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Water as a trophic currency in dryland food webs

Daniel C Allen^{1*}, Kevin E McCluney², Stephen R Elser³, and John L Sabo⁴

Water is essential for life on Earth, yet little is known about how water acts as a trophic currency, a unit of value in determining species interactions in terrestrial food webs. We tested the relative importance of groundwater and surface water in riparian food webs by manipulating their availability in dryland floodplains. Primary consumers (crickets) increased in abundance in response to added surface water and groundwater (contained in moist leaves), and predators (spiders and lizards) increased in abundance in response to added surface water, in spite of the presence of a river, an abundant water source. Moreover, the relative magnitude of organism responses to added water was greatest at the most arid site and lowest at the least arid site, mirroring cricket recruitment, which was greatest at the least arid site and lowest at the most arid site. These results suggest that water may be a key currency in terrestrial dryland food webs, which has important implications for predicting ecosystem responses to human- and climate-related changes in hydrology and precipitation.

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Although fresh water is essential to terrestrial life on Earth, surface water is scarce; 99% of liquid fresh water lies underground (Winter *et al.* 1998). It is even more uncommon in the arid, semi-arid, and dry-subhumid ecosystems (hereafter collectively referred to as “drylands”) that comprise 41% of the Earth’s terrestrial surface and in any ecosystem experiencing drought (Reynolds *et al.* 2007). Water availability affects interactions between plant species (Scholes and Archer 1997; Nippert and Knapp 2007), animal physiology and behavior (Tracy and Walsberg 2002; Ostrowski *et al.* 2006), and latitudinal biodiversity gradients (Hawkins *et al.* 2003). However, we know little about how water acts as a trophic currency, a unit of value in determining species interactions in terrestrial food webs, even in drylands (McCluney *et al.* 2012).

Groundwater contained in plants can be an important resource for animals in drylands. For example, crickets (*Gryllus alogus*) prefer to consume fresh groundwater-laden cottonwood (*Populus fremontii*) leaves as opposed to dried ones (Sabo *et al.* 2008), and they consume fewer fresh leaves when drinking water is present (McCluney and Sabo 2009). Sabo *et al.* (2008) estimated that the groundwater contained in naturally falling green cottonwood leaves could satisfy the water needs of cricket populations in riparian floodplains. Thus, there is the potential for plant-derived groundwater to influence food webs, even in floodplains where surface water is available.

We tested the role of groundwater and surface water in

determining the abundance of primary consumers and predators in a desert riparian food web via experimental supplementation of surface water (ie drinking water) and groundwater contained in leaves. We conducted our experiment in three 2–4-ha floodplains within a 30-km segment of one of the last free-flowing rivers in the southwestern US, where floodplains vary in stream permanence and site aridity. We hypothesized that primary consumers would increase in abundance in response to both water sources while predators would respond only to surface water, and that this effect would be (1) strongest during the dry season and (2) stronger at sites that are more arid.

Methods

Experimental design

We established three sites on the Upper San Pedro River in southeast Arizona that vary in aridity and stream permanence (WebFigure 1; Turner and Richter 2011). The river dried at the “dry” site during the experiment, while differences in soil moisture characterize the “intermediate” and “wet” floodplains (mean soil gravimetric water content [%] ± standard error: wet, 6.37 ± 1.61; intermediate, 4.98 ± 0.98). Plant communities across these floodplains are composed of cottonwood (*P fremontii*) and willow (*Salix gooddingii*) gallery forests, with the occasional mesquite (*Prosopis velutina*), saltcedar (*Tamarix ramosissima*), or seep willow (*Baccharis glutinosa*) growing in the understory. Summers in southeast Arizona begin with a dry phase that transitions into a wetter phase (“monsoon season”); we added water continuously throughout both seasons (dry and monsoon) as we expected effects of water additions to lessen during the monsoon.

We established nine 625-m² experimental plots per site

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($n = 27$ plots encompassing 1.7 ha in total), arranged into three spatial blocks (three plots per block) located ≥ 15 -m apart. Blocks were spread throughout the floodplain: one proximal to the river, one as distal as possible, and one intermediate. We generated three water treatments ($n = 3$ plots per treatment per site, randomly assigned within blocks). Specifically, there was a control treatment and two water treatments: a groundwater treatment that added water in the form of freshly picked green cottonwood leaves, and a surface water treatment that added “water pillows” (devices containing a silicate gel that hold ~ 30 g of water, which provide water in a manner similar to moist soil [McCluney and Sabo 2009]) and “chick waterers” (devices that continuously provide a small pool of water [McCluney and Sabo 2010]). Our water additions achieved a fourfold increase in ambient groundwater flux from naturally falling green cottonwood leaves (Sabo *et al.* 2008). We added water for 42 days ($\sim 333\,000$ cottonwood leaves and $\sim 20\,000$ water pillows) and replenished water sources daily; water pillows and unconsumed leaves from the previous day were removed. The added water was never entirely consumed in any plot in either treatment (DCA pers obs), so our additions essentially gave animals unlimited access to water.

For the groundwater treatment we added 900 fresh green cottonwood leaves per plot per day. Cottonwood leaves were picked daily (the picking site was rotated daily), stored in airtight plastic bags, and kept on ice until they were added to plots ~ 1 – 2 hours before sundown. For the first 6 days, leaves were attached to thin pieces of wood, but for the last 36 days leaves were placed in mesh bags (~ 2.5 cm mesh size). Leaf litter in these forests averages 5–10 cm in depth and $210\,000\text{ cm}^{-3}\text{ m}^{-2}$ (McCluney and Sabo 2009), so the biomass in our leaf additions was negligible as compared with leaf litter standing stocks. For the surface water treatment, we added 50 water pillows (Zilla Products, Franklin, WI) and 4 chick waterers.

We surveyed for primary consumers (juvenile and adult crickets [*G. alogus*]) and invertebrate predators (lycosid spiders [*Hogna antelucana*]) nightly, surveying a single site each night and rotating the survey site nightly. Water resources were added to plots in a 7 column \times 7 row grid, and counts from transects both on- and off-line with water resources were weighted by transect widths and the potential area to generate an average count per plot (WebFigures 2 and 3). Juvenile crickets do not have fully developed wings, whereas wings are present in adult crickets. Large spiders were classified as having a length (head to tip of abdomen) > 1 cm. We sampled for recently hatched (“early-instar”) crickets twice, beginning 10 days after our experiment, using a 1-m^2 quadrat and removing all crickets from four quadrats per plot for 5 minutes. We surveyed for vertebrate predators (lizards) during the day, with two surveyors observing the plot for lizards by sight and by sound for 15 minutes. Here, we focus on *Aspidoscelis uniparens*, a ground-dwelling lizard hereafter referred to as “whiptail lizard”.

Statistical analyses

We analyzed survey data using linear mixed-effects models in a repeated measures framework where water treatment, site, and seasonal factors were fixed effects and block was nested within site as a random effect. Because we were only interested in how our treatment effects varied between seasons, we omitted a survey factor from the model. Including survey as a random factor did not affect our results (WebTable 1). Cricket and spider data were square-root transformed to meet model assumptions, while a Poisson distribution was used for whiptail lizard data and a heterogeneous first-order autoregressive variance–covariance structure was used to account for correlations between repeated measurements (this structure was the best fit using an Akaike information criterion). We used a priori planned contrasts to test for differences in organism abundances between our water treatments with Cicchetti’s method to control for Type I errors (Toothaker 1993), the specific set of contrasts depending on which terms were statistically significant (eg if the treatment \times season interaction was significant, the contrasts would test for treatment differences in organism abundance within each season only, rather than testing for differences between a treatment in one season against a treatment in another season). For early-instar cricket abundance we used a repeated measures analysis of variance (ANOVA) model crossing water and site factors, with a Poisson distribution, while Tukey’s multiple comparison procedure was used to test for differences between sites. We calculated the water treatment effect size at each site for each taxa (primary consumers, ground- and surface water treatments relative to controls; predators, surface water treatments relative to controls only) during the dry and monsoon seasons using Cohen’s d (Cohen 1988). We used a two-way ANOVA with site and season factors and Cicchetti’s method with a priori planned contrasts to test for differences in effect size between sites within seasons. Statistical analyses were conducted using SAS 9.2 (SAS Institute Inc, Cary, NC) software.

Results

The abundance of primary consumers (ie adult and juvenile crickets) was greater in plots with groundwater and surface water additions, while the abundance of predators (ie large spiders and whiptail lizards) was greater only in surface water plots (Table 1; Figure 1). We found a significant treatment \times site interaction for juvenile crickets, indicating that the treatment effect differed between sites. Juvenile crickets, large spiders, and whiptail lizards had significant treatment \times season interactions (although adult crickets did not), showing that the treatment effect differed between seasons, as significant differences in the dry season were not evident in the monsoon period for these animals.

We found that the water treatment effect size differed

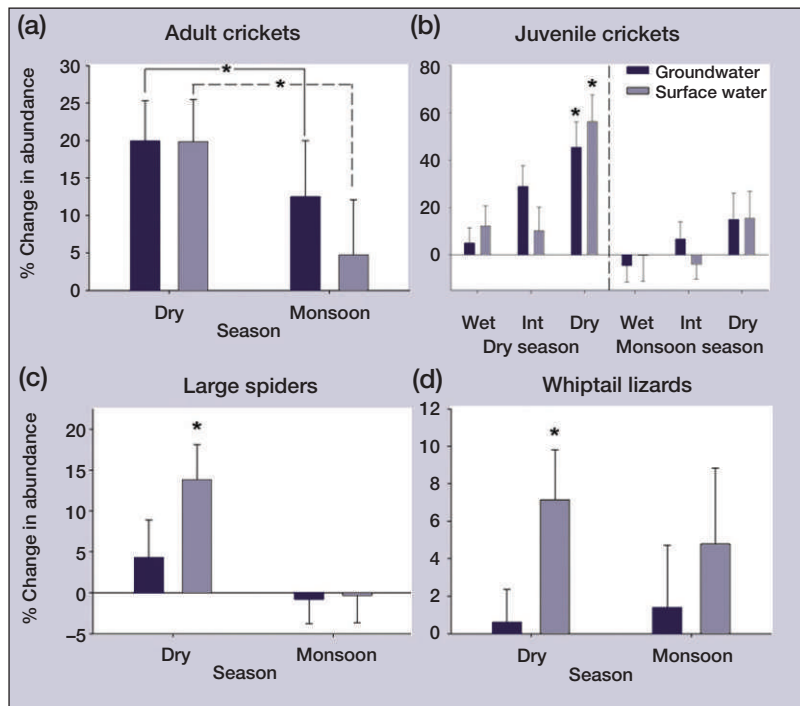


Figure 1. Percent change in abundance relative to controls for each organism. Bars and whiskers are means and standard errors, respectively. Asterisks indicate significant differences ($P < 0.05$) between the water treatment and controls. In (a), asterisks are bracketed to indicate that while we present the results by season, the post-hoc test used pooled data from both seasons. In (b), “Wet”, “Int”, and “Dry” refer to the wet, intermediate, and dry sites, respectively (see methods).

between sites during the dry season but not during the monsoon season (Table 1). Post-hoc tests confirmed that effect sizes at the most arid site were highest and significantly greater than those at the least arid site during the dry season (Figure 2a; $P < 0.05$). Although we did not find an effect of water treatment on early-instar cricket abundance, we did observe significant differences in recruitment between sites (Table 1). Post-hoc tests showed that cricket reproduction was lowest at the dry site and highest at the wet site (Figure 2b). Models using adult cricket abundance covariates suggested that early-instar cricket abundance was not related to adult cricket abundance using count data from the dry ($P = 0.401$) and monsoon ($P = 0.267$) seasons, or from post-experiment quadrat samples ($P = 0.583$).

Discussion

The most striking result of this study is that the abundance of riparian animals was greater where we added surface water and groundwater resources, despite the presence of a river, an abundant and natural water source. Sabo *et al.* (2008) found that habitats proximal to the river were lower in air temperature and higher in humidity compared to distal habitats, and that crickets preferred fresh green cottonwood leaves only in the distal habitats. However, we found significant results despite manipulating water avail-

ability in habitats proximal, intermediate, and distal to the river. Moreover, water sources had different effects on the numerical responses of animals in the food web. Water limitation was strong enough that the water additions increased the abundance of adult crickets during both the dry and monsoon seasons. Yet treatment differences for juvenile crickets and predators were not evident in the monsoon period. Furthermore, primary consumers responded to additions of both groundwater and surface water while predators responded only to surface water. Thus, the trophic structure (ie relative abundance of primary consumers and predators) was different for each water source.

Another interesting facet of this study is that our water treatment effects varied across sites, probably due to differences in overall site aridity. For example, we found a treatment \times site interaction for juvenile crickets with treatment differences evident only at the driest site. Moreover, the water treatment effect size was strongest at the most arid site and weakest at the least arid site during the dry season, while early-instar cricket recruitment was highest at the least arid site and lowest at the most arid site. The abundance of early-instar crickets did not appear to be related to the abundance of adult crick-

ets, suggesting this effect was in fact due to site differences in aridity. However, we did not find a “legacy” effect of our water addition treatments on cricket recruitment, which is most likely due to cricket movement patterns after the monsoon rains began. Nevertheless, these results have considerable theoretical and conservation-oriented ramifications. Overall, our results suggest that water limitation is variable even within this desert ecosystem, with differences between sites related to hydrology. Since aridity, surface flow, and local environmental conditions are controlled primarily by proximity to groundwater in the San Pedro River floodplains (Lite and Stromberg 2005), our observations on water effect sizes and early-instar cricket recruitment suggest that groundwater depth influences key components of an aboveground animal community.

Because primary consumers had access to groundwater contained in cottonwood leaves we expected the observed response, but predators have been shown to increase prey consumption in the absence of water (ie foraging prey for water; McCluney and Sabo 2009). Unexpectedly, predators did not respond to increased prey (cricket) availability in the groundwater treatment areas. This may be due to the experimental duration, as our water additions may not have lasted long enough to document any time lag effects of predators to increased cricket abundances that might occur. Seasonal variation in precipitation events, groundwater levels, and the fre-

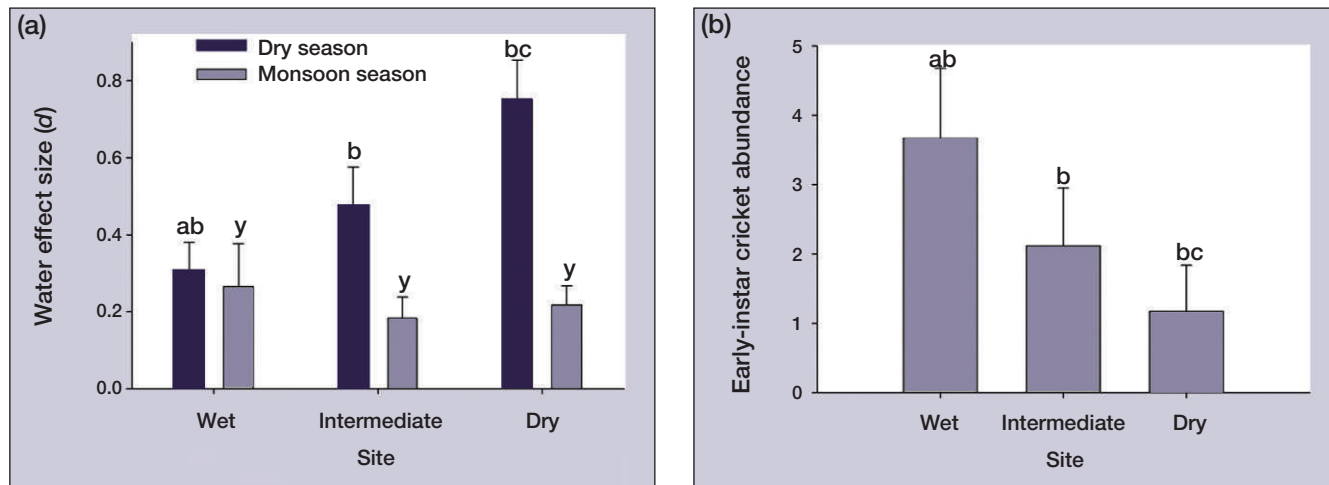


Figure 2. (a) Water treatment effect sizes (Cohen's *d*) for plot abundance at each site for the dry and monsoon seasons. Significant differences from post-hoc tests ($P < 0.05$) within each season are represented by the letters abc and xyz for the dry and wet seasons, respectively (treatments with different letters are significantly different). (b) Early-instar cricket abundances by site from samples taken during the monsoon season. Significant differences from post-hoc tests ($P < 0.05$) within each season are represented by the letters abc.

quency of scouring floods on these floodplains could ultimately shape food web structure at larger temporal and spatial scales, which should be an area for future study.

While there is the potential for the groundwater effect of our green cottonwood leaf additions to be confounded by a biomass effect, several factors make this unlikely. First, although we did not have a dried cottonwood leaf treatment, the amount of leaf biomass we added was negli-

gible when compared with standing stocks of leaf litter biomass. Second, other experiments have shown that crickets prefer to consume fresh cottonwood leaves rather than dried leaves only when other water sources are absent (Sabo *et al.* 2008; McCluney and Sabo 2009), and that they do not respond differently to dried green leaves than to dried brown ones (Sabo *et al.* 2008). Third, and most importantly, we specifically generated our groundwa-

ter and surface water treatments to contain the same amount of water, and cricket responses to green cottonwood leaf additions were no different than their responses to surface water additions in this experiment. This indicates that any cricket response due to added biomass in the leaves is indeed negligible when compared to their response to the water contained therein.

We acknowledge that our results come from a single river and so may not apply broadly, but we note three aspects of our study system that suggest wider relevance to other river systems at mid-latitudes where dry conditions prevail: (1) similar gallery forests and invertebrate communities are a unifying feature of riparian zones throughout the western and Great Plains regions of the US (Busch and Smith 1995; Stromberg *et al.* 1996; Benke and Cushing 2005), (2) the depth to groundwater gradient we report is representative of that of rivers in the West with minimal to moderate human impact on water table levels (Glennon 2002), and (3) climate studies predict that warming and changes in precipitation patterns will occur across much of the southern US; thus, if dry conditions are not the norm now, they will likely be within the next few decades (IPCC 2007). Our findings may not apply to more mesic areas where the balance between precipitation and evapotranspiration and/or the recharge and pumping of groundwater are net pos-

Table 1. Summarized results from repeated measures ANOVAs on abundance of juvenile and adult crickets, large spiders, whiptail lizards, and early-instar crickets

Organism	Effect	$F_{dfn, dfd}$	P
Adult crickets	Water	11.57 _{2,12}	0.0016
	Water × site	1.14 _{4,12}	0.3840
	Water × season	0.92 _{2,12}	0.4249
	Water × site × season	0.50 _{4,12}	0.7365
Juvenile crickets	Water	7.48 _{2,12}	0.0078
	Water × site	4.65 _{4,12}	0.0169
	Water × season	6.77 _{2,12}	0.0108
	Water × site × season	2.04 _{4,12}	0.1525
Large spiders	Water	2.49 _{2,12}	0.1246
	Water × site	0.11 _{4,12}	0.9767
	Water × season	5.73 _{2,12}	0.0179
	Water × site × season	1.60 _{4,12}	0.2375
Whiptail lizards	Water	3.21 _{2,12}	0.0716
	Water × site	0.49 _{4,12}	0.7433
	Water × season	6.21 _{2,12}	0.0141
	Water × site × season	0.27 _{4,12}	0.8917
Water treatment effect size	Site	3.01 _{2,30}	0.0642
	Season	17.52 _{2,30}	<0.001
	Site × season	4.17 _{2,30}	0.0252
Early-instar crickets	Water	1.12 _{2,26}	0.3415
	Site	5.40 _{2,26}	0.0109
	Water × site	0.65 _{4,26}	0.6320

Notes: Significant P values ($P < 0.05$) appear in bold font.

itive; in these areas, water may have less relevance as a trophic currency in terrestrial food webs.

Our results have important implications for predicting how terrestrial food webs will respond to human- and climate-related changes in hydrology and precipitation. Altered streamflows have been linked to the declines of cottonwood riparian forests in the western US (Busch and Smith 1995; Stromberg *et al.* 1996), and our findings indicate that an important conduit for groundwater delivery to terrestrial food webs is being lost in the process. Moreover, groundwater pumping and related river drying is becoming increasingly common (Glennon 2002). Thus, while water management decisions leading to increased river drying events will obviously affect aquatic ecosystems, our study shows that they are likely to affect terrestrial ecosystems as well. Finally, climate models predict globally distributed changes in precipitation and soil moisture, and increased drought frequency and duration in many regions (IPCC 2007). Management decisions should anticipate that alterations in aridity and hydrology may lead to dramatic changes in the structure of terrestrial food webs due to the importance of water as a trophic currency.

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