue forces Rubisco to use more ^{13}C than normal. As Rubisco uses the heavier isotope, the isotopic value of leaves becomes higher (more positive) and this is incorporated into the $\delta^{13}C$ of leaf tissue (Farquhar et al., 1982). If flooding-induced stomatal closure influences photosynthesis and performance in *Tamarix ramosissima*, an analysis of $\delta^{13}C$ could help to explain responses to flooding.

Effects of flooding on *Tamarix ramosissima* are of obvious importance for its invasive success. Yet, no studies have investigated physiological responses of *T. ramosissima* under flooding. Accordingly, this study sought to identify the physiological effects of flooding on *T. ramosissima*. This included two greenhouse studies and a field study.

The main objective of the greenhouse studies was to determine a mechanism to explain why *T. ramosissima* loses competitive ability during flooding. This was approached by examining physiological effects of flooding on photosynthesis and root respiration. Specifically, effects of flooding over time and effects of soil type were investigated. It was hypothesized that *T. ramosissima* would show an increase in root alcohol dehydrogenase activity. This would indicate a stress response to anaerobic conditions. Similarly, it was hypothesized that soil type would cause an increase in root alcohol dehydrogenase activity as a result of anaerobic conditions that correlate with soil particle size. It was also hypothesized that flooding could cause a decrease in photosynthesis, which could influence leaf $\delta^{13}C$ values.

The main objective of the field study was to compare physiological responses of *Tamarix ramosissima* with other species in the community under natural flooding regimes. The field study was used to assess interspecific differences in transpiration rates, stomatal conductance, leaf water potential, canopy cover, and leaf $\delta^{13}C$ values as influenced by flooding. It was hypothesized that many physiological responses would decrease during flooding. Shifts in canopy cover between species were expected to occur due to tolerance or intolerance of flooding.

2.1. Site description

The study and collection site was at the Commanche Boat Ramp at Cedar Bluff Reservoir, Trego County, KS, USA (38°46′ N, 99°41′ W). The site is prone to invasion by species such as *Tamarix ramosissima*, *Phragmites australis* (Cav.) Trin. ex Steud., and *Typha angustifolia* L. Other common nonnative species in this area are *Melilotus officinalis* (L.) Lam., *Baccharis salicina* Torr. & A. Gray, and *Saccharum ravennae* (L.) L. A native dominant species is *Populus deltoides*. Floods are common at the site following heavy rains. The main soil type at the Commanche Boat Ramp is Armo silt loam (Watts et al., 1990).

2.2. Physiological responses to flooding and soil type

Juvenile *Tamarix ramosissima* was collected in autumn of 2008, and identified from *Flora of the Great Plains* (Great Plains Flora Association, 1986). Plants were brought to the Fort Hays State University greenhouse (Hays, KS, USA) and planted in potting soil mixed with one ounce of Osmocote® fertilizer per pot (19% N, 6% P, 12% K) (Scotts Miracle-Gro Co.; Marysville, OH, USA). Pot sizes were 3.8 L. Plants were allowed to grow 4 months before experimentation. During this time, plants were watered every two to three days.

Eight total plants were used to examine plant responses over time to flooding. Experimental *T. ramosissima* plants were healthy in appearance and were approximately 31 cm in height. Four plants were randomly selected as a control; they were watered

every two to three days, and water was allowed to drain from pots. The remaining plants were individually placed in plastic tubs with dimensions of 61 x 40 x 22 cm. Each tub was filled with water to 12 cm depth, which was enough to saturate the soil. Plants were flooded for four weeks during January 2009. Photosynthesis measurements were made weekly on all plants. At the end of experimentation, roots were harvested from all plants for root alcohol dehydrogenase (ADH) assays.

For the soil type experiment, individuals of *Tamarix ramosissima* were collected in autumn of 2009. An Armo silt loam soil was collected from the same location. Plants and soil were brought to the Fort Hays State University greenhouse. Plants were transplanted in 3.8 L and 1.9 L pots. Pot sizes were randomly dispersed across treatments. No plants were limited by pot size. Plants were grown in potting soil for one month to establish the root system and improve survival of transplants. Following this, plants were potted in different soil types. The Armo silt loam soil was mixed with sand to create five soil mixtures: 100% Armo, 75% Armo, 50% Armo, 25% Armo, and 100% sand. Plants were placed on trays and were watered from the bottom, where < 2.5 cm of water was added once per week. Plants were grown in the soil mixtures for three months before flooding treatments began.

Thirty plants were used to examine how soil type influences responses to flooding in *Tamarix ramosissima*. Plants were healthy in appearance and approximately 31 cm in height. Fifteen plants were randomly selected for the drained (control) treatments with three plants (n =3) in each soil type. Plants were watered from the bottom once per week. The remaining 15 plants were placed individually into tubs. Tubs were filled with enough

water to saturate the soil. Plants were rotated between tubs weekly to ensure equal conditions.

Plants were flooded for three weeks in January 2010. The greatest effects of flooding on *T. ramosissima* occurred during the first two weeks (see Results), and the most important information could be gathered within three weeks of flooding. Photosynthesis measurements and root harvesting were completed in the same manner as the flooding duration experiment.

Photosynthesis was measured weekly for each plant by using an LI-6400 (Li-Cor Biosciences, Inc.; Lincoln, NE, USA) infrared gas analyzer system in differential mode. Light response curves were constructed by measuring photosynthesis at 2000, 1500, 1000, 500, 200, 100, 50, 20, and 0 μmol quanta m^{-2} s^{-1}. Measurements from light response curves used for comparisons between treatments included 1) maximum photosynthesis (P_{max}), the maximum measured rate of CO_2 uptake (Larcher, 2003); 2) net quantum efficiency (net qe), the linear increase of CO_2 uptake by the plant under increasing light, representing the relation between available radiation and photosynthetic yield (Larcher, 2003); and 3) photosynthesis at 1500 μmol quanta m^{-2} s^{-1} (A_{1500}). Stomatal conductance (g_s) and transpiration (E) were measured at the same nine light levels and were used in treatment comparisons.

Leaves were placed into the leaf chamber, covering an area of 2 cm^2. Every effort was made to equalize the leaf area being measured across plants by forming a single leaf layer in the chamber (Horton et al., 2001; Mounsif et al., 2002; Gries et al., 2003; Moore et al., 2008). Leaves were marked for use in weekly measurements. Relative humidity in

the chamber was 25%, CO_2 levels were 385 ppm, and block temperature was 25°C. Measurements were made after plants became adjusted to conditions, determined when photosynthesis and stomatal conductance stabilized, typically requiring 10-20 minutes.

Root samples were harvested at the end of greenhouse studies, rinsed in tap water, and frozen in liquid nitrogen. Root ADH assays were completed following the procedure described by Maricle et al. (2006). Roots were ground in liquid nitrogen with a chilled mortar and pestle. Cold extraction buffer was added to the resulting powder at 5 mL g^{-1}. The mixture was ground thoroughly and poured into a microcentrifuge tube, where it was centrifuged at 10,000 x g for ten minutes. The resulting supernatant was used as enzyme extract in the assay.

The reaction mixture for ADH assays was assembled in a 1.0 mL cuvette containing 950 µL of assay buffer, 20 µL of 4 mM NADH, and 10 µL of enzyme extract. Background rates of NADH oxidation were measured for one minute at 340 nm in a Shimadzu UV 160 UV-visible light spectrophotometer (Shimadzu Corporation; Kyoto, Japan). The reaction was initiated by adding 20 µL of 0.5 M acetaldehyde. Enzyme activity was calculated by the difference in NADH oxidation in the presence and absence of acetaldehyde. The corrected slope was divided by the extinction coefficient for NADH at 340 nm (6.22 mol m^{-3} cm^{-1}) and the fresh weight of root tissue. Final ADH activity was recorded in µmol NADH oxidized per gram of fresh root weight per minute.

Observations on appearance of plants were recorded for both greenhouse experiments. Specific observations were development of new shoot growth, leaf

chlorosis, and leaf drying. These observations were used to support findings of physiological measurements.

2.3. Field study

A field study was conducted from May to August, 2010 at the Commanche Boat ramp. Heavy rains occurred in mid May and early June, flooding the site. Species examined for physiological data were *Tamarix ramosissima*, *Phragmites australis*, and *Populus deltoides*, Species examined for canopy cover were *Tamarix ramosissima*, *Phragmites australis*, *Populus deltoides*, *Melilotus officinalis*, *Typha angustifolia*, *Baccharis salicina*, and *Saccharum ravennae*. All species identifications were verified using *Flora of the Great Plains* (Great Plains Flora Association, 1986)

Five 25 m transects were established at the study site near the waterline. Transects were oriented perpendicular to the shore, and were spaced 10 m apart. Points were marked on each transect at five meter intervals, for a total of 30 points. Elevation and GPS coordinates were recorded for each point by using a Garmin® eTrex® Vista Cx GPS unit accurate to 2 m (Garmin; Olathe, KS, USA). Individual plants for study were chosen by placing a 0.30 m line perpendicular to the right side of each transect point. The first plant to intersect the line was marked for study with flagging tape.

Soil moisture content was measured monthly by sampling 100 g of the top 15 ± 5 cm of soil at each point with a 2.0 cm soil probe (Oakfield Apparatus Company; Oakfield, WI, USA). Soil was sealed in plastic bags, brought back to Fort Hays State University, and placed in metal tins. 100 ± 0.5 g of soil was added to each tin. Tins were

placed into a drying oven at 40°C and were weighed daily until there was no change in mass. Percent moisture was calculated from mass lost.

A sample of soil from all points was used for measurement of soil water potential in a WP4-T Dewpoint Potentiameter (Decagon Devices, Inc; Pullman, WA, USA). Leaf water potential was measured once per month in all marked plants with a model 1000 pressure chamber (PMS Instrument Company; Albany, OR, USA). A leaf or branch was randomly selected on each plant for measurement.

Equations from Campbell and Norman (1998) were used in calculating leaf transpiration rates of marked plants once per month. Relative humidity of air was measured with an RH300 digital psychrometer (Extech Instruments; Waltham, MA, USA). Wind speed was measured with an AM-4204 hot wire anemometer (Lutron Electronic Enterprise Co.; Taipei, Taiwan). Leaf width was measured for all plants except *Tamarix ramosissima* with a Titan® electronic digital caliper (Star Asia-USA LLC (Titan Tools); Auburn, WA, USA). The relevant measure for *T. ramosissima* is stem width, since leaves are scalar, small in size, and grow closely to the stem. An SC-1 leaf porometer (Decagon Devices, Inc; Pullman, WA, USA) was used to measure stomatal conductance and leaf temperature. Additional stomatal conductances were measured monthly with the same process, but not used in calculating transpiration rates. These measurements were used in examining effects of flooding on the different species.

Leaf transpiration was calculated from Campbell and Norman (1998) as:

$$\lambda E = \lambda g_v \frac{e_s(T_L) - e_a}{P_a} \quad (1)$$

where λ is the latent heat of vaporization, E is vapor flux density, e_a is vapor pressure of the air, e_s (T_L) is vapor pressure at the leaf surface, and P_a is atmospheric pressure.

Total conductance to water vapor (g_v) was calculated from:

$$g_v = \frac{1}{\frac{1}{g_{va}} + \frac{1}{g_{vs}}} \tag{2}$$

where g_{vs} is stomatal conductance and g_{va} was boundary layer conductance, calculated as:

$$g_{va} = 0.147\sqrt{\frac{u}{d}} \tag{3}$$

where u is wind speed (m s^{-1}) and d is the characteristic dimension of the leaf (0.72 x leaf width, in m).

Vapor pressure at the leaf surface ($e_s(T_L)$) was calculated by:

$$e_s(T_L) = a\exp\left(\frac{bT}{T+c}\right) \tag{4}$$

where a is 0.611 kPa, b is 17.502, c is 240.97°C, and T_L is leaf temperature (°C). Vapor pressure of the air (e_a) was calculated from:

$$h_r = \frac{e_a}{e_s(T_L)} \tag{5}$$

where h_r is relative humidity and e_s (T_L) is vapor pressure at the leaf surface. Atmospheric pressure (P_a) was calculated by:

$$P_a = 101.3\exp\left(\frac{-X}{8200}\right) \tag{6}$$

where X is elevation (m).

Water depth was measured with a meter stick at each point twice per month for the duration of the study. Canopy cover for each transect point was measured by species with a model-C concave spherical densiometer (Bartlesville, OK, USA) in the months of June, July, and August. The spherical densitometer is a concave mirror that contains squares that are divided into quarters for a total of 96 quarters. Canopy cover was estimated by counting total number of covered quarters by species in the four cardinal directions. Counted quarters were averaged by species and multiplied by 1.04 to calculate percent of canopy cover for each species (Lemmon, 1956).

2.4. Stable isotope preparation

Leaf samples were randomly collected monthly from field plants for $\delta^{13}C$ analysis. Collected leaves represented new growth to correspond to any effects during experimentation. Leaf samples were dried overnight at 40°C. A Wiley mill (Thomas Scientific; Swedesboro, NJ, USA) was used to grind leaf samples. Ground samples were able to pass through a 20 mesh screen. Ground samples (1.0 ± 0.1 mg) were packaged in tin capsules and sent to Washington State University's stable isotope lab for $\delta^{13}C$ analysis.

2.5. Data analysis

All data were analyzed with SPSS 12.0 for windows (SPSS Inc.; Chicago, IL, USA). A repeated measures analysis of variance (ANOVAR) was used in greenhouse experiments for maximum photosynthesis, net quantum efficiency, transpiration at 1500 μmol quanta m^{-2} s^{-1}, stomatal conductance at 1500 μmol quanta m^{-2} s^{-1}, and

photosynthesis at 1500 μmol quanta m^{-2} s^{-1}. A two sample t-test was used to compare root 16 alcohol dehydrogenase activity for responses to flooding duration. Root alcohol dehydrogenase activity for the soil treatments was analyzed with analysis of variance (ANOVA). Post hoc comparisons were performed with Tukey's LSD. Qualitative appearances of plants were not statistically analyzed, but categorized by percentages to indicate plants that developed new growth, leaf chlorosis, or leaf drying.

Data were transformed as needed for normal distribution. For field data, canopy cover and soil moisture data were transformed using an arcsine transformation since the data were proportions. Water depth was coded into a 1 or 0. One indicated coverage of water and 0 indicated no water, which resulted in a normal distribution of data. Stomatal conductance and transpiration data were transformed using log(x+1). Soil water potential was transformed using e^x.

Analysis of covariance (ANCOVA) was performed for canopy cover. Covariates were Julian dates, soil water potential, and water depth. Sampling units for canopy cover were five transects with six points on each. Any missing variables or cases that were labeled "dead" were removed from the data set. An ANCOVA was performed for stomatal conductance from *Populus deltoides* (*n*=17), *Phragmites australis* (*n*=9), and *Tamarix ramosissima* (*n*=30). Covariates were air temperature, Julian dates, soil water potential, and water depth. A multivariate analysis of covariance (MANCOVA) was performed for plant water potential, transpiration, and a second round of stomatal conductance measures between species. Covariates were water depth, Julian dates, soil moisture, relative humidity, and air temperature.

$\delta^{13}C$ data were analyzed with ANCOVA for May, June, and July for *Tamarix ramosissima* (*n*=13) and *Populus deltoides* (*n*=10). One *Phragmite australis* plant was destroyed by a non-demonic intrusion, so $\delta^{13}C$ was not analyzed. Covariates were air temperature, Julian dates, soil water potential, and water depth.

Julian dates were used instead of months to determine if time influenced response variables. Pearson correlations were also run alongside both ANCOVAs and the MANCOVA to determine if any variables were correlated. All analyses were performed at α=0.05.

3.1. Physiological Responses to Flooding and Soil Type

3.1.1: Photosynthesis at 1500 µmol quanta m^{-2} s^{-1} (A_{1500})

Photosynthetic light response curves were measured weekly for four weeks to study effects of flooding over time (Fig. 1). Photosynthesis rates were hyperbolic with respect to irradiance. Flooding reduced photosynthesis, stomatal conductance, and transpiration in weeks one and two. Photosynthetic light response curves were also measured weekly for three weeks to study effects of soil type on photosynthesis (Fig. 2). Light response curves were similar for all soil treatments. Specific differences between treatments, soils, and times are as follows:

When considering differences in flooding over time, photosynthesis at 1500 µmol quanta m^{-2} s^{-1} (A_{1500}) ranged from 5.6 to 19.5 µmol CO_2 m^{-2} s^{-1} for the drained treatment and from 1.8 to 27 µmol CO_2 m^{-2} $s^{-1}$for the flooded treatment (Fig. 3). A_{1500} was significantly greater in week four compared to week one ($F=13$, $p=0.02$). There were no differences between treatments ($F=1.2$, $p=0.32$), and there was no week*treatment interaction in A_{1500} ($F=2.9$, $p=0.17$).

When considering differences in soil type and water treatments, A_{1500} ranged from 2.4 to 16 µmol CO_2 m^{-2} s^{-1} across soil type and water treatments (Fig. 4). A_{1500} was significantly greater in week one compared to week three ($F=8.6$, $p<0.01$). A_{1500} for the drained treatment was significantly higher compared to the flooded treatment (Fig. 4; $F=5.8$, $p=0.03$) across all soil types. There were no differences between soil treatments ($F=1.4$, $p=0.27$), and there was no soil*water interaction ($F=0.13$, $p=0.94$).

3.1.2: Maximum photosynthesis (P_{max})

The flooded treatment for responses to flooding over time had a maximum photosynthesis (P_{max}) range from 7.5 to 14 μmol CO_2 m^{-2} s^{-1} during the first two weeks, which increased by weeks three and four (Fig. 5; F=13, p=0.02). P_{max} for the drained treatment had a similar pattern for the first two weeks, but decreased by week four (F=13, p=0.02). There were no significant differences between drained and flooded treatments (F=1.0, p=0.29). There was no significant treatments*weeks interaction (F=2.9, p=0.17).

P_{max} was significantly different between weeks across soil treatments for responses to soil type (Fig. 6; F=5.6, p=0.01). P_{max} was highest for the drained treatment in week three at 17 μmol CO_2 m^{-2} s^{-1}. The lowest P_{max} was 2.9 μmol CO_2 m^{-2} s^{-1} in week one for the flooded treatment (Fig. 6). P_{max} for the soil treatments was significantly higher in drained plants compared to flooded plants (Fig. 6; F=8.0, p=0.01). However, there were no differences between soil treatments (F=1.7, p=0.20), nor in any interactions ($F \leq 0.77$, $p \geq 0.61$).

3.1.3: Net quantum efficiency (net qe)

Mauchly's sphericity ($x^2 \geq 9.3$, $p < 0.01$) was violated for net qe in greenhouse experiments. A Greenhouse-Geisser correction ($\varepsilon \geq 0.40$) was applied to both data sets. Net quantum efficiency (qe) had a range from 0.01 to 0.11 CO_2 $quantum^{-1}$ across treatments and weeks (Figs. 5-6). No statistical differences were seen between weeks, treatments, or their interaction (Fig. 5; $F \geq 0.10$, $p \geq 0.11$) for greenhouse experiments.

3.1.4: Stomatal conductance (g_s) and transpiration (E) at 1500 µmol quanta m^{-2} s^{-1}

Mauchly's sphericity (x^2=12, p=0.04) was violated for g_s comparisons between treatments for responses to flooding over time. A Greenhouse-Geisser correction (ε=0.58) was applied to the g_s data. After correction of g_s, patterns of maximum g_s and E were similar to P_{max} and A_{1500} for responses to flooding over time. Duration of flooding had the most effect on g_s and E, with measures in the flooded treatment increasing over four weeks (Fig. 7; F≥5.8, p≥0.02). There were no difference between treatments for E and g_s (F≥0.01, p≤0.95), and there were no treatment*week interaction for E and g_s (Fig. 7; F≤2.6, p≥0.2).

Similar responses were observed for g_s and E across soil treatments. g_s and E for the soil treatments were affected by the duration of flooding, with both measurements increasing over time (Fig. 8; F≤27, p<0.01). Also, g_s and E were higher in drained treatments compared to flooded treatments (Fig. 8; F≤11, p<0.01). There were no interactions between soil treatments and weeks (F≤1.7, p≥0.13). Soil type was not significant for E or g_s (F≤1.6, p≥0.21), and there were no soil*water treatment interactions (F≤0.24, p≥0.87).

3.1.5: Root alcohol dehydrogenase (ADH) activity

Root alcohol dehydrogenase (ADH) activity ranged from 0.26 to 0.95 µmol g^{-1} min^{-1} across treatments for flooding effects over time. Root ADH activities were not different between drained and flooded treatments (Fig. 9; t=-1.2, p=0.27).

There was no difference in root ADH activity between soil type (Fig. 10; $F=2.6$, $p=0.07$). However, root ADH activity was significantly higher in flooded treatments compared to drained treatments ($F=16.5$, $p<0.01$) when compared across soil types. ADH activity ranged from 3.9 to 13 μmol $g^{-1}min^{-1}$ in the flooded treatment, and from 0.71 to 2.6 μmol $g^{-1}min^{-1}$ in the drained treatment. There was no soil type*water treatment interaction ($F=1.3$, $p=0.32$).

3.1.6: Qualitative descriptions for greenhouse experiments

Table 1 describes the appearance of plants throughout greenhouse experiments. Most of the flooded plants in the flooding duration experiment had new growth that developed during flooding. All flooded plants developed leaf chlorosis, and drying of leaf tissue. Drained plants had no new growth develop or leaf chlorosis, but most plants had drying of leaf tissue.

All plants in the soil treatments had new growth that developed during experimentation (Table 1). Some of the plants in the 100% Armo drained treatment developed leaf chlorosis, and all drained plants had drying develop in leaf tissue. All plants in flooded treatments developed leaf chlorosis.

3.2. Field Study

3.2.1: Stomatal conductance, transpiration, and leaf water potential

Physiological responses of log(x+1) stomatal conductance (g_s), log(x+1) transpiration (E), and leaf water potential (Ψ) were significantly different for Julian date, coded water depth, and relative humidity ($F \leq 31$, $p<0.01$). No differences were observed

between leaf Ψ, E, and g_s for arcsine soil moisture or air temperature ($F \leq 1.7$, $p \geq 0.19$). There was a significant difference between species for the physiological measurements of leaf Ψ, log(x+1) E, and log(x+1) g_s (Fig. 11, 12; $F=2.9$, $p=0.13$). More specifically, species had a significant interaction with leaf Ψ (Fig. 11; $F=3.5$, $p=0.04$) and log(x+1) g_s. ($F=3.2$, $p=0.05$), but species did not interact with log(x+1) E (Fig. 11; $F=2.5$, $p=0.10$).

Tamarix ramosissima had a leaf Ψ of -1.4 MPa (Fig. 11). This was significantly lower than *Phragmites australis* at -0.88 MPa ($p=0.05$). *Populus deltoides* had a leaf Ψ of -0.94 MPa, which was significantly higher than *Tamarix ramosissima* ($p=0.03$). Leaf Ψ was not different between *Populus deltoides* and *Phragmite australis* ($p=0.90$). Log(x+1) E ranged from 0.0005 to 0.0006 mol H_2O m^{-2} s^{-1} across species and treatments (Fig. 11). Log (x+1) E was not different between species ($F=2.5$, $p=0.10$). However, log(x+1) E had a significant positive correlation with log(x+1) g_s (Table 2; $r=0.8$, $p<0.01$). Mean log(x+1) g_s ranged from 1.5 to 1.7 mmol H_2O m^{-2} s^{-1} across species and treatments (Fig. 12). Mean log(x+1) g_s was higher in *Phragmites australis* compared to *Tamarix ramosissima* ($p= 0.02$).

There were no significant interactions between Julian date and leaf Ψ or g_s (Fig. 13, 14; $F \leq 2.8$, $p \geq 0.10$), but Julian date had a significant interaction with log(x+1) E (Fig. 12; $F=6.9$, $p=0.01$). Variability was seen for log(x+1) E within months. Log(x+1) E was significantly higher in June at 0.001 mol H_2O m^{-2} s^{-1} compared to July at 0.0003 mol H_2O m^{-2} s^{-1} (Fig. 13; $F=6.9$, $p=0.01$). Log(x+1) E was observed to also increase from May to June and July to August (Fig. 13). Additionally, coded water depth had a significant

interaction with leaf Ψ (F=4.1, p=0.05), and relative humidity had a significant interaction with *E* (F=21, p<0.01).

Julian date did not have a significant correlation with log(x+1) *E* (Table 2; r=-0.26, p=0.05), but instead was negatively correlated with air temperature (r=-0.413, p<0.01). Coded water depth was positively correlated with log(x+1) *E* (r=0.29, p=0.03) and arcsine soil moisture (r=0.84, p<0.01), but was not correlated to leaf Ψ(r=0.21, p=0.12). Relative humidity was negatively correlated with coded water depth (r=-0.33, p=0.01), log(x+1) *E* (r=-0.55, p<0.01), arcsine soil moisture (r=-0.38, p=0.01), and air temperature (r=-0.34, p=0.01).

3.2.2: Stomatal conductance and arcsine canopy cover

Given the species* g_s interaction, *Tamarix ramosissima* had log(x+1) g_s of 1.5 mmol H_2O m^{-2} s^{-1}, which was marginally lower than log(x+1) g_s for *Phragmites australis* at 1.7 mmol H_2O m^{-2} s^{-1} (Fig. 12; F=2.8, p=0.07). Log(x+1) g_s ranged from 1.3 to 2.0 mmol H_2O m^{-2} s^{-1} during the study (Fig. 14). Coded water depth interacted with log(x+1) g_s (ANCOVA, F=4.5, p=0.04). Coded water depth was negatively correlated with log(x+1) g_s (Table 3; r=-0.29, p=0.03). Julian date, e^x soil Ψ, and air temperature did not interact with log(x+1) g_s (F≤3.7, p≥0.06). Julian date and air temperature were negatively correlated (r=-0.71, p<0.01).

There were no significant interactions on arcsine canopy coverage by e^x soil Ψ, Julian date, and coded water depth (F≤0.31, p≥0.58). Canopy cover ranged from 18 to 77% (arcsine transformed 0.18 to 0.77; Fig. 16). e^x soil Ψ was positively correlated with

Julian date ($r=0.39$, $p<0.01$) and water depth ($r=0.41$, $p<0.01$) (Table 4). Arcsine canopy cover did not correlate with any covariates ($r\leq0.11$, $p\geq0.17$).

Arcsine canopy cover was different between species (Fig. 15; $F=9.1$, $p<0.01$). Total canopy cover for *Populus deltoides* was 52% (arcsine transformed 0.52; Fig. 15), which was higher than cover for *Tamarix ramosissima*, *Phragmites australis*, *Melilotus officinalis, Baccharis salicina*, or *Saccharum ravennae* ($p<0.01$). Canopy cover for *Typha angustifolia* was not different from *Populus deltoides* ($p=0.24$) (Fig. 15). However, *Typha angustifolia* was significantly higher in arcsine canopy cover than all other species (Fig. 15; $p<0.01$). All other species were not significantly different from each for arcsine canopy cover (Fig. 15; $p\leq0.94$).

3.2.3: Leaf $\delta^{13}C$

Leaf $\delta^{13}C$ ranged from -27 to -29‰ and was not different between species (Fig. 16; $F=0.01$, $p=0.94$). $\delta^{13}C$ was not different between Julian dates ($F=0.01$, $p=0.92$). $\delta^{13}C$ was not significantly different between e^x soil Ψ, air temperature, and coded water depth ($F\leq1.5$, $p\geq0.24$). $\delta^{13}C$ did not correlate with any covariates (Table 5). However, there were correlations that did occur within the covariates. Water depth correlated with air temperature ($r=0.49$, $p=0.02$) and e^x soil Ψ correlated with air temperature ($r=-0.51$, $p=0.01$).

3.2.4: Species deaths

By the end of the field season, 14 plants had died. Four *Populus deltoides* plants had died, with one being destroyed from non-demonic intrusion. Seven *Tamarix*

ramosissima plants, one *Saccharum ravennae* plant, and two *Melilotus officinales* plants had also died at the end of the field season.

The main objective of the greenhouse studies was to determine why *Tamarix ramosissima* loses its competitive ability to genera such as *Populus* and *Salix* during flooding. The main objective of the field study was to compare physiological responses of *Tamarix ramosissima* and other species in a community to natural flooding. The field study was used to assess how physiological measurements and canopy cover were related to flooding.

4.1. Greenhouse experiments

4.1.1. Photosynthesis

The greenhouse studies examined responses of *Tamarix ramosissima* as a result of flooding over time and in different soil types. Maximum photosynthesis (P_{max}) was affected most by the duration of flooding, but not by drained or flooded treatments for. In the flooded treatment the greatest reduction in P_{max} and A_{1500} was in week one (Fig. 5), but continued to increase for the remainder of flooding. Flooding causes stomatal closure, and reduces photosynthesis (Kozlowski, 1984, 1997). This could explain P_{max} being lower for the flooded treatment in week one. A subsequent increase in P_{max} might have been due to plants acclimating to flooding. For the drained treatment, P_{max} decreased during week four indicating stomatal closure. P_{max} for the drained treatment was lower compared to the flooded treatment. P_{max} for the drained treatment was expected to be higher than the flooded treatment. This was not observed because flooded treatments did not cause stomatal closure.

Soil type did not have an effect on P_{max}. However, P_{max} for the soil treatments was affected by duration of flooding and flooding treatments. Again, P_{max} for the flooded treatments was lowest in week one, but increased in week three (Fig. 6). This might also be due to plants acclimating to flooding due to increased ADH activity.

P_{max} in the drained soil treatments was higher than in the flooded treatments throughout the duration of flooding. Plants were able to keep stomata open, allowing for higher P_{max}. This occurred in a related study by Chen et al. (2005), where photosynthesis in drained treatments was higher in *Lepidium latifolium* L. compared to flooded treatments. *Lepidium latifolium* is another invasive species in riparian zones in the western U.S. that causes similar problems to that of *Tamarix ramosissima*.

A_{1500} had a similar response to that of P_{max}. A_{1500} was most affected by duration of flooding. The flooded treatments had lower A_{1500} in week one (Fig. 3), but then increased for the remainder of flooding. A_{1500} for drained treatments were lower during treatment than in the flooded treatment, and decreased during week four in the experiment for flooding over time. A_{1500} for soil types also responded in the same manner to that of P_{max}.

P_{max} and A_{1500} were higher in the flooded treatment than the drained treatment in responses to flooding over time. P_{max} and A_{1500} increased during the length of flooding. Flooded plants for both these measurements acclimated to flooding. After two weeks, stomatal closure was not a limiting factor for photosynthesis in the flooded treatment, but stomatal conductance was limiting for the drained treatment plants. The same pattern was seen in P_{max} and A_{1500} in the flooded soil treatments.

Net qe was not different between soil types, length of treatment, or flooding treatments. Net qe is proportional to photosynthetic yield (Larcher, 2003). In a related study (Gardiner and Krauss, 2001), apparent quantum efficiency was used to assess flooding responses in bottomland *Quercus pagoda* Raf. In this study, Gardiner and Krauss (2001) observed that flooding reduced apparent quantum efficiency and photosynthesis in plants. *Quercus pagoda* is a riparian species, and experiences similar fluctuations in hydrology as *Tamarix ramosissima*. Understanding photosynthesis responses to flooding and light availability in *Q. pagoda* could aid in the understanding of flooding responses in *T. ramosissima*.

Mechanisms that cause fluctuations in P_{max} and A_{1500} during flooding can be explained by changes in g_s. g_s was higher in the flooded treatment in flooding responses to time. Again, measurements were lowest in week one compared to the remaining weeks for the flooded treatment. This further indicated that flooded plants had acclimated to flooding, and stomatal closure was not limiting for photosynthesis. For the soil type experiment, drained treatments had higher g_s, but g_s increased in the flooded treatments during the treatment period. Measures of transpiration (E), which largely depend on g_s, showed similar patterns between drained and flooded treatments.

Photosynthesis measurements in both greenhouse experiments indicated there were differences for flooding treatments in regards to length of flooding. The only experiment that indicated differences between drained and flooded treatments was the experiment examining responses to soil type. In this experiment, no differences were detected for soil type. Each experiment had small samples sizes (n=3 to n=4), which

could mask statistical differences. For future research, samples sizes should be increased for statistical analysis.

New growth occurred in greenhouse experiments within the flooded treatments (Table 1). Under flooded conditions, plants use escape mechanisms to "cope" with anaerobic stress (Vartapetian and Jackson, 1997). Plants often grow adventitious roots under flooding, allowing more intake of O_2 for respiration (Kozlowski, 1984). This could be an escape mechanism that *Tamarix ramosissima* uses under anaerobic stress, and it could be a reason why photosynthesis measurements increased in the flooded treatments over time. Tissue growth and possible hormone production in *T. ramosissima* should be investigated in further research as a possible escape mechanism.

Low photosynthesis rates in the drained treatments in the first greenhouse experiment could be explained by the physical appearance of the plants (Table 1). Some of the plants had chlorosis that occurred in leaf tissue. Also, drying in leaf tissue occurred in all drained treatment plants, which indicated tissue death. All plants were treated with slow release fertilizer during transplantation to replace lost nutrients, but nutrient deficiency is common in flooded plants due to a shortage of ATP synthesis (Drew and Sisworo, 1977). Flooded plants in both experiments exhibited chlorosis. For future research, plant tissue analysis should be conducted to determine the cause of chlorosis in leaf tissue.

4.1.2. Root respiration

Flooding causes displacement of oxygen in soils, inducing anaerobic conditions (Blom and Voesenek, 1996). These conditions cause anaerobic respiration to occur in a plant, which increases alcohol dehydrogenase (ADH) activity (Kimmerer, 1987). For flood tolerant species, a decrease in root ADH activity is a functional adaption indicating tolerance to oxygen deficient conditions (Larcher, 2003). However, for flooding intolerant species, increased ADH activity can indicate oxygen stress (Maricle et al., 2006).

No differences were detected in root ADH activity between treatments for flooding effects over time. Root ADH activities were expected to increase in flooded treatments due to anaerobic conditions. In a similar study by Kimmerer (1987), root ADH activity increased in *Populus deltoides* due to anaerobic stress. *Populus deltoides* is a riparian species that competes with *T. ramosissima* and is phreatophytic. Understanding root ADH activity responses in *P. deltoides* to anaerobic conditions could allow insight to similar responses in *T. ramosissima*. Root ADH activity in the soil treatments was different between flooded and drained treatments. ADH activity was highest in the flooded treatments, which indicated increased anaerobic respiration capacity in flooded conditions.

Soil type was also expected to cause an increase in root ADH activity as a result of anaerobic conditions that correlate with particle size. This was not supported. Gas dispersion in soils is affected by physical properties such as soil-air content, soil texture, and soil-pore network structure (Hamamoto et al., 2009). Physical properties of soil types

were not measured, but inference can be made from ADH activities in plants. High ADH activities would have correlated with low oxygen in flooded soils that contained smaller particles. Armo silt loam has a high water capacity (Watts et al., 1990) due to a smaller pore size that can create greater anaerobic conditions compared to sand. However, no physiological differences were measured between plants and different soil types. Perhaps differences in soil particle size become less important in flooded conditions.

As mentioned previously, both greenhouse experiments had small sample sizes. Small sample sizes could have affected the statistical analysis for ADH activity. A greater sample size would have allowed more differences to be detected between soil type and water treatments for root ADH activities. For future research, increasing sample size and measuring soil physical properties could further explain oxygen stress in *Tamarix ramosissima*. Root ADH activity and other metabolic responses to anaerobiosis should be further investigated within *T. ramosissima* to determine the flood tolerance of this species.

4.2. Field Study

4.2.1. g_s, *E*, and leaf Ψ

The field study examined physiological responses and shifts in canopy cover of *Tamarix ramosissima* and other species as a result of natural flooding. Measurements were g_s (Fig.13), *E*, and leaf Ψ for *T. ramosissima*, *Phragmites australis*, and *Populus deltoides*. These measurements were significantly different due to species, Julian date, water depth, and relative humidity. There was a significant interaction between *E* and

dates of measurements (Fig. 12). *E* decreased the most during July. Interactions between *E*, date of measurements, and relative humidity could be due to an increase in air temperature, which caused the vapor pressure deficit to increase, increasing *E*. This was observed from July-August and May-June (Fig. 13). Relative humidity was negatively correlated with air temperature. Relative humidity was also negatively correlated with water depth which could indicate a secondary relationship between other variables. Reduction in stomatal opening can be decreased by increased air temperatures and decreases in relative humidity, which lowers *E* (Larcher, 2003). *E* was also negatively correlated with water depth. Flooding caused stomates to close which lowered *E*.

The two physiological responses that had significant interactions with species were leaf Ψ (Fig. 11) and g_s (Fig. 13). Leaf Ψ can be considered as the work needed to elevate water to the leaf tissue (Larcher, 2003; Taiz and Zeiger, 2006). *Tamarix ramosissima* leaf Ψ was significantly lower than *Phragmites australis* and *Populus deltoides*. Under flooded soils, water uptake in plants can become reduced, simulating conditions of drought (e.g., stomatal closure) (Bradford and Hsiao., 1982; Pezeshki, 2001). This can cause leaves to become dehydrated, changing leaf Ψ (Bradford and Hsiao, 1982). g_s for *T. ramosissima* was lower than *Phragmites australis*. There was a significant interaction between leaf Ψ and water depth, which was expected due to stomates closing from flooding, which could lead to changes in leaf Ψ. However, water depth was not correlated with leaf Ψ. This indicated that there was no direct relationship between water depth and leaf Ψ.

g_s in *Populus deltoides* was not different from *Phragmites australis* or *Tamarix ramosissima*. Differences were expected to be seen between species for *E* and highest in *Phragmites australis*, since it is highly flood tolerant (Gries et al., 1989). However, no differences were detected.

Water depth interacted with and was negatively correlated with g_s, but not the other covariates. When water depth decreased, an increase in g_s occurred. There were only marginal differences in g_s between species. g_s was highest in *Phragmites australis*. As mentioned previously, *Phragmites australis* is a flood tolerant species, which could explain the high g_s during the field study.

4.2.2. Canopy cover

Canopy cover was not related to any covariates. Canopy cover was significantly different by species composition. The species with the highest total canopy cover were *Typha angustifolia* and *Populus deltoides*. Both of these species had similar total canopy covers. *Typha angustifolia* is considered to have a high tolerance to flooding (Crawford and Braendle, 1996; Kercher and Zedler, 2004). *Typha angustifolia* has been observed to increase biomass under flooding (Kercher and Zedler, 2004). This could further explain the dominance of canopy cover for *Typha angustifolia*. *Populus deltoides* also had higher canopy cover than *Tamarix ramosissima*, *Phragmites australis*, *Melilotus officinalis*, *Baccharis salicina*, and *Saccharum ravennae*. All transects started within *Populus deltoides* dominated stands. *Populus deltoides* within these areas was well established, which could cause canopy cover to be high for this species.

Canopy coverage was not different between *Tamarix ramosissima*, *Phragmites australis*, *Melilotus officinalis*, *Baccharis salicina*, and *Saccharum ravennae*. Fourteen plants died by the end of the field study, which could cause differences in canopy cover to occur between species. Also, *T. ramosissima* had the highest number deaths which resulted in a significant reduction in canopy cover. Reasons for plant deaths were most likely due to flooding.

Phragmites australis was expected to have a higher canopy cover due to its high flood tolerance. In areas invaded by *Phragmites australis*, monotypic stands commonly form, often replacing native vegetation (Tulbure et al., 2007). The same occurrence happens with *Typha angustifolia* (Grace and Wetzel, 1981). *Typha angustifolia* was the dominant species in flooded areas at this site. Seasonal shifts were apparent in some species. Future research at this site should be carried out to examine competition among all species to explain shifts in canopy cover.

Canopy cover was not correlated with any covariates. Canopy cover was expected to correlate with changes in water depth and soil Ψ. As flooding increased at the field site, flood intolerant species were shown to have increased leaf Ψ and decreased g_s and E. Decreases in g_s and E indicated stress responses in plants which would cause some species to die, changing canopy cover. Fluctuations in soil Ψ can cause changes in leaf Ψ due to water availability for uptake (Larcher, 2003). Changes in leaf Ψ can cause wilting or dehydration in leaf tissue. These types of changes can cause shifts in canopy cover from leaves lost from dehydration. In the present study, no changes were observed in leaf Ψ suggesting species were adapted to flooding.

Correlations occurred between soil Ψ and measurement dates. Soil Ψ was also correlated with water depth. These correlations were expected. Soil Ψ becomes more positive as soil water content increases in loam soils (Sylvia et al., 2005). Soil Ψ could have became more positive initially due to an increase in water depth and soil moisture. As the field season progressed, water depth decreased due to lack of rain events which could cause soil Ψ to become more negative. At the end of the field season, a rain event occurred, which caused an increase in soil Ψ.

4.2.3. $\delta^{13}C$

Leaf $\delta^{13}C$ values were not significantly different between any species or covariates during the field study. Both *Populus deltoides* and *Tamarix ramosissima* are C_3 plants. The enzyme Rubisco discriminates against ^{13}C (Rounick and Winterbourn, 1986), which is especially noticeable in C_3 plants. In healthy C_3 plants, leaf $\delta^{13}C$ is typically around -28‰ (Farquhar et al., 1982; Fry, 2006). $\delta^{13}C$ values can change due to stomatal closure, usually causing $\delta^{13}C$ values to increase in C_3 plants. Stomatal closure during flooding would cause the isotopic values for *P. deltoides* and *T. ramosissima* to change. However, other stress factors can cause stomates to close, such as an increase in air temperature and decreases in leaf Ψ. *Tamarix ramosissima* had lower g_s than *P. deltoides*, indicating stomates were closed for *T. ramosissima*. $\delta^{13}C$ values in *T. ramosissima* were expected to increase more than *P. deltoides* due to lower g_s. Instead, both *P. deltoides* and *T. ramosissima* had similar $\delta^{13}C$. Leaf $\delta^{13}C$ values were not correlated with any covariates. Isotope values for *P. deltoides* and *T. ramosissima* were

expected to correlate with water depth and air temperature, since these variables had the most effect on stomatal closure. Consequently, air temperature and water depth might not be the main limiting factors for stomatal closure. Sample sizes for both species were small (*P. deltoides*, *n*=10, *T. ramosissima*, *n*=13). An increase in sample size could help to detect differences for isotope values and help determine relationships between covariates.

4.3. Conclusions

This study examined physiological responses of *Tamarix ramosissima* to flooding in both greenhouse and field settings. Specific physiological measurements examined within the greenhouse experiments were photosynthesis and root respiration enzyme activity, and in the field measurements were leaf Ψ, E, g_s, and $\delta^{13}C$.

Physiological responses were affected the most by the duration of flooding, and not by soil type within greenhouse experiments. *T. ramosissima* could have escape mechanisms such as formation of adventitious roots and shoot production that allowed it to survive in flooding in similar research by Brotherson and Field (1987) and Sprenger et al. (2001).These escape mechanisms could also allow *T. ramosissima* to outcompete native species under flooding and allow *T. ramosissima* to acclimate to duration of flooding. During these events the species could have adaptive mechanisms, which should be further tested.

It has been reported in studies by Sher et al. (2000) and Sher and Marshall (2003) that *Tamarix ramosissima* seedlings were outcompeted by *Populus deltoides* seedlings under flooding. In both cases, physiological measurements were not reported to explain

competition mechanisms. However, both of these studies did report measures of height and biomass, which were higher in *P. deltoides* compared to *T. ramosissima*. In the field portion of this study, *P. deltoides* had higher canopy cover then *T. ramosissima* in adult plants. It was reported in Sher et al. (2000) and Sher and Marshall (2003) that *P. deltoides* seedlings tended to establish first, which crowded *T. ramosissima*. This is consistent with the canopy cover results in the present study.

Sher and Marshall (2003) also applied soil treatments that were similar to the present greenhouse experiment examining physiological responses to soil type. Their findings indicated that both *P. deltoides* and *T. ramosissima* had the greatest growth rate in clay soil because clay allowed for root establishment by seedlings. No differences were found for physiological responses to soil type in the present study, but should be investigated further to explain the results of Sher and Marshall (2003) on a physiological basis.

In another study, *Tamarix ramosissima* had a lower survival rate in flooded conditions compared to other species (Vandersande et al., 2001). However, Vandersande et al. (2001) did not examine physiological responses to flooding, but survival rates and biomass. It is possible that *T. ramosissima* did not survive flooding due to increased oxygen stress and lower photosynthesis rates as observed in greenhouse treatments in the present study. Additionally, *T. ramosissima* had lower g_s compared to other species in field settings, which could further explain the results of Vandersande et al. (2001). Physiological measurements such as an increase in root ADH, and changes in E and g_s

could also be used to explain results of the Gladwin and Roelle (1998) study where *T. ramosissima* did not survive 25 days of flooding.

Flooding has similar effects on plants compared to drought. During drought, *T. ramosissima* has been observed to maintain control of stomata at lower plant Ψ (Cleverly et al., 1997; Devitt et al., 1997). Cleverly et al. (1997) reported lower plant Ψ and lower g_s for *T. ramosissima* under drought conditions compared to *Salix exigua* Nutt., *Prosopis pubescens* Benth., and *Pluchea sericea* (Nutt.) Coville. In the present study, g_s in *T. ramosissima* was lower for leaf Ψ compared to *Phragmites australis* and *Populus deltoides*. The present study seems to support the studies of Devitt et al. (1997) and Cleverly et al. (1997) for drought; however, flooding presents a new set of stress conditions that drought does not. Flooding causes plants to undergo anaerobic fermentation from lack of oxygen. It is more likely that the physiological responses of *T. ramosissima* under flooding in the field were a result of anaerobic stress and not the ability of each species to survive drought. This is further supported by the observation that ADH activity was higher in flooded treatments for the greenhouse study examining responses to soil type.

Carbon isotope analysis has been used to examine water use efficiency in *T. ramosissima*. Busch and Smith (1995) observed that *T. ramosissima* had a higher $\delta^{13}C$ value than *Salix gooddingii* and *Pluchea sericea* indicating higher water use efficiency. Water use efficiency in a plant is determined by the amount of CO_2 uptake coupled with water loss through stomata (Larcher, 2003). Plants reduce water loss by stomatal closure, resulting in a reduction in CO_2 uptake. Carbon isotope analysis can also be used to detect

stomatal closure from stress conditions such as flooding. In the present study, differences in leaf $\delta^{13}C$ were not detected between *Populus deltoides* and *T. ramosissima*. However, the results from Busch and Smith (1995) could be used to gain insight of what would be expected for isotopic values for *T. ramosissima* under flooding.

The present study wanted to determine the physiological responses of *T. ramosissima* to flooding, and to explain a mechanism for loss of competitive ability during flooding. Root ADH activity increased in *T. ramosissima*. This indicated flooding causes anaerobic stress within the species. Photosynthesis decreased in greenhouse experiments, but increased over time, due to possible acclimation to flooding treatments. These results indicated soil type did not have an effect on root ADH activity, nor on photosynthesis in *T. ramosissima*. g_s and leaf Ψ were lower in *T. ramosissima* compared to the flood tolerant species *Phragmites australis* and the riparian species *Populus deltoides*. *Tamarix ramosissima* is less flood tolerant than *Phragmites australis* and *Populus deltoides*. Shifts in canopy cover for species were not directly linked to flooding, fluctuations in soil moisture, or soil Ψ. Instead, canopy cover was more different by species, which could indicate competition between dominant species at the field site.

The results of this study can aid in future management practices for *Tamarix ramosissima*. It is evident that flooding affects *T. ramosissima* in natural settings. Also, controlled flooding could potentially be used as part of an integrated management practice to help reduce establishment of *T. ramosissima* in invaded areas. Integrated practices could improve management success, and allow native vegetation to re-establish along riparian systems within invaded areas. However, more research should be

completed on the physiological responses of *T. ramosissima* to understand tolerance to flooding.

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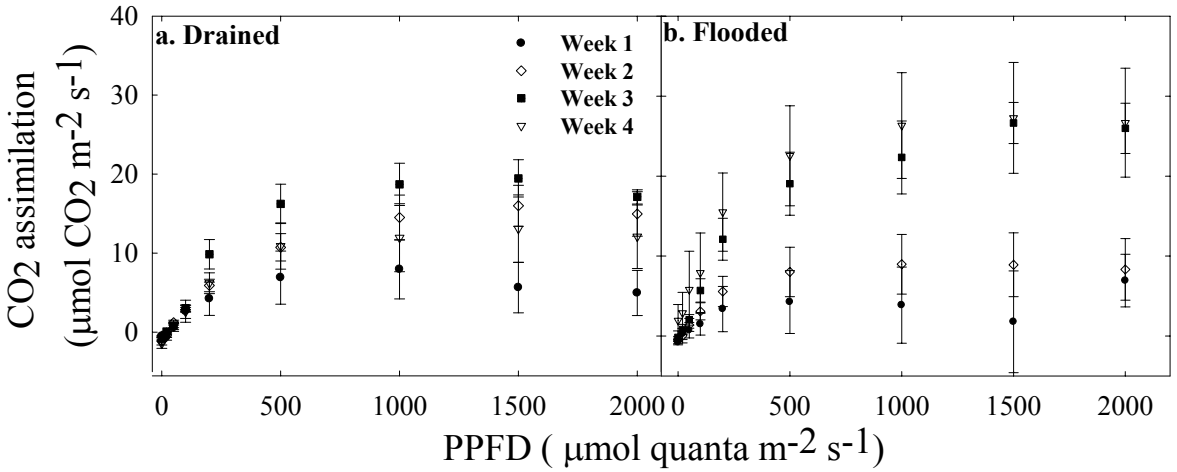

Figure 1: Light response curves for *Tamarix ramosissima*. Panels *a* and *b* represent drained and flooded measurements. Measurements were taken weekly for four weeks. Points represent means of four individuals per treatment ± SE.

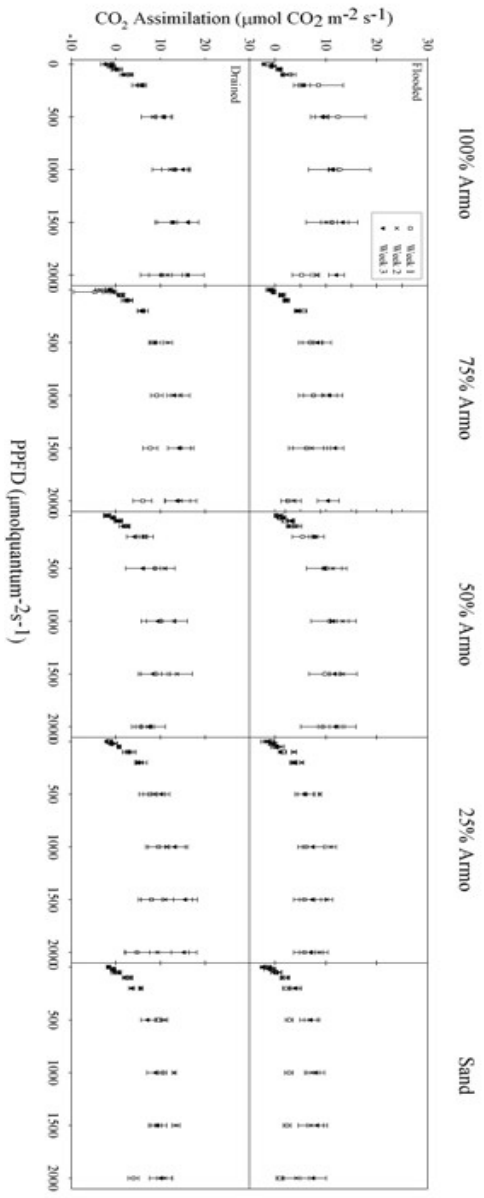

Figure 2: Light response curves for *Tamarix ramosissima* in different soil types. The top panels represent flooded plants in five soil mixtures. The bottom panels represent drained plants in five soil mixtures. Measurements were taken weekly for three weeks. Points represent means of three individuals per treatments ± SE.

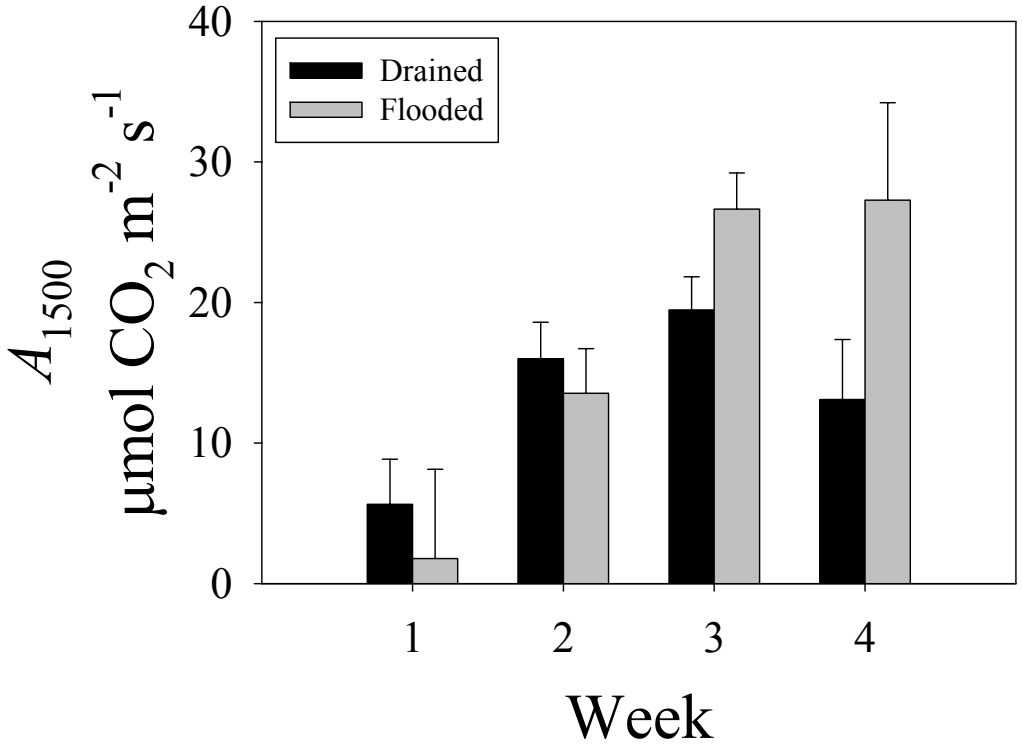

Figure 3: Photosynthesis at 1500 μmol quanta $m^{-2}s^{-1}$ (A_{1500}) for *Tamarix ramosissima*. Measurements were taken weekly for four weeks. Bars represent means of four individuals per treatment ± SE.

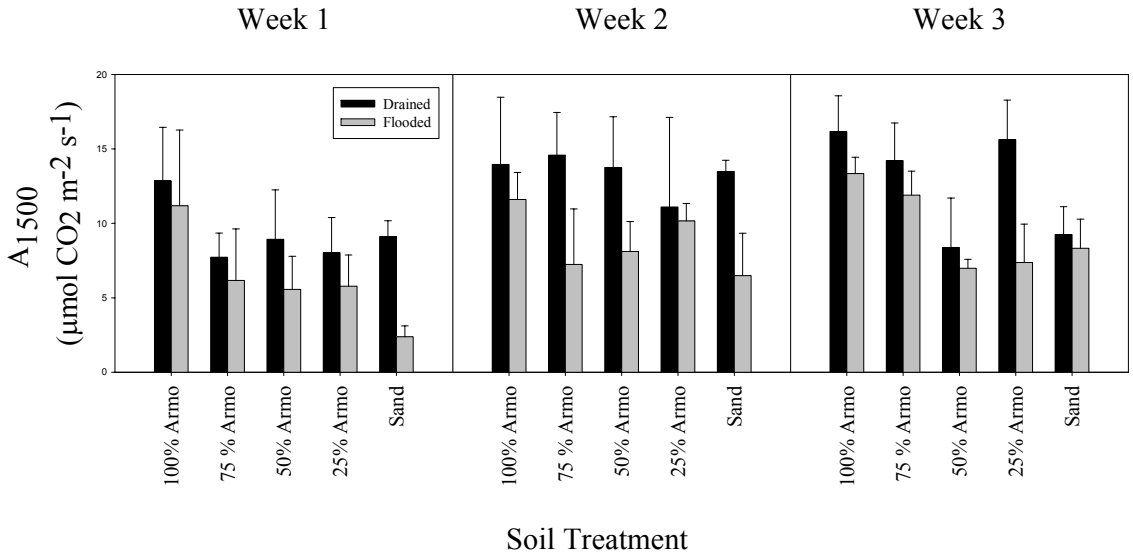

Figure 4: Photosynthesis at 1500 µmol quanta m^{-2} s^{-1} (A_{1500}) for *Tamarix ramosissima* in different soil mixtures. Measurements were taken weekly for three weeks. Bars represent means of three individuals per treatment ± SE.

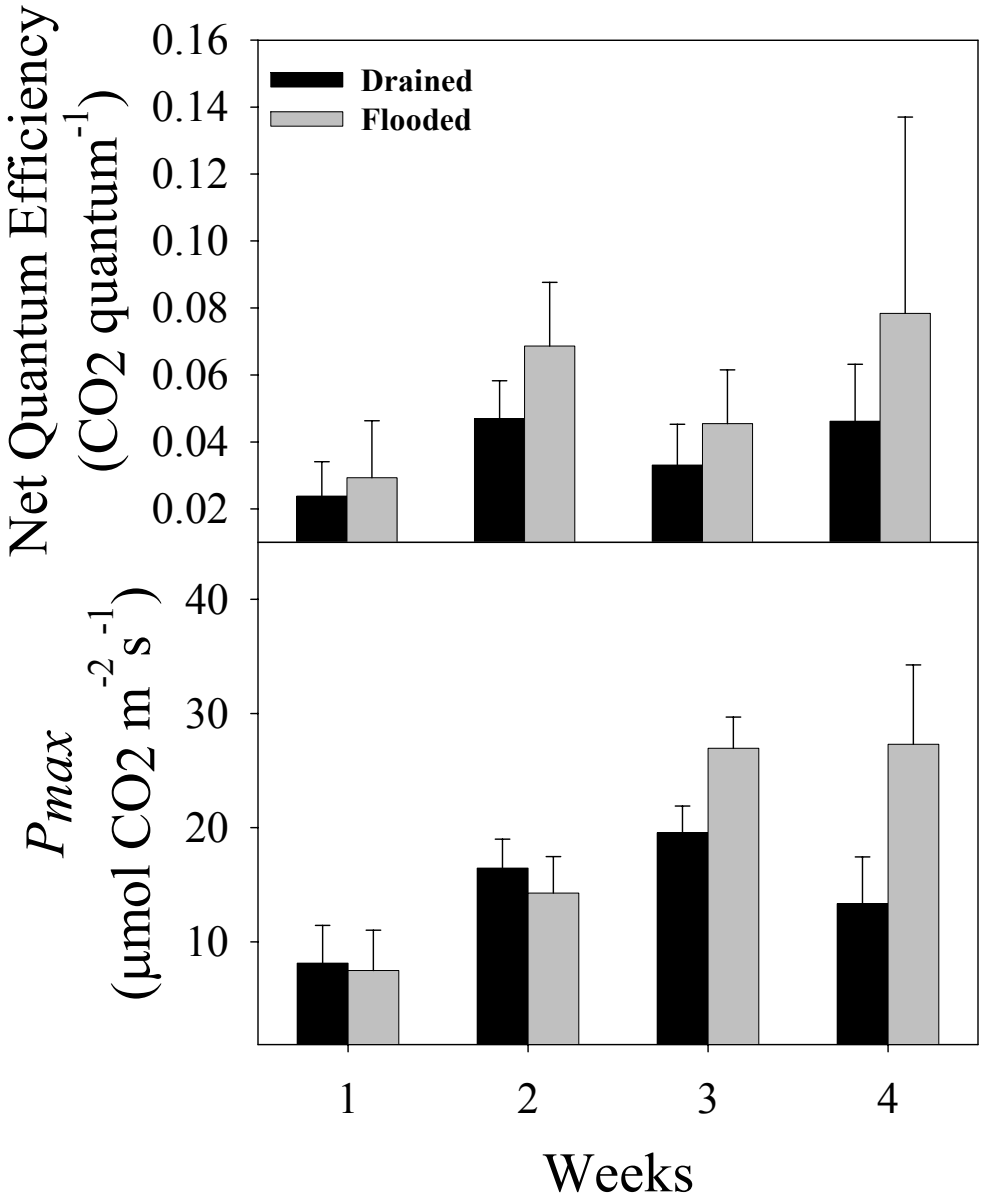

Figure 5: Net quantum efficiency (top) and maximum photosynthesis (P_{max}) (bottom) in *Tamarix ramosissima*. Measurements were taken weekly for four weeks. Bars represent means of four individuals per treatment ± SE.

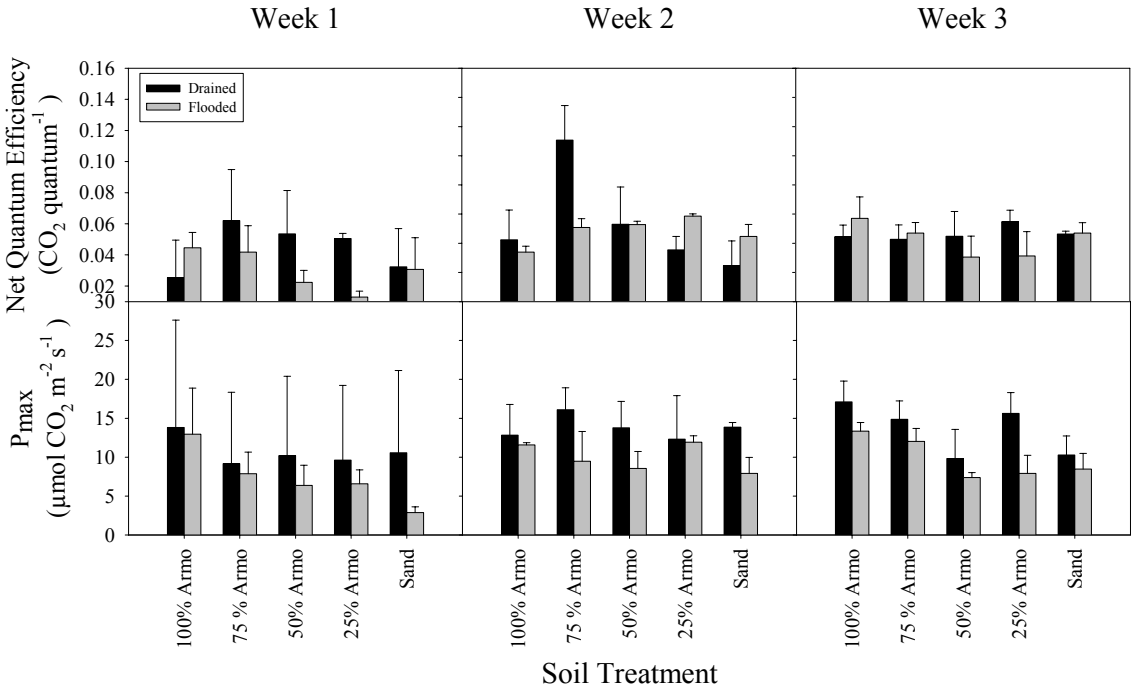

Figure 6: Net quantum efficiency (top) and maximum photosynthesis for *Tamarix ramosissima* in different soil mixtures. Measurements were taken weekly for three weeks. Bars represent means of three individuals per treatment ± SE.

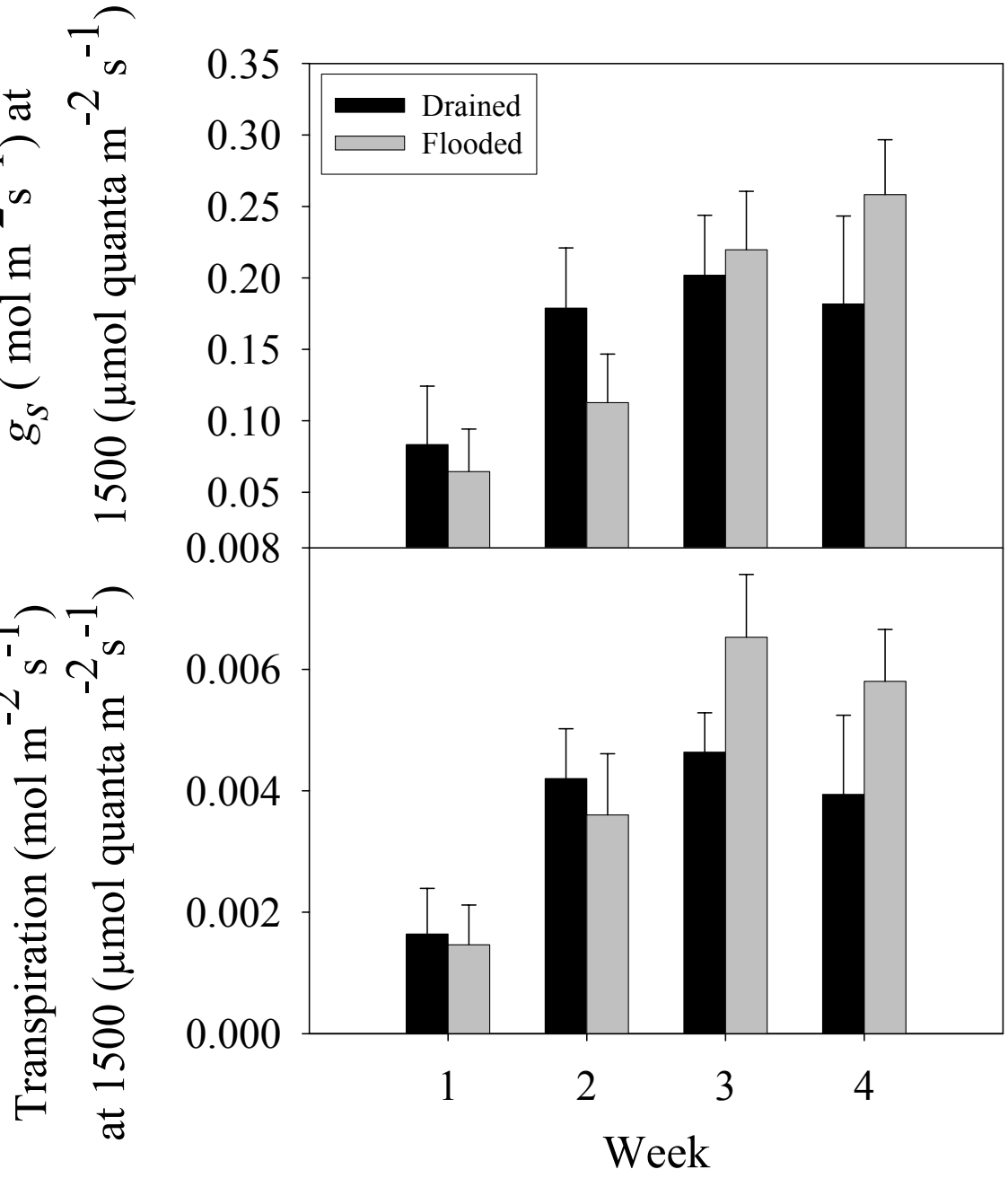

Figure 7: Stomatal conductance (top) and transpiration rate (bottom) in *Tamarix ramosissima*. Measurements were taken weekly for four weeks. Bars represent means of four individuals per treatment ± SE.

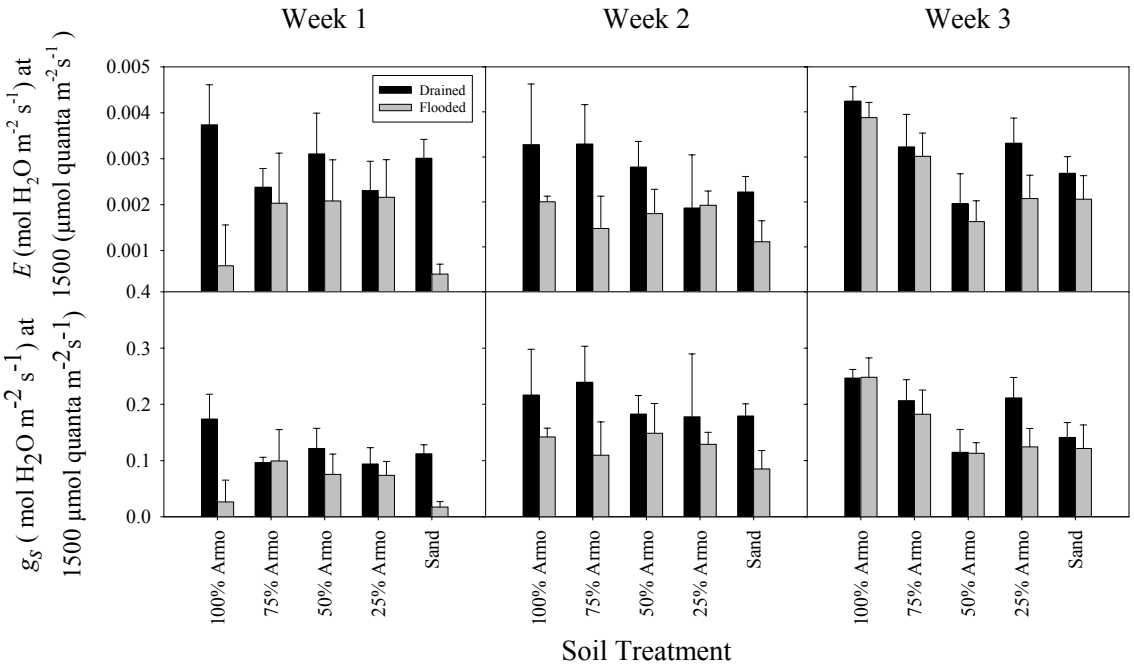

Figure 8: Transpiration rate (top) and stomatal conductance for *Tamarix ramosissima* in different soil mixtures. Measurements were taken weekly for three weeks. Bars represent means of three individuals per treatment ± SE.

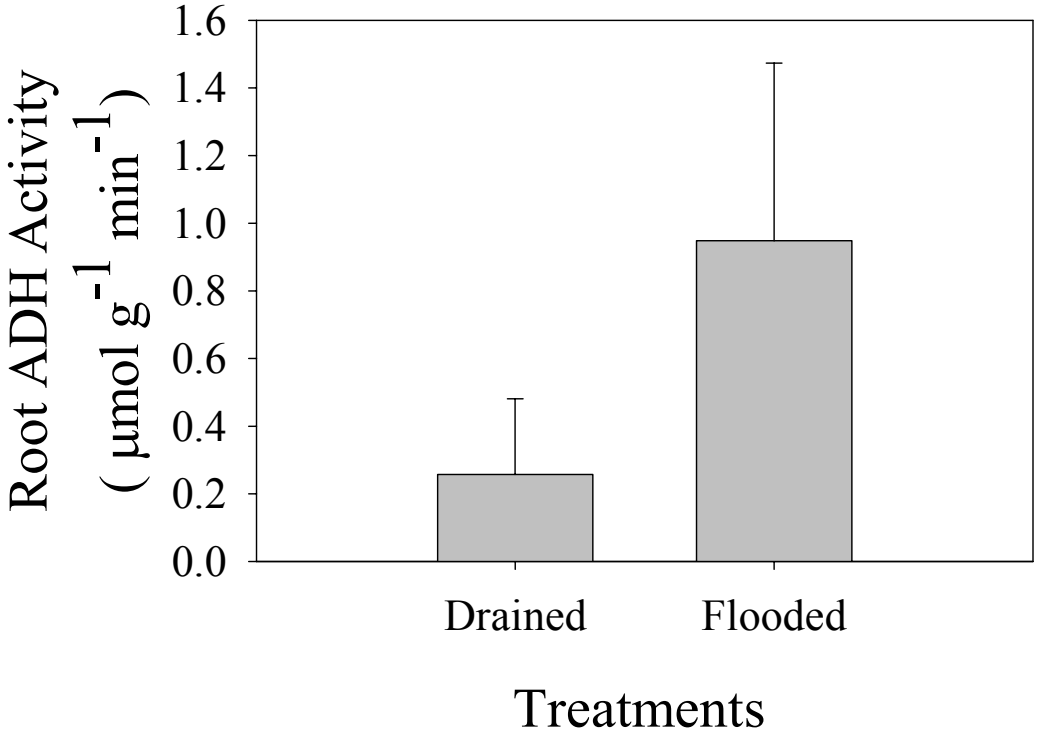

Figure 9: Root alcohol dehydrogenase (ADH) activity for *Tamarix ramosissima*. Bars represent means of four individuals per treatment ± SE. Root ADH was measured at the end of the four week treatment.

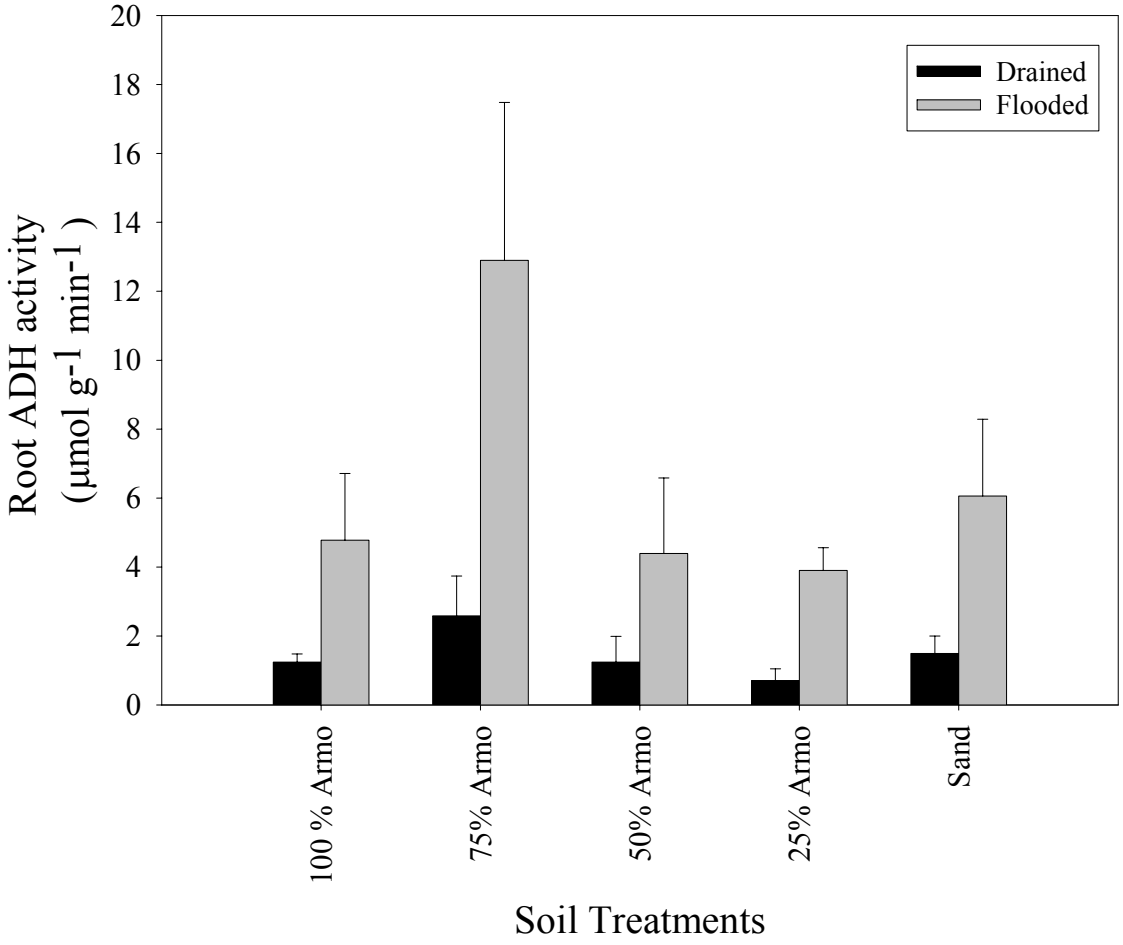

Figure 10: Root alcohol dehydrogenase (ADH) activity for *Tamarix ramosissima* in different soil mixtures. Black bars represent flooded treatments and grey bars represent drained treatments.Measurements were taken at the end of treatment. Bars represent means of three individuals per treatment ± SE.

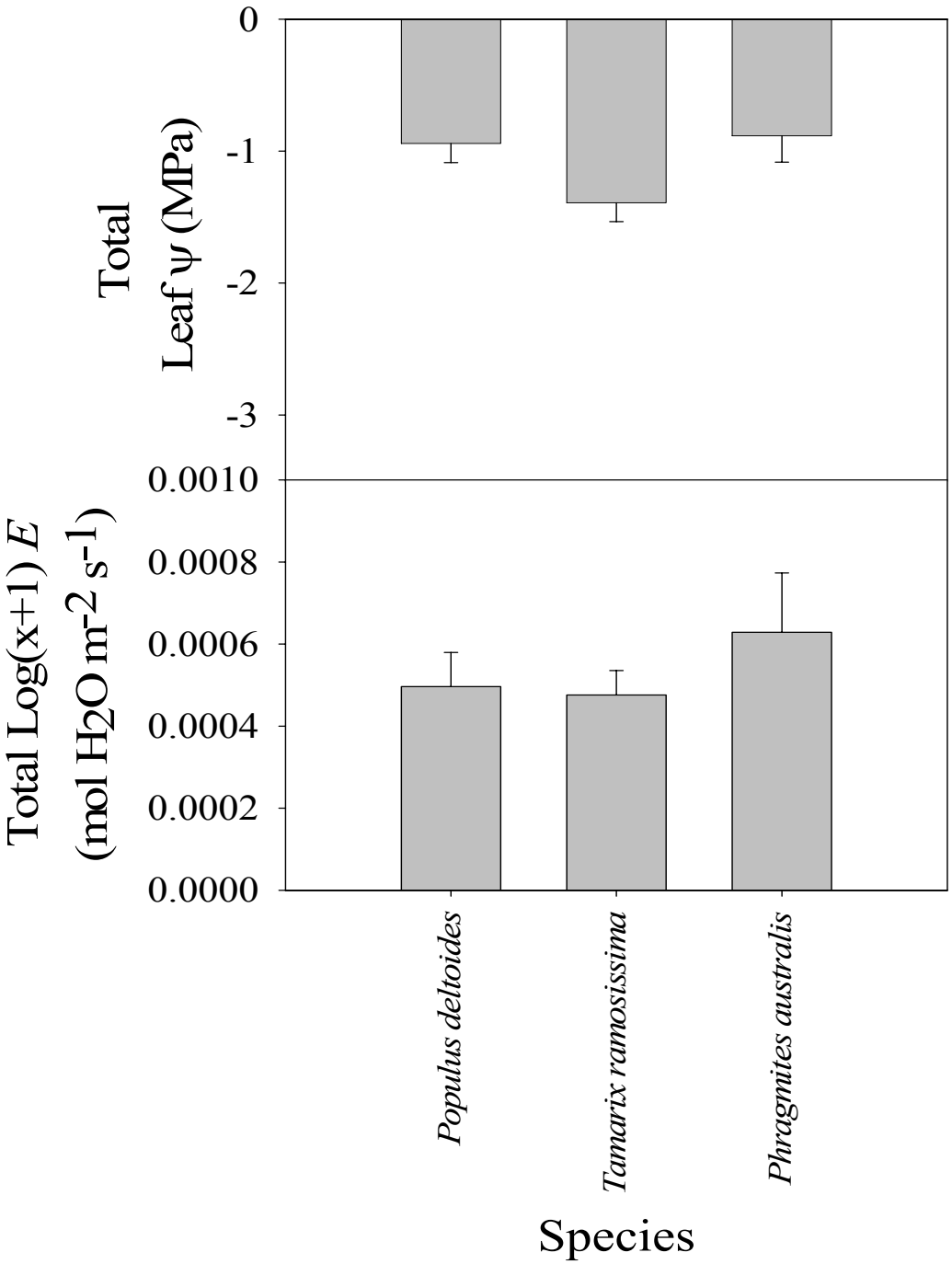

Figure 11: Total leaf Ψ (top), log(x+1) *E* (bottom) in *Tamarix ramosissima*, *Populus deltoides*, and *Phragmites australis*. Measurements were taken monthly from May to August 2010. Bars represent means of individuals for the total sampling period ± SE.

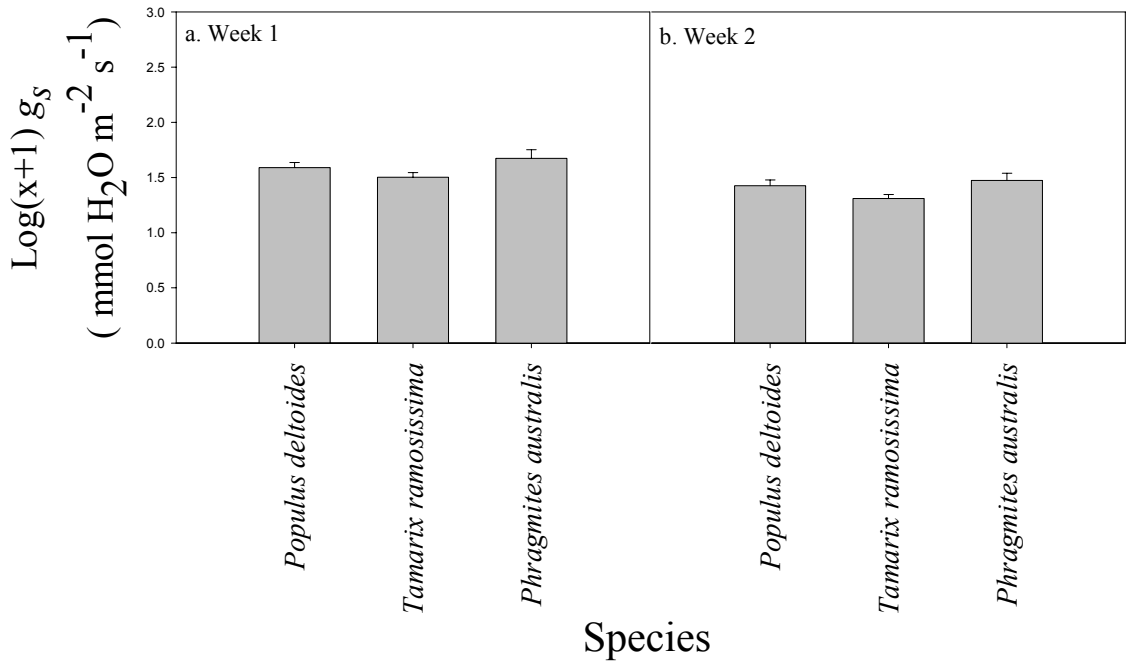

Figure 12: Total log(x+1) g_s in *Tamarix ramosissima*, *Populus deltoides*, and *Phragmites australis* for week one (*a*) and week two (*b*) within sampling months. Measurements were taken monthly from May to August 2010. Bars represent means of individuals for the total sampling period ± SE.

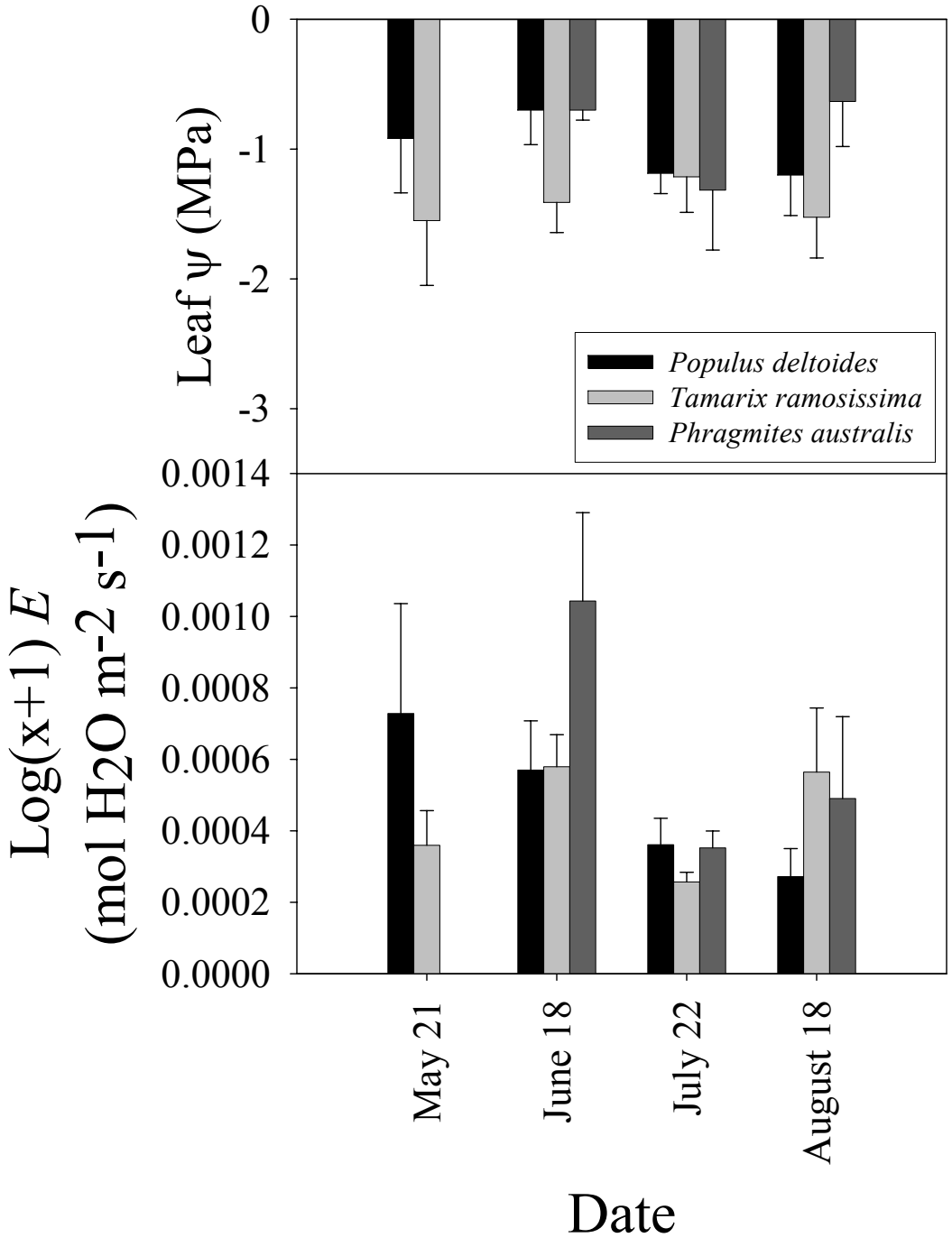

Figure 13: Leaf Ψ (top), and log(x+1) *E* (bottom) in *Tamarix ramosissima*, *Populus deltoides*, and *Phragmites australis*. The X-axis represents dates of measurement. Bars represent means of individuals in each month ± SE.

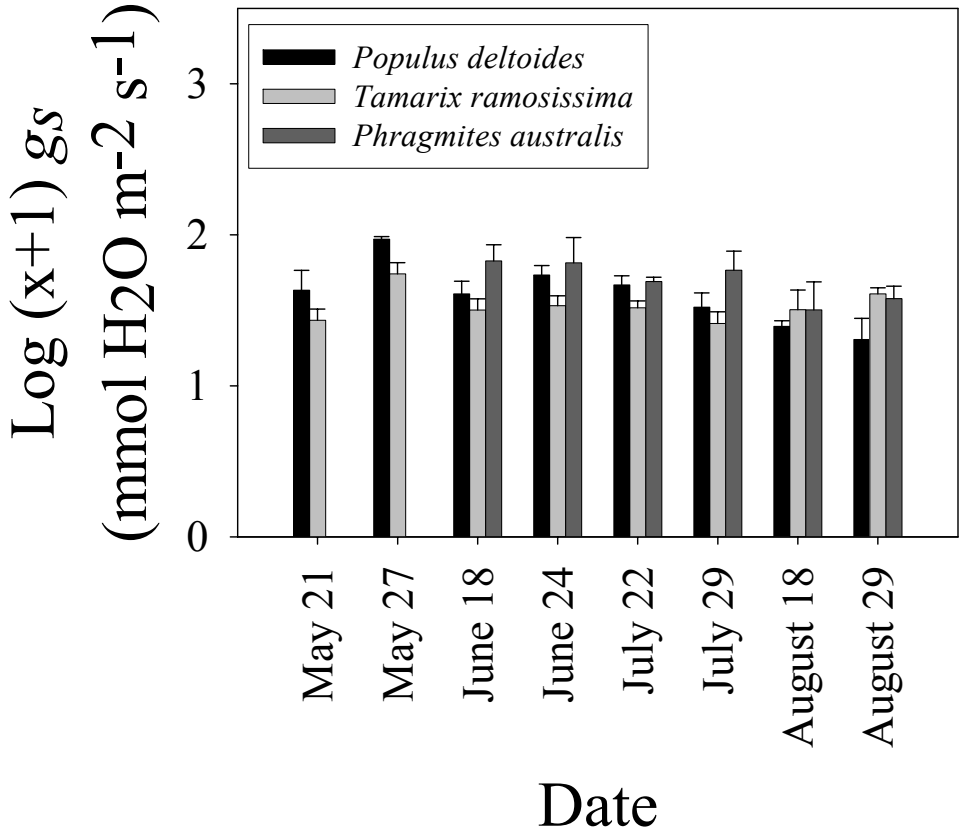

Figure 14: Log(x+1) g_s in *Tamarix ramosissima*, *Populus deltoides*, and *Phragmites australis*. The X-axis represents dates of measurements. Bars represent means of individuals for measurements at each date ± SE.

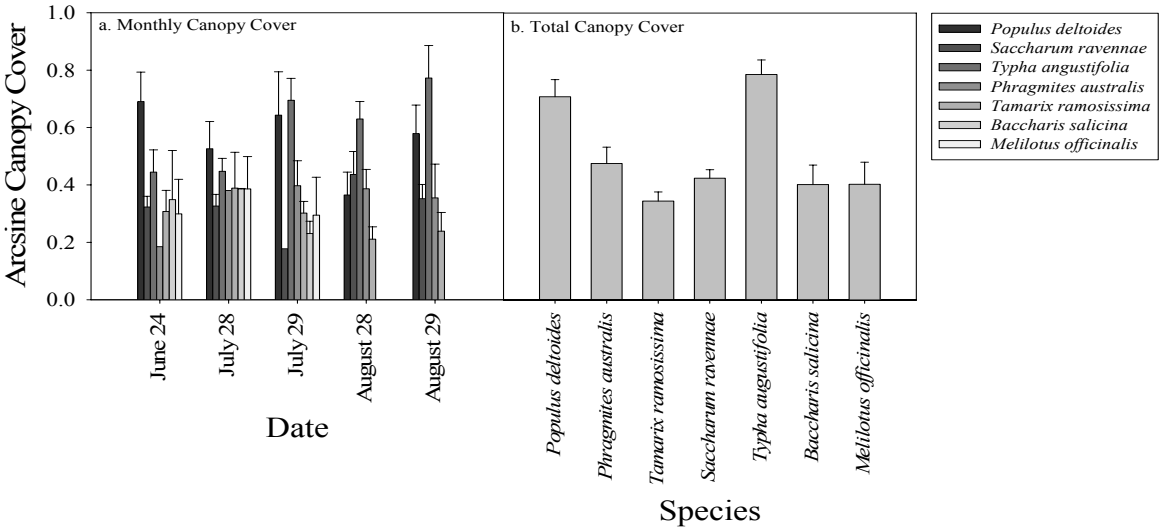

Figure 15: Canopy cover (*a*) and Total canopy cover (*b*) in, *Populus deltoides*, *Phragmites australis*, *Tamarix ramosissima*, *Saccharum ravennae*, *Typha angustifolia*, *Baccharis salicina*, *and Melilotus officinalis*. Measurements were taken monthly from June to August 2010. Bars represent means of canopy cover for individual species ± SE.

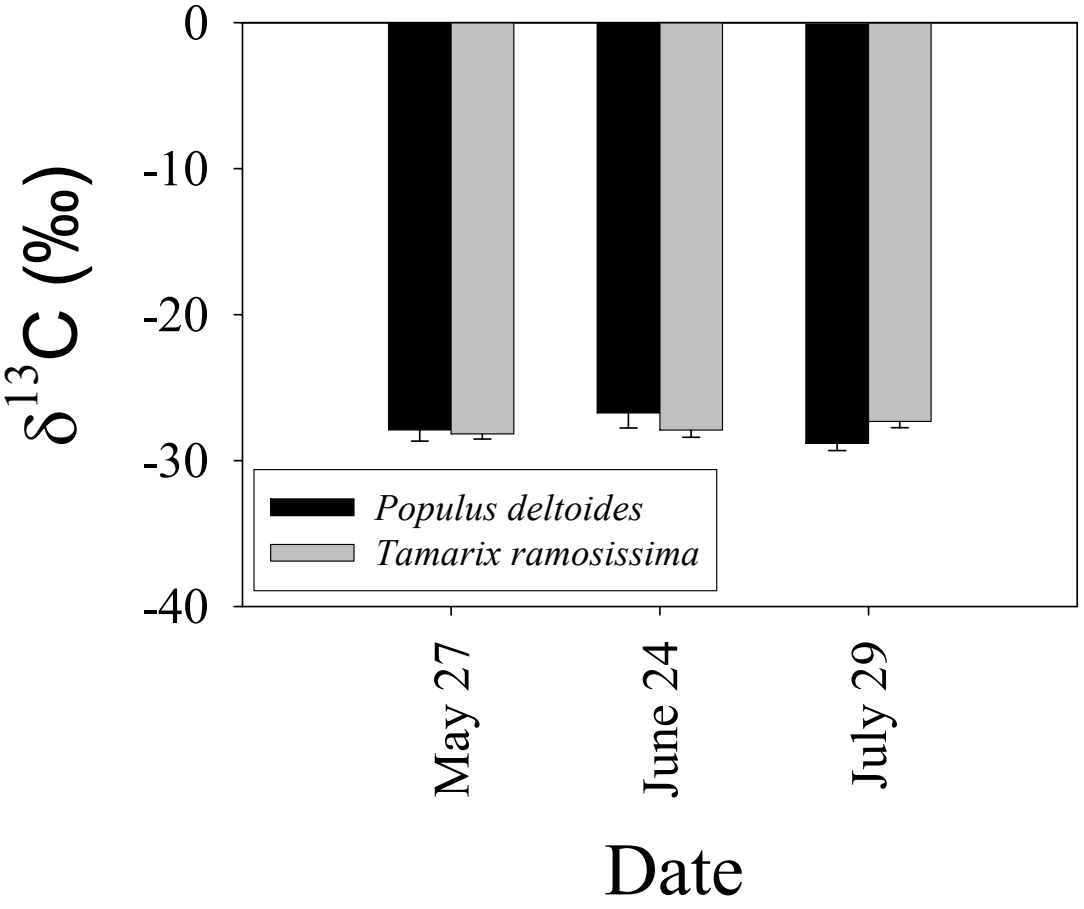

Figure 16: Leaf $\delta^{13}C$ in *Populus deltoides and Tamarix ramosissima*. Measurements were taken monthly from May-August 2010. Bars represent means of individual species in each month ± SE.

Treatment or Soil type	Flooding or Drained	% of Plants with new growth	% of Plants that developed leaf chlorosis or drying
Response to time	Drained	0%	75% chlorosis 100% drying
Response to time	Flooded	75%	100% chlorosis 100% drying
100 % Armo	Drained	100%	33% chlorosis 100% drying
75% Armo	Drained	100%	100% drying
50% Armo	Drained	100%	100% drying
25% Armo	Drained	100%	100% drying
100% Sand	Drained	100%	100% drying
100 % Armo	Flooded	100%	100% chlorosis 100% drying
75% Armo	Flooded	100%	100% chlorosis 100% drying
50% Armo	Flooded	100%	100% chlorosis 100% drying
25% Armo	Flooded	100%	100% chlorosis 100% drying
100% Sand	Flooded	100%	100% chlorosis 100% drying

Table 1: Description of appearances of plants throughout greenhouse experiments. Observations were made on the appearance of plants in each treatment. Percentages indicate the number of plants in each treatment that developed new growth and leaf chlorosis or drying.

		Coded Water Depth (cm)	Leaf Ψ(MPa)	Air Temperature (°C)	Log (x+1) g_s (mmol H_2O m^{-2} s^{-1})	Arcsine Soil Moisture %	Log (x+1) E (mol H_2O m^{-2} s^{-1})	Relative Humidity (%)
Julian Date	r	-0.040	-0.056	-0.413	-0.110	-0.052	-0.256	0.104
	p	0.770	0.683	0.002	0.418	0.702	0.057	0.445
	n	56	56	56	56	56	56	56
Coded Water Depth (cm)	r		0.211	0.152	0.092	0.844	0.289	-0.332
	p		0.119	0.263	0.502	0.000	0.030	0.012
	n		56	56	56	56	56	56
Leaf Ψ(MPa)	r			0.126	0.006	0.069	0.025	-0.053
	p			0.355	0.963	0.615	0.858	0.697
	n			56	56	56	56	56
Air Temperature (°C)	r				-0.132	0.127	0.130	-0.341
	p				0.334	0.349	0.340	0.010
	n				56	56	56	56
Log (x+1) g_s (mmol H_2O m^{-2} s^{-1})	r					0.092	0.798	-0.064
	p					0.500	0.000	0.639
	n					56	56	56
Arcsine Soil Moisture	r						0.253	-0.347
	p						0.060	0.009
	n						56	56
Relative Humidity (%)	r						-0.546	1
	n						0.000	.
	p						56	56

Table 2: Correlations of response variables and covariates from field data over the entire sampling period. Variables are correlated at the 0.05 level.

		Coded Water Depth (cm)	e^x Soil Ψ(MPa)	Log (x+1) g_s (mmol H_2O m^{-2} s^{-1})	Air Temperature (^oC)
Julian Date	r	-0.066	-0.068	-0.188	-0.705
	p	0.627	0.618	0.165	0.000
	n	56	56	56	56
Coded Water Depth (cm)	r		-0.216	-0.286	0.221
	p		0.111	0.033	0.102
	n		56	56	56
e^x Soil Ψ(MPa)	r			-0.116	0.084
	p			0.395	0.539
	n			56	56
Log (x+1) g_s (mmol H_2O m^{-2} s^{-1})	r				-0.011
	p				0.933
	n				56

Table 3: Correlations of Log (x+1) g_s and covariates from field data over the entire sampling period. Variables are correlated at the 0.05 level.

		Arcsine Canopy Cover	Coded Water Depth (cm)	e^x Soil Ψ(MPa)
Julian Date	r	-0.061	-0.030	0.388
	p	0.421	0.689	0.000
	n	175	175	175
Arcsine Canopy Cover	r		0.105	0.014
	p		0.168	0.857
	n		175	175
Coded Water Depth (cm)	r			0.408
	p			0.000
	n			175

Table 4: Correlations of canopy cover and covariates from field data over the entire sampling period. Variables are correlated at the 0.05 level.

		$\delta^{13}C$	Coded Water Depth	e^{x} Soil Ψ(MPa)	Air Temperature (^{o}C)
Julian Date	r	-0.007	0.134	0.314	0.014
	p	0.976	0.541	0.145	0.951
	n	23	23	23	23
$\delta^{13}C$	r		-0.052	-0.016	0.227
	p		0.813	0.941	0.297
	n		22	23	23
Coded Water Depth	r			-0.269	0.490
	p			0.214	0.018
	n			23	23
e^{x} Soil Ψ(MPa)	r				-0.507
	p				0.013
	n				23

Table 5: Correlations of $\delta^{13}C$ and covariates from field data over the entire sampling period. Variables are correlated at the 0.05 level.