

Patterns of *Tamarix* water use during a record drought

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Abstract During a record drought (2006) in southwest Kansas, USA, we assessed groundwater dynamics in a shallow, unconfined aquifer, along with plant water sources and physiological responses of the invasive riparian shrub *Tamarix ramosissima*. In early May, diel water table fluctuations indicated evapotranspirative consumption of groundwater by vegetation. During the summer drought, the water table elevation dropped past the lowest position previously recorded. Concurrent with this drop, water table fluctuations abruptly diminished at all wells at which they had previously been observed despite increasing evapotranspirative demand. Following reductions in groundwater fluctuations, volumetric water content declined corresponding to the well-specific depths of the capillary fringe

in early May, suggesting a switch from primary dependence on groundwater to vadose-zone water. In at least one well, the fluctuations appear to re-intensify in August, suggesting increased groundwater uptake by *Tamarix* or other non-senesced species from a deeper water table later in the growing season. Our data suggest that *Tamarix* can rapidly shift water sources in response to declines in the water table. The use of multiple water sources by *Tamarix* minimized leaf-level water stress during drought periods. This study illustrates the importance of the previous hydrologic conditions experienced by site vegetation for controlling root establishment at depth and demonstrates the utility of data from high-frequency hydrologic monitoring in the interpretation of plant water sources using isotopic methods.

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Introduction

Future climate projections of more variable precipitation and intense drought during the growing season (Easterling et al. 2000; IPCC 2001; Alley et al. 2007) point to the strong possibility of reduced freshwater availability for human consumption and ecosystem functioning, particularly during summer periods of high demand (Karl and Trenberth 2003; Pimentel et al. 2004; Jenerette and Larsen 2006; Barnett et al. 2008). Climate warming and an intensification of the global water cycle (i.e. more extreme events) are expected to reduce subsurface water availability (Labat et al. 2004; Huntington 2006; Oki and Kanae 2006) and result in increased water stress for plants, a condition that has broad implications for both the structure and

function of natural and agricultural ecosystems (Jasper et al. 2006).

In semiarid riparian ecosystems with shallow water tables, the effects of climate warming are expected to be pronounced as these areas have not historically experienced long periods of water limitation (Jasper et al. 2006). In western Kansas and other semiarid regions of the western United States, river discharges have been reduced as a result of warming trends, human alteration/regulation of river systems, and increased use of groundwater (VanLooy and Martin 2005; Barnett et al. 2008). This reduction has been accompanied by increases in riparian vegetation cover and often, a decline in the water table (Shafroth et al. 2002; VanLooy and Martin 2005), and has significant ramifications for the ecohydrology of riparian zones.

Increased concerns regarding the future of riparian ecosystems have focused attention on the water-use dynamics of invasive species and the impacts on the biodiversity and hydrologic budgets of riparian zones (Chapin et al. 2000; Crall et al. 2006; Stromberg et al. 2007). The invasive large shrub *Tamarix* inhabits 400,000–600,000 ha of riparian habitat throughout the western USA (Zavaleta 2000; Friedman et al. 2005; Shafroth et al. 2005). *Tamarix* alters ecosystem structure and function through the accumulation of surface salts, changes in fire frequency and intensity, and reductions in species diversity and wildlife habitat (Di Tomaso 1998; Chapin et al. 2000; Glenn and Nagler 2005; Shafroth et al. 2005). Like native riparian trees, *Tamarix* can transpire large quantities of water (Sala et al. 1996; Cleverly et al. 1997; Nagler et al. 2005). However, unlike many co-occurring native phreatophytes, constant physiological functioning has been reported for *Tamarix*, even during periods of water stress (Cleverly et al. 1997; Devitt et al. 1997; Gries et al. 2003; Pataki et al. 2005; Xu et al. 2007). Many native riparian trees and shrubs have a lower tolerance for water stress (Pockman and Sperry 2000; Horton et al. 2001), and therefore the ability of *Tamarix* to maintain constant gas exchange and growth through periods of greatly reduced water availability may contribute to the proliferation of these species in the western United States. Assessing the sensitivity of physiological responses to changes in water-resource availability is critical for predicting the population and community responses to changing environments and for determining the trajectory of vegetation change under altered climatic conditions (Dukes and Mooney 1999; Davis et al. 2005; Newman et al. 2006).

In the investigation described here, we assessed the responses of *Tamarix ramosissima* Ledeb. (hereafter, *Tamarix*) to declining water availability in the 2006 growing season (April–September) at a site in southwest Kansas, USA. Our assessment was based on both hydrologic and plant physiological measurements. We used diel

water table fluctuations, changes in volumetric water content above the water table, and the stable oxygen isotopic signature ($\delta^{18}\text{O}$) of *Tamarix* xylem water and water sources as indicators of plant dependence on multiple water sources. We assessed the impacts of drought on *Tamarix* physiology using standard plant physiological measurements. The goals of this research were to determine if and when *Tamarix* shifted water sources during drought and if a decline in water availability impacted leaf-level physiological processes. Due to the severity of the 2006 drought at the studied location, this event provided a rare opportunity to glean insights into *Tamarix* responses to the water limitations that are projected to become increasingly common in semiarid riparian zones in a potentially hotter and drier future.

Materials and methods

Field site and environmental monitoring

This research was conducted at a Kansas Geological Survey and Kansas State University research site located in riparian habitat adjacent to the Cimarron River 17 km south of Ashland, Kansas, USA (37°11'19"N, 99°45'55"W). The site overlies a shallow unconfined aquifer that is hydraulically connected to the river. The near-surface sediments consist primarily of coarse silts through medium sands. *Tamarix*, which first appeared at the site in 1939 following a flood (communicated by D. Arnold), is the predominant species in the riparian zone. Herbaceous species [primarily *Sporobolus airoides* (Torr.) Torr., *Panicum virgatum* L., and *Schizachyrium scoparium* (Michx.) Nash] are distributed among the *Tamarix*. In this paper, we report on work at two experimental plots (plots 1 and 3, each 7.5 ha) within the research site. Each plot has two well sites that are designated numerically (1.1, 1.2, 3.1, 3.2 for plots 1 and 3, respectively). In plot 3, all *Tamarix* was cut at ground level in 2005, and significant aboveground regrowth (1–1.5 m in height compared to 2–3 m in height for uncut *Tamarix* in plot 1) had occurred by August 2006. At each site, *Tamarix* individuals occur in close proximity (~ 1 –2 m) to each well. Further details on conditions at the site and the experimental layout have been previously described (Butler et al. 2005, 2008).

The wells in the experimental plots were installed in August 2004. Each well is 6.45 m in depth (top of screen 1 m below land surface) and equipped with an integrated pressure transducer/datalogger unit (in situ MiniTroll, 206.8 kPa) that records pressure-head readings (absolute pressure) every 15 min. Pressure-head readings are corrected for atmospheric pressure, which is measured on

site at the same frequency. Water table position is calculated using the corrected pressure-head measurement and the known sensor elevation. A neutron-probe access tube was installed adjacent to each well in August 2004 and volumetric water content is measured biweekly during the growing season using a model 503 DR Hydromprobe moisture depth gauge (Campbell Pacific Nuclear). Readings are taken every 15 cm to a depth of 3 m, and standard counts are recorded in the field prior to and after measurements. Volumetric water content ($\text{m}^3 \text{m}^{-3}$) is calculated with an equation based on laboratory calibrations and an adjustment for PVC pipe (Butler et al. 2005).

A weather station (Hobo weather station logger and sensors; Onset Computer) was installed in plot 3 in October 2004. Measurements of air temperature, precipitation, relative humidity, global irradiance, wind speed and direction, and atmospheric pressure are logged at 15-min intervals (Butler et al. 2005). In addition, daily maximum and minimum air temperatures and total daily precipitation are recorded at the city of Ashland, 17 km north of the site. A continuous record of daily measurements at Ashland extends from the year 1900 to the present.

Plant physiology

Five *Tamarix* individuals in the vicinity (within 5 m) of each well were randomly selected and repeatedly sampled over the summer. We measured the light-saturated photosynthetic rate (A_{sat}), stomatal conductance to water (g_s), and leaf transpiration (E). Gas exchange measurements were performed on new, mature leaves growing in full sunlight using a LI-6400 gas exchange system with a red/blue light source and a CO_2 injector (LI-COR). Light intensity inside the sample cuvette was $2,000 \mu\text{mol m}^{-2} \text{s}^{-1}$, CO_2 concentration was 380 p.p.m., and the relative humidity was maintained at ambient. All measurements were performed between 1100 and 1300 hours Central Standard Time (CST) on clear days and corrected for projected leaf area within the gas exchange cuvette using a LI-3100 leaf area meter (LI-COR). Water potential measurements were performed using a Scholander pressure bomb (PMS Instruments) at predawn (0400–0600 hours CST) and midday (1300–1500 hours CST) for two to five samples per individual per well site. Water potential samples were averaged for each individual prior to analysis. Physiology data were analyzed using a mixed-effects model ANOVA in SAS 8.02. In the analysis, date of sampling, treatment (cut versus uncut *Tamarix*), and their interaction were fixed effects, while well site (1 or 2) within plot (1 or 3) was a random effect. Sample date was a repeated measure because the same individuals were re-sampled over the course of the summer.

Stable isotopic analysis

On each sampling date, 10-cm subsections of plant stems were collected from each individual, stored in Exetainer vials (Labco) on ice, and then transported to the laboratory within 24 h for storage at -20°C . One soil pit was dug adjacent to each well on each sampling date for collection of soil samples at 10- and 30-cm depths. Soil samples (30–50 g) were removed from the vertical profile immediately after excavation. The samples were frozen and stored at -20°C until analysis. Groundwater was collected from each well and stored in Exetainer vials with no headspace at 4°C . Water was removed from plant and soil samples using cryogenic vacuum extraction (Ehleringer and Osmond 1989). Extracted water samples were directly equilibrated with a headspace of CO_2/He for 24 h at 30°C (Epstein and Mayeda 1953). The headspace gas was then analyzed for $\delta^{18}\text{O}$ on a gas bench connected to a ThermoFinnigan Conflow III interface and Finnigan Delta-plus continuous flow stable isotope ratio mass spectrometer. Within-run variation of sample replicates was 0.19‰, and the laboratory precision associated with the working standard (deionized tap water) was 0.20‰.

Results

The 2006 growing season was much warmer and drier than the long-term mean conditions for Ashland (Fig. 1). The high maximum daily air temperature (T_{max}) and low precipitation during 2006 were comparable to the great droughts of the 1930s, the period of the driest and hottest consecutive growing seasons for the last century at this location (Fig. 1, inset table). In the long-term data set (1900–2006), 6 years had total growing season precipitation ≤ 251 mm, and 20 years had a mean $T_{\text{max}} \geq 31.2^\circ\text{C}$. However, only 2 years, 1934 and 1954, had both a mean $T_{\text{max}} \geq 31.2^\circ\text{C}$ and precipitation ≤ 251 mm, the conditions recorded over the 2006 growing season. Although the Cimarron River is considered a perennial stream at the site, the severity of the 2006 drought resulted in the flow ending in early June and not resuming until mid-September.

The water table elevation declined by approximately 0.5 m at each well from early May to early September 2006 (Fig. 2). By August, water table elevations were 15–20 cm below the lowest positions recorded since the start of monitoring in August 2004 (Figs. 2, 3, horizontal dashed line). As the water table declined across the summer, the magnitude of diel water table fluctuations also changed. At wells 1.1, 1.2, and 3.1 (Fig. 2), diel water table fluctuations were present early in the growing season. The magnitude of these fluctuations in May and June varied between wells, with the greatest amplitude at well 1.1, the

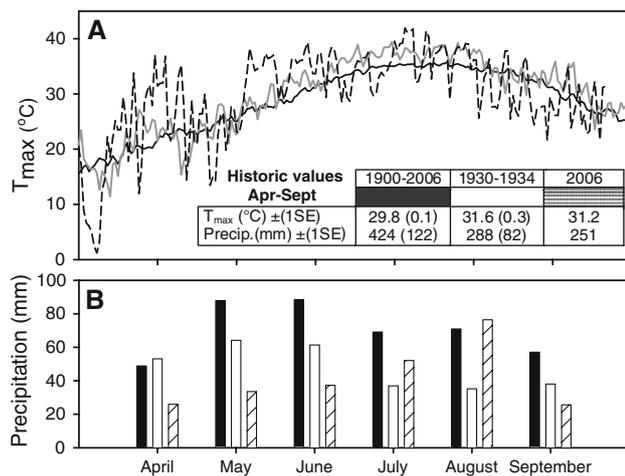


Fig. 1a, b Growing season (April–September) climate history for Ashland, Kansas, USA. **a** Variation in maximum daily air temperature (T_{max}) over the entire recorded history (black line), during the driest and hottest consecutive period of the recorded history (gray line), and during 2006 (dashed black line). Values for 1900–2006 and 1930–1934 are means. Inset table: April–September mean for each period with across-year variation (± 1 SE). **b** Mean monthly precipitation (black bar) for 1900–2006 and 1930–1934 (open bar), and monthly precipitation for 2006 (hatched bar)

location with the shallowest water table. As the water table declined beyond the previously recorded low in late June, the daily amplitude of the groundwater fluctuations abruptly diminished (Fig. 2, inset table). At wells 1.1, and 1.2 the fluctuations diminished but continued with further declines in the water table (Fig. 2). At well 3.1, fluctuations nearly disappeared as the water table dropped below the previously recorded low (Fig. 2). However, small diel fluctuations resumed at that well by mid-August (0.005-m mean increase in the daily amplitude from 11 August–7 September compared to 19 July–10 August), despite a 18.5-cm decline in the water table elevation below the previously recorded low. At well 3.2, diel fluctuations were minor for the entire summer, and there was no change in the mean daily amplitude as the water table dropped below the previous recorded low (Fig. 2).

Volumetric water contents in the vadose zone declined during the drought (Fig. 3). Consistent with the physics of subsurface flow in response to a falling water table, the greatest declines in volumetric water content occurred at depths near the position of the water table at the start of the growing season (henceforth, initial water table). For example, at well site 1.1, the volumetric water content declined from 0.35 to 0.15 $m^3 m^{-3}$ at a depth of 0.1 m from mid-May to early September. At depths in the vicinity of the initial water table, the volumetric water content was greatly reduced for three of the four well sites: 1.1 (54% reduction at depth of 0.1 m), 3.1 (45% reduction at depth of 0.6 m), and 3.2 (77% reduction at depth of 0.9 m,

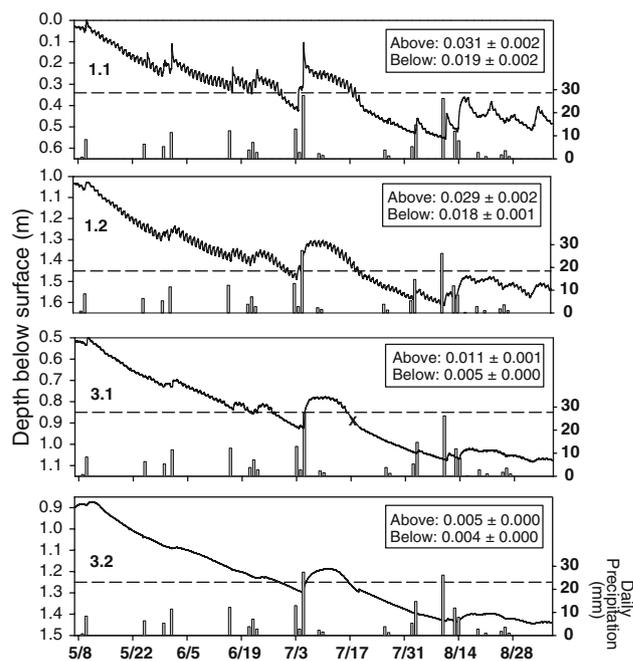
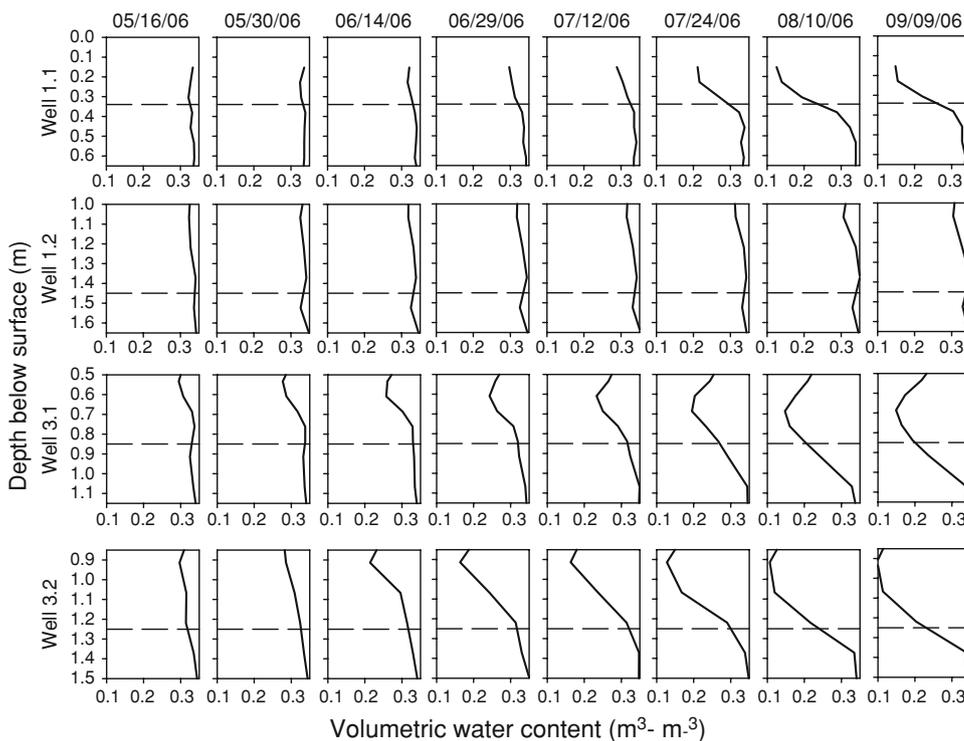


Fig. 2 Changes in water table elevation and diel water table fluctuations from May to September 2006 for each well site (1.1, 1.2, 3.1, 3.2). Within each panel, the heavy black line designates the water table elevation (left y-axis). Horizontal dashed lines denote the previously measured water table minimum. Vertical bars on the bottom of each panel are the magnitude of daily precipitation (lower right y-axis). At well 3.1, the cross in bold designates a 4-day interruption of water table monitoring from 16 to 19 July due to premature battery failure. Insets report the mean (± 1 SE) daily change in water table elevation (m) between 8 a.m. and 6 p.m. (the time course associated with the maximum and minimum groundwater amplitude; Butler et al. 2007) for all days above and below the previous water table minimum, respectively

consistent with the heavier dependence on vadose-zone water; Fig. 3). At well site 1.2, changes in volumetric water content at analogous depths were less than at the other sites, most likely because of the finer sediment textures at those depths. Finer sediments would be less subject to drainage over this time frame and also would allow development of a thicker capillary fringe and thus extended contact with the water table.

The $\delta^{18}O$ signature of *Tamarix* xylem water and shallow soil water (10-cm and 30-cm depths) varied by well sites and sample time, but groundwater $\delta^{18}O$ varied minimally (Fig. 4). Soil water at 10 cm had the heaviest isotopic signatures, reflecting dry soils (i.e., evaporative enrichment; Butler et al. 2008). At sites 1.1 and 3.2, the $\delta^{18}O$ of soil water at 30 cm was more similar to 10-cm depth $\delta^{18}O$, while the $\delta^{18}O$ of soil water at 30 cm at sites 1.2 and 3.1 more closely resembled groundwater $\delta^{18}O$ (Fig. 4). The xylem $\delta^{18}O$ was most similar to the $\delta^{18}O$ of groundwater at 25 May, 13 July, and 2 August at all sites. On 20 June, xylem $\delta^{18}O$ was most similar to soil water at 30 cm at sites

Fig. 3 Changes in volumetric water content by depth below surface for each well site from May to September 2006. Well-specific depths below surface correspond to Fig. 2. The horizontal dashed lines denote the previously measured water table minimum. The soil texture for the soil depths depicted was sand for wells 1.1, 3.1 and 3.2. The soil texture for well 1.2 was sand and silt

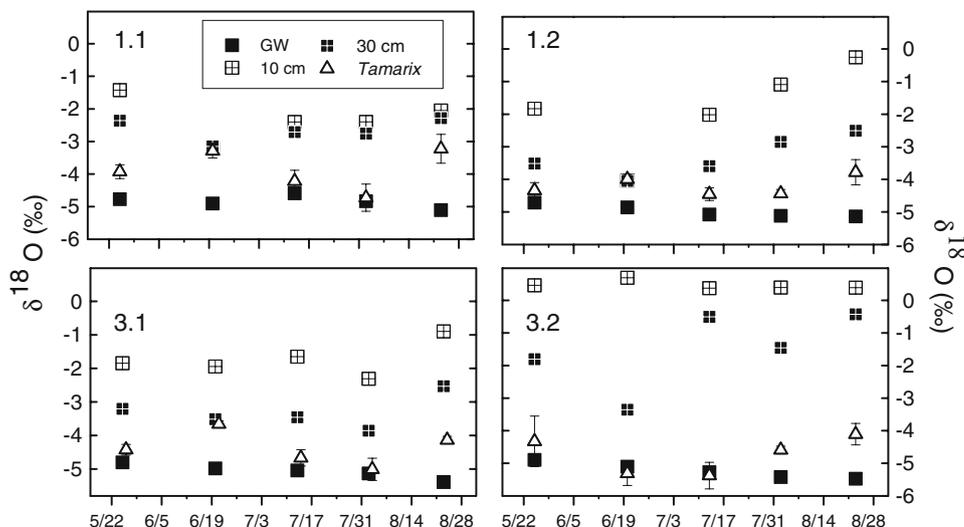


1.1, 1.2, and 3.1. During the 24 August sampling period, xylem $\delta^{18}\text{O}$ was not unique to either soil water at 30 cm or groundwater sources.

None of the physiological plant responses we measured varied significantly between wells within a given plot (1.1 vs. 1.2; 3.1 vs. 3.2; $P > 0.05$), but gas exchange rates were significantly higher ($P < 0.05$) for *Tamarix* in plot 3 compared to plot 1 (Fig. 5). A_{sat} rates displayed a similar pattern at all well sites, peaking on 20 June and then remaining relatively stable during the final three sampling dates (Fig. 5). Patterns of g_s were similar to A_{sat} at all well sites, except during the final sampling period when the

intercellular CO_2 concentrations were also lowest (data not shown). On 24 August, we measured nighttime (2400–0200 hours CST) rates of g_s on the same branches used for daytime gas exchange at each location. Nighttime g_s was approximately 77% less than daytime rates (0.027 and 0.119 mol $\text{H}_2\text{O m}^{-2} \text{s}^{-1}$ for night and midday g_s , respectively). None of the sampled *Tamarix* individuals were observed to have shed leaves in response to the drought. Leaf water potentials declined across the site from early to midsummer, with the lowest values in mid-July (Fig. 6). This period corresponds with the highest T_{max} of the summer (Fig. 1a). For the final two sampling periods (2, 24

Fig. 4 Mean (± 1 SE) stable oxygen isotopic signature ($\delta^{18}\text{O}$) of plant xylem water (triangle) and contributing water sources (10-cm depth, 30-cm depth, and groundwater) sampled across the 2006 growing season. Results are grouped by well site (1.1, 1.2, 3.1, 3.2). $\delta^{18}\text{O}$ of plant samples and 10-cm and 30-cm soil water samples were nearly equivalent (and symbols appear overlaid) at well 1.2 on 20 June



August), predawn and midday water potentials increased to values similar to those recorded during the early season despite the continued drought (Fig. 6).

Discussion

Evapotranspirative consumption of groundwater produces the diel fluctuations in the water table that are commonly observed in shallow wells in vegetated riparian zones (White 1932; Loheide et al. 2005; Butler et al. 2007). Groundwater use by terrestrial plants with roots extending to the capillary fringe is often the major mechanism responsible for these fluctuations. The diel fluctuations consist of a drop in the water table elevation from mid-morning to late afternoon followed by a rise in the water table from inflow during the night, corresponding to the common pattern of plant water use. Fluctuations were present at wells 1.1, 1.2, and 3.1 at the beginning of the 2006 growing season. However, the hot and dry conditions during mid-summer 2006 resulted in a dampening to near disappearance of these fluctuations as the water table declined past the previously recorded low (Fig. 2). Potentially, the loss of the diel signal may simply reflect an inability to detect plant water uptake if root density is lower in close proximity to that measured by the well or if high soil hydraulic conductivity minimizes inflow to replace plant-consumed groundwater. At this site however, the most likely explanation of changes in the strength of diel fluctuations is that *Tamarix* and other co-occurring plant species reduced groundwater uptake following the water table decline beyond the previously recorded low as a result of diminished access to groundwater. The diel fluctuations abruptly diminished at wells 1.1, 1.2, and 3.1 over 25–29 June as the water table dropped beyond the

previous low (Fig. 2), despite an increasing evapotranspirative demand (ET_0 was 5.7, 5.5, 6.3, 8.1, and 9.1 mm day⁻¹ for 25–29 June, respectively; Allen et al. 1998). The signals were briefly restored to their earlier strength in early July when precipitation increased the water table elevation above the previously recorded low (Fig. 2). However, the diel signals again abruptly diminished shortly thereafter. At well 3.1, the signal virtually disappeared with further water table declines and remained near-absent until mid-August, when, despite further drops in the water table, a clear, quantifiable re-emergence of the fluctuation occurred.

The differences in the responses between wells are thought to primarily reflect differences in sediment texture and the thickness of the capillary fringe, but may also be a result of differences in the distribution of functional roots by depth or root growth rates, both of which vary according to the position of the water table and the rate of water table decline (Naumburg et al. 2005; Cleverly et al. 2006). Previously, the rate of root growth for *Tamarix* was shown to vary between 1 and 13 mm day⁻¹ (Fenner et al. 1984; Horton and Clark 2001; Naumburg et al. 2005). The corresponding decline in the water table at well 3.1 between 16 July and 10 August was 7.4 mm day⁻¹, which suggests that root elongation to re-establish contact with the water table is within the range of potential root growth for this species. In the early part of the growing season when the water table was closer to the ground surface, it is likely that groundwater consumption by direct evaporation contributed to the diel fluctuations. However, by mid-August 2006, it is unlikely that direct evaporation was significantly contributing to the diel fluctuations recorded at any of the wells, as the water table was sufficiently deep or the near-surface volumetric water contents sufficiently low to eliminate direct evaporation as a primary driver for the

Fig. 5 Light-saturated photosynthetic rate (A_{sat} ; filled circles, left y-axis) and stomatal conductance to water (g_s ; open circles, right y-axis) sampled across the 2006 growing season. Results are grouped by well sites as means (± 1 SE). For A_{sat} , a significant statistical difference existed between plots (1 or 3; $P = 0.004$) and for date ($P < 0.001$). For g_s , a significant interaction between plot and date was present ($P = 0.028$)

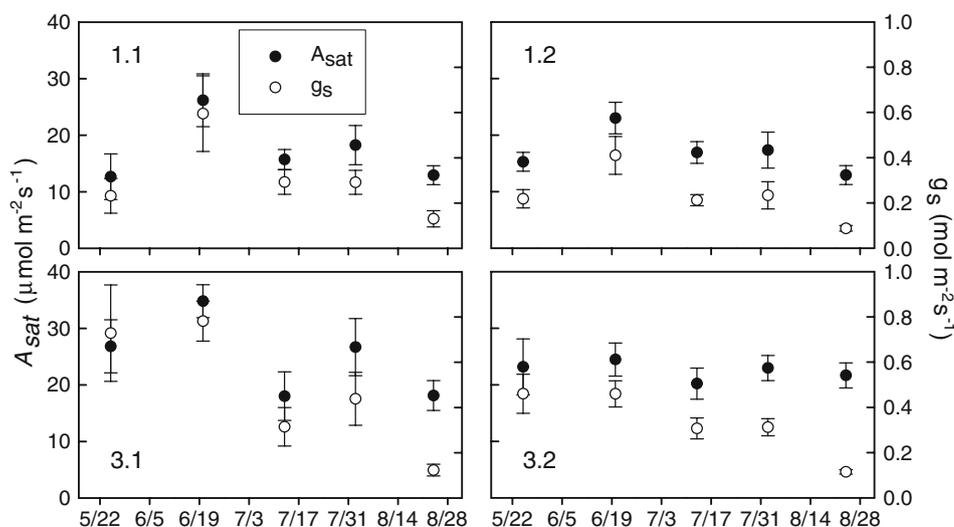
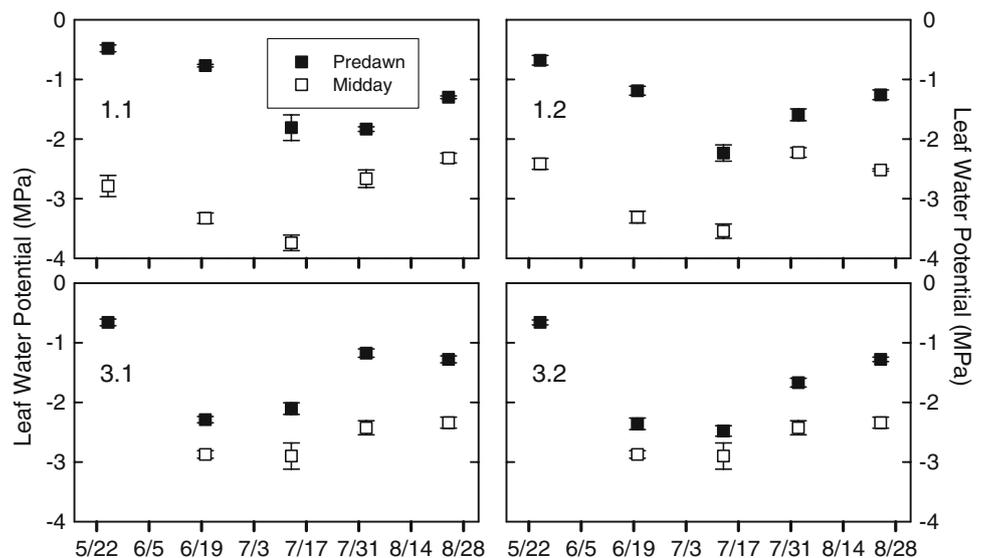


Fig. 6 Mean (± 1 SE) predawn (filled square) and midday (open square) leaf water potentials. All results are grouped according to the well site measured (1.1, 1.2, 3.1, 3.2). Midday water potential measurements were not performed at well sites 3.1 and 3.2 on 25 May because of a depleted gas supply. A significant interaction between plot and date was present for predawn water potential ($P < 0.001$) and for midday water potential ($P = 0.025$)



observed fluctuations. By mid-July, most herbaceous plants had senesced, reducing the functional importance of this plant community for the diel fluctuations.

Changes in volumetric water content by depth provide additional insight into changing patterns of *Tamarix* water use during drought (Fig. 3). The decreases in volumetric water content that were concurrent with the dampening of diel fluctuations in wells 1.1, 1.2, and 3.1 (Fig. 2) can be attributed to two possible mechanisms or their interaction. As the water table declined, the sediments drained, as would be expected, and the volumetric water content decreased. However, the close association of the dampening water table fluctuations and the declining volumetric water content is highly suggestive of a second mechanism: root-mediated water uptake at a specific soil depth. Using well 3.1 as an example, the progressive changes in volumetric water content centered at 0.6–0.7 m depth starting in late June are temporally consistent with the near-disappearance of the diel fluctuations. These changes are highly suggestive of root-mediated water uptake. In that case, water uptake would have occurred via roots established prior to the 2006 growing season in the vicinity of the initial water table elevation. Thus, the depth of plant water uptake may not have changed, but the source of water used by *Tamarix* and other non-senesced plant species may have changed as a result of water table declines during the drought. This combination of soil moisture data and diel water table fluctuations reinforces the facultative characteristics of *Tamarix* at this site. These data are among the first direct hydrologic illustrations of multiple shifts in the source of water used in response to a rapid environmental change. Thus, water use by *Tamarix* (and other non-senesced species) appears to have shifted from groundwater

to vadose-zone water above the capillary fringe in response to drought.

Previous work suggests that the hydrologic conditions experienced by the plant community are an important control on root distribution and groundwater uptake, i.e., groundwater uptake would be expected to decrease as the water table dropped past its previous low because the plants would not have developed a root network to extract water from greater depths (Scott et al. 2000; Shafroth et al. 2000; Butler et al. 2007). These results support this concept. The diel water table fluctuations decreased very abruptly as the water table fell past the previously recorded low position (Fig. 2), despite increasing evapotranspirative demand and relatively high rates of leaf-level gas exchange. The association of the position of the previous water table low and changes in the diel fluctuations at multiple wells eliminates direct evaporation as a mechanism driving the diel signal. If the diel fluctuations were driven by evaporation (White 1932; Gardner and Hillel 1962), and not by direct contact between plant roots and the capillary fringe, there would have been no change in the diel signal as the water table declined past the previous low: a phenomena observed twice (late June and mid-July) at all three wells where the diel signal occurred early in the growing season. Nighttime transpiration would be a potential explanation for the reduction in the fluctuations if the nighttime fluxes balanced daytime fluxes (Moore et al. 2008). However, measurements of nighttime transpiration were much lower than daytime transpiration, and thus the two are unbalanced. Sediment texture can play a pivotal role in determining the response of the plant community to water stress. At this site, the vadose zone was composed of coarse silts to medium sands, which provided an important

reservoir of water when the water table dropped below the primary zone of root water uptake. Thus, the response of a plant community to prolonged water stress must be interpreted in terms of the physiological characteristics of the plants as well as the retentive capacity of the shallow sediments.

At the beginning of the growing season, the water table was closest to the ground surface and the $\delta^{18}\text{O}$ of *Tamarix* xylem water was most similar to groundwater (Fig. 4). This isotopic signature is consistent with the diel fluctuations observed at three of the four well sites and the relatively small changes in the volumetric water content profiles (Fig. 3; Butler et al. 2008). The heavier xylem $\delta^{18}\text{O}$ on 20 June at well 1.1, 1.2, and 3.1 is likely a result of rainfall on 16 June mixing with and pushing downward isotopically heavier water. The corresponding rise in the water table at those well sites demonstrates that water moved downward to the water table in response to rainfall (there was no water in the river at this time). The xylem $\delta^{18}\text{O}$ of *Tamarix* at well 3.2 was always most similar to that of groundwater, consistent with the dampened water table responses to most precipitation events. The similarity between plant and groundwater signatures at wells 3.1 and 3.2 during mid-summer is potentially misleading, as diel water table fluctuations are nearly absent. Water left behind in the vadose zone as the water table declined would not be isotopically distinct from groundwater, unless enriched rainfall infiltrates from upper intervals, because fractionation does not occur via root uptake and this region is beyond the zone of evaporative enrichment. Thus, a shift to xylem water with a heavier isotopic signature may be an indication of downward movement of recharging water, and not a switch in water sources used. During late August, xylem $\delta^{18}\text{O}$ was heavier at all well sites, presumably reflecting the downward movement of isotopically heavier water in response to rainfall in early August. The hydrologic data support the assertion that *Tamarix* is utilizing a mix of groundwater (as indicated by the diel fluctuations; Fig. 2; Butler et al. 2008) and relatively deep vadose zone water (as indicated by the decreases in volumetric water content; Fig. 3) and do not have a large consumption of near-surface sources.

The stable isotope results suggest cautious interpretation of groundwater $\delta^{18}\text{O}$ from well samples if supporting hydrologic data are not available. Samples from wells are averages representative of some undefined portion of the screened interval, and not necessarily the $\delta^{18}\text{O}$ at the water table. For example, the water table on 20 June at well 1.1 was approximately 0.3 m below ground surface (top of well screen is 1.0 m below ground surface), so soil water from the 30-cm depth should reflect conditions at the water table. The -2‰ difference between the soil sample and the sample from well 1.1 demonstrates that measurements of

water samples from wells may not be the same as point measurements from the water table. Typically, the contribution of a few sources to the $\delta^{18}\text{O}$ mixture in plant xylem can be partitioned using a mixing model (Nippert and Knapp 2007). At this site, the similarity of $\delta^{18}\text{O}$ in vadose zone water and groundwater minimizes the usefulness of an “isotope-only” approach for water source determination because xylem water could reflect a mixture of near-surface and groundwaters or be composed entirely of vadose-zone water of a mixed composition. The difficulty of differentiating water sources in complex subsurface hydrogeologic regions using stable isotopes has been previously illustrated (Busch et al. 1992; Busch and Smith 1995; Horton et al. 2003). Our results demonstrate the usefulness of high-frequency hydrologic monitoring for gaining insight into changes in the vertical distribution of $\delta^{18}\text{O}$ in the vadose zone and groundwater over time. Clearly, more attention needs to be given to the details of subsurface water flow and well construction for reliable interpretations of water sources using isotopic measurements.

Leaf physiology was relatively constant for *Tamarix* over the summer, despite low precipitation and progressive increases in T_{max} (for similar drought responses also see Cleverly et al. 1997; Xu et al. 2007). We expected the previous site history (cut *Tamarix* in plot 3 versus uncut plot 1) to impact physiological responses during the summer drought because microenvironments vary between plots, and cut individuals would have to allocate comparatively more resources aboveground for regrowth. Across the site, leaf gas exchange rates were high (Fig. 4), as photosynthetic rates remained near the upper range reported for woody C_3 species across the summer ($\sim 20 \mu\text{mol m}^{-2} \text{s}^{-1}$; Larcher 1995). *Tamarix* in plot 3 had higher gas exchange rates, likely from higher light intensities and higher nutrient allocation within a smaller canopy (Fig. 5). For *Tamarix* in plot 1, the absolute difference between predawn and midday water potentials declined over the summer (Fig. 6). This change suggests that increased stomatal regulation reduced whole-plant transpiration during the summer drought (Reich and Hinckley 1989), consistent with reductions in leaf-level gas exchange (Fig. 5). The cut *Tamarix* (plot 3) responded differently, with an increasing absolute difference between predawn and midday water potentials over the same period. Thus, despite decreased (3.1) or steady (3.2) gas exchange rates during this period, whole-plant transpiration was likely increasing. The midday water potentials we measured are similar to other reported values in dry mid-summer conditions (-2 to -3 MPa; Anderson 1982; Devitt et al. 1997; Mounisif et al. 2002; Horton et al. 2001). Gries et al. (2003) reported 30% cavitation at -4.5 MPa and 100% cavitation at -7 MPa in *Tamarix ramosissima*. The range of water potentials we measured makes it unlikely that widespread cavitation had occurred in either plot.

Therefore the *Tamarix* leaf physiology largely reflects canopy regrowth in plot 3, and moderate water stress in plot 1 during the summer drought.

Conclusion

In this work, we demonstrated the value of frequent measurements of water table position and volumetric water content for improving interpretations of changes in the primary zone of root water uptake based on $\delta^{18}\text{O}$ data. The previous hydrologic conditions on site were an important constraint on root establishment at depth, and impacted the source of water used by the plant community. Our data suggests that *Tamarix* rapidly shifted its primary water source in response to declines in the water table. The use of multiple water sources by *Tamarix* minimized leaf-level water stress even during an historic drought for this site.

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