Terrestrial carbon balance in a drier world: the effects of water availability in southwestern North America

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Abstract

Global modeling efforts indicate semiarid regions dominate the increasing trend and interannual variation of net CO2 exchange with the atmosphere, mainly driven by water availability. Many semiarid regions are expected to undergo climatic drying, but the impacts on net CO2 exchange are poorly understood due to limited semiarid flux observations. Here we evaluated 121 site-years of annual eddy covariance measurements of net and gross CO2 exchange (photosynthesis and respiration), precipitation, and evapotranspiration (ET) in 21 semiarid North American ecosystems with an observed range of 100 – 1000 mm in annual precipitation and records of 4–9 years each. In addition to evaluating spatial relationships among CO2 and water fluxes across sites, we separately quantified site-level temporal relationships, representing sensitivity to interannual variation. Across the climatic and ecological gradient, photosynthesis showed a saturating spatial relationship to precipitation, whereas the photosynthesis–ET relationship was linear, suggesting ET was a better proxy for water available to drive CO2 exchanges after hydrologic losses. Both photosynthesis and respiration showed similar site-level sensitivity to interannual changes in ET among the 21 ecosystems. Furthermore, these temporal relationships were not different from the spatial relationships of long-term mean CO2 exchanges with climatic ET. Consequently, a hypothetical 100-mm change in ET, whether short term or long term, was predicted to alter net ecosystem production (NEP) by 64 gCm–2 yr–1. Most of the unexplained NEP variability was related to persistent, site-specific function, suggesting prioritization of research on slow-changing controls. Common temporal and spatial sensitivity to water availability increases our confidence that site-level responses to interannual weather can be extrapolated for prediction of CO2 exchanges over decadal and longer timescales relevant to societal response to climate change.

Keywords: carbon dioxide, climate, ecosystem, evapotranspiration, net ecosystem exchange, net ecosystem production, photosynthesis, productivity, respiration, semiarid, water

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Introduction

Semi-arid ecosystems dominate the global trend of increasing net CO2 uptake from the atmosphere and contribute the greatest fraction to atmospheric CO2 interannual variation (Poulter et al., 2014; Ahlström et al., 2015). In many semiarid regions, interannual variability of precipitation far exceeds current precipitation trends, creating natural experiments for predicting ecosystem response to future climate. Because water is a primary control of CO2 exchange in semiarid ecosystems (Huxman et al., 2004; Bai et al., 2008), there is growing concern that future changes in water availability may alter their important capacity to mitigate anthropogenic emissions (Sala et al., 2012; Carvalhais et al., 2014). In this paper, we use observations from an ecological and climatic gradient in semiarid southwestern North America, where precipitation is expected to
Net exchange of CO₂ between ecosystems and the atmosphere may be quantified as net ecosystem production (NEP), the small difference between opposing fluxes of assimilation via gross ecosystem photosynthesis (GEP), and release by ecosystem respiration (Rₑₑₑ) (Eqn 1).

$$\text{NEP} = \text{GEP} - R_{\text{eco}}$$  \hspace{1cm} (1)

In this paper, we use the term ‘CO₂ exchanges’ to refer collectively to NEP and its component fluxes GEP and Rₑₑₑ. CO₂ exchanges are controlled both by fast-changing factors, primarily ecophysiological sensitivity to weather, and by slow-changing ecosystem demographic factors including plant community (species, age, structure) and biogeochemical pools, which reflect climate and legacies of disturbance (Barford et al., 2001; Schwalm et al., 2012; Vicente-Serrano et al., 2013; Friend et al., 2014; Reichstein et al., 2014). These slow-changing factors constrain ecophysiological response to weather (Knapp & Smith, 2001; Huxman et al., 2004; Sala et al., 2012), meaning CO₂ exchanges depend on interactions between slow and fast factors. Slow factors are less well studied than fast ones, and ecosystem process models often emphasize fast ecophysiology, such as meteorological controls on photosynthesis. Observations are lacking to assess the accuracy of extrapolating well-studied fast ecophysiology to predict NEP over decadal and longer timescales, resulting in highly uncertain projections of future climate over the timescales important for societal decision-making (Sitch et al., 2008; Friedlingstein et al., 2013).

The well-studied relationship between precipitation and vegetation productivity supports inferences about GEP under altered water availability. First, the productivity response is expected to follow an initially modest trajectory but increase in magnitude after slow plant community adaptation; this has been inferred, using a space-for-time substitution, from steeper spatial relationships between productivity and precipitation across sites with different climates than temporally among years at a site (Hsu et al., 2012; Sala et al., 2012; Jin & Goulden, 2014). Moreover, ecosystem adaptation to altered climatic water availability may change the sensitivity of production to temporal variation in water availability (i.e., altered slow factors regulate fast response). Because temporal slopes tend to be steeper at drier sites (Huxman et al., 2004; Hsu et al., 2012; Sala et al., 2012; Jin & Goulden, 2014), we can expect that climatic drying in southwestern North America would increase ecosystem sensitivity to interannual weather variation. Increased sensitivity would then multiply the impact of expected increases in precipitation variability. While spatial and temporal precipitation–productivity relationships are among the most extensive datasets of climate–ecosystem interactions, it remains unclear whether the above expectations can be extrapolated to NEP, because the impacts of water availability on respiration are less well understood.

Observed relationships between water availability and respiration are relatively scarce in comparison with those of productivity. Temperature has received much emphasis as a kinetic driver of Rₑₑₑ over short timescales (i.e., hours to days), but recent studies indicate that water availability, mediated by vegetation activity, is an important control of annual-scale Rₑₑₑ (Mahecha et al., 2010; Wang et al., 2010). Diverse measurements indicate that GEP is a strong driver of Rₑₑₑ probably because it provides photosynthates for both autotrophic and heterotrophic respiration (Ayres & Lombardero, 2000; Högberg et al., 2001; Janssens et al., 2001; Ryan & Law, 2005; Baldocchi, 2008; Wang et al., 2010). The typical approach in prior syntheses of annual eddy covariance datasets has been to combine site-years, often resulting in linear spatial relationships between Rₑₑₑ and GEP with slopes of ~0.7–0.9, sometimes with separate relationships for site classes (i.e., vegetation, disturbance) (Baldocchi, 2008; Lasslop et al., 2010; Yu et al., 2013; Chen et al., 2015). However, site-specific differences in Rₑₑₑ may dominate variability in annual NEP across sites (Valentini et al., 2000), possibly because legacies of disturbance alter the relationship between long-term mean respiration and productivity (Baldocchi, 2008; Chen et al., 2015). Therefore, in the present analysis, we maintained the distinct identity of each site and quantified an offset between the mean annual CO₂ flux at each site and the spatial relationship.

An additional challenge is quantifying water available to drive ecosystem CO₂ exchanges. Soil moisture is commonly recognized as a primary control on both photosynthesis and respiration in semiarid systems. However, soil moisture measurements can be difficult to compare across sites, and asynchrony of soil moisture with other ecological constraints (e.g., phenology, energy) may confound annual-scale analysis. As the input to soil moisture, precipitation (P) is the most common proxy for water availability, although the annual local water balance reflects hydrologic partitioning of P to runoff and drainage losses (Q), storage changes (S), and ET (Eqn 2).

$$P = ET + Q - S$$  \hspace{1cm} (2)
In semiarid regions, annual $S$ is small (Scott, 2010). Meanwhile, intense precipitation may exceed infiltration capacity, especially during the southwest monsoon, causing significant runoff which does not contribute to local CO$_2$ exchanges. Runoff tends to be larger in wetter years and at wetter sites, increasing the amount by which precipitation overestimates available water (Ponce-Campos et al., 2013). Therefore, in addition to precipitation, we used ET as a proxy of water availability. In semiarid ecosystems, ET represents primarily the efflux of soil moisture, and it has long been recognized as a more accurate metric of the water available to drive plant and soil CO$_2$ cycling (Rosenzweig, 1968; Schwalm et al., 2010; Ponce-Campos et al., 2013). However, a lack of measurements has limited understanding of the relationship between ET and CO$_2$ exchanges, especially for semiarid sites, where ecosystem function is particularly sensitive to water. Maturing eddy covariance datasets help answer this challenge by simultaneously quantifying ecosystem-scale ET with NEP and its components GEP and $R_{ec}$ (Goulden et al., 1996). Use of ET would also capture any influence from ecosystem access to groundwater (Thompson et al., 2011), although the available data suggest that groundwater does not play a significant role in the network of semiarid, upland sites studied here.

Here we quantified the effects of water availability (P, ET) on NEP and its components GEP and $R_{ec}$ across 21 eddy covariance sites representing the climatic and ecological demography of semiarid southwestern North America. We used the interannual variation of ecosystem CO$_2$ exchanges to quantify site-level temporal relationships (Laenenoth & Sala, 1992; Knapp & Smith, 2001; Huxman et al., 2004). Cross-site spatial relationships were fit to site mean values across the climatic and ecological gradients, and we employed a space-for-time substitution to draw inferences about ecosystem CO$_2$ exchange under future climatic water availability (Hsu et al., 2012; Sala et al., 2012; Jin & Goulden, 2014). To improve understanding of semiarid ecosystem–atmosphere CO$_2$ exchanges, we addressed three questions: (i) How does the temporal sensitivity of semiarid ecosystem CO$_2$ fluxes to interannual water availability vary among sites with different climatic water availability? (ii) How do the temporal sensitivities of ecosystem CO$_2$ fluxes to interannual water availability compare to cross-site spatial relationships with climatic water availability? (iii) What is the relative importance of spatial and temporal water availability variations in regulating semiarid NEP? In contrast to models, atmospheric inversions, or remote-sensing estimates, the unique dataset of semiarid ecosystem measurements assembled here allows in-depth analysis of how NEP and its component fluxes respond to spatial and temporal variations in water availability.

### Methods and materials

#### Study sites

We identified 21 eddy covariance flux sites with 4–9 years of measurements (mean of 6 years, total $n = 121$) representing the climate and ecosystems of the southwestern US and northern Mexico (Fig. 1, Table 1, Fig. S1), a region that is water-limited at the annual scale (i.e., potential evapotranspiration > precipitation). Observations were made between 1999 and 2013, with most occurring after 2004 (Table 1). The major regional ecosystem types represented are desert, arid tropical scrub, chaparral, grassland, savanna, pinyon, and juniper woodlands, and forests including ponderosa, mixed conifer, oak/pine, and tropical deciduous forest. Site descriptions are available for the US sites at www.ameriflux.lbl.gov and for the Mexico sites at www.fluxdata.org. Climate for the study sites and region was characterized with mean annual precipitation and temperature (Fig. S1) for the period 1950–2000 using the 30 arc-second WorldClim dataset (www.worldclim.org). Based on the ANUSPLIN algorithm, WorldClim is comparable to PRISM (www.prism.oregonstate.edu) but offers worldwide coverage (Parra & Monahan, 2008). Mean annual precipitation ranged from 150 to 750 mm, while mean annual temperature ranged from 1 to 24 °C. Most sites had some history of management or disturbance, although the availability and precision of such data varied (Table S1). One chaparral site (so2) had a stand-replacing fire. The postfire observations were treated separately and appear as a 21st site in the analysis (so2B).

#### Flux data collection and processing

We used annually integrated sums of precipitation and high-frequency (30 min) measurements of net CO$_2$ exchange and water vapor flux and estimates of GEP and $R_{ec}$ derived from the net CO$_2$ exchange measurements. Measurements of terrestrial-atmosphere gas flux were made at the ecosystem level using the eddy covariance technique (Goulden et al., 1996). Data collection and regular calibrations of eddy covariance flux measurement systems followed accepted guidelines (Lee et al., 2006). Observations of net CO$_2$ exchange with insufficient turbulent mixing were screened using a friction velocity filter (Reichstein et al., 2005). Gross fluxes were initially partitioned from the net CO$_2$ exchange measurements based on the observed relationship between nighttime respiration and temperature, which was then used to separately derive daytime GEP and $R_{ec}$ (Reichstein et al., 2005). At several sites with recurring periods of insufficient nighttime turbulent mixing to determine a robust respiration-temperature relationship, gross fluxes were instead partitioned using a light response curve fit to daytime net CO$_2$ flux (Lasslop et al., 2010). Previous comparisons have shown good agreement among approaches at the annual scale (differences <10%) (Desai et al.,...
Here, we found that the choice of partitioning method did not alter any of our conclusions. Annual CO2 and water vapor flux sums were calculated using a hydrologic year running November 1 to October 31. At two sites, fluxes for the months of November and December were estimated in one hydrologic year (emg-2007, so2-1999) using the mean weekly observed fluxes of the remaining years. November and December are relatively dormant months at these Mediterranean chaparral sites, together comprising only 9–12% of mean annual fluxes.

Separation of fast and slow factors controlling ecosystem CO2 exchanges

We interpreted our results using an ecological approach developed to separate temporal and spatial variability in plot-scale precipitation–productivity relationships and associate them with fast and slow controls, respectively (Fig. 2a) (Lauenroth & Sala, 1992; Huxman et al., 2004; Sala et al., 2012). Site-level temporal relationships represent ecophysiological responses to fast-changing factors such as weather (i.e., annual water availability), while spatial relationships determined from mean annual values at each site reflect slow-changing controls such as plant community adaptation to climate (Lauenroth & Sala, 1992; Chen et al., 2015) (Fig. 2b). Employing a space-for-time substitution allows inferences to be drawn about ecosystem response to future conditions (Hsu et al., 2012; Sala et al., 2012; Jin & Goulden, 2014). We modified the existing approach by quantifying site offsets (Fig. 2a), which are attributed to slow controls not captured by the spatial relationship, such as confounding environmental factors or legacies of disturbance (Baldocchi, 2008; Chen et al., 2015). This spatial–temporal approach differs from the more common practice in synthesis studies of eddy covariance data in which a single relationship between two variables is determined across the pooled site-years or classes thereof (e.g., vegetation class, disturbance). The single response determined in this manner is usually similar to the spatial relationship but is weighted by unequal years of observation among sites.

Results

GEP ranged from 67 to 1140 gC m⁻² yr⁻¹ (Fig. 3). The spatial relationship of GEP to precipitation was positive and gradually saturating (Fig. 3a), consistent with prior observations of ANPP or remotely sensed greenness.
The temporal and spatial slopes between GEP and ET (Fig. S3) with a slope of 0.78 gC mm⁻¹ H₂O, but the relationship was relatively weak ($R^2 = 0.27, P < 0.01$). Instead, there was a stronger spatial relationship between $R_{\text{eco}}$ and GEP (Fig. 4, $R^2 = 0.65, P < 0.001$). This CO₂ balance between GEP and $R_{\text{eco}}$ defines NEP (Eqn 1), and the spatial slope indicated an average increase of 64 gC m⁻² annually respired for each 100 gC m⁻² of increased annual photosynthesis. Temporal slopes between $R_{\text{eco}}$ and GEP showed no trend across the productivity gradient. The temporal slope fit to interannual deviations from the means of all sites was 0.56 ($R^2 = 0.52, P < 0.001$), meaning that on average across the 21 semiarid ecosystems, 56% of GEP interannual variation was counteracted by $R_{\text{eco}}$ interannual variation within the same year (Fig. 4 inset). Three sites with known disturbance (Table S1, lpa, fmf, fwf) had the lowest temporal slopes (Fig. S4). The temporal and spatial slopes between $R_{\text{eco}}$ and GEP were not different. Therefore, respiration showed the same average relationship to interannual productivity variation, which depends upon interannual water availability, as to long-term site productivity, which depends upon climatic water availability.
Fig. 2 Interpretation of spatial (red) and temporal (black) relationships in multi-site ecosystem synthesis studies including illustration with hypothetical observations (a) and a conceptual diagram showing timescales of several factors regulating ecosystem function (b). Slow factors regulate the cross-site spatial relationship between average values of an environmental driver (e.g. water availability) and the CO2 flux, while fast factors control the CO2 flux response to temporal variability of the driver. In (a), the site offset represents slow factors not scaling with the driver, such as disturbance effects on soil carbon or plant stem density. In (b), the vertical axis represents a gradient from abiotic to biotic factors. Please see the online version of the article for references to color.

Fig. 3 Relationships of annual gross photosynthesis (GEP) with precipitation (P) (a) and with evapotranspiration (ET), a metric of water available to drive ecosystem CO2 cycling after subtracting hydrologic losses from precipitation (b). Linear fits estimate the temporal (that is, interannual) relationships at each site (small black lines). In (a) the spatial relationship of GEP to mean precipitation P (red curve) is described by a negative exponential (Huxman et al., 2004) $GEP = 1218(1 - exp(-0.00532P))$, $n = 21$ sites, $R^2 = 0.52$, $P < 0.001$), while in (b) the spatial relationship to mean ET is linear: $GEP = 1.79ET - 139$, $n = 21$, $R^2 = 0.73$, $P < 0.001$. In (b) the inset shows the annual GEP and ET expressed as deviations from each site’s mean using the same units as the main figure. The temporal slope fit to this combination of all sites (1.46 gCmm$^{-1}$H$_2$O, $n = 121$ site-years, $R^2 = 0.71$, $P < 0.001$) was not different from the spatial slope ($P > 0.05$). To identify individual sites, see Fig. S2.

Semiarid ecosystems showed a positive linear spatial relationship between climatic water availability (mean ET) and NEP with a slope of 0.95 gC mm⁻¹ H₂O (Fig. 5a). The spatial relationship intercepted the ET axis (horizontal) at 286 mm, suggesting a water availability threshold for net CO₂ source/sink function in southwestern North America during the early 21st century. Temporal slopes between ET and NEP were positive and showed no trends in sensitivity of NEP to ET across the site gradient in climatic water availability. The temporal slope fit to interannual deviations at all sites was 0.62 gC mm⁻¹ H₂O, $R^2 = 0.26$, $P < 0.001$, not shown.

We used partial variance decomposition (Bevington & Robinson, 2002) to quantify the percentage of NEP variance explained by the relationships of GEP with ET and of $R_{eco}$ with GEP including spatial relationships, site offsets, and temporal relationships, as well as unexplained variability around the temporal models (Fig. 2a). We found 63% of NEP variance could be explained by just the spatial relationships of GEP with ET (42%) and of $R_{eco}$ with GEP (21%) (Fig. 5b). Most of the remaining NEP variability (26%) was related to site offsets. Meanwhile, only an additional 8% of NEP variance was explained by the addition of temporal relationships for each site, while 4% remained unexplained.

Discussion

We found a tendency toward similar spatial and temporal responses of annual CO₂ exchanges to water availability variations across a climatic and ecological gradient of semiarid ecosystems (Figs 3b and 4). Therefore, we did not find evidence supporting the expectation that ecosystem response to altered water availability would initially follow a shallow temporal slope, then a steeper spatial slope representing slow climate adaptation. Instead, similar spatial and temporal slopes increase our confidence that fast ecophysiological responses are useful for predicting NEP under future climatic water availability. A central tendency in temporal sensitivities of CO₂ exchanges to water among sites suggested that climatic drying (or wetting) should not be expected to change CO₂ exchange sensitivity to moisture. Most of the unexplained NEP variance across this regional dataset was related to site offsets in mean CO₂ fluxes, suggesting a need for future research to prioritize site-specific controls.

Productivity relationships with available water

A linear spatial relationship between GEP and ET suggests that semiarid ecosystems use marginal differences in climatic water availability with common efficiency (Fig. 3b) and that saturating relationships between productivity and precipitation (Fig. 3a), (Huxman et al., 2004; Hsu et al., 2012; Jin & Goulden, 2014) reflect, at least in part, increasing hydrologic losses at wetter sites (Eqn 2) (Ponce-Campos et al., 2013). Here, a horizontal intercept of ~80 mm ET in the spatial relationship (Fig. 3b) implies a minimum threshold of climatic water availability below which vegetation productivity is negligible, and all water remaining after runoff losses is evaporated. While this represents an extrapolation, the inclusion of dry sites makes the extrapolation small relative to the range of observations.

A common temporal relationship between GEP and ET across the climatic and ecological gradient (Fig. 3b inset) implies that if expected regional drying drives ecosystem shifts (e.g., forest to savanna and grassland to shrubland), this will not necessarily constrain a site’s capacity for response to water availability. Vegetation change can alter the amount of precipitation which becomes ecosystem-available (i.e., the hydrologic partitioning of P between ET and Q, Eqn 2), but this would be captured by our use of ET as the water availability metric (Scott et al., 2014). Our finding that temporal and spatial slopes did not differ from one another contrasts with results suggesting that reduced climatic water availability would drive down productivity initially along a shallower interannual slope, then subsequently
along a steeper spatial slope reflecting vegetation community adaptation (Sala et al., 2012; Jin & Goulden, 2014). Our sites were similar to these studies in both climatic precipitation and ecosystem functional types, and our finding of similar spatial and temporal slopes likely results from use of ET, which removes from consideration the portion of precipitation not available to drive local CO₂ cycling (Eqn 2). It is likely that at a site, more (less) precipitation results in more (less) hydrologic loss (Zhang et al., 2001; Ponce-Campos et al., 2013), flattening the apparent temporal slopes of productivity to precipitation. Meanwhile, the underlying efficiency with which ecosystems utilize an increment of available water for productivity ($\Delta$GEP/$\Delta$ET) appears to remain relatively constant both temporally and spatially (Fig. 3b). Unexplained variability in the temporal relationship of ET with GEP could reflect interannual differences in hydrologic partitioning of ET between evaporation and transpiration, ecosystem constraints resulting from water availability in earlier years, or the timing and size of precipitation events throughout the year. However, unexplained temporal variation contributed <5% to NEP variance (Fig. 5b).

Respiration relationships with available water and productivity

Our finding that $R_{\text{eco}}$ was related weakly to ET (Fig. S3) and more strongly to GEP (Fig. 4) is consistent with direct and indirect control of $R_{\text{eco}}$ by water. ET represents primarily the efflux of soil moisture remaining after hydrologic losses from precipitation (Eqn 2), which can limit heterotrophic respiration of accumulated labile carbon until a precipitation pulse wets the soil (Sponseller, 2007; Jenerette et al., 2008). However, this direct control of heterotrophic respiration by water is more likely to regulate the timing of respiration within a season than alter annual sums of $R_{\text{eco}}$. Annual respiration is more likely controlled by water availability indirectly through plant production of photosynthates (Mahecha et al., 2010; Wang et al., 2010), which are respired by plant tissue and root-associated mycorrhizae and stimulate heterotrophic respiration (Högberg et al., 2001; Janssens et al., 2001; Ryan & Law, 2005; Sampson et al., 2007; Baldocchi, 2008; Vargas et al., 2011).

A common temporal slope of $R_{\text{eco}}$ to GEP (0.56) found by combining all sites (Fig. 4 inset) builds upon the finding that respiration was half as sensitive as productivity to drought (Schwalm et al., 2010) by showing that this relationship holds more generally for wetting or drying within the entire range of observed variation. The temporal slope also falls within reported ratios of autotrophic respiration to productivity in forests ($R_a$/GEP ~ 0.53–0.57) (Waring et al., 1998; Litton et al., 2007). This may mean that in these semiarid ecosystems, interannual variation of $R_{\text{eco}}$ reflects mainly the response of plants to changes in water availability and resulting

Fig. 5 The relationship between annual net ecosystem production and evapotranspiration (a) and the percentages of NEP variance explained by the spatial and temporal relationships among productivity, respiration, and evapotranspiration (b). In (a), the linear spatial relationship was $\text{NEP} = 0.95 \times \text{ET} - 271$; $n = 121$; $P < 0.001$; $R^2 = 0.60$. At the horizontal intercept of the spatial model ($\text{NEP} = 0$) ET is 286 mm yr⁻¹. In (b), GEP was predicted from spatial and temporal relationships with ET (Fig. 3b), and $R_{\text{eco}}$ was predicted from relationships with GEP (Fig. 4). The four model components (bars) shown are described in Fig. 2a.
photosynthate production. In such a scenario, multi-
year mean $R_{\text{eco}}$ at a site may be viewed as a baseline
regulated by slow-changing factors including plant bio-
mass and soil carbon pools. Although we lack the mea-
surements to separately quantify the components of
$R_{\text{eco}}$ here, this scenario illustrates how separation of
temporal and spatial relationships across multitempo-
ral, multisite studies (Fig. 2) can suggest new hypothe-
ses for ecosystem function.

The spatial slope of $R_{\text{eco}}$ to GEP (0.64) for southwest
North American semiarid ecosystems (Fig. 4) was
smaller than that reported in several prior studies
(−0.7 to 0.9) (Law et al., 2002; Baldocchi, 2008; Lasslop
et al., 2010; Chen et al., 2015). It was more similar to that
found in a recent synthesis across eddy covariance sites
in China (0.68) with greater representation of semiarid
ecosystems (Yu et al., 2013). One possible explanation
for the lower spatial slope found here is that this study
represents a period of drought in southwestern North
America (Seager & Vecchi, 2010; Scott et al., 2015) dur-
ing which ecosystem respiration is elevated relative to
productivity (Van der Molen et al., 2011; Scott et al.,
2015). Therefore, the drier sites often functioned as car-on sources to the atmosphere (Fig. 4), increasing the
vertical intercept and reducing the slope of the spatial
relationship. Although there has been discussion in the
literature about spurious correlation between $R_{\text{eco}}$
and GEP, a recent analysis of FLUXNET sites found a similar
relationship between these two fluxes ($R_{\text{eco}} = 0.71\text{GEP} + 153$, $R^2 = 0.76$) and showed that
most of their correlation was not spurious, especially
for annual sums (Baldocchi et al., 2015).

Relationships of NEP with interannual and climatic
differences in available water

Our results show that semiarid NEP depends on how
water availability drives counteracting responses in
productivity and respiration, both spatially and tempo-
 rally. The spatial relationship of $R_{\text{eco}}$ with GEP (Fig. 4)
intersects the 1:1 line at $\sim315 \text{ gCm}^{-2} \text{ yr}^{-1}$, suggesting
that sites with average productivity above
315 gCm$^{-2} \text{ yr}^{-1}$ tended to function as net CO$_2$
sinks ($R_{\text{eco}} < \text{GEP}$), while those sites below this productivity
threshold tended to be sources ($R_{\text{eco}} > \text{GEP}$). We calcu-
late a similar source/sink threshold at a productivity of
$\sim250 \text{ gCm}^{-2} \text{ yr}^{-1}$ in the ChinaFlux dataset of Yu et al.
(2013). Our productivity threshold of 315 gCm$^{-2} \text{ yr}^{-1}$
corresponds to a climatic water availability of $\sim255$ mm
(Fig. 3b), illustrating why NEP tended to switch from
negative to positive near this value of ET (Fig. 5a).
Mass conservation precludes the driest sites from func-
tioning indefinitely as carbon sources, and caution
should be applied in extrapolating these results, which
represent a period of drought in southwestern North
America (Seager & Vecchi, 2010; Scott et al., 2015).
Drought may shift a number of long-lasting constraints
such as plant community and soil carbon pools, possi-
ble reducing GEP and increasing $R_{\text{eco}}$ (Van der Molen
et al., 2011), similar to the ‘disturbance offset’ suggested
in other multisite flux data syntheses (Baldocchi, 2008;
Chen et al., 2015).

Using the empirical approach shown in Fig. 2 and
the combined observations from the 21 sites, we find
that NEP was equally sensitive to interannual varia-
tions in water availability and differences in average
climatic water availability (Fig. 6). First we posit a
change, which could be positive or negative, of 100 mm
in available water, estimated from ET. For the case
where the change represents interannual weather varia-
tion (Fast pathway), we use the temporal slopes of GEP
to ET and $R_{\text{eco}}$ to GEP. Temporal variation of 100 mm
in available water is predicted to change GEP by
146 gCm$^{-2} \text{ yr}^{-1}$, of which 56% is counteracted by
$\Delta R_{\text{eco}}$ within the same year, resulting in predicted
$\Delta$NEP magnitude of 64 gCm$^{-2} \text{ yr}^{-1}$. For a difference in
climatic water availability (slow pathway), we use the
spatial slopes, which predict $\Delta$GEP of $179 \text{ gCm}^{-2} \text{ yr}^{-1}$,
64% of which is counteracted by long-term mean respi-
ration, resulting in the same predicted $\Delta$NEP magni-
tude of $64 \text{ gCm}^{-2} \text{ yr}^{-1}$. This result (Fig. 6) contrasts
with our initial expectation that NEP would be more
sensitive to climatic shifts than to interannual variation,
inferred from steeper spatial than temporal slopes in
precipitation–productivity relationships (Hsu et al.,
2012; Sala et al., 2012; Jin & Goulden, 2014). Our pre-
dicted NEP sensitivity to water falls within the range
estimated from models and atmospheric inversions
over Australia, 25–100 gCm$^{-2} \text{ yr}^{-1}$ per mm (deviation
from mean growing season P) (Poulter et al., 2014), pro-
viding terrestrial observation-based support for the
idea that semiarid region NEP dominates the interan-
nual variability of global atmospheric CO$_2$ (Ahlström
et al., 2015).

We are cautious about extrapolating the NEP
responses predicted in Fig. 6. The results represent a
specific region and time period, as mentioned above.
Furthermore, we employ a space-for-time substitution
assuming that water availability is the main driver of
differences in ecosystem CO$_2$ cycling in space and time,
and we cannot account for future climatic changes not
represented by our climatic and ecological gradient.
Notably, changes in atmospheric temperature, vapor
pressure deficit (VPD), and CO$_2$ concentration could
influence plant community structure or alter GEP by
changing leaf-level water-use efficiency (Morgan et al.,
2007; Donohue et al., 2013; Keenan et al., 2013; Friend
et al., 2014). Here, we found no relationship between

Because CO₂ exchanges showed common spatial and temporal relationships to water availability, most of the unexplained NEP variation was related to slow (i.e., persisting throughout the observation years) site-specific offsets from the spatial relationships (Fig. 5b, offsets for each site shown in Table S1). We detected no associations between offsets and mean annual temperature, vapor pressure deficit, seasonality of precipitation, or plant functional type. Although complex terrain can pose challenges for eddy covariance measurement and data processing (Baldocchi, 2008), we detected no association of site offsets with elevation or with sites described in the literature as having somewhat complex terrain (see Table 1 for literature references). Errors in partitioning of NEP into its component fluxes could contribute to offsets, but offset magnitude at many sites (up to 50–70%) exceeded expected systematic partitioning errors (~10%) (Desai et al., 2008; Lasslop et al., 2010). Many of the largest offsets suggested associations with site demography and history, supporting the ‘disturbance offset’ concept (Baldocchi, 2008; Chen et al., 2015). For example, the most positive GEP offsets were associated with disturbances that killed some plants without changing the biome type (Fig. S2, Table S1, sites fmf, emg), consistent with demographic shifts toward younger plants during recovery from moderate disturbance (Baldocchi, 2008; Amiro et al., 2010). A stand-replacing chaparral fire was associated with a change in GEP offset from positive to negative (so2, so2B), consistent with reductions in stem density, leaf area, and root development. At the high-elevation sites vcm and nr1, negative GEP offsets could be due to snow sublimation, which reduces the fraction of water available to support photosynthesis. In the carbon balance regulating NEP, the most positive Reco offset relative to GEP (Figs 4 and S4, Table S1) was associated with drought at scw, where plant mortality likely reduced photosynthesis while increasing substrate for heterotrophic respiration (Harmon et al., 2011). The chaparral site (so2) Reco offset switched from positive to negative following wildfire (so2B), possibly because combustion reduced the carbon pools available to support long-term average respiration. At vcm, a negative Reco offset could indicate asynchrony of temperature and water limitations on respiration at this high-elevation, seasonally dry site, or respiration inhibition related to elevated nitrogen deposition (Janssens et al., 2010).

Directions for future work to improve understanding of terrestial CO₂ exchanges

While offsets at some sites were consistent with plausible causes (Table S1), a rigorous analysis was precluded because these sites, like many others, lack consistent observations of slow factors likely to regulate offsets (Fig. 2) (Litton et al., 2007; Baldocchi, 2008; Tang et al., 2014). Studies based on coordinated flux mesonetworks deployed across forest age gradients offer a valuable counterexample (Amiro et al., 2010), but a greater number and diversity of sites reporting nonflux observations are needed to support inferences about slow-changing controls from synthesis studies. Alternatively, very long term records at a site may reveal shifts in mean flux relationships, such as water-use efficiency (Keenan et al., 2013). We expect maturing datasets in semiarid ecosystems may be promising for such site-based study, because the slow factors likely driving site offsets (Fig. 2) tend to change more frequently and
rapidly in semiarid ecosystems than in forests (e.g., drought alters grassland species assemblage (Moran et al., 2014), recurrent fire alters chaparral biomass pools (Keeley, 1986)).

Our results support the use of ecosystem-scale ET to represent water availability, although it remains an imperfect proxy. As compared with precipitation, ET showed a stronger relationship with GEP (Fig. 3). In eddy covariance studies, ET is measured using the same instruments and methodology as the CO₂ exchanges, and represents the same spatial footprint, whereas precipitation measurements involve different instrumental challenges and assumptions (Rasmussen et al., 2012; Shuttleworth, 2012). Use of ET instead of P removed hydrologic losses from the estimated water availability (Eqn 2). Although Q likely varies with terrain, soils, and the within-year distribution of precipitation events, our results confirm that losses increase in wetter years and at wetter sites, impacting both spatial and temporal models of productivity (Fig. 3). Further advances in understanding of hydrologic controls on ecosystem CO₂ exchanges depend on quantifying how precipitation is partitioned among hydrologic losses, transpiration, and abiotic evaporative losses (Newman et al., 2006).

The spatial–temporal empirical framework used here (Fig. 2) integrates several decades of ecological thought on fast and slow factors controlling productivity with the promising field of whole-ecosystem carbon and water flux observations. We suggest this approach of maintaining site identity could be employed in cross-site synthesis studies whenever sufficient data exist to quantify site mean fluxes and site-level temporal relationships. Although robust statistical treatment of individual sites is challenging when site records are relatively short (~10 years), inferences about ecosystem function may be drawn from the collective patterns of site-level temporal relationships across gradients of important drivers (Huxman et al., 2004). There is a need to compare the results of the present study across global networks of long-term eddy covariance sites, including for controls other than water and/or nonlinear relationships. Separation of fast and slow controls across broad networks of ecosystem measurements should enable learning about timescales of important factors regulating ecosystem function, informing priorities for observation and improving predictive ecosystem models.

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Author contributions

J.A.B., R.L.S., and M.L.G. conceived the study. J.A.B. assembled the data, produced preliminary results, and wrote the manuscript. All authors analyzed data, contributed to the interpretation of results, and helped revise the manuscript. The authors declare no conflict of interest.

References


Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Climate for the region and the 21 sites.
Figure S2. Relationships of GEP with ET, as in Main Text Fig. 3b, with site codes added.
Figure S3. Relationships of Reco with ET.
Figure S4. Relationships of Reco with GEP, as in Main Text Fig. 4, with site codes added.
Table S1. Site disturbance histories and site offsets from spatial relationships.