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Sensitivity of riparian ecosystems in arid and semiarid environments to moisture pulses

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Abstract:

Structural and functional dynamics of riparian vegetation in arid and semiarid basins are controlled by hydrological processes operating at local, landscape and catchment scales. However, the importance of growing-season precipitation as a control on evapotranspiration (ET) and carbon cycling in these ecosystems varies considerably across the riparian landscape, depending largely on access to the near-surface water table. Here we describe key findings from ongoing ecohydrological studies along the Upper San Pedro River (USPR) in semiarid, south-eastern Arizona, USA. Depth to the water table varies substantially across the riparian landscape along the USPR drainage, and is a key factor controlling the sensitivity of cottonwood (*Populus fremontii*) water-source use, transpiration rate and photosynthetic metabolism to inputs of monsoonal moisture during the growing season. Landscape-scale functional variation in cottonwood forests has been incorporated into spatially explicit ET models for estimating water balance components along the USPR. However, of greater importance for understanding controls on water and carbon exchange processes in the riparian corridor is the conversion of sacaton (*Sporobolus* spp.) grasslands on pre-entrenchment floodplain terraces to communities dominated by the deep-rooted woody legume, mesquite (*Prosopis velutina*). Mesquite is now the dominant cover in the riparian corridor and has increased by more than 300% in the USPR basin since 1972. The physiognomic shift from grassland to mesquite woodland on pre-entrenchment floodplain terraces alters the sensitivity of ET and CO_2 exchange to inputs of growing-season precipitation. Because mature mesquite shrubs and trees have greater access to groundwater in these habitats than sacaton, ET and gross ecosystem production (GEP) are relatively decoupled from variation in monsoonal precipitation. However, decomposition of litter and soil organic matter in floodplain ecosystems remains highly coupled to monsoonal moisture inputs after mesquite encroachment. Responses of net ecosystem exchange of CO_2 (NEE) to inputs of monsoonal rainfall are therefore not simple, but depend on vegetation composition and the connection of dominant plants to the water table. The heterogeneous vegetation patterns and groundwater depths in the riparian landscape offer unique opportunities for understanding fundamental ecohydrological processes linking carbon and water cycles in both riparian and upland ecosystems. Copyright © 2006 John Wiley & Sons, Ltd.

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INTRODUCTION

Ecological processes in arid and semiarid regions are critically tied to watershed hydrology. Water is the most limiting resource to biological activity in these environments, so the timing and magnitude of ecosystem production, evapotranspiration (ET) and nutrient cycling are expected to be closely coupled to inputs of

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growing-season precipitation (Noy-Meir, 1973). As such, future changes in the size, frequency and/or seasonal timing of moisture inputs are predicted to have large impacts on vegetation distribution and ecosystem function in arid and semiarid regions (Neilson, 2003; Weltzin *et al*., 2003).

Recharge of soil moisture resulting from a single or a series of rainfall events produces a hierarchy of biological responses among key organisms involved in ecosystem water and carbon cycling (Reynolds *et al*., 2004). Plants facilitate the movement of water from the soil to the atmosphere, and through photosynthesis provide the energy necessary for many key biogeochemical processes. Because plants do not use precipitation inputs equally during the growing season (Ehleringer *et al*., 1991), there is some uncertainty in how arid and semiarid ecosystems are likely to respond to change in precipitation (Weltzin *et al*., 2003). For example, woody plants respond physiologically to large inputs of moisture during the growing season, but only if water in deep soil layers is limiting (Golluscio *et al*., 1998; Williams and Ehleringer, 2000). Developmental stage and life history characteristics of woody plants further determine their sensitivity to moisture inputs (Dawson and Ehleringer, 1991; Donovan and Ehleringer, 1992; Wan *et al*., 1994; Schwinning and Ehleringer, 2001). Conversely, grasses and many other herbaceous plants with shallow root systems and limited access to deep, stable moisture sources, are more sensitive to moisture inputs than are deep-rooted perennials (Ehleringer *et al*., 1991; Golluscio *et al*., 1998; Scott *et al*., 2000).

Understanding interactions and feedbacks among changes in land cover, precipitation regime and the exchange of energy and matter at ecosystem and larger scales is an important, contemporary challenge in ecology and hydrology (Hannah *et al*., 2004). Rooting depth, or more generally the availability of a stable moisture source, strongly controls the timing and magnitude of water and carbon cycling in arid and semiarid environments (Jackson *et al*., 2000, 2001; Huxman *et al*., 2005). Therefore, patterns of ecosystem carbon and water cycling are likely to be highly variable in the complex riparian landscapes of arid and semiarid regions. Riparian habitats, in these otherwise water-limited environments, are characterized by steep spatial gradients in root-zone water availability, frequent disturbance by flooding and fire, highly variable precipitation inputs in time and space and often rapid changes in surface flows and groundwater depth. The importance of climate, and specifically the role of rainfall variation, as a driver of ecosystem gas exchange dynamics in riparian ecosystems is likely to depend on the prevalence of deep soil moisture or groundwater available to dominant plants (Scott *et al*., 2003, 2004, 2006a; Williams and Scott, in press). Therefore, alteration of vegetation structure and distribution in riparian landscapes, affecting large-scale patterns of groundwater and precipitation use, has important ramifications for basin-level water and carbon budgets (Dahm *et al*., 2002; Goodrich *et al*., 2000a; Scott *et al*., 2006a, 2006b; Tabacchi *et al*., 2000). Because riparian landscapes in arid and semiarid environments are heterogeneous with respect to water table depth and vegetation structure, they offer unique opportunities to investigate the sensitivity of material and energy exchanges between the ecosystem and atmosphere in response to seasonal precipitation inputs, and the basic mechanisms linking hydrological and ecological dynamics.

In a comprehensive analysis of data from the international terrestrial flux observation network, FLUXNET (Baldocchi *et al*., 2001), Law *et al*. (2002) found a negative correlation between ET and net ecosystem exchange (NEE) of CO_2. This correlation is to be expected, since transpiration, the dominant component of ET in many ecosystems, and CO_2 diffusion into leaves during photosynthesis share a common pathway through stomatal pores. However, NEE is the sum of two opposing CO_2 fluxes: the gross photosynthetic flux of CO_2 from the atmosphere (GEP; gross ecosystem production) and ecosystem respiration (R_e), which includes respiration from autotrophic (R_a) and heterotrophic (R_h) organisms. The value of NEE conventionally has a negative sign when there is a net flux of CO_2 from the atmosphere to the ecosystem. Values for *GEP* and *R* are conventionally reported with a positive sign, and therefore:

$$NEE = R_e - GEP \tag{1}$$

$$NEE = (R_a + R_h) - GEP \tag{2}$$

Changes in ET, GEP, and R_e in arid and semiarid ecosystems are often coupled to growing-season moisture inputs that wet upper soil layers in which plant roots and soil microbial communities are most active (Hastings *et al*., 2005; Scott *et al*., 2006a). However, in riparian zones, deep-rooted phreatophytes, which are frequently the dominant plants in these ecosystems, obtain a large fraction of their water from the near-surface water table or capillary fringe, and in many cases do not take up growing-season precipitation (Snyder and Williams, 2000). As a result, ET, GEP and R_a in riparian vegetation may be relatively insensitive to inputs of growing-season moisture from flooding or directly from rainfall, but may be responsive to seasonal and event-driven changes in groundwater depth (Horton *et al*., 2001; Gazal *et al*., 2006). Heterotrophic respiration (R_h) associated with decomposition of litter and oxidation of soil organic matter is very sensitive to moisture inputs regardless of the source water used by dominant plants (Huxman *et al*., 2004). Consequently, in riparian ecosystems dominated by deep-rooted woody plants with a stable source of water, NEE, which is an integration of all CO_2 fluxes, is expected to respond in a non-linear fashion to growing-season moisture inputs. Under certain circumstances, severe flooding in riparian vegetation may damage plant canopies and redistribute soil organic matter such that ET, GEP, R_a and R_h are affected.

Here we highlight completed and ongoing ecohydrological studies conducted in riparian ecosystems along the Upper San Pedro River (USPR) in south-eastern Arizona. These studies have focused on leaf-, canopy- and ecosystem-scale gas exchange in stream side and floodplain vegetation along the USPR over the past 10 years (Gazal *et al*., 2006; Goodrich *et al*., 2000a; Hultine *et al*., 2004; Schaeffer *et al*., 2000; Scott *et al*., 2000, 2003, 2004, 2006a, 2006b; Snyder and Williams, 2000, 2003; Yepez *et al*., 2003). We have identified several examples in which monsoonal moisture inputs during the growing season produce unequal and even divergent responses of CO_2 and H_2O exchange in riparian vegetation. These findings shed light on the often complex interactions between hydrological and ecological dynamics in semiarid environments and argue for more detailed and mechanistic studies on how ecosystem components respond to pulsed resource supply.

THE UPPER SAN PEDRO RIVER AND STUDY SITES

The San Pedro River has its origin in northern Sonora, Mexico, and flows freely northward across the international border and through the upper and Lower San Pedro River basins to its confluence with the Gila River in south-central Arizona. Annual rainfall averages about 300 mm at our study sites along the San Pedro River in the upper basin near Tombstone, Arizona. About 65% of the annual rainfall at these locations occurs during the summer monsoon season (July through September) and the remainder arrives during winter months (Goodrich *et al*., 2000b).

Much of our work has focused on three dominant vegetation communities along the riparian corridor of the USPR: cottonwood/willow (*Populus fremontii/Salix gooddingii*) forest along the active channel, mesquite (*Prosopis velutina*) woodland and sacaton (*Sporobolus* spp.) grassland. The mesquite woodland and sacaton grassland occur predominantly on pre-entrenchment floodplain terraces above the active channel (Figure 1) and have varying degrees of connection to the water table (Stromberg *et al*., 1996). River down-cutting about 100 years ago decoupled vast expanses of sacaton grassland from the near-surface water table and from seasonal flood pulses that sustained their high productivity (Bahre, 1991; Stromberg *et al*., 1996). Ecological dynamics during the growing season in remnant sacaton grassland on these upper terraces are highly coupled to direct precipitation inputs (Scott *et al*., 2000). Deep-rooted mesquite has invaded these grasslands, and in the absence of fire, has converted large sections of pre-entrenchment floodplains to woodland (Bahre, 1991; Scott *et al*., 2006b).

Because of geomorphic and hydrogeologic variation along the river drainage (Pool and Coes, 1999; Leenhouts, 2006), the streamside cottonwood/willow forest is subjected to substantial site-specific variation in water-table depth and seasonal drought stress. Perennial sections of the river support extensive and dense cottonwood forest of varying age structure (Schaeffer *et al*., 2000; Stromberg, 1998; Stromberg *et al*., 2006). Because groundwater depths are small in these sections of the river, cottonwood transpiration is rarely limited
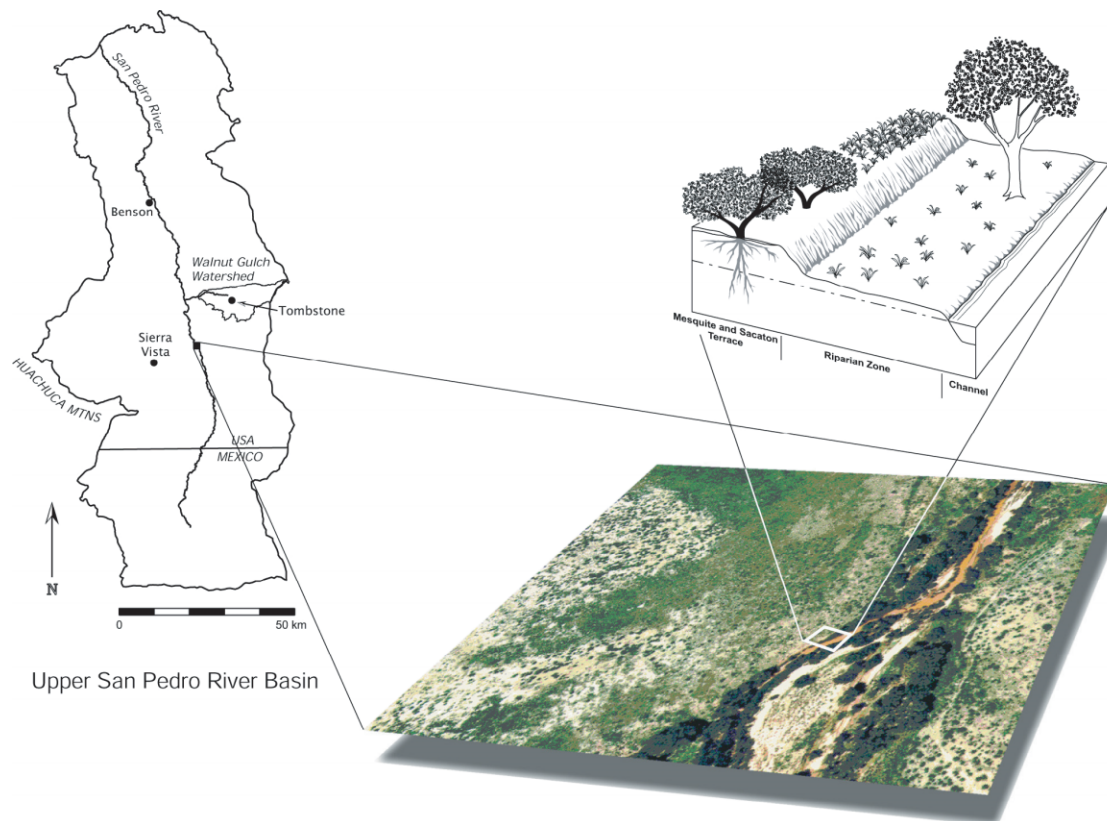
Figure 1. Location of research area on the Upper San Pedro River and representation of pre-entrenchment floodplain terrace supporting sacaton (*Sporobolus* spp.) grassland and mesquite (*P. velutina*) woodland, and streamside riparian forest dominated by cottonwood (*P. fremontii*)

by water availability. Intermittently flowing sections of the river support sparse cottonwood forest subjected to comparatively greater magnitudes of water limitation and physiological stress, especially during the hot, pre-monsoon drought period in late May and June. The understory vegetation in the cottonwood/willow forest is dominated by sacaton and seep willow (*Baccharis glutinosa*). The understory vegetation is patchy and locally abundant, and is not highly sensitive to monsoonal moisture pulses (Scott *et al.*, 2006b).

The narrow fetch of the cottonwood forest along the USPR is unsuitable for estimation of ecosystem-level ET and CO_2 fluxes using micrometerological approaches, such as eddy covariance. We have estimated stand-level transpiration of cottonwood and willow at perennial and intermittent reaches of the river using sap flow measurements (Gazal *et al.*, 2006; Schaeffer *et al.*, 2000), and investigated photosynthetic responses to monsoonal moisture inputs from leaf gas exchange and carbon isotope ratio measurements (Schaeffer, 1998; Williams *et al.*, 1998; Potts and Williams, 2004). A micrometeorological tower with eddy covariance instrumentation has been operating continuously at a pre-entrenchment floodplain-terrace site in a dense mesquite woodland since 2001 (Scott *et al.*, 2003, 2004). Similar eddy covariance instrumentation was installed in the sacaton grassland in 2003 (Scott *et al.*, 2006a). Both H_2O and CO_2 fluxes are quantified half-hourly at these sites to investigate daily, seasonal and inter-annual controls over fluxes in mesquite- and grass-dominated floodplain ecosystems (Scott *et al.*, 2003, 2004, 2006a). The large mesquite trees at the woodland site have roots extending to the water table ∼10 m below the surface. The understory plant community beneath the mesquite canopy is sparsely covered by C3 and C4 herbaceous dicots and grasses, and owing to the high plant production, the soil surface is covered by a thick and highly decomposable litter layer from mesquite

leaves and twigs. The floodplain grassland is uniformly covered by large, tussok-forming sacaton grasses and is only marginally connected to the near-surface water table (Scott *et al.*, 2006a).

SENSITIVITY OF RIPARIAN COTTONWOOD FOREST TO MONSOONAL MOISTURE INPUTS

We have investigated patterns of leaf stomatal conductance, sapflow, source water and carbon isotope ratio variation in cottonwood and willow trees at perennial and intermittent sections of the USPR (Gazal *et al.*, 2006; Schaeffer, 1998; Schaeffer *et al.*, 2000; Snyder and Williams, 2000; Potts and Williams, 2004; Williams *et al.*, 1998). Streamside habitats on perennially flowing sections of the river have shallow groundwater tables (1–3 m) that do not vary appreciably during the growing season. In contrast, conditions along intermittent sections of the river are less suitable for cottonwood and willow—obligate riparian species requiring access to continual groundwater supply for survival in this semiarid environment (Stromberg, 1998).

Water sources available to cottonwood trees include groundwater, stream water (including flood water) and precipitation. The proportion of tree transpiration derived from these sources varies over the season and among habitats supporting cottonwood forest. Where the water table is shallow along perennial sections of the river, cottonwood obtains 90–100% of its transpiration water from this readily available source, even after significant inputs of monsoonal rainfall (Snyder and Williams, 2000). However, where groundwater is less accessible along intermittently dry sections of the river, cottonwood relies significantly on direct inputs of precipitation and/or floodwater for its transpiration demands. Up to 25% of the water transpired by cottonwood was from shallow soil layers wetted by monsoonal rainfall at a site where the water-table depth exceeded 4 m (Snyder and Williams, 2000). Likewise, leaf stomatal conductance increased significantly from the pre-monsoon dry period to the wet monsoon period at sites where cottonwood had limited access to groundwater. But along perennially flowing sections of the river, stomatal conductance did not increase significantly (Table I). Goodding willow (*Salix gooddingii*), a co-dominant tree in these forests, had a very similar response to monsoonal moisture inputs at perennial and intermittent reaches of the river.

Scaled sap flow and tree-ring carbon isotope ratio measurements in cottonwood show that canopy-scale photosynthetic metabolism and transpiration fluxes are much more sensitive to growing-season moisture pulses along intermittently flowing sections of the river than along perennially flowing sections. Canopy transpiration

Table I. Average midday (10:00–13:00 h) leaf-level stomatal conductance (g_s; mmol m^{-2} s^{-1}) (1 SE) for cottonwood (*P. fremontii*) and willow (*Salix gooddingii*) measured during pre- (June) and peak-monsoon (August) periods at intermittent and perennial sections of the Upper San Pedro River in south-eastern Arizona, USA. Measurements are from four trees of each species per site. Three to five leaves were measured from several different locations in a given tree and averaged to obtain a single value for each tree

	Pre-monsoon	Peak-monsoon
Cottonwood		
Perennial reach	243 (21)[c]	325 (54)[b,c]
Intermittent reach	164 (7)[a]	331 (30)[b]
Willow		
Perennial reach	171 (30)[a,c]	229 (58)[b,c]
Intermittent reach	93 (18)[a]	238 (30)[b]

Superscript letters (a,b,c) are compared within a species and within a given variable, and where different, denote significance at $\alpha = 0.05$ (from Schaeffer, 1998).

in cottonwood, the dominant component of total ET in this ecosystem (Schaeffer *et al.*, 2000; Scott *et al.*, 2006b), almost doubled from the dry pre-monsoon period in early July to the monsoon period in late August at an intermittently flowing section of the river (Figure 2; Gazal *et al.*, 2006). Conversely, canopy transpiration increased by only 30% or less in response to monsoonal moisture inputs at a perennially flowing section of the river (Figure 2).

Carbon isotope ratio ($\delta^{13}C$) values of biomass from C3 plants, such as cottonwood, reflect variation in leaf internal-to-ambient CO_2 concentration ratios (c_i/c_a) during photosynthesis (Farquhar *et al.*, 1989), an index of stomatal 'openness'. Tree-ring cellulose $\delta^{13}C$ values integrate changes in canopy-scale c_i/c_a (Francey and Farquhar, 1982) and provide a record of long-term patterns in canopy photosynthetic responses to environment. Potts and Williams (2004) extracted and analyzed sub-annual increments of tree-ring tissue from early- and late-season growth from cottonwood at perennial and intermittent sections of the USPR (Figure 3).
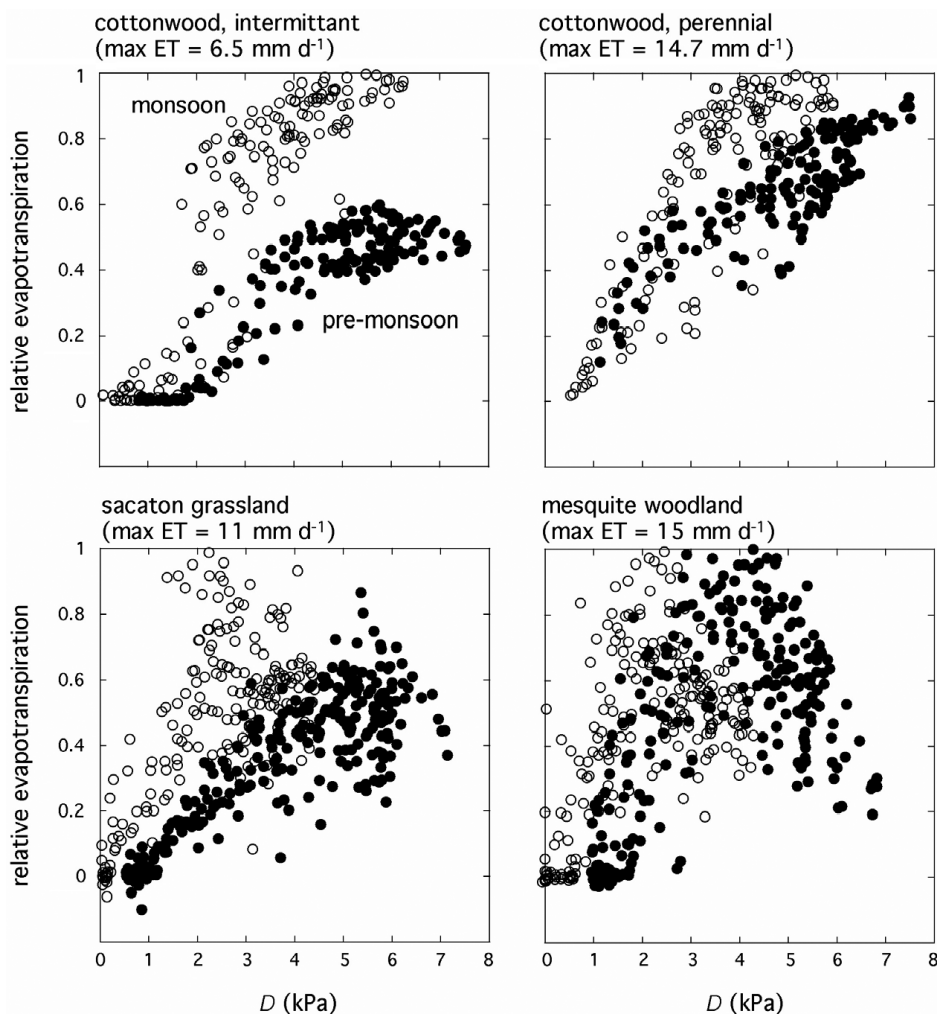

Figure 2. Relative sensitivity of evapotranspiration to monsoonal moisture input for cottonwood forest at perennial and intermittent stream reaches and for sacaton grassland and dense mesquite woodland on pre-entrenchment floodplain terraces. Thirty-minute averaged ET rates are plotted against vapour pressure deficit (*D*) for daytime intervals (05 : 30–17 : 00 h) over two 10-day periods: day of year 182–192 (closed symbols, 'pre-monsoon') and day of year 240–250 (open symbols, 'monsoon'). Data are from Gazal *et al.*, 2006 for cottonwood, and from Scott *et al.* (2006a) for mesquite woodland and sacaton grassland

The difference in $\delta^{13}C$ between early- and late-season ring-tissue fractions was significantly correlated ($r^2 = 0.59$, $p = 0.005$) with monsoon-period streamflow condition (Q90; the 90% flow exceedence—an index of maximum river flow rates corrected for extreme low-flow and flooding events) at an intermittently flowing section of the river, but not at a perennially flowing section of the river ($r^2 = 0.003$, $p = 0.85$). Canopy-level photosynthetic metabolism in riparian forest apparently is sensitive to variation in monsoon activity only where groundwater is relatively inaccessible. Q90 provides a single integrated value of moisture availability, and is defined as the daily stream flow value that was exceeded 90% of all days during the monsoon season. Q90 was positively correlated to precipitation amount and negatively correlated to atmospheric vapour pressure deficit (Potts and Williams, 2004).

Taken together, these results suggest ET and GEP of the riparian forest canopy are highly sensitive to monsoonal moisture inputs where access to groundwater is limited, but less so elsewhere along the river where the water table is shallow. Ecosystem water and CO_2 fluxes are likely to be controlled more by radiation, temperature and atmospheric humidity along perennially flowing sections of the river than by direct inputs of monsoonal precipitation and/or flood flows (Gazal *et al.*, 2006). Where groundwater is shallow, NEE is potentially decoupled from monsoonal moisture inputs. Unfortunately, we have not measured soil or ecosystem-scale respiration, important components of NEE (Equation (1)), in cottonwood/willow forest, so sensitivity of NEE to variation in monsoon strength is not known. Furthermore, the contribution of understory plants, such as seep willow and sacaton, to ET could be substantial where local abundance is high (Scott *et al.*, 2006b), but source water for these plants is likely similar to that of cottonwood. Therefore, sensitivity of understory vegetation in cottonwood/willow forest to monsoonal moisture inputs likely parallels that of the dominant overstory canopy (Scott *et al.*, 2006b). Because of limited information on understory vegetation processes and ecosystem respiration, a complete understanding of how NEE and ET are coupled to monsoonal moisture inputs in cottonwood/willow forest is still lacking.

ECOHYDROLOGICAL CONSEQUENCES OF WOODY-PLANT ENCROACHMENT INTO FLOODPLAIN GRASSLAND

Encroachment of mesquite (*P. velutina*) into former grassland on pre-entrenchment floodplain terraces of the USPR and in upland areas of the basin is likely to have large effects on patterns and magnitudes of CO_2 and ET fluxes. Between 1973 and 1992 mesquite cover in the basin increased 371% (Goodrich *et al.*, 2000b; Kepner *et al.*, 2000); this deep-rooted woody plant now forms the dominant cover over 67% of the land in the basin. Pre-entrenchment floodplain terraces of the river once supported extensive sacaton (*Sporobolus* spp.) grasslands (Bahre, 1991). These large tussock grasses have shallower root systems than mesquite and do not access groundwater where water-table depths exceed 3 m (Scott *et al.*, 2006b), which is now the case for many of the sites occupied by this grass on pre-entrenchment terraces of the USPR.

Encroachment of mesquite into these grasslands provides an opportunity to investigate the complex interactions between water and carbon cycle processes and the sensitivity of these processes to environmental drivers. Sacaton on pre-entrenchment terraces is largely dependent on local rainfall for moisture since flooding rarely inundates these upper terraces. Mesquite on these pre-entrenchment terraces uses water from the near-surface water table, reducing its dependence on rainfall during the growing season (Fravolini *et al.*, 2005; Scott *et al.*, 2006b; Snyder and Williams, 2000, 2003).

Woody-plant encroachment into remnant sacaton grassland has the potential to decouple primary productivity from monsoonal rain inputs because deep-rooted woody plants access H_2O sources unavailable to shallow-rooted grasses. ET is more sensitive to monsoonal moisture inputs in sacaton grassland than in mesquite woodland (Figure 2). However, increases in primary productivity associated with shrub access to deep sources of water can be offset by larger respiratory fluxes from soil microbial communities that remain highly responsive to summer rain (Scott *et al.*, 2006a). We hypothesize that imbalances between ecosystem respiration and photosynthesis develop as grasslands are invaded by deep-rooted woody plants (Figure 4).
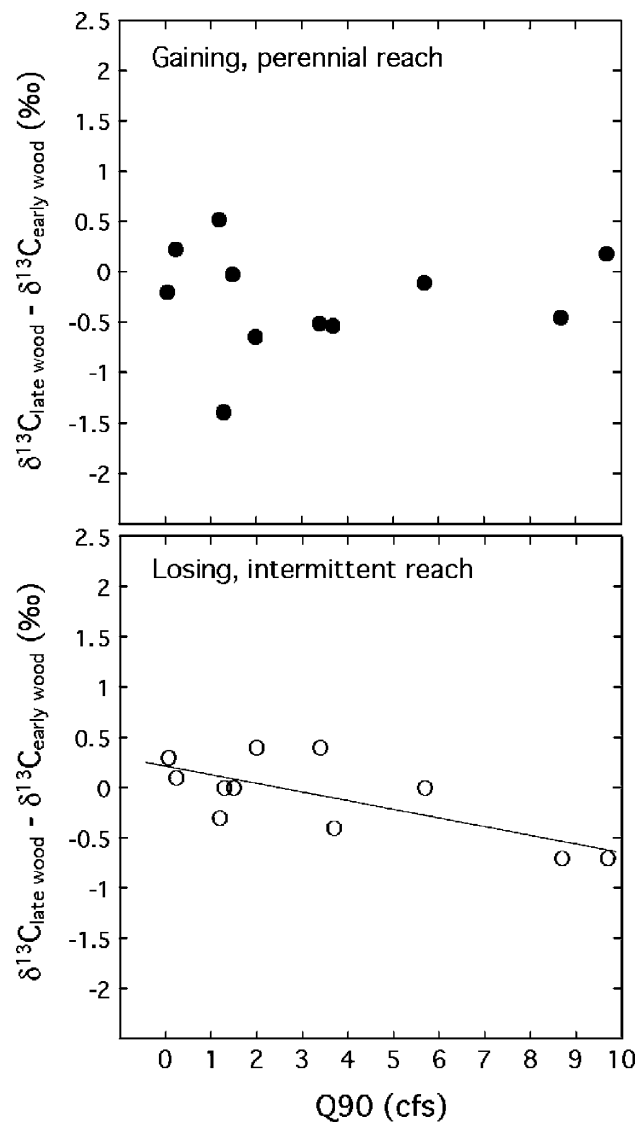
Figure 3. Carbon isotope ratio (δ^{13}C) values for tree-ring holocellulose in cottonwood (*Populus fremontii*). Shown are the changes in δ^{13}C values from early- to late-wood fractions of an 11-year tree-ring record for populations at perennial and intermittent sections of the Upper San Pedro River in south-eastern Arizona, USA. Negative values indicate that canopy-level c_i/c_a values during the monsoon-period were higher (greater stomatal 'openness') compared to pre-monsoon values. Q_{90} is the 90% exceedence stream flow value during the monsoon period (July–September 15) for each year (Potts and Williams, 2004). Flow records were taken from the San Pedro River's Charleston stream gauge (#09741000; US Geological Survey Water Resources Division), which is midway between the intermittent and perennially flowing sections of the river where tree cores were collected. A statistically significant correlation between the intra-annual δ^{13}C shift and Q_{90} was found only for trees at the intermittently flowing section of the river ($r^2 = 0.59$, $p = 0.005$). Figure modified from Potts and Williams (2004), used with permission

This imbalance leads to non-linear responses of NEE to climate variability across different vegetation compositions. However, the degree of this imbalance is dependent upon vegetation physiognomy. In riparian floodplains, deep-rooted woody plants access groundwater and maintain a consistently high rate of leaf gas exchange through the growing season. Thus, the imbalance between photosynthesis and respiration in mesquite woodland may be greater than in the grasslands on pre-entrenchment terraces (Scott *et al.*, 2006a).
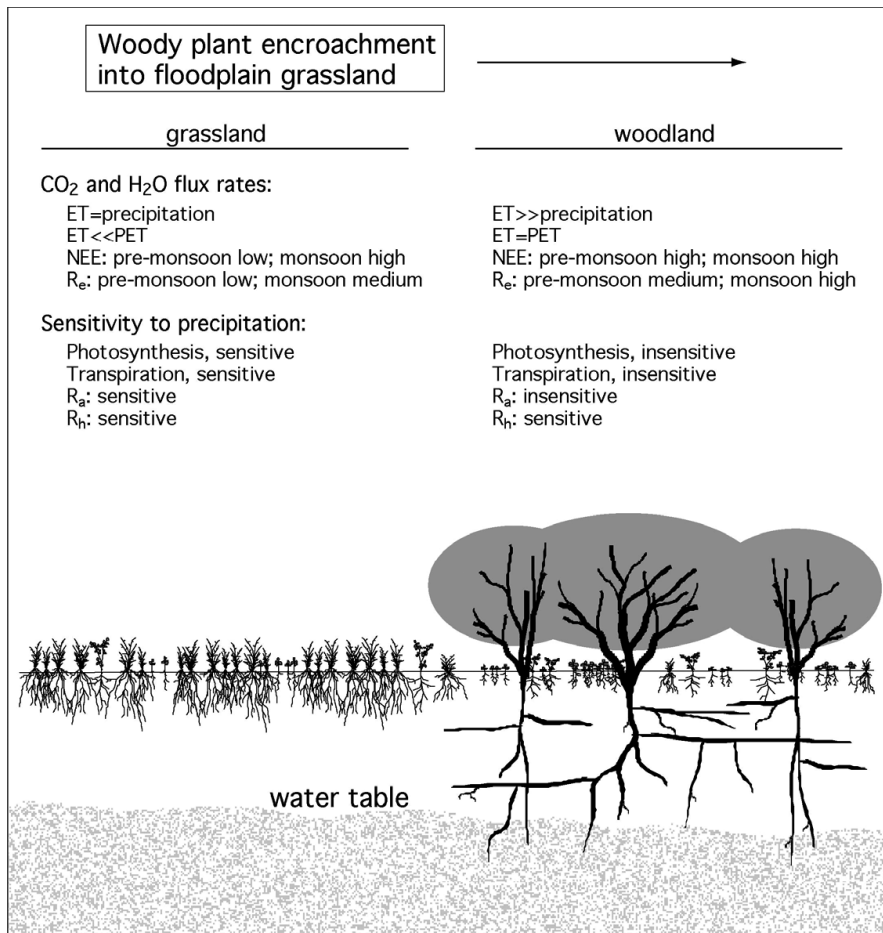
Figure 4. Diagrammatic representation of woody-plant encroachment into riparian grassland and predictions of changes in carbon and water fluxes

Photosynthetic gas exchange and water potential of mature mesquite shrubs in upland environments are very sensitive to even small pulses (10 mm) of monsoonal rainfall (Fravolini *et al*., 2005). However, in the riparian setting, groundwater is accessible at significant depths. Only a small fraction of the transpiration water used by large mesquite plants in the riparian setting is derived from monsoon season precipitation (Scott *et al*., 2006b), but this fraction varies with water-table depth (Snyder and Williams, 2000) and plant size (Potts *et al*., in press). Our conceptual model describes the dependence of ecosystem function on vegetation physiognomy (Figure 4). In a riparian grassland system, ecosystem photosynthesis, respiration and ET are driven by summer inputs of precipitation. Productivity is likely to be strongly connected to annualized precipitation in these grasslands, as a result of summer input dominating yearly totals. Similar to the situation for the cottonwood/willow system, in a riparian mesquite woodland, light and temperature will replace precipitation in controlling ecosystem photosynthesis, as access to groundwater overcomes water limitations of the dominant woody plants. Respiration and soil carbon dynamics will continue to be linked to summer precipitation in mesquite woodland leading to a decoupling of ecosystem CO_2 uptake and release and a complex pattern of NEE with respect to precipitation.

Biological activity of grassland on pre-entrenchment floodplain terraces of the USPR, where groundwater depths exceed 3 m, is driven by summer rain pulses that recharge surface soil layers (Scott *et al*., 2000).

However, for grasslands that have been converted to mesquite, several key ecosystem processes are decoupled from rainfall pulses. Cumulative ET from sacaton grassland matched or slightly exceeded summer precipitation inputs, whereas ET from a mesquite woodland system greatly exceeded summer precipitation by more than 300% and did not fluctuate with rain inputs (Scott *et al.*, 2000, 2004, 2006a). Such differences in the magnitude of ET are also the case for NEE at grassland and woodland sites (Scott *et al.*, 2006a).

Use of groundwater is advantageous for woody species in riparian settings (Smith *et al.*, 1998). However, along the continuum from grassland to mesquite woodland, facultative use of soil water does not occur evenly. ET estimated from mature mesquite woodland by the eddy covariance technique shows no significant change in transpiration by mesquite from pre- to peak-monsoon periods (Figure 2; Scott *et al.*, 2003; Yepez *et al.*, 2003). When mesquite reaches a critical size, they may no longer rely on soil water and mainly use groundwater as a near-exclusive source for transpiration. These results suggest the potential for a non-linear relationship between the degree of grassland invasion by mesquite and ecosystem ET, photosynthesis and respiration as a result of tree access to a resource unavailable to the grassland system (Figure 4).

The presence of abundant, readily decomposable litter and soil organic matter in fully developed mesquite systems sets the stage for high ecosystem-scale CO_2 respiratory efflux following rain pulses (Martens and McLain, 2003). Nighttime average CO_2 efflux from mesquite woodland was highly sensitive to monsoon rainfall pulses that moisten these surface soil layers (Figure 5; Scott *et al.*, 2004). Prior to monsoon-onset, nighttime CO_2 fluxes were negligible, and assumed to be primarily a function of the metabolic activity of autotrophs. Significant CO_2 efflux starts with the arrival of rainfall pulses and decreases rather rapidly as soils dry, suggesting that the activity of heterotrophic organisms is the primary source for this carbon loss. The greatest CO_2 respiratory efflux occurred after large precipitation pulses during the wet monsoon year of 2002. Thus, the majority of the carbon lost from this system (and ultimately, carbon balance) depends on the magnitude, timing and frequency of monsoon moisture pulses.
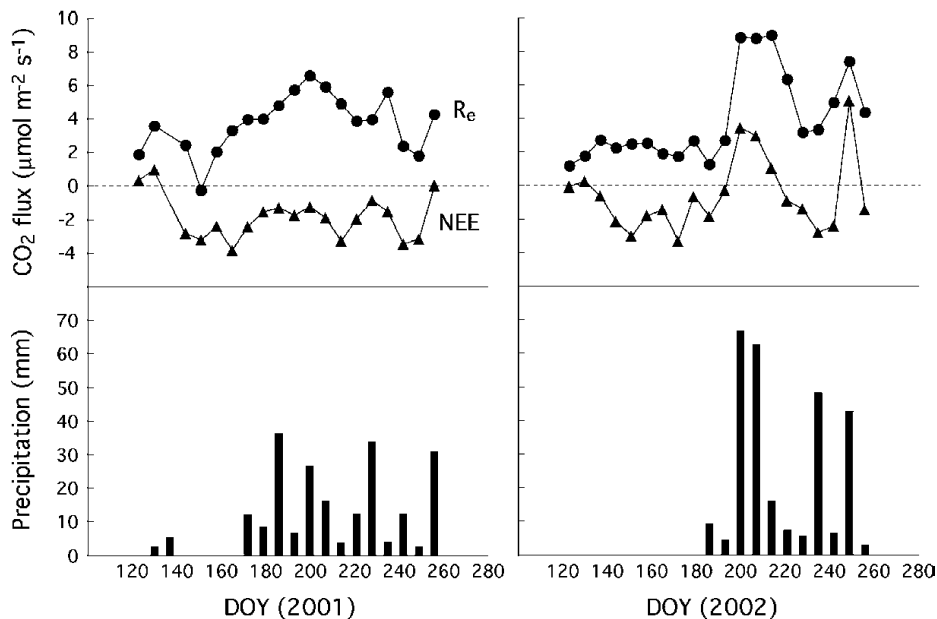

Figure 5. Weekly average fluxes of nighttime ecosystem respiration (R_e) and NEE of CO_2 for a mesquite woodland on a pre-entrenchment floodplain terrace along the Upper San Pedro River in south-eastern Arizona, USA, during the growing season in 2001 and 2002. Net CO_2 exchange (NEE) was calculated as the day-length-weighted sum of the weekly average daytime and nighttime CO_2 fluxes. Negative values of CO_2 flux indicate net uptake by the ecosystem. Lower panels show weekly accumulated precipitation at the study site. Figure modified from Scott *et al.* (2004), used with permission

Scott *et al*. (2006a) showed that the R_e increase in response to monsoon rains was much greater in mesquite woodland than in sacaton grassland. Given the above pattern and this vegetation composition contrast, the source of the high R_e following rainfall pulses in the riparian mesquite ecosystem appears to be from the decomposition of litter and soil organic matter, rather than from autotrophic respiration of mesquite trees. Nighttime ecosystem respiration can be partitioned into its sources using carbon isotope ratio ($\delta^{13}C$) measurements of atmospheric CO_2 (Pataki *et al*., 2003). The $\delta^{13}C$ signal of respiration from mesquite is -26 to $-28‰$, and that from the litter and soil organic matter is -24 and $-21‰$ (D. G. Williams, unpublished results). Keeling plots (CO_2 isotopic mixing relationships) for a riparian mesquite woodland near our eddy flux site showed a $6.6‰$ positive shift in the $\delta^{13}C$ value of R_e from pre- to peak-monsoon (Figure 6). Pre-monsoon R_e had a $\delta^{13}C$ value of $-28.3‰$, very close to the value of mesquite leaves ($-27.6‰$). The peak-monsoon $\delta^{13}C$ value of R_e was $-21.7‰$. If the high R_e fluxes observed during the monsoon period were due to enhanced autotrophic respiration of mesquite, the $\delta^{13}C$ value of R_e would either stay constant or shift to more negative values, reflecting less water stress and higher c_i/c_a during the humid monsoon period (Fessenden and Ehleringer, 2003). Rather, the $\delta^{13}C$ values of R_e shifted to more positive values and approached values similar to ^{13}C-enriched litter and soil organic matter values after inputs of monsoonal moisture, suggesting enhanced heterotrophic respiration associated with decomposition of litter and/or soil organic matter. C4 plant autotrophic respiration ($\delta^{13}C$ value of approximately $-14‰$) likely does increase in these ecosystems with the onset of the monsoon, but since these plants make up only a small component of this heavily wooded ecosystem (Yepez *et al*., 2003), it is unlikely they are responsible for the extremely high R_e observed with the input of growing-season precipitation.

Seasonal ET is less sensitive to summer precipitation than is R_e in the riparian mesquite ecosystem because mesquite accesses a stable groundwater moisture source. However, because heterotrophic respiration remains dependent on rainfall pulses wetting the litter and surface soil, ET and NEE become relatively decoupled during the monsoon period. Because mesquite is the dominant plant in these floodplain ecosystems, and transpiration by mesquite from the groundwater is the dominant ET source (Scott *et al*., 2003; Yepez *et al*., 2003), ET and GEP (a measure of ecosystem photosynthesis) remain positively correlated in wet and dry
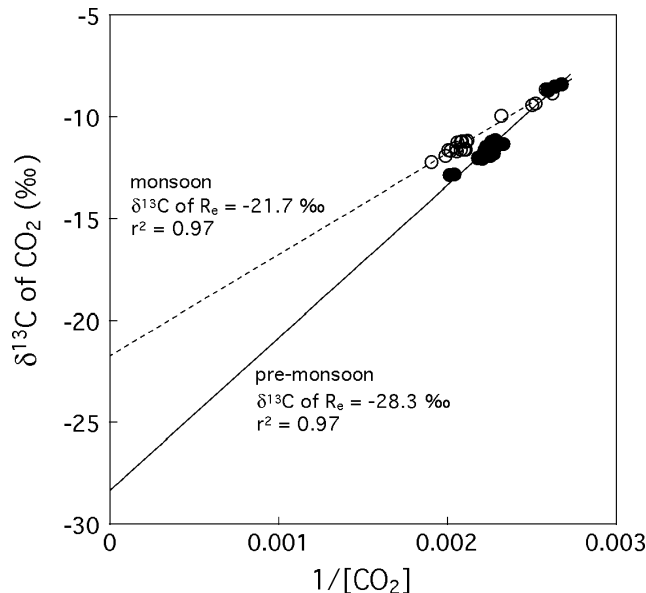

Figure 6. Nighttime 'Keeling plots' of CO_2 for a mesquite woodland on a pre-entrenchment floodplain terrace along the Upper San Pedro River in south-eastern Arizona, USA. Atmospheric CO_2 samples for Keeling plots were collected during pre- and peak-monsoon periods. The *y*-intercepts of the linear regressions indicate the $\delta^{13}C$ value of ecosystem respiration
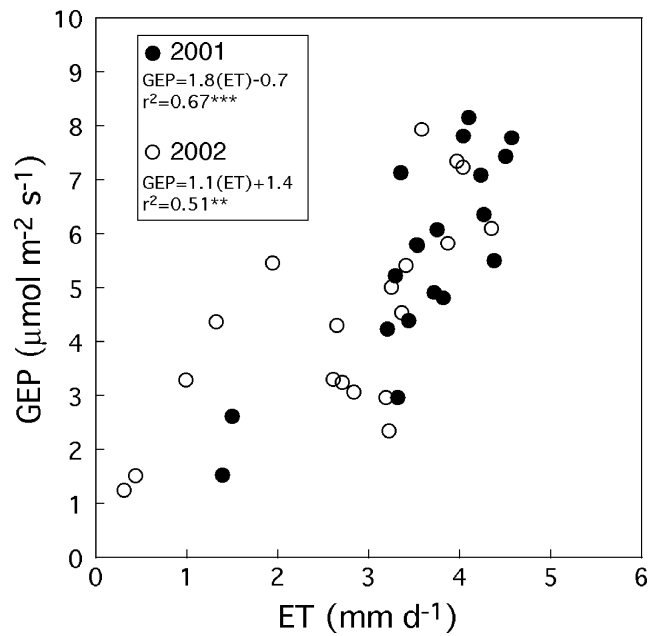
Figure 7. Relationship between weekly averaged gross ecosystem production (GEP) and evapotranspiration (ET) for a mesquite woodland on a pre-entrenchment floodplain terrace along the Upper San Pedro River in south-eastern Arizona, USA, during the growing seasons of 2001 and 2002. Data from Scott *et al.* (2004). GEP and ET were significantly correlated at the $p < 0.01$ (**) in 2002 and at the $p < 0.001$ (***) level in 2001
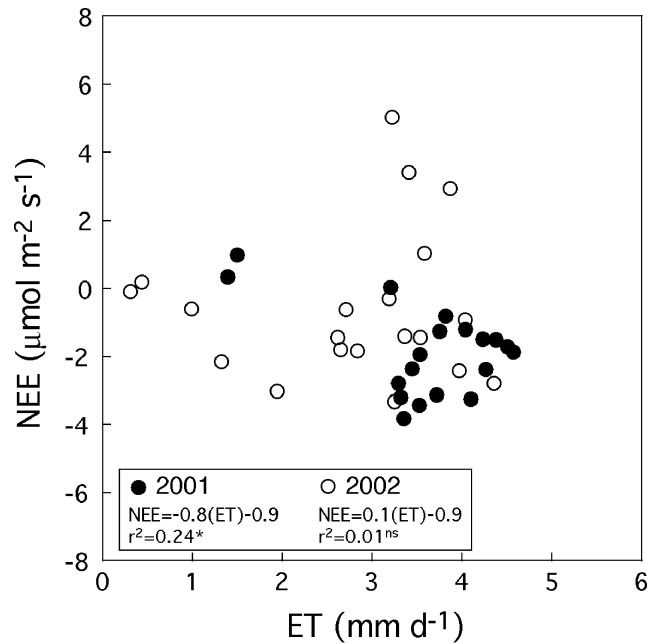

Figure 8. Relationship between weekly averaged net ecosystem exchange of CO_2 (NEE) and evapotranspiration (ET) for a mesquite woodland on a pre-entrenchment floodplain terrace along the Upper San Pedro River in south-eastern Arizona, USA, during the growing seasons of 2001 and 2002. Data from Scott *et al.* (2004). NEE and ET were significantly correlated at the $p < 0.05$ (*) level in 2001, but were not significantly correlated (ns) in 2002

monsoon years (Figure 7; Scott *et al.*, 2004). However, the relationship was not as strong during the wetter monsoon year of 2002, possibly due to episodes of high soil evaporation following inputs of rainfall (Yepez *et al.*, 2003). Furthermore, because of the highly sensitive responses of ecosystem respiration to rainfall inputs, the relationship between ET and NEE differs between wet and dry monsoon years (Figure 8). These variably coupled processes generate complex and unanticipated responses of net ecosystem carbon exchange to precipitation inputs.

Taken together, these responses reveal the highly dynamic and complex nature of carbon and water exchange processes in semiarid riparian ecosystems. Our studies provide valuable insight into how vegetation shifts and changes in root system depth or access to groundwater affect the processing of energy and matter at the ecosystem scale.

CONCLUSION AND FUTURE STUDIES

Many studies have focused on effects of changes in single factors (e.g. vegetation structure or precipitation change) on ecosystem processes. However, changes in a number of environmental factors are likely to interact in a complex way. Interactions between these factors on ecological and hydrological processes at large scales may be as important as their individual effects. In fact, the sign of response of ecosystem water use to environmental changes associated with these interactions is unknown. The short- and long-term effects of climate change will be related partially to vegetation composition and functional type responsiveness to precipitation changes, and in a broader context, to plant metabolic responses to rising atmospheric CO_2, increased temperature and local-scale biotic interactions.

Riparian landscapes in arid and semiarid environments provide exceptional opportunities to study ecohydrological impacts of land-cover change. The main goal of our research is to develop an understanding of how ecological and hydrological processes respond to precipitation variability and vegetation change in semiarid ecosystems. On the basis of a number of efforts at individual sites, we are now poised to answer fundamental questions about how land-cover change and access to groundwater impact ecosystem processes across diverse physiographic settings.

Our current studies are focused on leaf-, canopy- and ecosystem-scale exchange of water and carbon across gradients in groundwater depth and woody-plant encroachment (Scott *et al.*, 2006a). We expect carbon efflux to be highly coupled with the stage of woody-plant encroachment as well as the ecosystem physiographic setting (e.g., upland, riparian). As mesquite cover increases within grassland, poorer quality and less abundant grass litter is replaced by higher quality, more abundant mesquite litter. However, limited access to deeper water sources in upland settings will dampen the accumulation of high quality litter, reducing the magnitude of heterotrophic respiration in upland environments. Ongoing studies will allow us to disentangle the factors controlling ecosystem exchange of energy and matter within global change and ecohydrological contexts.

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