



## 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* invades riparian zones, but loses competitiveness under flooding. Metabolic effects of flooding could be important for *T. ramosissima*, but have not been previously investigated. Photosynthesis rates, stomatal conductance, internal (intercellular)  $\text{CO}_2$ , transpiration, and root alcohol dehydrogenase (ADH) activity were compared in *T. ramosissima* across soil types and under drained and flooded conditions in a greenhouse. Photosynthesis at  $1500 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$  ( $A_{1500}$ ) in flooded plants ranged from 2.3 to  $6.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  during the first week, but  $A_{1500}$  increased to  $6.4\text{--}12.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  by the third week of flooding. Stomatal conductance ( $g_s$ ) at  $1500 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$  also decreased initially during flooding, where  $g_s$  was 0.018 to  $0.099 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$  during the first week, but  $g_s$  increased to  $0.113\text{--}0.248 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$  by the third week of flooding. However, photosynthesis in flooded plants was reduced by non-stomatal limitations, and subsequent increases indicate metabolic acclimation to flooding. Root ADH activities were higher in flooded plants compared to drained plants, indicating oxygen stress. Lower photosynthesis and greater oxygen stress could account for the susceptibility of *T. ramosissima* at the onset of flooding. Soil type had no effect on photosynthesis or on root ADH activity. In the field, stomatal conductance, leaf water potential, transpiration, and leaf  $\delta^{13}\text{C}$  were compared between *T. ramosissima* and other flooded species. *T. ramosissima* had lower stomatal conductance and water potential compared to *Populus deltoides* and *Phragmites australis*. Differences in physiological responses for *T. ramosissima* could become important for ecological concerns.

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### 1. Introduction

Riparian systems are especially vulnerable to exotic species due to disturbances such as floods, droughts, human alterations, and fires that can open areas to invasion (Naiman and Décamps, 1997). One species in the western United States that takes advantage of disturbances in riparian systems is *Tamarix ramosissima* Lebed. (saltcedar).

*T. ramosissima* is problematic because it displaces native species of willow (*Salix* L.), cottonwood (*Populus* L.) (Frasier and Johnsen, 1991; DiTomaso, 1998), and mesquite (*Prosopis* L.) (Cleverly et al., 1997). *T. ramosissima* also narrows waterways, causing subsequent flooding (Busch and Smith, 1995), and removal of this species can also cause increased problems with bank erosion and increased sedimentation in reservoirs (Barz et al., 2008). A critical review of

the ecological effects of *Tamarix* species is provided by Stromberg et al. (2009).

*T. ramosissima* has several competitive advantages over native riparian tree species during drought that result from its physiological characteristics. For example, *T. ramosissima* has greater control over stomatal conductance compared to native species, which limits water loss (Anderson, 1982). *T. ramosissima* can physiologically withstand lower water potentials (Devitt et al., 1997), yet it is also phreatophytic, which allows it to reach ground water readily (Brotherson and Field, 1987).

A number of previous studies have compared *T. ramosissima* to other riparian species, but the competitive advantage of *T. ramosissima* is unclear under flooding. Physiological or metabolic differences between species have not been reported. For example, Vandersande et al. (2001) demonstrated adult individuals of *T. ramosissima* lost their competitive advantage, stopped growing, and dislodged after 58 days of flooding. However, Brotherson and Field (1987) showed *T. ramosissima* can withstand flooding up to 70 days. Seedlings of *T. ramosissima* are apparently less flooding tolerant and are typically out competed when flooded. For example, Gladwin and Roelle (1998) showed *T. ramosissima* seedlings died under 25 days of flooding, whereas *Populus deltoides* Bartt.

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seedlings survived. In a study by Sher et al. (2000), *P. deltoides* seedlings were able to out compete *T. ramosissima* under flooding. However, Sprenger et al. (2001) reported *P. deltoides* seedlings were out competed by *T. ramosissima* seedlings under 30 days of flooding. From the preceding, it appears *T. ramosissima* is less flooding tolerant compared to native riparian tree species in most cases. Morphological differences between species, such as size (Sprenger et al., 2001) and adventitious rooting (Vandersande et al., 2001), have been proposed to account for differences in flooding tolerance. Although there has been extensive work regarding survival and competition of *T. ramosissima* during flooding, the biochemical and physiological mechanisms that make *T. ramosissima* susceptible to flooding are not known.

One explanation for loss of competitiveness of *T. ramosissima* under flooding could be increased oxygen stress during flooding, indicating a sensitivity to waterlogged sediments (Blom and Voesehek, 1996). General mechanisms used by plants to tolerate hypoxia during flooding include increased anaerobic metabolism (Drew, 1997) and increased ventilation of submerged tissues by adventitious roots and aerenchyma tissue in roots (Blom et al., 1994). Previous work has indicated *T. ramosissima* can form adventitious roots when flooded (Tomanek and Ziegler, 1960; Zedler and Kercher, 2004), but it has a decreased ability to form adventitious roots when compared to other riparian trees and shrubs (Vandersande et al., 2001). Moreover, *T. ramosissima* has a limited ability to form aerenchyma in roots (with aerenchyma apparently confined to primary tissues; Tomanek and Ziegler, 1960), suggesting sensitivity to anaerobic conditions is important for determining flooding tolerance in *T. ramosissima*.

Anaerobic respiration is inherently less efficient than aerobic respiration (Drew, 1997); energy shortages from decreased ATP synthesis could contribute to flooding sensitivity in *T. ramosissima*. Oxygen stress in flooded plants is measurable by increased activities of alcohol dehydrogenase (ADH) in roots (Maricle et al., 2006). ADH plays an important regulatory role in alcohol fermentation in flooded plants (Kimmerer, 1987). Accordingly, oxygen stress is one potential explanation for decreased performance of *T. ramosissima* under flooding; if *T. ramosissima* is more sensitive to anaerobic sediments compared to native riparian species, then this could represent a significant disadvantage.

Physiological stress caused by flooding in roots can also be manifested as decreased photosynthesis in leaves (Pezeshki, 2001). Stomata typically close during flooding (Kozłowski, 1984), potentially lowering photosynthesis and gas exchange rates (Pezeshki, 2001). Any treatment reducing photosynthesis would be expected to decrease plant growth and performance.

While instantaneous measures of stomatal conductance can be assessed by gas exchange or porometer measures, longer-term indices of stomatal behavior can be meaningful when considering effects of flooding over the scale of weeks. Whole leaf stomatal regulation can be assessed through analysis of leaf  $\delta^{13}\text{C}$  (Farquhar et al., 1982). Stomatal closure decreases intake of atmospheric  $\text{CO}_2$ , and changes the dynamics of carbon isotope discrimination by plants. In  $\text{C}_3$  plants like *T. ramosissima*, the enzyme Rubisco discriminates against  $^{13}\text{C}$  during photosynthesis (O'Leary, 1981). For  $\text{C}_3$  plants,  $\delta^{13}\text{C}$  values typically increase with stomatal closure (Farquhar et al., 1982). If flooding-induced stomatal closure influences photosynthesis in *T. ramosissima*, an analysis of  $\delta^{13}\text{C}$  could help to explain responses to flooding.

Effects of flooding on *T. 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 measure the physiological effects of flooding on *T. ramosissima* in greenhouse and field studies. The main objective of this study was to investigate physiological effects of flooding on gas exchange and respiratory metabolism in *T. ramosissima*. This could

provide a mechanism to explain why *T. ramosissima* loses competitive ability in the field during flooding. Specifically, effects of soil type were investigated under drained and flooded soil conditions in greenhouse experiments. It was hypothesized flooding would cause oxygen deficiency in *T. ramosissima*, which would limit aerobic respiration (Drew, 1997) and decrease photosynthesis through stomatal closure (Gravatt and Kirby, 1998). Oxygen deficiency that limits aerobic respiration would be evident as an increase in root alcohol dehydrogenase activity in flooded plants (Maricle et al., 2006). Similarly, it was hypothesized an increase in root alcohol dehydrogenase activity would occur as a result of anaerobic conditions that correlate with decreased soil particle size.

Once an understanding of flooding on *T. ramosissima* had been established, comparative measures were performed in a field setting. The main objective of the field study was to test if the greenhouse study results would be supported by field data. Physiological responses of *T. ramosissima* were compared with other species under natural flooding regimes. It was hypothesized the limited flooding tolerance of *T. ramosissima* in the field would be evident in decreased stomatal conductance and transpiration (Pezeshki et al., 1996; Atkinson et al., 2008), and concomitant increased leaf  $\delta^{13}\text{C}$  (Farquhar et al., 1982). Additionally, the superior drought tolerance of *T. ramosissima* was expected to be manifested as a lower water potential compared to other species in a flooded community (Cleverly et al., 1997). It is hoped this understanding could be used to understand invasion dynamics of *T. ramosissima* and potentially develop new management strategies (or support existing strategies) for *T. ramosissima* in riparian areas.

## 2. Materials and methods

### 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 main soil type at the Commanche Boat Ramp is Armo silt loam (Watts et al., 1990). Mean annual precipitation at the site is 56.5 cm (Kansas State University Research and Extension data); around 80% of annual precipitation occurs during the growing season (Adler and HilleRisLambers, 2008). Floods are common at the site following heavy rains. The site is invaded by species such as *T. ramosissima*, *Phragmites australis* (Cav.) Trin. ex Steud., and *Typha angustifolia* L. A native dominant species is *P. deltoides*. Other common non-native species in this area are *Melilotus officinalis* (L.) Lam., *Baccharis salicina* Torr. & A. Gray, and *Saccharum ravennae* (L.) L.

### 2.2. Physiological responses to flooding and soil type

Individuals of *T. ramosissima* were collected in autumn of 2009 and identified from *Flora of the Great Plains* (Great Plains Flora Association, 1986). Armo silt loam was collected from the same location. Plants and soil were brought to the Fort Hays State University greenhouse (Hays, KS, USA; 38°52'N, 99°22'W). Plants were transplanted in 3.8L and 1.9L pots. Pot sizes were randomly dispersed across treatments. Plants were grown in potting soil mixed with 28 g of Osmocote® fertilizer per pot (19% N, 6% P, 12% K) (Scotts Miracle-Gro Co.; Marysville, OH, USA) for one month for plants to establish a root system and to improve survival. Following this, plants were potted in different soil types. Armo silt loam was mixed with sand to create five soil mixtures: 100% Armo, 75% (by volume) Armo, 50% Armo, 25% Armo, and 100% sand (with no potting soil or fertilizer). 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 of *T. ramosissima* to flooding of medium duration. Plants were healthy in appearance, approximately 31 cm in height, and had approximately 30–35 branches each. 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 for the flooding treatment, again with three plants ( $n=3$ ) in each soil type. Tubs were filled with 12 cm of water. Plants were flooded for three weeks (e.g., Copolovici and Niinemets, 2010) in January 2010. Sulfate reduction was evident in many of the pots, indicating highly reducing, anoxic sediment. Photosynthesis was measured weekly for each plant during early to mid-morning hours with an LI-6400 infrared gas analyzer system in differential mode (Li-Cor Biosciences, Inc.; Lincoln, NE, USA). Light response curves were constructed by measuring photosynthesis at 2000, 1500, 1000, 500, 200, 100, 50, 20, and 0  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ . Young leaves at the top and ends of each plant were placed into the leaf chamber, covering an area of 2  $\text{cm}^2$ . Leaves were marked for repeated use in weekly measurements. Relative humidity in the chamber was 25%,  $\text{CO}_2$  levels were 385 ppm, and chamber temperature was 25 °C. Measurements were made after plants became adjusted to conditions, determined when photosynthesis and stomatal conductance stabilized, typically requiring 10–20 min. Measurements from a PPFD of 1500  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$  were used for statistical comparisons between treatments and included (1) photosynthesis at 1500  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$  ( $A_{1500}$ ), (2) stomatal conductance ( $g_s$ ), (3) internal (intercellular)  $\text{CO}_2$  concentration ( $C_i$ ), and (4) transpiration ( $E$ ).

Root samples were harvested at the end of the greenhouse study, rinsed in tap water, and frozen in liquid nitrogen. Root ADH activities were assayed following the spectrophotometric procedure described by Maricle et al. (2006).

### 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. Individuals examined for physiological data were fourteen *T. ramosissima*, three *P. australis*, and seven *P. deltoides* individuals. All species identifications were verified using *Flora of the Great Plains* (Great Plains Flora Association, 1986).

Five 25 m transects were established at the site near the waterline. Transects ran perpendicular to the shore, and were 10 m apart. Points were marked on each transect at 5 m intervals, for a total of 30 points. 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. All measures were performed from May through August, 2010. Water depth was measured with a meter stick at each point twice per month for the duration of the study.

Soil moisture content was measured monthly by sampling 100 g of the top  $15 \pm 5$  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 to Fort Hays State University, and  $100 \pm 0.5$  g of soil was placed in metal tins. Tins were dried at 40 °C and were weighed daily until there was no change in mass. Percent moisture was calculated from mass lost.

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

Transpiration rates of marked plants were calculated once per month, following a procedure by Campbell and Norman (1998). 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) at a height of 1.5 m. Leaf width (or stem width for *T. ramosissima*) was measured for all plants with a Titan® electronic digital caliper (Star Asia-USA LLC (Titan Tools); Auburn, WA, USA). An SC-1 leaf porometer (Decagon Devices, Inc; Pullman, WA, USA) was used to measure stomatal conductance and leaf temperature.

Leaf transpiration ( $E$ ) 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  $\lambda$  is the latent heat of vaporization (44,000  $\text{J mol}^{-1}$ ),  $e_a$  is vapor pressure of the air (kPa),  $e_s(T_L)$  is vapor pressure at the leaf surface (kPa), and  $P_a$  is atmospheric pressure (kPa).

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

$$g_v = \frac{1}{(1/g_{va}) + (1/g_{vs})} \quad (2)$$

where  $g_{vs}$  is stomatal conductance (obtained from the leaf porometer) and  $g_{va}$  was boundary layer conductance ( $\text{mol m}^{-2} \text{s}^{-1}$ ), calculated after Campbell and Norman (1998) as:

$$g_{va} = 0.147 \sqrt{\frac{u}{d}} \quad (3)$$

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

Vapor pressure at the leaf surface ( $e_s(T_L)$ ) was assumed to be saturated, and it was calculated by:

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

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 after Campbell and Norman (1998) as:

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

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

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

where  $X$  is elevation (m) (Campbell and Norman, 1998).

### 2.4. Stable isotope preparation

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

### 2.5. Data analysis

All data were analyzed with SPSS 12.0 for Windows (2003 SPSS Inc.; Chicago, IL, USA). A repeated measures analysis of variance (ANOVAR) was used in the greenhouse experiment for  $A_{1500}$ ,  $g_s$ ,  $C_i$ , and  $E$  at 1500  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ . Root alcohol dehydrogenase

activity was analyzed with analysis of variance (ANOVA). Post hoc comparisons were performed with Tukey's LSD.

Field data were transformed as needed for normal distribution. Assumptions of the analysis were tested by plotting transformed data to determine normal distribution and running a one sample Kolmogorov–Smirnov test. Soil moisture data were transformed using an arcsine transformation since the data were proportions. Water depth was coded into a 1 (coverage of water) or 0 (no water), which resulted in a normal distribution. Stomatal conductance and transpiration data were transformed using  $\log(x+1)$ . Soil water potential was transformed using  $e^x$ .

Any missing variables or cases that were labeled “dead” were removed from the field data set. An analysis of covariance (ANCOVA) was performed for stomatal conductance from field plants in a repeated measures design. Covariates were air temperature, Julian date, soil water potential, and water depth. A multivariate analysis of covariance (MANCOVA) was performed for plant water potential and transpiration. Covariates were water depth, Julian date, soil moisture, relative humidity, and air temperature.  $\delta^{13}\text{C}$  data were analyzed with ANCOVA for *T. ramosissima* and *P. deltoides*. One *P. australis* plant was destroyed by a deer, so  $\delta^{13}\text{C}$  was not analyzed. Covariates were air temperature, Julian dates, soil water potential, and water depth. Pearson correlations were also run alongside both ANCOVAs and the MANCOVA to determine if any variables were correlated. All analyses were performed at  $\alpha = 0.05$ .

### 3. Results and discussion

This study examined physiological responses of *T. ramosissima* to flooding in both greenhouse and field settings. Flooding impacts *T. ramosissima* metabolically, as roots had increased ADH activity and leaf-level gas exchange was reduced. Nonetheless, *T. ramosissima* showed an ability to acclimate to flooding within three weeks, indicating moderate tolerance to flooding. Responses to flooding might help explain ecological phenomena relevant to invasion by *T. ramosissima*.

#### 3.1. Physiological effects of flooding on gas exchange in *Tamarix ramosissima*

Photosynthetic light response curves were measured weekly for three weeks to study effects of flooding and soil type on photosynthesis in *T. ramosissima* (Fig. 1). Photosynthesis at  $1500 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$  ( $A_{1500}$ ) ranged from 2.3 to  $16.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$  across treatments and weeks (Fig. 2). Flooding reduced  $A_{1500}$  during the first two weeks (Fig. 2;  $F = 8.0, P < 0.01$ ), but  $A_{1500}$  increased thereafter.  $A_{1500}$  was significantly higher in drained plants compared to flooded plants ( $F = 10.8, P < 0.01$ ). However, there were no differences between soil treatments, nor were there any interactions ( $F = 1.1, P \geq 0.36$ ).

Flooding can cause photosynthesis rates to decrease in plants (Pezeshki, 2001), often due to stomatal closure (Kozłowski, 1984).  $A_{1500}$  and  $g_s$  for plants in the flooded treatments were lowest in week one, but increased by week three (Fig. 2). This increase is similar to results of Pezeshki et al. (1996), where the flooding-tolerant *Taxodium distichum* L. had similar gas exchange results as *T. ramosissima* in the present study. Recovery of photosynthesis following flooding indicates *T. ramosissima* is at least moderately tolerant of flooding (Copolovici and Niinemets, 2010), which could be important for its invasive success.

Physiological responses were affected the most by flooding duration, and not by soil type. Measures of transpiration ( $E$ ), which largely depend on stomatal conductance ( $g_s$ ), were similar to patterns of photosynthesis between weeks and treatments

(Figs. 2–3). Both  $g_s$  and  $E$  were higher in drained treatments compared to flooded treatments ( $F \geq 1.6, P < 0.01$ ).  $g_s$  and  $E$  were initially reduced by flooding (Figs. 2–3;  $F \geq 10.3, P < 0.01$ ), but both  $g_s$  and  $E$  increased as the experiment progressed. Soil type did not influence  $g_s$  or  $E$  ( $F \leq 1.6, P \geq 0.21$ ), and there were no interactions ( $F \leq 0.7, P \geq 0.67$ ). However, fluctuations in  $A_{1500}$  during flooding were not caused by changes in  $g_s$ . Flooded plants had non-stomatal (e.g., metabolic) limitations on photosynthesis, resulting in lower  $A_{1500}$ . Non-stomatal limitations on photosynthesis also occurred in a related study of flooding-tolerant *Populus angustifolia* James (Rood et al., 2010), where photosynthesis in drained treatments was higher than in flooded treatments.

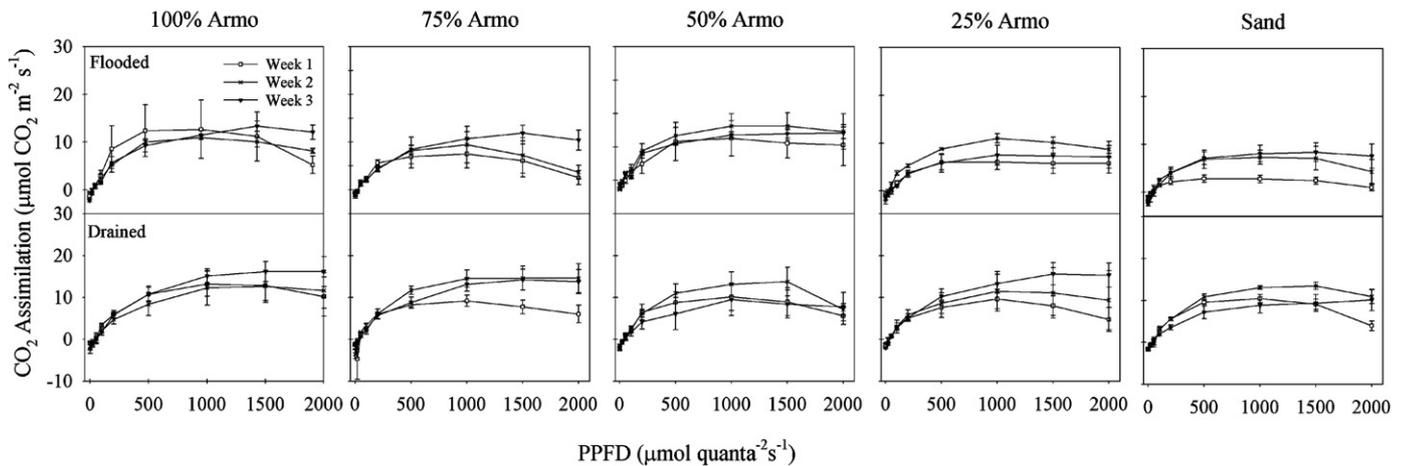
The ability of *T. ramosissima* to acclimate to flooded conditions is apparent in gas exchange data during the first three weeks of flooding (Figs. 1–2). Both  $A_{1500}$  and  $g_s$  in *T. ramosissima* decreased with flooding. This decrease in  $A_{1500}$  did not come from stomatal closure, as  $C_i$  was unchanged by flooding (Fig. 3;  $F < 0.01, P = 0.96$ ). This was somewhat surprising, as we hypothesized stomatal closure under flooding would reduce  $A_{1500}$ , similar to measurements of other flooding-sensitive species (Gravatt and Kirby, 1998). Stomatal closure has been linked to flooding in many plants, for example in flooding-sensitive *Forsythia* (Atkinson et al., 2008) and in citrus seedlings (Rodríguez-Gamir et al., 2011), but also in flooding-tolerant species like *T. distichum* (Krauss et al., 2009) and *P. angustifolia* (Rood et al., 2010). However, flooding-induced stomatal closure only reduces photosynthesis in some cases, such as in flooding-sensitive barley (Yordanova et al., 2005). Stomatal closure did not reduce photosynthesis in more tolerant species like *T. distichum* (Krauss et al., 2009) and *P. angustifolia* (Rood et al., 2010). Similarly,  $A_{1500}$  in *T. ramosissima* in the present study was reduced by non-stomatal limitations, despite reduced  $g_s$ , suggesting *T. ramosissima* is more flooding tolerant than previously hypothesized.

In the present study, new shoot growth and discoloration were observed in both flooded and drained plants. Most plants had new shoot growth (86.7% of flooded plants, and 93.3% of drained plants) by week 3, but yellowing of leaves was more evident in flooded plants (100% of individuals) compared to drained plants (13.3% of individuals), indicating possible anaerobic stress. Flooding survival by *T. ramosissima* could be aided by escape mechanisms such as formation of adventitious roots and shoot growth (Brotherson and Field, 1987; Sprenger et al., 2001). However, *T. ramosissima* is less adept at these escape mechanisms compared to native riparian species (Vandersande et al., 2001), making them unlikely to be important in the invasive success of *T. ramosissima*.

In previous studies (Sher et al., 2000; Vandersande et al., 2001; Sher and Marshall, 2003), *T. ramosissima* seedlings were out competed by *P. deltoides* or other riparian species under flooding. Physiological measurements were not reported in these studies. However, measures of height, biomass, and survival were greater in native species compared to *T. ramosissima*. It is possible *T. ramosissima* did not survive flooding due to increased oxygen stress and lower photosynthesis rates. Similarly, physiological measurements such as an increase in root ADH, and changes in  $E$  and  $g_s$ , could also help to explain the results of Gladwin and Roelle (1998), where *T. ramosissima* did not survive 25 days of flooding.

#### 3.2. Physiological effects of flooding on root metabolism in *Tamarix ramosissima*

Flooding causes displacement of oxygen in soils, inducing anoxic conditions (Blom and Voeselek, 1996). This causes anaerobic respiration to occur in plants, which typically increases alcohol dehydrogenase (ADH) activity in roots (Kimmerer, 1987). For flood tolerant species, a decrease in root ADH activity is a functional adaptation indicating tolerance to oxygen deficient conditions (Crawford and



**Fig. 1.** 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  $\pm$  SE.

Braendle, 1996). However, for flooding intolerant species, increased ADH activity can indicate oxygen stress (Maricle et al., 2006).

In the present study, root ADH activity was higher in plants in flooded treatments compared to drained treatments ( $F=16.5$ ,  $P<0.01$ ), indicating oxygen stress. ADH activity ranged from  $3.9$  to  $12.9 \mu\text{mol g}^{-1} \text{min}^{-1}$  in the flooded treatment, and from  $0.71$  to  $2.6 \mu\text{mol g}^{-1} \text{min}^{-1}$  in the drained treatment (Fig. 4). In a similar study by Kimmerer (1987), root ADH activity increased in the riparian species *P. deltoides* due to anaerobic stress. Understanding root ADH activity in riparian species in response to anaerobic conditions could allow assessment of oxygen stress in *T. ramosissima* and competitors.

There was no difference in root ADH activity between soil types (Fig. 4;  $F=2.6$ ,  $P=0.07$ ), and there was no soil type  $\times$  water treatment interaction ( $F=1.3$ ,  $P=0.32$ ) in the present study. It could be possible that differences in soils become less important in flooded

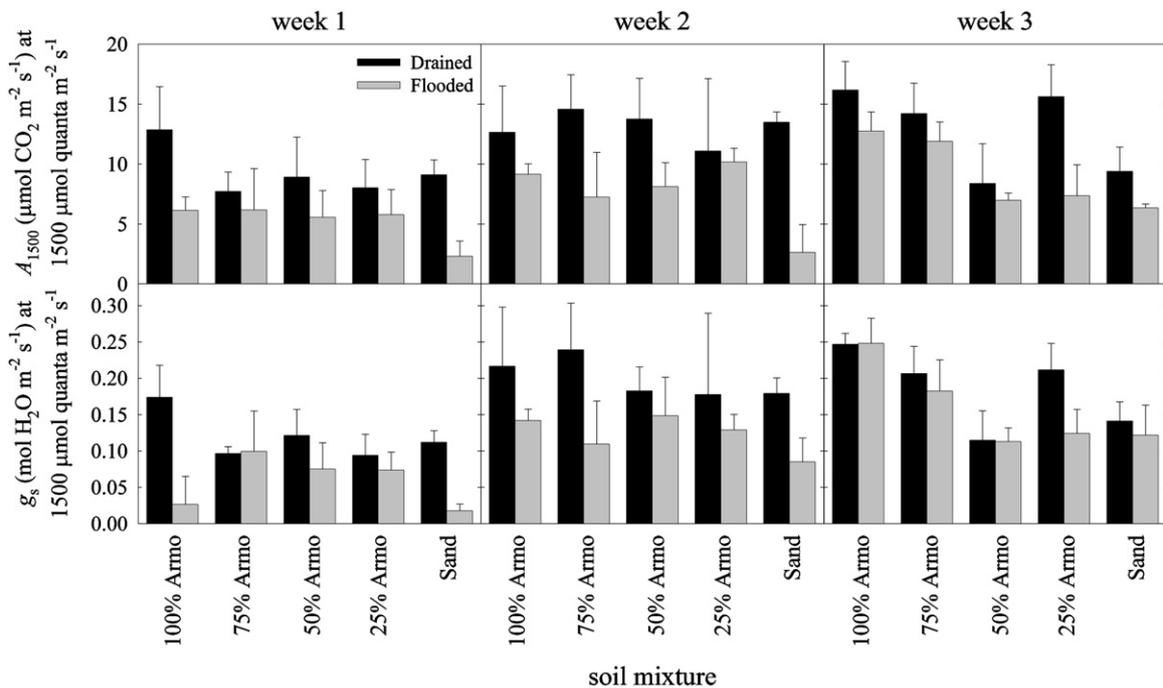
conditions. Furthermore, small sample sizes could have affected the statistical analysis for ADH activity. For future research, increasing sample size and measuring soil physical properties could further explain oxygen stress in *T. ramosissima*.

### 3.3. Comparing responses to flooding between *Tamarix ramosissima* and co-occurring species in the field

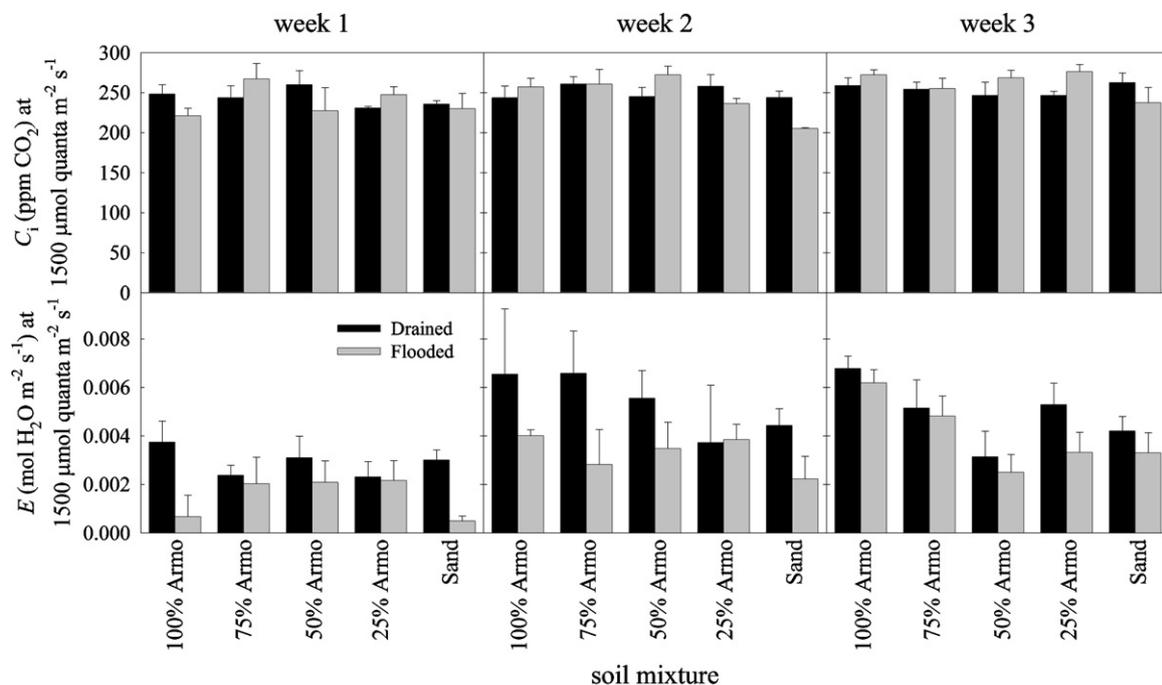
*T. ramosissima* appeared less flooding tolerant compared to co-occurring riparian and wetland species, indicated by leaf  $\Psi$  and  $g_s$ .

#### 3.3.1. $E$ , $g_s$ , and leaf $\Psi$ of *Tamarix ramosissima*, *Phragmites australis*, and *Populus deltoides*

Transpiration ( $E$ ) ranged from  $1.1$  to  $1.4 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$  across species and treatments (Fig. 5).  $E$  and leaf water potential ( $\Psi$ ) were significantly different across Julian dates and relative



**Fig. 2.** Photosynthesis ( $A_{1500}$ , top row) and stomatal conductance ( $g_s$ , second row) at  $1500 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$  for *Tamarix ramosissima* in different soil mixtures. Measurements were taken weekly for three weeks. Black bars represent drained treatments and grey bars represent flooded treatments. Bars are means of three individuals per treatment  $\pm$  SE. Statistics for main effects regarding  $A_{1500}$  were: flooding,  $P<0.01$ ; weeks,  $P<0.01$ ; soil,  $P=0.39$ ; all interaction terms,  $P \geq 0.36$ . Statistics for main effects regarding  $g_s$  were: flooding,  $P<0.01$ ; weeks,  $P<0.01$ ; soil,  $P=0.25$ ; all interaction terms,  $P \geq 0.39$ .



**Fig. 3.** Internal (intercellular) CO<sub>2</sub> concentration ( $C_i$ , top row) and transpiration rate ( $E$ , second row) at 1500  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$  for *Tamarix ramosissima* in different soil mixtures. Measurements were taken weekly for three weeks. Black bars represent drained treatments and grey bars represent flooded treatments. Bars are means of three individuals per treatment  $\pm$  SE. Statistics for main effects regarding  $C_i$  were: flooding,  $P=0.36$ ; weeks,  $P=0.02$ ; soil,  $P=0.32$ ; all interaction terms,  $P \geq 0.36$ . Statistics for main effects regarding  $E$  were: flooding,  $P < 0.01$ ; weeks,  $P < 0.01$ ; soil,  $P = 0.21$ ; all interaction terms,  $P \geq 0.67$ .

humidities (Table 1;  $F \geq 3.5$ ,  $P < 0.04$ ).  $E$  was higher in June at 2.4  $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$  compared to July at 0.60  $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$  ( $F=6.9$ ,  $P=0.01$ ).  $E$  increased from May to June and from July to August. No differences were detected in leaf  $\Psi$  and  $E$  due to soil moisture, air temperature, or water depth (Table 1;  $F \leq 2.9$ ,  $P \geq 0.07$ ).

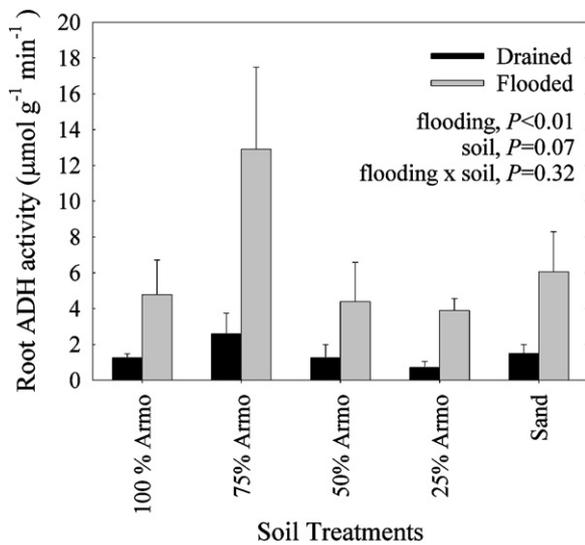
Leaf  $\Psi$  can be considered the work needed to elevate water to the leaf tissue (Larcher, 2003). *T. ramosissima* had a leaf  $\Psi$  of  $-1.40$  MPa, which was lower than  $\Psi$  in *P. australis* ( $-0.88$  MPa) and *P. deltoides* ( $-0.94$  MPa) ( $P \leq 0.05$ ) (Fig. 5). Leaf  $\Psi$  was not different between *P. deltoides* and *P. australis* ( $P=0.91$ ). Lower leaf  $\Psi$  in *T. ramosissima* could indicate more energy was spent to lower water

potential compared to other species under flooding, a potential energy sink that could put *T. ramosissima* at a competitive disadvantage when flooded.

Under flooded soils, water uptake in plants can become reduced, which can cause leaf dehydration and lower leaf  $\Psi$  (Bradford and Hsiao, 1982). *T. ramosissima* can maintain control of stomata at low plant  $\Psi$  (Cleverly et al., 1997; Devitt et al., 1997). The present study seems to complement the drought studies of Devitt et al. (1997) and Cleverly et al. (1997); however, flooding presents stress conditions in addition to decreased  $g_s$  and lowered  $\Psi$ . It is more likely physiological responses of *T. ramosissima* under flooding were a result of anaerobic stress and not decreased water uptake. This is further

**Table 1**  
Correlations of response variables and covariates from field data over the entire sampling period. Sample sizes reflect a repeated measures design, and bold font represents variables correlated at the 0.05 level.

		Coded water depth (cm)	Leaf $\Psi$ (MPa)	Air temperature ( $^{\circ}\text{C}$ )	Arcsine soil moisture (%)	$\log(x+1) E$ ( $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$ )	Relative humidity (%)
Julian date	$r$	-0.040	-0.056	-0.413	-0.052	-0.256	0.104
	$p$	0.770	0.683	<b>0.002</b>	0.702	0.057	0.445
	$n$	56	56	56	56	56	56
Coded water depth (cm)	$r$		0.211	0.152	0.844	0.289	-0.332
	$p$		0.119	0.263	<b>0.000</b>	<b>0.030</b>	<b>0.012</b>
	$n$		56	56	56	56	56
Leaf $\Psi$ (MPa)	$r$			0.126	0.069	0.025	-0.053
	$p$			0.355	0.615	0.858	0.697
	$n$			56	56	56	56
Air temp. ( $^{\circ}\text{C}$ )	$r$				0.127	0.130	-0.341
	$p$				0.349	0.340	<b>0.010</b>
	$n$				56	56	56
Arcsine soil moisture (%)	$r$					0.253	-0.347
	$p$					0.060	<b>0.009</b>
	$n$					56	56
Relative humidity (%)	$r$					-0.546	1
	$p$					<b>0.000</b>	-
	$n$					56	56



**Fig. 4.** Root alcohol dehydrogenase (ADH) activity for *Tamarix ramosissima* in different soil mixtures. Black bars represent drained treatments and grey bars represent flooded treatments. Measurements were taken at the end of three weeks of treatment. Bars represent means of three individuals per treatment  $\pm$  SE.

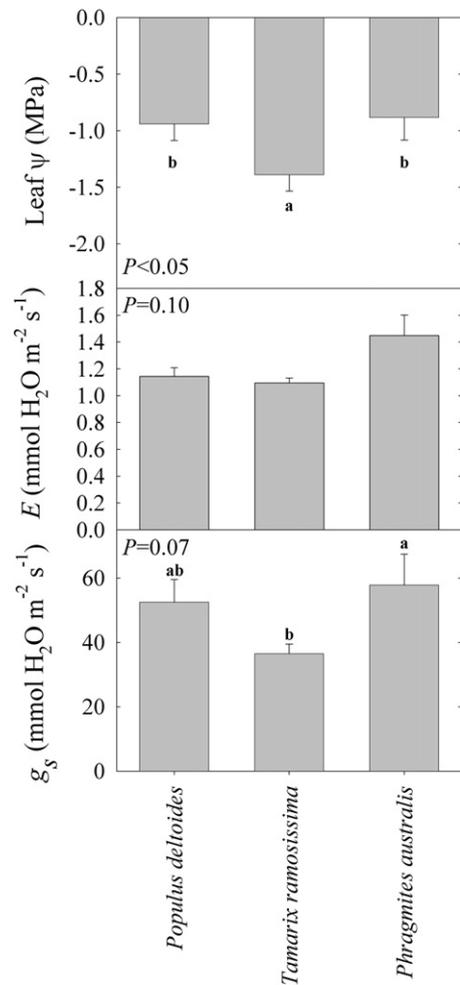
supported by the observation that root ADH activity was higher in flooded treatments for the greenhouse study.

Stomatal conductance ( $g_s$ ) is a measure that has numerous important correlates. Since photosynthetic  $\text{CO}_2$  uptake and transpiration ( $E$ ) both occur through stomata, variations in  $g_s$  can also indicate variations in photosynthesis and  $E$ , and therefore general response to flooding. *T. ramosissima* had a mean  $g_s$  of  $36.5 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ , which was marginally lower than  $g_s$  for *P. australis* at  $57.8 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$  (Fig. 5;  $F=2.8$ ,  $P=0.07$ ).  $g_s$  was negatively correlated with water depth (Table 2;  $P=0.03$ ).

*P. australis* is a flood tolerant species, which could explain the high  $g_s$  and  $E$  during the field study when compared to *T. ramosissima* and *P. deltoides*.  $E$  was significantly different between Julian dates and relative humidities (Table 1;  $P<0.04$ ). In other environmental variables, increased air temperatures and decreased relative humidity caused a reduction in stomatal conductance, which lowered  $E$  (Table 1;  $P\leq 0.01$ ).  $E$  was expected to be highest in *P. australis* since it is highly flood tolerant (Gries et al., 1989). However, no differences in  $E$  were detected between species in the present study ( $F=2.5$ ,  $P=0.10$ ).

### 3.3.2. Leaf $\delta^{13}\text{C}$

Carbon isotope analysis has been used to examine stomatal behavior and water use efficiency in *T. ramosissima*. In the present



**Fig. 5.** Leaf  $\Psi$  (top),  $E$  (middle), and  $g_s$  (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  $\pm$  SE.

study, *T. ramosissima* had a leaf  $\delta^{13}\text{C}$  of  $-27.0 \pm 0.21\text{‰}$  (standard error), which was higher than *P. deltoides* at  $-28.0 \pm 0.35\text{‰}$  (data not shown;  $F=9.4$ ,  $P<0.01$ ). Similarly, Busch and Smith (1995) observed *T. ramosissima* had a higher  $\delta^{13}\text{C}$  value than *Salix gooddingii* C.R. Ball and *Pluchea sericea* (Nutt.) Coville, indicating higher water use efficiency.

Carbon isotope analysis can be used to detect stomatal closure from stress conditions such as flooding. Stomatal closure usually causes  $\delta^{13}\text{C}$  to increase in  $\text{C}_3$  plants such as *P. deltoides* and

**Table 2**

Correlations of  $\log(x+1)g_s$  and covariates from field data over the entire sampling period. Sample sizes reflect a repeated measures design, and bold font represents variables correlated at the 0.05 level.

		Coded water depth (cm)	$e^x$ soil $\Psi$ (MPa)	$\log(x+1)g_s$ ( $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ )	Air temperature ( $^\circ\text{C}$ )
Julian date	$r$	-0.066	-0.068	-0.188	-0.705
	$p$	<b>0.627</b>	0.618	0.165	<b>0.000</b>
	$n$	56	56	56	56
Coded water depth (cm)	$r$		-0.216	-0.286	0.221
	$p$		0.111	<b>0.033</b>	0.102
	$n$		56	56	56
$e^x$ soil $\Psi$ (MPa)	$r$			-0.116	0.084
	$p$			0.395	0.539
	$n$			56	56
$\log(x+1)g_s$ ( $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ )	$r$				-0.011
	$p$				0.933
	$n$				56

**Table 3**  
Correlations of  $\delta^{13}\text{C}$  and covariates from field data over the entire sampling period. Sample sizes reflect a repeated measures design, and bold font represents variables correlated at the 0.05 level.

		$\delta^{13}\text{C}$ (‰)	Coded water depth (cm)	$e^x$ soil $\Psi$ (MPa)	Air temperature ( $^{\circ}\text{C}$ )
Julian date	<i>r</i>	0.061	−0.024	−0.037	−0.689
	<i>p</i>	0.690	0.876	0.811	<b>0.0001</b>
	<i>n</i>	45	45	45	45
$\delta^{13}\text{C}$ (‰)	<i>r</i>		−0.034	0.002	−0.027
	<i>p</i>		0.825	0.989	0.862
	<i>n</i>		45	45	45
Coded water depth (cm)	<i>r</i>			−0.249	0.191
	<i>p</i>			0.099	0.209
	<i>n</i>			45	45
$e^x$ soil $\Psi$ (MPa)	<i>r</i>				0.039
	<i>p</i>				0.797
	<i>n</i>				45

*T. ramosissima* (Farquhar et al., 1982). In healthy  $\text{C}_3$  plants, leaf  $\delta^{13}\text{C}$  is typically around  $-28.0\%$  (Farquhar et al., 1982; Fry, 2006). *T. ramosissima* had higher  $\delta^{13}\text{C}$  values than *P. deltoides*, indicating *T. ramosissima* closed stomates during flooding. Leaf  $\delta^{13}\text{C}$  values did not relate to any environmental variables in the field study (Table 3;  $P \geq 0.69$ ). Carbon isotope values for *P. deltoides* and *T. ramosissima* were expected to correlate with water depth, since this variable had the greatest effect on stomatal closure (Table 2;  $P = 0.03$ ). Consequently, water depth might not be the main factor influencing  $\text{CO}_2$  availability and leaf  $\delta^{13}\text{C}$  in *T. ramosissima*.  $\delta^{13}\text{C}$  was not significantly different between Julian dates, soil  $\Psi$ , air temperature, or water depth ( $F \leq 0.95$ ,  $P \geq 0.34$ ). However, other factors can cause stomates to close, such as an increase in air temperature and decreases in leaf  $\Psi$ .

#### 4. Conclusions

The main goal of the present study was to determine the physiological responses of *T. ramosissima* to flooding. Greenhouse results indicated oxygen deficiency occurred in flooded *T. ramosissima* plants, which corresponded with decreased photosynthesis. Contrary to expectations, stomatal closure did not limit photosynthesis. Instead, non-stomatal limitations reduced  $A_{1500}$ . Following three weeks of flooding, physiological acclimation was evident in *T. ramosissima*, indicating metabolic acclimation and moderate flooding tolerance within a greenhouse setting. Field results suggest *T. ramosissima* is less flood tolerant than the flood tolerant species *P. australis* and the riparian species *P. deltoides*. In the field,  $g_s$  and leaf  $\Psi$  were lower in *T. ramosissima* compared to *P. australis* and *P. deltoides*. Decreased photosynthetic production by *T. ramosissima* during flooding, paired with increased oxygen deficiency, likely contribute to its lack of competitiveness in flooded systems. A possible decrease in competitiveness is important to note because flooding could decrease invasive success of *T. ramosissima* along riparian systems, which could allow riparian ecosystems to return to a more original state.

It is evident flooding affects *T. ramosissima* in natural and greenhouse 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. However, more research should be completed on the physiological responses of *T. ramosissima* to understand tolerance to flooding.

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