TRANSPERSION, GROWTH AND SURVIVAL OF NATIVE RIPARIAN AND
INTRODUCED SALTCEDAR TREES IN MIXED STANDS
ON THE SAN PEDRO RIVER, U.S.A.

by

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Western riparian zones have undergone significant landscape changes over the past several decades, with introduced saltcedar (*Tamarix* spp.) as a crucial component of this transformation. Saltcedar, now a dominating presence along many western rivers, due to its high tolerance to drought, salinity and stress, is considered to be a high-water-use plant that can desiccate disturbed river systems. Where native and saltcedar plant communities occur together, it is important to understand water use patterns and the physiological responses of each species to environmental stress factors, as a way to project an eventual course of succession processes and management options at a given site. Stress and disturbance in the form of reduced stream flows and land use changes may influence these interactions. Understanding the conditions that allow for saltcedar dominance is critical in determining riparian water budgets, and developing effective management strategies. Sap flux sensors were used to measure the physiological response of co-occurring communities of saltcedar and native trees to these environmental stress factors during the pre-monsoon period in early summer, a time of maximum stress for riparian vegetation. The results suggest that native trees are still competitive with saltcedar so that a mixed plant community is likely to continue on the San Pedro River on the condition that current groundwater levels and river flows are maintained. If base flows and depth to groundwater continue to decline, this competitive balance between saltcedar and native trees likely could change.
CHAPTER 1

INTRODUCTION

1.1 Background

Terrestrial riparian zones consist of unique plant assemblages that are dependent on growing along primary channels and floodplains of rivers and streams. They serve as rich havens of biodiversity, contain abundant habitats that provide unique niche ecosystems to support an assortment of wildlife exclusive to that area. Overall, plant community species that occupy riparian zones are exclusive to their locale, having adapted to fluvial disturbances specific for their region (Naiman and Decamps, 1997).

Phreatophytes are riparian tree species that typically grow in southwestern riparian forests utilizing groundwater as their primary water source. They prevail in areas where infrequent rainfall and flood events are inadequate to support the survival and growth of non-phreatophytic plants (Thomas, 2014).

Phreatophytic trees that establish along riparian areas in the southwestern USA comprise a wide assortment of species that vary broadly in their structural and functional characteristics as regards to above and below ground plant architecture, transpiration rates, tolerance to drought and groundwater fluctuations, and flexibility in accessing alternate water sources (Lite and Stromberg, 2005; Snyder and Williams, 2000; Thomas, 2014).
Over the past century, natural river processes of major western U.S. rivers have been significantly affected by human intervention. In essence, the natural flow regimes of all major western U.S. rivers have been regulated through construction of dams, channelization, land use changes, and water diversions of groundwater to meet agricultural and human needs. (Ohmart et al., 1988; Rood et al. 1995; Glenn et al. 1996; Howe and Knopf, 1997; Poff et al. 1997; Smith et al. 1998; Everitt, 1998; Molles et al. 1998). This has resulted in reduced stream base flows and water tables in riparian zones of semi arid and arid areas. Consequently, greater saline content and xeric conditions now exist along river banks of these areas. In many cases, shifts in riparian plant community composition as well as senescence of woody communities are the end result of such changes to river hydrology (Nilsson and Berggren, 2000).

Such circumstances have facilitated the spread of non-native saltcedar along major western riparian river systems and reservoirs and diminished the availability of mesic native tree habitats (Smith et al., 1998; Friedman et al., 2005; Glenn and Nagler, 2005, Ringold et al., 2008). Saltcedar, a small tree or shrub native to Africa and Eurasia, was intentionally brought to the United States in the early 19th century (Robinson, 1965; Brock, 1994). Saltcedar species (*Tamarix ramosissima* and related hybrids) have rapidly proliferated along western rivers. *Tamarix's* swift spread occurred between the 1940s to 1960s, during a period of intensive regulation of major western U.S. rivers that involved construction of dams, and implementation of water diversion for human use (Glenn and Nagler, 2005, Nagler et al., 2011). Along disturbed river systems, saltcedar plant communities can establish as vast monocultures, as observed on floodplains of the Lower
Colorado River; or, as mixed stands nearby native riparian trees, as observed on riparian zones of the San Pedro, Rio Grande and Colorado Rivers. (Ohmart et al., 1988; Howe and Knopf, 1991; Stromberg, 1998; Glenn et al., 1998; Dahm et al., 2002).

In the past gallery forests of cottonwood willow riparian trees were one of the most prevalent vegetation types along the length of many low elevation rivers of the southwest USA. Currently, riparian forests are composed of native pioneer cottonwood-willow (*Populus fremontii-Salix gooddingii*) phreatophytic trees along with introduced stress-tolerant saltcedar (*Tamarix ramosissima* and related species and hybrids) distributed along active perennial and intermittent reaches of river channels in semiarid regions, they are mainly reliant on groundwater availability and as such influence critical hydrological processes (Stromberg, 1993).

Certain thresholds of stream flows and ground water levels foster the establishment of particular phreatophytic riparian tree species (Lite and Stromberg, 2005). *Populus fremontii* (Fremont cottonwood) trees, a drought sensitive species, are evident at perennial or intermittent river reaches where groundwater levels range between 2.3 - 3 meters in depth; (Stromberg et al. 1993; Stromberg et al. 1996). Whereas both saltcedar (*Tamarix ramosissima*) and mesquite (*Prosopis velutina*), found along intermittent and ephemeral river reaches, have been noted to access groundwater at depths of 4 and 6 meters respectively (Canadell et al., 1996; Horton et al. 2003, Glenn and Nagler, 2005; Lite and Stromberg, 2005). As man-made modifications to river hydrology continued, thresholds of groundwater levels and stream flows required to
maintain native cottonwood-willow communities were not sustained in many major western U.S. rivers, resulting in a rapid decline of riparian areas over the past several decades, and a shift in riparian species composition that allowed for greater abundance of drought tolerant saltcedar (*Tamarix ramosissima*) (Shafroth et al. 1998, 2002; Stromberg, 1998; Levine and Stromberg, 2001; Stromberg and Chew, 2002; Tallent-Halsell and Walker, 2002).

Previous studies have expressed the concern that *Tamarix*'s continual spread along western rivers may lead to a deterioration in riparian ecological functions and adversely affect habitat areas (DiTomaso, 1998; Chapin et al., 2000). Numerous neotropical bird species utilize riparian passageways as migratory routes and nesting sites. Their coordinated exodus through these pathways corresponds to the flowering and seed production of native trees, which serve as food and habitat sources (Ohmart et al., 1998). Areas where saltcedar has developed into dense stands are alleged to serve as poor substitute habitat in place of native trees.

Saltcedar establishment and persistence in disturbed river systems of semiarid riparian zones is largely due to its collective physiological adaptations that allows saltcedar to function as a replacement for native tree species. (Neill, 1985; Hughes, 1993; Friederici, 1995; Barrow, 1998; DiTomosa, 1998; Smith et al., 1998; Zavaleta, 2000). Included among these adaptations are rapid growth rates (Friederici, 1995); excessive seed production, quick germination and seedling establishment (Neill, 1985; Brotherson
Transpired groundwater by riparian phreatophytes represents a substantial part of riparian water budgets most especially in arid and semiarid regions wherein potential evapotranspiration (PET) is far greater than annual rainfall amounts. (Anderson, 1995; Tillman et al. 2012). Moreover, increasing urban development and agricultural expansions in western regions have placed greater demands on water budgets making it progressively more challenging for water managers to preserve water supplies, respond to urban and agricultural needs, while simultaneously sustaining riparian habitats (Jackson et al., 2001).

Several studies have expressed the concern that the spread of introduced saltcedar species along many western waterways, in many cases occupying greater areas than native riparian trees, may alter groundwater budgets (Sala et al., 1996; DiTomaso, 1998). Water budgets of semiarid riparian areas can be affected by the spread of non-native species, if their incursion results in greater transpired water rates per unit ground area; or, if non-native ground cover is greater than natives and non-native plants are directly accessing groundwater from underground stream aquifers (Hultine and Bush, 2011). Attentive monitoring of changes in riparian vegetation cover, particularly in arid and semiarid regions increases our knowledge of ecohydrological conditions that may contribute towards shifts in riparian communities and what their long term effects on groundwater budgets may be (Tillman et al. 2012).
Earlier transpiration studies of saltcedar reported exceptionally high rates of water use relative to native species. Later, it was realized that the techniques applied for measurement of riparian transpiration tended towards overestimation of water use (Shafroth et al., 2005). However more current research have modified these rates and indicates that transpired groundwater by tamarisk is actually similar to that of native riparian species with water use rates ranging between 0.75 to 1.45 m yr\(^{-1}\) with an average rate of approximately 1 m yr\(^{-1}\) (Devitt et al. 1998; Cleverly et al. 2002, 2006; Nagler et al., 2005; Westenburg et al. 2006; Owens and Moore, 2007; Nagler et al. 2008a, 2008b; Shafroth et al., 2010)

Considerable discussion has ensued among land use managers as to the best saltcedar management options for western riparian areas (Anderson, 1998; Stromberg and Chew, 2002). Saltcedar eradication programs are considered as viable management alternatives for some land use managers. To some extent, using collective mechanical and chemical methods for saltcedar removal can be effectual in achieving desired results on an immediate basis (Taylor and McDaniel, 1998; McDaniel and Taylor, 2003). A logical supposition would be that upon removal of any phreatophytic tree/shrub species (including *Tamarix*), riparian transpiration rates would decline and higher river flows would result. However, not all riparian restoration efforts have been completely successful (Briggs, 1996; Anderson, 1998). On the Pecos River, Texas in 1999, for instance, large scale removal of saltcedar using chemical applications resulted in widespread mortality of salt cedar; however increase in river flows were documented (Hart et al. 2005). Removal of riparian vegetation may result in raised groundwater
tables; however their removal also creates greater bare-soil areas which leads to higher soil evaporation.

To date, wide scale saltcedar removal has not been attempted along any major western rivers. Such an effort likely would have far-reaching consequences on habitat conditions as well as affect native and non-native riparian species distribution and would largely depend upon the replacement vegetation that establishes in place of saltcedar (Hultine et al., 2010; Shafroth et al., 2008). More recently, leaf-eating Diorhabda beetles have been released in western riparian areas as bio-control agents for the sole purpose of reducing the spread of saltcedar (DeLoach et al., 1996; Lewis et al., 2003; Quimby et al., 2003). This approach could possibly provide an alternative, cost-effective option for the control of saltcedar over larger spatial scales.

As more research is collected on western riparian ecosystem dynamics and restoration projects continue, research scientists who have spent a considerable portion of their professional careers investigating this long debated issue are becoming more convinced of an alternative perspective of Tamarix spread. An elucidation that species shift from native vegetation to Tamarix on selected western rivers occurs as a replacement mechanism, whereby Tamarix colonizes riparian areas no longer hydrologically viable to support native vegetation establishment (Harris 1966; Haase 1972; Horton 1977; Engel-Wilson & Ohmart 1978; Everitt 1980; Anderson 1996; Smith et al. 1998).
Researchers who support this alternate analysis, suggest that *Tamarix* operates as a replacement rather than displacement species whereby it mostly establishes in environments that have lower water tables, higher soil salinities and lack stream flows. In essence, saltcedar, a stress and drought tolerant species establishes primarily in locations that no longer can support mesic, native pioneer species.

Exceptionally drier climate conditions have persisted in many southwestern regions that are experiencing a long term drought. Human populations are rising rapidly in several major southwestern cities resulting in rapid urban development; all of which are expected to place greater demands on existing water supplies. This will eventually cause further declines in groundwater levels and likely will impact hydrologic conditions in riparian areas.

Environmental thresholds that support a species' replacement are theorized to occur in a non-linear fashion such that small alternations in ecosystems can weaken riparian equilibrium to the advantage of one species over another (Lansen and Alp, 2015).

If hydrologic conditions continue to be altered on U.S. southwestern rivers, it will likely promote succession processes in which saltcedar ultimately becomes the dominant riparian species on disturbed river systems of the southwest (Busch and Smith, 1995; DiTomosa, 1998; Smith et al., 1998; Merritt and Poff, 2010).
The natural flow regime of many southwest rivers have been altered considerably; however their flows have not been eliminated altogether. Mixed stands of native and non-native species often predominate along these river systems. Although this is the most common ecosystem type along many southwestern disturbed river systems, little is known about their ecology (Nagler et al., 2011).
CHAPTER II

PRESENT STUDY

II. 1 Explanation of Dissertation Format

This dissertation consists of two chapters and two appendices. Chapter I is the introduction explaining the background for this research and the research objectives.

Appendices A and B, are manuscripts that will be submitted to peer-reviewed journals.

Appendix A is the first manuscript titled, “Survival, growth and physiological response to environmental variables for Arizona ash (Fraxinus veluntia), cottonwood (Populus fremonti) and introduced saltcedar (Tamarix spp.) trees on the Upper San Pedro River, Arizona, U.S. My research work represented the following: self manufacturing of sap flow sensors, supervised installation of sap flow sensors/field equipment, ground water data collection, mapping of vegetation, measured vegetation species, collected and formatted data and conducted data analysis. In kind field work support was provided by two previously trained family members and limited initial assistance for some site equipment was rendered by various U.S. Government Agency(s). My advisor and mentor, Dr. Edward P. Glenn and I collaborated on the statistical analysis, remote sensing imagery and writing of the manuscript.
Appendix B is the second manuscript titled, “Transpiration, Stomatal Conductance and Growth and Survival of Cottonwood \((Populus fremonti)\) Mesquite \((Prosopis glutinosa)\) and Saltcedar \((Tamarix spp.)\) Trees in Mixed Stands on a Riparian Floodplain in the Southwestern United States. My research study for this paper represented the following work: self manufacturing of sap flow sensors, supervised and installed sap flow sensors/field equipment, recorded vegetation measurements, ground water data collection, data collection, data formatting and final data analysis. In kind field work support was provided by one previously trained family member and limited assistance was rendered by various U.S. Government Agency(s) and by staff members from the Nature Conservancy San Pedro River Conservation Ranch. My advisor and mentor, Dr. Edward P. Glenn and I collaborated on the statistical analysis, remote sensing imagery and writing of the manuscript.

1.2 Research Objectives

The purpose of the work presented here is to gain an improved understanding of hydrologic interactions between introduced saltcedar and native riparian trees in stressful environmental conditions. Transpiration studies were conducted during the summer pre-monsoon seasons, a time of maximum stress for riparian vegetation when groundwater is at its greatest depth. The goal was to observe if introduced salt cedar species would exhibit greater tolerance to physiological stress conditions, and out-compete the native riparian trees in terms of growth and survival over the long term. Understanding the
environmental influences that affect the outcome of non-native species dominance within these areas is critical to developing effective management and conservation strategies.

**Objective 1:**

Determine if transpiration rates are significantly different between native and introduced saltcedar riparian species established in co-occurring plant communities under two different hydrologic regimes: perennial and intermittent stream flows.

Determine if competition for water between these co-occurring riparian plant communities. Evaluate species water use patterns per adjacent co-occurring riparian plant species

**Objective 2:**

Evaluate plant physiological response of both native and introduced saltcedar to high atmospheric demand conditions during pre-monsoon season

**Objective 3:**

As a basis for monitoring long-term changes in riparian ecosystem condition resulting from changes in river water availability, after a 5-7 year time frame, determine if the sampled riparian plant communities continued to grow in stable associations at these study sites.
Synthesis of Study

The primary objective of this study was to observe if introduced saltcedar species would exhibit greater tolerance to stressful environmental conditions, and out-compete native riparian trees in terms of growth and survival over the long term. Our hypothesis was that saltcedar would have greater water use and demonstrate better endurance to physiological stress conditions than native riparian trees, traits that would eventually allow saltcedar to become the dominant riparian plant community.

Sap flux sensors were used to measure transpiration and stomatal conductance of introduced saltcedar and native riparian plants in mixed stands at perennial and intermittent steam flow reaches, during the pre-monsoon period, a time of great physiological stress for riparian vegetation.

Results from both studies indicate that saltcedar did not have high ET rates in comparison to native trees. Moreover, stomatal conductance patterns of saltcedar and native tree species both peaked in the early morning hours and were negatively correlated with vapor pressure deficit. A resurvey of sampled trees seven years later to measure their canopy growth and survival with the aid of high-resolution satellite imagery was conducted. Our purpose was to track the survival of individual trees and evaluate their plant canopy areas to determine whether the sampled saltcedar plants eventually developed into a more dominant riparian community over native riparian trees.

At the intermittent reach, the cottonwoods showed appreciable expansion of canopy areas; while saltcedar plants did not increase appreciably in canopy area between
2006 and 2015, but the two cottonwood canopies increased by 6.3 and 11.5 times, respectively. At the perennial reach, all trees but one survived to 2015, and canopy areas showed increases of 1.1-3.5 times since 2007.

We conclude that as long as depth to groundwater along the San Pedro River can be maintained at 3.0 m or less during the pre-monsoon green-up period, and given occasional pulse floods to germinate new cohorts of trees, mixed stands of mesquites, saltcedars and cottonwoods can be expected to persist.
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APPENDIX A

Survival, growth and physiological response to environmental variables for Arizona ash (Fraxinus velutina), cottonwood (Populus fremontii) and introduced saltcedar (Tamarix spp.) trees on the Upper San Pedro River, Arizona, U.S.A

Abstract

Even protected and unregulated river systems are subject to degradation due to changes in regional hydrological conditions and introduction of exotic species. We measured transpiration and stomatal conductance of two mesic native tree species (Fraxinus velutina and Populus fremontii) and the introduced, stress-tolerant species, Tamarix spp., on the Upper San Pedro River in the southwestern U.S. Despite protection, the river has lost about 60% of its base flow since 1944 due in part to groundwater extraction for growing urban centers in the basin, and many reaches have converted from perennial to intermittent. We conducted sap flow measurements on trees in an intermittent reach of the river during the pre-monsoon period in June and July, 2006, a period of maximum stress for riparian vegetation in this ecosystem. We then followed growth and survival of sampled trees through 2015 with high-resolution satellite imagery. Saltcedar is sometimes considered to be a high-water-use plant that can desiccate invaded river systems. However, we found that saltcedar transpiration rates were lower than ash or cottonwoods and were only 42% of potential evapotranspiration. Stomatal conductance of all three tree species peaked in early morning and were negatively
correlated with vapor pressure deficit. All trees survived to 2015, but only the cottonwoods showed appreciable expansion of canopy areas (6-12 fold increase). Despite changes in base flow, depth to water (2.5-3.0 m) and the recession rate of the aquifer during the pre-monsoon period (0.5 m) were still within the range that supports cottonwoods and other mesic tree species. However, if hydrological conditions deteriorate further, a succession process with saltcedar replacing native trees could take place in the future.

Introduction

Human activities have negatively impacted riparian forests throughout the world’s arid and semiarid zones through alteration of the natural flow regime (Poff et al., 1997; Kingsford et al., 2006; Poff and Zimmerman, 2010; Orellana et al., 2012; Perry et al., 2012). It can be difficult to determine the consequences of human impacts on riparian zones, however, due to lack of long-term observational records on many river systems (Webb et al., 2007). Water diversions for agriculture and urban use and flood control structures can have obvious impacts on riparian ecosystem (Poff et al., 1997). However, even unregulated and protected rivers can be impacted by regional and global changes in hydrology and climate (Perry et al., 2012; Nguyen et al., 2014). Introduced species can also have hydrological and ecological impacts on river systems (DiTomosa, 1998). Impacts of introduced species are more difficult to quantify than direct impacts of river regulation, and their potential impact often depend on other changes taking place on river
systems (Stromberg et al., 2009a). There is controversy on whether invasive species are drivers or passengers of ecological change in ecosystems where environmental stress factors are increasing (MacDougall and Turkington, 2005).

The present study was conducted on the Upper San Pedro River in southeastern Arizona, U.S. This river originates in Mexico and flows north into the U.S., ultimately discharging into the Gila River in the Lower Colorado River Basin. Much of the riparian zone is protected within the San Pedro Riparian National Conservation Area (SPRNCA), a 55 km long portion of the river. Created in 1988, the SPRNCA is the U.S.’s only designated Riparian National Conservation Area (Stromberg et al., 1996; Stromberg and Tellman, 2009). Agriculture, groundwater extraction and livestock grazing have been eliminated within the SPRNCA. However, regional groundwater pumping to support population growth in the basin (Mac Nish et al. 2009) and possible changes in upland vegetation in the area Nie et al. 2012) have raised concerns about the health of the riparian forest along the river (Stromberg et al., 2009b). Furthermore, like other southwestern rivers, the riparian zone has been colonized by introduced saltcedar (Tamarix ramosissima and related species and hybrids) (Gaskin and Schaals, 2002).

Concerns about the health of the SPRNCA riparian forest are partly due to an observed decrease in flows in the river over the past century (Thomas and Pool, 2006). Groundwater contributions to the river base flow (estimated as the lowest seven-day flow period of the year) decreased by 66% from 1942-2000 (Thomas and Pool, 2006) and in 2005 the U.S. Geological Survey stream gage at Charleston in the SPRNCA recorded
zero flow over a seven-day period for the first time since it was installed in 1904 (Mac Nish et al., 2009). Similar flow reductions did not occur in other southeastern Arizona and southwestern New Mexico rivers over the same period (Thomas and Pool, 2006). The long-term decrease includes decreases in total annual flows as well as base flows, but is due mainly to reductions in summer flows, while winter flows are so far unaffected (Thomas and Pool, 2006; Hirschboek, 2009). Nguyen et al. (2014) reported an overall decrease in the Normalized Difference Vegetation Index (NDVI) in portions of the riparian corridor since 1984. There is concern that saltcedar might eventually replace much of the native riparian forest, including cottonwoods (Populus fremontii), willow (Salix gooddingii) and mesquite (Prosopis glandulosa) (Stromberg et al., 1996, 2005, 2006). Saltcedar could impact the hydrology of the river if it uses more water than native species as some studies have suggested (DiTomosa, 1998).

The goal of this study was to compare water use patterns of native trees and introduced saltcedar in the Upper San Pedro River. Our study site was downstream of the urban centers of Sierra Vista and Fort Huachuca, where base flows have been reduced over the past 60 years. We compared transpiration and stomatal conductance of Arizona ash (Fraxinus velutina), cottonwood, and saltcedar on the banks of a formerly perennial but now intermittent reach of river. Southeastern Arizona has a monsoon-driven precipitation cycle, with 60% of annual precipitation arriving July to September, and the rest arriving in winter (Goodrich et al., 2008). The study was conducted during the pre-monsoon season in June and July, 2006. This is a time of maximum stress for riparian vegetation because trees have leaved-out but surface flows are minimal or absent, and
groundwater is at its greatest depth. We then resurveyed plants with the aid of high-resolution satellite imagery from 2007 to 2015 to compare canopy growth and survival of the plants sampled in 2006. Our working hypothesis was that saltcedar would have greater water use than ash or cottonwood, would exhibit greater tolerance to physiological stress conditions, and would out-compete the native trees in terms of growth and survival over the long term.

Materials and Methods

Study Site. The study site (31°46.03'N, 110°12.18'W) was near the historic mining town (now abandoned) of Contention, Arizona. The site is within the SPRNCA and is now classified as "Intermittent-Wet-Condition Class 2", defined as a reach with streamflow 60-100% of the year, groundwater depth of 2.5-3.5 m in the driest time of year, and annual groundwater fluctuation of 0.5-1.0 m per year (Leenhouts et al., 2005). We conducted our study from DOY 168 to DOY 194 in 2006, but the measurement intervals varied among trees. The trees were relatively young, apparently established as seedlings after a flood in 2000 scourd the floodplain, creating space for new cohorts of trees to germinate (Figure 1). Two clusters of trees in mixed stands were monitored for sap flow(Figure 2). In the first cluster of trees, two ash trees and two saltcedar trees were measured from DOY 168 to DOY 182. In the second cluster of trees two cottonwoods and one saltcedar tree were measured from DOY 173 to DOY 194 (Figure 2).
Characteristics of each tree are in Table 1 as well as repeat measures of canopy area in 2015. Trees were separated by 3-7 m of bare soil or low groundcover.

Measurement of transpiration with sap flow sensors. Sap flow sensors used in this study were comprised of three main components: a flexible heat source wrapped around the plant stem, three differentially wired thermocouples inserted into the cambium to measure axial heat loss, and a thermopile wrapped around these components to measure radial heat loss. The heat source consisted of a thin resistive heating wire 0.08 mm diameter type T constantan heating wire (Omega Engineering Inc., Stamford, CT), cut into a 3.2 m length and measured an approximate resistance range of 290-320 Ω. This wire was wrapped around the plant stem and secured with tape creating a band of heating wire approximately 35-40 mm in width. The thermocouple unit was constructed using 0.13 mm diameter (36 gauge AWG) duplex insulated copper-constantan ANSI type T thermocouple wires (Omega Engineering Inc., Stamford, CT) cut into lengths of 100 mm, 150 mm, and 200 mm. One end of each length thermocouple wire were twisted together, soldered and trimmed to create tips approximately 2 mm long for insertion into the plant stem. The reference thermocouple was inserted at the center of the heat source, and the remaining two thermocouples were inserted 15 mm above and below the heat source to detect conductive axial heat loss.

The thermopile component was created using 0.28 mm diameter (30 gauge AWG) duplex insulated copper-constantan ANSI type T thermocouple wires (Omega Engineering, Inc., Stamford, CT). This wire was used to make thermocouple junctions
connected in a series which were inserted midpoint along a 152 mm wide strip of craft foam, cut to fit individual shrub stems. These junctions were aligned in pairs placed on opposite sides of the foam backing. The range of thermocouple junctions per thermopile was from 6-14 dependent upon the width of the thermopile. The thermopile was positioned tightly around the stem so that junctions were placed at midpoint of the heat source. Plant stems were lightly sanded with sandpaper prior to applying the sensor gauge to remove small knobs and ridges on the plant and provide better contact between the stem and heat source. Sap flow sensors were applied to plant branches at three levels: low, mid, and upper canopy levels.

Sensors were insulated with two layers of pipe foam insulation and several layers of insulation material lined with reflective backing as an outer cover to reduce any influence of thermal perturbations from the surrounding climate conditions. A constant heat of low intensity was applied to the heater and the temperatures were measured every 15 seconds using a CR-10 datalogger (Campbell Scientific, Inc., Logan, UT). The amount of heat supplied to the stems was controlled with a voltage regulator set at 8 and 10 volts dependent on the stem size. The datalogger and voltage regulator were powered by two 12-volt Deep Cycle Marine batteries as well as a solar panel that was attached to the batteries as a source of daily recharge. Heat input, thermocouple and thermopile raw data were sampled every 5 seconds and averaged every 30 minutes. Data was downloaded every 2-4 days using a laptop computer. Malfunctioning sensor units were replaced with installation of new sensors as soon as errors were detected.
Accuracy of measurement using sap flow devices have been determined to be within ± 10% when compared to water loss rates measured directly using a lysimeter balance (Sakuratani, 1981). A critical analysis of reported sources of error in sap flow calculations using the stem heat balance method (SHB) have determined several factors that affect the accuracy of sap flow measurements. The next four paragraphs discuss limitations of sap flow sensors and methods this research study applied to reduce potential measurement errors.

Sudden changes in rates of transpiration or environmental temperatures in field settings may produce large temperature changes in the heated stem segment, causing a lag in sap flow gauge response due to thermal inertia of the plant stem. In these cases, the assumption of steady state conditions could result in significant errors of sap flow measurements. Incorporating a heat storage term in the heat balance equation corrects this situation and provides dynamic resolution (Grime and Sinclair, 1999). However, findings from other research studies have suggested that the influence of stem heat storage is negligible except at low or zero flows (Baker and Nieber, 1989; Groot and King, 1992; Grime et al., 1995).

Energy partitioning between conductive and convective heat loss is dependent upon the rate of plant sap flow. Changes in the velocity of sap flow are directly proportional to convective heat fluxes and inversely proportional to temperature differences upstream and downstream from the heat source. Errors in sap flow estimates can occur when sap flow heat convection is large and temperature differences are less
than 1ºK. These inaccuracies can be corrected through application of equations that operate as filters to define maximum sap flow velocities based upon the plant stem cross-sectional area (Grime and Sinclair, 1999).

Monitored stem temperature differences are related to heat inputs and stem sap flow velocity. Temperature differences should be non-existent in the absence of either sap flow or heat input. However, temperature changes in the microclimate can influence stem temperatures causing differences in excess of 1 ºC that can create negative correlations between rates of sap flow and temperature changes (Shackel et al., 1992). This environmental effect can be corrected by either placing additional insulation around the stem at the site of the sensor, or by applying an empirical correction using values of temperature differences from unheated gauges (Guitierrez et al., 1994). This study minimized this influence by adding multiple layers of insulation to the plant stem to diminish microclimate influences.

Estimation of radial conductive heat flux is based upon the assumption of radial uniformity in stem temperature across the heated stem cross section and requires determination of sheath conductance (K_{rad}) under minimum or zero flow conditions. Errors can occur in this computation during high water stress conditions as daytime sap flow will be much lower under these circumstances and nighttime rehydration of stem tissues may be significant enough to affect accurate estimates of sheath conductance. However, inaccuracies in radial longitudinal conductive heat losses balance each other out so that estimates of heat flux carried by plant sap flow are scarcely affected (Baker
and Nieber, 1989; Grime and Sinclair, 1999). For this study, the sheath conductance ($K_{rad}$) value was determined using the data between 2:00 - 4:00 am (Mountain Standard Time) each day. This value was monitored on a daily basis for each sensor to determine an accurate $K_{rad}$ value.

The sap flow method used in this study relies upon the heat balance of a plant stem segment given by the equation (Kjelgaard et al. 1997):

$$Q_H - Q_f - Q_{up} - Q_{dn} - Q_{rad} = 0$$  \hspace{1cm} (1)

where $Q_H$ represents heat input; $Q_f$ refers to the convective heat carried by sap flow; $Q_{up}$ and $Q_{dn}$ apply to the heat conducted upstream and downstream through plant stem, and $Q_{rad}$ is radial heat loss away from the stem and heat source (all units in Watts). The components of Eq. 2 were calculated as follows:

$$Q_H = \frac{V_{in}^2}{R_H}$$  \hspace{1cm} (2)

where $V_{in}$ is the voltage supplied to the heater and $R_H$ is the corresponding heater resistance ($\Omega$). Up and down stream conduction can be determined from
\[ Q_{up} = 0.42 \left( \pi \frac{diam^2}{4} \right) \left( \frac{\delta T_{up}}{L_{up}} \right) \quad (3) \]

\[ Q_{dn} = 0.42 \left( \pi \frac{diam^2}{4} \right) \left( \frac{\delta T_{dn}}{L_{dn}} \right) \quad (4) \]

where 0.42 \( \text{W} \text{ m}^{-1} \text{ °C}^{-1} \) is the approximate thermal conductivity of woody plant stems (Grime and Sinclair, 1999), \( diam \) refers to the plant stem diameter (m) at the heater, \( \delta T_{up} \) and \( \delta T_{dn} \) are the temperature differences between the heater and thermocouples located upstream and downstream (°C), and \( L_{up} \) and \( L_{dn} \) is the distances from heaters edge to the upstream and downstream thermocouples. A radial conductance, \( K_{rad} \) \( \text{W} \text{ °C}^{-1} \), must be calculated during a time of zero or near zero flow in order to determine radial heat loss \( (Q_{rad}) \).

\[ K_{rad} = \frac{Q_H - Q_{up} - Q_{dn}}{\delta T_{rad}} \quad (5) \]
where $\delta T_{\text{rad}}$ ($^\circ$C) is measured by the thermopile to derive the temperature difference between the heat source and outside of the insulation. Zero flow was assumed to occur between 2:00-4:00 am although $K_{\text{rad}}$ required recalculation whenever there was a significant change in minimum air temperatures. Once $K_{\text{rad}}$ has been calculated, radial heat loss was determined as:

$$Q_{\text{rad}} = K_{\text{rad}} \times \delta T_{\text{rad}} \quad (6)$$

Convective heat carried by sap flow ($Q_f$) can then be determined by rearranging Eq. 2,

$$Q_f = Q_{\text{nt}} - Q_{\text{ap}} - Q_{\text{do}} - Q_{\text{rad}} \quad (7)$$

The convective heat loss due to sap flow ($Q_f$) is then converted into an equivalent mass flow ($S_i$)

$$S_i = \frac{3600Q_f}{4.19\delta T_{\text{up-dn}}} \quad (8)$$
where units of S are in g h\(^{-1}\), 4.19 refers to the specific heat of liquid water (J\(^{-1}\)g\(^{-1}\)\(^\circ\)C\(^{-1}\)), 3600 are the number of seconds in one hour, and \(\delta T_{up} - T_{dn}\) (°C), refers to the difference in temperature between upstream and downstream thermocouples. Prior to removal of the gauged branch and harvest of its leaves, a dry weight: leaf area relationship was determined for each species.

First, the area of a 22.5 cm x 28 cm sheet of ¼-inch graph paper was calculated (cm\(^2\)) and divided by the number of squares on the sheet to establish an area relationship per square on the graph paper \(\frac{\text{cm}^2}{\text{square}}\). This value was then converted to units of \(\frac{\text{m}^2}{\text{square}}\).

Near the end of the study period, 50 fresh leaves were sampled from 5 different plants per riparian species type. These selected riparian plants from which leaf samples were harvested were situated adjacent to the study site; and were typical of plants in our study in terms of age, height and canopy traits. Fresh leaves of an individual species were arbitrarily placed in a single layer fashion on the same sheet of ¼-inch graph paper. The number of grid intersections the fresh leaves covered were added up and multiplied by the area per square (m\(^2\)) to represent the degree of the fraction of paper covered. Fresh leaves, were then weighed to determine hydrated (wet) weight (g); dried in an oven overnight and leaf dry weight (g) recorded the following morning to establish a leaf: weight relationship per species.

Leaves of all gauged branches were harvested at the end of the measurement period to determine leaf area per branch based on their dry weight. Sapflow (g h\(^{-1}\)) was
converted to transpiration on a leaf-area basis ($E_L$) (terminology and units follow Ewers and Oren, 2000). Transpiration per m$^2$ leaf area ($E_L$) was then translated to transpiration on a ground area basis ($E_G$):

$$E_G = E_L \times \text{LAI}$$

(9)

In order to ensure that the sap flow gauges were functioning accurately, daily climate conditions and individual sensor heat energy components were inspected graphically. Leaf Area Index (LAI) was measured under each canopy with a Licor 2000 LAI Meter (LiCor., Lincoln, NE). The height and canopy area were determined based on canopy diameter. These parameters were measured at the widest and narrowest points of the canopy.

*Environmental Data.* Climate provides the forcing for the transpiration process. Therefore, monitoring daily meteorological functions is important so as to better interpret the response by a particular species to atmospheric demand. Meteorological variables of solar radiation (LI-200X, LiCor, Lincoln, NE), wind speed and direction (R.M. Young Co., Traverse City, MI), relative humidity, and air temperature (HMP35D, Vaisala, Helsinki, Finland) were measured from a 2-meter height close to the site. Measurements were taken every 5 seconds and an average value recorded every 30 minutes by a datalogger.
ET\textsubscript{o} refers to the evaporation rate from a theoretical extensive green grass crop surface having a uniform set height of 0.12 m, an albedo of 0.23, and a surface resistance of 69 s m\textsuperscript{-1}. This hypothetical grass cover completely shades ground surfaces, has infinite water supplies and is actively growing under the existing climate conditions occurring at the site of interest (Shuttleworth, 1993). Calculating ET\textsubscript{o} estimates the maximum potential amount of water that can be consumed by this vegetation cover under current climate conditions at the study site. In this study we computed a standard reference crop evaporation rate using temperature, relative humidity, solar radiation, and wind speed measurements to evaluate variations in atmospheric evaporation demand and its impacts on measured seep willow transpiration. The Arizona Meteorological Network (AZMET) equation developed for southern Arizona was used for calculating reference crop evaporation ET\textsubscript{o} in units of mm h\textsuperscript{-1} (Brown, 1989)

\[ ET_o = W*R_n + (1-W)*VPD*FU2 \quad (10) \]

where W refers to a dimensionless partitioning factor, R\textsubscript{n} is net radiation in units of mm hr\textsuperscript{-1} of equivalent evaporation, VPD is vapor pressure deficit in units of kPa, and FU2 refers to an empirical wind function in units of mm h\textsuperscript{-1} kPa\textsuperscript{-1}. Determining the dimensionless partitioning factor (W) required first computing three separate variables: the saturation vapor pressure (e\textsubscript{s}), the slope of the saturation vapor pressure curve, S, and the psychometric constant, γ. Once these were calculated, the partitioning factor was computed.
Depth to groundwater (DTW) was measured in an observation well placed near the sap flow measurement sites on the lower terrace of the river where trees were rooted. DTW was measured at half-hourly intervals with a pressure transducer and reported as daily mean values. Annual river flows for the San Pedro gauge near Tombstone was obtained from the USGS Water for the Nation website (http://waterdata.usgs.gov/nwis).

Stomatal conductance. Examining plant stomatal conductance ($G_s$) of water provides an indication of stomatal control exerted at the leaf level during daylight hours. Plant conductance values also represent potential photosynthetic rate and carbon uptake rate because carbon gain and water loss are locked into a tight feedback control loop (Wainwright et al. 1999). Sap flux data can be used to calculate $G_s$ on a leaf area or ground area basis. We calculated $G_s$ on a ground area basis in mm h$^{-1}$ (Ewers and Oren 2000):

$$G_s = \frac{E_g (K_G)}{VPD} \quad (11)$$

where VPD is vapor pressure deficient (kPa) and $K_G$ is the conductance coefficient (kPa), calculated from atmospheric pressure corrected for temperature effects by the formula:
The term $E_g(K_g)/D$ is the ratio of transpiration to atmospheric water demand, and it is related to the degree of stomatal opening at a given time of day (Monteith and Unsworth 1990). This calculation assumes that VPD at the leaf surface is the same as bulk VPD over the canopy (Jarvis and McNaughton 1992). This assumption is not valid when VPD is below about 0.6 kPa (Ewers and Oren 2000; Ewers et al. 2007) but VPD values in this study were well above this threshold.

**Satellite imagery.** High-resolution images were available from Google Earth for June 7, 2007; June 4, 2010; August 29, 2012, and January 3, 2015. These were inspected to track the survival of individual trees, and plant canopy areas of surviving trees were measured on the 2015 image. Leaves had fallen from cottonwood trees in the 2015 image but canopy area was measured by the width of the branches making up the crown of the trees. A single Enhanced Vegetation Index (EVI) pixel (250 m x 250 m) from the Moderate Resolution Imaging Spectrometer (MODIS) sensors on the Terra satellite was obtained from the Oak Ridge National Laboratory DAAC site (http://daac.ornl.gov). The images covered the period DOY 49, 2000 to DOY 353, 2014 at 16-day intervals. The center of the pixel was at 31.776668 N, -110.2095 W and the pixel footprint encompassed the groups of measured in the study.
Results

Mean LAI per species ranged from 1.08-1.79 (P = 0.25) during the sap flow measurement period in 2006 (Table 1). Daily rates of $E_G$ were relatively constant over the measurement periods for each species (Figure 3), with mean values of 4.95 mm d$^{-1}$ (SE = 0.12) for ash, 3.49 mm d$^{-1}$ (SE = 0.08) for cottonwood and 2.57 mm d$^{-1}$ (SE = 0.07) for saltcedar (each significantly different at P < 0.001). Daily means of environmental factors are in Figure 4. $T_{air}$ (Figure 4A), VPD (Figure 4C), $ET_o$ (Figure 4D) and $R_S$ (Figure 4E) did not show a net trend over the pre-monsoon season, but decreased briefly during the few scattered rain events that occurred during the measurement period (Figure 4E). Mean $ET_o$ was 6.08 mm d$^{-1}$ (SE = 0.27), hence $E_G$ was 81% of $ET_o$ for ash, 57% for cottonwood and 42% for saltcedar. DTW decreased by 0.46 m over the pre-monsoon period, from 2.90 m to 3.35 m (Figure 4B).

Mean daily $E_G$ by all three species was positively (P < 0.05) correlated with $T_{air}$, $R_S$ and $ET_o$ and cottonwood and saltcedar $E_G$ were also positively correlated with VPD (Table 2). Table 2 also shows that the environmental factors were moderately to strongly correlated with each other, making it difficult to pinpoint the prime determinants of $E_G$ for each species on a daily basis. By contrast to $E_G$, correlation coefficients between mean daily $G_S$ and environmental were negative for VPD, $T_{air}$, $ET_o$ and DTW for all three species (Table 3). There was no overall trend in either $E_G$ or $G_S$ with regard to DTW.

Diurnal plots of half-hourly values showed that $E_G$ of all three species peaked between 0800 and 1000 hours then decreased slowly through the rest of the daylight
period (Figure 5A). \( R_S \) peaked at 1200 hours while VPD peaked at 1600 hours. On the other hand, \( G_S \) peaked at 0800 hours for all three species and diurnal curves were truncated relative to \( R_S \) (Figure 5B). Multiple regression equations relating daily hourly values of \( G_S \) to VPD and \( R_S \) were similar for all three species (Table 3). For all three, \( R_S \) was a positive factor and VPD was a negative factor \((P < 0.001)\). Beta coefficients showed that negative control of \( G_S \) was 3-9 times more important than positive control of \( G_S \) by \( R_S \) depending on species.

The plants for which sap flow was measured in 2006 were re-surveyed with high-resolution imagery available on Google Earth. All plants survived to 2015 (Table 1). Ash and saltcedar trees did not increase appreciably in canopy area between 2006 and 2015, but the two cottonwood canopies increased by 6.3 and 11.5 times, respectively. MODIS EVI values varied from year to year (Figure 7A) as did river flows (Figure 7B). EVI was significantly correlated with the log of annual river flows \((r = 0.57, P = 0.026)\) for the years 2000-2014.

**Discussion**

Contrary to our working hypothesis, saltcedar had significantly lower \( E_G \) than the native trees. Saltcedar ET was only 42% of \( E_{To} \), within the range of other recent measurements of saltcedar ET on the in the southwestern U.S. (reviewed in Nagler and Glenn, 2013). Earlier estimates reporting high ET rates for saltcedar (reviewed in
DiTomosa, 1998) were based on artificial conditions, in which saltcedar was grown in lysimeter tanks with high water tables and subject to advection effects that increased ET (Glenn and Nagler, 2005). The present study also did not show that saltcedar had greater physiological tolerance of the stress factors encountered during the pre-monsoon season at this site. Saltcedar can extract water from a greater depth (Horton and Clark, 2001; Horton et al., 2001, 2003) and is more tolerant of salinity (Glenn et al., 1998, 2013) than mesic native trees. However, groundwater levels and recession rates at the Contention site were within the range tolerated by cottonwoods and ash trees (Stromberg et al., 2005, 2006), and well records show that the groundwater near the river is non-saline (conductivity < 0.5 dS m⁻¹) (data not shown). Under these conditions saltcedar did not have a competitive advantage over ash or cottonwood. Although all plants survived from 2006 to 2015, only cottonwood showed an appreciable increase in canopy area.

Analyses of the stomatal response to environmental factors showed that for ash, cottonwood and saltcedar, Gₛ was negatively correlated with VPD on both a daily and hourly basis. Gₛ peaked between 0700-0800 hours and all three showed marked midday depression of Gₛ relative to the radiation curve. Beyond about 0800 hours atmospheric water demand as estimated by VPD apparently exceeded the capacity of all three species to support transpiration, resulting in partial stomatal closure to restrict water loss. Nevertheless, ash was able to transpire at 80% of the rate of ETₒ and was the highest water user of the three species at this site. E₉ increased further into the day than Gₛ presumably because even at reduced stomatal conductance, higher VPD led to increased water loss through partially open stomata.
Despite the conversion of this river reach from perennial to intermittent, we conclude that native trees are still competitive with saltcedar and a mixed plant community can be expected to persist on the Upper San Pedro River. However, an important proviso to this conclusion is that current groundwater levels and river flows should be maintained. If the reduction in base flows noted since 1942 continues, it can be expected that depth to groundwater will increase, and the competitive balance between saltcedar and native trees could change (Stromberg et al., 1996, 2009b).
References


Table 1. Plant canopy area, height and LAI of plants measured for transpiration and stomatal conductance in 2006 and resurveyed for survival and canopy area increase with high-resolution satellite imagery in 2015.

<table>
<thead>
<tr>
<th>Plant</th>
<th>Dates (DOY)</th>
<th>Canopy Area (m) 2006</th>
<th>Height (m) 2006</th>
<th>LAI 2006</th>
<th>Canopy Area (m) 2015</th>
<th>2015/2006 Canopy Area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ash 1</td>
<td>168-180</td>
<td>11.6</td>
<td>4.6</td>
<td>1.28</td>
<td>10.4</td>
<td>0.90</td>
</tr>
<tr>
<td>Ash 2</td>
<td>168-180</td>
<td>15.6</td>
<td>4.6</td>
<td>0.884</td>
<td>34.8</td>
<td>2.29</td>
</tr>
<tr>
<td>SC 1</td>
<td>168-180</td>
<td>8.2</td>
<td>4.0</td>
<td>1.72</td>
<td>9.4</td>
<td>1.15</td>
</tr>
<tr>
<td>SC 2</td>
<td>168-180</td>
<td>9.8</td>
<td>2.7</td>
<td>2.26</td>
<td>13.1</td>
<td>1.34</td>
</tr>
<tr>
<td>SC 3</td>
<td>173-194</td>
<td>20.8</td>
<td>5.5</td>
<td>1.38</td>
<td>28.4</td>
<td>1.36</td>
</tr>
<tr>
<td>CW 1</td>
<td>173-194</td>
<td>4.7</td>
<td>3.4</td>
<td>1.28</td>
<td>54.2</td>
<td>11.5</td>
</tr>
<tr>
<td>CW 2</td>
<td>173-194</td>
<td>17.8</td>
<td>7.0</td>
<td>1.79</td>
<td>112</td>
<td>6.30</td>
</tr>
</tbody>
</table>
Table 2. Correlation between ash. cottonwood (CW) and (SC) transpiration rates ($E_G$), stomatal conductance ($G_S$) and environmental variables during the pre-monsoon period at a site on the Middle San Pedro River. VPD = vapor pressure deficit; $T_{air}$ = mean daily air temperature; $R_S$ = solar radiation; $ET_o$ = potential evapotranspiration; DTW = depth to groundwater.

<table>
<thead>
<tr>
<th></th>
<th>VPD</th>
<th>$T_{air}$</th>
<th>$R_S$</th>
<th>$ET_o$</th>
<th>DTW</th>
</tr>
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<tbody>
<tr>
<td><strong>Ash $E_G$</strong></td>
<td>0.09ns</td>
<td>0.60*</td>
<td>0.82***</td>
<td>0.63*</td>
<td>-0.55ns</td>
</tr>
<tr>
<td><strong>CW $E_G$</strong></td>
<td>0.93***</td>
<td>0.45*</td>
<td>0.74***</td>
<td>0.39ns</td>
<td>0.42ns</td>
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<tr>
<td><strong>SC $E_G$</strong></td>
<td>0.64*</td>
<td>0.58*</td>
<td>0.71**</td>
<td>0.69**</td>
<td>-0.06ns</td>
</tr>
<tr>
<td><strong>Ash $G_S$</strong></td>
<td>-0.94</td>
<td>-0.82***</td>
<td>-0.60*</td>
<td>-0.82***</td>
<td>-0.48ns</td>
</tr>
<tr>
<td><strong>CW $G_S$</strong></td>
<td>-0.84***</td>
<td>-0.76***</td>
<td>-0.34ns</td>
<td>-0.73***</td>
<td>0.32ns</td>
</tr>
<tr>
<td><strong>SC $G_S$</strong></td>
<td>-0.84***</td>
<td>-0.74***</td>
<td>-0.51*</td>
<td>-0.75***</td>
<td>0.67***</td>
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<tr>
<td><strong>VPD</strong></td>
<td>0.81***</td>
<td>0.70***</td>
<td>0.94***</td>
<td>0.49**</td>
<td></td>
</tr>
<tr>
<td><strong>$T_{air}$</strong></td>
<td></td>
<td>0.46*</td>
<td>0.74***</td>
<td>0.01 ns</td>
<td></td>
</tr>
<tr>
<td><strong>$R_S$</strong></td>
<td></td>
<td></td>
<td>0.78***</td>
<td>-0.24ns</td>
<td></td>
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<tr>
<td><strong>$ET_o$</strong></td>
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<td></td>
<td></td>
<td>-0.44*</td>
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Table 3. Multiple linear regression analyses of day-time values of $G_S$ for cottonwoods, mesquites and saltcedar growing together on the Lower San Pedro River. Equations took the form: $G_S$ (mm d$^{-1}$) = Constant + Coefficient VPD * VPD + Coefficient $R_S$ * $R_S$.

<table>
<thead>
<tr>
<th></th>
<th>Ash</th>
<th>Cottonwood</th>
<th>Saltcedar</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Constant</strong></td>
<td>56.2</td>
<td>36.0</td>
<td>24.4</td>
</tr>
<tr>
<td><strong>Coefficient VPD</strong></td>
<td>-13.8</td>
<td>-8.79</td>
<td>-5.91</td>
</tr>
<tr>
<td><strong>Coefficient $R_S$</strong></td>
<td>5.06</td>
<td>4.95</td>
<td>7.34</td>
</tr>
<tr>
<td>$\beta$ Coefficient VPD</td>
<td>-0.97</td>
<td>-0.99</td>
<td>-1.06</td>
</tr>
<tr>
<td>$\beta$ Coefficient $R_S$</td>
<td>0.10</td>
<td>0.15</td>
<td>0.36</td>
</tr>
<tr>
<td><strong>F</strong></td>
<td>69.4</td>
<td>75.4</td>
<td>113</td>
</tr>
<tr>
<td><strong>P</strong></td>
<td>$&lt; 0.001$</td>
<td>$&lt; 0.011$</td>
<td>$&lt; 0.001$</td>
</tr>
<tr>
<td>$r^2$</td>
<td>0.86</td>
<td>0.87</td>
<td>0.91</td>
</tr>
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Figure 1. Examples of trees measured for transpiration and stomatal conductance at the Contention site on the Upper San Pedro River in 2006. Top: ash and adjacent saltcedar trees. Bottom: cottonwood and adjacent saltcedar trees.

Figure 2. Diagram showing spacing between sampled trees in 2006.

Figure 3. Transpiration on a ground area basis ($E_G$) for ash, cottonwood and saltcedar at the Contention site on the Upper San Pedro River, Arizona.

Figure 4. Environmental variables measured at the sap flow station at Contention on the Upper San Pedro River in 2006. Bars in (E) show rainfall events.

Figure 5. Diurnal response of transpiration ($E_G$) (A) and stomatal conductance ($G_S$) (B) for ash, cottonwood and saltcedar at the Contention site on the Upper San Pedro Reserve, 2006. Also shown are diurnal curves for radiation ($R_S$) and vapor pressure deficit (VPD).

Figure 6. (A) EVI of a 250 m x 250 m area encompassing sap flow stations at Contention by MODIS imagery, 2000-2014; (B) annual river flows measured at the Tombstone gauge on the San Pedro River.
APPENDIX B

Transpiration, Stomatal Conductance and Growth and Survival of Cottonwood (*Populus fremontii*) Mesquites (*Prosopis glutinosa*) and Saltcedar (*Tamarix* spp.) Trees in Mixed Stands on a Riparian Floodplain in the Southwestern United States

Abstract

Saltcedar (*Tamarix* spp.), a stress-tolerant shrub from Asia, has spread widely in southwestern U.S. riparian zones, mainly in disturbed river systems where depth to water or salinity has increased. There is concern it could come to dominate many more river systems to the detriment of riparian water resources and wildlife. We used heat-balance sap flow sensors to measure transpiration and stomatal conductance of saltcedar and native trees growing together on a moderately disturbed reach of the Lower San Pedro River in Arizona. Due to groundwater extraction for human use, the river has become intermittent rather than perennial and depth to groundwater has increased, but the river still supports a mixed population of cottonwoods (*Populus fremontii*), mesquites (*Prosopis glandulosa*) and saltcedars. During the pre-monsoon period in 2007 (DOY 144-182), the water table decreased from by about 0.3 m to a depth of 3 m, and cottonwood transpiration and stomatal conductance decreased over the same period. By contrast, mesquite and saltcedar transpiration increased. However, all three species showed midday depression of both transpiration and stomatal conductance in response to
high vapor pressure deficits, with peak stomatal conductance occurring at 0700 to 0800 hours. Transpiration was 40-50% of potential evapotranspiration and leaf area indices were relatively low, ranging from 1.0-1.7 among species. Saltcedar did not have unusually high water use compared to cottonwood and mesquites. Resurvey of the plants in 2014 with high-resolution imagery showed only one mortality among the 11 trees, and all the surviving plants had increased in canopy area to form partially closed canopies. This study suggests that saltcedar can grow in apparently stable associations with native trees on moderately disturbed river systems, providing multi-structured habitat for birds and other wildlife.

Introduction

Riparian zones are reservoirs of biodiversity in arid and semiarid regions, but they are threatened by water diversions, land use changes and introduction of non-native species (Nilsson and Berggren, 2000; Poff and Zimmerman, 2010). In the southwestern United States, saltcedar (Tamarix ramosissima and related species and hybrids) (Gaskin and Schaal, 2002), a stress-tolerant shrub or small tree introduced in the 19th Century, has spread widely in riparian zones (Nagler et al., 2011). The spread of saltcedar is possibly changing the riparian water balance through greater evapotranspiration compared to native trees (Sala et al., 1996; DiTomosa, 1998). There is also concern that saltcedar has lower habitat value for wildlife than native vegetation (DiTomaso, 1998; Chapin et al., 2000). The spread of saltcedar has been described as an invasion process, in
which saltcedar displaces native trees such as cottonwoods (\textit{Populus} spp.) willows (\textit{Salix} spp.) and mesquites (\textit{Prospolis} spp.) DiTomosa, 1998). However, an alternative point of view is that saltcedar simply replaces mesic native vegetation when their niche requirements are no longer fulfilled (Glenn and Nagler, 2005; Stromberg et al., 2009). Saltcedar has spread most rapidly on disturbed river systems in which depth to groundwater or salinities or both have increased due to altered pulse flood regimes (Horton and Campbell, 1974; Busch and Ingram, 1992; Busch and Smith, 1995; Horton and Clark, 2001; Glenn and Nagler, 2005; Nagler et al., 2011).

Ecological thresholds for species replacement in riparian wetlands are thought to be non-linear, such that small changes can tip the balance in favor of one species over another (Lansen and Alp, 2015). There is concern that as conditions are altered on southwestern U.S. rivers, a succession process can take place with saltcedar eventually becoming dominant on both human-altered river systems (e.g., Busch and Smith, 1995; DiTomosa, 1998; Smith et al., 1998; Merritt and Poff, 2010). Attempts have been made to establish threshold conditions under which saltcedar will increase at the expense of native vegetation (e.g., Stromberg et al., 2005).

It is sometimes overlooked, however, that saltcedar can grow in apparently stable associations with native vegetation; this occurs in its native range in Asia, where \textit{Tamarix} spp. commonly grow in floodplains along with \textit{Populus} and \textit{Salix} spp (Hao and Li, 2014; Li et al., 2013; Yu et al., 2013). Saltcedar and native trees also grow in mixed stands in North America in such river systems as the Middle Rio Grande (Sher et al., 2000), the
delta of the Colorado River in Mexico (Nagler et al., 2005, 2009), headwater streams in
the Sonoran Desert in Mexico (Scott et al., 2009), the Bill Williams (Horton et al., 2003;
Stromberg et al., 2012), and the Upper Verde (Johnson et al., 2010) and San Pedro Rivers
in Arizona (Stromberg et al., 2005).

Where they occur together, it is important to understand water use patterns and
the physiological responses of each species to environmental stress factors, as a way to
predict the eventual trajectory of the succession processes and management options at a
given site. Numerous studies have concluded that saltcedar has competitive advantages
over native trees under stress conditions. Stress factors include depth to water greater
than about 3 m or a water table that declines greater than about 0.5 m during the growing
season (e.g., Busch and Ingraham, 1992; Horton and Campbell, 1974; Horton and Clark,
2001; Horton et al., 2001, 2003) or salinities greater than about 2 g l\(^{-1}\) in the soil solution
(Glenn et al., 1998). On the other hand, under non-stress conditions native trees usually
out-compete saltcedar in seedling establishment and early growth (Sher et al., 2000; Sher
and Marshall, 2003; Bhattacharjee et al., 2009) eventually over-toping them and
becoming dominant or co-dominant woody species (Bunting et al., 2013; Nagler et al.,
2005; Johnson et al., 2010).

This study compared transpiration and stomatal conductance of saltcedar with
native cottonwood (Populus fremontii) and mesquite (Prosopis glandulosa) trees on a
moderately disturbed floodplain on the Lower San Pedro River in southeastern Arizona,
U.S. Our study was conducted on a stretch of river that had been scoured by floods in
2000 (Haney, 2005), creating new cohorts of both native trees and saltcedar growing in mixed stands by the time the study was initiated in 2007. We used sap flux sensors to measure the physiological response of saltcedar and the native trees to environmental stress factors, and we followed up by measuring growth and survival of the sampled trees seven years after physiological measurements were made. Our goal was to see if saltcedar had physiological advantages over cottonwoods and mesquites that allowed it to ultimately become dominant.

Materials and Methods

Study Site. The study site (32°56.6'N, 110°45.227'W) was in The Nature Conservancy's San Pedro River Preserve on the Lower San Pedro River just above its confluence with the Gila River (Haney, 2005). The San Pedro River was formerly perennial over most of its length, but extraction of water for agriculture and urban growth has made many reaches ephemeral, including the stretch in the preserve. The property was formerly used for agriculture and aquaculture, and after purchase by The Nature Conservancy in 1998, 2.6 million m³yr⁻¹ of groundwater pumping was retired to enhance groundwater levels in the riparian zone. The property was also fenced to exclude cattle.

Southeastern Arizona has a monsoon-driven precipitation cycle, with 60% of annual precipitation arriving July to September, and the rest arriving in winter (Goodrich et al., 2008). We conducted our study in 2007 during the pre-monsoon period in early
summer, a time of maximum stress for riparian vegetation. Trees are fully leafed out at this time of year but groundwater levels are at their deepest extent and the vadose zone is normally dry. The trees were relatively young, apparently established as seedlings after the 2000 flood scoured the floodplain, creating space for new cohorts of trees to germinate (Figure 1). Characteristics of each tree are in Table 1. Two clusters of trees in mixed stands were monitored for sap flow from DOY 144 to DOY 182 (Figure 2). In the first cluster of trees, two mesquite trees (Prosopis glutinosa), two cottonwood trees and two saltcedar trees were measured. In the second cluster of trees three cottonwoods and two saltcedars were measured (Table 1). Cottonwood and saltcedar canopies were separated by 2-5 m in these clusters.

Measurement of transpiration with sap flow sensors. Sap flow sensors used in this study were comprised of three main components: a flexible heat source wrapped around the plant stem, three differentially wired thermocouples inserted into the cambium to measure axial heat loss, and a thermopile wrapped around these components to measure radial heat loss. The heat source consisted of a thin resistive heating wire 0.08 mm diameter type T constantan heating wire (Omega Engineering Inc., Stamford, CT), cut into a 3.2 m length and measured an approximate resistance range of 290-320 Ω). This wire was wrapped around the plant stem and secured with tape creating a band of heating wire approximately 35-40 mm in width. The thermocouple unit was constructed using 0.13 mm diameter (36 gauge AWG) duplex insulated copper-constantan ANSI type T thermocouple wires (Omega Engineering Inc., Stamford, CT) cut into lengths of 100 mm, 150 mm, and 200 mm. One end of each length thermocouple wire were twisted together,
soldered and trimmed to create tips approximately 2 mm long for insertion into the plant stem. The reference thermocouple was inserted at the center of the heat source, and the remaining two thermocouples were inserted 15 mm above and below the heat source to detect conductive axial heat loss.

The thermopile component was created using 0.28 mm diameter (30 gauge AWG) duplex insulated copper-constantan ANSI type T thermocouple wires (Omega Engineering, Inc., Stamford, CT). This wire was used to make thermocouple junctions connected in a series which were inserted midpoint along a 152 mm wide strip of craft foam, cut to fit individual shrub stems. These junctions were aligned in pairs placed on opposite sides of the foam backing. The range of thermocouple junctions per thermopile was from 6-14 dependent upon the width of the thermopile. The thermopile was positioned tightly around the stem so that junctions were placed at midpoint of the heat source. Plant stems were lightly sanded with sandpaper prior to applying the sensor gauge to remove small knobs and ridges on the plant and provide better contact between the stem and heat source. Sap flow sensors were applied to plant branches at three levels: low, mid, and upper canopy levels.

Sensors were insulated with two layers of pipe foam insulation and several layers of Insulation material lined with reflective backing as an outer cover to reduce any influence of thermal perturbations from the surrounding climate conditions. A constant heat of low intensity was applied to the heater and the temperatures were measured every 15 seconds using a CR-10 datalogger (Campbell Scientific, Inc., Logan, UT). The
amount of heat supplied to the stems was controlled with a voltage regulator set at 8 and 10 volts dependent on the stem size. The datalogger and voltage regulator were powered by two 12-volt Deep Cycle Marine batteries as well as a solar panel, that was attached to the batteries as a source of continuous recharge. Heat input, thermocouple and thermopile raw data were sampled every 5 seconds and averaged every 30 minutes. Data was downloaded every 2-4 days using a laptop. Malfunctioning sensor units were replaced with installation of new sensors as soon as errors were detected.

Accuracy of measurement using sap flow devices have been determined to be within ± 10% when compared to water loss rates measured directly using a lysimeter balance (Sakuratani, 1981). A critical analysis of reported sources of error in sap flow calculations using the stem heat balance method (SHB) have determined several factors that affect the accuracy of sap flow measurements. The next four paragraphs discuss limitations of sap flow sensors and methods this research study applied to reduce potential measurement errors.

Sudden changes in rates of transpiration or environmental temperatures in field settings may produce large temperature changes in the heated stem segment, causing a lag in sap flow gauge response due to thermal inertia of the plant stem. In these cases, the assumption of steady state conditions could result in significant errors of sap flow measurements. Incorporating a heat storage term in the heat balance equation corrects this situation and provides dynamic resolution (Grime and Sinclair, 1999). However, findings from other research studies have suggested that the influence of stem heat
storage is negligible except at low or zero flows (Baker and Nieber, 1989; Groot and King, 1992; Grime et al., 1995).

Energy partitioning between conductive and convective heat loss is dependent upon the rate of plant sap flow. Changes in the velocity of sap flow are directly proportional to convective heat fluxes and inversely proportional to temperature differences upstream and downstream from the heat source. Errors in sap flow estimates can occur when sap flow heat convection is large and temperature differences are less than 1ºK. These inaccuracies can be corrected through application of equations that operate as filters to define maximum sap flow velocities based upon the plant stem cross-sectional area (Grime and Sinclair, 1999).

Monitored stem temperature differences are related to heat inputs and stem sap flow velocity. Temperature differences should be non-existent in the absence of either sap flow or heat input. However, temperature changes in the microclimate can influence stem temperatures causing differences in excess of 1 ºC that can create negative correlations between rates of sap flow and temperature changes (Shackel et al., 1992). This environmental effect can be corrected by either placing additional insulation around the stem at the site of the sensor, or by applying an empirical correction using values of temperature differences from unheated gauges (Guitierrez et al., 1994). This study minimized this influence by adding multiple layers of insulation to the plant stem to diminish microclimate influences.
Estimation of radial conductive heat flux is based upon the assumption of radial uniformity in stem temperature across the heated stem cross section and requires determination of sheath conductance ($K_{rad}$) under minimum or zero flow conditions. Errors can occur in this computation during high water stress conditions as daytime sap flow will be much lower under these circumstances and nighttime rehydration of stem tissues may be significant enough to affect accurate estimates of sheath conductance. However, inaccuracies in radial longitudinal conductive heat losses balance each other out so that estimates of heat flux carried by plant sap flow are scarcely affected (Baker and Nieber, 1989; Grime and Sinclair, 1999). For this study, the sheath conductance ($K_{rad}$) value was determined using the data between 2:00 - 4:00 am (Arizona Time) each day. This value was monitored on a daily basis for each sensor to determine an accurate $K_{rad}$ value.

The sap flow method used in this study relies upon the heat balance of a plant stem segment given by the equation (Kjelgaard et al. 1997):

$$Q_H - Q_f - Q_{up} - Q_{dn} - Q_{rad} = 0 \quad (1)$$

where $Q_H$ represents heat input; $Q_f$ refers to the convective heat carried by sap flow; $Q_{up}$ and $Q_{dn}$ apply to the heat conducted upstream and downstream through plant stem, and
$Q_{\text{rad}}$ is radial heat loss away from the stem and heat source (all units in Watts). The components of Eq. 2 were calculated as follows:

$$Q_H = \frac{V_{in}^2}{R_H}$$  \hspace{1cm} (2)

where $V_{in}$ is the voltage supplied to the heater and $R_H$ is the corresponding heater resistance ($\Omega$). Up and down stream conduction can be determined from

$$Q_{up} = 0.42 \left( \pi \frac{\text{diam.}^2}{4} \left( \frac{\delta T_{up}}{L_{up}} \right) \right)$$  \hspace{1cm} (3)

$$Q_{dn} = 0.42 \left( \pi \frac{\text{diam.}^2}{4} \left( \frac{\delta T_{dn}}{L_{dn}} \right) \right)$$  \hspace{1cm} (4)

where 0.42 (W m$^{-1}$ °C$^{-1}$) is the approximate thermal conductivity of woody plant stems (Grime and Sinclair, 1999), diam. refers to the plant stem diameter (m) at the heater, $\delta T_{up}$ and $\delta T_{dn}$ are the temperature differences between the heater and thermocouples located upstream and downstream (°C), and $L_{up}$ and $L_{dn}$ is the distances from heaters edge to the upstream and downstream thermocouples. A radial conductance, $K_{\text{rad}}$ (W °C$^{-1}$), must be
calculated during a time of zero or near zero flow in order to determine radial heat loss (Q_{rad}).

\[
K_{rad} = \frac{Q_H - Q_{ap} - Q_{dn}}{\delta T_{rad}}
\]  

(5)

where \( \delta T_{rad} \) (°C) is measured by the thermopile to derive the temperature difference between the heat source and outside of the insulation. Zero flow was assumed to occur between 2:00-4:00 am although \( K_{rad} \) required recalculation whenever there was a significant change in minimum air temperatures. Once \( K_{rad} \) has been calculated, radial heat loss was determined as:

\[
Q_{rad} = K_{rad} \times \delta T_{rad}
\]  

(6)

Convective heat carried by sap flow (Q_f) can then be determined by rearranging Eq. 2,

\[
Q_f = Q_H - Q_{ap} - Q_{dn} - Q_{rad}
\]  

(7)
The convective heat loss due to sap flow \( (Q_f) \) is then converted into an equivalent mass flow \( (S) \)

\[
S_f = \frac{3600Q_f}{4.19\delta T_{up-dn}} \tag{8}
\]

where units of \( S \) are in \( \text{g h}^{-1} \), 4.19 refers to the specific heat of liquid water \( (J^{-1}\text{g}^{-1}\text{C}^{-1}) \), 3600 are the number of seconds in one hour, and \( \delta T_{up} - T_{dn} \) \( (\text{C}) \), refers to the difference in temperature between upstream and downstream thermocouples.

Prior to removal of the gauged branch and harvest of its leaves, a dry weight: leaf area relationship was determined for each species.

First, the area of a 22.5 cm x 28 cm sheet of \( \frac{1}{4} \)-inch graph paper was calculated \( (\text{cm}^2) \) and divided by the number of squares on the sheet to establish an area relationship per square on the graph paper \( \frac{\text{cm}^2}{\text{square}} \). This value was then converted to units of \( \frac{\text{m}^2}{\text{square}} \).

Near the end of the study period, 50 fresh leaves were sampled from 5 different plants per riparian species type. These selected riparian plants from which leaf samples were harvested were situated adjacent to the study site; and were typical of plants in our
study in terms of age, height and canopy traits. Fresh leaves of an individual species were arbitrarily placed in a single layer fashion on the same sheet of ¼-inch graph paper. The number of grid intersections the fresh leaves covered were added up and multiplied by the area per square (m²) to represent the degree of the fraction of paper covered. Fresh leaves, were then weighed to determine hydrated (wet) weight (g); dried in an oven overnight and leaf dry weight (g) recorded the following morning to establish a leaf: weight relationship per species.

Leaves of all gauged branches were harvested at the end of the measurement period to determine leaf area per branch based on their dry weight. Sapflow (g h⁻¹) was converted to transpiration on a leaf-area basis (Eₗ) (terminology and units follow Ewers and Oren, 2000). Transpiration per m² leaf area (Eₗ) was then translated to transpiration on a ground area basis (E₉):

\[ E₉ = Eₗ \times \text{LAI} \]  

(9)

In order to ensure that the sap flow gauges were functioning accurately, daily climate conditions and individual sensor heat energy components were inspected graphically. Leaf Area Index (LAI) was measured under each canopy with a Licor 2000 LAI Meter (LiCor., Lincoln, NE). The height and canopy area were determined based on
canopy diameter. These parameters were measured at the widest and narrowest points of
the canopy.

*Micro Meteorological Station.* Climate provides the forcing for the transpiration
process. Therefore, monitoring daily meteorological functions is important so as to better
interpret the response by a particular species to atmospheric demand. Meteorological
variables of solar radiation (LI-200X, LiCor, Lincoln, NE), wind speed and direction
(R.M. Young Co., Traverse City, MI), relative humidity, and air temperature (HMP35D,
Vaisala, Helsinki, Finland) were measured from a 2-meter height close to the site.
Measurements were taken every 5 seconds and an average value recorded every 30
minutes by a datalogger.

$E_T\text{,}$ refers to the evaporation rate from a theoretical extensive green grass crop
surface having a uniform set height of 0.12 m, an albedo of 0.23, and a surface resistance
of $69 \text{ s m}^{-1}$. This hypothetical grass cover completely shades ground surfaces, has infinite
water supplies and is actively growing under the existing climate conditions occurring at
the site of interest (Shuttleworth, 1993). Calculating $E_T\text{,}$ estimates the maximum
potential amount of water that can be consumed by this vegetation cover under current
climate conditions at the study site. In this study we computed a standard reference crop
evaporation rate using temperature, relative humidity, solar radiation, and wind speed
measurements to evaluate variations in atmospheric evaporation demand and its impacts
on measured seep willow transpiration. The Arizona Meteorological Network (AZMET)
equation developed for southern Arizona was used for calculating reference crop evaporation $E_{T_0}$ in units of mm h$^{-1}$ (Brown, 1989)

$$E_{T_0} = W \cdot R_n + (1-W) \cdot VPD \cdot FU2 \quad (10)$$

where $W$ refers to a dimensionless partitioning factor, $R_n$ is net radiation in units of mm hr$^{-1}$ of equivalent evaporation, $VPD$ is vapor pressure deficit in units of kPa, and $FU2$ refers to an empirical wind function in units of mm h$^{-1}$ kPa$^{-1}$. Determining the dimensionless partitioning factor ($W$) required first computing three separate variables: the saturation vapor pressure ($e_s$), the slope of the saturation vapor pressure curve, $S$, and the psychometric constant, $\gamma$. Once these were calculated, the partitioning factor was computed.

*Stomatal conductance.* Examining plant stomatal conductance ($G_S$) of water provides an indication of stomatal control exerted at the leaf level during daylight hours. Plant conductance values also represent potential photosynthetic rate and carbon uptake rate because carbon gain and water loss are locked into a tight feedback control loop (Wainwright et al. 1999). Sap flux data can be used to calculate $G_S$ on a leaf area or
ground area basis. We calculated $G_s$ on a ground area basis in mm h$^{-1}$ (Ewers and Oren 2000):

$$G_s = \frac{E_g(K_G)}{VPD} \quad (11)$$

where VPD is vapor pressure deficient (kPa) and $K_G$ is the conductance coefficient (kPa), calculated from atmospheric pressure corrected for temperature effects by the formula:

$$K_G = 115.8 + 0.4226T_{air} \quad (12)$$

The term $E_g(K_G)/D$ is the ratio of transpiration to atmospheric water demand, and it is related to the degree of stomatal opening at a given time of day (Monteith and Unsworth 1990). This calculation assumes that VPD at the leaf surface is the same as bulk VPD over the canopy (Jarvis and McNaughton 1992). This assumption is not valid when VPD is below about 0.6 kPa (Ewers and Oren 2000; Ewers et al. 2007) but VPD values in this study were well above this threshold.

**Satellite imagery.** High-resolution images were available from Google Earth for June 7, 2007; June 4, 2010; February 4, 2013; and December 6, 2014. These were inspected to track the survival of individual trees, and plant canopy areas of surviving trees were measured on the 2014 image.
Results

Mean LAI per species ranged from 1.03-1.71 ($P = 0.71$) during the sap flow measurement period in 2007 (Table 1). Daily rates of cottonwood $E_G$ decreased from 3.2 mm d$^{-1}$ on DOY 144 to 1.7 mm d$^{-1}$ on DOY 182 in 2007 (Figure 1A). By contrast, mesquite and saltcedar $E_G$ each increased from about 3.5 mm d$^{-1}$ to about 5 mm d$^{-1}$ over the same period (Figure 1B,C). Daily means of environmental factors are in Figure 2. $T_{air}$, VPD and $E_{To}$ increased over the study period whereas $R_S$ was relatively constant. A single rainfall event occurred on DOY 162, reducing $E_G$ briefly for all species (see Figure 1) and reducing VPD, $R_S$, $T_{air}$ and $E_{To}$ for that day (Figure 2A-D). Depth to water increased from 2.75-2.8 m at the start of the study to 3.05 m at the end (Figure 2E).

$E_G$ by the three species appeared to respond differently to environmental factors based on a correlation analysis of daily mean values (Table 2). Cottonwood $E_G$ was negatively correlated with $T_{air}$, VPD, $E_{To}$ and DTW, with DTW producing the highest negative correlation ($r = -0.844$, $P < 0.001$). By contrast, saltcedar and mesquite $E_G$ were positively correlated with $T_{air}$, VPD, $E_{To}$ and DTW, showing opposite trends to cottonwood. Although statistically significant, the positive correlations between mesquite $E_G$ and VPD, $T_{air}$, $E_{To}$ and DTW were only moderate whereas they were stronger for saltcedar. Mesquite and saltcedar $E_G$ were weakly correlated with $R_S$ ($P < 0.05$) whereas the correlation coefficient for cottonwood $E_G$ was non-significant. Table 2 also shows that the environmental factors were moderately to strongly correlated with each other,
making it difficult to pinpoint the prime determinants of $E_G$ for each species on a daily basis.

By contrast to $E_G$, correlation coefficients between mean daily $G_S$ and environmental conditions were negative for VPD, $T_{air}$, $E_T$ and DTW for all three species (Table 3). Diurnal plots of half-hourly values showed that $E_G$ of cottonwood peaked at 800 hours compared to 900 hours for mesquite and 1200 hours for saltcedar (Figure 2A). $R_S$ peaked at 1200 hours while VPD peaked at 1650 hours (Figure 2A). $G_S$ peaked at 0700-0800 hours for all three species and diurnal curves were truncated relative to $R_S$ (Figure 2B). Since cottonwood $E_G$ decreased over the study period, we considered it possible that the diurnal response to environmental factors changed as well. However, diurnal curves of $E_G$ and $G_S$ for cottonwood constructed at the beginning of the study period and at the end of the study period were similar except that peak values were lower in the latter period (not shown). Multiple regression equations relating daily hourly values of $G_S$ to VPD and $R_S$ were similar for all three species (Table 3). For all three, $R_S$ was a positive factor ($P < 0.001$) and VPD was a negative factor ($P < 0.001$).

The plants for which sap flow was measured in 2007 were re-surveyed with high-resolution imagery available on Google Earth. Images available for 2010 and 2013 showed that one of the five cottonwoods apparently died by 2010 but all other plants remained alive and increased in canopy area. Canopy areas measured on a DOY 340, 2014 image showed increases of 1.1-3.5 times the areas in 2007 (Table 1), and canopies of adjacent plants were now in contact. Differences among species were not significant
by one-way ANOVA (P = 0.15); within-species differences were larger than between-species differences and the sample size was small. Canopies between adjacent plants had closed by 2014 and the area of a canopy was in part determined by how much space was available between plants (Figure 6).

**Discussion**

In this study, as in others that directly compared ET rates of riparian species (reviewed in Glenn and Nagler, 2005), saltcedar did not have high ET rates compared to cottonwood or mesquites. At the start of the pre-monsoon period, $E_G$ rates were about the same for each species, less than 40% of $E_{To}$. LAIs of plants were also similar and below values > 3.0 expected for dense, closed canopies (Shuttleworth, 1993). The biggest difference between species was the decrease in $E_G$ noted for cottonwood during the pre-monsoon season while $E_G$ of mesquite and saltcedar tended to increase. The decrease in cottonwood $E_G$ was strongly correlated with an increase in DTW. The threshold depth to water for cottonwood saplings is in the range of 2.6-3.0 m (Stromberg et al., 2005) close to the depth of water in this study. Cottonwoods are sensitive to the rate of recession of the groundwater during the pre-monsoon period, with a threshold of 0.5 m (Stromberg et al., 2005), greater than the value noted in this study. By contrast to cottonwoods, saltcedars can access water as deep as 8 m below the surface (Horton 2001, 2003), and
mesquite can obtain water from even deeper sources (Bleby et al., 2010). Since the plants in this study grew in mixed stands, it is reasonable to conclude that the ability of saltcedar and mesquite to extract water from a greater depth than cottonwood could give them a competitive advantage during the pre-monsoon season, as they could be expected to lower the water table beyond the threshold depth for cottonwood. Both saltcedar (Yu et al., 2013) and mesquite (Bleby et al., 2010) are capable of hydraulically redistributing deep water to shallower soil layers, giving them a potential advantage over more shallow-rooted plants at all soil depths.

On the other hand, DTW decreases during the monsoon season (Haney, 2005), and in the long run cottonwoods can have a competitive advantage over saltcedars and mesquites because they grow taller and can shade out shorter competitors (Nagler et al., 2005; Bunting et al., 2013). At this site, all but one of the starting trees were still alive in 2014 and had grown to form a partially closed canopy of mixed species. Not only the sampled trees, but throughout the study area, mixed stands persisted, with cottonwoods tending to dominate near the active channel and saltcedars and mesquite dominating further away from the active channel (Figure 6). Mesquites also grew on the former agricultural fields near the river.

Analyses of the stomatal response to environmental factors showed that for all three species, $G_S$ was negatively correlated with VPD on both a daily and hourly basis. Diurnal curves showed that $G_S$ peaked between 0700-0800 hours and all three showed marked midday depression of $G_S$ relative to the radiation curve. Beyond about 0800
hours atmospheric water demand as estimated by VPD apparently exceeded the capacity of all three species to support transpiration, resulting in partial stomatal closure to restrict water loss. VPD was 2.0 kPa by 0900 hours and peaked at over 5 kPa by 1600 hours. At this site, all three species exercised control over stomatal conductance during the pre-monsoon period. \( E_G \) increased further into the day than \( G_S \) presumably because even at reduced stomatal conductance, higher VPD led to increased water loss through partially open stomata. These results are similar to those reported for *Tamarix* spp. and *Populus euphratica* spp. in the lower Tarim River in China's arid region (Chen et al., 2013).

Similar to the San Pedro River in this study, diversion of water for human use has converted the river from perennial to intermittent, and groundwater levels have decreased. During a drought period both *Tamarix* spp. and *P. euphratica* showed midday depression of transpiration, stomatal conductance and photosynthesis. In addition, all three parameters decreased with increasing depth to groundwater, which ranged from 2-8 m in the study plots (Chen et al., 2013).

We conclude that despite apparently shallower rooting depth for cottonwoods, at this restored site saltcedar, cottonwoods and mesquites are able to co-exist in mixed stands, at least up to the point of canopy closure. While the decrease for cottonwood was negatively correlated with VPD and \( T_{air} \), which tended to increase over the same period, the strongest negative correlation was with depth to groundwater. Depth to groundwater was also the main determinant of photosynthesis and transpiration for *Populus* and *Tamarix* in the native range of these species in China (Li et al., 2013). So long as depth to groundwater along this reach of the San Pedro River can be maintained at 3.0 m or less.
during the pre-monsoon green-up period, and given occasional pulse floods to germinate new cohorts of trees, mixed stands of mesquites, saltcedars and cottonwoods can be expected to persist. Such mixed stands offer both midstory and overstory canopy structures that provide good habitat for generalist as well as riparian-obligate birds (van Riper et al., 2002; Paxton et al., 2011) as well as habitat for other wildlife (Bateman et al., 2015).


Li, J., B. Yu, C. Zhao. 2013. Physiological and morphological responses of Tamarix ramosissima and Populus euphratica to altered groundwater availability. Tree Physiology 33:57-68.


Table 1. Plant canopy area, height and LAI of plants measured for transpiration and stomatal conductance in 2007 and resurveyed for survival and canopy area increase with high-resolution satellite imagery in 2014.

<table>
<thead>
<tr>
<th>Plant</th>
<th>Canopy Area 2007 (m²)</th>
<th>Height 2007 (m)</th>
<th>LAI</th>
<th>Canopy Area 2014 (m²)</th>
<th>Fractional Increase</th>
</tr>
</thead>
<tbody>
<tr>
<td>CW1</td>
<td>5.91</td>
<td>8.82</td>
<td>0.35</td>
<td>69.2</td>
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<td>1.50</td>
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<td>2.87</td>
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</tr>
<tr>
<td>M 1</td>
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<td>1.08</td>
<td>12.4</td>
<td>3.5</td>
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<td>M 2</td>
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<td>SC 4</td>
<td>12.3</td>
<td>6.71</td>
<td>2.61</td>
<td>13.3</td>
<td>1.08</td>
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</table>
Table 2. Correlation between cottonwood (CW), mesquite (MESQ) and saltcedar (SC) transpiration rates (E<sub>G</sub>) and environmental variables during the pre-monsoon period at a site on the Middle San Pedro River. VPD = vapor pressure deficit; T<sub>air</sub> = mean daily air temperature; R<sub>S</sub> = solar radiation; E<sub>T0</sub> = potential evapotranspiration; DTW = depth to groundwater.

<table>
<thead>
<tr>
<th></th>
<th>VPD</th>
<th>T&lt;sub&gt;air&lt;/sub&gt;</th>
<th>R&lt;sub&gt;S&lt;/sub&gt;</th>
<th>E&lt;sub&gt;T0&lt;/sub&gt;</th>
<th>DTW</th>
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<tbody>
<tr>
<td>CW E&lt;sub&gt;G&lt;/sub&gt;</td>
<td>-0.511***</td>
<td>-0.699***</td>
<td>0.0886ns</td>
<td>-0.322*</td>
<td>-0.844***</td>
</tr>
<tr>
<td>MESQ E&lt;sub&gt;G&lt;/sub&gt;</td>
<td>0.395*</td>
<td>0.481**</td>
<td>0.162ns</td>
<td>0.387*</td>
<td>0.458**</td>
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<tr>
<td>SC E&lt;sub&gt;G&lt;/sub&gt;</td>
<td>0.884***</td>
<td>0.917***</td>
<td>0.523***</td>
<td>0.845***</td>
<td>0.783***</td>
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<tr>
<td>CW G&lt;sub&gt;S&lt;/sub&gt;</td>
<td>-0.876***</td>
<td>-0.949***</td>
<td>-0.239ns</td>
<td>-0.696***</td>
<td>-0.933***</td>
</tr>
<tr>
<td>Mesq G&lt;sub&gt;S&lt;/sub&gt;</td>
<td>-0.914***</td>
<td>-0.769***</td>
<td>-0.608***</td>
<td>-0.836***</td>
<td>-0.621***</td>
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<tr>
<td>SC G&lt;sub&gt;S&lt;/sub&gt;</td>
<td>-0.659***</td>
<td>-0.452**</td>
<td>-0.191ns</td>
<td>-0.457**</td>
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<tr>
<td>VPD</td>
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<td>0.934***</td>
<td>0.461**</td>
<td>0.861***</td>
<td>0.796***</td>
</tr>
<tr>
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<td>0.299ns</td>
<td>0.749***</td>
<td>0.827***</td>
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<tr>
<td>R&lt;sub&gt;S&lt;/sub&gt;</td>
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<td>0.737***</td>
<td>0.263ns</td>
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<tr>
<td>E&lt;sub&gt;T0&lt;/sub&gt;</td>
<td>1.00</td>
<td></td>
<td></td>
<td>0.604***</td>
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Table 3. Multiple linear regression analyses of day-time values of $G_S$ for cottonwoods, mesquites and saltcedar growing together on the Lower San Pedro River. Equations took the form: $G_S$ (mm d$^{-1}$) = Constant + Coefficient VPD * VPD + Coefficient $R_S$ * $R_S$

<table>
<thead>
<tr>
<th></th>
<th>Cottonwood</th>
<th>Mesquite</th>
<th>Saltcedar</th>
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</thead>
<tbody>
<tr>
<td><strong>Constant</strong></td>
<td>15.0</td>
<td>22.9</td>
<td>23.1</td>
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<tr>
<td>Coefficient VPD</td>
<td>-2.80</td>
<td>-4.80</td>
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<tr>
<td>Coefficient $R_S$</td>
<td>3.88</td>
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<tr>
<td>$\beta$ Coefficient VPD</td>
<td>-1.08</td>
<td>-1.10</td>
<td>-1.05</td>
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<tr>
<td>$\beta$ Coefficient $R_S$</td>
<td>0.365</td>
<td>0.575</td>
<td>0.646</td>
</tr>
<tr>
<td><strong>F</strong></td>
<td>328</td>
<td>2596</td>
<td>0.946</td>
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<td><strong>P</strong></td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
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<tr>
<td>$r^2$</td>
<td>0.966</td>
<td>0.996</td>
<td>0.946</td>
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Figure Captions.

Figure 1. Examples of trees measured for transpiration and stomatal conductance in 2007. Top: cottonwoods and adjacent saltcedar trees. Bottom: mesquite and adjacent saltcedar trees.

Figure 2. Diagram showing spacing between sampled trees in 2007.

Figure 3. Transpiration on a ground area basis (EG) for cottonwood, mesquite and saltcedar at the Nature Conservancy sites on the San Pedro River, Arizona. The dip in EG at DOY 162 was due to a rainfall event.

Figure 4. Environmental variables measured at the sap flow sites at the Nature Conservancy San Pedro Reserve.

Figure 5. Diurnal response of transpiration (EG) (A) and stomatal conductance (Gs) (B) for cottonwood, mesquite and saltcedar at the Nature Conservancy San Pedro Reserve, DOY 144-182, 2007. Also shown are diurnal curves for radiation (Rs) and vapor pressure deficit (VPD).

Figure 6. The study area as it appeared on June 7, 2007 (Top) and December 6, 2014 (Bottom). The 2014 scene shows the two clusters of trees that were measured in 2007 (white circles). In the December, 2014 scene saltcedars appear as orange canopies due to
senescence of leaves; cottonwoods appear as light green canopies as leaves are still on trees; and mesquites are deeper green canopies compared to cottonwoods.
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