Ecological Applications, 15(3), 2005, pp. 1009–1018

ECOHYDROLOGY IN A COLORADO RIVER RIPARIAN FOREST: IMPLICATIONS FOR THE DECLINE OF *POPULUS FREMONTII*

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Abstract. *Populus fremontii* (Fremont cottonwood) was once a dominant species in desert riparian forests but has been increasingly replaced by the exotic invasive *Tamarix ramosissima* (saltcedar). Interspecific competition, reduced flooding frequency, and increased salinity have been implicated in the widespread decline of *P. fremontii*. To elucidate some of the multiple and interacting mechanisms of this decline, we examined ecological processes in a control stand of *P. fremontii* along the Colorado River in Utah, USA, as well as a disturbed stand characterized by high groundwater salinity and invasion of *T. ramosissima*. Sap flux data showed that *P. fremontii* at the saline site experienced large reductions in afternoon canopy stomatal conductance relative to the control. Thus, average daily stand transpiration was 4.8 ± 0.1 mm/d at the saline site in comparison to 9.3 ± 0.2 mm/d at the control site over a two-month period. Light-saturated photosynthesis and apparent quantum yield were also reduced in saline *P. fremontii*. Stable isotope analysis indicated that trees at the saline site utilized evaporatively enriched groundwater that was likely derived from a nearby pond of irrigation runoff; this was also the probable source of high salinity. Interspecific competition for water at the saline site is unlikely, as *T. ramosissima* is still a minor species that is present only in the understory. However, reduced tissue N content in *P. fremontii* at the saline site suggested that physiological stress during salinity and halophyte invasion may be exacerbated by altered N relations.

Key words: Colorado River (USA); ecohydrology; gas exchange; invasive species; Populus fremontii; *riparian; salinity; sap flow; stable isotopes;* Tamarix ramosissima; *transpiration.*

Introduction

Riparian ecosystems provide essential habitat for a variety of species in the desert southwest of the United States. In these areas, *Populus fremontii* S. Wats. (Fremont cottonwood) is a common riparian species that becomes established following flooding and depositional events in alluvial plains (Braatne et al. 1996). Human-caused alterations in hydrology, grazing, and invasive species have had a large impact on riparian areas once dominated by *P. fremontii* and its co-occurring species. Stands of *P. fremontii* have been reduced to a small fraction of their former extent, having been replaced by secondary successional species, upland species, and exotic invasives (Braatne et al. 1996, Stromberg 2001). A number of mechanisms have been ascribed to the decline of *P. fremontii*, including drought stress (Horton et al. 2001*c*), salinity stress (Shafroth et al. 1995, Glenn et al. 1998), and interspecific competition (Di Tomaso 1998).

Management and restoration of riparian ecosystems requires an understanding of the importance of potential mechanisms of ecosystem degradation and shifts in community structure. Damming and flood control of rivers in the western United States have been linked to water table decline and subsequent drought stress of *P. fremontii* (Stromberg et al. 1996, Horton et al. 2001*a*). *Populus fremontii* is a phreatophyte that is highly vulnerable to cavitation, experiencing almost complete embolism when water potentials drop below −2 MPa (Leffler et al. 2000, Pockman and Sperry 2000). *Populus fremontii* is also intolerant of high salinity, showing reductions in transpiration and relative growth rate of seedlings when salt concentrations exceed 2000 mg/L (Glenn et al. 1998, Vandersande et al. 2001). This contrasts with the exotic invasive *Tamarix ramosissima* Ledeb., a Eurasian native that has replaced *P. fremontii* in many areas of the Southwest. *Tamarix ramosissima* is a facultative phreatophyte that has shown greater tolerance of water table decline and drought stress than *P. fremontii*. As a halophyte, *T. ramosissima* can excrete salts from its leaves that become deposited onto the soil surface following leaf abscission, salinizing the upper soil layers (Di Tomaso 1998).

Several studies of differential seedling recruitment, survival, and stress physiology have been conducted in *P. fremontii* and *Tamarix* spp., with important implications for regeneration and population dynamics in

Manuscript received 19 August 2004; accepted 24 September 2004. Corresponding Editor: J. Belnap.
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PLATE 1. Mortality of *Populus fremontii* at the Scott M. Matheson Preserve in Moab, Utah, USA. Seedlings of the exotic invasive species *Tamarix ramosissima* are visible in the foreground. Photo credit: D. Pataki.

riparian corridors (Stromberg 1997, Glenn et al. 1998, Vandersande et al. 2001). Comparative studies of leaf-level physiology and gas exchange in both seedlings and mature individuals have shown that *P. fremontii* is more sensitive to temporal and spatial fluctuations in water table depth and groundwater salinity than *Tamarix* spp., which can maintain higher rates of gas exchange at low leaf water potential and high vapor pressure deficit (Busch and Smith 1995, Glenn et al. 1998, Horton et al. 2001*a*, *b*, Vandersande et al. 2001). There have been fewer studies of whole ecosystem function in mature invaded and uninvaded stands of *P. fremontii*. Previous studies of ecosystem water balance have shown that stands of *T. ramosissima* may have higher rates of evapotranspiration than native stands, in part because of high leaf to sapwood area ratios (Sala et al. 1996, Smith et al. 1998).

In this study, we examined water relations and gas exchange at both leaf and ecosystem scales in two stands of *P. fremontii* along the Colorado River in Moab, Utah, USA. One stand contained an understory of *T. ramosissima* and was characterized by groundwater total dissolved solids (TDS) exceeding 5000 mg/L near the top of the water table and 2000 mg/L at depth. The second stand was a control without invasion and with groundwater TDS of <500 mg/L. We addressed the question: how is riparian ecosystem function perturbed by salinity and halophyte invasion in stands of *Populus fremontii*?

MATERIALS AND METHODS

Study sites.—Two stands of *P. fremontii* were chosen in the Scott M. Matheson Wetlands Preserve in Moab, Utah, USA, located along the Colorado River at 38.6° N, 109.5° W, 1230 m elevation. Mean annual temperature in this area is 13.8°C, with ~220 mm of annual precipitation (Brough et al. 1987). The sites were chosen according to site history and initial measurements of groundwater depth and salinity.

The saline site was characterized by groundwater TDS ranging from 5120 mg/L at 1.5 m below the water table surface to 2150 mg/L at 12 m in June of 2002, just prior to the initiation of ecological measurements. The depth to water table at this time was 0.3 m at the control site and 0.9 m at the saline site. The saline site contained a dense understory of 1–2 m tall individuals of *T. ramosissima*, and was located near an area of substantial mortality of *P. fremontii* that occurred in the mid- to late 1990s (see Plate 1). The individuals in this area were likely established in the floods of 1983–1984 that occurred along the Colorado River (Rood et al. 1996). A control site was chosen that was considered

TABLE 1. Stand characteristics of the control and saline sites during the growing season.

Stand characteristics	Control	Saline site
Groundwater TDS (mg/L)	280–430	2150–5120
Depth to groundwater (m)	0.1–2.4	0.7–2.7
Stand leaf area index (m^2/m^2)	4.8	3.3
Cross-sectional area at 1.4 m height *P. fremontii* (m^2/ha)	66.7	34.7
Leaf : sapwood area at 1.4 m *P. fremontii* (m^2/cm^2)	0.16	0.13
Mean diameter at 1.4 m *P. fremontii* (cm^2)	19.8 ± 1.4	15.9 ± 1.3**
Mean depth to heartwood at 1.4 m *P. fremontii* (cm)	3.2 ± 0.3	3.8 ± 0.4*
Specific leaf area *P. fremontii* (cm^2/g)	119.6 ± 5.7	105.7 ± 2.7*

Notes: TDS refers to total dissolved solids. Mean sampled values are given ± SE. An asterisk indicates that control and saline values are different at $\alpha = 0.01$ by t test; two asterisks indicate significance at $\alpha = 0.05$.

relatively undisturbed: groundwater TDS was <500 mg/L at all measured depths (3, 6, and 12 m). In addition, the control site was not invaded by *T. ramosissima*, although it did contain isolated understory saplings of *Salix nigra* Marsh. (black willow) and *Elaeagnus angustifolia* L. (Russian olive).

Groundwater measurements.—Groundwater was monitored by installing stainless steel drive point piezometers that were accessed with 1.3-cm ID poly tubing. Water levels were measured using an electric tape and water samples were collected using a peristaltic pump. Four piezometers were installed at varying depths at each site to obtain groundwater samples at 1.5, 6, 9, and 12 m. Specific conductivity (SpC) was measured with the Hydrolab Minisonde 4a probe (Hydrolab-Hach, Loveland, Colorado, USA) on sample water after each piezometer was purged of a minimum of three casing volumes of water. Values of TDS were then derived according to the following site-specific relationship (Gardner and Solomon 2003):

$$\mathrm{TDS(mg/L)} = \mathrm{SpC}(\mu\mathrm{S/cm}) \times 0.7308. \quad (1)$$

Sap-flow and gas-exchange measurements.—In July 2002, 12 m diameter plots were established at each site, within which 18 individuals of *P. fremontii* were instrumented with 20 mm long constant heat sap flow gauges according to the design of Granier (1987). Sensors were installed at ~1.4 m above the ground and were supplied with 200 mW of power per tree. Millivolt differences were recorded on a Campbell 23× datalogger instrumented with an AM 16/32 multiplexer (Campbell Scientific, Logan, UT, USA) logging every 30 s and averaging every 30 min. These data were used to estimate sap flux (J_S, $g \cdot m^{-2} \cdot s^{-1}$) as described by Granier (1987). Temperature and relative humidity were also logged at each site at the same frequency with a sensor installed within the canopy at approximately one-half canopy height (Vaisala HMP 45 C, Campbell Scientific, Logan, Utah, USA), representing the area of maximum leaf area. Sap flux and environmental data were recorded from 17 July–21 September 2002. Sap flux-measured trees were cored with an increment borer at sensor height at the conclusion of the study to visually estimate the depth to heartwood and calculate total cross-sectional sapwood area. Depth to sapwood did not exceed 4 cm on average at either site (Table 1).

Diurnal measurements of leaf gas exchange were made at the saline site on 1 September 2002 to compare transpiration of *P. fremontii* and *T. ramosissima*, as stems of *T. ramosissima* individuals were too small to estimate sap flux with constant heat gauges. Measurements were made with the LI 6400 portable photosynthesis system (LI-COR, Lincoln, Nebraska, USA) equipped with a CO_2 injector system and a red/blue LED light source. Environmental conditions in the cuvette were prescribed to approximate ambient temperature, relative humidity, and light conditions at the time of measurement. Measurements were conducted in the lower canopy on five individuals of each species.

Midday light response curves were obtained at both sites on 7–8 September 2002, with photosynthetically active radiation (I) varied from 1500 to 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at eight intervals with 200–300 s between intervals. Lower canopy leaves of two individuals were measured on each species at each site for a total of six light response curves. Light response curves were fitted with the following model:

$$A + R_d = \frac{\phi I + A_{max} - \sqrt{(\phi I + A_{max})^2 - 4\Theta\phi I A_{max}}}{2\Theta} \quad (2)$$

where ϕ is apparent quantum yield, R_d is dark respiration, A_{max} is the maximum, light-saturated rate of assimilation, I is photosynthetically active radiation, and Θ is a curvature parameter (Leverenz 1987). Apparent quantum yield was derived from the slope of the linear, light-limited portion of the light response curve above the compensation point by ordinary least-squares regression. A_{max} and Θ were derived by fitting the data to Eq. 2 with a nonlinear, Gaussian procedure (PROC NLIN, SAS Institute 1989).

Midday intercellular to ambient CO_2 concentration ratios (c_i/c_a) at $I = 1200$ $\mu mol \cdot m^{-2} \cdot s^{-1}$ were estimated from gas-exchange measurements on five individuals each of control and saline *P. fremontii* on 8 September. These measurements were conducted under environmental conditions close to ambient with vapor pressure deficit of 2 kPa and air temperature of 25°C.

To express gas-exchange rates of *T. ramosissima* on a leaf area basis, shoots were harvested following gas-exchange measurements to estimate one-sided, projected shoot area (LI 3100 area meter, LI-COR, Lincoln, Nebraska, USA).

Stable isotope measurements.—Three shade leaf samples were collected from the lower canopy of all sap-flow monitored individuals of *P. fremontii* and 10 individuals of *T. ramosissima* at the saline site. At the control site, three leaf samples were collected from 16 of 18 sap-flow monitored individuals due to canopy inaccessibility of the other two trees. Leaf samples were collected on 5 August 2002, and dried at 70°C for at least 48 hours.

Dried leaf samples were placed in liquid nitrogen and ground to number 40 mesh with a mortar and pestle while still frozen. The three leaves of each individual tree were combined and homogenized into one sample during grinding. A 2-mg subsample of ground leaves was loaded into tin cups and flash-combusted in an elemental analyzer coupled to an isotope ratio mass spectrometer (IRMS) for $\delta^{13}C$ and $\delta^{15}N$ determination (delta S, Finnigan MAT, San Jose, California, USA). The analytical precision of these measurements was 0.03‰ for $\delta^{13}C$ and 0.09‰ for $\delta^{15}N$.

Small stems were removed from the lower canopy of 10 individuals of each species at each site on a weekly basis from 5 August to 14 September 2002. Stems were placed into vacutainers, sealed with parafilm, and placed into a cooler containing dry ice immediately after collection. Samples remained frozen until water was extracted by cryogenic vacuum distillation and measured for oxygen isotope ratio on an IRMS by the CO_2-equilibration method (Fessenden et al. 2002). Water was also extracted and measured from 10-mL soil samples collected by coring at 30-cm increments from the soil surface to the saturated zone, which occurred at 2.5–3 m depth at both sites by late summer. A subset of water samples were measured for hydrogen isotope ratio (δD) by reduction of H_2O to H_2 with a Zn catalyst at 500°C followed by IRMS analysis. Measurement precision was ±1‰ for δD and ±0.2‰ for $\delta^{18}O$.

Isotope ratios were expressed with the conventional δ notation:

$$\delta = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right) \times 1000 \qquad (3)$$

where R is the absolute ratio of the heavy to the light isotope. $\delta^{13}C$, $\delta^{18}O$ and δD, and $\delta^{15}N$ were referenced to the V-PDB, V-SMOW, and atmospheric air standard, respectively.

Estimating canopy leaf area.—To determine stand leaf area, eight 0.3-m² litter traps were distributed under the canopy within each experimental plot. From September–December, abscised leaves were collected while still moist, identified, and sorted by species. The projected area of a subsample of each species was measured with a leaf area meter (LI 3100, LI-COR, Lincoln, Nebraska, USA). These sample leaves were dried for at least 48 hours at 70°C, and weighed to obtain the specific leaf area (SLA, cm²/g). The remainder of collected leaves was also dried and weighed. The leaf area of each species (A_{li}) was then obtained by multiplying SLA by the total dry mass for that species.

Results

Leaf area and stand characteristics.—Basal area of *P. fremontii* was twice as large at the control site as at the saline site; however, leaf area index (LAI) and leaf : sapwood area ratios were only 50% and 23% larger, respectively (Table 1). The discrepancy can be explained by differences in sapwood area; despite the fact that *P. fremontii* individuals at the saline site were smaller (t test, $P < 0.05$, Table 1), tree core data indicated that these trees produced equal or marginally significantly more sapwood than at the control (heteroscadastic t test, $P < 0.01$, Table 1). Leaf area index estimated by litterfall was 4.8 m²/m at the control site and 3.3 m²/m at the saline site.

Sap flow and canopy-scale transpiration.—Sap flux density (J_S) of *P. fremontii* expressed on a sapwood-area basis was greatly reduced at the saline site relative to the control (Fig. 1). Averaged over the study period, daily J_S was 38% lower at the saline site. Site-to-site differences in J_S were not explained by the vapor pressure deficit (D), which was similar at both sites (Fig. 1). Sap flux density was scaled to canopy transpiration of *P. fremontii* at each site according to Pataki et al. (2000). The resulting values of E_C were 9.3 ± 0.2 mm/d on average at the control site, vs. 4.8 ± 0.1 mm/d at the saline site, a reduction of 50%. Differences between the saline and control site were greater for E_C than J_S due to lower plot-scale sapwood area to ground area ratio at the saline site. Daily transpiration at both sites responded strongly to D for the duration of the study (Fig. 2).

Half-hourly sap flux data were separated into morning (07:00–12:00) and afternoon (12:30–19:00) periods, averaged, and related to average D during the same period. The slope of the increase in sap flux of *P. fremontii* with D was greater in the morning than in the afternoon at both sites (Fig. 3). In the afternoon, sap flux at the two sites diverged more strongly than in the morning, indicating greater stomatal closure at the saline site in the afternoon. This was quantified by fitting a polynomial equation to each relationship and subtracting morning from afternoon fitted values at each site. The difference between modeled morning and afternoon sap flux was much larger at the saline site than at the control (Fig. 3c).

Leaf-level gas exchange.—At the saline site, *P. fremontii* showed lower rates of assimilation (A), stomatal

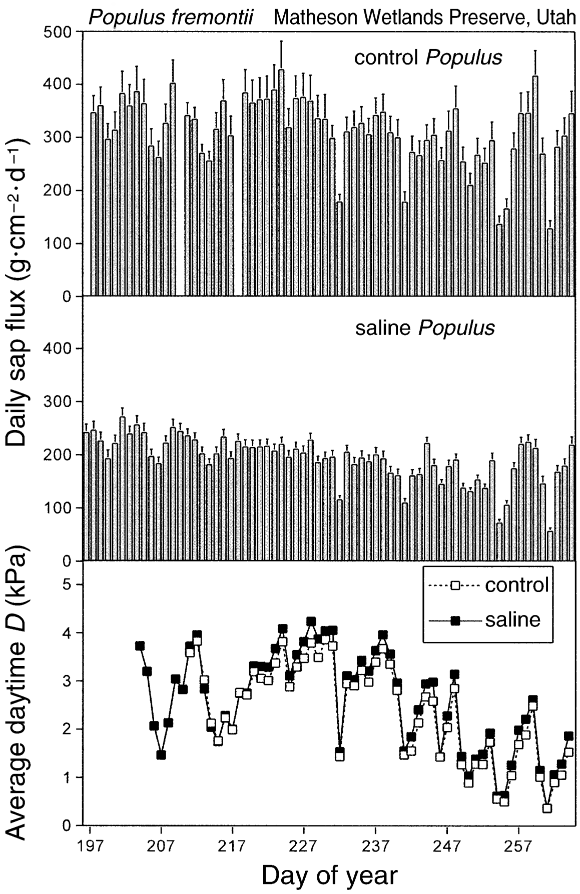

FIG. 1. The daily sum of sap flux and mean daytime vapor pressure deficit (D) for the control and saline sites during the length of the study period. Errors bars indicate the standard error.

conductance, and transpiration than *T. ramosissima* on a leaf area basis under ambient environmental conditions (Fig. 4). For both species, stomatal conductance was highest early in the morning, while assimilation and transpiration peaked in mid-morning. These measurements were conducted on shade leaves of both species. While we could not access sun leaves at the top of the canopy of *P. fremontii*, we compared the light response of shade leaves of both saline and control *P. fremontii* as well as *T. ramosissima.*

T. ramosissima and control *P. fremontii* showed similar A_{max} of 20.6 ± 1.9 and 24.1 ± 2.6 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Fig. 5, Table 2). In comparison, A_{max} of saline *P. fremontii* was greatly reduced, reaching only 9.8 ± 0.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$. In *T. ramosissima* and control *P. fremontii*, apparent quantum yield was close to the typical value for C_3 plants at 20°C of 0.05 mol/mol (Björkman and Ehleringer 1977). However, saline *P. fremontii* showed a reduced apparent quantum yield of 0.036 ± 0.002 mol/mol (Table 2).

Carbon, nitrogen, and oxygen stable isotopes.—The oxygen isotope ratio ($\delta^{18}O$) of stem water was used to evaluate differences in water sources between species and sites. $\delta^{18}O$ of groundwater varied at the two sites, with a value of −14.5‰ at the top of the water table at the control site and −12.0‰ at the saline site, indicating different sources of groundwater at the two sites. The relationship between oxygen and deuterium isotope ratios of meteoric water (derived from precipitation) may be used to further evaluate differences between groundwater samples. In this study, the stable isotope composition of many groundwater samples fell on the global meteoric water line (Fig. 6), which has a slope of 8 (Craig 1961). However some wells, including shallow groundwater at the saline site, were isotopically enriched and showed a relationship between oxygen and hydrogen stable isotope ratios with a shallow slope of 4.9. Soil water collected at 30-cm intervals in the unsaturated zone showed even greater deviation from the meteoric water line with a slope of 3.9 (Fig. 6), indicative of evaporation in the shallow soil as is common (Allison et al. 1983).

At the control site, $\delta^{18}O$ of stem water of *P. fremontii* was similar to groundwater (Fig. 7a). However, $\delta^{18}O$ of stem water at the saline site in both *P. fremontii* and *T. ramosissima* was more similar to evaporatively enriched soil water measured ~1.5 m above the top of the water table than to $\delta^{18}O$ of groundwater in the saturated zone (Fig. 7b). Therefore, *P. fremontii* and *T. ramosissima* at the saline site likely shared the same water source in the unsaturated zone, or in an isotopically enriched zone within or near the water table that was not measured.

The carbon isotope composition ($\delta^{13}C$) of leaves was similar for *T. ramosissima* and *P. fremontii* at both sites (ANOVA, $P > 0.5$, Fig. 8). In contrast, the nitrogen

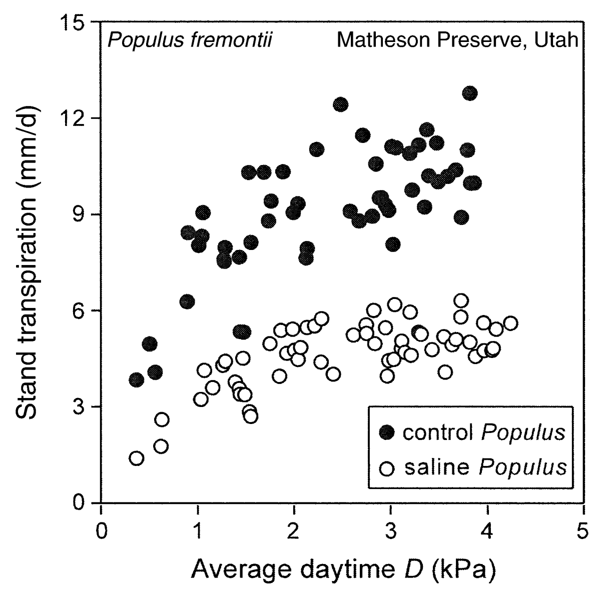

FIG. 2. Daily stand transpiration of canopy trees estimated from sap flux at the control and saline sites in relation to mean daytime vapor pressure deficit (D).

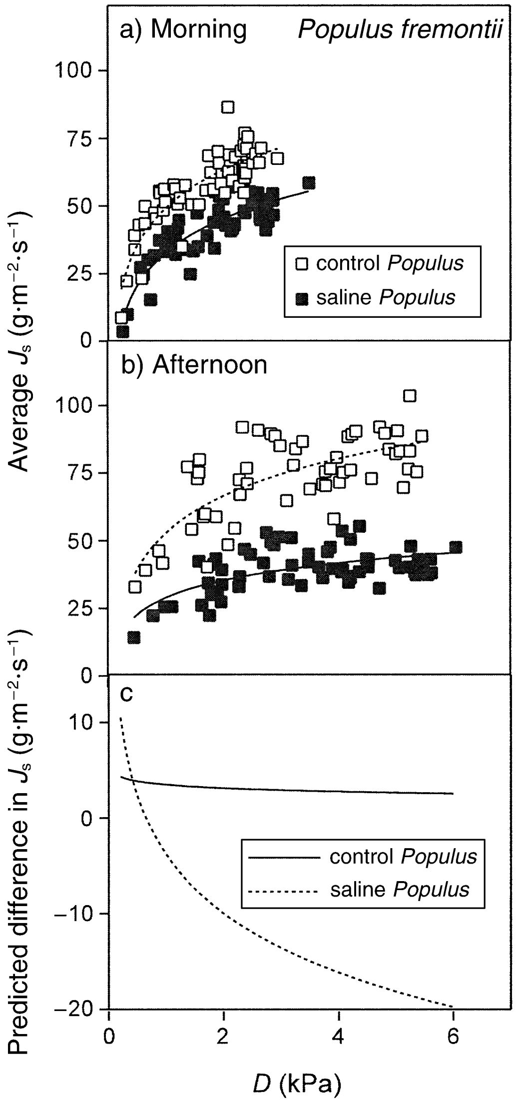

FIG. 3. (a, b) Morning and afternoon average sap flux (J_S) for control and saline trees in relation to average vapor pressure deficit (D) during the same period. The line shows a second-order polynomial fit of the data. (c) Predicted morning minus afternoon J_S for the control and saline site using the polynomial fits shown above.

isotope composition ($\delta^{15}N$) was distinct for *T. ramosissima*, *P. fremontii* at the control site, and *P. fremontii* at the saline site (ANOVA with least squares difference post hoc test, $P < 0.05$, Fig. 8). $\delta^{15}N$ of *P. fremontii* was more enriched at the saline site than at the control, and was most enriched in *T. ramosissima* at the saline site. The nitrogen content of leaves was similar in control *P. fremontii* and saline *T. ramosissima*, but was reduced in saline *P. fremontii* (ANOVA with least-squares difference post hoc test, $P < 0.05$, Fig. 8).

DISCUSSION

Sap flux rates of control *P. fremontii* were similar to those reported by Schaeffer et al. (2000) and to a review of several species of *Populus* measured by a variety of sap flux techniques (Lambs and Muller 2002). E_C of control *P. fremontti* was similar to both sap flux-scaled transpiration and Bowen ratio-derived evapotranspiration of pure stands of *T. ramosissima* (Sala et al. 1996, Devitt et al. 1998). However, E_C of control *P. fremontii* was higher than canopy transpi-

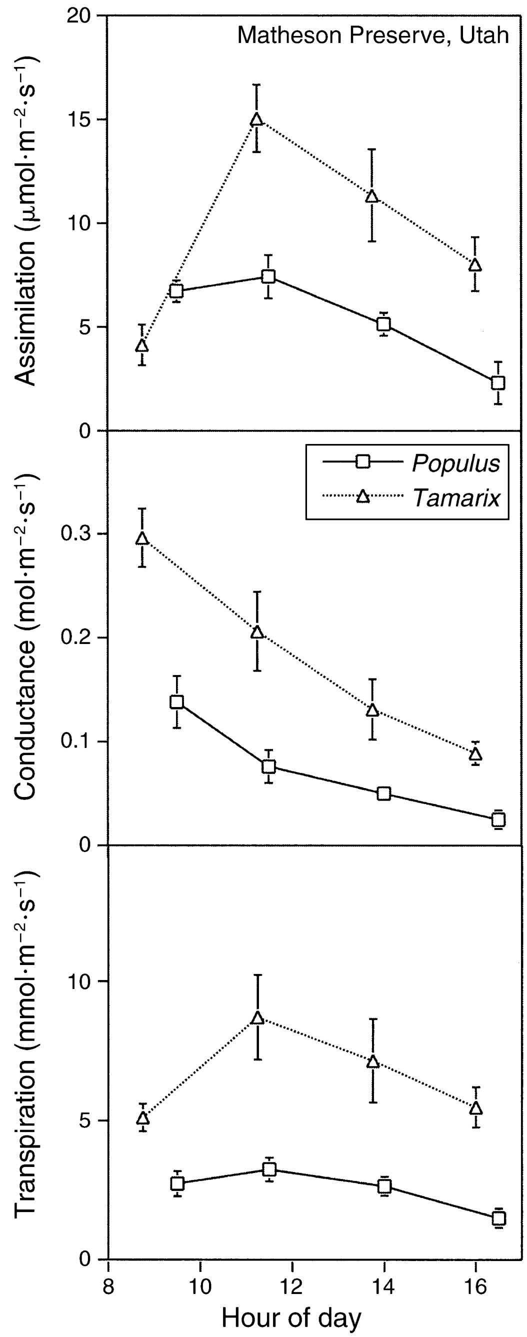

FIG. 4. Leaf-level net assimilation, stomatal conductance, and transpiration of *Populus fremontii* and *Tamarix ramosissima* for a diurnal period at the saline site. Error bars show ± SE.

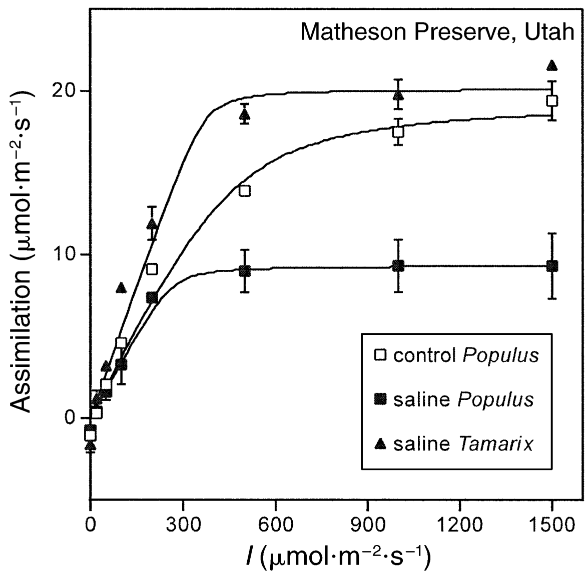

FIG. 5. The response of assimilation to photosynthetically active radiation (I) for *Populus fremontii* at the control and saline sites and for *Tamarix ramosissima* at the saline site, measured by leaf gas exchange. The lines show the modeled fit derived from Eq. 2 (see *Materials and Methods: Sap flow*).

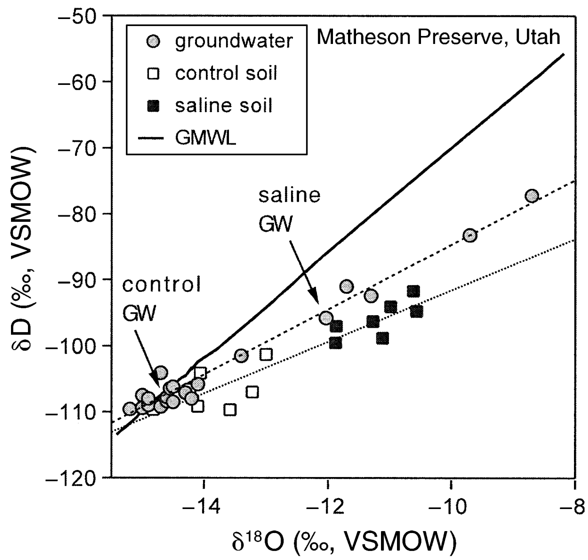

FIG. 6. The hydrogen isotope ratio (δD) plotted against the oxygen isotope ratio ($\delta^{18}O$) of waters collected at the Matheson Wetland Preserve (symbols, dashed lines), compared to the Global Meteoric Water Line (solid line). Groundwater (GW) values at the control and saline sites are indicated by arrows; the other groundwater samples were collected at additional wells located throughout the Matheson Preserve. Soil waters are plotted on one line and have a slope of 3.9; groundwaters have a slope of 4.9. VSMOW, Vienna Standard Mean Ocean Water.

ration of mixed cottonwood–willow stands along the San Pedro River in Arizona (Schaeffer et al. 2000). Much of this difference is likely due to higher LAI in the current study. In addition, radial trends in sap flux were not measured in the current study, which may have led to overestimation of E_C, as an assumption of uniform rather than declining sap flux with depth was applied. This would particularly affect the saline plot in which depth to heartwood was 3.8 cm on average, in comparison to the sensor length of 2 cm. Therefore, the difference between E_C in saline and control plots may be even greater than estimated. However, Lambs and Muller (2002) reported uniform rates of sap flux in the outer 4 cm of *Populus nigra* and *Populus* × *euramericana*.

Reduced rates of sap flux in the saline stand were largely attributable to afternoon stomatal closure, which was negligible in the control stand but pronounced in the saline stand (Fig. 3). We attribute this difference to salinity stress rather than direct effects of drought stress, i.e., declining water table depths, in the saline stand. Although *P. fremontii* appeared to be utilizing soil water rather than groundwater in the saline stand (Fig. 7), there was little evidence of soil moisture limitations at the saline site; there was <2 mm of precipitation in July and August, yet daily sap flux did not decline (Fig. 1) and was strongly correlated with D throughout the study (Fig. 2). In contrast, soil moisture limitation would cause declining transpiration over time and alter the relationship between sap flux and D, e.g., Pataki et al. (2000). In addition, total transpiration exceeded precipitation inputs in this ecosystem. During the 68 days of sap flux monitoring, 323 mm of water was transpired by the saline stand, in comparison to 191 mm of precipitation in all of 2002. Therefore, transpired water in this stand may be replenished by capillary action or lateral flow of groundwater; a capillary action mechanism is consistent with the fine particle size at 1.5 m depth at the saline site, which often prevented water collection from the well at this depth due

TABLE 2. Apparent quantum yield (ϕ), maximum light-saturated assimilation (A_{max}), and a curvature parameter (Θ).

Species and site	ϕ (mol/mol)	Θ	A_{max} (μmol·m^{-2}·s^{-1})
Control *Populus*	0.047 ± 0.002	0.90 ± 0.03	24.1 ± 2.6
Saline *Populus*	0.036 ± 0.002	0.98 ± 0.01	9.8 ± 0.5
Saline *Tamarix*	0.055 ± 0.014	0.99 ± 0.03	20.6 ± 1.9

Note: Parameters were determined by fitting least-squares linear regression and Eq. 2 to gas-exchange measurements.

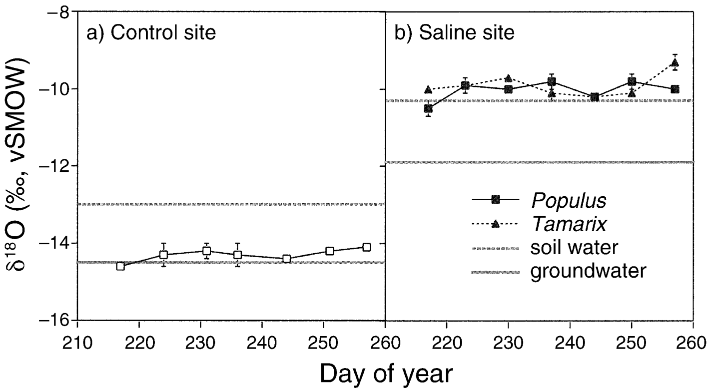

FIG. 7. The oxygen isotope ratio ($\delta^{18}O$) of stem waters (symbols), groundwater (solid gray line), and soil water (dashed gray line). Panel (a) shows the control site, and (b) shows the saline site. The soil water value is the most enriched measured in the soil profile, which occurred at 90 cm below the soil surface at the control site and 120 cm below the soil surface at the saline site. Groundwater was measured at the top of the water table, which occurred at ~240 cm at the control site and 270 cm at the saline site. Error bars indicate ± SE.

to slow recovery. Alternatively, there may have been some uptake of groundwater directly or via hydraulic redistribution that was not detectable from stable isotope measurements at the saline site.

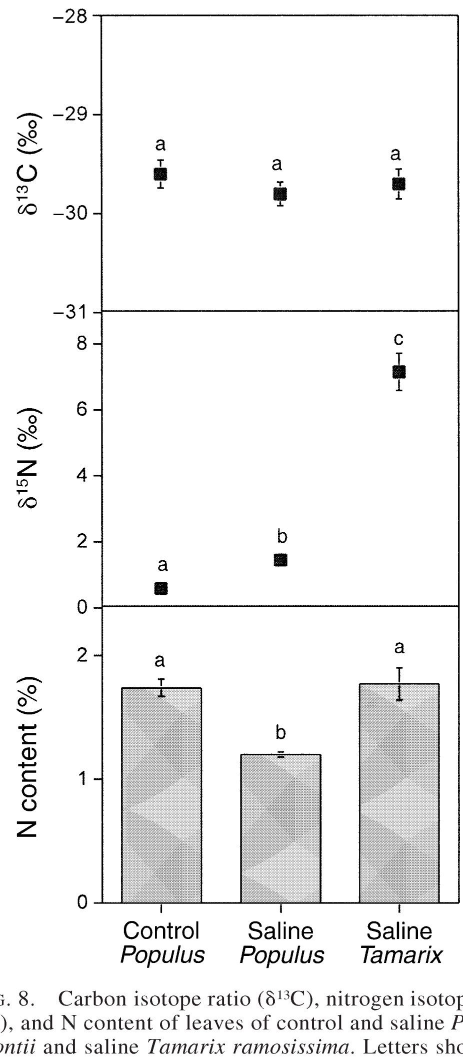

FIG. 8. Carbon isotope ratio ($\delta^{13}C$), nitrogen isotope ratio ($\delta^{15}N$), and N content of leaves of control and saline *Populus fremontii* and saline *Tamarix ramosissima*. Letters show significant differences by analysis of variance, least-squares difference post hoc test (α = 0.05). Error bars indicate ± SE.

Physiological effects of salinity are difficult to distinguish from drought stress, as both are associated with low soil water potential and subsequent stomatal closure and reductions in photosynthesis (Staples and Roenniessen 1984). In this study, afternoon stomatal closure in saline *P. fremontii* caused lower E_C in the saline stand as well as lower leaf area-based gas-exchange rates of saline *P. fremontii* relative to co-occuring, understory *T. ramosissima* (Fig. 4). Although this difference may be partially explained by lower gas exchange in mature *P. fremontii* vs. juvenile *T. ramosissima*, similar patterns have been reported from controlled environment studies on seedlings (Glenn et al. 1998, Vandersande et al. 2001) and from potted plants grown in field conditions (Nagler et al. 2003), indicating that gas exchange of halophytic *T. ramosissima* is generally not affected by moderate salinity. However, in the current study we wished to exclude the possibility that the differences observed were attributable only to differences between sun and shade leaves, as sun leaves of *P. fremontii* could not be accessed. Shade leaves of control *P. fremontii* showed much higher values of A_{max} and ϕ than shade leaves of saline *P. fremontii*; in fact, A_{max} and ϕ were similar for control *P. fremontii* and *T. ramosissma* (Fig. 5, Table 2). Sala et al. (1996) reported similar leaf-area based rates of gas exchange in the two species under non-saline conditions, which may lend support to the hypothesis that gas exchange of *T. ramosissima* was not adversely affected by salinity in the present study.

There were no differences in bulk leaf carbon isotopes between species or sites (Fig. 8). Differences between control and saline *P. fremontii* were expected based on previous studies (Busch and Smith 1995) and current gas-exchange measurements, which showed instantaneous values of c_i/c_a of 0.74 ± 0.01 for control trees and 0.64 ± 0.01 for saline trees under similar ambient conditions. In part, this discrepancy may be due to the fact that shade leaves were measured in this study, obscuring potential differences in $\delta^{13}C$ higher in the canopy. It is also possible that despite the instantaneous measurements, in the long-term reductions in stomatal conductance were offset by concurrent reductions in photosynthetic capacity, resulting in no change in c_i/c_a. However, we hypothesize that bulk leaf carbon, which is primarily fixed early in the growing season during leaf expansion, was not indicative of salinity stress that occurred later in the season. Early in the growing season, the high water table levels at the saline site associated with winter flooding of the nearby pond may have diluted salt concentrations and reduced salinity stress for *P. fremontii*. This is supported by the seasonal cycle of groundwater salinity at the saline site; in early March 2003, total suspended solids declined to 1620 mg/L from 2970 mg/L in September 2002 at 6 m depth.

The control and saline sites appeared to differ in nutrient as well as water relations. There were significant differences in leaf nitrogen isotopes among both species and sites. *Tamarix ramosissima* showed the most enriched values, while control *P. fremontii* was the most depleted (Fig. 8). In addition, leaf N content was similar between control *P. fremonttii* and *T. ramosissima*, but reduced in saline *P. fremontii* (Fig. 8). While species differences in foliar ^{15}N within the saline site may be due to a number of factors pertaining to species-specific N assimilation and translocation, greater overall ^{15}N enrichment at the saline site and low foliar N content in saline *P. fremontii* followed expected trends. High pH associated with salinity results in increased volatilization and gaseous losses of NH_3, enriching the remaining substrate in ^{15}N (van Groenigen and van Kessel 2002). In addition, ionic effects of high salinity interfere with uptake of both NH_4^+ and NO_3^- in nonhalophytes (Greenway and Munns 1980, Hawkins and Lewis 1993), potentially disrupting N relations of *P. fremontii*. Finally, salt-excreting *T. ramosissima* litter salinifies the upper soil layers where nitrogen is most available, putting *P. fremontii* at a competitive disadvantage for nutrient uptake. Further studies of soil biogeochemical cycling, plant available nitrogen, and soil microbial activity during invasion of *T. ramosissima* may further elucidate these potential effects.

Differences in groundwater salinity at the two sites are likely related to the differences in isotopic enrichment of groundwater. There are two potential mechanisms for isotopic enrichment of meteoric water: evaporative enrichment or water derived from precipitation at a lower elevation than mountain, winter precipitation recharge (Kendall and Coplen 2001). At the saline site, water from the north side of the Colorado River derived from low elevation precipitation recharge and an upstream pond of irrigation runoff that floods and evaporates annually are potential water sources (Gardner and Solomon 2003). During winter, the saline site experiences water table depths very near or at the soil surface due to flooding of the pond; previous measurements of tritium content indicate that the source of this water is not the regional groundwater discharge from the Glenn Canyon aquifer group, but rather irrigation runoff (Gardner and Solomon 2003). Subsequent annual flooding and associated anaerobic conditions may restrict the rooting depth of trees at the saline site, resulting in uptake of water at shallower depths than the control site (Fig. 7).

Differences in isotopic composition between groundwater and soil water have often been used to evaluate water sources of riparian trees (Busch et al. 1992, Snyder and Williams 2000, Horton et al. 2003). In this study, we used isotopic measurements to determine not only the source of transpiration, but also the sources of groundwater and the mechanisms underlying variability in groundwater salinity. In this ecosystem adjacent to a populated area, annual flooding and evaporation of irrigation runoff has resulted in high salinity in some areas of the Matheson Preserve, with adverse effects on leaf level gas exchange, stand transpiration, and growth of *P. fremontii*. This may be an important mechanism of disturbance in other riparian ecosystems affected by irrigation runoff and evaporation in semiarid regions. These results suggest that studies at the intersection of ecology and hydrology may reveal previously unknown causes and effects of riparian ecosystem disturbance that can be applied to conservation and management of the remaining stands of *P. fremontii*.

Acknowledgments

We thank A. Allred, C. Cook, M. Lott, W. Ike, and C.-F. Kitty for their assistance with data collection, S. Bellagama and D. Fagan for access to the Matheson Wetlands Preserve, and The Nature Conservancy for supporting this research. D. R. Bowling and K. Hultine provided helpful comments on an earlier version of this manuscript.

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