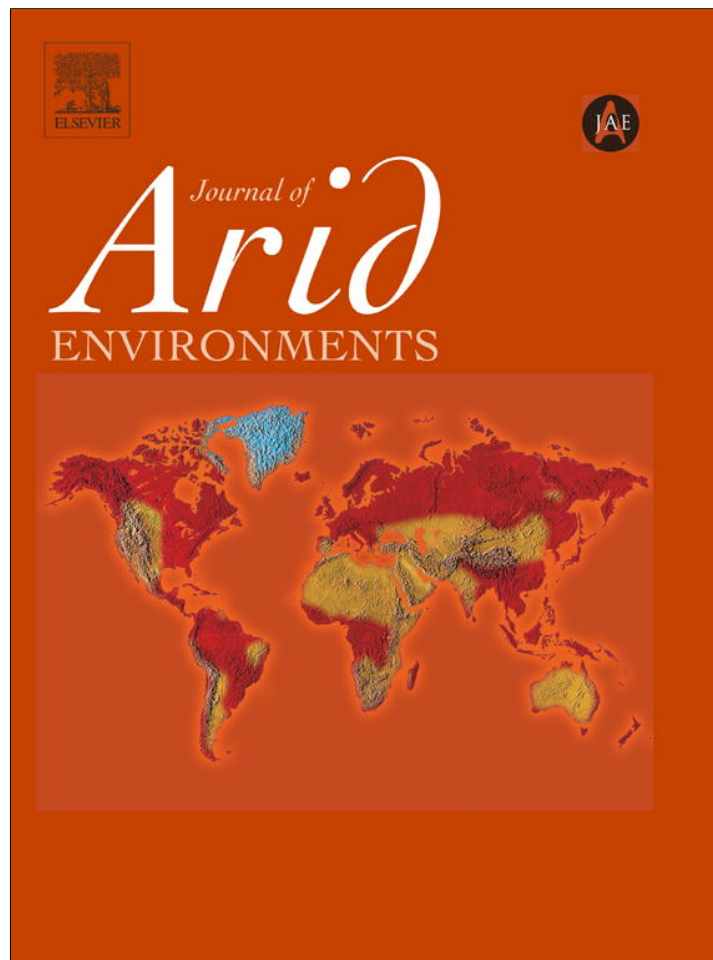




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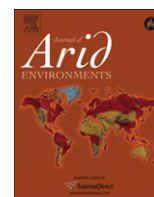
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Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenvFloral ecology and insect visitation in riparian *Tamarix* sp. (saltcedar)D.C. Andersen^{a,*}, S.M. Nelson^b^a United States Geological Survey, Fort Collins Science Center, c/o Bureau of Reclamation, 86-68220, PO Box 25007, Denver CO 80225, USA^b Bureau of Reclamation, 86-68220, PO Box 25007, Denver, CO 80225, USA

ARTICLE INFO

Article history:

Received 14 August 2012

Received in revised form

30 November 2012

Accepted 6 March 2013

Available online

Keywords:

Coniatus splendidulus

Desert riparian

Flowers

Ground water depth

Las Vegas Wash

Nectar

Pollination

Saltcedar

Soil moisture

Tamarix ramosissima

ABSTRACT

Climate change projections for semiarid and arid North America include reductions in stream discharge that could adversely affect riparian plant species dependent on stream-derived ground water. In order to better understand this potential impact, we used a space-for-time substitution to test the hypotheses that increasing depth-to-groundwater (DGW) is inversely related to *Tamarix* sp. (saltcedar) flower abundance (*F*) and nectar production per flower (*N*). We also assessed whether DGW affected the richness or abundance of insects visiting flowers. We examined *Tamarix* floral attributes and insect visitation patterns during 2010 and 2011 at three locations along a deep DWG gradient (3.2–4.1 m) on a floodplain terrace adjacent to Las Vegas Wash, an effluent-dominated Mojave Desert stream. Flower abundance and insect visitation patterns differed between years, but no effect from DGW on either *F* or *N* was detected. An eruption of a novel non-native herbivore, the splendid tamarisk weevil (*Coniatus splendidulus*), likely reduced flower production in 2011.

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1. Introduction

Streamside plant communities commonly contain species that require animals for pollination. Although the woody, wind-pollinated poplars and cottonwoods (*Populus* sp.) structurally dominate many riparian ecosystems in cold- and warm-temperate deserts of the northern hemisphere, insect-pollinated woody plants such as mesquite (*Prosopis* sp.) can be major components of warm desert riparian vegetation in both the northern and southern hemisphere (Pasicznik et al., 2001; Simpson et al., 1977). Insect-pollinated willows (*Salix* sp.) and various entomophilous herbaceous species are common in desert riparian settings where flow is perennial. The structurally dominant woody riparian plants in some south-temperate drylands are large, animal-pollinated trees. For example, in Australia, river red gum (*Eucalyptus camaldulensis*) is likely pollinated by non-flying mammals (Carthew and Goldingay, 1997) as well as arthropods. Riparian pollinators are drawn to zoophilous plants by the food and/or water present in pollen, nectar, and other exudates. The floral traits of these plant

species, including the quality and quantity of nectar, can strongly influence both the diversity of flower visitors and pollination success (Willmer, 2011).

Nectar is an aqueous solution, and thus one of the factors that affects nectar production is plant-available soil moisture (Carroll et al., 2001; Zimmerman and Pyke, 1988). In the semiarid and arid western United States, climate change is already altering hydrology, and climate model projections include reductions in annual maximum as well as base flows in many streams, even if water extraction for human use remains stable (Perry et al., 2012). Because floodplain ground water level in many reaches is determined by river stage and thus discharge, flow reduction will increase depth to ground water (hereafter, DGW) on river floodplains, and thereby potentially reduce soil water availability to phreatophytic riparian plants. The extent to which a reduction in soil water availability will affect riparian plant floral ecology, riparian pollinators, and plant–pollinator interactions is largely unknown, because we lack information on most plant species' response to shifts in DGW. A reduction in flower production may be a common consequence of water stress (Inouye et al., 2003; Miller-Rushing and Inouye, 2009; Tepedino and Stanton, 1980).

In order to better understand how climate-induced hydrological shifts may affect dryland riparian ecology, we assessed flower

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abundance, nectar production, and insect visitation to flowers along a riparian DGW gradient in a stand of riparian *Tamarix* sp. (saltcedar) in the Mojave Desert along Las Vegas Wash, near Las Vegas, Nevada. *Tamarix* is currently the most common non-native woody species in riparian areas of southwestern North America (Friedman et al., 2005) and its effects and control are of major management concern (Shafroth et al., 2009). In this region, the species blooms from spring until autumn, but there is little quantitative information on variability in *Tamarix* flower production, or the factors affecting it, and few studies have examined *Tamarix* pollinators (Durst et al., 2008; Wiesenborn et al., 2008).

2. Materials and methods

2.1. Study area

Las Vegas Wash (LVW) drains the Las Vegas metropolitan area and surrounding 1550 km² Las Vegas Valley, in the Mojave Desert of southern Nevada. The area has a mean annual precipitation of <11 cm, distributed bimodally with peaks produced by winter frontal storms in February and localized thunderstorms associated with the North American monsoon in July and August (1981–2010 data; Gorelow, 2005). The mean extreme minimum and maximum daily temperatures in July are 19.6 °C (range 13.3–25.6 °C) and 44.7 °C (range 41.7–47.2 °C). In January, the same values are –4.5 °C (range –13.3–2.8 °C) and 20.3 °C (range 11.1–25.0 °C), respectively (National Weather Service Station 264436, 1940–2012 data). Although historically an intermittent or interrupted-perennial stream, the lowest 16 km of LVW, including the study area, now features a nearly constant discharge due to inflows of treated municipal wastewater from three facilities that together add about $550 \times 10^3 \text{ m}^3 \text{ d}^{-1}$ ($6.4 \text{ m}^3 \text{ s}^{-1}$) to the channel (http://www.lvwash.org/html/what_flow_reclaimed.html accessed 28 Nov 2011). Flash floods occur when storm runoff adds to the effluent inflow. Severe channel-bed degradation and bank erosion has occurred over the past 50 years (Duan and Scott, 2007), and some former floodplain surfaces, including the study area, are no longer subject to inundation. *Tamarix* sp. invasion and other vegetation shifts have accompanied the hydrological and geomorphological changes. The *Tamarix* present along LVW likely consists of *Tamarix ramosissima*, *Tamarix chinensis*, or their hybrids (Friedman et al., 2008; Gaskin and Schaal, 2002).

We worked in a *Tamarix* stand along the effluent-dominated portion of the LVW, ~200 m upstream of an erosion-control check-dam and a USGS stream gaging station (# 09419700, Las Vegas Wash at Pabco Road near Henderson, NV) (Fig. 1). The stand consisted of dense, mature *Tamarix* ranging from 4.5 to 7.5 m in height intermixed with patches of quailbush (*Atriplex lentiformis*). Herbaceous vegetation was sparse. We selected three point locations (hereafter referred to as G1, G2, and G3) along a presumptive water table elevation gradient running perpendicular to the channel. Each point was in a small open area surrounded by *Tamarix* and progressively farther from the rip-rapped channel margin (Fig. 1). Soil stratigraphy (layers of silt and clay intermixed with layers of gravel) was similar throughout the area, based on observations made while installing a monitoring well in each of the three openings. We selected six representative *Tamarix* trees for monitoring at each location.

2.2. Stream discharge, ground water dynamics, and soil moisture changes

Real-time (15-min) and historic (daily mean) discharge data for Las Vegas Wash are available from the USGS Pabco Road gage. We measured water level at 1-hr intervals in each well beginning on 22



Fig. 1. Rectified aerial image showing locations G1, G2, and G3 (large circles) along the depth-to-groundwater gradient perpendicular to Las Vegas Wash, Nevada. The positions of some of the individual *Tamarix* (small circles) monitored at each location are also shown. Surface water, flowing from left to right, is confined within rip-rapped banks on the inner border of the construction roads. The USGS gaging station (# 09419700) is located in the bottom right of the image, immediately upstream of the concrete erosion-control structure.

April 2010, a few days after well installation, using Onset® Hobo U20-001-04 pressure sensor/loggers. Barometric corrections were based on readings from a fourth sensor/logger hung above the water in Well G3. Each well consisted of commercial 5-cm PVC narrow-slotted well casing installed vertically in one end of a short trench excavated (and backfilled) by a backhoe.

We used a real-time kinematic global positioning system (GPS; Trimble R8) to determine horizontal and elevational position of the ground surface at each tree, each well casing top (TOC), and the water surface at the channel margin on 2 March 2011. Positional accuracy (x, y, z) was estimated to be ± 2 cm (Terry Waddle, USGS, personal communication). We corrected water table elevational at each well relative to the common (GPS) datum from manual measurement of depth from the TOC to the water table and then referenced water table elevation changes, measured with the HOBO sensors, to that same datum. These data allowed us to calculate changes in DGW at each monitored tree.

To index surface soil moisture conditions, we installed three gypsum soil moisture blocks (Delmhorst Instrument Co. GB-1) at widely spaced positions near the *Tamarix* drip line around each well. Blocks were placed at a 30-cm depth in soil undisturbed by well installation. Percentage saturation was read with a Delmhorst Model KS-D1 moisture meter during each site visit.

2.3. Flower abundance

We monitored *Tamarix* flower abundance at 1- to 2-month intervals during the 2010 and 2011 growing seasons. *T. ramosissima* bear small (<2 mm across) white-to-pink flowers on racemes in either simple or compound panicles. To estimate panicle-level flower abundance, we collected at least one panicle from each of three separate branches on each of the six trees at each location when flowers were abundant, and fewer when flowers were uncommon. We collected panicles from 1.5 to ~4 m above the ground, without regard to aspect, and counted the number of racemes on the panicle and the number of buds, flowers, and fruits on a raceme from each of the lower, middle and upper portion of the panicle. In cases where compound panicles were present, several representative panicles were collected from lower, middle, and upper positions from within the compound panicle. We estimated the overall abundance of panicles on each tree visually, by classifying the proportion of the outer surface covered with blooming flowers as either none, $\leq 1\%$, $>1\%$ but $\leq 10\%$, $>10\%$ but $\leq 60\%$, and

>60%. For a site-level index of flower abundance, we assigned to each tree the midpoint of its range class (i.e., 0, 0.5, 5.5, 35, or 80) and summed the values for the six trees.

2.4. Nectar production

We assessed *Tamarix* nectar production during each site visit, using methods for flowers with low nectar volume (Morrant et al., 2009). We collected 100 fresh, fully opened flowers by pinch-cutting the pedicel at the raceme rachis with forceps, and then vigorously shook the flowers in 1 ml of distilled water for 1 min. We performed the same procedure using unopened, late-stage flower buds to assess whether sugar content was affected by the flower collection process. We presumed no nectar would be present in the buds. Flower collection time ranged from 2- to 7-hr after sunrise. Nectar sugar concentration (sucrose equivalent) was measured using a Bellingham & Stanley refractometer (Eclipse model 0-45 Brix). We tested for differences along the DGW gradient using paired *t*-tests with Bonferroni corrections. On several visits we also assessed nectar concentration in flowers from *Tamarix* growing in the general area but immediately adjacent to the surface water margin, where we judged DGW to be < 1 m.

2.5. Arthropod floral visitors

Arthropods potentially important as pollinators of *Tamarix* were documented during each visit using visual surveys that began between 0900 and 1400 h. The three study locations were sequentially monitored, each for a 10-min period (total of 30-min each location) with the time allocated among the 6 focal trees. The kinds and abundances of insects noted present on flowers were documented, with voucher specimens collected in most cases. Arthropods not on flowers were ignored. We considered each visit (sampling occasion) during a growing season to be an independent replicate and used 2-factor ANOVA to test for differences in mean pollinator abundance and taxa richness between the three locations and two years. We used principle components analysis (PCA) to summarize and describe trends in the data.

3. Results

3.1. Climatology and surface and ground water hydrology

The latter part of winter 2009–2010 was wet, but little rain fell during the 2010 *Tamarix* growing season (April thru October; Fig. 2A). In contrast, the 2011 growing season featured substantial monsoon-related (July) precipitation. The moisture block data (Fig. 2B) indicated that surface soil moisture was recharged by winter precipitation and subsequently declined throughout the growing season in both 2010 and 2011. The pattern of recharge and decline at G1 differed from that at G2 and G3 (Fig. 2B), suggesting environmental conditions at G1 differed in some way from those at G2 and G3.

Discharge data indicated that flows during the study period were relatively uniform, with a daily mean of $\sim 8 \text{ m}^3/\text{s}$, punctuated by several 70–100 $\text{m}^3 \text{ s}^{-1}$ flood events (Fig. 3). The water table in each well rapidly rose and fell in response to each flood pulse (Fig. 3). However, after each of the November and December 2010 events the post-flood “base” water table level was higher than the pre-flood base, presumably due to storm-related channel aggradation raising the local stream stage. A dredging operation in March 2011 to remove sediment and vegetation immediately upstream of the erosion control structure (Fig. 1) lowered the local base stage, which in turn lowered ground water levels about 15 cm (Fig. 3).

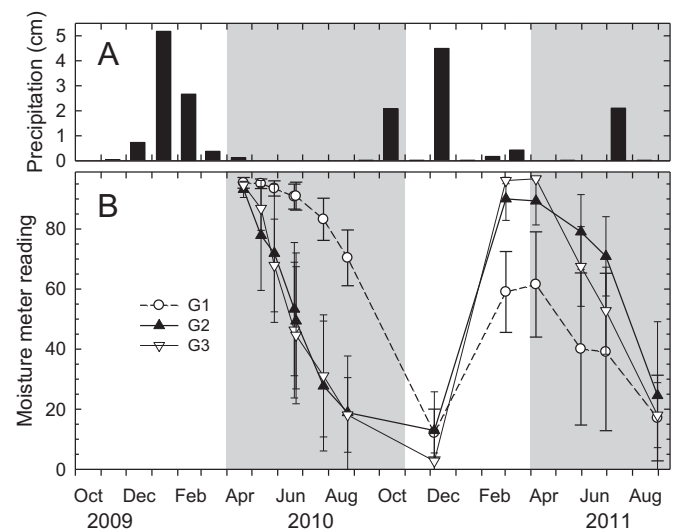


Fig. 2. (A) Total monthly precipitation measured in the Las Vegas metropolitan area [climate station Las Vegas WSO Airport, Nevada (264436)] immediately prior to and thru the period when *Tamarix* flowers were monitored. The growing season months (April thru October) are shaded. (B) Temporal pattern of surface soil moisture under *Tamarix* at sites G1, G2, and G3. Plotted values are means $\pm$ SE of readings for moisture blocks ($n = 3$) installed at a 30-cm depth.

3.2. *Tamarix* stand structure and depth-to-groundwater gradient

The trees (aboveground stems) monitored at G1, G2 and G3 ranged in size (diameter at approximately breast height, DBH) from 9.5 to 32.5 cm. There was a non-significant trend for individual trees to become smaller from G1 to G3 (Table 1; ANOVA: $F = 0.153$; $df = 2,15$; $P = 0.86$). DGW under the 18 monitored trees ranged from 3.21 to 4.31 m when surveyed on 2 March 2011, with a gradient in mean DGW increasing from 3.2 m at G1, nearest the channel, to 4.1 m at G3 (Table 1). LVW flows had been stable during the two months prior to the survey, indicating the gradient was not transient, and the direction of the gradient supported our assumption that LVW discharge level determined ground water level under the *Tamarix*. The short response time between storm-driven change in LVW discharge and ground water dynamics (Fig. 3) suggests that surface and ground water levels are tightly coupled.

3.3. Floral biology

Flowers were abundant at G1, G2 and G3 in April 2010 (Fig. 4, Panel A). At that time, the mean total number of flowers in an individual raceme, i.e., including all phenological stages from bud to fruit, varied among the three locations (ANOVA: $F = 6.47$; $df = 2, 142$; $P = 0.002$), but only G2 ($\bar{x} = 44.0$) and G3 ($\bar{x} = 33.1$) differed significantly (Bonferroni pairwise comparisons: $P = 0.001$) (Fig. 4B). The number of blooming flowers per raceme did not differ among locations (ANOVA, $P = 0.61$) (Fig. 4C). We estimated that an individual (simple) panicle contained $22.1 \pm 2.4 \text{ SE}$ ($n = 48$) racemes and that each compound panicle was made up of 18.7 ± 4.8 ($n = 6$) simple panicles. Thus, the mean total production from a compound panicle on that date was 15,700 flowers. Based on the size of individual compound panicles relative to the size of an entire tree's surface area, we conservatively estimated the total number of compound panicles on a tree to range between 20 and 50.

The number of blooming flowers per raceme tended to rise over the growing season (Fig. 4C), but this value did not differ among the locations on any survey date (separate ANOVAs, all $P \geq 0.15$). Similarly, no difference in the number of racemes per panicle was evident among locations in comparisons made in each of April and

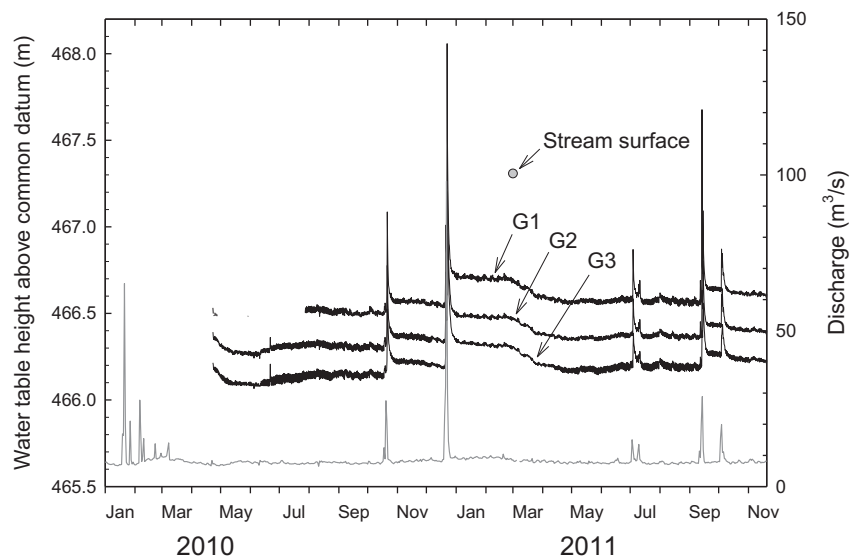


Fig. 3. Water table elevation at locations G1, G2, and G3 (black lines), stream water surface elevation from our 2 March 2011 survey (circle), and daily mean discharge as measured at the nearby USGS gage (gray line at bottom) along Las Vegas Wash, Nevada. The water table data are the hourly average plotted at ~8-hr intervals. Note the post-storm rise in the water table elevation in October and December 2010 and the March 2011 decline at all three locations.

June 2010 and in June 2011 (separate ANOVAs; all $P \geq 0.19$), nor was there a consistent trend among the sites across those dates (Fig. 4D).

Spring floral abundance and phenology differed between 2010 and 2011. Seven of the 18 monitored trees were classified as having “abundant” open flowers on 8 April 2010, whereas one year later (5 April 2011), only one tree was so classified, and only 4 trees were classified as having abundant buds. The site-level index of blooming flower abundance indicated blooms were most abundant at G1 during the 2010 growing season, with flower numbers lower but more or less equal at G2 and G3 (Fig. 4A). A similar pattern, but with flower abundance reduced at all sites, was evident early in the 2011 growing season (April), but by mid-summer Site G3 appeared to harbor most of the flowers in bloom (Fig. 4A).

We observed a universal decline in the visual appearance of *Tamarix* foliage “thickness” in 2011, as well as the death of one monitored tree and branch loss (>10% of the canopy) on two others. At the 30 June 2011 visit, we documented the presence of a herbivorous insect, the splendid tamarisk weevil (*Coniatus splendidulus* Fabricius, 1781) on several of the monitored trees. Although we did not estimate weevil abundance, the species’ unusual pupation cages were evident on the foliage of most monitored trees by August 2011.

3.4. Nectar production

Nectar was never observable in individual flowers, suggesting the volume was extremely low throughout the growing season. Sugar was present in slurries made with flowers from both morning and mid-day collections (Table 2). However, the sugar

Table 1

Mean ($\pm$ SE) *Tamarix* size and depth to the water table at the four locations along the depth-to-groundwater gradient where *Tamarix* flowers were monitored in Las Vegas Wash, Nevada. Water table elevation is for midday, 22 April 2010.

Site	n	Tree diameter at breast height (cm)	Depth to the water table at tree (m)
G1	6	21.6 (2.39)	3.19 (0.049)
G2	6	20.6 (3.19)	3.37 (0.074)
G3	6	19.5 (2.34)	4.07 (0.048)

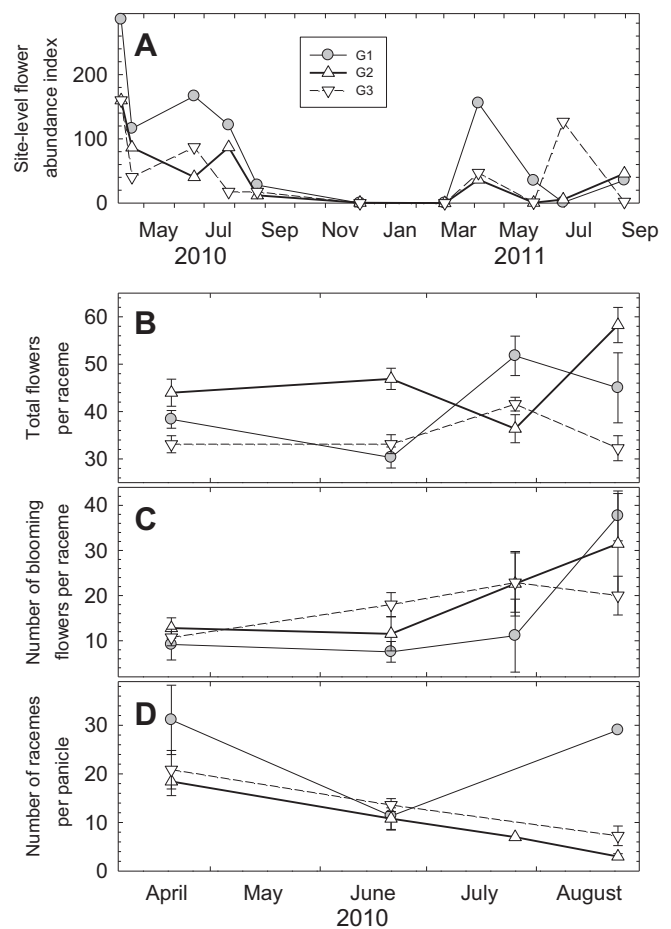


Fig. 4. *Tamarix* floral production at sites G1, G2, and G3 along a depth-to-groundwater gradient (DGW) near Las Vegas Wash, Nevada. G1 has the smallest DGW and G3 the largest. (A) Site-level index of blooming flower abundance for both 2010 and 2011 growing seasons. (B) Mean ($\pm$ SE) number flowers in all phenological stages on individual racemes. (C) Mean ($\pm$ SE) number of blooming flowers on individual racemes. (D) Mean ($\pm$ SE) number of racemes per individual (simple) panicle.

Table 2

Nectar concentrations (% sucrose equivalent) found in the liquid from slurries made from 100 fresh *Tamarix* blossoms. Sites G1–G3 are located along a depth-to-groundwater (DGW) gradient, with G1 having the smallest DGW. “Stream margin” refers to flowers collected at nearby sites where DGW was much smaller than at G1. Tabulated value is the mean or range, with sample size in parentheses.

2010	Time of day ^a	Site			2011	Time of day	Site			
		G1	G2	G3			Stream margin	G1	G2	G3
21-Apr	08:00–13:00	– ^b	– ^b	– ^b	7-Apr	09:00–10:30	0.5 (2)	0.25–1.0 (2)	0.5 (1)	0.5 (3)
23-Jun	10:00–11:00	0.0 (1)	0.0 (2)	–	30-Jun	14:00–15:00	0.0 (2)	–	0.0 (4)	0.0 (4)
27-Jul	12:30–13:30	0.5 (1)	0.5 (1)	0.5 (1)						
25-Aug	08:00–09:00	0 (2)	0.12 (2)	0.25–0.5 (2)						
25-Aug	11:00–12:00	0.25 (2)	0.06 (3)	0.06–0.12 (2)						

^a Sunrise times for 21 Apr, 25 Jun, 27 Jul and 25 Aug are 06:00, 05:25, 05:44, and 06:07.

^b We have no quantitative values for 21 April 2010, but a visual inspection of ~400 flowers resulted in no unambiguous detection of nectar.

concentrations varied inconsistently through the season and no difference was detected along the DGW gradient ($P \geq 0.63$). The nectar concentration in flowers collected from plants growing at the stream margin, zero to 0.5%, was essentially the same as that in flowers from the monitored plants (Table 2). No sugar was detected in the flower bud assay.

3.5. Arthropod pollinators

Neither arthropod richness nor abundance differed among locations along the DGW gradient, nor did we detect a *location* $\times$ *year* interaction (Table 3). Abundance, but not richness, differed between years (Table 3). Abundance per sampling occasion was much higher in 2010 ($\bar{x} = 21.0$) compared to 2011 ($\bar{x} = 7.6$). Mean richness per occasion in 2010 was 4.1 and in 2011 was 3.7. Total richness was similar between the years, with 24 taxa detected in 2010 and 26 detected in 2011. Overall, 22 families/superfamilies and 44 taxa used *Tamarix* flowers (Table 4).

The patterns resulting from PCA indicated that pollinator communities differed between 2010 and 2011 (Fig. 5). Eigenvalues were 0.916 for the first axis and 0.037 for Axis 2, with 95.3% of species data variance explained. Axis 1 sample scores were highly correlated with insect abundance ($r = 0.95$, $P < 0.001$) and richness ($r = 0.50$, $P = 0.013$). Most of the 2010 samples are in the positive portion of Fig. 5, whereas all of the 2011 samples are in the negative part. The two years also featured different taxa. For example, a wasp (Sphecidae-5), was the most abundant ($n = 12$) member of this family and was only detected in 2010. Other taxa within this family were seen only in 2011. A total of twenty individual butterflies representing five families were detected in 2010, whereas no butterfly was recorded in 2011. Only 13.6% of taxa were recorded in both years.

Table 3

Results of 2-factor ANOVA for each of richness and abundance of arthropods using *Tamarix* flowers at three locations along a depth-to-groundwater gradient on the Las Vegas Wash floodplain during the 2010 and 2011 growing seasons.

Source	DF	SS	MS	F	P
Richness					
Year	1	5.042	5.0417	0.49	0.4912
Location	2	4.750	2.3750	0.23	0.7948
Year*location	2	6.083	3.0417	0.30	0.7459
Error	18	183.750	10.2083		
Total	23	199.625			
Abundance					
Year	1	1426.04	1426.04	6.44	0.0206
Location	2	125.08	62.54	0.28	0.7571
Year*location	2	104.08	52.04	0.24	0.7928
Error	18	3983.75	221.32		
Total	23	5638.96			

Grand Mean 3.6250 CV 88.14.

Grand Mean 13.292 CV 111.93.

The decline in total visitor abundance from 2010 to 2011 reflected declines in most visitor taxa. For example, 181 European honeybees (*Apis mellifera*) were detected in 2010, whereas the same sampling effort resulted in detection of only 17 in 2011. Casual observations suggested these declines were restricted to the monitored *Tamarix* trees. For example, large numbers of European honeybees were observed at the stream margin in March 2011, but none were found on *Tamarix* trees just a few meters distant. A

Table 4

Kinds and abundances of arthropods observed on *Tamarix* flowers at the Las Vegas Wash study site during the 2010 and 2011 growing seasons.

Order/Family/or Superfamily	Taxon	Abundance	
		2010	2011
Pieridae	<i>Colias eurytheme</i>	2	0
Pieridae	<i>Pieris rapae</i>	1	0
Lycaenidae	<i>Brephidium exilis</i>	1	0
Lycaenidae	<i>Leptotes marina</i>	2	0
Hesperiidae	<i>Ochlodes yuma</i>	14	0
Chrysomelidae	Chrysomelidae 1	0	1
Dermestidae	Dermestidae 1	13	1
Staphylinidae	Staphylinidae 1	0	1
Bombyliidae	Bombyliidae 1	1	0
Bombyliidae	Bombyliidae 2	0	1
Calliphoridae	Calliphoridae 1	0	6
Conopidae	Conopidae 1	1	0
Diptera	Diptera A	0	1
Diptera	Diptera B	0	1
Diptera	Diptera C	0	1
Diptera	Diptera D	0	1
Syrphidae	Syrphidae 1	1	2
Syrphidae	Syrphidae 2	0	1
Syrphidae	Syrphidae 3	1	0
Andrenidae	<i>Andrena</i> 1	0	1
Andrenidae	<i>Andrena</i> 3	0	1
Andrenidae	<i>Andrena</i> B5	0	1
Apidae	<i>Apis mellifera</i>	181	17
Apidae	<i>Ceratina arizonensis</i>	2	3
Apidae	<i>Melissodes</i> sp.	1	0
Chalcidoidea	Chalcidoidea 1	0	1
Chrysidae	Chrysidae 1	0	1
Colletidae	<i>Hylaeus mesillae</i>	0	1
Halictidae	<i>Agapostemon melliventris</i>	1	0
Halictidae	<i>Agapostemon obliquus</i>	1	0
Halictidae	<i>Lasioglossum (Dialictus)</i> sp. 1	2	10
Halictidae	<i>Lasioglossum (Evylaeus)</i> sp. 1	0	3
Halictidae	<i>Nomia m. melanderi</i>	3	0
Ichneumonoidea	Ichneumonoidea 1	0	2
Ichneumonoidea	Ichneumonoidea 2	0	2
Ichneumonoidea	Ichneumonoidea 3	0	3
Megachilidae	<i>Megachile (Eutricharaea)</i> sp. 1	4	0
Pompilidae	Pompilidae 1	1	0
Sphecidae	Sphecidae 1	2	0
Sphecidae	Sphecidae 2	1	0
Sphecidae	Sphecidae 3	1	0
Sphecidae	Sphecidae 4	0	1
Sphecidae	Sphecidae 5	12	0
Vespidae	<i>Polistes</i> sp.	4	3

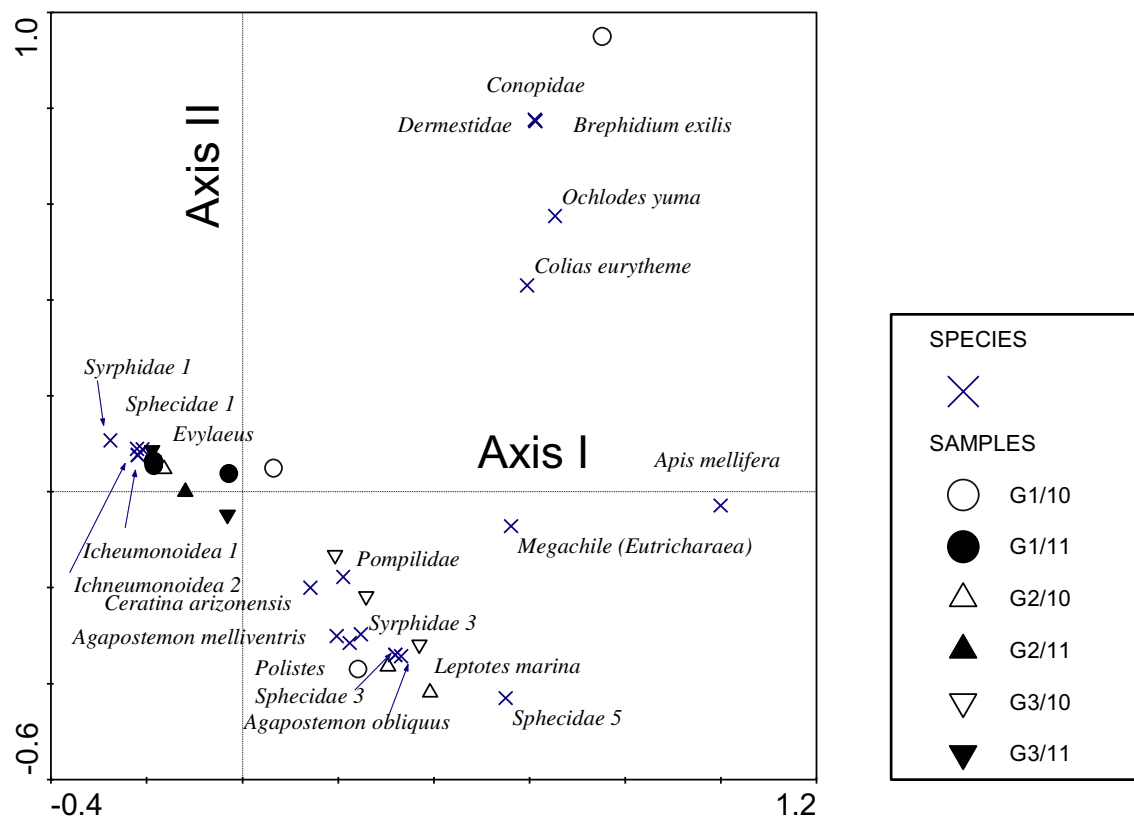


Fig. 5. Principle components analysis of kinds and abundances of insect visitors at *Tamarix* flowers recorded at three locations (G1, G2, and G3) along a depth-to-groundwater gradient (DGW) at the Las Vegas Wash study site. G1 has the smallest DGW and G3 the largest. Data are for three sampling occasions in each of 2010 (open symbols) and 2011 (filled symbols) growing seasons. Samples from most of 2011 are overlain in the far left of the diagram, along with those from April 2010. The distinctive July 2010 sample from G1 is at the top of the plot. Only taxa with 5% fit are presented.

similar pattern was noted in May 2011, when numerous bees, flies, and butterflies were observed collecting nectar on a catclaw acacia (*Acacia greggii*) growing near the *Tamarix* stand, but only five visitors were noted at *Tamarix* trees during 1.5 h of surveying.

Locations differed in taxa found on sampling occasions to a greater extent in 2010 than in 2011, leading to a large separation along Axis II (Fig. 5). In 2011, locations were all tightly clustered together (Fig. 5), suggesting very little difference in the taxa mix over the sampling year. This was likely caused by the few individuals present and absence of a gradient in abundance over the course of the growing season. Samples at the negative end of Axis I all contained very few insects. In general no location had a characteristic pollinator community that would differentiate it from another location. However, the July 2010 sample at G1 contained large numbers of dermestid beetles (*Dermestidae*), which differentiated this location from others (Fig. 5).

4. Discussion

4.1. Flower production

Despite the importance of *Tamarix* spp. as a non-native tree of southwestern riparian ecosystems (Shafroth et al., 2009), its floral ecology remains incompletely understood. Horton (1957) reported that flowers first appear in racemes produced near the tip of the prior-year's branches, and subsequently in panicles at or near the ends of new (current-year) stems. Multiple flowering peaks are a normal occurrence during each growing season (Horton, 1957; Horton and Flood, 1962; Tomanek and Ziegler, 1962). Tomanek and Ziegler (1962:10), working in western Kansas, noted that a

"flowering branch" (presumably equivalent to a raceme) 8-cm long "often" supported an average of 50–60 flowers. They noted that branches of different age produced flowers at different times, and noted that a few branches "contained all stages from flower buds to mature seeds." Our site-level (Fig. 4A) and tree-level (Fig. 4B–D) observations on flower abundance corroborate these findings, although in most cases we found fewer flowers per raceme (Fig. 4B). Our data may be unique in allowing quantification of the common statement that *Tamarix* flower abundance can be "extremely large." For example, our flower and raceme count data for April 2010 indicate that a tree with 35 compound panicles, which we consider conservative, would be supporting 550,000 flowers.

Our failure to detect a relationship between DGW and flower abundance may be a consequence of the large DGW values at the sites we examined (Table 1). Horton et al. (2001a, b) reported evidence of water stress in Sonoran Desert *Tamarix* when DGW was greater than about 2.5 m, and possibly less, depending on the DGW conditions the plants had been exposed to. Nagler et al. (2009) concluded on the basis of physiological and isotopic measurements that *Tamarix* were stressed at a site where DGW ranged from 2.5 to 3.3 m. Nagler et al. (2009) dismissed—we think prematurely—DGW as a contributing factor, but their data were inadequate to identify an alternative agent. Our minimum DGW value (3.2 m at G1) suggests that all 18 monitored trees at G1, G2, and G3 may have been experiencing some level of moisture stress.

An alternative explanation for our result is that the DGW-flower abundance relationship is weak or non-existent along the gradient, which would be the case if trees were not water stressed. Assuming, as argued above, that our DGW values were sufficient to

induce water stress, some and perhaps complete relief from that stress could have arisen from trees relying on precipitation rather than, or in addition to, stream-derived ground water. This argument is given some support by the high level of surface soil moisture under *Tamarix* at the start of each growing season and its subsequent decline (Fig. 2B), coupled with the absence of any competing understory vegetation at our study site. Horton et al. (2003) found isotopic evidence that *Tamarix* has the ability to use both ground water and water derived from other sources, such as local precipitation, and Nippert et al. (2010) present physiological data supporting the idea that *Tamarix* can rapidly shift water sources from ground water to vadose zone water in response to declines in the water table.

4.2. Nectar production

We found no evidence to support our hypothesis that nectar production declines as DGW increases. Rather, nectar production varied as much among trees within a site as among sites. Pooling the 2010 and 2011 results, the absence of nectar in June samples (Table 2) suggests there may be a stand-level mid-summer production decline. As with flower abundance, our inability to detect a DGW effect on nectar production could reflect its true absence. Support for this interpretation is provided by the similarly high values for sugar concentration in the April 2011 flower collections for G1, G2, and G3, where DGW > 3 m, and in flowers collected at the same time from plants adjacent to the channel, where DGW was judged to be <0.5 m (Table 2).

Alternatively, we may have failed to detect a true relationship (i.e., produced a Type II error) because of our relatively simple nectar assessment method. Neither the daily nor seasonal nectar secretion pattern in *Tamarix* flowers is known, and we did not exclude visitors to the flowers we used in our tests. It is possible that in some cases visitors had already removed nectar from the flowers we collected for testing. An argument against this, however, was the presence of nectar in both morning and midday assessments.

4.3. Pollinators

We found no evidence of a shift in the pollinator community associated with *Tamarix* along the DGW gradient. Like Wiesenborn et al. (2008), we found the introduced honey bee to be a very common component of the pollinator community. Taxonomic richness was also similar between his study and ours. Wiesenborn et al. (2008) noted 17 families present at his Colorado River site (160 km south of Las Vegas Wash), whereas we recorded 22 families. Pendleton et al. (2011) suggested Melyridae beetles might be important *Tamarix* pollinators, but none were detected during our surveys.

We found a large difference in pollinator abundance between years. Temporal variation has been observed in other pollinator studies (Petanidou et al., 2008), and variation in rainfall has been positively correlated to abundance of desert riparian arthropods (e.g., Durst et al., 2008). In our case, however, growing season precipitation was highest in 2011 (Fig. 2), when pollinator abundance was lowest. The March 2011 drop in the water table produced by dredging may have stressed plants and reduced flower production (Fig. 4A), which then led to reduced pollinator abundance, but this seems unlikely given that the size of the drop (~15 cm) was smaller than the difference in DGW between sites G2 and G3. The most reasonable explanation for the drop in flower abundance, and thereby pollinators, was the extensive herbivory by the non-native weevil, *Coniatus splendidulus*. This insect was first noted in the Wash in June of 2010 (Eckberg and Foster, 2011) and appeared to be undergoing a population irruption in our study area

in 2011. Both adults and larvae are thought to feed on *Tamarix* flowers and foliage.

The taxa richness we found using Las Vegas Wash *Tamarix* is smaller than richness values reported for other woody, animal-pollinated dryland riparian plant species. For example, Golubov et al. (1999) reported 81 species visiting nectar-producing flowers of the facultatively riparian *Prosopis glandulosa* near a Chihuahuan Desert water catchment, and Simpson and Neff (1987) collected 64 solitary bee species visiting flowers of *Prosopis velutina* growing along Sonoran Desert washes. Boldt and Robbins (1990) found 37 insect species visiting *Baccharis salicifolia* flowers at widespread riparian sites in the southwestern United States and northern Mexico. Although they recorded only one bee, *A. mellifera*, they noted that Krombein et al. (1979) had listed 27 bee species as visiting the flowers. Comparisons among floral visitation studies are problematic, however, because of differences in sampling intensity, the variety of sampling methods, and the timing and duration of the study. Few studies have compared pollinator communities along moisture gradients in deserts. Minckley (2008) compared bee faunas captured in pan traps at adjacent Sonoran desert riparian and upland scrub habitats and reported species richness slightly higher in riparian habitat (102 versus 93 species). More species of specialist (oligolectic) bees occurred in the scrub habitat, whereas more species of generalist (polylectic) bees occurred in riparian habitats.

The overall importance of *Tamarix* as a resource for native riparian pollinators remains unclear. *Tamarix* was used by native pollinators along Las Vegas Wash, especially during the first study year, and Wiesenborn et al. (2008) documented numerous native pollinators on *Tamarix* at a site along the lower Colorado River in Arizona. Tepedino et al. (2008) suggest that *Tamarix*, because it blooms through the entire growing season, may increase native bee abundance by filling the mid-summer gap in floral resources that normally appears in native vegetation. However, the drop in pollinators that accompanied the decline in *Tamarix* flower numbers from the first to second year of our study, together with the relatively large variety and abundance of pollinators observed in the second year at nearby non-*Tamarix* areas, is consistent with the hypothesis that the *Tamarix* was attracting pollinators that depend primarily on (e.g., nest in) other vegetation or habitat types. Richardson and Rejmánek (2011, Appendix S3) suggest that most non-native animal-pollinated woody plants readily infiltrate prevailing pollinator networks.

The idea that pollinators from other habitats are visiting *Tamarix* opportunistically when flowers (and associated resources) are extremely abundant, described by Durst et al. (2008) as the “tourist” hypothesis, and the gap-filling hypothesis of Tepedino et al. (2008) are not mutually exclusive. Population studies of native pollinators in areas ecologically matched except for the presence of *Tamarix* with and without biocontrol agents that impact flower production would provide insight into the importance of *Tamarix* to native pollinator communities.

Acknowledgments

This work was supported by the U.S. Geological Survey and the Bureau of Reclamation's Science and Technology Program. Special thanks to Jason Eckberg and the Southern Nevada Water Authority for assistance in well installation. We thank Rick Wydoski for help collecting soil moisture data, Terry Waddle (USGS Fort Collins Science Center) for the topographic survey, Virginia Scott (University of Colorado) for identifying arthropods, and Joan Daniels and the anonymous reviewers for comments on the manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

- Boldt, P.E., Robbins, T.O., 1990. Phytophagous and flower-visiting insect fauna of *Baccharis salicifolia* (Asteraceae) in the southwestern United States and northern Mexico. *Environmental Entomology* 19, 515–523.
- Carroll, A.B., Pallardy, S.G., Galen, C., 2001. Drought stress, plant water status, and floral trait expression in fireweed, *Epilobium angustifolium* (Onagraceae). *American Journal of Botany* 88, 438–446.
- Carthew, S.M., Goldingay, R.L., 1997. Non-flying mammals as pollinators. *Trends in Ecology & Evolution* 12, 104–108.
- Duan, J.G., Scott, S., 2007. Selective bed-load transport in Las Vegas Wash, a gravel-bed stream. *Journal of Hydrology* 342, 320–330.
- Durst, S.L., Theimer, T.C., Paxton, E.H., Sogge, M.K., 2008. Temporal variation in the arthropod community of desert riparian habitats with varying amounts of saltcedar (*Tamarix ramosissima*). *Journal of Arid Environments* 72, 1644–1653.
- Eckberg, J.R., Foster, M.E., 2011. First account of the splendid tamarisk weevil *Coniatius splendidulus* Fabricius, 1781 in Nevada. *Pan Pacific Entomologist* 87, 51–53.
- Friedman, J.M., Auble, G.T., Shafroth, P.B., Scott, M.L., Merigliano, M.F., Preehling, M.D., Griffin, E.K., 2005. Dominance of non-native riparian trees in western USA. *Biological Invasions* 7, 747–751.
- Friedman, J.M., Roelle, J.E., Gaskin, J.F., Pepper, A.E., Manhart, J.R., 2008. Latitudinal variation in cold hardiness in introduced *Tamarix* and native *Populus*. *Evolutionary Applications* 1, 598–607.
- Gaskin, J.F., Schaal, B.A., 2002. Hybrid Tamarix Widespread in U.S. Invasion and Undetected in Native Asian Range. *Proceedings of the National Academy of Sciences, USA* 99, pp. 11256–11259.
- Golubov, J., Eguarte, L.E., Mandujano, M.C., Lopez-Portillo, J., Montana, C., 1999. Why be a honeyless honey mesquite? Reproduction and mating system of nectarful and nectarless individuals. *American Journal of Botany* 86, 955–963.
- Gorelow, A., 2005. Climate of Las Vegas, Nevada. National Weather Service.
- Horton, J.L., Hart, S.C., Kolb, T.E., 2003. Physiological condition and water source use of Sonoran Desert riparian trees at the Bill Williams River, Arizona, USA. *Isotopes in Environmental and Health Studies* 39, 69–82.
- Horton, J.L., Kolb, T.E., Hart, S.C., 2001a. Physiological response to groundwater depth varies among species and with river flow regulation. *Ecological Applications* 11, 1046–1059.
- Horton, J.L., Kolb, T.E., Hart, S.C., 2001b. Responses of riparian trees to interannual variation in ground water depth in a semi-arid river basin. *Plant, Cell and Environment* 24, 293–304.
- Horton, J.S., 1957. Inflorescence development in *Tamarix pentandra* Pallas (Tamaricaceae). *Southwestern Naturalist* 2, 135–139.
- Horton, J.S., Flood, J.E., 1962. Taxonomic notes on *Tamarix pentandra* in Arizona. *Southwestern Naturalist* 7, 23–28.
- Inouye, D.W., Saavedra, F., Lee-Yang, W., 2003. Environmental influences on the phenology and abundance of flowering by *Androsace septentrionalis* (Primulaceae). *American Journal of Botany* 90, 905–910.
- Krombein, K.V., Hurd Jr., P.D., Smith, D.R., Burks, B.D., 1979. *Catalog of Hymenoptera in America North of Mexico*. Smithsonian Institution Press, Washington DC.
- Miller-Rushing, A.J., Inouye, D.W., 2009. Variation in the impact of climate change on flowering phenology and abundance: an examination of two pairs of closely related wildflower species. *American Journal of Botany* 96, 1821–1829.
- Minkley, R., 2008. Faunal composition and species richness differences of bees (Hymenoptera: Apiformes) from two North American regions. *Apidologie* 39, 176–188.
- Morant, D.S., Schumann, R., Petit, S., 2009. Field methods for sampling and storing nectar from flowers with low nectar volumes. *Annals of Botany* 103, 533–542.
- Nagler, P.L., Morino, K., Didan, K., Erker, J., Osterberg, J., Hultine, K.R., Glenn, E.P., 2009. Wide-area estimates of saltcedar (*Tamarix* spp.) evapotranspiration on the lower Colorado River measured by heat balance and remote sensing methods. *Ecohydrology* 2, 18–33.
- Nippert, J.B., Butler, J.J., Kluitenberg, G.J., Whittemore, D.O., Arnold, D., Spal, S.E., Ward, J.K., 2010. Patterns of *Tamarix* water use during a record drought. *Oecologia* 162, 283–292.
- Pasiecznik, N.M., Felker, P., Harris, P.J.C., Harsh, L.N., Cruz, G., Tewari, J.C., Cadoret, K., Maldonado, L.J., 2001. The *Prosopis juliflora* – *Prosopis pallida* Complex: a Monograph. HDRA, Coventry, UK.
- Pendleton, R.L., Pendleton, B.K., Finch, D., 2011. Displacement of Native Riparian Shrubs by Woody Exotics: Effects on Arthropod and Pollinator Community Composition. *Natural Resources and Environmental Issues* 16: Article 25. Available at: <http://digitalcommons.usu.edu/nrei/vol16/iss1/25> (accessed 2.07.12.).
- Perry, L.G., Andersen, D.C., Reynolds, L.V., Nelson, S.M., Shafroth, P.B., 2012. Vulnerability of riparian ecosystems to elevated CO₂ and climate change in arid and semiarid western North America. *Global Change Biology* 18, 821–842.
- Petanidou, T., Kallimanis, A.S., Tzanopoulos, J., Sgardelis, S.P., Pantis, J.D., 2008. Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. *Ecology Letters* 11, 564–575.
- Richardson, D.M., Rejmánek, M., 2011. Trees and shrubs as invasive alien species – a global review. *Diversity and Distributions* 17, 788–809.
- Shafroth, P.B., Brown, C.A., Merritt, D.M., 2009. Saltcedar and Russian Olive Control Demonstration Act Science Assessment. U.S. Geological Survey, Scientific Investigations Report 2009-5247, p. 143.
- Simpson, B.B., Neff, J.L., 1987. Pollination ecology in the arid southwest USA. *Aliso* 11, 417–440.
- Simpson, B.B., Neff, J.L., Moldenke, A.R., 1977. *Prosopis* flowers as a resource. In: Simpson, B.B. (Ed.), *Mesquite: Its Biology in Two Desert Scrub Ecosystems*. Dowden, Hutchinson, and Ross, Stroudsburg, PA, pp. 92–114.
- Tepedino, V.J., Bradley, B.A., Griswold, T.L., 2008. Might flowers of invasive plants increase native bee carrying capacity? Intimations from Capitol Reef National Park, Utah. *Natural Areas Journal* 28, 44–50.
- Tepedino, V.J., Stanton, N.L., 1980. Spatiotemporal variation in phenology and abundance of floral resources on shortgrass prairie. *Great Basin Naturalist* 40, 197–215.
- Tomanek, G.W., Ziegler, R.L., 1962. *Ecological Studies of Salt Cedar*. Final Report to Bureau of Reclamation. Fort Hays Kansas State College, Hays, Kansas.
- Wiesenborn, W.D., Heydon, S.L., Lorenzen, K., 2008. Pollen loads on adult insects from tamarisk flowers and inferences about larval habitats at Topock Marsh, Arizona. *Journal of the Kansas Entomological Society* 81, 50–60.
- Willmer, P., 2011. *Pollination and Floral Ecology*. Princeton University Press, Princeton, New Jersey.
- Zimmerman, M., Pyke, G.H., 1988. Experimental manipulations of *Polemonium folioissimum* – effects on subsequent nectar production, seed production and growth. *Journal of Ecology* 76, 777–789.