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Wide-area estimates of saltcedar (*Tamarix* spp.) evapotranspiration on the lower Colorado River measured by heat balance and remote sensing methods[†,‡]

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ABSTRACT

In many places along the lower Colorado River, saltcedar (*Tamarix* spp) has replaced the native shrubs and trees, including arrowweed, mesquite, cottonwood and willows. Some have advocated that by removing saltcedar, we could save water and create environments more favourable to these native species. To test these assumptions we compared sap flux measurements of water used by native species in contrast to saltcedar, and compared soil salinity, ground water depth and soil moisture across a gradient of 200–1500 m from the river's edge on a floodplain terrace at Cibola National Wildlife Refuge (CNWR). We found that the fraction of land covered (f_c) with vegetation in 2005–2007 was similar to that occupied by native vegetation in 1938 using satellite-derived estimates and reprocessed aerial photographs scaled to comparable spatial resolutions (3–4 m). We converted f_c to estimates of leaf area index (LAI) through point sampling and destructive analyses ($r^2 = 0{\cdot}82$). Saltcedar LAI averaged 2·54 with an f_c of 0·80, and reached a maximum of 3·7 with an f_c of 0·95. The ranges in f_c and LAI are similar to those reported for native vegetation elsewhere and from the 1938 photographs over the study site. On-site measurements of water use and soil and aquifer properties confirmed that although saltcedar grows in areas where salinity has increased much better than native shrubs and trees, rates of transpiration are similar. Annual water use over CNWR was about 1·15 m year^{-1}. Copyright © 2008 John Wiley & Sons, Ltd.

KEY WORDS tamarisk; *Pluchea*; *Populus*; *Prosopis*; ground water; MODIS; EVI

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INTRODUCTION

In their natural state, riparian corridors in the southwestern US experienced periodic pulse floods that washed salts from the soil and replenished and freshened the aquifers (Poff *et al.*, 1997; Mahoney and Rood, 1998; Glenn and Nagler, 2005; Pataki *et al.*, 2005). These flood plains supported a mosaic of mesic trees and salt-tolerant shrubs, interspersed with areas of emergent marsh vegetation (e.g. Clover and Jotter, 1944). As a result of flow regulation and water diversions, more saline conditions have been created. As a result, gallery forests of cottonwood and willow (*Populus fremontii* and *Salix goodingii*) along the river banks and mesquites (*Prosopis* spp.) on the terraces have been replaced by saltcedar (*Tamarix ramosissima* and related species, see Gaskin and Schaal, 2002), an introduced shrub. Although conditions are more saline than previously (e.g. Olmsted and McDonald, 1967; Pataki *et al.*, 2005), saltcedar can develop dense stands, and therefore, it has been assumed, uses more water than plants originally distributed across the flood plain (Di Tomaso, 1998; Zavaleta, 2000). These suppositions have resulted in legislation to fund efforts to remove saltcedar (HR2720, US 109th Congress, 2005).

We question these suppositions (Glenn and Nagler, 2005), and in the study reported here, compare plant water use by saltcedar and native shrubs in reference to their variation in leaf area index (LAI), soil salinity, depth of water table, moisture availability and climatic conditions at the Cibola National Wildlife Refuge (CNWR) on the lower Colorado River where historical photographs were available to contrast vegetation cover then with current conditions.

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METHODS

Site description

CNWR is located between Yuma, AZ and Blythe, CA, on the lower Colorado River. Annual rainfall is under 10 cm year^{-1} and temperatures range from 4 to 42 °C over the year. Saltcedar is deciduous in this climate, losing leaves in November and initiating new leaves in March (growing season *ca* 230 days).

CNWR contains approximately 4295 ha of riparian vegetation, of which 2816 ha is classified as saltcedar near-monocultures (>90% saltcedar), and the remainder is mainly saltcedar in association with 10% or greater cover of native trees including cottonwood and willow (44 ha), honey mesquite (*Prosopis. glandulosa*) and screwbean mesquite (*Prosopis. pubescens*) (1075 ha), or native shrubs including arrowweed, quailbush (*Atriplex lentiformis*) and fourwing saltbush (*Atriplex. canescens*) (78 ha). CNWR also supports a small amount of marsh habitat (282 ha), which was much more extensive before dams were built on the river (Olmsted and McDonald, 1967; United States Bureau of Reclamation, 1996).

Our study site was on a floodplain terrace bordered by desert hills on the west and the 'old river channel' on the east (Figure 1). This channel was formerly the main channel of the Colorado River but since 1964 most of the river flow has been diverted into a new channel parallel and to the east of the old channel; low flows of 8–15 m^3 s^{-1} enter the old channel, while the main channel carries 200–400 m^3 s^{-1} (United States Bureau of Reclamation, 2008). Four study plots were established on the terrace. Three of the plots were defined by a set of five observation wells approximately 100 m apart with an additional well in the centre of the plot (Nagler *et al.*, 2008). The wells were installed in June, 2006, and were sampled for depth and salinity at approximately monthly intervals through June, 2008. Names of these three plots, distances from the river and lat/long position at the centre of the plot are: Swamp (200 m) (33·2746, −114·6583), Slitherin (750 m) (33·2761, −114·7096) and Diablo (1500 m) (33·2659, −114·6992). Saltcedar was the dominant plant at each site, growing in dense stands interrupted by areas of light, sandy soil. An additional plot, designated Diablo East, was established east of Diablo and 870 m from the river (33·2687, −114·6895). This plot had a mixed plant community of saltcedar with occasional arrowweed shrubs and stunted screwbean mesquite trees occurring together, and it allowed us to measure transpiration on all three plant types at the same time. An observation well was installed in this plot in March, 2008 and it was sampled at monthly intervals through June, 2008. Transpiration was measured by sap flux sensors at Slitherin, Swamp and Diablo East.

Comparison of flood plain vegetation, 1938 and 2005

Figure 1. Saltcedar study sites at CNWR on the lower Colorado River, displayed on a 2005 Enhanced Thematic Mapper satellite image. CR points to the two channels of the Colorado River, with the old river channel on the left and the new channel on the right. Numbered study areas are Slitherin (1), Diablo (2), Diablo East (3), Swamp (4), the lower portion of the CNWR (5) and the whole CNWR (6).

To detect large-scale changes in vegetation patterns in the study area, we compared aerial photographs from 1938, the year Hoover Dam was completed, with high-resolution (*ca* 4 m) Quickbird imagery acquired in 2005 (Digital Globe, Inc., Longmont, CO). The 1938 images were acquired with black-and-white film and were digitized in a GIS with a resolution of about 2–3 m (Norman *et al.*, 2006). This was sufficient to distinguish individual trees, marshes and shrub areas using visual methods described in Nagler *et al.* (2005a). Cottonwood and willow trees could be identified by the size of their crowns (10–20 m in diameter) and the distinct long shadows they cast on understory vegetation, due to the height of their trunks. Mesquite trees were identified by their smaller shadows in relation to canopy diameter than cottonwoods and willows. Marsh areas were visible as uniform patches of vegetation near water. Fractional vegetation cover (f_c) was determined by a point-intercept method, by importing the images into SigmaPlot (Systat Software, Inc., San Jose, CA), and layering a 200 point grid over the image (Nagler *et al.*, 2004; Glenn *et al.*, 2008). Each grid intersection was scored as vegetated or unvegetated, and f_c was calculated as vegetated grid intersections divided by total intersections falling in the study area (but excluding water). The 95% confidence intervals (CI) were determined for each estimate based on the binomial distribution.

Depth to ground water, salinity, and vadose zone moisture measurements

Wells were installed and sampled as described in Nagler *et al.* (2008). Soil samples were collected at 25-cm intervals during well installation and were measured for texture (percentage sand, silt and clay by hydrometer) and

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[†] [Corrrection made here after online publication].

electrical conductivity (EC) of a saturated paste extract. At each monthly sampling interval, the well was plumbed to determine depth to water, then the well was pumped to remove at least three volumes of water from the casing, and a sample was withdrawn for measurement of EC in units of dS m^{-1} using a hand-held EC meter calibrated against NaCl solutions (Nagler *et al.*, 2008).

Volumetric soil moisture (m^3 m^{-3}) of the vadose zone was measured at 25-cm intervals with a neutron hydroprobe (CPN, Inc., Concord, CA), using the PVC well casings as neutron probe access tubes (Nagler *et al.*, 2008). All five wells at Swamp, Slitherin and Diablo were measured in June, 2007. Wells at the Swamp and Diablo sites were measured 3 times per day, at approximately 8:30–9:45 a.m., 11:30–12:00 noon, and 3:30–4:00 p.m., on three consecutive days to determine if vadose zone moisture levels were static or variable through the day.

Sap flux measurements

Sap flux was measured by the heat-balance method as described in Sala *et al.* (1996); Grime and Sinclair (1999); Kjelgaard *et al.* (1997); Nagler *et al.* (2003, 2007). Methods used in the present study closely followed those described in detail in Glenn *et al.* (2008). We used home-made sensors described in Scott *et al.* (2006). In the tissue-heat-balance method we used, an intact branch containing leaves was wrapped by a heating wire and a constant, low intensity heat was applied to each branch. Thermocouples embedded in the branch measure temperatures upstream and downstream from the heat source, and a thermopile outside the heating wire in the surrounding layer of insulation measures heat lost radially from the branch. A heat-balance equation is then solved to calculate heat transported by convection in the transpiration stream, versus diffusion in the stem and radially in the insulation layer, and the results are expressed in terms of grams of water transported per hour (Kjelgaard *et al.*, 1997).

Branches ranged from 5 to 15 mm in diameter. The sensors and thermopile were wrapped in insulating foam and covered with reflective foil to minimize solar heating. An instrument station containing a solar panel, four 6-V batteries, one to three multiplexers, a voltage regulator and a data-logger was established in each plot. The periods of data collection for saltcedar were July 20–September 2, 2007 (43 days), for the Slitherin site; June 22–July 8 (16 days) for Diablo East; and June 20–July 17, 2007 (27 days) for the Swamp site. Data for mesquite and arrowweed at Diablo East were collected from July 7 to September 4, 2007. However, sensors on some of the smaller branches showed a steady decline in transpiration after August 2, presumably due to tissue damage to the branch either by continuous heating or by a wound reaction to the sensor itself. Therefore, only data from July 7 to August 2 (26 days) were analysed.

At the end of the experiment, gauged branches were harvested for determination of leaf dry weight and leaf area per branch. Calculation of sap flux requires a correction for diffusive heat loss that occurs in the absence of sap flux, which is usually accomplished by assuming that sap flux goes to zero between 2 and 4 a.m. each day, and using temperature readings during those hours as zero points. However, saltcedar is now known to transpire at night (Moore *et al.*, 2008). Therefore, at the end of each sap flux measurement period, we continued to measure temperatures for 2 h after harvesting the branch above the point of sensor attached, and those temperature values were used as zero points for calibrating sensors. Data were collected from 8 arrowweed, 10 mesquite, and 20 saltcedar plants (8 at Slitherin, 5 at Diablo East and 7 at Swamp).

Scaling sap flow to plant and stand levels

Sapflow (J) was converted to transpiration on a leaf-area basis (E_L) (terminology and units follow Ewers and Oren, 2000) by harvesting all leaves on each gauged branch at the end of the measurement period. We determined dry weight of leaves on each gauged branch, then determined specific leaf area (SLA) (m^2 g^{-1}) on several hundred fresh leaves sampled from 10 different plants per species during the sap flux measurement periods using methods in Nagler *et al.* (2004). SLA for each species was: saltcedar, 0·0079 m^2 g^{-1} (SE = 0·0004); arrowweed, 0·0062 m^2 g^{-1} (SE = 0·0003) and mesquite, 0·0081 m^2 g^{-1} (SE = 0·0005). SLA is not constant and must be determined separately for each species during the period of sap flow measurement (e.g. Pataki *et al.*, 2005). E_L was expressed on a daily basis in units of mm H_2O m^{-2} leaf area d^{-1} and on an instantaneous basis during the day in units of mmol H_2O m^{-2} s^{-1} for comparison with stomatal conductance. To scale leaf-level measurement of transpiration to a canopy-area basis (E_C), we determined plant leaf-area index (LAPS), defined as one-sided m^2 leaf area per m^2 of horizontal plant surface, then we calculated E_C as:

$$E_C = \text{LAPS} \times E_L \qquad (1)$$

To scale E_L to transpiration on a ground-area basis (E_G) at each site, we first determined LAI, defined as m^2 of leaf area per m^2 of ground area, from LAPS and estimates of fractional cover (f_c) of vegetation at each site:

$$\text{LAI} = \text{LAPS} \times f_c \qquad (2)$$

Then E_G was calculated as:

$$E_G = E_L \times \text{LAI} \qquad (3)$$

LAPS was measured under several hundred plant canopies at each site with a LiCor LAI 2000 leaf-area meter (LiCor, Inc., Lincoln, NE) in June, July and August, 2007. Measurements were made in canopies that were extensive enough (>3-m in diameter) so that the shallowest sensor angle collected light that passed through the canopy so as not to violate the geometric assumptions built into the calculation procedure for LAI by the Licor LAI 2000 (see Nagler *et al.*, 2004). Licor LAI 2000 readings were calibrated by recording LAPS under selected canopies for which we also harvested leaves to determine LAPS. We placed a 0·25 m^2 PVC plastic frame horizontally over the canopy at the point where LAPS was measured by the Licor LAI 2000, then harvested all the leaves within the frame. The leaves from these quadrant samples were then dried and weighed, and expressed as LAPS based on SLA measurements.

To calculate f_c, we used high-resolution (1 m) aerial photographs collected by Dr Chris Neale (Utah State University) in June, 2007. The photographs covered an area of approximately 8 ha around each sap flow measurement station. Fractional cover on the photographs was determined by the point-intercept method described above.

Estimation of f_c and LAI by MODIS enhanced vegetation index

We used the enhanced vegetation index (EVI) from the moderate resolution imaging spectrometer (MODIS) sensors on the Terra satellite to estimate f_c and LAI over the study site. EVI data are supplied as 250-m resolution, pre-processed, georectified and atmospherically corrected, 16-day composites of near-daily images (Huete *et al.*, 2002). EVI values from summer, 2005 (June 10–September 10) were acquired for nine MODIS pixels over the study area representing a range of vegetation densities from nearly bare soil to complete plant cover. These were then regressed against values of f_c determined for the same areas on the 2005 Quickbird image. The on-line, Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC) (2008) MODIS subset tool was used to select pixels of interest. This tool displays the foot print of a selected MODIS pixel on a high-resolution Google Earth image, allowing the precise area of coverage to be located. For each site, we determined f_c of the area within the selected pixel using the point-intercept method on the 2005 Quickbird image, and then we acquired the 2005 EVI data for that pixel from the ORNL DAAC archive. EVI was then regressed against f_c across the sites to develop an equation for predicting f_c from EVI. The sites included the Swamp, Slitherin, Diablo and Diablo East plots, two additional areas of dense saltcedar, three areas of moderate or sparse saltcedar and one area of nearly bare desert soil adjacent to the study area.

Using the same method, we developed a relationship between EVI and LAI using LAPS and f_c data collected in 2006 (Nagler *et al.*, 2008) and 2007 (the present study) at the Swamp, Slitherin, Diablo, and Diablo East plots, as well as for the desert plot. LAI for each site was calculated from LAPS and f_c, by Equation (2), then LAI was regressed against EVI over the sites. For the desert site, we used the mean LAPS value determined for mesquite at the Diablo East site to determine LAI, since the few shrubs in the desert pixel were mesquites.

Calculation of E_G by MODIS EVI and maximum daily air temperature (T_a)

The calculation procedures and rationale for the algorithm used to estimate evapotranspiration ET from EVI and maximum daily air temperature (T_a) from ground stations are described in Nagler *et al.* (2005c). This algorithm was developed by correlating ET measured over multiple years at nine riparian flux tower sites with MODIS EVI and T_a. Daily T_a data were averaged to cover the 16-day MODIS reporting periods. We first converted EVI, which ranged from 0·091 to 0·542 in the original study (Nagler *et al.*, 2005c), to a full scale between 0 and 1 (EVI*):

$$\text{EVI}^* = 1 - (0{\cdot}542 - \text{EVI})/0{\cdot}451 \tag{4}$$

We then used EVI* and T_a values to calculate ET:

$$\text{ET (mm d}^{-1}) = 11{\cdot}5 \times (1 - \exp^{(-1{\cdot}63\text{EVI}^*)}) \times 0{\cdot}832/ (1 + \exp^{-(T_a - 27{\cdot}9)/2{\cdot}57}) + 1{\cdot}07 \ (r^2 = 0{\cdot}74) \tag{5}$$

Equation (5) has three components: (i) an EVI* term, which stands for foliage density, (ii) a temperature term, which is a proxy for atmospheric water demand and (iii) a constant, which is minimum ET (the same as bare soil evaporation). The first and second components are multiplied and the third is added. The expression containing EVI* is based on the formula for light extinction through a canopy. The temperature term is in the form of a sigmoidal curve, where there is a minimum temperature where atmospheric drivers for ET fluxes are mostly absent; a middle, exponential portion of the curve which fits the vapour pressure deficit: temperature response in the Penman–Monteith equation (Monteith and Unsworth, 1990) and an upper limit, where stomatal limitations constrain ET fluxes. Hence, air temperature is a scalar from 0 to 1·0 that accounts for both atmospheric water demand and for stomatal limitations to ET, at the low and high end of the temperature scale. The constant (1·07 mm day^{-1}) is required because in the original study (Nagler *et al.*, 2005c), none of the tower-based values of ET reached zero even in winter. This empirical formula is only valid for the plant species, vegetation densities and meteorological conditions for which it was calibrated. Saltcedar, which stands at CNWR fall within those ranges of conditions. The error or uncertainty in the ET estimates is in the range of 20–30% due to simplifying assumptions in the model and errors associated with flux tower measurements of ET.

We determined ET for the single MODIS pixel centred on each study site, for masks prepared for the lower portion of CNWR that encompassed our sap flow sites (Figure 1) and for riparian vegetation over the entire CNWR. The CNWR mask was prepared to encompass all the areas of riparian habitat within CNWR, but excluding pixels containing open water or active or abandoned agricultural fields, both of which are present within CNWR (see Nagler *et al.*, 2008).

Other methods and data sources

Meteorological data was obtained from the AZMET station located at Parker, Arizona, the nearest reporting station on the Colorado River, located approximately 25 km north of our study site (AZMET, 2008). Reference crop potential evapotranspiration (ET_o) was calculated from meteorological data by the Penman–Monteith equation (Allen *et al.*, 1998). Canopy conductance (G_S) on a leaf-area basis (mmol m^{-2} s^{-1}) was calculated by the formula (Phillips and Oren, 1998; Ewers and Oren, 2000):

$$G_S = E_L/D \times K_G \tag{6}$$

where K_G is the stomatal conductance coefficient (kPa), calculated from atmospheric pressure corrected for temperature effects by the formula:

$$K_G = 115{\cdot}8 + 0{\cdot}4226T \tag{7}$$

The term $E_L/D \times K_G$ is the ratio of transpiration to atmospheric water demand, and it is related to the degree of stomatal opening at a given time of day (Monteith and Unsworth, 1990).

$^{13}C/^{12}C$ ratios in plant tissues can also be used as indicators of stress and degree of stomatal opening during photosynthesis (e.g. Farquhar *et al.*, 1989; Ehleringer and Cook, 1998; Ehleringer *et al.*, 2002). $\delta^{13}C$ (‰) expresses the enrichment of ^{13}C in the sample compared to an atmospheric standard. Plant tissues have negative $\delta^{13}C$ values, and less negative values indicate greater enrichment in ^{13}C, and therefore more plant stress during carbon fixation, than more negative numbers. In July, 2007, we sampled leaf tissues from randomly selected saltcedar plants near each observation well at Slitherin, Swamp and Diablo East sites. Samples were analysed by the SIRFER Laboratory, University of Utah, Salt Lake City, UT (Ehleringer and Cook, 1998).

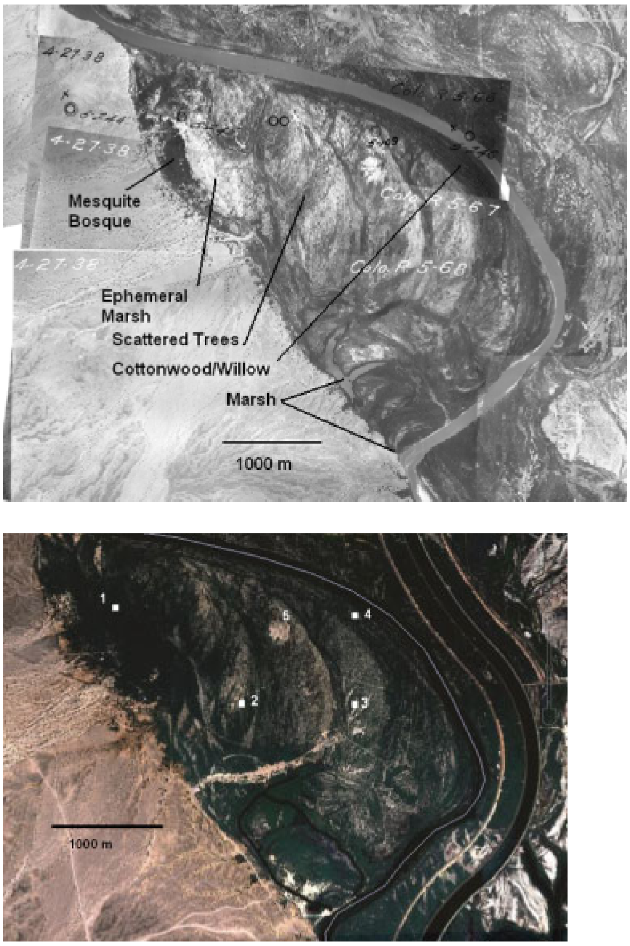

Figure 2. A portion of the CNWR on the lower Colorado River where study plots were located, showing the area from aerial photographs taken on April 27, 1938 (a) and on a Quickbird satellite image in May, 2005 (b). Panel a shows where large mesquites, cottonwoods and willows were visible in the 1938 photomosaic but not on the 2005 image. Numbered areas on panel b show the location of Slitherin (1), Diablo (2), Diablo East (3), and Swamp (4) plots, and an area of geothermal spring upwelling (5), also visible on the 1938 photomosaic.

RESULTS

Comparison of 1938 and 2005 imagery

Large-scale vegetation patterns in 2005 were remarkably similar to those in 1938 (Figure 2), with f_c of 0·83 (95% CI = 0·051) and 0·81 (95% CI = 0·057), in 2005 and 1938, respectively. The study area is a flood plain terrace dissected by several over-flow channels, with an extensive marsh area at the southern end of the terrace. In 1938, the Colorado River occupied a single channel. However, the majority of river flow was subsequently diverted into a new channel, while the old river channel has been preserved with a smaller flow of water to maintain wildlife habitat. Dense vegetation in both years was confined to the banks of the river channel where Swamp is located, to the ephemeral over-flow channels crossing the terrace and to a marsh area along the western edge of the terrace. The rest of the terrace was more thinly vegetated, with areas of bare soil visible between plant stands as at Diablo (Figure 3) and Diablo East. An anomalous circular bare spot (site 5 in Figure 2) was present on the flood plain in both 1938 and 2005; this proved to be an area where a plume of geothermal water (>50 °C) approaches the soil surface (J. Osterberg, unpublished observations).

In 1938, the northern part of the marsh area where Slitherin is located was dry, and the dry area has been subsequently filled with saltcedar. It appears that a former ephemeral marsh area has been converted to a saltcedar area rooted into ground water. This is the only expansion of vegetation that is evident between the 2 years. However, the species composition of the terrace has changed. In 1938, the banks of the river supported dense stands of cottonwood and willow trees (Figure 3a) with crowns 10–20 m wide, forming a continuous band 200-m wide along the river channel. Large trees were also scattered across the terrace amidst shrubs and along the over-flow channels (Figure 3b). These trees were likely to have been large cottonwood and mesquite trees, as the trunks of these now-dead trees are still present on the flood plain. By 2005, large trees had disappeared from these locations, and saltcedar now dominates the

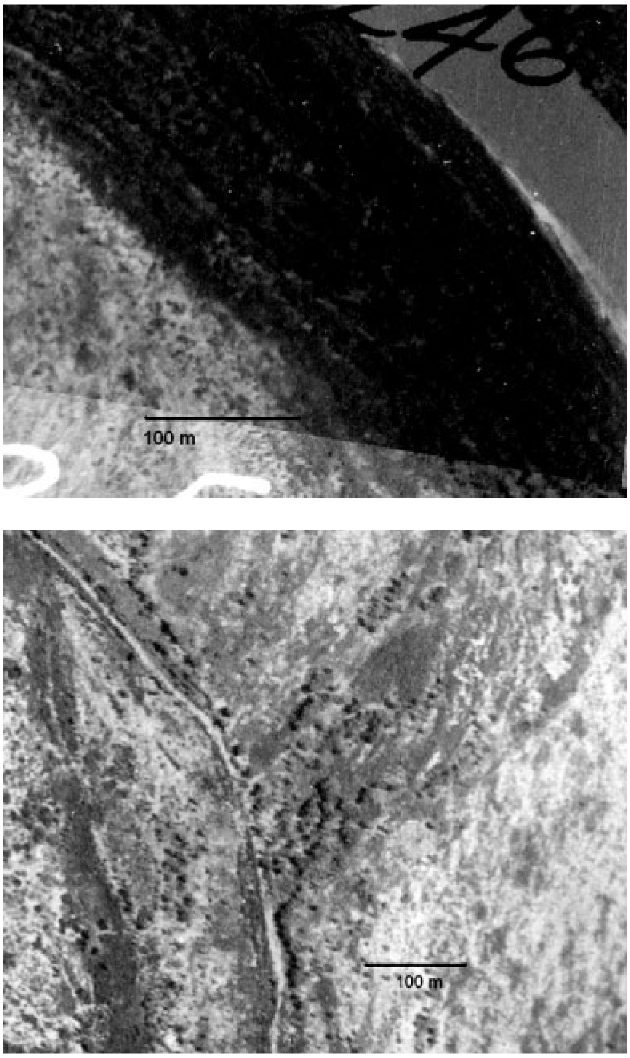

Figure 3. Closeup images of the CNWR on the lower Colorado River from aerial photographs taken on April 27, 1938, showing large native trees growing in the vicinity of the current Swamp plot (a) and Diablo plot (b). Trees at Swamp are probably a mix of cottonwoods and willows, whereas trees at Diablo are probably large mesquites and cottonwoods. Scale bars are approximate.

entire terrace area except for some marsh vegetation at the southern end of the terrace.

Depth to water, salinity, and vadose zone moisture at sap flux sites

Soil texture and salinities in the vadose zone and aquifer at the four study plots are in Table I. Vadose zone soils were layered at each site but, on average, were loams. Aquifer soils ranged in texture from sand at Diablo East to loam at Swamp. The water table was 2·5 m beneath the surface at Swamp (nearest the river) and increased to 3·32 m at Slitherin and Diablo. EC of the aquifer was only 3·3 dS m^{-1} at Swamp (compared to *ca* 1·5 dS m^{-1} for Colorado River water at 950 mg l^{-1} total dissolved salts), but ranged from 7·1 to 15·9 dS m^{-1} at the other sites. Saturated soil extracts from the vadose zone soils had ECs similar to the aquifer EC at Slitherin, Diablo, and Diablo East, but EC in the vadose zone at Swamp was 38·3 dS m^{-1} despite the low EC in the aquifer.

Depth to water showed a slight seasonal trend, being highest in winter when plants were not active, and lowest in summer (Figure 4a–c). The trend was more pronounced for Slitherin and Diablo than for Swamp, which was nearest the river. As in a previous study (Nagler *et al*., 2008), the Swamp site had a pool of soil moisture near field capacity above the aquifer, extending to within 1 m of the soil surface (Figure 4d), while Slitherin and Diablo had lower levels of vadose zone moisture. At both Diablo and Swamp, vadose zone moisture levels at the 0·4–4 m soil depths were very stable over short time periods, varying by $<2\%$ over the course of a day and day-to-day over the course of 3 days (not shown).

The aquifer EC was stable over time at Swamp (Figure 5a), whereas it was more spatially and temporally variable at the sites further from the river (Figure 5b, c). Aquifer salinity increased linearly with distance from the river, whereas vadose zone salinity was highest near the river (Figure 5d).

Table I. Soil and aquifer properties at four sites at CNWR on the lower Colorado River.

	Swamp	Slitherin	Diablo	Diablo east
Vadose zone:				
% Sand	48.3 (4.7)	45.2 (5.0)	54.2 (6.2)	52.5 (4.3)
% Silt	38.6 (3.5)	39.2 (3.4)	31.8 (4.3)	31.0 (2.9)
% Clay	13.1 (1.7)	15.6 (1.8)	14.0 (2.2)	16.5 (13.5)
Texture class	Loam	Loam	Loam	Loam
EC (dS m^{-1})	38.3 (4.6)	13.8 (3.2)	20.0 (2.3)	5.0 (1.2)
Aquifer:				
% Sand	34.0 (8.8)	63.8 (12.3)	84.0 (8.6)	95.0
% Silt	47.0 (5.6)	27.5 (10.1)	10.6 (6.2)	2/0
% Clay	19.0 (4.0)	8.8 (2.4)	5.4 (2.4)	3.0
Texture class	Loam	Sandy loam	Loamy sand	Sand
EC (dS m^{-1})	3.30 (0.06)	8.97 (0.42)	15.9 (0.49)	7.1 (0.19)
Depth (m)	2.50 (0.01)	3.32 (0.03)	3.21 (0.03)	2.50 (0.04)

Vadose zone texture classes are the mean of samples taken at approximately 25 cm intervals from the soil surface to the top of the aquifer when wells were installed. Vadose zone EC was determined in saturated past extracts of the same soil samples. Aquifer soil texture classes were from samples taken from the top 25 cm of the aquifer when wells were installed. Aquifer EC and depth to the top of the aquifer are means of monthly measurements after installation of wells. Numbers in parentheses are standard errors.

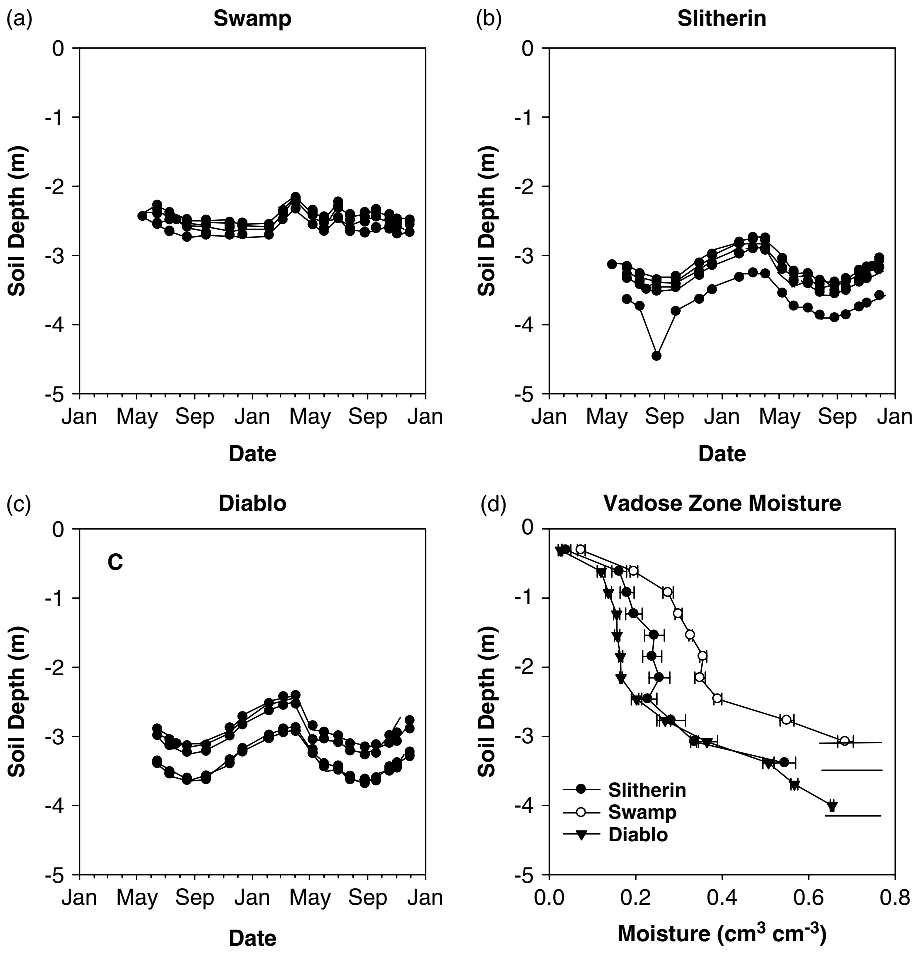

Figure 4. Depth to the aquifer at the Swamp (a), Slitherin (b) and Diablo (c) sites at CNWR on the lower Colorado River. Each datum is the depth measured at an individual observation well (five wells per site) at monthly intervals. Soil moisture levels above the aquifer measured in each well in June, 2007 are in (d); horizontal lines show approximate depth to the aquifer. Error bars are standard errors of means.

Plant leaf-area index and fractional cover

LAPS measured by leaf harvest and by the LAI 2000 for the same shrubs are in Table II. As many as 35 saltcedar plants from Slitherin and Swamp sites were sampled. A regression equation passing through the origin was significant ($r^2 = 0{\cdot}081$, $P < 0{\cdot}001$), but mean Licor LAI 2000 results were 15% lower than mean leaf harvest results. The difference between means was marginally significant ($P = 0{\cdot}068$ by paired t-test). Mesquite LAPS was nearly the same by both methods. Arrowweed had higher LAPS values by the Licor LAI 2000 than by leaf harvest, but the results were not significant, due to the low sample size (five plants). When all plants were pooled, the Licor LAI 2000 LAPS was 16% higher than leaf harvest LAPS ($P = 0{\cdot}022$), similar to the results with saltcedar alone. Therefore, we multiplied all Licor values by 0·84 to account for the fact that the Licor LAI 2000 measures non-photosynthetic tissues as well as leaves.

Licor LAI 2000 results at the three sites for June–August are in Table III. For all species and sites, LAPS tended to be constant over the summer. LAPSs at Slitherin and Swamp were high (mean = 3·59), whereas saltcedar at Diablo East was significantly ($P < 0{\cdot}05$)

Table II. LAPS of riparian shrubs measured with a LAI 2000 leaf-area meter and by a leaf harvest method.

Plant species	LAPS (Licor)	LAPS (Harvest)	*P*
Saltcedar			
Mean	3·26	2·78	0·068
SE	0·245	0·223	
N	35	35	
Mesquite			
Mean	1·53	1·49	0·914
SE	0·239	0·279	
N	5	5	
Arrowweed			
Mean	2·64	1·56	0·126
SE	0·290	0·327	
N	5	5	
Combined			
Mean	2·97	2·50	0·022
SE	0·210	0·195	
N	45	45	

Licor measurements were made under the canopy of each shrub, then a 0·25 m^2 frame was placed on the canopy at the point of Licor measurement and all the leaves in the frame were harvested to determine LAI by the leaf harvest method. *P* values indicate the probability that the means of the two methods are the same for each species and for pooled data by paired t-test.
SE, standard error; *n*, total number of readings.

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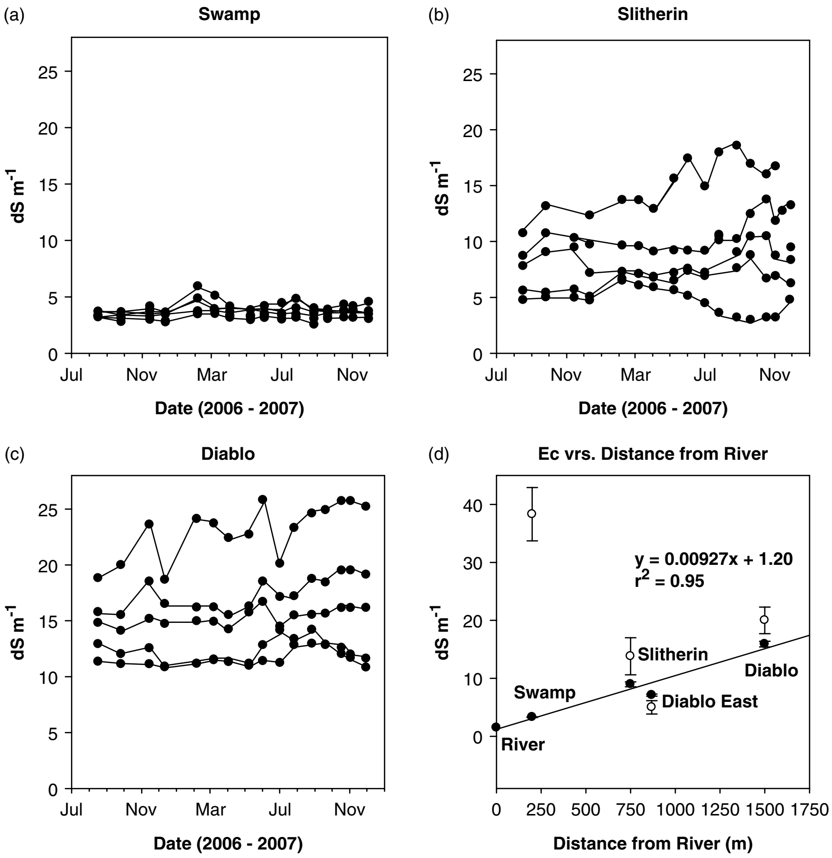

Figure 5. EC of the aquifer at the Swamp (a), Slitherin (b) and Diablo (c) sites at CNWR on the lower Colorado River. Each datum is the EC measured at an individual observation well (five wells per site) at monthly intervals. Mean ECs at each site are plotted against distance from the river in (d), showing aquifer (closed circles) and vadose zone EC (open circles). Error bars are standard errors of means.

lower (mean = 2·00). Mesquite and arrowweed at Diablo East also had low LAPSs of 1·28 and 1·55, respectively.

Fractional cover, determined for an 8-ha plot around each tower site on aerial photographs, was 0·95 (SE = 0·05) for Slitherin, 0·78 (SE = 0·07) for Swamp and 0·67 (SE = 0·10) for Diablo East, with mean $f_c = 0{\cdot}80$ across sites, similar to the value determined on the 2005 Quickbird image. LAIs (LAPS × f_c) were 3·70 for Slitherin, 2·56 for Swamp and 1·34 for Diablo East, with mean LAI = 2·53 across sites, all significantly different ($P < 0{\cdot}05$) by Tukey's Means Test (Table III).

Sap flux results and correlation with meteorological variables

Daily values of saltcedar E_L averaged across sensors at each site were consistent over the summer, ranging from 2 to 3 mm m^{-2} d^{-1} (Table III, Figure 6a). Swamp E_L was significantly ($P = 0{\cdot}042$) lower than Slitherin by Tukey's means comparison test. Mesquite and arrowweed had much higher E_L than saltcedar, and mesquite was higher than arrowweed (10·92 vs 8·40 mm m^{-2} d^{-1}) ($P < 0{\cdot}001$). Slitherin had the highest E_C due to high LAPS and f_c, and Diablo East had much lower E_C than Swamp or Slitherin due to lower LAPS and f_c compared to the other sites. E_C values were higher for mesquite and arrowweed than for saltcedar, but the differences were not as large as for E_L, due to lower LAPS of mesquite and arrowweed compared to saltcedar. Estimates of saltcedar

Table III. LAPS of saltcedar (SC), mesquite (M), and arrowweed (AW) at three sites in CNWR on the Colorado River in 2007.

Site	June	July	August	Mean
Swamp SC				
Mean	2·58a	3·39a	3·65a	3·28
SE	0·08	0·09	0·07	—
N	93	40	40	—
Slitherin SC				
Mean	4·05b	3·86b	3·75a	3·89
SE	0·19	0·07	0·12	—
N	24	42	41	—
Diablo East SC				
Mean	1·97c	2·03c	2·00b	2·00
SE	0·07	0·18	0·10	—
N	64	11	16	—
Diablo East M				
Mean	1·42d	1·15d	1·27d	1·28
SE	0·11	0·11	0·09	—
N	21	13	13	—
Diablo East AW				
Mean	2·02c	1·24d	1·38d	1·55
SE	0·12	0·22	0·13	—
N	32	13	13	

LAI was measured with a Licor 2000 leaf-area meter by taking five readings at different locations under the canopy of individual plants; *n* is the total number of readings taken at each sampling event and SE is the standard error of the mean. Different letters following the mean values in a column denote significant differences between sites at $P < 0{\cdot}05$.
SE, standard error; SC, saltcedar; *n*, total number of readings; AW, arrowweed.

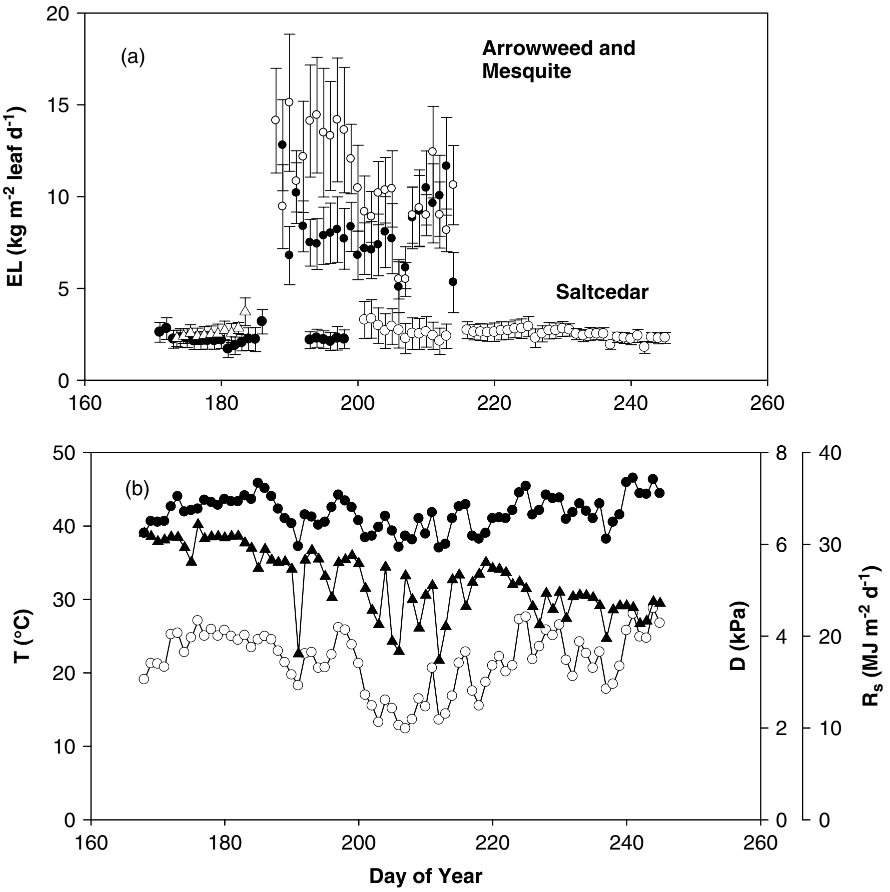

Figure 6. (a) Daily sap flux estimates of transpiration (E_L) for saltcedar, arrowweed, and mesquite plants measured over the summer of 2007 at CNWR on the Colorado River. Bars show standard errors. Symbols represent mesquite (small closed circles) and arrowweed (small open circles) at Diablo East; and saltcedar at Swamp (large closed circles), Diablo East (open triangles), and Slitherin (large closed circles). (b) Climatic conditions measured at the Parker, AZ AZMET Station, showing maximum daily temperature (T, closed circles), vapour pressure deficit (D), and solar radiation (R_s) over the study.

E_G by sap flow from June 22 to September 4, ranged from 3·74 to 9·46 mm d^{-1} for stands of different densities and LAIs. Giving equal weight to each site, mean E_G over the study area was 6·40 mm d^{-1} from June 22 to September 4, 2007. Mesquite and arrowweed were not factored into this estimate because they were minor constituents of the vegetation and we did not estimate fractional cover of these species.

Meteorological determinants of E_L *and* G_S

The climate was extremely hot, dry and sunny over the measurement period (Figure 6b), with mean daily $T_{\max}$ of 41·8 °C, potential ET of 16 mm d^{-1}, and only 2 mm of total precipitation over the measurement period. No significant ($P > 0{\cdot}05$) correlations were found between daily meteorological data and E_L, except for a weak correlation between mesquite E_L and wind speed ($r = 0{\cdot}43$, $P = 0{\cdot}04$). On an hourly basis, E_L was strongly correlated with air temperature, vapour pressure deficit and solar radiation for saltcedar at Swamp and Slitherin, but only weakly correlated with these variables at Diablo East (Table IV). Arrowweed and mesquite E_L were also strongly correlated with meteorological variables. By contrast, GS was less well correlated with environmental variables (Table IV). G_S of saltcedar at Slitherin was moderately correlated with T, D and R_S ($P < 0{\cdot}05$), but correlations were either non-significant ($P > 0{\cdot}05$) or, in

Table IV. Correlation coefficients between leaf-level transpiration (E_L) or stomatal conductance (G_S) and air temperature (T_a), vapour pressure deficit (D), and solar radiation (R_S) for riparian plants at CNWR on the lower Colorado River.

	Swamp saltcedar	Slitherin saltcedar	Diablo East saltcedar	Diablo East arrowweed	Diablo East mesquite
E_L:					
T_a	0·796***	0·912***	0·021 NS	0·915***	0·814***
D	0·789***	0·910***	0·008 NS	0·893***	0·754***
R_S	0·957***	0·960***	0·438*	0·926***	0·742***
G_S:					
T_a	−0·053 NS	0·535**	−0·536**	0·371 NS	0·228 NS
D	−0·063 NS	0·505*	−0·529**	0·307 NS	0·134 NS
R_S	0·390 NS	0·841***	−0·172 NS	0·550**	0·273 NS

Transpiration and meteorological data are hourly values averaged over each multi-day measurement period in summer, 2007. Asterisks denote significance at $P < 0{\cdot}05$ (*), $P < 0{\cdot}01$ (**) or $P < 0{\cdot}001$ (***); NS = not significant ($P > 0{\cdot}05$).

E_L, leaf-level transpiration; G_S, stomatal conductance; T_a, air temperature; D, vapour pressure deficit; R_S, solar radiation; asterisks denote significance at $P < 0{\cdot}05$ (*), $P < 0{\cdot}01$ (**), or $P < 0{\cdot}001$ (***); NS = not significant ($P > 0{\cdot}05$).

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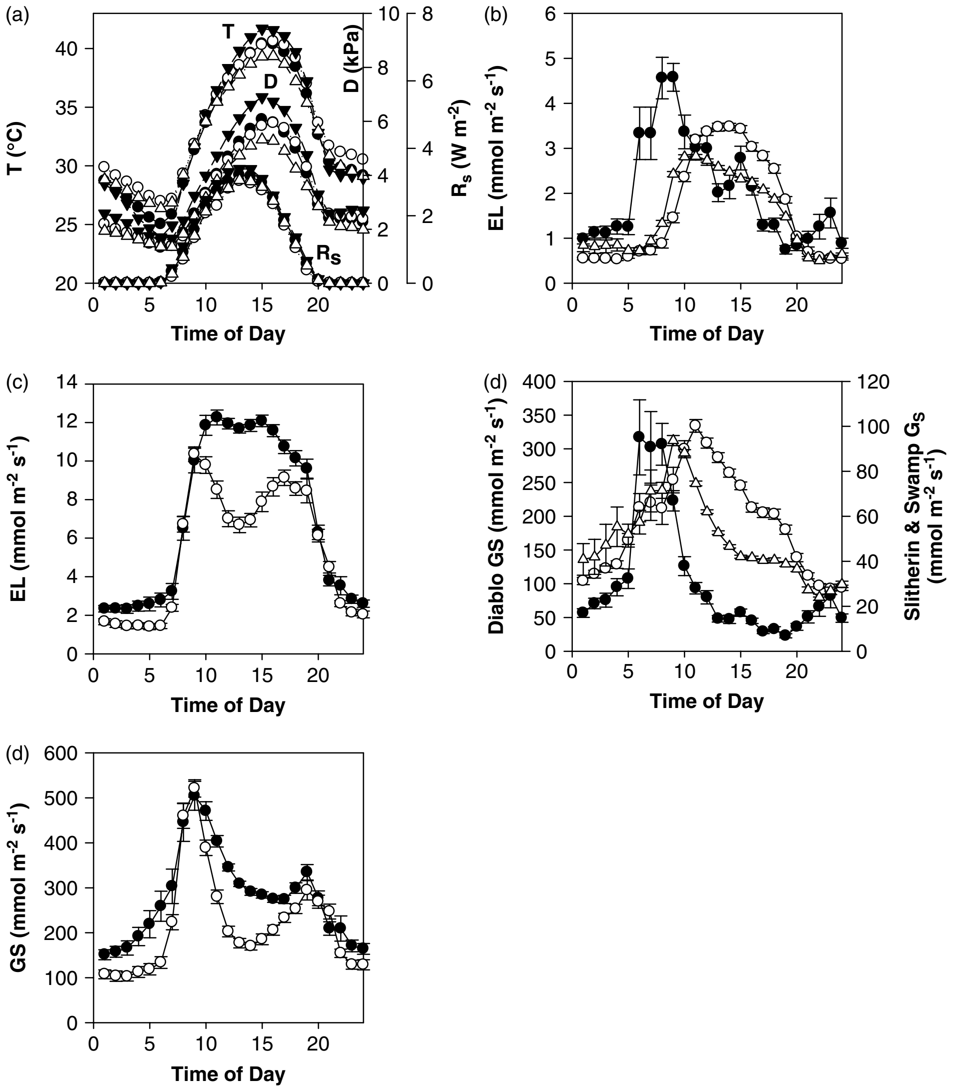

Figure 7. Diurnal curves of climatic variables, transpiration and stomatal conductance at CNWR on the Colorado River. (a) Air temperature (*T*), vapour pressure deficit (*D*), and solar radiation (R_S) during sap flow measurement intervals for saltcedar at Diablo East (closed circles), Slitherin (open circles) and Swamp (closed triangles); and for mesquite and arrowweed at Diablo East (open triangles). (b) Transpiration (E_L) of saltcedar at Diablo East (closed circles), Sliterhin (open circles) and Swamp (open triangles). (c) E_L of arrowweed (open circles) and mesquite (open circles) at Diablo East. (d) Stomatal conductance (G_S) of saltcedar at Diablo East (closed circles), Slitherin (open circles), and Swamp (open triangles). Note different *y*-axis scale for Slitherin and Swamp. (e) G_S for arrowweed (closed circles) and mesquite (closed circles) at Diablo. Data points are hourly values averaged over the measurement period for each plant type and station; bars show standard errors.

the case of saltcedar at Diablo East, significantly negative ($P < 0{\cdot}05$) for other plants and locations.

Diurnal curves for E_L, G_S, and meteorological data are in Figure 7. Mesquite and arrowweed showed severe midday depression of E_L and G_S, with peak values occurring before 10 a.m. and after 5 p.m. Saltcedar at Diablo East and Swamp also had peak E_L and G_S before 10 a.m. and they showed little recovery in the afternoon. Only at Slitherin did saltcedar follow a typical diurnal pattern, with peak E_L at 2 p.m. and peak G_S at noon, indicating less stress than at the other two sites.

^{13}C *enrichment values*

δ^{13}C values in leaf samples from Slitherin (−26·78, SE = 0·31) were significantly ($P < 0{\cdot}05$) lower than leaf samples from Swamp (−24·85, SE = 0·58) or Diablo East (−24·04, SE = 0·58). This analysis supports the LAI and G_S results, suggesting that saltcedar at Swamp and especially at Diablo East are more stressed than plants at Slitherin.

MODIS f_c*, LAI and ET estimates*

MODIS satellite data were used to scale the point measurements of f_c, LAI and ET over larger spatial and longer temporal intervals. MODIS EVI values for individual pixels were strongly correlated with f_c (Figure 8A) and LAI (Figure 8B) values determined for the same areas of coverage on high-resolution imagery. LAI and f_c were also strongly correlated with each other (Figure 8C) as expected since f_c is used in the calculation of LAI from LAPS. Using the linear regression equation of best fit, f_c over the study site by MODIS EVI was 0·801 (SE = 0·023), similar to the mean cover

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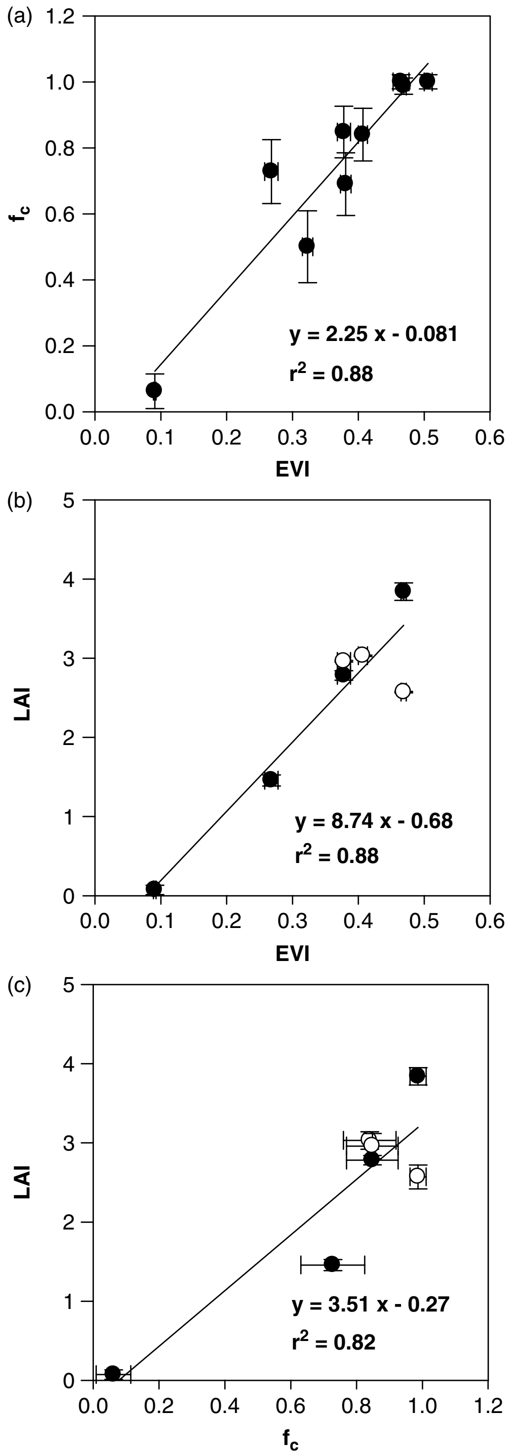

Figure 8. (a) Regression of MODIS EVI on fractional cover (f_c) and (b) LAI and (c) f_c on LAI for vegetation at the CNWR on the lower Colorado River. Closed circles in (b) and (c) are for 2007 data and open circles are from 2006 data (Nagler *et al.*, 2008). Bars show standard errors.

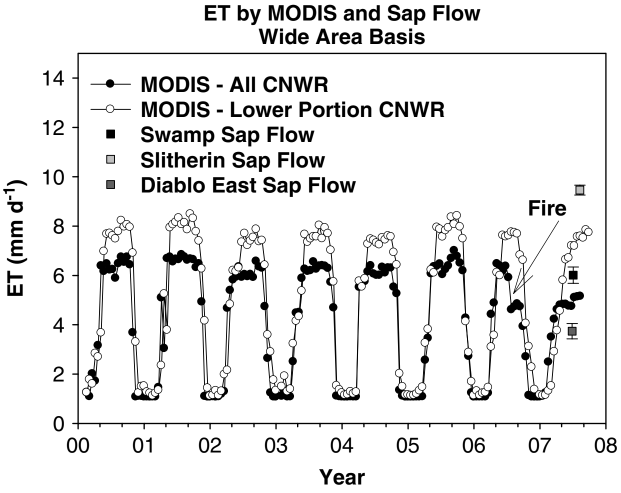

Figure 9. Wide-area, MODIS ET estimates for riparian vegetation at the CNWR, showing the whole refuge and the lower floodplain terrace where Swamp Slitherin and Diablo East plots were located. Also shown are the sap flux estimates of E_G in 2007.

over the plots and of the 2005 estimate from the Quickbird image. LAI estimated by MODIS EVI was 2·68 (SE = 0·09), close to the mean of Licor LAI 2000 measurements at the plots.

MODIS ET estimates varied less across sites than sap flux estimates, but generally matched individual site values (Table V). MODIS ET measured over the lower CNWR study site was 7·41 mm d^{-1} (SE = 0·089) for the period during which sap flow data was collected, 16% higher than the mean ET over the sap flow measurement sites (Table V). However, if the Diablo East sap flux results are excluded the mean sap flow, ET was 7·74 mm d^{-1}, very close to the MODIS estimate.

ET for the two masked areas of CNWR from 2000 to 2007 are in Figure 9. The masked area prepared for the entire CNWR had lower ET rates than the lower CNWR study site due to lower plant cover and EVI values. The effect of a fire in the upper part of CNWR in 2006 is evident in the MODIS ET estimates for that year. Over the whole CNWR in 2007 f_c was 0·424 (SE = 0·019) and LAI was 1·40 (SE = 0·085), reflecting the effects of fire and the presence of relatively sparse riparian areas over parts of the flood plain north of the river channel.

Using MODIS estimates, annual ET was calculated for the entire CNWR for each year from March 15 to November 1 from 2000 to 2006. Mean annual saltcedar ET was stable year-to-year and averaged 1147 mm $year^{-1}$ (SE = 40), while ET_o at Parker, AZ was 2446 mm $year^{-1}$, hence the crop coefficient ($k_c = ET/ET_o$) was 0·47 for saltcedar at CNWR. This is similar to the ratio of E_G to ET_o measured by sap flow sensors in 2007, 0·43.

DISCUSSION

Changes in flood plain vegetation and hydrology over time

The same over-flow channels and marsh areas evident on the flood plain terrace in 1938 were still present in 2005. These were likely ephemeral features when the river was subject to overbank flooding, but they have become permanent, relic landscape features now that overbank flooding has been virtually eliminated on the river. Olmsted and McDonald (1967) documented the increase in ground water salinity and reduction in surface flows brought about by construction of Hoover

Dam and water diversions for agriculture along this stretch of the lower Colorado River. They noted that

Table V. Sap flux and MODIS estimates of plant water use at study sites at the CNWR on the Colorado River.

Plant species/site	Sap flow E_L (kg m^{-2} d^{-1})	Sap flow E_C (kg m^{-2} d^{-1})	LAI (m^2 m^{-2})	Sap flow E_G (mm d^{-1})	MODIS E_G (mm d^{-1})
Saltcedar–Swamp					
Mean	2·35a	7·71a	2·56a	6·01a	7·45a
SE	0·121	0·42	0·04	0·33	0·17
N	23	23	173	23	6
Saltcedar–Slitherin					
Mean	2·56a	9·96b	3·69b	9·46b	8·45b
SE	0·046	0·18	0·08	0·17	0·11
N	43	43	107	43	6
Saltcedar–Diablo East					
Mean	2·89a	5·58c	1·34c	3·74c	5·74c
SE	0·20	0·39	0·04	0·26	0·17
N	16	16	91	16	6
Mesquite–Diablo East					
Mean	8·24b	10·55a	No cover	No cover	NA
SE	0·732	0·93	Data	Data	—
N	27	27	—	—	—
Arrowweed–Diablo East					
Mean	10·92c	16·93d	No cover	No cover	NA
SE	0·501	0·77	Data	Data	—
N	27	27	—	—	—
Saltcedar–Mean	2·60	7·75	2·53	6·40	7·48
SE	0·16	1·27	0·68	1·67	0·27
N	3	3	3	3	3

Sap flux results were expressed as transpiration on a leaf-area basis (E_L), a canopy-area basis (E_C) ($E_L \times$ LAPS), and a ground-area basis (E_G) ($E_L \times$ LAI). MODIS E_G was calculated for the single pixel encompassing each sap flow site averaged over the total period of sap flow collection (June 22–September 4), encompassing 6, 16-day MODIS data collection intervals.
E_L, leaf-area basis; E_C canopy-area basis; E_G ground-area basis.

Table VI. LAI, evapotranspiration (ET), and the salinity in mg l^{-1} TDS that produces half-maximal growth for selected species on western US rivers.

	Saltcedar	Mesquite	Arrowweed	Cottonwood
LAI	2·8[a] 1·5–3·3[b] 2·0–3·9[c] 0·9–4·1[d]	1·9[e] 1·5[c] 1·9–2·4[f]	3·7[a] 1·6[c]	3·5[a] 3·1–3·8[g] 2·5–3·5[h] 1·75–2·75[i]
ET (mm d^{-1})	5·3–11·5[b] 3·7–9·5[c] 6·0–9·0[j] 6–10[k]	5–6[l] 8·2[c]	6·0[m] 10·6[c]	6–12[g] 8–9[j] 4·8–9·3[h] 3·1–5·7[i]
Salt Tolerance	35 000[n]	6000–12 000[o]	16 000[n]	5000[n] 2000–5000[p]

Literature values were selected to represent the range of conditions reported on different river systems, including both stressed and unstressed plants.
[a] Mean of values at eight sites on the lower Colorado River (Nagler *et al.*, 2004).
[b] Range for salt-stressed and unstressed plants on a tributary of the lower Colorado River (Sala *et al.*, 1996).
[c] This study.
[d] Range for plants on the Middle Rio Grande, New Mexico (Cleverly *et al.*, 2002, 2006).
[e] *Prosopis velutina* in a Sonoran Desert riparian corridor (Stromberg *et al.*, 1993).
[f] Savanna mesquites (Ansley *et al.*, 2002).
[g] Range for water-stressed and unstressed, irrigated plots (Nagler *et al.*, 2007).
[h] Salt-stressed and unstressed plants on the lower Colorado River (Pataki *et al.*, 2005).
[i] Range for water-stressed and unstressed plants on Upper San Pedro River (Gazal *et al.*, 2006).
[j] Range on the Middle Rio Grande (Cleverly *et al.*, 2006).
[k] Range for unirrigated and irrigated on the Virgin River, Nevada (Devitt *et al.*, 1997).
[l] Woodland and shrubland mesquites on the Upper San Pedro, Arizona (Nagler *et al.*, 2005c; Scott *et al.*, 2006).
[m] Dense stands on the lower Colorado River (Westenberg *et al.*, 2006).
[n] Greenhouse salt-gradient study (Glenn *et al.*, 1998).
[o] Greenhouse study salt-gradient study (Felker *et al.*, 1981).
[p] Range of salinities in an aquifer producing half-maximal ET of trees on lower Colorado River (Pataki *et al.*, 2005).

salt-tolerant plants such as arrowweed and quailbush had become dominant on the river terraces. Our study area at CNWR was impacted by diversion of the main river channel away from the site. The old river channel north of the study area currently has flows of about 8–15 m^3 s^{-1}, because the majority of river water is now carried by a deep, engineered channel parallel to the old channel (United States Bureau of Reclamation, 2008). By contrast, before Hoover Dam was constructed, the old river channel carried 100–1000 m^3 s^{-1} and frequently flooded the terrace, depending on the stage of the river (United States Bureau of Reclamation, 1996).

The aquifer under the riparian flood plain is now saline, with salinity increasing in proportion to distance from the river channel. Table VI compares physiological properties, including salt tolerance, of the riparian species found on the flood plain. In greenhouse trials, saltcedar had 50% growth reduction on 35 g l^{-1} total dissolved solids (TDS), whereas cottonwood had 50% growth reduction on only 5 g l^{-1} TDS, and mesquite and arrowweed were intermediate. On the basis of the greenhouse studies, the only viable niche for cottonwoods would be near the river channel (e.g. at Swamp), but the vadose zone there has been salinized by the capillary rise of water and accumulation of salts. Without overbank flooding, mesic trees are no longer able to establish on the riverbanks, and saltcedar has become dominant. Away from the river, the aquifer is too saline for cottonwoods and willows and supports mainly saltcedar, interspersed with occasional salt-affected, shrubby mesquites and arrowweed growing as an understory species.

There is no indication that saltcedar has expanded the vegetation zone or grows in higher density than the native species that formerly occupied the terrace. Saltcedar was undoubtedly already present at CNWR in 1938, as it was noted in the Colorado River in Grand Canyon as a species that grew in mixed associations with native trees and shrubs in that year (Clover and Jotter, 1944). We believe that the increased dominance of saltcedar at our study site was due to salinization of the aquifer due to reduced surface flows in the old river, and to lack of overbank flooding to leach salts and germinate new cohorts of trees along the riverbank.

LAI and water use of saltcedar and native species

Saltcedar had higher LAPS than screwbean mesquite and arrowweed plants in this study, as noted also by Sala *et al.* (1996) on the Virgin River in Nevada. However, the mean LAI of saltcedar stands at CNWR were within the range of other tree or shrub associations on other western US rivers (Table VI). The range of LAI values within and among studies was high, and local site conditions rather than species were the most important determinant of LAI. Smith *et al.* (1998) speculated that saltcedar might have systematically higher LAI than native plants on western rivers, leading to increased water consumption. However, literature values show that saltcedar LAI is within the range of native riparian species.

Similarly, Table VI shows that saltcedar ET values are also within the range of other riparian species. As with LAI, ET varied widely within and among studies and local site conditions were more important than species in determining water consumption. In general, riparian ET is about 50% of ET_o on western rivers, regardless of species composition (Nagler *et al.*, 2005c). Since f_c did not change between 1938 and 2005, and saltcedar LAI and ET is within the range of native species, it is logical to conclude that no net increase in water consumption has occurred due to the replacement of native species by saltcedar at our study site.

Environmental controls on transpiration

Leaf-level rates of saltcedar transpiration ranged narrowly, from 2·4 to 2·9 mm m^{-2} d^{-1} among sites, similar to values reported for natural stands of saltcedar in other studies (Sala *et al.*, 1996; Devitt *et al.*, 1997; Horton *et al.*, 2001a,b; Pataki *et al.*, 2005). For example, Sala *et al.* (1996) reported rates of 3·5 mm m^{-2} d^{-1} for saltcedar, mesquite and arrowweed on the Virgin River in Nevada. Similar to this study, Sala *et al.* (1996) reported that saltcedar tended to have relatively constant rates of sap flow at the leaf-level, and that the main determinants of canopy-level and stand-level ET rates were LAI and f_c, respectively. In that study, mesquite and arrowweed had leaf-level rates similar to saltcedar, but in our study mesquite and arrowweed had markedly higher rates than saltcedar, ranging from 8 to 11 mm m^{-2} d^{-1}. Mesquite and arrowweed occur as occasional small, isolated plants in sparsely vegetated areas of CNWR, hence the plants receive light from all sides of the canopy, leading to higher leaf-level transpiration than would occur in closed canopies.

All plants in this study showed evidence of nocturnal transpiration, as E_L and G_S did not go to zero at night. Nocturnal transpiration accounted for up to 36·6% of total daily transpiration for well-watered saltcedar on the Middle Rio Grande (Moore *et al.*, 2008), and was 20–25% of total saltcedar E_L at CNWR. Each morning at dawn, saltcedar foliage was thickly covered with highly saline water of guttation excreted from hydrathodes, as also noted in other studies (Duncan *et al.*, 1993).

Although seasonal trends in E_L as a function of environmental variables are expected, sap flow measurements in this study were restricted to the height of the growing season, and no correlations between daily values of E_L and environmental variables were found. Arrowweed and mesquite had biphasic diurnal curves for E_L and G_S, indicating a moderate amount of midday depression of stomatal conductance (Xu and Shen, 2005). Saltcedar at Swamp and Diablo East lacked a second (afternoon) peak of G_S, which is considered to be a more severe form of midday depression than a biphasic response (Xu and Shen, 2005). G_S at Diablo East was severely depressed after 8 : 30 a.m., setting a limit on E_L and presumably also carbon fixation and growth at this site. Stomatal conductance peaked at about noon at Slitherin, but decreased sharply in the afternoon and did not follow the bell-shaped curves typical of unstressed vegetation. Hence, all the plants appeared to be under stress throughout the summer at CNWR. Devitt *et al.* (1997) also reported peak E_L and G_S between 8 and 10 a.m. for unirrigated saltcedar on the Virgin River.

Saltcedar at Slitherin was clearly in a more favourable environment than at Swamp or Diablo East, as seen by diurnal patters of G_S and E_L, f_c, LAPS and ^{13}C enrichment. The environmental factors controlling saltcedar transpiration at CNWR are not yet clear. Meteorological conditions were extreme, but could not explain the differential response of saltcedar at different sites, because conditions were presumably similar across the flood plain. Aquifer depth differed slightly among sites and showed some seasonal variation, but the aquifer was relatively shallow compared to other studies, in which saltcedar extracted water from as deep as 10 m (Horton *et al.*, 2001a,b, 2003). Salinity also varied among sites, but saltcedar at Diablo East, which showed the greatest stress, had lower ground water salinity than plants at Slitherin, which had the least signs of stress, and all sites were well within the tolerance limit of saltcedar (Glenn *et al.*, 1998; Pataki *et al.*, 2005).

Soil texture in the aquifer differed among sites and can limit the rate of transpiration that can be supported in phreatophytes (Hultine *et al.*, 2006). Sands, as at Diablo East, produce cavitations at the root–soil interface at much lower critical transpiration rates than in heavier-textured soils, as occurred at Slitherin and Swamp (Sperry *et al.*, 1998). Vegetation density over the flood plain was highest in the former marsh areas and secondary channels, even though these areas no longer receive surface flows. It is possible that soil texture differences in these areas are responsible for the higher plant densities in these areas, but further research is needed to determine the limiting factors for plant growth on this flood plain. Ground water temperatures at Diablo East are 2–3 °C warmer than at the other sites, suggesting an influence of the geothermal plume on the aquifer at this site, and perhaps contributing to the inhibition of plant growth (J. Osterberg, unpublished data).

Wide-area estimates of saltcedar ET by MODIS

MODIS vegetation indices can be used to monitor a variety of ecosystem physiological processes (Waring *et al.*, 2006; Glenn *et al.*, 2007, 2008). MODIS EVI estimates of f_c, LAI and ET were generally well-correlated with point measurements made on the ground. The validity of the MODIS ET estimates depends on a high correlation between EVI and transpiration, and on the validity of using maximum daily temperature as a scalar (Nagler *et al.*, 2005c). Sap flow measurements were nearly constant on a leaf-area basis, and variations over the study site were due to variations in LAI and f_c, which were accurately modelled by MODIS EVI. Hourly rates of saltcedar transpiration were strongly correlated with temperature and vapour pressure deficit at Slitherin and Swamp, supporting the use of maximum daily temperature as a scalar. Equation (5) has a non-linear response of E_G to T_{max}, consistent with the observed partial stomatal closure (decrease in G_S) as D increased during the day. However, saltcedar at Diablo East were more stressed than at other sites and did not respond to temperature or vapour pressure deficit, and the MODIS estimate of ET was higher than that measured by sap flow sensors.

MODIS ET estimates support flux tower studies (Devitt *et al.*, 1998; Cleverly *et al.*, 2002, 2006; Westenberg *et al.*, 2006) showing a rather narrow range of wide-area, annual saltcedar ET, 800–1400 mm year^{-1}, with a mean value of 1000 mm year^{-1}, about half of ET$_o$. As noted by Owens and Moore (2007), early reports of very high water use by saltcedar were likely erroneous, and projections of high water salvage potential through saltcedar removal are unrealistic.

CONCLUSIONS

At CNWR, a formerly mixed mesic and saline flood plain, with intermittent flooding supporting a variety of shrubs and trees, has become a permanently saline system as in other human-impacted arid wetlands (Jolly *et al.*, 2008), supporting in this case mainly saltcedar. Eliminating saltcedar would not, by itself, lead to the establishment of desirable replacement species, water savings, or improvement in habitat over most of the floodplain (Shafroth *et al.*, 2005). Restoration efforts to support wildlife habitat should be aimed at creating a mixed tree–saltcedar zone along the banks of the river, where ground water salinities are permissive. This would require periodic overbank flooding or irrigation during the establishment year but would not necessarily require saltcedar removal, as trees outcompete saltcedar shrubs under favourable conditions and eventually overtop them (Sher *et al.*, 2002; Nagler *et al.*, 2005b; Dewine and Cooper, 2008). A mixed habitat of saltcedar with 10–20% native overstory trees and proximity to water provides optimal bird habitat (Hinojosa-Huerta, 2006; Hinojosa-Huerta *et al.*, 2006, 2008; Sogge *et al.*, 2008; van Riper *et al.*, 2008), which are the main species of concern on the lower Colorado River (Lower Colorado River Multi-species Conservation Program, 2004). However, a restored plant community would likely use more, rather than less, water than the current saltcedar stands.

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