

# Landscape and environmental controls over leaf and ecosystem carbon dioxide fluxes under woody plant expansion

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## Summary

**1.** Many regions of the globe are experiencing a simultaneous change in the dominant plant functional type and regional climatology. We explored how atmospheric temperature and precipitation control leaf- and ecosystem-scale carbon fluxes within a pair of semi-arid shrublands, one upland and one riparian, that have undergone woody plant expansion.

**2.** Through a combination of leaf-level measurements on individual bunchgrasses and mesquites shrubs and ecosystem-scale monitoring using eddy covariance techniques, we sought to quantify rates of net carbon dioxide (CO<sub>2</sub>) flux, CO<sub>2</sub> flux temperature sensitivity and the responsiveness of these parameters to seasonal rains and periods of soil dry-down.

**3.** We found significant differences in physiological acclimation between the two plant functional types, in that the shrubs consistently conducted photosynthesis across a broader temperature range than co-occurring grasses during dry periods, yet maximum photosynthetic rates in grasses were twice that of mesquites during the wetter monsoon season. Landscape position modulated these temperature sensitivities, as the range of functional temperatures and maximum rates of photosynthesis were two to three times greater within the riparian shrubland in dry times.

**4.** Also, it was unexpected that ecosystem-scale CO<sub>2</sub> uptake within both shrublands would become most temperature sensitive within the monsoon, when mesquites and grasses had their broadest range of function. This is probably explained by the changing contributions of component photosynthetic fluxes, in that the more temperature sensitive grasses, which had higher maximal rates of photosynthesis, became a larger component of the ecosystem flux.

**5. Synthesis:** Given projections of more variable precipitation and increased temperatures, it is important to understand differences in physiological activity between growth forms, as they are likely to drive patterns of ecosystem-scale CO<sub>2</sub> flux. As access to stable subsurface water declines with decreased precipitation, these differential patterns of temperature sensitivity among growth forms, which are dependent on connectivity to groundwater, will only become more important in determining ecosystem carbon source/sink status.

**Key-words:** eddy covariance, landscape position, mesquite (*Prosopis velutina*), photosynthesis, plant–climate interactions, semi-arid, temperature optima, vegetation change, woody plant encroachment

## Introduction

Surface air temperatures have increased over the last 30 years across the semi-arid Southwestern United States (Cubasch

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*et al.* 2001; Backlund *et al.* 2008), and this region is predicted to experience warmer daytime temperatures, with more frequent warmer nights (Cubasch *et al.* 2001; Tebaldi *et al.* 2006; Christensen *et al.* 2007; Backlund *et al.* 2008; Weiss, Castro & Overpeck 2009). The US south-west is also predicted to become drier, on average, but with more extreme rain events. Western North America has experienced a 15% decrease in precipitation since 1900 (Cubasch *et al.* 2001), and models forecast, with fair confidence, reduced and more variable precipitation with longer interstorm rain-free periods (Overpeck & Cole 2006; Christensen *et al.* 2007; Backlund *et al.* 2008), and with slightly less confidence, more marked interannual variability in summer rains associated with the North American monsoon (Cubasch *et al.* 2001). In order to better understand ecosystem-scale responses to climate change, there has been substantial interest in quantitatively linking plant and ecosystem responses to temperature and water stress (Medlyn, Loustau & Delzon 2002b; Medlyn *et al.* 2002a; Barron-Gafford, Grieve & Murthy 2007; Lloyd & Farquhar 2008; Sage, Way & Kubien 2008; Montpied, Granier & Dreyer 2009; Kanniah, Beringer & Hutley 2010; Barron-Gafford *et al.* 2012; Munson *et al.* 2012).

Interacting with climatic change is land cover-scale shifts in the dominant plant functional type, creating an opportunity to study the nexus of physical geography, plant ecophysiology and climate science. One of the most notable transitions in vegetative cover is woody plant encroachment (WPE) into historical grasslands (Knapp *et al.* 2008b), which can alter interception of solar radiation (Breshears *et al.* 1998; Villegas *et al.* 2010), nutrient cycling and availability (Hibbard *et al.* 2001; McLain, Martens & McClaran 2008; Throop & Archer 2008), net ecosystem exchange of carbon and water (Jackson *et al.* 2000; Hughes *et al.* 2006; Scott *et al.* 2006b; Barron-Gafford *et al.* 2012), ecosystem structure and function (Jackson *et al.* 2002; Huxman *et al.* 2005; Munson *et al.* 2012) and controls to landscape hydrological dynamics (Seyfried *et al.* 2005). WPE has been documented throughout regions of varied water status (Jackson *et al.* 2002; Knapp *et al.* 2008b; Ravi *et al.* 2009; Van Auken 2009; Naito & Cairns 2011; Jenerette & Chatterjee 2012), including the US central plains grasslands (Briggs *et al.* 2005; McKinley *et al.* 2008), south-west desert grasslands (Buffington & Herbel 1965) and mesquite (*Prosopis spp.*) expansion world-wide (Harding & Bate 1991; Archer 1994; McClaran 2003).

In water limited systems, plant growth form influences plant and ecosystem phenology through differential growth responses to precipitation and the temporal persistence of plant activity across periods of drought or high temperature stress (Smith, Monson & Anderson 1996). In contrast to grasses, which allocate relatively little to deep roots, woody plants can develop root systems that extract shallow water resources (e.g. Ogle & Reynolds 2004), or deep, extensive rooting networks, often allowing them to act as phreatophytes in landscape positions with stable groundwater sources or areas of deep soil water recharge (Smith, Monson & Anderson 1996). This feature can effectively decouple woody plant physiological activity from incident rainfall (Williams *et al.*

2006). Physiological processes in grasslands tend to be more sensitive to incident precipitation than woodland or mixed vegetation ecosystems because shallowly rooted grasses have less connectivity to stable water sources at depth (Ehleringer *et al.* 1991; Golluscio, Sala & Lauenroth 1998; Jackson *et al.* 2000; Scott *et al.* 2000; Potts *et al.* 2006; Williams *et al.* 2006). Such differences in plant growth/life-forms traits therefore modify both ecosystem-scale hydrological patterns important to surface processes (Canadell *et al.* 1996; Jackson *et al.* 2000; Schenk & Jackson 2002; Huxman *et al.* 2005; Seyfried *et al.* 2005) and plant carbon and water fluxes that are important to biosphere–atmosphere feedbacks (Evanari *et al.* 1975; Hultine *et al.* 2004, 2006; Jenerette *et al.* 2009).

Leaf physiological traits are another fundamental component of biosphere–atmosphere gas exchange (Wright *et al.* 2004; Enquist *et al.* 2007). Leaf physiology is primarily associated with rates and patterns of plant carbon assimilation ( $A$ , photosynthesis), which responds to variations in vapour pressure deficit (VPD), light,  $[CO_2]$  and temperature through both biochemical shifts and leaf morphological features that affect internal gas diffusion (Schulze & Caldwell 1994). The temperature response of  $A$  generally follows a dual Arrhenius function with a peaked response, such that at low temperatures  $A$  increases to an optimum beyond which rates decline depending on thermal tolerance (Farquhar, von Caemmerer & Berry 1980; Leuning 2002).  $C_4$  species tend to have higher rates of  $A$  at elevated temperatures compared with most  $C_3$  plants, but have enzyme kinetics that more strongly restrict the range of physiologically optimal temperatures (Berry & Björkman 1980). However, the expressed convexity of the temperature response across entire growing seasons depends not only on photosynthetic pathway ( $C_3$  or  $C_4$ ), but also the degree of physiological temperature acclimation (tendency of a species to maintain homeostasis in a changing environment), which can be affected by plant resource availability (Barron-Gafford *et al.* 2012). In semi-arid settings, water availability depends strongly on landscape position. In riparian areas, plant rooting attributes and access to stable groundwater may allow for temperature acclimation for deep-rooted woody  $C_3$  plants as compared to shallow rooted  $C_4$  grasses. In contrast, at upland locations, the lack of stable groundwater resources may result in both growth forms having more constrained seasonal physiological adjustment due to more prevalent water stress. The combination of these biological and resource availability features in controlling  $A$ , suggest emergent properties of ecosystem-scale biosphere–atmosphere exchange and temperature response that may be tied to landscape position.

There are clear topographical/landscape position influences on ecosystem responses to precipitation, both in terms of timing and amount of precipitation. While riparian woodlands are less sensitive to summer monsoon precipitation, whether those rains are small or large (Scott *et al.* 2006a; Potts *et al.* 2008), mesquites in upland shrublands are more responsive to larger precipitation events than smaller pulses (Fravolini *et al.* 2005). Knapp *et al.* (2008a) suggested dry-land ecosystems that become stressed under current precipitation regimes of

frequent small events may become only 'intermittently stressed' under predicted less frequent, but larger rains because such events more completely recharge to greater soil depths. These forecasted conditions may better benefit mesquites, which appear to respond more favourably to large events, than grasses, which have evolved a rooting habit capable of quickly capturing smaller pulses. In this context, we explored the concomitant controls of temperature and precipitation on leaf- and ecosystem-scale CO<sub>2</sub> flux in upland and riparian mesquite-encroached semi-arid grasslands.

Using these paired ecosystems, both a mix of C<sub>4</sub> grasses and C<sub>3</sub> mesquites, as a model for ecosystems of differential access to stable groundwater, we addressed the following questions:

(i) How does temperature differentially limit net CO<sub>2</sub> uptake in C<sub>4</sub> grasses and C<sub>3</sub> mesquites in contrasting landscape positions through periods of varying precipitation and temperature extremes?; (ii) Does access to groundwater modulate when rates of ecosystem-scale CO<sub>2</sub> uptake are more or less temperature sensitive?; and (iii) How do the component fluxes of CO<sub>2</sub> uptake and efflux contribute to ecosystem-scale temperature sensitivity? In addressing these questions, we will better understand emergent features at the ecosystem scale of how temperature and precipitation variation differentially influence carbon dynamics within mixed vegetation ecosystems experiencing dramatic changes in available soil moisture, such as what may occur under projected climatic change scenarios.

## Materials and methods

### STUDY SITES AND SPECIES

This study used two former south-east Arizona USA semi-arid grasslands that have been converted to shrubland following prolonged woody plant encroachment. The riparian site (31.566°N, 110.133°W) is located on an old alluvial terrace at an elevation of 1237 m, bordering the San Pedro River. Soils consist mainly of gravelly sandy loam layers interspersed with clay and gravel lenses (Scott *et al.* 2006b). The eddy covariance tower footprint at this site is dominated by velvet mesquite (*Prosopis velutina*), with a canopy cover of ca. 51%. Understorey canopy is principally the C<sub>4</sub> bunchgrass, big sacaton (*Sporobolus wrightii*; ca 27% total cover), and an additional 32% of understorey intercanopy soil space fills in with annual herbaceous species, most commonly *Viguiera dentata* (Cav.) Spreng. Mesquite height averaged 3.7 m, mean bunchgrass canopy height was 1.25 m, with a mean depth to groundwater of 6.5 m (Scott *et al.* 2006b; Potts *et al.* 2008). The upland site is located in the Santa Rita Experimental Range (31.8214° N, 110.8661° W, elevation: 1116 m) SSE of Tucson, AZ, USA. Soils here are a deep sandy loam (Scott *et al.* 2009). Mesquite cover at this site is approximately 35%, with vegetation of the intercanopy space dominated by a mosaic of perennial C<sub>4</sub> bunchgrasses (*Eragrostis lehmanniana* Nees, *Digitaria californica* Benth and *Bouteloua eriopoda*) and seasonally bare soil. Intercanopy plant cover of perennial grasses, forbs and sub-shrubs is approximately 22% (Scott *et al.* 2009). Mesquite averaged 2.5 m in height, and the mean depth to groundwater at the upland site probably exceeds 100 m, as nearby wells measured depths to groundwater of 100 and 154 m. Mean annual precipitation (1971–2000) from stations around the

riparian shrubland ranges from 313 to 386 mm (Scott *et al.* 2006b) and is (1937–2007) 377 mm at the upland site (Scott *et al.* 2009), with about 50% falling between July–September during the North American Monsoon.

### EDDY COVARIANCE MEASUREMENTS

Ecosystem-scale carbon dioxide, water vapour and energy fluxes were monitored at the riparian site from 2003 to 2008 and at the upland since 2004 till present (Scott *et al.* 2006b, 2009). Detailed descriptions of instrumentation, sensor heights and orientations, and data processing procedures are given elsewhere (Scott *et al.* 2004, 2006b, 2009; Potts *et al.* 2008). Briefly, at both sites, instrumentation on 8 m towers measures all variables needed to quantify 30 min averages of net ecosystem exchange of CO<sub>2</sub> (*NEE*), air temperature (*T*<sub>air</sub>), VPD, air pressure, photosynthetic photon flux density (*PPFD*), shortwave and net radiation, and precipitation. We filtered CO<sub>2</sub> flux data over poor turbulent mixing periods by removing data associated with a friction velocity (*u*<sup>\*</sup>) below 0.15 m<sup>2</sup> s<sup>-1</sup> (Scott *et al.* 2006b). Ecosystem-scale gross ecosystem productivity (*GEP*) was calculated as:

$$GEP = R_{Eco} - NEE \quad \text{eqn 1}$$

where *R*<sub>Eco</sub> is ecosystem respiration, derived from the night-time *NEE* data processed using procedures in Reichstein *et al.* (2005). We converted *NEE* to net ecosystem productivity (*NEP* = -*NEE*), so that ecosystem-level data follows the sign convention of leaf-level ecophysiological data.

Eddy covariance data from 2007 was divided into 40-day blocks representing the pre-monsoon (DOY 140–180), monsoon (190–230) and post-monsoon (280–320) periods for each site. These periods were selected because they represent typical climatic conditions of their respective seasons and encompass periods when canopies were present and stable. Each seasonal batch of *NEP* data was separated into 16 2.5 °C temperature bins from 0 °C to 40 °C. Within each bin, *NEP* was regressed against *PPFD* to assess T-effects at different light levels across the day and season (Huxman *et al.* 2003; Barron-Gafford *et al.* 2012). Light-saturated *NEP* rate for each 2.5 °C bin of *T*<sub>air</sub> was modelled using a rectangular hyperbola (nonlinear least-squares regression; SigmaPlot 11.0, spss, Chicago, IL, USA):

$$NEP = \left( \frac{\alpha_e I \times PPFD \times NEP_{sat}}{NEP_{sat} + (\alpha_e I \times PPFD)} \right) - R_e \quad \text{eqn 2}$$

where  $\alpha_e$  is the apparent ecosystem quantum yield, *NEP*<sub>sat</sub> is light-saturated net CO<sub>2</sub> exchange, and *R*<sub>e</sub> is respiratory CO<sub>2</sub> exchange at *PPFD* = 0 (Ruimy *et al.* 1995). The *NEP*<sub>sat</sub> at each of 16 temperature bins were plotted for each site for each seasonal period to assess a T-response function for each ecosystem. The *Q*<sub>10</sub> of *R*<sub>Eco</sub> was calculated as:

$$Q_{10} = \frac{R_{Eco} \text{ rate at } T_{air} + 10^\circ\text{C}}{R_{Eco} \text{ rate at } T_{air}} \quad \text{eqn 3}$$

where *T*<sub>air</sub> was referenced to a common temperature of 25 °C. Rates of *R*<sub>Eco</sub> at this common temperature (*R*<sub>Eco25</sub>) were also used for between-ecosystem comparisons.

### LEAF-LEVEL PHYSIOLOGICAL MEASUREMENTS OF GAS AND WATER EXCHANGE

Measurements of leaf-level night-time leaf respiration (*R*<sub>Leaf</sub>) and daytime net photosynthesis (*A*) were conducted across a 25 + °C range

of  $T_{\text{air}}$  on mesquites and grasses at each site throughout 2007. Following the methods described by Barron-Gafford *et al.* (2012), we used a LI-6400 portable photosynthesis system (LI-COR, Lincoln, NE, USA) with a red–blue light source (LI-6400-02b) providing constant  $PPFD$  of  $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$  during daytime  $A$  estimations. Cuvette  $\text{CO}_2$  was held to 375 p.p.m. by mixing outside air with  $\text{CO}_2$  from a cylinder injection assembly attached to the instrument. A small, white reflective cap was placed on top of the cuvette to minimize heat gain by the chamber, while still allowing for thermal dissipation by the chamber's cooling fans. An initial measurement flux was taken at ambient  $T$  to serve as an indicator of  $R_{\text{Leaf}}$  or  $A$  under ambient conditions and as a metric against which to compare the  $T$ -response curve. Finding a similar reading prior to the initialization of the response curve and at that same  $T$  during the subsequent response curve confirmed, we did not induce any perturbation by our protocol. After this initial measurement, the temperature of a Pelletier-exchange cooled temperature block was set to  $5^\circ\text{C}$  to lower chamber  $T$  to its minimum reachable level. Once chamber  $T$  had stabilized, the two infrared gas analysers within the instrument were matched, and gas exchange data were logged. After this, the block temperature was increased in  $3\text{--}5^\circ\text{C}$  increments, and the leaf was given a minimum of 2 min to stabilize in response to cuvette  $T$ . This was repeated until the maximum potential chamber temperature was reached. Leaf temperature was continuously measured with a fine-wire type-T thermocouple pressed to the underside of the leaf. We occasionally added a small amount of water to the instrument's  $\text{CO}_2$  soda lime scrubber to avoid excessive VPD at higher temperatures, with care taken to avoid any condensation in the instrumentation tubing. Five individual mesquite and five individuals of the dominant grass (*S. wrightii* at the riparian *E. lehmanniana* and at the upland) were sampled at each site, with measurements taken on intact leaves midway up the south side of the canopy. Estimates of gross photosynthesis ( $A_{\text{Gross}}$ ) were made by summing  $A$  and  $R_{\text{Leaf}}$ . All gas exchange leaf samples were harvested after measurement and stored in paper envelopes. Sample leaf area was determined (CI-202, CID Bio-Science, Camas, WA, USA), and then samples were air-dried.

These protocols were repeated during three periods throughout the growing season: the pre-monsoon drought (DOY 171–173), monsoon peak (DOY 223–225) and post-monsoon dry-down (DOY 284–286) in 2007. We chose these periods to identify the influence of landscape position on (i) patterns of photosynthetic upregulation in response to warm-season rains, (ii) changes in  $T$ -sensitivity among plant functional types in response to prolonged soil moisture availability and (iii) acclimation potential as the system returned to a dry state.

#### DETERMINATION OF TEMPERATURE OPTIMA AND THE DEGREE OF TEMPERATURE-LIMITATIONS TO $\text{CO}_2$ UPTAKE AND STATISTICAL ANALYSIS

$A_{\text{max}}$  and  $NEP_{\text{max}}$  and optimum temperature ( $T_{\text{opt}}$ ) for each were estimated from the single peak of a temperature response curve fit to the leaf- and ecosystem-level data. A custom model was developed in MATLAB 2009b (MathWorks, Natick, MA, USA) to fit the data, based on the energy of activation and deactivation model presented by Leuning (2002) for estimating the temperature sensitivity of maximum catalytic rate of the carbon-fixing enzyme *Rubisco* and the maximum electron transport rate (Barron-Gafford *et al.* 2012; Richardson, Chatterjee & Jenerette 2012). The model estimates a peak in the temperature response function and allows for asymmetry in the sub- and supraoptimal portions of the response curve. From there, a metric of the convexity of the temperature response function was derived by

quantifying the range of temperatures over which a leaf or ecosystem was assimilating 50% ( $\Omega_{50}$ ) and 75% ( $\Omega_{75}$ ) of  $A_{\text{max}}$  and  $NEP_{\text{max}}$ .  $\Omega_{50}$  and  $\Omega_{75}$  illustrate the difference between the upper and lower temperatures at which  $A_{\text{max}}$  and  $NEP_{\text{max}}$  declined by 75% and 50%, respectively.  $\Omega_{50}$  illustrates variation in the temperature sensitivity at the edge of the plant's or ecosystem's functional range, while  $\Omega_{75}$  illustrates a plant or ecosystem's ability to assimilate carbon in the range of temperatures most immediate to  $T_{\text{opt}}$ .

A split-plot, repeated-measures analysis of variance (RM-ANOVA; Statistix v. 8.0, Analytical Software, Tallahassee, FL, USA) was used to test for differences in leaf-level  $A_{\text{max}}$ ,  $T_{\text{opt}}$ ,  $\Omega_{50}$  and  $\Omega_{75}$ , and  $R_{\text{Leaf}}$  between the two sites (landscape position), three sampling periods and two plant functional types. The between-treatment, whole-plot effect was growth form (mesquite versus grass), using the growth-form-by-replicate interaction as the whole-plot error term and an  $\alpha$  of 0.05. The within-treatment, subplot effects were seasonal periods (pre-monsoon, monsoon, post-monsoon) and the growth-form-by-season interaction, using the growth-form-by-season-by-replicate interaction as the subplot error term. An RM-ANOVA was used to test for differences in ecosystem-level  $NEP_{\text{max}}$ ,  $T_{\text{opt}}$ ,  $\Omega_{50}$  and  $\Omega_{75}$ , and  $R_{\text{Eco}}$  between the two sites (landscape position) and the same three sampling periods (pre-monsoon, monsoon, post-monsoon).

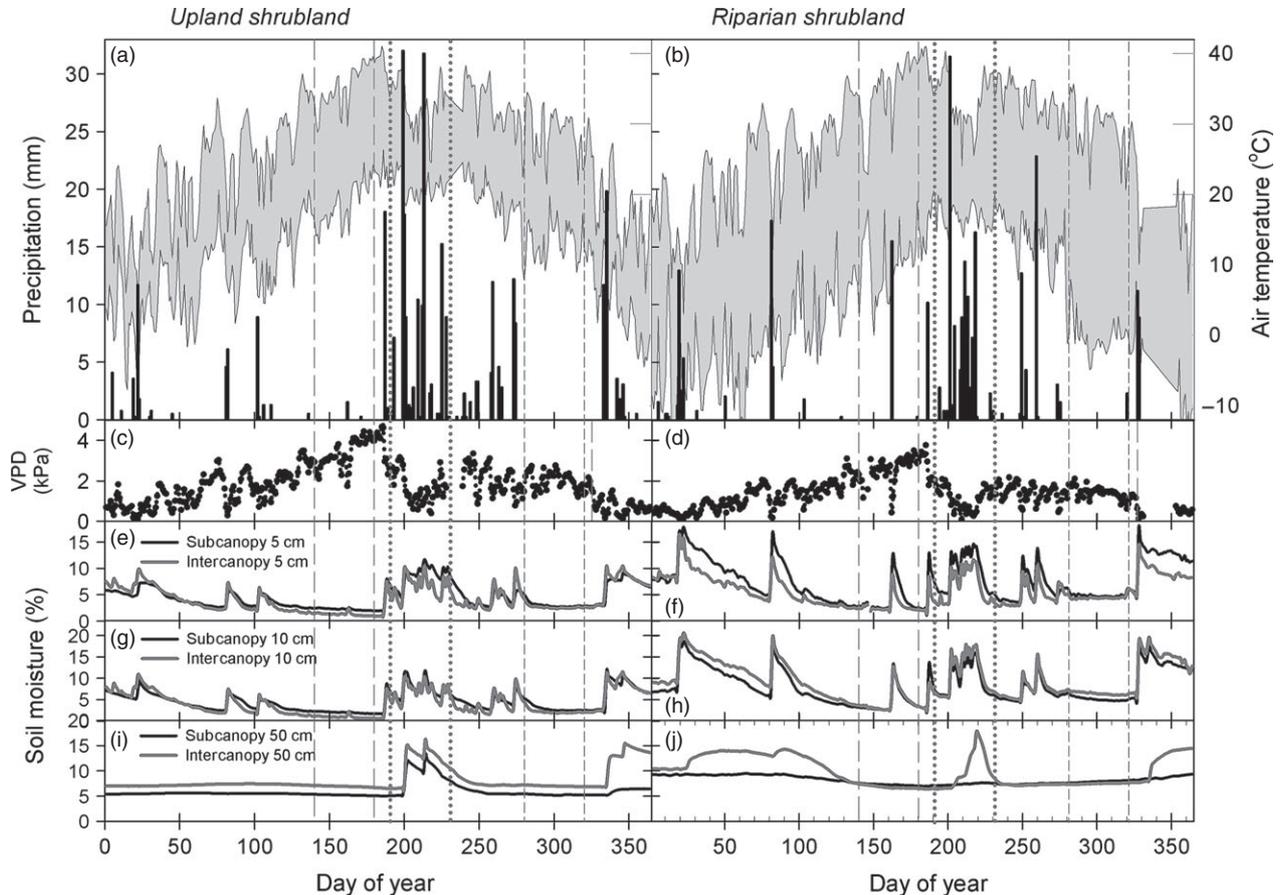
## Results

### ENVIRONMENTAL DYNAMICS

Total 2007 precipitation at the riparian and upland site was 263 mm and 330 mm, respectively (Fig. 1a,b). Average weekly air temperature ( $T$ ) peaked during the pre-monsoon at  $\sim 40^\circ\text{C}$  (DOY 140–180) and was consistently warmer at the upland site. Average  $T$  differed as little as  $1^\circ\text{C}$  between the sites during the monsoon (DOY 190–230) and by  $8.4^\circ\text{C}$  in dry periods (DOY 280–320; Fig. 2c). Average daily temperature fluctuation (daily  $T_{\text{max}} - T_{\text{min}}$ ) at the riparian site ( $23.4^\circ\text{C}$ ) was greater than at the upland site ( $14.2^\circ\text{C}$ ) due to lower  $T_{\text{min}}$  at the riparian site, not differences in  $T_{\text{max}}$ . With the exception of late winter, VPD was higher at the upland site (Fig. 1c,d, Fig. 2d). Pre-monsoon weekly average diel VPD were 1.1 kPa higher at the upland site and 0.5 kPa through monsoon and post-monsoon periods. Average 5, 10 and 50 cm soil moisture were 4.4, 4.3 and 7.0% in upland site soils vs. 6.8, 8.8 and 9.0%, respectively, at the riparian site (Fig. 1e–h). Rainfall increased weekly average 5 and 10 cm soil moisture more at the riparian site than at the upland site. Upland site soils were consistently drier at 50 cm than at the riparian site (Fig. 2e).

### ECOSYSTEM-SCALE FLUX AND TEMPERATURE RESPONSES

By DOY 85, weekly average net ecosystem exchange of  $\text{CO}_2$  ( $NEE$ ) at the riparian site were negative, indicating net  $\text{CO}_2$  uptake, while the upland site did not attain negative weekly average  $NEE$  until DOY 203 (Fig. 2a). For the pre-monsoon, the riparian site was a net  $\text{CO}_2$  sink ( $\Sigma NEE = -24.5 \text{ gC m}^{-2}$ ), while the upland site was a net source ( $+ 13 \text{ gC m}^{-2}$ ; Fig. 2b). At the start of the monsoon,  $\Sigma NEE$  was  $-73.6$  and  $+ 27.2 \text{ gC m}^{-2}$  at the riparian and upland



**Fig. 1.** Precipitation and weekly averages of daytime maximum and minimum temperatures for the upland (a) and riparian (b) shrublands, and average weekly levels of vapour pressure deficit (VPD) within these same ecosystems (c, d), for the entire 2007 year. Weekly averages of soil moisture at the 5 cm (e), 10 cm (g) and 50 cm (i) depths within the upland shrubland and at the riparian site for these same depths (f, h, j, respectively). Vertical dashed lines represent the partitioning between the seasonal periods; long dash = pre-monsoon; dotted = monsoon; short dash = post-monsoon.

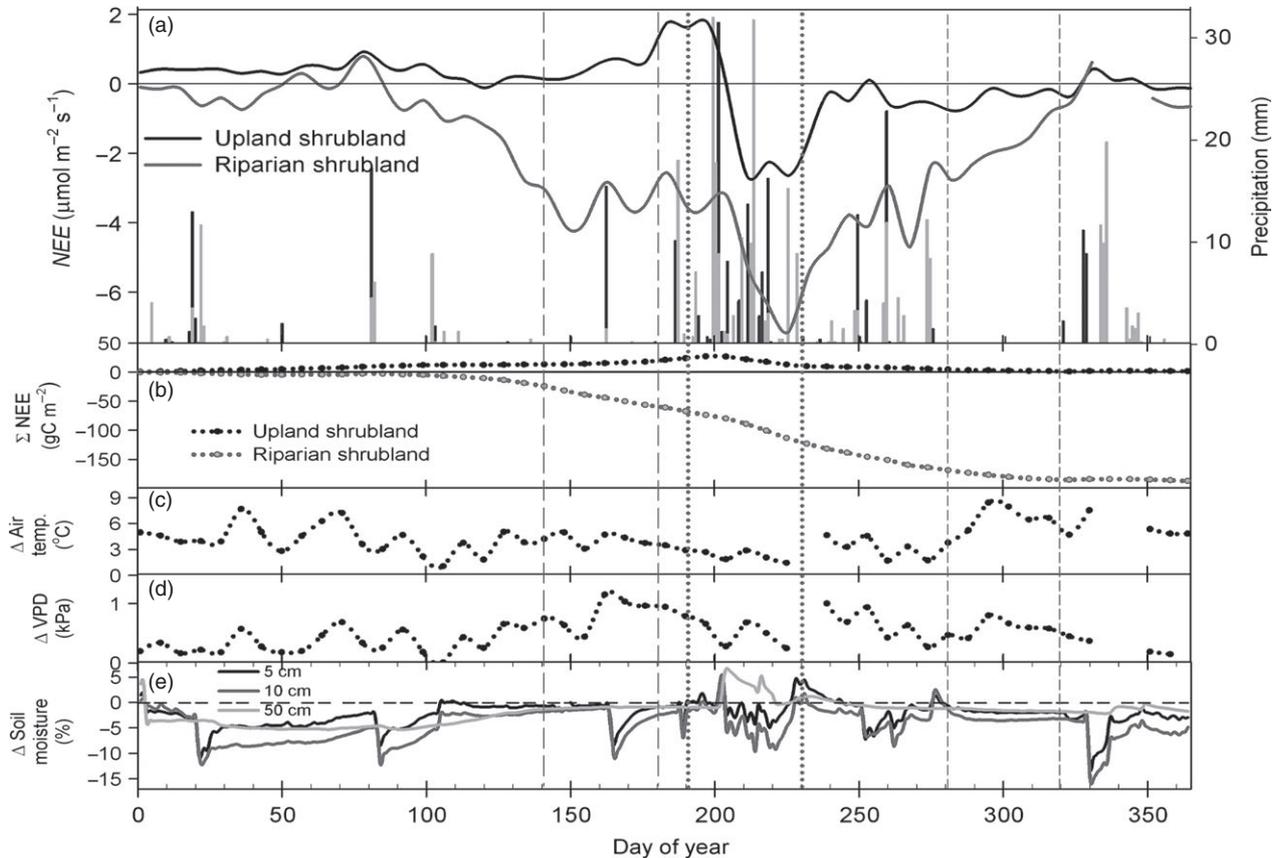
sites, respectively (Fig. 2a,b). By the end of the monsoon, the riparian site received 193 mm rain with a  $\Sigma NEE$  of  $-123 \text{ gC m}^{-2}$ , the upland site received 222 mm and a  $\Sigma NEE + 10.3 \text{ gC m}^{-2}$ . During the post-monsoon period,  $NEE$  continued to show that both sites were a net sink for CO<sub>2</sub>.

The temperature response of ecosystem-level net ecosystem productivity ( $NEP$ ; illustrated as positive values *sensu* ecosystem photosynthesis) and ecosystem respiration ( $R_{Eco}$ ) differed significantly between upland and riparian shrubland sites and varied between seasonal periods (Fig. 3a–c). Pooled across sites, maximum rates of  $NEP$  ( $NEP_{max}$ ) were greatest within the monsoon period ( $F_{2,16} = 37689$ ;  $P < 0.0001$ ). Lowest  $NEP_{max}$  was attained at the upland site during the pre-monsoon period and over the post-monsoon at the riparian site. There was a significant two-way site-by-season interaction ( $F_{2,16} = 5449$ ;  $P < 0.0001$ ), due to  $T_{opt}$  at the upland site varying between seasonal periods (19.7 °C, 28.1 °C and 22.1 °C for pre-monsoon, monsoon and post-monsoon, respectively), but not at the riparian site (27.1, 27.7 and 26.3 °C).  $NEP_{max}$  also had a significant site-by-season interaction ( $F_{2,16} = 4852$ ;  $P < 0.0001$ ), because  $NEP_{max}$  increased 420% from pre-monsoon to the monsoon in the upland, but

only 45% at the riparian site. Post-monsoon  $NEP_{max}$  declined 50% from monsoon period levels at both sites.

$\Omega_{50}$  and  $\Omega_{75}$  for the riparian site  $NEP$  were ca. twice that at the upland, averaging 52 + 4% higher across the seasonal periods ( $F_{1,4} = 65737$  and 151190, respectively;  $P < 0.0001$ ). Both shrublands reduced  $\Omega_{50}$  and  $\Omega_{75}$  in from pre-monsoon to the monsoon, indicating greater ecosystem  $T$ -sensitivity during the period of greatest water availability. The reduction in  $NEP \Omega_{50}$  was more pronounced for the riparian (38%) than the upland (7%) site. Post-monsoon  $\Omega_{50}$  and  $\Omega_{75}$  increased 30% at the upland site, while the riparian site  $\Omega_{50}$  of increased 39% and 29% in  $\Omega_{75}$ , indicating a broader ecosystem  $T$ -response than during the monsoon (Fig. 3).

$R_{Eco}$  temperature responses also differed between seasonal periods for both sites, although the riparian site consistently had more negative  $R_{Eco25}$  (Fig. 3d–f;  $F_{1,4} = 2114.55$ ;  $P < 0.0001$ ). During the pre-monsoon, there was little  $R_{Eco}$  in the upland site, and the  $Q_{10}$  of  $R_{Eco}$  was 0.98, indicating limited  $R_{Eco}$   $T$ -response, while  $R_{Eco25}$  at the riparian site was  $-2.8 \mu\text{mol m}^{-2} \text{ s}^{-1}$  and  $Q_{10} = 1.5$  (Fig. 3d).  $R_{Eco25}$  was most negative over the monsoon ( $F_{2,16} = 684.60$ ;  $P < 0.0001$ ), with a curvilinear  $T$ -response; the  $Q_{10}$  of the riparian site was 2.2 for the 15–25 °C range, but only 1.0 for



**Fig. 2.** (a) Net ecosystem exchange of carbon ( $NEE$ ) and precipitation throughout the entire annual cycle, and (b) cumulative  $NEE$  ( $SNEE$ ) across this same time period for both an upland and riparian shrublands. Data are presented in atmospheric notation, such that  $CO_2$  uptake from the atmosphere is illustrated as a negative value and efflux to the atmosphere yield a positive value. The difference between weekly averages of air temperature (c;  $\Delta$ Air temp), vapour pressure deficit (d;  $\Delta$ VPD) and three depths of volumetric soil moisture (e;  $\Delta$ Soil moisture) in the upland relative to the riparian shrublands, such that positive values of  $\Delta$ Air temp and  $\Delta$ VPD indicate a warmer and drier environment in the upland than the riparian ecosystem. Vertical dashed lines represent the partitioning between the seasonal periods; long dash = pre-monsoon; dotted = monsoon; short dash = post-monsoon.

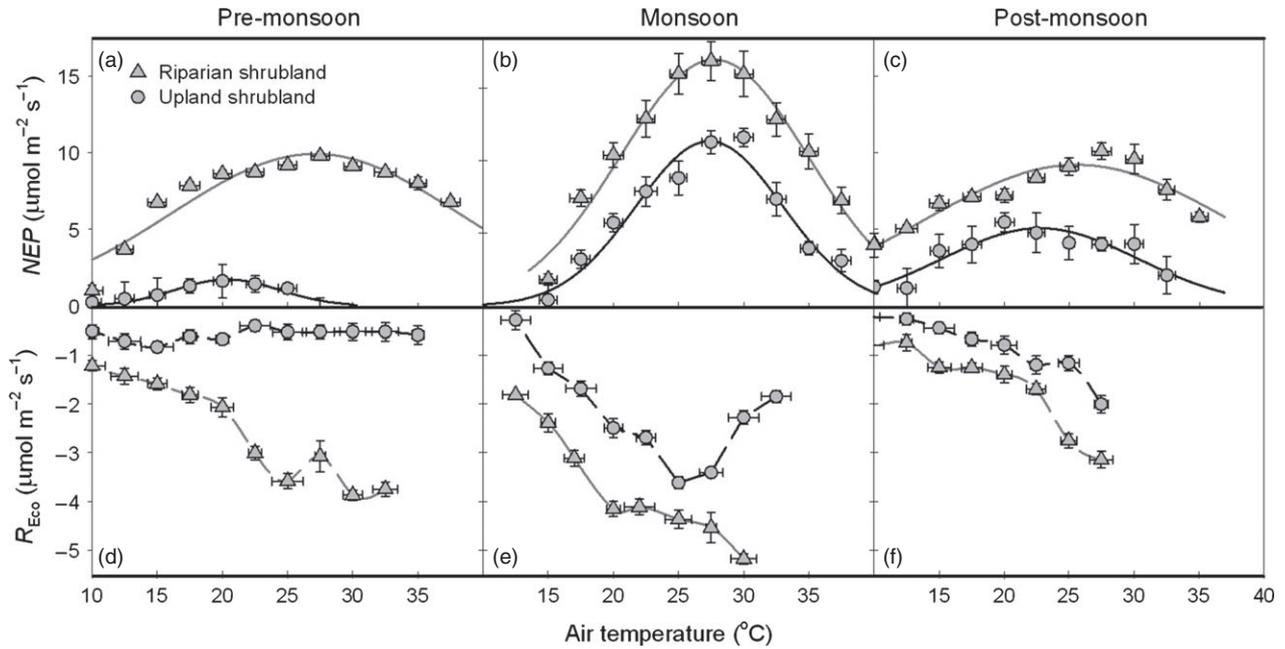
the 25–35 °C range. There was a significant site-by-season interaction ( $F_{2, 16} = 181.14$ ;  $P < 0.0001$ ) in that the monsoon increased  $R_{Eco}$  more markedly at the upland site (844%) than at the riparian (57%), with  $R_{Eco25}$  of  $-3.4$  and  $-4.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively.  $R_{Eco25}$  declined 56% at the upland and 45% at the riparian site over the post-monsoon, but was 4 times higher than pre-monsoon levels (Fig. 3d,f).

#### COMPONENTS FLUXES ~ LEAF-SCALE TEMPERATURE RESPONSES

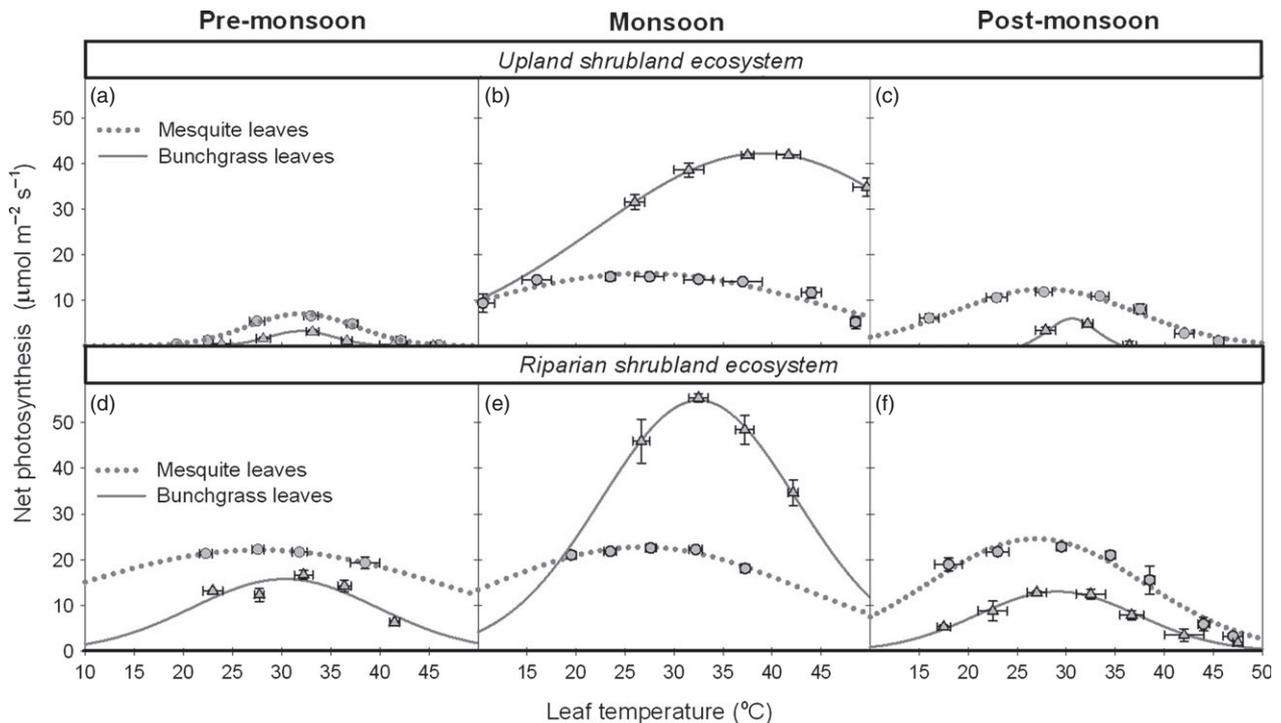
$A_{max}$  and  $T_{opt}$  differed between seasonal periods ( $F_{2,40} = 732.33$  and  $8.64$ ;  $P < 0.05$  for  $A_{max}$  and  $T_{opt}$ , respectively), with significant three-way site-by-species-by-season interactions in both variables ( $F_{2,40} = 7.02$  and  $11.52$ ;  $P < 0.05$  for  $A_{max}$  and  $T_{opt}$ , respectively; Fig. 4). At both sites, higher  $A_{max}$  were attained by bunchgrasses during the monsoon ( $48.8 \pm 3.1$ ) compared with mesquite ( $19.8 \pm 1.7$ ), while mesquite  $A_{max}$  were higher in the pre- ( $14.9 \pm 1.3$  and  $10.1 \pm 1.1$  for mesquite and grasses, respectively) and post-monsoon ( $17.8 \pm 1.8$  and  $9.90 \pm 1.2$  for mesquite and grasses, respectively). At the upland site,  $A_{max}$  increased

124% and 1041% between pre-monsoon and monsoon periods, in mesquite and grasses, respectively (Fig. 4). Post-monsoon  $A_{max}$  in mesquites were 21% lower than monsoon peaks, and 86% lower in grasses, which remained higher than pre-monsoon levels.  $\Omega_{50}$  and  $\Omega_{75}$  of  $A$  for both growth forms peaked in the monsoon and were greater in mesquites across the pre-monsoon, monsoon and post-monsoon periods, respectively (Fig. 4). Monsoon  $\Omega_{50}$  were 64% and 81% higher than pre-monsoon  $\Omega_{50}$  in the upland site mesquite and grasses, respectively, and post-monsoon  $\Omega_{50}$  and  $\Omega_{75}$  reductions were more substantial in grasses (Fig. 4).

Although  $A_{max}$  and  $T_{opt}$  for mesquites and grasses differed between seasonal periods of differing water availability, they were less variable in riparian site plants (Fig. 4). Riparian site mesquite  $A_{max}$  were seasonally invariant and averaged  $22.6 \pm 0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ .  $A_{max}$  of riparian site grasses increased 234% from pre-monsoon to monsoon periods and dropped to 75% of pre-monsoon levels in the post-monsoon (Fig. 4d–f).  $A_{max}$  was  $7.3 \mu\text{mol m}^{-2} \text{s}^{-1}$  higher in mesquites than grasses in pre- and post-monsoon periods, but mesquite  $A_{max}$  were  $32.2 \mu\text{mol m}^{-2} \text{s}^{-1}$  lower than in grasses during the monsoon.  $\Omega_{50}$  and  $\Omega_{75}$  for riparian mesquites were



**Fig. 3.** (a–c) Net ecosystem productivity ( $NEP$ ) throughout the pre-monsoon, monsoon and post-monsoonal periods across the range of temperatures that the upland (black circles) and riparian shrublands (grey triangles) experienced. (d–f) Ecosystem respiration rates ( $R_{\text{Eco}}$ ) across these same seasonal periods are shown for both sites. Data are presented in the traditional plant-physiological manner in which positive rates of  $NEP$  indicate net CO<sub>2</sub> uptake from the atmosphere, rather than in atmospheric notation, to aid in comparison between ecosystem- and leaf-level data.



**Fig. 4.** (a–c) Leaf-level rates of maximum net photosynthesis across a 25  $^{\circ}\text{C}$  range of temperatures for C<sub>3</sub> mesquites and C<sub>4</sub> grasses within and upland shrubland during the pre-monsoon, monsoon and post-monsoonal periods. (d–f) Same as above but for the C<sub>3</sub> mesquites and C<sub>4</sub> grasses located in the riparian ecosystem. Measurements were carried out on five individuals within each shrubland in each seasonal period.

greatest in the pre-monsoon and were lower and similar over the monsoon and post-monsoon. Riparian grass  $\Omega_{50}$  and  $\Omega_{75}$  in the monsoon were 11% and 26% higher than pre-monsoon

ranges. Changes in  $\Omega_{75}$  were greater than  $\Omega_{50}$  for mesquites, while the opposite was true for grasses, indicating a greater expansion and contraction in area around  $A_{\text{max}}$  in mesquites,

and more change at the edges of the  $T$ -response for riparian site grasses (Fig. 4d–f).  $T_{\text{opt}}$  did not change in riparian mesquites (27 °C), while grass  $T_{\text{opt}}$  was 33 °C in pre-monsoon and monsoon and 29 °C in post-monsoon periods.

Pooled across the plant functional types, seasonal rates of  $A_{\text{max}}$  were greater at the riparian than the upland site, although differences were smaller during the monsoon. Pre-monsoon, rates of  $A_{\text{max}}$  were three times greater in riparian mesquites than in upland site plants (22.4 + 1.9 vs. 7.4 + 0.7, respectively), and more than four times that of grasses (16.6 + 1.6 vs. 3.7 + 0.7; Fig. 4a,d). Post-monsoon,  $A_{\text{max}}$  was nearly twice as great at the riparian site for both mesquite (Fig. 4c, mesquite: 22.5 + 2.0 vs. 12.6 + 1.6) and grasses (Fig. 4f; 13.8 + 1.3 vs. 6.0 + 1.2). Pre- and post-monsoon  $\Omega_{50}$  for both growth forms were nearly twice as great in riparian plants than in upland plants, although these landscape differences became muted within the monsoon (Fig. 4d–f).

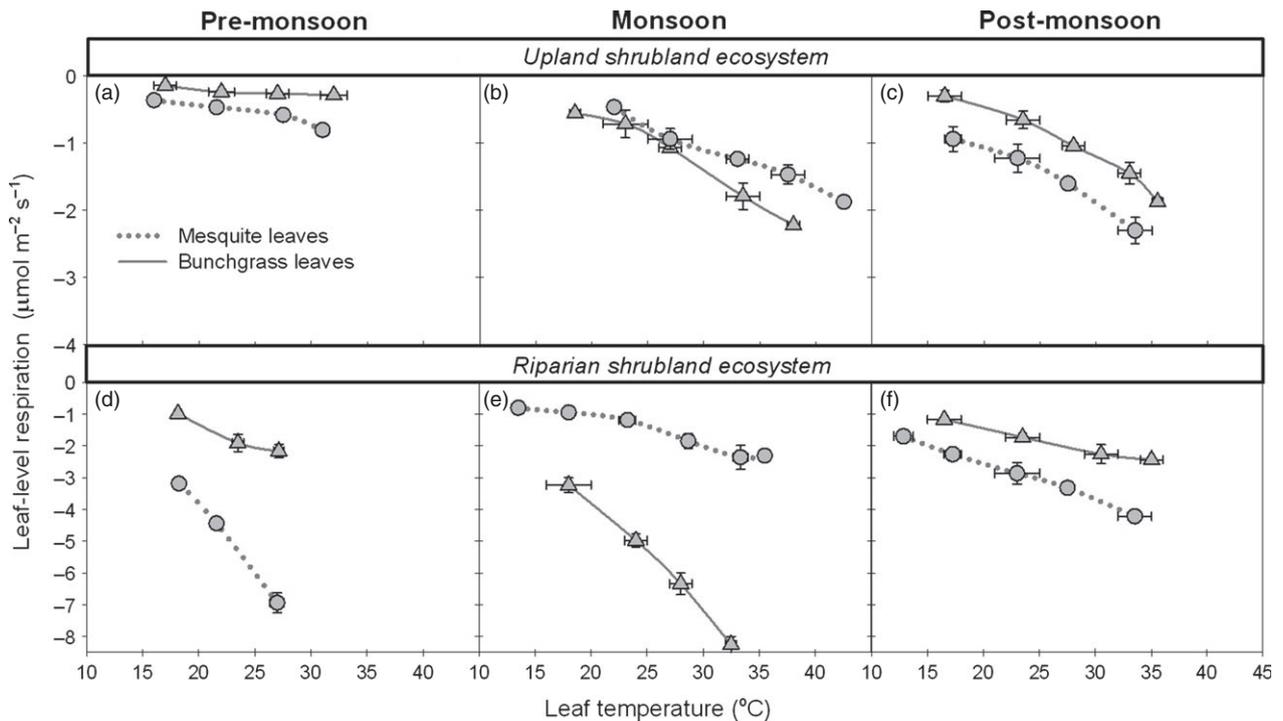
$R_{\text{Leaf}}$  showed a near-linear  $T$ -response in all periods, regardless of landscape position or growth form (Fig. 5). Upland  $R_{\text{Leaf25}}$  became progressively more negative through time for both growth forms, with greatest rates in the post-monsoon ( $F_{2,40} = 57.71$ ;  $P < 0.0001$ ; Fig. 5).  $R_{\text{Leaf25}}$  was higher in grasses than in mesquite during the monsoon, with the opposite in the pre- and post-monsoon.  $R_{\text{Leaf}}$   $Q_{10}$  in upland mesquites was greater in the monsoon (1.89) than pre- (1.50) or post-monsoon (1.58; Fig. 5a–c). Seasonally pooled  $R_{\text{Leaf25}}$  at the riparian site were twice that of upland plants ( $F_{1,40} = 2244.09$ ;  $P < 0.0001$ ; Fig. 5). Leaf-level  $R_{\text{Leaf25}}$ :  $A_{\text{Gross}}$  were more  $T$ -sensitive during pre-monsoon than monsoon periods, indicated by curvilinear responses in upland site

plants and steeply sloped responses in riparian site plants (Fig. 6a,c). During the monsoon, riparian plant  $R_{\text{Leaf}}$  had slightly negative response ( $Q_{10}$  of 1.6 + 0.1), while upland plants had a  $Q_{10}$  indicating stronger  $T$ -response (1.9 + 0.1). At the ecosystem level,  $R_{\text{Eco}}$  was rarely more than 45% of  $GEE$  (Fig. 6b,d), except across temperatures where  $NEP$  was nearly negative (dashed lines in Fig. 6). At both sites, pre-monsoon  $R_{\text{Eco}}:GEE$  peaked at lower  $T$  than in the monsoon, and these correspond with respective  $T_{\text{opt}}$  for  $NEP$ .

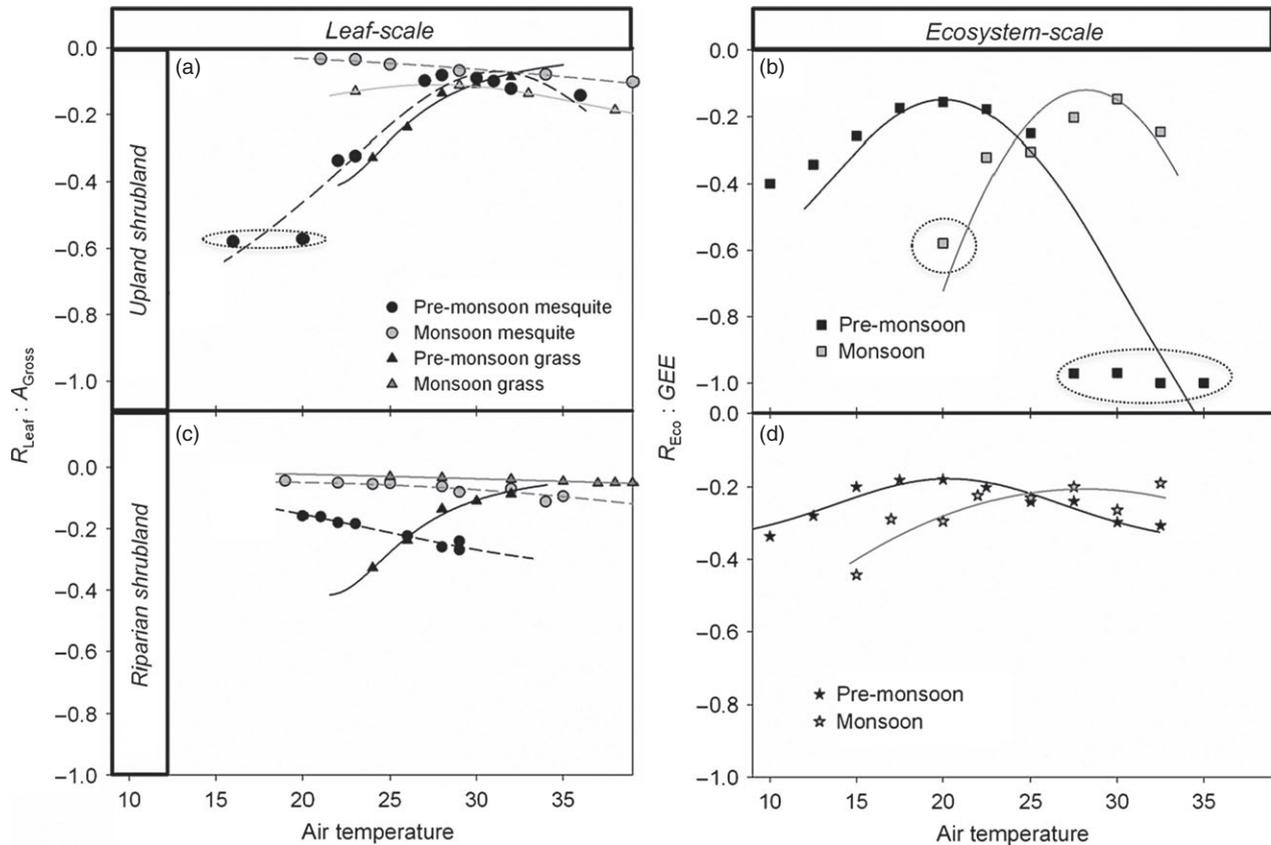
## Discussion

How components of ecosystems combine to collectively exchange materials and energy with the atmosphere and the associated hydrological network is an important challenge. The complexities of growth form, photosynthetic pathway and the potential for acclimation and/or genetic adaptation all suggest emergent properties of how environmental variables are related to ecosystem exchanges at larger spatial scales. This study provides comprehensive quantification of the temperature sensitivity of both the dominant vegetative components within semi-arid shrublands and the entire ecosystems themselves. By repeating measurement campaigns across seasonal periods and landscape positions, we were able to compute changes in thermal sensitivity due to periods of varying precipitation and estimate the role of component fluxes in driving ecosystem-scale responses.

Our results show several important conclusions, which are described in detail below. First, there was a difference in the physiological acclimation among the two plant functional



**Fig. 5.** (a–c) Rates of leaf-level respiration across a 25 °C range of temperatures for  $C_3$  mesquites and  $C_4$  grasses within an upland shrubland during the pre-monsoon, monsoon and post-monsoonal periods. (d–f) Same as above but for the  $C_3$  mesquites and  $C_4$  grasses located in the riparian ecosystem. Measurements were carried out on five individuals within each shrubland in each seasonal period.



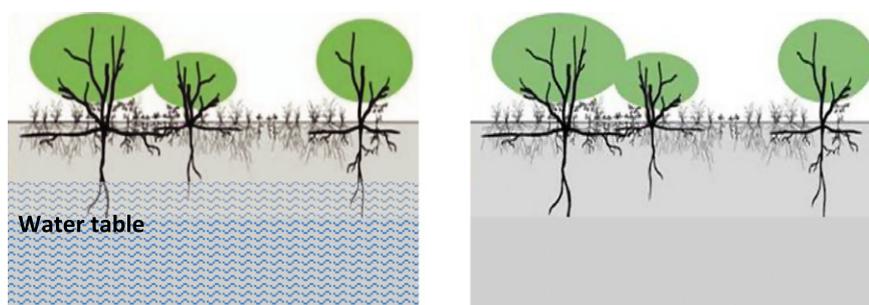
**Fig. 6.** The ratio of leaf-level respiration to gross photosynthesis ( $R_{\text{Leaf}} : A_{\text{Gross}}$ ) across a range of temperatures for the dominant vegetation within an upland (a) and riparian shrubland (c) during the pre-monsoon (black shapes) and the monsoonal (grey shapes) periods. Circles represent leaf-level responses of the mesquites, and the triangles correspond to the grasses. The ratio of ecosystem-level respiration to gross photosynthesis ( $R_{\text{Eco}} : GEE$ ) across a range of temperatures for the upland (b) and riparian shrubland (d) during the pre-monsoon (black shapes) and the monsoonal (grey shapes) periods. Dashed lines encircle temperature blocks when net ecosystem productivity was, itself, nearly negative (Fig. 3) such that virtually all CO<sub>2</sub> flux was an efflux from the ecosystem.

types. Mesquites were able to maintain net carbon assimilation across a range of temperatures 40–75% greater than co-occurring grasses during dry periods, but grasses outperformed mesquites during the monsoon. Secondly, landscape position played an important role in modulating these temperature sensitivities, as the range of functional temperatures and maximum rates of  $A$  were two to three times greater within the riparian shrubland in dry times. Thirdly, there was a disconnect between ecosystem- and leaf-scale temperature sensitivities of carbon uptake. Ecosystem carbon fluxes were most temperature sensitive within the monsoon for both shrubland locations, when mesquites and grasses displayed their largest ranges of photosynthetic temperature tolerance. This shows that ecosystem-scale functional restrictions were not due to constraints in plant photosynthetic capacity within either growth form, but rather were tied to the shifting relative contributions of component fluxes. Finally, the relative contribution of respiration to gross CO<sub>2</sub> uptake at both leaf- and ecosystem scales were more temperature sensitive in the upland ecosystem than the riparian shrubland. Soil- and leaf respirations from the nitrogen-rich mesquite leaves were both major contributors to ecosystem CO<sub>2</sub> fluxes. Collectively, our results highlight both a differential physiological acclimation to temperature among these plant

functional types and that the relative contribution of these component fluxes directed ecosystem-scale temperature sensitivity of the shrublands depending on access to soil moisture (as summarized in Fig. 7).

#### DIFFERENTIAL TEMPERATURE SENSITIVITY OF GRASSES AND WOODY PLANTS AND THE ROLE OF LANDSCAPE POSITION IN MODULATING PLANT ACTIVITY

Plant functional types differed significantly in their rates of  $A_{\text{max}}$ , the range of temperatures across which they were able to conduct net  $A$ , and their responsiveness to the onset of precipitation. Importantly, we detected a greater physiological capacity in mesquites than grasses within dry periods, such that  $A_{\text{max}}$  and  $\Omega_{50}$  in mesquites were nearly twice those of bunchgrasses. Collectively, these findings illustrate that ecosystems undergoing vegetative change are likely to see enhanced performance in the woody plants relative to native grasses, particularly under predicted precipitation patterns of longer interstorm periods of drought (Cubasch *et al.* 2001; Overpeck & Cole 2006; Backlund *et al.* 2008). Our classic understanding of historical woody plant expansion, developed



Landscape position	Riparian	Upland
Climate change analogue	Continued saturating precipitation	Prolonged or seasonal drought
Influence of air temperature on overstorey shrub CO <sub>2</sub> uptake	Shrubs / trees relatively unconstrained by temperature stress	C <sub>3</sub> shrubs / trees outperformed bunchgrasses during dry periods
Influence of air temperature on understorey plant CO <sub>2</sub> uptake	Bunchgrasses photosynthesis enhanced by presence of "lifted" water	Bunchgrass photosynthesis constrained during periods of drought
Effects of ecosystem sensitivity to temperature stress	NEP less sensitive to temperature stress and ecosystem is more productive	Ecosystem productivity more modulated by air temperature

**Fig. 7.** Conceptual diagram illustrating the effects of access to soil moisture on the effects of climatic stressors on plant and ecosystem function. Having a connectivity to sub-surface water augmented plant and ecosystem capacity for carbon assimilation and mitigated the constraining force of atmospheric temperature on those rates of carbon uptake. A lack of that access to sub-surface water, whether through landscape position or projected climate change will probably exacerbate differences among plant functional types and increase the sensitivity of the individual plant functional types and the entire ecosystem to climatic stress.

through extensive observation and experimentation, suggests that high levels of herbivory by livestock yields (i) spread of mesquite seed and (ii) less above-ground grass biomass and fine fuel, which greatly reduces or eliminates grassland fires (see Archer, Schimel & Holland 1995; Van Auken 2000 and references within). Here, we have identified a potential mechanism for continued expansion despite much better range management practices that keep livestock grazing in check and efforts to restore native semi-arid grasslands. Rises in atmospheric CO<sub>2</sub> concentrations may exacerbate this landscape transition given its potential to overly favour C<sub>3</sub> relative to C<sub>4</sub> species. Previous work has suggested that elevation has not been a primary cause of woody expansion in the past (Madany & West 1983; Conley, Conley & Karl 1992; Archer, Schimel & Holland 1995), although this may need to be revisited in light of climate change projections. One might predict that as more ecosystems lose subsurface waters (Seager *et al.* 2007), native grasses will become more reliant on incident precipitation to mitigate restrictions imposed by atmospheric temperature on plant and ecosystem function. Hence, greater access to subsurface water and increased atmospheric CO<sub>2</sub> concentrations would both benefit woody plant productivity and expansion (Fig. 7; climate change analogue).

#### DISCONNECT BETWEEN ECOSYSTEM- AND LEAF-SCALE TEMPERATURE SENSITIVITIES

Despite a considerable increase in  $NEP_{max}$ , both shrublands experienced a significant increase in temperature sensitivity from the pre-monsoon to monsoon conditions. This reduced

range of functional temperatures, in spite of increased peak performance, was contrary to our expectations, given that both ecosystems would have more available soil water during the monsoon than any other time of year. We found that the increased temperature sensitivity of the upland shrubland was not due to a restriction in the leaf-level plant physiological capacity of either growth form, as  $\Omega_{50}$  and  $\Omega_{75}$  actually increased an average of 68% and 83% in the mesquites and grasses from the pre-monsoon to the monsoon (Fig. 4a,b). Rather, the ecosystem-scale reduction in  $\Omega_{50}$  and  $\Omega_{75}$  was tied to (i) the relative contribution of component fluxes and the transition of dominant contribution from a species with a wider range of temperature function (mesquites) to one more constrained by temperature (grasses) and (ii) the significant increase in green leaf area of grasses in response to summer rains (personal observation). During the pre-monsoon, grasses had minimal rates of  $A$  and were contributing little to total ecosystem-scale flux, but in the transition to the monsoon, average grass  $A_{max}$  was nearly three times (157%) that of the mesquites and therefore probably the dominant contributor to total ecosystem flux. Bunchgrasses in this region typically have very low functional leaf area index (LAI) in the pre-monsoon, but LAI increases ~620% in periods of peak performance (Hamerlynck *et al.* 2010), while mesquite LAI remains relatively constant at ~1.6 (Scott *et al.* 2004).  $\Omega_{50}$  and  $\Omega_{75}$  of  $NEP$  increased to their highest levels among all seasonal periods for both shrublands in the post-monsoon, and we hypothesize that this is due to the concomitant effects of a 45% and 72% greater  $\Omega_{50}$  and  $\Omega_{75}$  in the mesquites than the grasses and a greater capacity for assimilation in mesquites than

grasses in the post-monsoon, as quantified by an average of 89% higher  $A_{\max}$ .

We found that a greater connectivity to groundwater both relaxed dependence of ecosystem performance on precipitation and enhanced potential for ecosystem-scale temperature acclimation. Sap flux-based measures of whole-tree transpiration in upland mesquite have illustrated a significantly reduced total daily water use between conditions of lower available soil moisture and higher VPD, relative to an environment characterized by abundant soil moisture and relatively lower evaporative demand (Dugas, Heuer & Mayeux 1992). Reduced rates of  $NEP$  at higher temperatures and lower  $\Omega_{50}$  and  $\Omega_{75}$  within our upland relative to the riparian shrubland were not due to higher  $R_{\text{Soil}}$  efflux countering plant uptake at higher temperatures in the upland (Fig. 6b), but rather may be linked to reduced rates of  $A$  under the combined atmospheric conditions of high temperatures and high VPD at the upland site (Fig. 2c,d).

#### THE RELATIVE CONTRIBUTION OF RESPIRATION TO GROSS CO<sub>2</sub> FLUX AT THE LEAF- AND ECOSYSTEM-SCALES

There was a strong temperature response of ecosystem-scale respiration ( $R_{\text{Eco}}$ ;  $Q_{10} > 1.5$ ) within the riparian shrubland during all seasons and in the upland during the monsoon and post-monsoon (Fig. 3d–f). The near-zero efflux rates and lack of a temperature response in  $R_{\text{Eco}}$  within the dry upland during the pre-monsoon were probably tied to the lack of soil moisture and minimal rates of leaf-level  $A$  within both growth forms that would yield few root exudates to feed microbial respiration.  $R_{\text{Eco}25}$  was significantly greater in the riparian site than the upland site during all seasonal periods, but the greatest differences between the shrublands came during this pre-monsoon period when efflux rates were an order of magnitude larger (Fig. 3d). Relatively high  $R_{\text{Eco}}$  rates have been documented in mixed and mesquite-dominated riparian ecosystems during the dry pre-monsoon because of mesquite access to groundwater (Scott *et al.* 2006b). By also measuring component fluxes of mesquite and grass  $R_{\text{Leaf}}$ , we could estimate their relative contributions to ecosystem efflux. We found that a significant portion of  $R_{\text{Eco}}$  came from foliar respiration, as  $R_{\text{Leaf}25}$  within riparian shrubland was  $-6.0$  and  $-1.9 \mu\text{mol m}^{-2} \text{s}^{-1}$  in the mesquites and grasses. The relative proportion of  $R_{\text{Eco}}$  to gross ecosystem exchange of carbon ( $GEE$ ) remained between 20 and 40% for both shrublands, except at temperature extremes when  $NEP$  itself was near-zero, resulting in virtually all CO<sub>2</sub> exchange being an efflux from the ecosystem (Fig. 6b,d). The shape of this  $R_{\text{Eco}}:GEE$  temperature response function was much more convex in the upland shrubland, suggesting that the relative contribution of respiration to gross flux CO<sub>2</sub> flux was more sensitive to temperature than in the riparian shrubland. The temperature at which this  $R_{\text{Eco}}:GEE$  function and the temperature at which  $NEP_{\max}$  peaked corresponded almost exactly with one another within shrublands during each growing season, underscoring the fact that these ecosystems were functioning best at specific temperatures, beyond which their carbon balance became less of a net sink for CO<sub>2</sub>.

## Summary and conclusions

Leaf- and ecosystem-scale carbon fluxes were monitored throughout multiple seasonal periods to provide a quantitative linkage among atmospheric temperature, water availability and ecosystem processes across multiple landscape positions and temporal scales. We found connectivity to stable groundwater sources decoupled leaf- and ecosystem-scale temperature sensitivity relative to comparable sites lacking such access (Fig. 7). Groundwater access not only resulted in a near-doubling of the range of temperatures across which the ecosystem could assimilate CO<sub>2</sub> at near-peak rates, but also actual rates of net ecosystem productivity being 1.5 times greater when precipitation was relatively abundant and 5 times greater when it was not. Given projections of more variable regional precipitation and increased temperatures, differences in physiological capacity among growth forms are likely to drive patterns of ecosystem-scale carbon flux, depending on the degree of woody versus grass cover within shrublands. As access to stable subsurface water declines with decreased precipitation input, these differential patterns of temperature sensitivity among growth forms dependent on connectivity to groundwater will only become more important in determining ecosystem carbon source/sink status.

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