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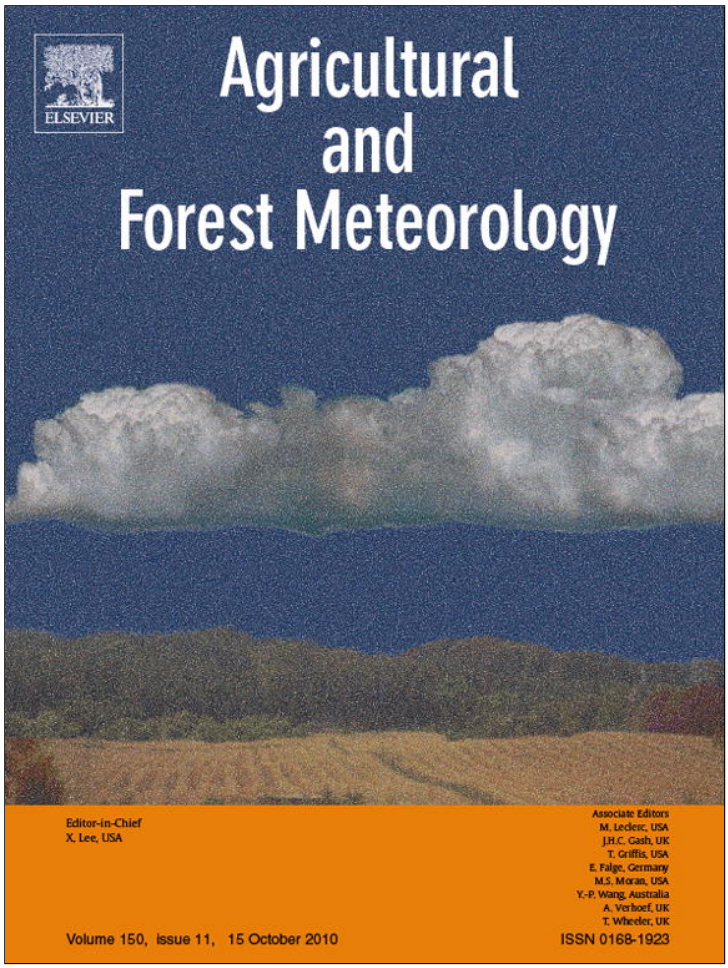

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Sap flux-scaled transpiration by tamarisk (*Tamarix* spp.) before, during and after episodic defoliation by the saltcedar leaf beetle (*Diorhabda carinulata*)

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ABSTRACT

The release of the saltcedar beetle (*Diorhabda carinulata*) has resulted in the periodic defoliation of tamarisk (*Tamarix* spp.) along more than 1000 river km in the upper Colorado River Basin and is expected to spread along many other river reaches throughout the upper basin, and possibly into the lower Colorado River Basin. Identifying the impacts of these release programs on tamarisk water use and subsequent water cycling in arid riparian systems are largely unknown, due in part to the difficulty of measuring water fluxes in these systems. We used lab-calibrated, modified heat-dissipation sap flux sensors to monitor tamarisk water use ($n = 20$ trees) before, during and after defoliation by the saltcedar leaf beetle during the 2008 and 2009 growing seasons (May–October) in southeastern Utah. We incorporated a simple model that related mean stem sap flux density (J_s) with atmospheric vapor pressure deficit (*vpd*) before the onset of defoliation in 2008. The model was used to calculate differences between predicted J_s and J_s measured throughout the two growing seasons. Episodic defoliation resulted in a 16% reduction in mean annual rates of J_s in both 2008 and 2009, with decreases occurring only during the periods in which the trees were defoliated (about 6–8 weeks per growing season). In other words, rates of J_s rebounded to values predicted by the model when the trees produced new leaves after defoliation. Sap flux data were scaled to stand water use by constructing a tamarisk-specific allometric equation to relate conducting sapwood area to stem diameter, and by measuring the size distribution of stems within the stand. Total water use in both years was 0.224 m, representing a reduction of about 0.04 m yr^{-1}. Results showed that repeated defoliation/refoliation cycles did not result in a progressive decrease in either leaf production or water use over the duration of the study. This investigation improves ground-based estimates of tamarisk water use, and will support future efforts to characterize impacts of the beetle on basin-wide hydrologic processes.

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1. Introduction

Balancing scarce water supplies to support expanding human enterprise while maintaining ecosystem function and diversity is a primary challenge for land managers, policy makers and scientists. Nowhere in the United States is this more apparent than in the arid west where rising population coupled with frequent drought has resulted in periodic and at times, critical water shortages. These shortages have spurred considerable efforts to improve the accounting of the inputs and outputs of water cycles at multiple scales. However, efforts to close water budgets of complex watersheds is a significant challenge given that major components of the water cycle such as storage and evapotranspiration (ET) are difficult to quantify at large spatial scales.

Water deliveries for agriculture and municipalities in the arid west are supplied primarily from major watersheds and river systems that also support native riparian vegetation and habitat (Patten, 1998). Delivering adequate water supplies while maintaining the necessary flow regimes to support desired riparian ecosystems is becoming increasingly difficult. Consequently, many riparian systems have undergone dramatic alteration over the last 50–100 years. One of the most visible changes that are in part due to altered flow regimes is the establishment of invasive plant species into native riparian areas (Stromberg et al., 1991, 2007; Shafroth et al., 1998, 2002; Lite and Stromberg, 2005). Among the most aggressive invasive riparian plant species is the Eurasian

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tree/shrub, tamarisk (*Tamarix* spp.) that is now the third most dominant woody species in the western United States riparian zones (Friedman et al., 2005). Tamarisk tends to form dense thickets with high leaf areas and thick litter layers that often result in monocultures with little or no native vegetation (DiTomaso, 1998). The rate of tamarisk expansion along riparian ecosystems has been estimated at 20 km yr^{-1} (Glenn and Nagler, 2005).

The impacts of tamarisk on regional water cycles are not well understood. Recent evidence suggests that the replacement of native vegetation such as cottonwood and willow with tamarisk results in very little if any net change in riparian evapotranspiration per unit ground area (Nagler et al., 2005, 2007; Shafroth et al., 2005). Nevertheless, tamarisk has the potential to occupy areas that previously had little or no native vegetation (Morisette et al., 2006), is more drought tolerant than most native riparian vegetation (Devitt et al., 1997; Pockman and Sperry, 2000), and may have more extensive root systems that allow it to extract water from deeper aquifers compared to native vegetation (Shafroth et al., 2000). Taken together, these factors suggest that the expansion of tamarisk in arid riparian systems may have significant impacts on hydrologic processes over broad spatial scales.

Tamarisk control and removal has become a priority of riparian ecosystem management, due in part to its potential negative impacts on stream flow and groundwater recharge. Among the most controversial, and potentially most successful tamarisk control approach is the release of the saltcedar leaf beetle, *Diorhabda carinulata* Bulle (Dudley, 2005; Hultine et al., 2009). The beetle feeds exclusively on tamarisk leaves, resulting in periods of defoliation that last several weeks or longer. These episodic defoliation events result in carbon starvation that in turn, reduce leaf production and growth and in some cases leads to tamarisk mortality. The advantage of the biocontrol program is that the beetle has the potential to spread and impact tamarisk over large areas. For example, the beetle was released in 2004 at only a few locations on the Colorado River, but by 2007, these releases and a small number of subsequent releases had resulted in tamarisk defoliation on over a 1000 river km in the upper Colorado River Basin (Hultine et al., 2009).

It is difficult to assess the impacts of defoliation is having on regional patterns of tamarisk ET and subsequent water cycling of the upper Colorado River Basin, due in part to challenges associated with estimating riparian ET rates to begin with. One approach is to use remote sensing techniques to estimate riparian ET from vegetation indices (Nagler et al., 2005, 2008, 2009; Dennison et al., 2009). Dennison et al. (2009) found that tamarisk defoliation along the Colorado and Dolores Rivers in Utah resulted in much smaller changes in annual riparian ET than changes in ET resulting from inter-annual climatic variability. However, remote sensing estimates of ET are typically calibrated from water vapor flux data from flux towers placed in riparian forests. Unfortunately, most riparian systems are comprised of narrow strips of vegetation (especially true for the upper Colorado River Basin) that are not suitable for flux tower measurements. Consequently alternative approaches, such as stem sap flux measurements, are necessary to calibrate remote sensing estimates of riparian ET, and subsequent impacts of the saltcedar leaf beetle on tamarisk transpiration in the upper Colorado River Basin.

In this paper, we report patterns of sap flux-scaled water use by tamarisk, before, during and after episodic defoliation by the saltcedar leaf beetle over two consecutive growing seasons (2008 and 2009) in southeastern Utah on the Colorado Plateau. The goal of the study was to: 1) determine whether herbivory by the saltcedar leaf beetle progressively decreases leaf production and stand transpiration after defoliation/refoliation cycles, and 2) provide accurate ground-based estimates of stand water use for scaling to large river reaches.

2. Materials and methods

2.1. Site description

The study took place at the University of Utah's Entrada Field Station (http://entrada.biology.utah.edu/) located approximately 65 km east of Moab in southeastern Utah. The field station is located on the Dolores River about 12 km from its confluence with the Colorado River. The river flows perennially through the field station and the USGS operates a stream gauge on site that includes 59-year records of stream discharge (http://waterdata.usgs.gov/ut/nwis/uv/?site_no=09180000). Precipitation patterns in southeastern Utah are bimodal with approximately 50% of the 230 mm of mean annual rainfall occurring during the summer monsoon (July–September). Relative humidity, air temperature and photosynthetic active radiation were measured continuously at the field station over the duration of the investigation. Relative humidity and air temperature were measured with a Vaisala HMP 45 AC humidity and temperature probe (Vaisala, Woburn, MA, USA), placed approximately 2.0 m above the ground surface. Photosynthetically active radiation (Q) was measured with a Li-Cor LI-190SZ quantum sensor (Li-Cor, Lincoln, NE, USA). Micrometeorological data were measured every 30 s and stored as 15 min averages with a Campbell CR1000X data logger (Campbell Scientific, Logan, UT, USA). Measurements of relative humidity and air temperature were used to calculate atmospheric vapor pressure deficit (vpd).

Historic aerial photographs show that tamarisk [*Tamarisk ramossisima* Ledeb. × *chinensis* Lour. (Gaskin and Schaal, 2002)] likely became established at the field station in the late 1950s after several large flood events. The study was conducted in a large tamarisk stand from late April of 2008 through the end of October of 2009, effectively capturing the entire 2008 and 2009 tamarisk growing seasons. The stand (38°47′53.42″N, 109°12′16.51″W, elevation 1277 m) was comprised almost exclusively of mature tamarisk trees with a few coyote willow (*Salix exigua*) thickets occurring along the river channel. Depth to groundwater was measured near the center of the stand with an In-Situ MiniTroll pressure transducer and datalogger system (In-Situ, Ft. Collins, CO) installed in a piezometer well. Soil texture was comprised primarily of sandy loams with about 60% sand fraction, and 10% clay fraction in the upper 1.5 m.

In the summer of 2004 through the summer of 2006, several thousand saltcedar leaf beetles were released at multiple locations including one release point near the confluence of the Colorado and Dolores Rivers. The beetles have since migrated successfully upriver and reached the field station during mid-summer of 2007. Three tamarisk defoliation events have since occurred at the station with each lasting several weeks until new leaves emerged. The first event initiated in mid-July of 2007, the second, in mid-June of 2008, and the most recent in mid-July of 2009.

2.2. Field sap flux measurements

Twenty mature tamarisk trees were selected for sap flux study. Each tree was either dominant or co-dominant in the stand. At the onset of the study, stem diameters at breast height ranged from 0.067 to 0.133 m with a mean diameter of 0.104 m. Granier-type sensors (Granier, 1987; Hultine et al., 2007) were constructed in the laboratory to measure sap flux density (J_S). Each sensor consisted of a pair of 10 mm long, 2 mm diameter stainless steel probes inserted approximately 15 cm apart along the axis of the hydroactive xylem (i.e., sapwood). A single sensor was inserted in each tree at approximately 1.5 m above the ground. Azimuth direction of each sensor was randomly selected to eliminate potential biases due to non-uniformity in sap flux around the stem. The upper

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Table 1
Stem diameter, sapwood area, sapwood depth at the probe insertion point, and regression coefficients for sap flux density measurements of tamarisk stems used to calibrate Granier-type sap flux probes. Standard error (SE) is ±1 standard error of the mean.

Stem #	Diameter (mm)	Sapwood area (mm^2)	Sapwood depth (mm)	β_1 ($g\,m^{-2}\,s^{-1}$)	β_2	R^2
1	42.5	211	4.7	110	1.09	0.99
2	49.0	238	4.9	172	1.11	0.99
3	49.0	255	3.5	175	1.65	0.95
4	49.5	940	8.2	514	1.35	0.99
5	44.5	749	8.5	429	1.71	0.98
6	36.5	232	8.2	507	0.95	0.97
7	42.0	499	5.3	241	1.05	0.91
8	35.0	461	6.3	152	0.93	0.99
9	36.5	505	5.1	127	1.01	0.99
10	40.0	379	4.4	104	0.84	0.99
11	33.5	423	5.0	106	1.10	0.99
Mean	41.6	445	5.8	240	1.16	0.98
SE	2.0	77	0.6	49.1	0.10	0.01

Model: $J_s = \beta_1 * K^{\beta_2}$.

probe (i.e., toward the canopy) was supplied with constant power of 200 mW, and the temperature difference between the heated (powered) probe and the lower, unheated reference probe was converted to sap flux density according to the equation:

$$J_s = \beta_1 K^{\beta_2} \quad (1)$$

where β_1 and β_2 are fitting parameters, and K is calculated from:

$$K = \frac{\Delta T_0}{\Delta T} - 1 \quad (2)$$

where ΔT is the temperature difference between the heated and unheated probes, ΔT_0 is the temperature difference obtained under zero flow conditions. We assumed that zero flow only occurred at night when *vpd* was at or near zero. At the conclusion of the 2008 growing season, the sensors were removed and new sensors were installed the following spring at different locations on the stem. Sap flux measurements in both 2008 and 2009 commenced during leaf flush on day 120, and concluded during leaf senescence around on day 305 during leaf. Mean daily sap flux was calculated for both daytime and nocturnal periods. Daytime was defined as periods when Q was above 10 $\mu mol\,m^{-2}\,s^{-1}$ (Hultine et al., 2007).

Heat-dissipation probes inevitably underestimate water flow through stems in cases where the length of the probe extends beyond the depth of conducting sapwood. In the present study, mean sapwood depth of tamarisk trees in the stand was 9.1 mm, whereas the probe length was 10 mm. Therefore, we applied a correction outlined by Clearwater et al. (1999) that accounts for inactive xylem within the measured region of the sensors:

$$\Delta T_{sw} = \frac{\Delta T - b\,\Delta T_m}{a} \quad (3)$$

where ΔT_{sw} is the temperature difference between probes within conductive sapwood, ΔT_m is the temperature difference between probes in inactive xylem (assumed to equal ΔT_0), and a and b are the proportion of probe in sapwood and inactive xylem, respectively.

2.3. Laboratory sap flux calibration

The original calibration of Granier style sensors was conducted on 20 mm length probes (Granier, 1987). However, because sapwood depth of tamarisk trees at our field site was consistently less than 20 mm, we constructed 10 mm length probes. Therefore, we produced tamarisk-specific sensor-calibration coefficients in the lab using a protocol developed by Taneda and Sperry (2008), and Bush et al. (in press). Approximately 2 m length stem segments, ranging in diameter from approximately 33.5–49.0 mm were harvested from the field site ($n = 11$ stems). After removal of all side branches, the stem segments were placed in sealed plastic bags with a wet towel and transported to the lab. The stems were cut under water into approximately 0.8 m segments and the ends were trimmed with a sharp razor blade. The stems were held upright with a ring stand and rubber gaskets with tubing attached to a vacuum pump were placed over the upper end while the lower end was placed in filtered 20 mM KCl solution on a balance. Flow rate was measured by the balance over a series of reduced pressures from approximately 0.024 MPa to 0.004 MPa. 10 mm long Granier-type sensors (described above) were inserted approximately 15 cm apart along the axis of the hydroactive xylem. The sensors were installed near the middle portion of the stem. The upper probe (i.e., toward the vacuum pump) was supplied with a constant power of 200 mW, while the lower reference probe received no power input. Voltage differences were measured between the heated and unheated probe at each pressure after flow rates were allowed to stabilize (20 min). Voltage differences at zero flow were determined for each sensor/segment two to three hours after voltage/flow measurements had concluded. Following the flow measurements, 0.1% safranin dye was pulled through the stem segments to measure the conducting sapwood area and sapwood depth between the two probes. This allowed the conversion of volume flow to mean sap flux density ($g\,m^{-2}\,s^{-1}$). The stems used for sap flux calibration all had sapwood depth that was less than the length of our 10 mm probes (Table 1). Therefore, we applied the Clearwater correction (Eq. (3)) that accounts for inactive xylem within the measured region of the sensors. After voltage differences were converted to temperature differences, the relationship between temperature differences (K, °C) during periods of sap flow (ΔT) and temperature differences during zero flow (ΔT_0) was calculated from Eq. (2).

Best-fit regression curves for the exponential function between mean J_s and K were calculated using Eq. (1), and were applied to voltage differences measured in the field.

2.4. Modeling of defoliation impacts on sap flux density

A major challenge for quantifying impacts of defoliation on annual rates of tamarisk water use is determining how much water tamarisk would use annually if defoliation were absent. Rates of water loss in riparian areas vary spatially due to variations in groundwater depth, soil texture, salinity, stand density, and leaf area index (LAI), while temporal variations in *vpd* and Q can have dramatic impacts on inter-annual patterns of water use within an area or stand. We therefore tested various models to relate mean J_s of the stand to atmospheric drivers *vpd* and Q, before the onset of beetle-induced defoliation in 2008. For mean daytime J_s, (J_{sd}) we tested a multivariate model that included the parameters, *vpd*, Q, and the interaction *vpd**Q. Because tamarisk trees also transpire nocturnally (Moore et al., 2008), we also modeled mean nocturnal J_s (J_{sn}) with nocturnal *vpd*. We incorporated an exponential sat-

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uration curve to relate mean daytime and nocturnal J_s with *vpd* (Hultine et al., 2007):

$$J_s = \beta_1(1 - e^{-\beta_2 vpd}) \quad (4)$$

where β_1 and β_2 are fitting parameters. The relationship between J_s and Q is also non-linear and was therefore fitted against ln(Q). The models were tested over a 41 day period from May 10 (DOY 130) to June 19 (DOY 170), a period in which the trees showed complete leaf flush, but before the adult beetles or larvae were visibly present.

2.5. Scaling sap flux from tree to stand

Sap flux density was scaled to stand transpiration by determining the relationship between sapwood area and stem diameter, and then determining the number of stems for various size classes within the stand. The relationship between stem sapwood area and stem diameter was determined by harvesting stems over the range of size classes that are typically found within the stand. Cross sections were cut from 15 tamarisk stems ranging in diameter from 0.018 to 0.14 m, and then photographed with a digital camera. The sapwood area (A_s), defined as the total area under the bark that was clearly lighter in color than heartwood was determined using the public domain image processing program, Image J (National Institutes of Health, http://rsb.info.nih.gov/ij). Because not all sapwood area is conductive, we measured the ratio of conductive sapwood area (A_c), determined from the staining technique described above, and A_s on 13 tamarisk stems. The analysis yielded a relationship of $A_c = 0.83A_s$ ($R^2 = 0.95$, $P < 0.0001$). Conducting sapwood area to stem diameter (D) relationships were determined using a power function given in Eq. (5):

$$A_c = \beta_1 * D^{\beta_2} \quad (5)$$

where β_1 and β_2 are fitting parameters.

Total conducting sapwood area per unit ground area was estimated by establishing ten 10 m × 10 m (100 m^2) plots within the stand, and measuring the diameter at breast height of every live tamarisk stem greater than 2 cm diameter in each plot.

2.6. Leaf area index measurements

Leaf area index (LAI, m^2 m^{-2}) was measured monthly during the growing season except during periods when the trees were directly impacted by the saltcedar leaf beetle. LAI measurements were conducted with a Li-Cor LAI 2000 leaf area meter (Li-Cor, Inc., Lincoln, NE), along four transects ($n = 6$ measurement locations per transect). Initial measurements were conducted before each growing season so that a baseline plant area index (PAI) could be determined. LAI was therefore calculated by subtracting PAI values measured at each location during the growing season from PAI measured at the same locations prior to the onset of the growing season. Because the LAI 2000 leaf area meter often underestimates stand LAI (Brantley and Young, 2007), litter traps were placed at each measurement location and litter fall was collected at the conclusion of the 2008 growing season. Leaf area of each litter trap was determined by weighing the total leaf mass and applying a previously determined equation (data unpublished) that relates leaf area to leaf mass (i.e., specific leaf area). LAI determined from litter fall was compared to the LAI 2000 measurements conducted just prior to senescence and yielded a calibration offset of 2.28.

2.7. Statistical analysis

Regression analysis was used to relate gravimetrically measured J_s to K. The response of daytime J_s to *vpd* and Q was analyzed using analysis of covariance (ANCOVA) where *vpd*, Q and *vpd**Q were used as independent variables in the regression equation. Regression analysis was used to relate nocturnal J_s to *vpd*. Regression analysis was also performed to relate A_c to A_s, and A_c to stem diameter. A standard Students T-test was used to test for mean differences between measured J_s and J_s modeled from *vpd* and Q. JMP 8.0 (SAS institute Inc., Cary, NC, USA.) was used for all statistical analysis, with $P \leq 0.05$ as the significance level.

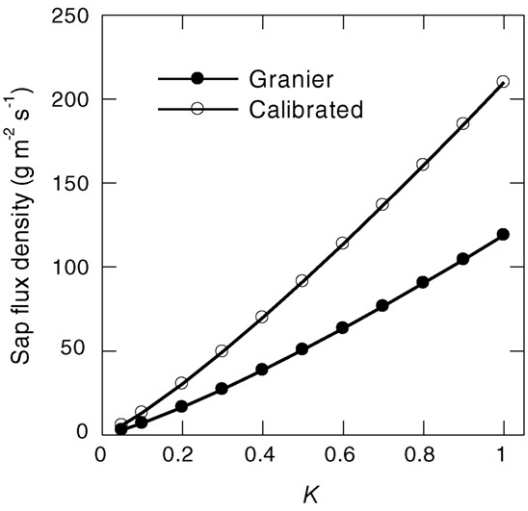

Fig. 1. The relationship between sap flux density (J_s) and K (the ratio between temperature differences during periods of sap flow and temperature differences during zero flow) for Granier calibrated heat-dissipation sensors and lab-calibrated heat-dissipation sensors.

3. Results

3.1. Lab sap flux calibration

The relationship between measured sap flux density and K (Eq. (2)) was highly significant in all the stems we measured and explained between 91 and 99% of the variation in the sap flux density models (Table 1). The β_1 coefficient ranged five fold from 104 to 514 g m^{-2} s^{-1}, and β_2 (the exponent in Eq. (1)) ranged two fold from 0.84 to 1.71 (Table 1). The mean β_1 coefficient for sap flux density was 240 (standard error = 49.1) g m^{-2} s^{-1}, and β_2 was 1.16 (SE = 0.10) (Table 1). The coefficients represent departures from the standard Granier equation where β_1, and β_2 were 119 g m^{-2} s^{-1} and 1.23, respectively (Granier, 1987). Differences between the tamarisk-specific-calibration coefficients and those from the orig-

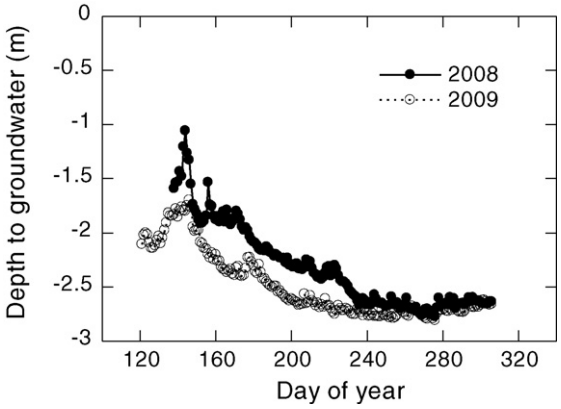

Fig. 2. Depth to groundwater measured during the 2008 and 2009 growing seasons at the Entrada Field station in southeastern Utah. Measurements were conducted near the center of a tamarisk stand used for sap flux studies in 2008 and 2009.

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Table 2
Coefficients and error terms yielded from the relationship between daytime (J_{sd}) and nocturnal (J_{sn}) sap flux density and vapor pressure deficit (Eq. (4), Fig. 3).

	β_1	β_2	β_1 error	β_2 error
Daytime J_s	43.5	1.63	1.18	0.23
Nocturnal J_s	34.8	0.27	37.0	0.35

Model: $J_s = \beta_1 * [1 - \exp(-\beta_2 * vpd)]$.

inal Granier equation are clearly visible when J_s is calculated from K (Fig. 1). In fact, the Granier coefficients would result in about a 50% reduction in J_s compared to the coefficients determined from lab calibration (Fig. 1).

3.2. Depth to groundwater

Water use by phreatophytic plants in semi-arid riparian areas is often tightly coupled to groundwater depth. Therefore, inter-annual variability in depth to groundwater could confound inter-annual comparisons of saltcedar beetle impacts on tamarisk water use. Groundwater was consistently 0.3–0.5 m deeper during the 2009 growing season compared to 2008 until about day 240, after which groundwater depth was similar between the two years (Fig. 2). Mean depth to groundwater in 2008 was −2.32 m (SE = 0.03) with a range of −1.06 to −2.77 m. Mean depth to groundwater in 2009 was −2.53 m (SE = 0.02) with a range of −1.70 to −2.81 m.

3.3. Field sap flux density and LAI measurements

In cases where soil water is readily available for plant uptake, such as in riparian areas, J_s is primarily constrained by atmospheric drivers *vpd* and *Q*. We therefore developed a multivariate model for mean daytime sap flux density (J_{sd}) using *vpd*, *Q* and the interaction between *vpd* and *Q* before the onset of defoliation by the saltcedar leaf beetle in 2008. The model yielded a significant relationship between J_{sd} and *vpd* ($F = 13.13$, $P = 0.0009$, $n = 41$ days). On the other hand, there was no relationship between either *Q* ($F = 1.84$, $P = 0.18$) or the interaction *vpd***Q* ($F = 1.24$, $P = 0.27$). After removing both *Q* and *vpd***Q* from the model, *vpd* explained 50% of the variation in J_{sd} ($F = 43.95$, $P < 0.0001$, Fig. 3a). Likewise, mean nocturnal *vpd* explained 30% of the variation in mean J_{sn} ($F = 24.28$, $P < 0.0001$, Fig. 3b). Coefficients β_1 and β_2 in the model used to predict J_s from *vpd* (Eq. (4)), along with error terms for β_1 and β_2 are shown in Table 2.

The saltcedar leaf beetle initially appeared in 2008 at the field site on or around day 170 (personnel observation). Within about two weeks after the beetles appeared, all tamarisk leaves turned from green to brown due to beetle-induced defoliation. However, J_{sd} initially increased during defoliation by the saltcedar leaf beetle and reached a maximum on day 177 (Fig. 4a) when the leaves had already turned brown. After Day 177, mean daily J_{sd} quickly decreased until about day 198 when it leveled off for about three weeks at around 10 g m^{-2} s^{-1}, less than one quarter of the expected value without defoliation (Fig. 4a). As the trees produced new leaves, mean daily J_{sd} increased until it returned to levels that were predicted by the model on around Day 240. Subsequently, rates of J_{sd} in September and October were similar to those predicted by the model (Table 3). For the entire growing season (May–October), rates of mean daily J_{sd} were about 16% lower than predicted (Table 3).

Patterns were somewhat different in 2009 as defoliation occurred more slowly, due to an apparent lower density of beetles during the initial infestation compared to 2008 (personnel observation). Consequently, there was no obvious spike in mean J_{sd} as there was in 2008 (Fig. 4b). The period of defoliation occurred over a longer period than in 2008 from about Day 190 until about Day 250 (Fig. 4b, Table 3). However mean J_{sd} again returned to values predicted by the model (i.e., Fig. 3a) and retained expected rates throughout the remainder of the growing season. Defoliation by the beetle resulted in about 15% lower rates of J_{sd} over the course of the growing season (Table 3).

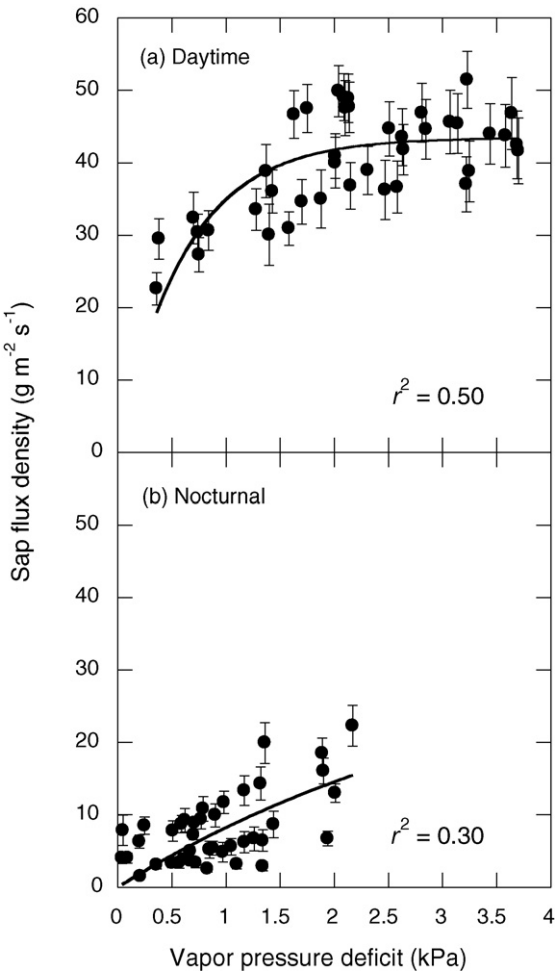

Fig. 3. Relationship between mean daily sap flux density and mean daily vapor pressure deficit of mature tamarisk trees ($n = 20$ trees) in southeastern Utah on days 130–170 during the 2008 growing season. (a) Relationship between mean daytime sap flux density and daytime vapor pressure deficit ($r^2 = 0.50$, $P < 0.0001$). (b) Relationship between nighttime sap flux density and nighttime vapor pressure deficit ($r^2 = 0.30$, $P < 0.0001$). Error bars are ±standard error of the means.

Nocturnal J_s (J_{sn}) also varied between 2008 and 2009. In 2008, beetle defoliation initially resulted in a very large increase in mean daily J_{sn} of more than three fold above the predicted magnitude before declining sharply beginning on Day 182 (Fig. 5a). Consequently, J_{sn} was 116% higher than predicted for the month of June (Table 3). Unlike J_{sd}, however, J_{sn} remained below the predicted magnitude even after the trees produced new leaves, until about Day 280, when J_{sn} more or less returned to values predicted by the model (Fig. 5a). For the entire growing season, J_{sn} was on average 15% lower than expected rates from the model. In 2009, a modest spike in J_{sn} was visible as defoliation commenced (Fig. 5b), resulting in 29% higher than expected values in J_{sn} during June (Table 2). Similar to 2008, J_{sn} remained lower than predicted even after refoliation was complete until about Day 275. Defoliation resulted in about 24% lower rates in mean J_{sn} during the 2009 growing season (Table 3).

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Table 3
Measured and predicted daytime (J_{sd}) and nocturnal (J_{sn}) sap flux density ($g\,m^{-2}\,s^{-1}$) measured on 20 mature tamarisk trees during the 2008, and 2009 growing seasons in southeastern Utah. Numbers in parentheses are ±1 standard error of the means.

Month	J_{sd}	J_{sd} Predicted	% Difference	J_{sn}	J_{sn} Predicted	% Difference
2008						
May	33.0 (1.4)	39.5 (0.9)	−16.5***	4.7 (0.5)	6.4 (0.6)	−26.8*
June	47.1 (1.0)	41.6 (0.9)	13.1***	19.2 (2.1)	8.9 (0.7)	116.3***
July	18.3 (1.9)	43.3 (0.0)	−57.8***	8.9 (1.4)	13.5 (0.4)	−34.3*
August	29.3 (2.3)	41.4 (1.0)	−29.3***	6.2 (0.6)	10.9 (0.8)	−43.6***
September	41.3 (0.3)	41.8 (0.2)	−1.3	4.3 (0.4)	7.6 (0.3)	−43.5***
October	37.1 (1.6)	37.2 (0.8)	−0.3	6.4 (0.6)	5.2 (0.6)	23.6
Season	34.2 (0.9)	40.8 (0.3)	−16.1***	8.2 (0.6)	8.7 (0.3)	−5.5
2009						
May	38.5 (1.6)	40.2 (0.9)	−4.3	6.3 (0.8)	7.5 (0.6)	−16.3
June	45.3 (0.4)	41.7 (0.4)	8.6***	11.2 (0.5)	8.7 (0.5)	28.9*
July	35.7 (1.6)	43.2 (0.1)	−17.3***	9.2 (0.6)	12.0 (0.4)	−23.1**
August	16.9 (0.7)	43.3 (0.1)	−60.9***	3.3 (0.4)	12.3 (0.5)	−73.3***
September	37.1 (1.4)	40.8 (0.8)	−9.1*	5.7 (0.5)	9.1 (0.7)	−37.7**
October	35.5 (1.9)	35.0 (1.3)	1.5	5.9 (0.4)	5.1 (0.6)	15.9
Season	34.8 (0.9)	40.7 (0.4)	−14.6***	6.9 (0.3)	9.1 (0.3)	−24.2***

*$P < 0.05$, **$P < 0.001$, ***$P < 0.0001$.

Tamarisk trees produced about the same amount of leaf area in 2009 compared to 2008 (except for periods of defoliation). In 2008, stand LAI peaked at 1.86 in mid June, whereas stand LAI in 2009 peaked at 2.10 in early July, a period in which the trees were already undergoing significant defoliation in 2008 (data not shown).

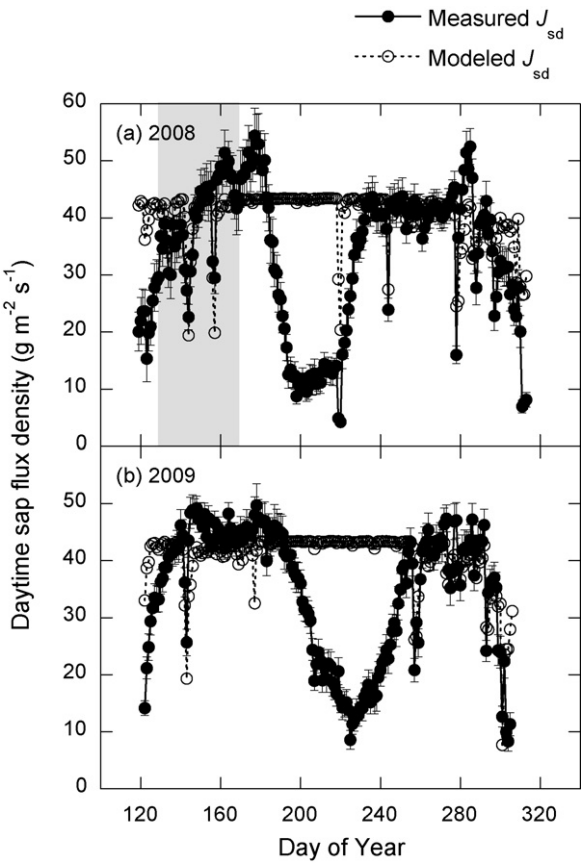

Fig. 4. Mean measured daytime sap flux density (closed circles) and modeled daytime sap flux density (open circles) of mature tamarisk trees ($n = 20$ trees) in southeastern Utah during the 2008 and 2009 growing seasons. Modeled sap flux density values were determined from the relationship between measured daytime sap flux density and daytime atmospheric vapor pressure deficit measured on days 130–170 in 2008 (gray bar). (a) Measured and modeled daytime sap flux density in 2008, and (b) measured and modeled daytime sap flux density in 2009. Error bars are ±standard error of the means.

3.4. Scaling from sap flux density to stand water use

We combined measurements of stem sap flux, conducting sapwood area (A_c) to stem diameter (D) relationships, and measurements of stand density to estimate seasonal water use of tamarisk trees during the 2008, and 2009 growing seasons. The relationship between A_c and D was highly significant ($R^2 = 0.95$, $P < 0.0001$, Fig. 6) and yielded the coefficients of 0.0858 for β_1 and 1.69 for β_2 respectively. The density of tamarisk A_c was 6.31 $m^2\,ha^{-1}$. Total

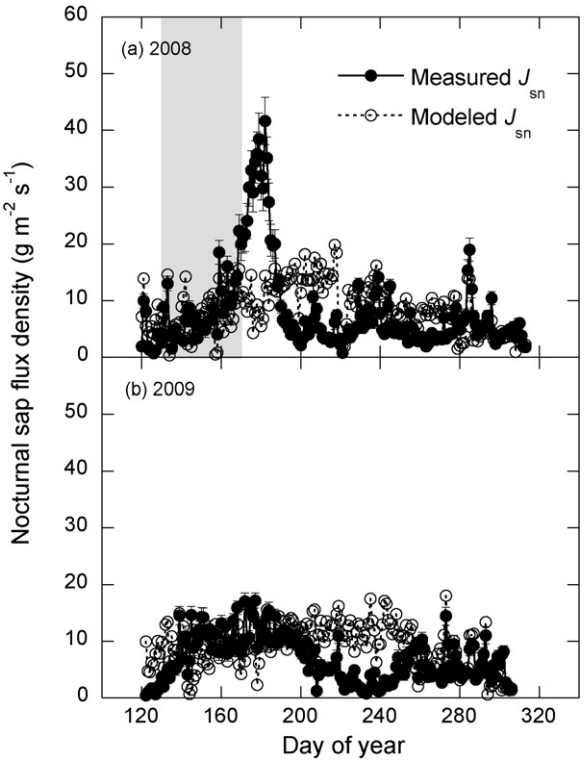

Fig. 5. Mean measured nocturnal sap flux density (closed circles) and modeled nocturnal sap flux density (open circles) of mature tamarisk trees ($n = 20$ trees) in southeastern Utah during the 2008 and 2009 growing seasons. Modeled sap flux density values were determined from the relationship between measured nocturnal sap flux density and nocturnal atmospheric vapor pressure deficit measured on days 130–170 (gray bar). (a) Measured and modeled nocturnal sap flux density in 2008, and (b) measured and modeled nocturnal sap flux density in 2009. Error bars are ±standard error of the means.

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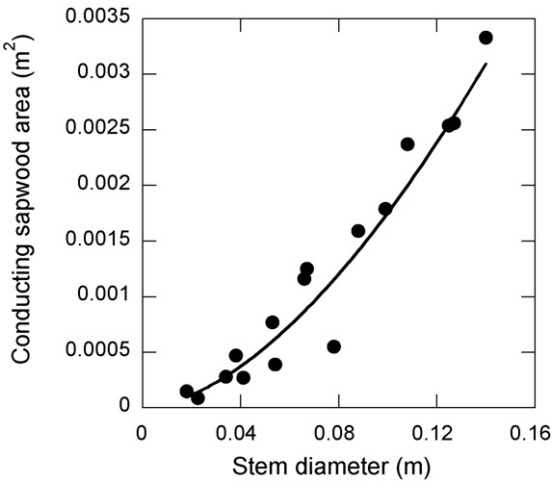

Fig. 6. the relationship between stem sapwood area and stem diameter of tamarisk trees ($R^2 = 0.95$, $P < 0.0001$, $n = 15$ trees) in southeastern Utah.

annual water use of the stand in 2008 was 0.224 m, of which 0.189 m occurred during the day and 0.035 m occurred at night (Fig. 7a). Total annual water use predicted by the model was 0.266 m (Fig. 7a), representing a savings of 0.042 m by defoliation. Total annual water use in 2009 was also 0.224 m, of which 0.194 m occurred during the day and 0.030 m occurred nocturnally (Fig. 7b). The sap flux model predicted that 0.268 m would have occurred without defoliation (Fig. 7b), representing a savings of 0.044 m of water.

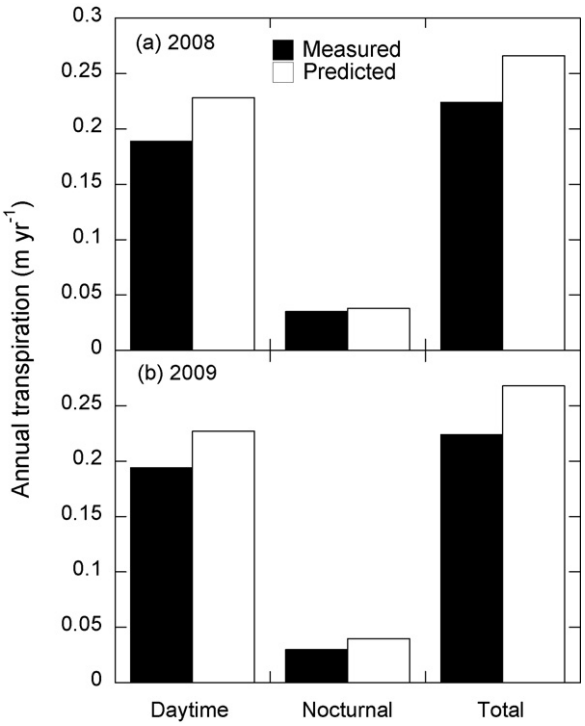

Fig. 7. The measured (closed bars) and predicted (open bars) annual amount of daytime, nocturnal and total transpiration from a mature tamarisk stand in southeastern Utah during the 2008 (a) and 2009 (b) growing seasons. Predicted values were determined from the relationship between sap flux density and atmospheric vapor pressure deficit during the spring of 2008, before the onset of tamarisk leaf defoliation by the saltcedar leaf beetle.

3.5. Error analysis of stand water scaled use from sap flux density measurements

Estimates of tree stand water use from measurements of stem sap flux requires several steps, all with the potential of adding significant error to the final scaled value. We suspect that by far, the largest source of error was with our model of J_s from *vpd*, and therefore focus on the error terms for coefficients β_1 and β_2 in Eq. (4) (Table 2). The error terms in the daytime model yielded an average error in J_{sd} of ±5% over the measured range of mean daytime *vpd* (data not shown). On the other hand, the error terms for the nocturnal model were much larger and yielded an average error of +275%, to −97% of J_{sn}, owing to the difficulty of measuring sap flux with heat-dissipation probes under conditions of relatively low flow rates (such as nighttime, or when *vpd* is near zero).

4. Discussion

The saltcedar beetle (*D. carinulata*) has now impacted tamarisk along more than 1000 river km in the upper Colorado River Basin (Hultine et al., 2009) and is expected to spread along many other river reaches throughout the upper basin, and possibly into the lower Colorado River Basin. Releases in Texas, California, Nevada and New Mexico have or may eventually have large impacts on tamarisk as well. Identifying the impacts of these release programs on tamarisk water use patterns and subsequent water cycling of arid riparian systems are largely unknown, due in part to the difficulty of measuring water fluxes in these systems.

Measurements of tamarisk water fluxes using lab-calibrated, modified heat-dissipation (Granier) sap flux sensors showed that defoliation by the saltcedar beetle resulted in about a 16% reduction in annual water use over two consecutive growing seasons. Decreases of annual tamarisk water use translated into an annual water savings of a little more than 0.04 m yr^{-1}. Whether these savings result in significant impacts on either riverine hydrology or riparian ecosystem processes remains unclear. Future impacts of the beetle on tamarisk water use may increase, particularly if defoliation results in widespread tamarisk mortality. Intensive long-term research will be required to identify the cascading impacts of the saltcedar leaf beetle on ecohydrology over large temporal and spatial scales.

The saltcedar leaf beetle may be expected to impact tamarisk water use in two ways. The first and most obvious is during the period of defoliation when the trees would otherwise have full canopies to transpire water to the atmosphere. The second is through a progressive decrease in stored carbohydrates (Hudgeons et al., 2007) resulting in reduced leaf production, and possibly reduced fine root productivity and maintenance following each defoliation event (Snyder and Williams, 2003). In the present study, tamarisk water use was clearly impacted during periods of defoliation (Figs. 3 and 4). However, we did not see a progressive decrease in leaf production or water use following each defoliation event. Likewise, beetle-induced mortality has been apparently absent at our field site (personal observation). These data and observations suggest that several weeks of defoliation over three consecutive growing seasons have failed to result in significant carbon starvation or subsequent carbohydrate limitations. If future defoliation events result in measurable reductions in leaf and root productivity and widespread mortality, stand water use rates will decrease substantially from those predicted by our sap flux model.

Large increases in J_s during the onset of defoliation, particularly nocturnal J_s in 2008, were clearly visible. These large increases were likely a function of how the beetles feed on the tamarisk leaves. They start by scraping away leaf waxes and the cuticle before attacking the mesophyll and the leaf vascular system as a whole

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(Dudley, 2005). The removal of the leaf surfaces results in large increases in leaf conductance and subsequent tissue water loss, particularly at night where leaf conductance is otherwise much lower than during the daytime. On the other hand, increases in J_s during the onset of defoliation was much more subtle in 2009. Defoliation occurred much more slowly in 2009 as there were fewer beetles that initially attacked tamarisk. This likely resulted in fewer leaves being foraged at any one time, and a much slower process of stand defoliation. By the time beetle densities increased later in the growing season, the canopies had already undergone significant damage and subsequent changes to stand water use were relatively small.

Comparison of interannual water use patterns by riparian plant species is often compromised by interannual variation in site meteorology and fluvial hydrology. We controlled for variation in meteorology by modeling water use patterns with atmospheric drivers *vpd* and *Q*. However, we were unable to control for seasonal variation in depth to groundwater, a potentially significant control over water use patterns by riparian tree species (Schaefer et al., 2000; Horton et al., 2001; Dahm et al., 2002; Hultine et al., 2010). In the present study, depth to groundwater was on average −2.32 m in 2008, and −2.53 m in 2009, a difference of about 0.2 m. Tamarisk spp. tend to thrive in locations where depth to groundwater is less than 6 m (Horton and Campbell, 1974). Moreover, fast root growth allows tamarisk to respond quickly to declining water tables (Horton and Clark, 2001; Lite and Stromberg, 2005; Stromberg et al., 2007). Given that tamarisk at our field site displayed similar interannual rates of water use in relation to *vpd* suggests that neither changes in depth to groundwater or repeated defoliation by the saltcedar leaf beetle had significant impacts on plant water relations or productivity during the investigation. Nevertheless, caution should be taken when comparing seasonal impacts of the saltcedar beetle on tamarisk where interannual fluctuations in depth to groundwater are relatively large (i.e., >0.5 m), or when stream or river reaches are compared that have large variations in groundwater depth.

Tamarisk defoliation by the saltcedar leaf beetle has now occurred over three consecutive growing seasons beginning in 2007. Our sap flux studies commenced prior to defoliation in 2008, meaning that the magnitude and pattern of tamarisk water use in 2007 was not characterized at our field site. While it is plausible that the initial defoliation event in 2007 resulted in lower rates of tamarisk water use compared to the 2008 and 2009 growing seasons, evidence suggests this is not likely. Mean annual sap flux rates measured at an adjacent location did not vary between the 2007, and 2008 growing season (data unpublished). Moreover, LAI during non-defoliation periods of the 2008 and 2009 growing seasons remained relatively constant. In fact, the highest stand LAI measured during the investigation occurred in July of 2009, suggesting that carbohydrate and starch reserves had not yet been depleted to the extent that decreased leaf production or significant stand dieback had developed.

Recent estimates suggest that evapotranspiration from tamarisk-dominated stands range from about 0.7 to 1.45 m yr^{-1} (Shafroth et al., 2005; Owens and Moore, 2007; Nagler et al., 2009; Stromberg et al., 2009), although rates as low as 0.3 m yr^{-1} have been reported (Nagler et al., 2005). Annual ET of tamarisk-dominated stands along the upper Colorado River and Dolores River was previously estimated at about 0.7 m yr^{-1} using remote sensing methods (Dennison et al., 2009). In the present study, ET modeled without defoliation was considerably lower: from 0.26 m yr^{-1} in 2008 to 0.27 m yr^{-1} in 2009. Differences between the two studies are likely due, in part to the fact that ET estimated from the Enhanced Vegetation Index (Huete et al., 2002) in the former study, was parameterized from Bowen Ratio and eddy covariance flux data collected in watersheds that are outside of the Colorado River Basin (Nagler et al., 2005). Moreover, flux tower measurements incorporate ET from all vegetation sources, bare soil, and open water. Flux tower measurements of ET are mostly un-obtainable in the upper Colorado River Basin because riparian vegetation is typically constrained to narrow strips along river reaches and streams. In the present study, ET was estimated from sap flux measurements using sensors that were calibrated specifically for tamarisk studies. Although some ET is likely derived from other vegetation along with bare soil and evaporation from the river, the major component of ET along most major river systems in the upper Colorado Basin is derived from tamarisk stands that currently dominate these riparian systems. Therefore, data from the present study should improve efforts to scale from tree stand to river reach using satellite observations.

Total annual water savings by the saltcedar leaf beetle amounted to about 0.04 m yr^{-1} in both 2008 and 2009. What impact that these water savings have on fluvial hydrology and stream discharge are unclear. Tamarisk defoliation along large, high-order stream systems will likely not result in significant alterations in hydrologic fluxes, even where widespread mortality results from multiple defoliation events. This is because the rate of stream discharge can be several orders of magnitude larger than ET fluxes from adjacent riparian vegetation. For example, ET from tamarisk stands along the lower Colorado River amounted to about one percent of the river's annual discharge (Nagler et al., 2009). Likewise, mechanical removal of tamarisk along the Pecos River in Texas resulted in no measurable changes in stream discharge (Hart et al., 2005). On the other hand, opposite patterns could emerge along lower-order streams that produce much smaller discharge rates relative to the vegetation cover in the associated riparian area. In many low-order stream systems in the upper Colorado Basin, tamarisk has not only displaced native vegetation along stream margins, but in many cases has spread to wider areas of the flood plain that were previously occupied by much lower densities of vegetation (Graf, 1978; Webb and Leake, 2006). The relatively deep root systems and greater resistance to xylem cavitation (Pockman and Sperry, 2000) provides the foundation that allows tamarisk to persist in habitats that are often unsuitable for cottonwood and willow species, particularly where surface flows are highly regulated. Therefore, several weeks of tamarisk defoliation along low-order upper basin tributaries could have measurable impacts on downstream discharge and groundwater recharge, even if direct impacts of the saltcedar leaf beetle along the Colorado River are negligible.

5. Conclusions

Stem sap flux measurements showed that defoliation by the saltcedar leaf beetle resulted in a savings of about 0.04 m yr^{-1} of annual tamarisk water use during the 2008 and 2009 growing seasons in southeastern Utah. It is currently unclear whether these savings are enough to impact hydrologic or riparian ecosystem processes of the upper Colorado River Basin. We expect that tamarisk defoliation will have little or no direct impact on river discharge along major watersheds, even if repeated defoliation events results in widespread mortality and/or large reductions in overall canopy cover. On the other hand, beetle-induced alterations of these processes may occur along riverine systems where the area of tamarisk canopy cover is large relative to stream discharge (i.e., low-order streams). Longer-term research should focus on potential impacts of tamarisk biocontrol on plant community structure (with an emphasis on secondary invasive species), canopy cover, and phenology, along with the cascading impacts on hydrologic and riparian (terrestrial and aquatic ecosystem) ecosystem processes. Future work should also consider the interactive impacts of tamarisk biocontrol and other global change forces on ecosystem services from valued riparian areas of the southwestern U.S.

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