



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) 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 CO_2 , and changes the dynamics of carbon isotope discrimination by plants. In C_3 plants like *T. ramosissima*, the enzyme Rubisco discriminates against ^{13}C during photosynthesis (O'Leary, 1981). For 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.

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