

When vegetation change alters ecosystem water availability

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Abstract

The combined effects of vegetation and climate change on biosphere–atmosphere water vapor (H₂O) and carbon dioxide (CO₂) exchanges are expected to vary depending, in part, on how biotic activity is controlled by and alters water availability. This is particularly important when a change in ecosystem composition alters the fractional covers of bare soil, grass, and woody plants so as to influence the accessibility of shallower vs. deeper soil water pools. To study this, we compared 5 years of eddy covariance measurements of H₂O and CO₂ fluxes over a riparian grassland, shrubland, and woodland. In comparison with the surrounding upland region, groundwater access at the riparian sites increased net carbon uptake (NEP) and evapotranspiration (ET), which were sustained over more of the year. Among the sites, the grassland used less of the stable groundwater resource, and increasing woody plant density decoupled NEP and ET from incident precipitation (P), resulting in greater exchange rates that were less variable year to year. Despite similar gross patterns, how groundwater accessibility affected NEP was more complex than ET. The grassland had higher respiration (R_{eco}) costs. Thus, while it had similar ET and gross carbon uptake (GEP) to the shrubland, grassland NEP was substantially less. Also, grassland carbon fluxes were more variable due to occasional flooding at the site, which both stimulated and inhibited NEP depending upon phenology. Woodland NEP was large, but surprisingly similar to the less mature, sparse shrubland, even while having much greater GEP. Woodland R_{eco} was greater than the shrubland and responded strongly and positively to P, which resulted in a surprising negative NEP response to P. This is likely due to the large accumulation of carbon aboveground and in the surface soil. These long-term observations support the strong role that water accessibility can play when determining the consequences of ecosystem vegetation change.

Keywords: carbon dioxide, ecosystem water-use, eddy covariance, evapotranspiration, mesquite (*Prosopis velutina*), net ecosystem production, riparian, sacaton semiarid (*Sporobolus wrightii*), vegetation change, water-use efficiency, woody plant encroachment

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Introduction

The vegetative composition of many ecosystems around the world is rapidly changing. One example among many is the proliferation woody plants into grasslands (Mayeux *et al.*, 1991; Archer, 1994; Noble, 1997; Van Auken, 2000). Vegetation change is not simply an expansion and contraction of species' ranges, but rather a change in linkages that affect the soil–plant–atmosphere continuum and dependent biophysical processes. In terms of water availability, grasses are generally more shallow-rooted than shrubs or trees so woody plant encroachment into grasslands may lead to exploitation of deepwater stores (if available), which, in

turn, impacts ecosystem ecohydrological function (Huxman *et al.*, 2005; Kulmatiski & Beard, 2013). The consequences of these potentially important shifts in composition and structure on the fundamental coupling of ecosystem water and carbon cycling, or ecohydrology, are not well understood.

While we see dynamic changes in vegetation composition in many settings across the globe, there is conflicting evidence from broadscale studies illustrating changes in ecosystem function. For example, a global study shows vegetation change having little effect on temporal dynamics of ecosystem water-use efficiency (Campos *et al.*, 2013). This is a puzzling result given that evapotranspiration (ET), the hydrological system component of water use efficiency, has decreased globally (Jung *et al.*, 2010), while rising atmospheric CO₂ and widespread woody plant encroachment can

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stimulate productivity, indicating positive ecosystem carbon rate processes with altered vegetation structure (Barger *et al.*, 2011; Donohue *et al.*, 2013). These findings are difficult to rectify with our conceptualization of how the composition of ecosystems is important to biogeochemical cycling and emergent properties at the ecosystem scale and the specific patterns of vegetation change (Eldridge *et al.*, 2011; Jenerette *et al.*, 2012; Kulmatiski & Beard, 2013). At the same time, while the availability of biosphere/atmosphere exchange data in sites that allow us to contrast vegetation structure is growing, we are still severely constrained by the lack of detailed studies exploring the interannual dynamics of ecohydrological fluxes. These types of studies would help us connect vegetation dynamics to changes in ecosystem function. Identifying potential changes in ecosystem function is needed to both understand feedbacks on climate and future dynamics of ecosystem services that may portend important tipping points and undesirable state change (Branosky *et al.*, 2012).

Scott *et al.* (2006a) examined carbon and water exchange for a riparian grassland, shrubland, and woodland (representing an encroachment gradient of mesquite, *Prosopis velutina*) along the San Pedro River of southeastern Arizona, USA. Over the course of one year, they found that ET and net ecosystem production of CO₂ (NEP) increased over the grassland to woodland gradient, suggesting that the woody plants make better use of groundwater reserves leading to greater carbon accumulation. Looking across three growing seasons, Jenerette *et al.* (2009) showed that the gross productivity at the grassland was more variable within and between the years than the woodland as the grasses had a greater sensitivity to precipitation. Similarly, Barron-Gafford *et al.* (2012) found that the shift from this C4-dominated grassland to a C3 woodland leads to changes in the response of leaf- to ecosystem-level CO₂ flux to temperature, such that a woodland maintains physiological function across a wider temperature range during precipitation-limited periods. The addition of mesquite trees has been shown to greatly increase soil carbon and nitrogen and respiration rates (microbial and root), especially under large mesquite, relative to soil under bunchgrass and bare ground (McLain & Martens, 2006; Cable *et al.*, 2009, 2012). However, soil under small- to medium-sized mesquite shrubs tend to have similar properties as grasses (Cable *et al.*, 2012), suggesting that once mesquite reach a large size, their impacts on soil carbon cycling dramatically increases. Thus, as a relatively uniform grassland changes into a more patchy and heterogeneous shrubland these results imply a more heterogeneous and reduced soil respiration and carbon storage response. Soil respiration and carbon storage should then

increase as that shrubland thickens and develops into a fully developed woodland dominated by large trees.

Like the large-scale syntheses above, much of what we have learned about ecosystem fluxes and vegetation change comes from studies ranging from a few months to a few seasons. The degree of variability in ecosystem ecohydrology across multiple years is key to understanding structure–function relationships, as interannual variability of precipitation magnitude and timing is especially large in these semiarid regions, resulting in highly variable NEP response and switching between being a source or sink of atmospheric CO₂ (Huxman *et al.*, 2004b; Hastings *et al.*, 2005; Scott *et al.*, 2009; Hamerlynck *et al.*, 2013). However, even in mesic regions, precipitation variability can result in unpredictable NEP dynamics (e.g., Saleska *et al.*, 2003; Falk *et al.*, 2008). Thus, it is the interannual variability in ecosystem function that allows us to mechanistically evaluate the coupling of structure and function (e.g., Huxman *et al.*, 2004a), highlighting the need for longer-term data sets in ecosystem science. There is considerable evidence that the more dynamic and complex response of ecosystem photosynthetic uptake rather than respiration drives a greater proportion of interannual variability in NEP seen at many sites (Schwalm *et al.*, 2010). While ecosystem respiration may appear more simply coupled to climate and less tied to deeper-soil water availability than gross photosynthesis, important antecedent conditions and long-term legacy effects also influence this process in addition to current conditions (i.e., temperature and moisture; Cable *et al.*, 2013, Ma *et al.*, 2012). The question remains: How does ecosystem access to a more stable source of (deeper) water affect the interannual variability of water and carbon exchange and their components?

To address this fundamental question, we present here a multiyear (5–9 years depending on the site) eddy covariance and ancillary hydrometeorological data from three proximate ecosystems that are representative of varying degrees of woody plant encroachment within a riparian corridor (Scott *et al.*, 2006a) to evaluate how soil water sources and accessibility affects the magnitude and variability of the biosphere/atmosphere exchanges of water and carbon dioxide. Riparian areas offer an excellent setting to understand how vegetation structure is related to ecosystem dynamics, as each of our settings plants have access to both shallow soil moisture pools and potentially deeper groundwater sources. Also, variation in rooting strategy allows for insight into how changes in vegetation structure and function depend on the accessibility of soil moisture and how ecohydrologic coupling of carbon and water cycling is affected by this feature. We start by comparing how access to groundwater affects the

average seasonal patterns of water and carbon exchange by comparing the riparian sites with the typical behavior of a nearby upland ecosystem without access to groundwater. Then, we examine the seasonal to annual magnitude and variability of the fluxes along the encroachment gradient and, with increasing focus on the details, unravel how water accessibility influenced the gross uptake and release of carbon dioxide and changed their relationship with environmental drivers.

Methods

Study sites

We used data collected along a gradient of riparian woody plant encroachment (grassland, grass–shrub mosaic, woodland), from three sites located on older, broad, and flat alluvial terraces adjacent to the main channel of the San Pedro River in southeastern Arizona. These sites are described in more detail by Scott *et al.* (2006a). Briefly, the grassland (31.562°N, 110.140°W, elevation 1230 m) is dominated by the perennial bunchgrass big sacaton (*Sporobolus wrightii*), but many small (ca. 2 m high) velvet mesquite (*Prosopis velutina*) are evidence of beginning encroachment. Within a 100 m radius of the small (2.8 m) eddy covariance tower, grass cover is ca. 65% with an average canopy height of 1 m with mesquite cover of ca. 20% (Barron-Gafford *et al.*, 2012). Mean depth to groundwater is 2.4 m measured in a collocated piezometer with a water level logger. The adjacent grass–shrub mosaic, or shrubland (31.566°N, 110.134°W, elevation 1237 m), has a 6.4 m eddy covariance tower embedded in a patchy matrix of velvet mesquite, (canopy cover of 51%, mean height 3.7 m) and an understory of dispersed sacaton bunchgrass (27% total cover, height 1.25 m) and bare intercanopy soil (32%) that seasonally fills in with annual herbaceous species, most commonly *Viguiera dentata* (Barron-Gafford *et al.*, 2013). The mean depth to groundwater is 5.4 m. The fully encroached woodland site (31.664°N, 110.178°W, elevation 1200 m) lies 12 km downstream and north of the grassland and shrubland sites in a similar alluvial depositional setting. Around the 14 m eddy covariance tower, large velvet mesquite dominate (70% canopy cover and 7 m mean canopy height), with an understory composed primarily of sacaton bunchgrass (24% understory cover) with scattered greythorn shrubs (*Zizyphus obtusifolia*) and ephemeral annual herbaceous species within 200 m of an eddy covariance tower (Barron-Gafford *et al.*, 2012). The depth to groundwater is ca. 10 m. Despite the increasing depth to groundwater, with increasing proportion of mesquite cover, the fractional access of vegetation to groundwater increases with increasing shrub encroachment (Scott *et al.*, 2008). Mean annual precipitation (1971–2000) in the San Pedro valley ranges from 313 to 386 mm, with about 60% falling between late June through September during the North American Monsoon (Adams & Comrie, 1997).

Vadose zone soil texture profiles at all three sites are similar and consist mainly of gravelly sandy loam layers interspersed with clay and gravel lenses (Scott *et al.*, 2006a). Sampling of soil carbon under mesquite trees, open/forb-covered areas, and sacaton grasses indicated about 30, 6, and 18 g organic C kg⁻¹, respectively, in the top 5 cm of soil (McLain & Martens, 2006). The deepest soils of the woodland bear a strong isotopic signature of C4 plants, suggesting that the shrubland and

woodland sites were recently dominated by grasslands (McLain & Martens, 2006). This is consistent with recent (less than 100 years) mesquite encroachment in the valley (Turner *et al.*, 2003), thought to result regionally from overgrazing, fire suppression, and climate change (Archer *et al.*, 1995; Van Auken, 2000).

Measurements

The eddy covariance technique was used to monitor ecosystem-scale carbon dioxide, water vapor, and energy fluxes at the grassland and shrubland sites from 2003 to 2008 and at the woodland site from 2001 to 2011 (only partial year data available in 2001 and 2002). Detailed descriptions of instrumentation and data processing procedures are available elsewhere (Scott *et al.*, 2004, 2006a). In summary, we installed instrumentation on tripods or towers to measure all variables needed to quantify 30 min averages of net ecosystem exchange of CO₂ (NEE), (ET), air temperature (T_{air}), vapor pressure deficit (VPD), air pressure, photosynthetically active radiation (PAR), shortwave and net radiation, and precipitation. We also monitored two profiles of the near-surface (ca. 0–1 m) vadose zone soil moisture at multiple (5–8) soil depths and the depth to groundwater in collocated piezometers. We recently discovered a specific instrumental bias in the sensitivity of each particular open-path infrared gas analyzer (IRGA, LI-7500; Li-Cor Inc, Lincoln, NE, USA) by using side-by-side tests with other open-path and closed-path IRGAs. To correct for this bias, we multiplied the 30-min vertical wind and CO₂ density covariance with a bias correction factor determined individually for each IRGA as compared to a network standard IRGA (R.L. Scott, unpublished data).

Hereafter, we use the ecosystem-centered metric of net CO₂ flux termed net ecosystem production of CO₂ whereby a positive value represents a net uptake, and a negative NEP indicates a net release, of CO₂ by the ecosystem (NEP = -NEE). We partitioned NEP into the component processes of ecosystem photosynthesis or gross ecosystem production (GEP) and ecosystem respiration (R_{eco}). First, NEP data were eliminated when the friction velocity, *u**, was less than the site specific, *u** threshold (Scott *et al.*, 2006a). Then, we fit an exponential function of air temperature to valid nighttime NEP data over a moving ca. 5 day window (Reichstein *et al.*, 2005). The window size varied to ensure that data from prestorm (dry) periods were not grouped together with data following storms. The exponential model was used to fill missing nighttime NEP data and model daytime R_{eco}. Missing daytime NEP values were filled using a second-order polynomial of incoming PAR fit to separate morning or afternoon data for the 5-day moving window; this procedure produced better fits of NEP to PAR (data not shown) than commonly used high-order light response models (Lasslop *et al.*, 2010). Finally, we calculated GEP as: GEP = R_{eco} + NEP. Our regression analysis below includes contrasts of 5 years of flux data (2003–2007) from all sites, and an additional 4 years (2008–2011) of the woodland data were used to produce more robust statistics where indicated. Furthermore, missing data from January–February 2003 for the grassland and shrubland were filled with daily average values of NEP, R_{eco}, GEP, and ET from January–February 2004–2007 as the data for this period of time normally has small NEP and ET fluxes (Fig. 1).

Using a function that depends on the number of missing observations, we computed the total random error in yearly NEP that accounted for random measurement error (Richardson *et al.*, 2006; Richardson & Hollinger, 2007) and gap-filling error

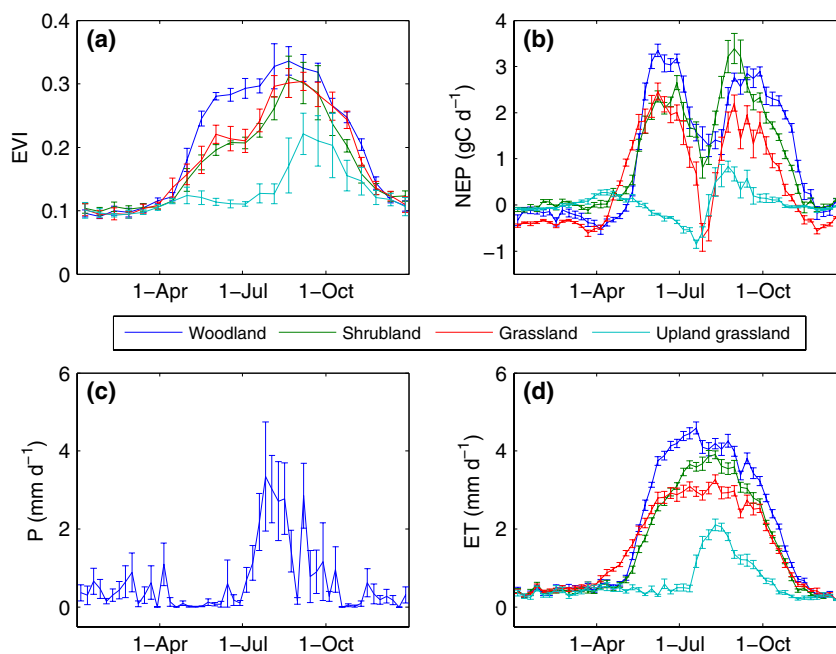


Fig. 1 (a) 2003–2007 16-day ensemble averages of MODIS Enhanced Vegetation Index (EVI), (b) net ecosystem production (NEP), (c) precipitation (P), and (d) evapotranspiration (ET). Error bars represent ± 1 standard error. Precipitation is shown for just one site as the other sites had very similar magnitude and seasonality. The upland grassland is from the nearby Ameriflux Kendall Grassland, representing a more typical site in this region without access to groundwater (data from Scott *et al.*, 2010).

(Dragoni *et al.*, 2007). The error in yearly sums ranged from 6.7–11.2 g C m⁻² yr⁻¹ across sites and years. Systematic errors due to site-specific biases, instrumentation, measurement technique, and calculations are expected to be larger but are relatively unknown (Lasslop *et al.*, 2010). Total uncertainty in yearly NEP using eddy covariance is estimated to be around ± 10 –30% (Goulden *et al.*, 1996; Hagen *et al.*, 2006; Loescher *et al.*, 2006; Moffat *et al.*, 2007). In terms of the open-path methodology and bias-correction employed in this paper, we conducted year-long comparisons of our open-path instrumentation at two different sites with a parallel closed-path instrumentation and found good agreement with integrated yearly NEP (within 10 g C yr⁻¹; R.L. Scott, unpublished data).

Daily ET was calculated by first filling the gaps in the 30 min data using 14-day moving-average look-up tables of ET and incoming PAR, averaged over 100 μ mol m⁻² s⁻¹ intervals (Falge *et al.*, 2001) and separated into morning or afternoon periods. Linear interpolation was used to fill any multi-day gaps in daily ET that occurred when a site lost power.

We used the MODIS Enhanced Vegetation Index (EVI; Huete *et al.*, 2002) to quantify the seasonality and variation in green biomass at the sites. The index is computed as a 16-day composite value over the 250 \times 250 m pixel that contains the eddy covariance tower (ORNL DAAC, 2012).

Results

Average seasonal variation and magnitude of vegetation greenness (EVI) and ecosystem carbon and water fluxes were similar across the three study sites (Fig. 1). However, these riparian systems differed strongly with

a nearby desert grassland, shown here as an example of a typical upland, non-groundwater using, ecosystem (data from Scott *et al.*, 2010). Although occasionally responsive to winter/spring and early summer precipitation (winter/spring – November–April; pre-monsoon – May–June), the desert grassland was mostly inactive until the summer rains occurred (monsoon period–July–September). In contrast, all three riparian sites initiated either new leaf growth or canopy greening in early May, with a corresponding net uptake of CO₂ that led to substantial NEP and high ET in the hot, dry premonsoon period (Fig. 1).

All four sites exhibited large reductions in NEP at the onset of the summer monsoon rainy season, around July 1. Following this initial reduction in net carbon acquisition by the ecosystem, plant canopies likely expanded in size, as is suggested by the uptick in EVI (Fig. 1a), and photosynthetic processes up-regulated in leaves (Barron-Gafford *et al.*, 2012) to overcome the substantial respiration fluxes stimulated by the summer rains (Cable *et al.*, 2012). This resulted in a secondary peak in August. When summer rains ended, NEP at the upland desert grassland quickly diminished, whereas high ET and NEP continued into October and November at the riparian sites (Fig. 1b,d).

Among the study sites, average maximum EVI, NEP, and ET were highest at the woodland, especially in the

premonsoon, and extended further into the fall than the other sites (Fig. 1). At the shrubland, NEP increased (118% from June to September) in response to the monsoon, while NEP decreased at the grassland (81%) and woodland (88%). Furthermore, positive CO₂ uptake by the shrubland extended into the fall intermediate in time to the woodland vs. the grassland. Interestingly, the grassland NEP increased earlier, dipped most dramatically at the monsoon onset, and was first to show marked autumn decreases. The woodland's average annual ET was larger than the other sites and exceeded precipitation (P) to a greater extent (ET–P = 449 mm yr⁻¹, compared with 279 mm yr⁻¹ at the shrubland and 259 mm yr⁻¹ at the grassland, Table 1), indicating significant groundwater exploitation by all systems, but especially the deeply rooted woodland. Considering the fractional canopy area (fc), this results in an average annual groundwater use per unit dominant canopy type of 641 547 and 398 mm yr⁻¹ for the woodland (fc = 0.70), shrubland (fc = 0.51) and grassland (fc = 0.65), respectively. Thus, both woody sites more effectively accessed groundwater despite greater depths to the water table at those sites.

Cross-year comparisons show that linear regressions between total annual NEP and total annual P were significant ($P < 0.05$) only at the shrubland (Fig. 2). Surprisingly, the woodland had a *negative* relationship with total monsoon NEP and P (Fig. 2). When ET was

regressed with NEP (Fig. 2), significant correlations were only found at the shrubland for the monsoon and at the grassland for the premonsoon. When all sites were pooled together, the ET–NEP correlations were significant for the monsoon ($R^2 = 0.53$), and premonsoon periods ($R^2 = 0.76$) and at the annual timescale ($R^2 = 0.39$).

In comparison with other North American ecosystems (Xiao *et al.*, 2008), we observed moderate to high levels of annual NEP, with a consistent minimum value occurring in 2003 (Fig. 3, Table 1). Precipitation was variable across the years for our sites (Fig. 3) with coefficients of variation (CV) of 8%, 15%, and 17% at the woodland, shrubland, and grassland, respectively, but these were consistently lower than the CV for NEP (15%, 17%, and 38%, respectively), about double that of the CV for P at the woodland and grassland and the same at the shrubland. At the woodland, four distinctly different years of precipitation resulted in similar cumulative ecosystem CO₂ flux (Fig. 3). Mean shrubland NEP was slightly lower than the woodland, but showed greater variability across years (Table 1). Mean grassland NEP was the lowest of the sites, with three of the 5 years having similar total NEP, resulting in even greater variability in net CO₂ uptake than the two woody sites. The two peak production years at the grassland were in 2005, which had a large monsoon precipitation total, and in 2007, in which the growing season followed a year of substantial flooding.

What controlled this variability across sites and years? Ecosystem respiration (R_{eco}) at the woodland displayed considerably less variation than the shrubland and grassland (CV = 3%, 11% and 24%, respectively), which appears to have been a strong determinant of the differences in NEP variability across sites (Fig. 4, Table 1). At the same time, relative year-to-year variation in GEP varied by a factor of four between the sites (CV = 6%, 12% and 24%, respectively), but the absolute variation in GEP was larger than in R_{eco} , which suggests within-site annual variation is driven by photosynthetic processes.

At the grassland, large storm flows in the river caused substantial rises in the water table and occasional flooding (Fig. 5). We observed complete ca. 0.5 m inundation of the site in late July, 2006. In 2005, storm flows and possible flooding (which was not confirmed visually) elevated the water table to within 1 m of the surface. This groundwater change was likely due in large part to lateral groundwater flows from riverbank recharge, as the increase in 0–1 m soil moisture storage was considerably less than the water table change. Relative to 2005, the flooding in 2006 suppressed NEP, though the monsoon rain total was even higher (Fig. 3). Postflooding (August–October) total R_{eco} in 2006 was 78 g C m⁻²

Table 1 Annual water and carbon fluxes. Precipitation (P) and evapotranspiration (ET) have units of mm. Net ecosystem production (NEP), ecosystem respiration (R_{eco}) and gross ecosystem production (GEP) have units of g C m⁻²

	2003	2004	2005	2006	2007	Mean	Standard deviation
Woodland							
P	232	226	228	272	255	243	20
ET	709	703	663	663	721	692	27
NEP	292	434	372	419	400	383	56
R_{eco}	765	761	771	818	769	777	23
GEP	1058	1196	1143	1237	1169	1160	67
Shrubland							
P	230	261	312	342	282	285	44
ET	491	607	601	555	567	564	47
NEP	268	332	419	404	382	361	62
R_{eco}	454	608	555	540	581	547	58
GEP	721	940	974	944	963	908	106
Grassland							
P	229	260	313	352	289	289	48
ET	472	506	554	552	654	548	69
NEP	135	126	269	135	244	182	69
R_{eco}	549	546	625	781	924	685	164
GEP	684	672	894	916	1169	867	204

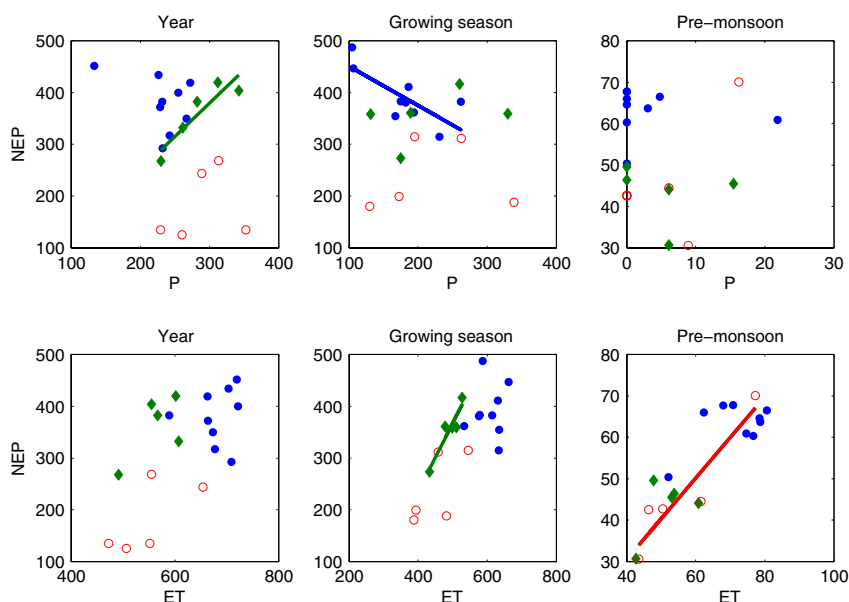


Fig. 2 Net ecosystem production (NEP, $\text{g C}^{-1}\text{season}$) vs. precipitation (P , mm) and evapotranspiration (ET , mm) for the year, growing season (1 May–31 Oct.), and premonsoon (1 June–21 June) totals at the woodland (blue circles), shrubland (green diamonds), and grassland (red open circles). Statistically significant linear relationships at a site ($P < 0.05$) are indicated with a regression line.

higher and total GEP was 53 g C m^{-2} lower than in 2005, despite 35 mm more rainfall. But the 2006 flooding left near-saturated values of soil moisture in the vadose zone that appeared to fuel subsequent NEP in 2007. In the spring of 2007, there was approximately 35 mm more of root zone (0–1 m) vadose zone soil moisture relative to spring 2006 (Fig. 5) that led to much higher pre-monsoon productivity (Fig. 3). Likewise, total premonsoon ET was about 30 mm higher in the 2007 premonsoon period (data not shown).

Contrary to the usual expectation, we observed no significant correlations between P and GEP at the sites. Rather, we found significant correlations between ET and GEP at the grassland and shrubland (Fig. 6). Little correlation was found between ET and GEP at the woodland as there was little variation with either variable ($CV = 7\%$ and 5% , respectively). Pooling the sites showed growing season ET was significantly correlated with GEP ($R^2 = 0.77$). As such, features that drive variation in GEP are those biotic (phenology) and abiotic (micrometeorological) factors that control not only the availability of water to drive photosynthetic processes, but also the uptake, transport, and ultimate delivery to the atmosphere of this important resource. In contrast to GEP, growing season R_{eco} was significantly correlated with P at the woodland, but not for the other sites. In the grassland, ET was a greater predictor of R_{eco} (Fig. 6), and this correlation was also significant ($R^2 = 0.38$) when results were pooled across sites. Combined, this suggests that the relative importance of

abiotic and biotic features that control both GEP and R_{eco} are site-specific, indicating a strong connection to ecosystem structure.

We examined the relationships between growing season fluxes and their known meteorological drivers by computing correlation coefficients using daily average variables (Fig. 7). For NEP at the woodland and grassland, meteorological forcing (T , VPD , PAR) was more positively associated with NEP, and soil moisture negatively related (with a trend toward shallower, more surface soil depths). Weaker correlations were found for the shrubland. There was no clear separation between the sites with ET ; increases in meteorological forcing were associated with decreases in ET , and increases in soil moisture were associated with increases in ET . Likewise the correlations for R_{eco} across all sites were similar, but GEP responded negatively to VPD at the grassland and shrubland and positively to increases in PAR at the woodland. While all sites' GEP was positively related to soil moisture with increasing depths associated with greater rooting volume, the correlations from the woodland were considerably weaker than the other two sites (Fig. 7).

Regressions of GEP and R_{eco} were significant for all sites and pooled across sites for the yearly and growing season periods, but only at the grassland did GEP and R_{eco} significantly covary across the premonsoon period (Fig. 8). Neither the slopes or intercepts of the regression lines were significantly different from one another, but the grassland plotted

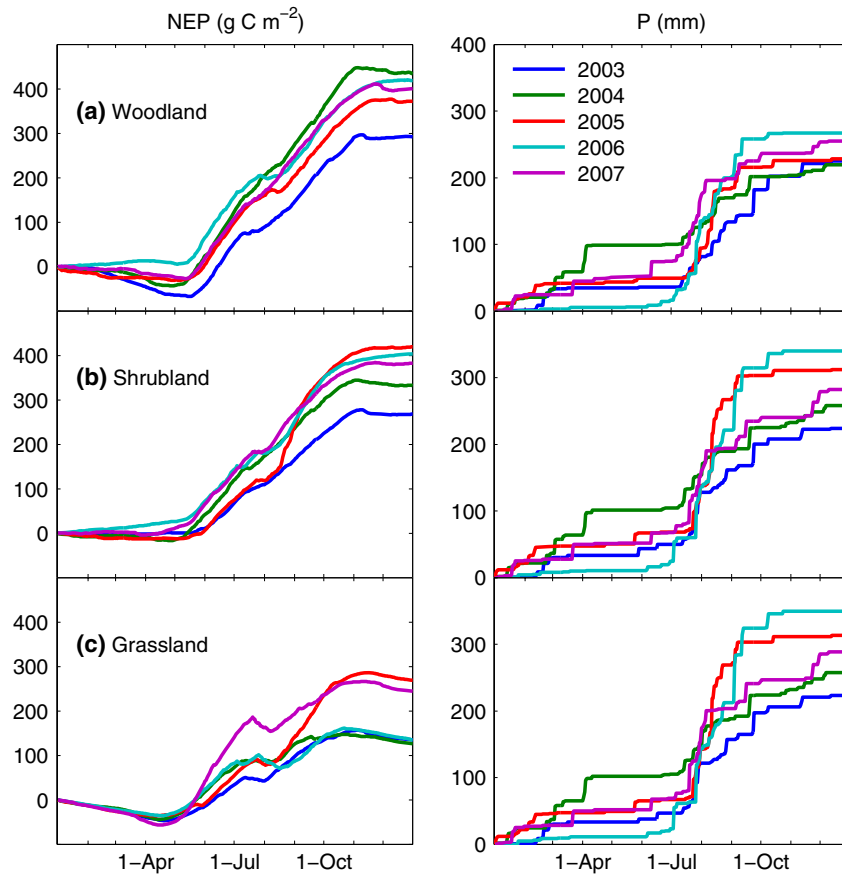


Fig. 3 Cumulative annual net ecosystem production (NEP) and precipitation (P).

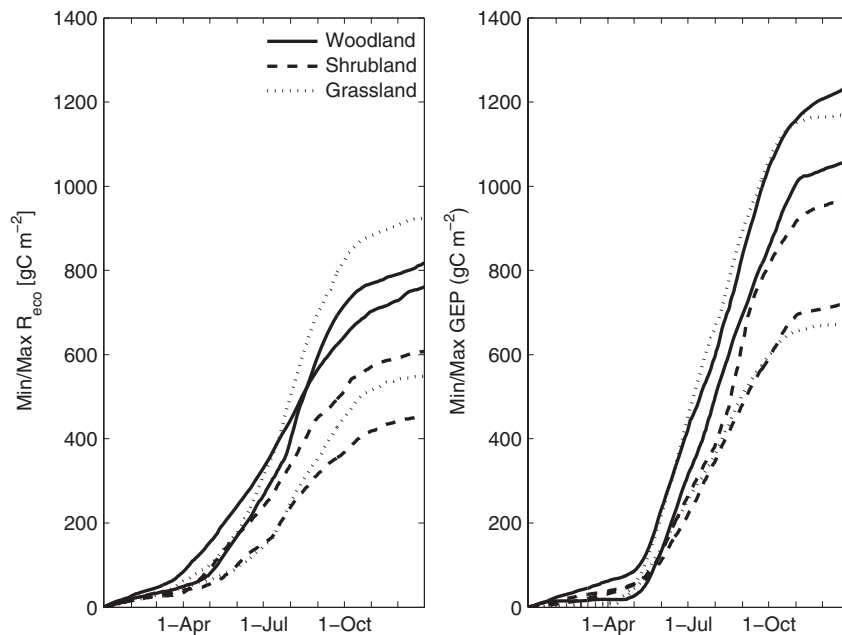


Fig. 4 Cumulative ecosystem respiration (R_{eco}) and gross ecosystem production (GEP) for the years with minimum and maximum efflux and production.

much closer to the global GEP/R_{eco} relationship found by Lasslop *et al.* (2010). For a given amount of productivity, the shrubland and woodland respiration

was generally lower than the grassland and the global average, which resulted in a higher net productivity at these woody sites.

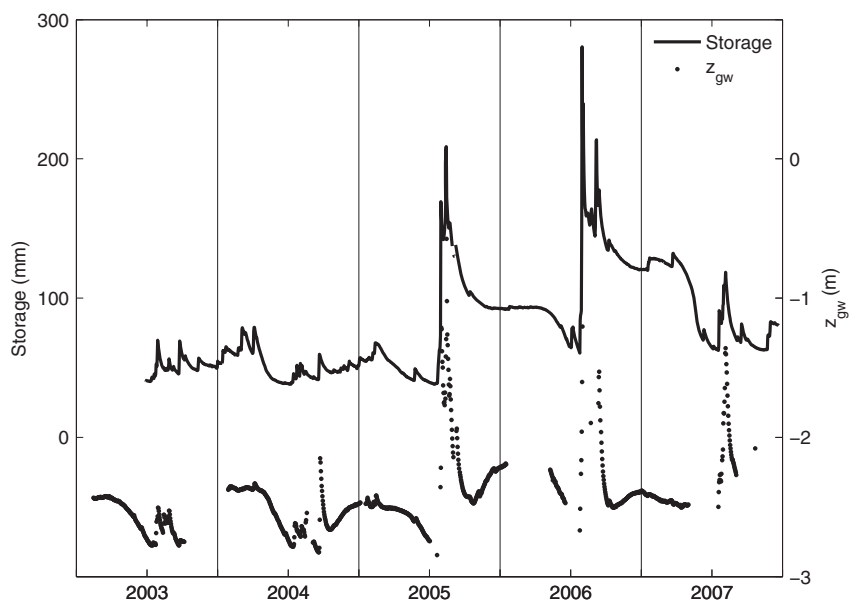


Fig. 5 Total (0–1 m) vadose zone soil water storage and depth to groundwater (z_{gw}) at the grassland. Groundwater measurements have more gaps due to instrument malfunctions.

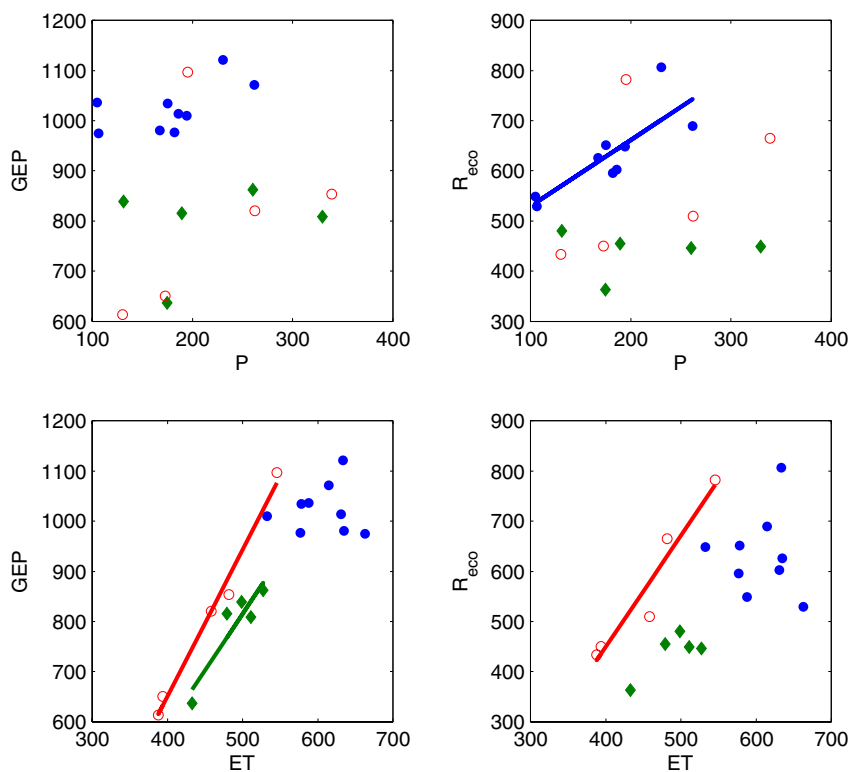


Fig. 6 Gross ecosystem production (GEP, $g C^{-1}season$) and ecosystem respiration (R_{eco} , $g C^{-1}season$) vs. precipitation (P, mm) and evapotranspiration (ET, mm) for the growing season (1 May–31 Oct) at the woodland (blue circles), shrubland (green diamonds), and grassland (red open circles). Significant linear relationships at a site ($P < 0.05$) are indicated with a regression line.

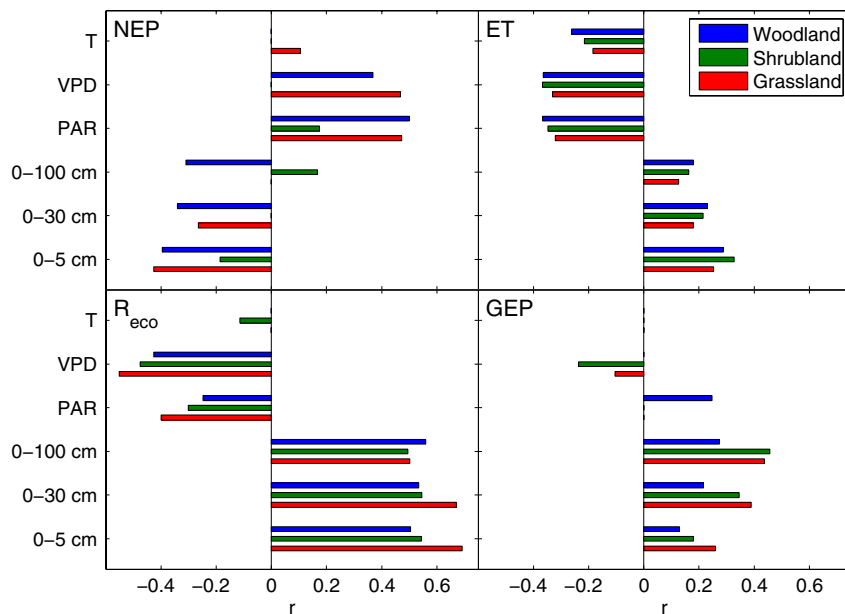


Fig. 7 Correlation coefficients between environmental variables of daily average air temperature (T), vapor pressure deficit (VPD), photosynthetically active radiation (PAR), and 0–5, 0–30, and 0–100 cm total soil water and ecosystem fluxes from 1 June through 30 September for all years. Only highly significant ($P < 0.01$) correlations are shown, non-significant correlations are not presented.

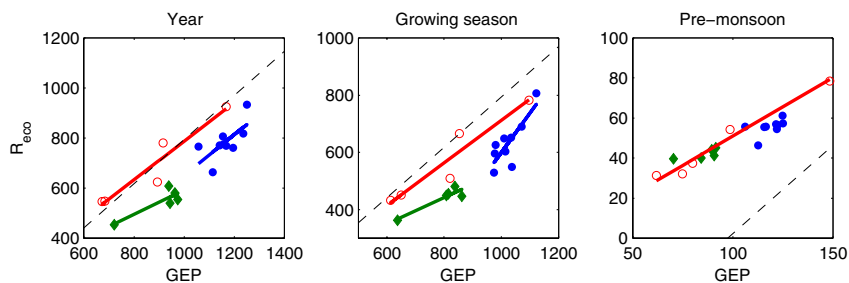


Fig. 8 Gross ecosystem production (GEP, $\text{g C}^{-1}\text{season}$) and ecosystem respiration (R_{eco} , $\text{g C}^{-1}\text{season}$) for yearly, growing season (1 May–31 Oct.), and premonsoon (1 June–21 June) totals at the woodland (blue circles), shrubland (green diamonds), and grassland (red open circles). Significant linear relationships ($P < 0.05$) are indicated with a line. Dashed line is from a global synthesis (Lasslop *et al.*, 2010).

Discussion

Vegetation change and water accessibility

Understanding the relationship between structure and function in terrestrial ecosystems is an important step towards predicting how future changes in plant dynamics feedback on climate (Chapin *et al.*, 1997). Changes in the structure of vegetation from grass dominated to woody plant-dominated landscapes across biomes has been shown to be a function of mean annual precipitation (Barger *et al.*, 2011) with the assumption that differences in plant water-use of available soil moisture, vs. rainfall impacts on soil carbon cycling, drives differences in productivity with a change in

plant structure (Huxman *et al.*, 2005; Kulmatiski & Beard, 2013). In this study, we found that the availability and access of groundwater associated with greater fractions of woody, rather than herbaceous, species in these riparian ecosystems led to significant changes in magnitude, variability, and importance of environmental drivers of the biosphere–atmosphere exchanges of water and carbon dioxide.

Increased access to groundwater led to changes in the seasonality of ecosystem-level carbon exchange and greatly expanded the functional growing season of all dominant plant types (Fig. 1). The fore-summer, premonsoon (May, June) are reliably hot and dry with large radiation loads and high vapor pressure deficits (VPD), presenting an extreme environmental challenge

for plants to maintain functional surfaces (Barron-Gafford *et al.*, 2012). The high levels of production at all sites were in part due to the extremely dry surface soils that restricts total ecosystem respiration by limiting heterotrophic respiration (e.g., Huxman *et al.*, 2004b), yet the differences in the relative leaf area across sites highlight intrinsic differences in photosynthetic capacity at the ecosystem scale as woody plant increase in abundance. The result is that net ecosystem productivity (NEP) was especially large at this time of year for the woodland, as compared to NEP during the monsoon, when the bulk of the annual precipitation occurs (Fig. 1). Differences among sites were also evident in the length of the growing season, which began earlier in the more cold-tolerant grassland and was extended with improved groundwater access at the woody sites, resulting in greater values of NEP persisting into the fall (Fig. 1). It is likely that this persistence into the fall is driven in part by both differences in access to groundwater and phenological constraints on grass growth forms that result in down-regulation of photosynthetic processes following reproduction at the height of the growing season (as in Craine *et al.*, 2012).

Woody plant encroachment alters ecohydrological relations between carbon and water

Despite access to groundwater, regressions of annual and growing season P and NEP and growing season ET and NEP were significant only at the shrubland site (Fig. 2). The shrubland had a greater size class distribution of mesquite, understory shrubs and grasses that were not likely accessing groundwater at 7 m depth (Potts *et al.*, 2008; Stromberg, 2013). This greater fraction of precipitation-reliant vegetation in comparison to the woodland or grassland likely led to a closer coupling of P and NEP (Fig. 2), which is also supported by the positive correlation of daily NEP with shallow 0–1 m root zone soil moisture at the shrubland (Fig. 7). Taken together, these data suggest that the transitional shrubland state may have periods of productivity that equal or even exceed the fully encroached woodland state in periods of high precipitation (e.g., years 2005 and 2006, Fig. 3) because of the greater density of precipitation-reliant understory and the more open, less shaded, understory environment.

Remarkably, greater precipitation led to decreased NEP (Fig. 2) in the woodland, likely due to the significant positive relationship between P and R_{eco} (Fig. 6). Likewise, daily shallow soil moisture was more negatively correlated with NEP (and most negative with 0–5 cm soil moisture, Fig. 7) at the grassland and woodland. Decades of carbon accumulation from the

highly productive N-fixing mesquite have led to soils with vast amounts of carbon and nitrogen and high C/N ratios (McLain & Martens, 2006) that, in turn, leads to relatively larger soil respiration pulses under the entire woodland and under the trees when it rains (Yepez *et al.*, 2007; Cable *et al.*, 2012). Likewise, large accumulations of carbon can build up in the soils under the grassland's bunchgrasses. In the presence of adequate soil moisture, both carbon pool size and C/N have been shown to be strong controllers of soil respiration in semiarid soils (Conant *et al.*, 2000). Furthermore, studies have shown a strong respiration response to moisture input measured in higher C/N soils (under mesquite and sacaton grasses), indicating that soil respiration at sites where these vegetation types are more abundant is not limited by carbon availability (Cable *et al.*, 2013). With the acquisition of carbon being considerably decoupled from water constraints and microbial decomposition often precipitation limited, the woodland's NEP response to precipitation is opposite to what one might expect based only on plant-based responses like net primary production (Huxman *et al.*, 2004a). But this unusual property might be found more broadly in other seasonally dry forests that have access to a constant supply of groundwater (e.g., Saleska *et al.*, 2003). The dynamics in these type of settings are poorly captured in ecosystem models (Saleska *et al.*, 2003), which presents a challenge, as these sites disproportionately impact regional biosphere/atmosphere exchange totals in some regions.

The impact of groundwater accessibility on annual net carbon exchange across our gradient of woody plant encroachment was more complex than ET because of the degree of coupling between precipitation and component C exchanges (Figs 3 and 6). Even while R_{eco} and GEP were both about 230 g C m^{-2} lower, on average, in the shrubland than in the woodland, average NEP was nearly equivalent (Table 1, Fig. 3). For this to occur, average R_{eco}/GEP decreased from 71% (woodland) to 64% (shrubland). This downward shift could be due to alterations in several aboveground and belowground characteristics. A fully encroached woodland has a greater allocation to large, extensive woody rooting systems (Barger *et al.*, 2011; Stromberg, 2013) and also supports a more extensive and denser canopy, which could increase autotrophic maintenance and growth respiration costs. In addition, mesquite are facultative N-fixers, and, in riparian areas, consistent access to groundwater facilitates sustained allocation to N-fixing capacity. This could lead to leaves with higher physiological capacity (Smith *et al.*, 1997), potentially driving up baseline aboveground respiration by the dominant woody plant as well as providing N-rich litter that could fuel extensive heterotrophic microbial

respiration in the woodland setting (McInain & Martens, 2006; Cable *et al.*, 2009, 2012).

Interannual variability in R_{eco} and GEP increased from the woodland to grassland (Fig. 4, Table 1). Grassland variability was probably due to a combination of biotic constraints and its location on a lower floodplain terrace that made it subject to larger water table rises and flooding. Such an event occurred in 2006 and, possibly, 2005, providing greater variability in water availability to the shallower-rooted bunchgrasses (Fig. 5). In comparison with 2003 and 2004 when no flooding occurred, we found that grassland NEP was substantially lower (Fig. 3). While gross productivity was comparable between the grassland and shrubland, NEP was lower because $R_{\text{eco}}/\text{GEP}$ was shifted upwards (Fig. 8). Grassland systems typically have higher proportional allocation to belowground biomass (Parton *et al.*, 1993), and increased access to groundwater could support greater live root biomass, increasing baseline maintenance respiration. In addition, more extensive live root mass would enhance soil organic carbon accumulation, increasing microbial activity and turnover, increasing the respiratory sensitivity to water pulses (Jenerette *et al.*, 2008). These two features were likely not matched by similar incremental increases in leaf-level photosynthetic capacity, canopy-level leaf area development following rainfall pulses or flooding, or extensions of the growing season, thereby resulting in a greater control over NEP by the changes in respiration costs. In the contrast, the relationship of GEP to R_{eco} at the shrubland and woodland was shifted downward from the global relationship, implying a lower base respiration. This may be due to the stronger degree of decoupling between water and carbon exchange at these sites in time along with a buildup of more recalcitrant forms of carbon in the soil or coarse woody debris (Fig. 8).

Implications for water availability

Across the woody plant encroachment gradient, even as depth to groundwater increased from grassland to shrubland to woodland, the woodland had the highest ET in excess of precipitation and the grassland was lowest (Table 1, Fig. 1). As opposed to the surrounding upland areas where P limits ET (Scott, 2010), all three sites used substantial quantities of non-locally recharged groundwater that represents a significant amount of basin aquifer outflow (Scott *et al.*, 2006b, 2008). Because woody plants have historically and are currently proliferating across the San Pedro basin (Stromberg *et al.*, 2010) and in intact riparian regions throughout the Southwest (Asner *et al.*, 2003), this increased extraction of groundwater from the aquifer (when not too deep)

may lead to decreased groundwater contributions (base flow) to streams and rivers. Mesquite trees, with their deep roots, access groundwater at depths beyond many other woody riparian species (Stromberg, 2013). Thus, mesquite, or any other deep-rooted shrub or tree species, expansion on floodplains increases the lateral extent of phreatophytes beyond a river's active channel region leading to larger groundwater extractions from aquifers.

Change in the vegetation composition of ecosystems is a global phenomenon with potentially large consequences for how mass and energy cycle between the land and atmosphere. Vegetation shifts may have more impact on these cycles if access to soil moisture pools change (shallow vs. deep pools) or if these pools change due to an altered climate regime like changes in precipitation intensity (Kulmatiski & Beard, 2013). This study is valuable as an illustrative example of what we can expect when woody plant encroachment into grasslands occurs in a setting where supplemental deep water sources may be available. While these systems represent an extreme regionally, in terms of the magnitude of fluxes, these large values and the variance has allowed us to illustrate the dynamics that are likely in operation in non-riparian settings, with similar proportional changes in ecosystem consequences that may be difficult to detect due to their relatively small magnitudes. The degree to which vegetation, such as woody plants, access a deeper soil water pool will likely increase ET and NEP over a longer functional growing season. The response of NEP will likely be much more complex as the encroachment proceeds because of the long-term adjustments to above and belowground biomass that directly affects R_{eco} .

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