The carbon balance pivot point of southwestern U.S. semiarid ecosystems: Insights from the 21st century drought

Russell L. Scott¹, Joel A. Biederman¹, Erik P. Hamerlynck², and Greg A. Barron-Gafford³,⁴

¹Southwest Watershed Research Center, USDA-ARS, Tucson, Arizona, USA, ²Eastern Oregon Agricultural Research Center, USDA-ARS, Burns, Oregon, USA, ³School of Geography and Development, University of Arizona, Tucson, Arizona, USA, ⁴B2 Earthscience, Biosphere 2, University of Arizona, Tucson, Arizona, USA

Abstract Global-scale studies indicate that semiarid regions strongly regulate the terrestrial carbon sink. However, we lack understanding of how climatic shifts, such as decadal drought, impact carbon sequestration across the wide range of structural diversity in semiarid ecosystems. Therefore, we used eddy covariance measurements to quantify how net ecosystem production of carbon dioxide (NEP) differed with relative grass and woody plant abundance over the last decade of drought in four Southwest U.S. ecosystems. We identified a precipitation “pivot point” in the carbon balance for each ecosystem where annual NEP switched from negative to positive. Ecosystems with grass had pivot points closer to the drought period precipitation than the predrought average, making them more likely to be carbon sinks (and a grass-free shrubland, a carbon source) during the current drought. One reason for this is that the grassland located closest to the shrubland supported higher leaf area and photosynthesis at the same water availability. Higher leaf area was associated with a greater proportion of evapotranspiration being transpiration (T/ET), and therefore with higher ecosystem water use efficiency (gross ecosystem photosynthesis/ET). Our findings strongly show that water availability is a primary driver of both gross and net semiarid productivity and illustrate that structural differences may contribute to the speed at which ecosystem carbon cycling adjusts to climatic shifts.

1. Introduction

Even though the average magnitude of biosphere-atmosphere carbon dioxide exchange in semiarid regions is small compared to more mesic grasslands and forests [Xiao et al., 2014], the contribution of these expansive semiarid regions is substantial and dominates the trend and interannual variability in the global land carbon sink [Ahlstrom et al., 2015]. For example, strong annual net carbon uptake in Southern Hemisphere semiarid lands as a response to La Niña-driven enhanced precipitation evidently played a substantial role in the unusually large global sink in 2011 [Poulter et al., 2014]. This was attributed both to the prior years of rapid alterations in semiarid vegetation cover and a strong and potentially growing sensitivity to forcing changes like precipitation [Pacala et al., 2001; Poulter et al., 2014]. Such a significant impact on the annual land carbon sink prompts the question of how long such increases in carbon storage persist after the precipitation returns to normal. In other words, how quickly does the net carbon exchange in semiarid areas respond to annual- to decadal-scale fluctuations in precipitation, and how soon does it reach a new equilibrium? Similarly, do the well-documented shifts in semiarid vegetation composition such as the recent proliferation of woody plant species into semiarid grasslands or the replacement of native species with exotic species [e.g., Noble, 1997; Van Auen, 2000; Wilcox et al., 2012] make these ecosystems’ carbon exchange more or less responsive to short- and long-term changes in precipitation?

For much of the last two decades, drought conditions have prevailed over the semiarid southwestern United States [Dai, 2013]. This “21st century drought” has varied in severity and location across these years resulting in a myriad of regional challenges for natural and human-dominated systems, such as water shortages, forest mortality, and wildfires [e.g., Barnett and Pierce, 2008; Bresehers et al., 2005; Mcauliffe and Hamerlynck, 2010; Westerling and Bryant, 2008]. Climate models have suggested the characteristics of this drought, including the prevalence of reduced winter precipitation and higher air temperatures, may represent a “new normal” [McAfee and Russell, 2008] and that this region will experience even more severe and protracted drought in the future [Cayan et al., 2010]. We do not know how the current drought, let alone predicted increased desiccation, has altered carbon exchange in this region [Archer and Predick, 2008; van der Molen et al., 2011].
Water is the dominant control on ecosystem carbon exchange in dryland regions [Noy-Meir, 1973]. Droughts change both ecosystem structure and functioning: shorter periods of high drought intensity in the early 2000s, embedded in the current long-term drought in the Southwest U.S., have induced extensive forest mortality [Williams et al., 2010], die-offs of native grasses and desert shrubs [McAuliffe and Hamerlynck, 2010; Polyakov et al., 2010], and altered productivity response to precipitation in semiarid grasslands that had significant mortality [Moran et al., 2014]. Studies on the relationship between productivity and precipitation indicate that rain use efficiency (the amount of productivity for a given amount of precipitation) increases for drier years and at drier sites [Huxman et al., 2004; Jin and Goulden, 2014], implying that ecosystems are more productively efficient in their water use during droughts. Ecosystem flux results quantifying net ecosystem production of carbon dioxide (NEP) point to a more rapid and less lagged response in semiarid grasslands than shrublands or savannas to fluctuations in water availability, possibly due to a faster turnover of herbaceous biomass pools [Emmerich and Verdugo, 2008; Kurc and Small, 2007; Scott et al., 2010, 2009]. Moreover, the NEP of many different semiarid ecosystem types such as shrublands [Luo et al., 2007; Petrie et al., 2014], grasslands [Ma et al., 2007; Scott et al., 2010], savannas [Scott et al., 2009], and desert scrub [Bell et al., 2012] throughout southwestern North America show high sensitivity to precipitation fluctuations with a tendency for being sources of carbon dioxide to the atmosphere during the dry years and carbon sinks in wet years. This implies a precipitation “pivot point” where the net carbon exchange for semiarid ecosystems may pivot between source and sink behavior.

In this paper, we characterize the response of the biosphere-atmosphere exchange of carbon dioxide to water availability across four Southwest U.S. semiarid ecosystems varying in relative shrub, tree, and grass abundance. We quantify (1) where the precipitation pivot point between net annual carbon source and sink lies in relation to current and predrought water availability and (2) how distinct semiarid plant community structure shapes their response to interannual precipitation variation through this prolonged early 21st century drought. We used eddy covariance observations of water vapor and carbon dioxide exchange collected over the last 7 to 11 years from distinct semiarid plant communities in southern Arizona, USA. These ecosystems represent a vegetation mosaic of shrublands, savannas, and grasslands found throughout the warm Sonoran and Chihuahuan Deserts of southwestern North America. In contrast to models, coarse-scale atmospheric inversions or satellite estimates of productivity, our data sets allow in-depth examination of the responses of NEP, and its component fluxes of gross ecosystem photosynthesis (GEP) and ecosystem respiration ($R_{eco}$), to variations in water availability. Shorter-term (1–5 years), site-based studies have yielded important results, but our maturing flux network data sets offer a new opportunity to assess annual-scale NEP response to water across a gradient of plant community structure that illustrate the value of long-term data collection [Moran et al., 2008b].

We test the hypothesis that the 21st century drought would cause a tendency for these southwestern ecosystems to be losing carbon accumulated in the wetter, previous decades. Moreover, we test the hypothesis that the magnitude of net carbon loss would be smaller in ecosystems with greater relative abundance of herbaceous, rather than woody, plants due to a faster adjustment of carbon pools to drought. Finally, we examined whether vegetation structure influences the ecosystem functional response to water availability at the annual to decadal timescales relevant to global carbon cycling.

2. Methods
2.1. Sites
The four southern Arizona sites used in this study represent common semiarid ecosystem types—grasslands, savannas, and shrublands—resulting from land cover change due to woody plant expansion. Climate at the sites (Table 1) is typical of the warm, dry conditions prevalent across the lower elevation regions of the Southwest. With long-term mean annual precipitation ranging from 320 to 420 mm and an annual air temperature of about 18°C, they have precipitation amounts that occur most frequently across the U.S. and air temperatures at the warmer end of the spectrum although this region is outside the climate space norm sampled by many Ameriflux sites (Figure S1 in the supporting information).

Two of the sites are 5 km apart and located on the University of Arizona’s Santa Rita Experimental Range, established in 1903 and located ~45 km south of Tucson, AZ [Sayre, 2003]. The first site, Santa Rita Mesquite Savanna (“sav-s” hereafter), is a semiarid grassland that has been encroached by the native tree, velvet mesquite (Prosopis velutina), over the last century. The site now consists of about 35% mesquite tree...
canopy cover, with intercanopy and undercanopy vegetation consisting mainly of native and exotic perennial warm season grasses with 15% plant cover that can dramatically increase with annual forbs and grasses during the rainy season. The Santa Rita Grassland ("gra-s") site is a pasture established after all mesquite were killed by herbicide application in 1957; it now has 11% mesquite cover and is dominated by the South African warm season bunchgrass, Lehmann Lovegrass (Eragrostis lehmanniana).

The other two sites, the Lucky Hills Shrubland ("shb-w") and Kendall Grassland ("gra-w"), are separated by about 10 km and located within the U.S. Department of Agriculture Agricultural Research Service (USDA-ARS) Walnut Gulch Experimental Watershed established in 1954 and located ~80 km east from the Santa Rita sites [Moran et al., 2008a]. The desert shrubland, shb-w, has a large diversity of shrubs that are typically found throughout the Sonoran and Chihuahuan Deserts. There is negligible perennial grass presence at this site, and there is little infilling of the bare intershrub spaces with annual grasses or forbs in the rainy season.

For our analysis, we used a "hydrologic year" of 1 November to 31 October to accommodate the seasonal cycles of precipitation and temperature such that precipitation falling within the hydrologic year was mainly used within that year as evapotranspiration (ET). In this region, dry and cool conditions are usually established by early November, and most of the vegetation has senesced or entered dormancy. Any winter precipitation evaporates or is stored as soil moisture that supports a limited spring growing season beginning in February or March and lasting 3–6 weeks until soil moisture is depleted [Scott et al., 2000]. May and June are predictably dry and hot. The summer growing season begins with the North American Monsoon rainfall that typically commences in July and ends mid-September. Sporadic but substantial rainfall can occur in association with remnant tropical storms from September to mid-October.

### 2.2. Measurements

At each site, the eddy covariance technique was used to measure ecosystem-scale carbon dioxide, water vapor, and energy fluxes. Measurements began in 2004 at sav-s and gra-w, in 2007 at shb-w, and 2008 at...
We installed instrumentation on tripods or towers to measure all variables needed to quantify 30 min averages of net ecosystem production of CO₂ (NEP), evapotranspiration (ET), air temperature (\(T_{\text{air}}\)), vapor pressure deficit, air pressure, photosynthetically active radiation (PAR), shortwave and net radiation, soil moisture, and precipitation. NEP is an ecosystem-centered metric of net CO₂ flux whereby a positive value represents a net uptake and a negative value indicates a net release of CO₂ by the ecosystem. We discovered a specific instrumental bias in the sensitivity of each particular open-path infrared gas analyzer (IRGA, LI-7500, Li-Cor Inc.) by using side-by-side tests with other open-path and closed-path IRGAs. To correct for this bias and ensure comparability across the sites, we multiplied the 30 min vertical wind and CO₂ density covariance with a bias correction factor determined individually for each IRGA by comparison with a closed-path analyzer (for more information on this correction, please see the supporting information).

The number of gaps across all years in the supporting meteorological data at the sites was small, usually less than 1% of all the 30 min periods in each study period year. With the exception of precipitation, these data were not gap filled to compute annual averages. All sites have redundant precipitation gauges on separate data loggers located either at the sites or within ~1 km of them. Differences in seasonal to annual totals between the paired gauges were less than ~10 mm or 3%. In the case of failed primary gauge measurements, data from the other gauge were used to fill the gaps so that annual precipitation sums were gap free.

The flux data were filtered for spikes, instrument malfunctions, and poor quality (representing ~7–11% of the ET and NEP data). The rejection criteria used to screen data were rain events, out-of-range signals, and spikes with the standard deviation of [CO₂], [H₂O], and/or sonic temperature greater than 2 standard deviations from the mean determined on a yearly basis.

Daily ET was calculated by first filling the gaps in the 30 min data using 14 day moving-average lookup tables of ET and incoming PAR, averaged over 100 μmol m⁻² s⁻¹ intervals [Falge et al., 2001] and separated into morning and afternoon periods. Linear interpolation was used to fill any multiday gaps.

We partitioned NEP into gross ecosystem photosynthesis (GEP) and ecosystem respiration (\(R_{\text{eco}}\)) by first eliminating NEP data when the friction velocity, \(u^*\), was less than 0.15 m s⁻¹ [Scott et al., 2010, 2009]. We then fit an exponential function of air temperature to the remaining nighttime NEP data over a moving ~5 day window [Reichstein et al., 2005], with varying window sizes to ensure data from pre-storm (dry) periods were not grouped together with post-storm data, since precipitation events result in immediate respiration pulses that change the relationship between temperature and nighttime NEP [Xu et al., 2004]. The resultant exponential functions were used to fill missing nighttime NEP data and model daytime \(R_{\text{eco}}\). Missing daytime NEP values were filled using a second-order polynomial of incoming PAR fit to separate morning or afternoon data for the 5 day moving window; this procedure produced better fits of NEP to PAR than commonly used higher-order light response models [Lasslop et al., 2010]. Finally, we calculated GEP as GEP = \(R_{\text{eco}}\) + NEP. GEP and \(R_{\text{eco}}\) are always positive with this sign convention.

Using a function that depends on the number of missing observations, we computed the total random error in yearly NEP that accounted for random measurement error [Richardson and Hollinger, 2007; Richardson et al., 2006] and gap-filling error [Dragoni et al., 2007]. The error in yearly sums was around ±3.0 g C m⁻² yr⁻¹ with little variation across the sites and years. Systematic errors due to site-specific biases, instrumentation, measurement technique, and calculations are expected to be larger but are relatively unknown [Lasslop et al., 2010]. However, we expected that systematic errors would tend to persist across sites and years within the same measurement network, and therefore, they should not seriously affect site-level interannual patterns [Baldocchi, 2008; Lasslop et al., 2010]. Total uncertainty in yearly NEP using eddy covariance is estimated to be around ±10–30% [Goulden et al., 1996; Hagen et al., 2006; Loescher et al., 2006; Moffat et al., 2007]. To validate the open-path IRGA methodology and bias correction employed in our study, we conducted multiple yearlong comparisons of our open-path instrumentation with parallel closed-path IRGA instrumentation and found good agreement in aggregated daily and yearly sums (annual NEP within ±10 g C yr⁻¹) after bias corrections (Table S1).

We used the NASA Moderate Resolution Imaging Spectroradiometer (MODIS) leaf area index (LAI) [Oak Ridge National Laboratory Distributed Active Archive Center, 2015] product to quantify the seasonality and variation in green leaf area at the sites (Table 1). The index is computed every 16 days at 1 km resolution. Only a handful of sporadic ground-based observations of LAI have been made at these sites throughout the years, but the magnitude and variation of these values are similar to the range and variability in the MODIS data.
2.3. Evapotranspiration as a Measure of Water Availability

Below we use ET as a proxy for ecosystem water availability (WA) when looking at the functional link between WA and productivity. ET is the preferred quantification of WA in this analysis of annual data for a number of reasons. First, the seasonal timing of GEP and ET are generally in phase, whereas other direct measures of water availability, like soil moisture, can be out of phase with these fluxes, especially during winter. Hence, ET captures when soil moisture becomes available to drive ecosystem fluxes. Second, ET is measured at the same spatial scale as the carbon flux. Third, using ET rather than P accounts for any hydrological losses (i.e., runoff and drainage) from the system that do not wet or stay in the near-surface soil and thereby become available to influence ecosystem C fluxes measured at this spatial scale [Scott, 2010].

3. Results

3.1. The Southwest Drought and Ecosystem Fluxes

The current drought in the Southwest began in the mid-1990s and was preceded by a wetter than average period in the 1980s to early 1990s (Figure 1a). Across the region, annual and cool season (November–March, in parentheses) precipitation averages for the periods 1978–1994 and 1995–2014 were 425 (177) and 326 (108) mm yr$^{-1}$, respectively. Thus, the current drought has had a greater relative reduction in cool season (~39%) than warm monsoon (~12%) rainfall. The flux measurements span a 6–10 year period characterized by a 12–20% decrease in precipitation relative to the preceding 30 years (Figure 1b), but importantly, these sites had already experienced around a decade of drought before eddy covariance measurements began (Figure 1a). Regional air temperatures were also warmer during this period by about 0.6°C or a 3% increase (data not shown) compared to the preceding 30 years.

The study sites were located in a similar hydroclimatological setting, although there were small differences in meteorological conditions (Table 1). As expected, temperatures were slightly lower at the higher-elevation sites. Precipitation differences among sites were not significant due to large interannual variability (Figure 2), but their ranking (shb-w < gra-w < sav-s < gra-s) was consistent with longer-term averages (Table 1). ET was significantly higher at the Santa Rita sites (sav-s, gra-s, Figure 2) where local topography is flatter and surface runoff is lower due to more permeable loamy sand soils and less developed channel networks [Scott, 2010].
Annual ET/P decreased similarly at each site as hydrological losses, quantified meteorologically by P-ET, were found to increase at all sites with increasing P (data not shown). Every site varied between annual carbon source and sink functioning during the study period, predicted in large part by annual precipitation (Figure 3). Seasonal climatology and ecosystem responses were relatively consistent across the sites. For example, the “wet” monsoon year of 2014 and the El Niño-driven wet cool season precipitation year 2010 resulted in increased NEP across all sites. Conversely, poor monsoon years of 2009 and 2011 reduced NEP amounts. Variation in cross-site mean NEP was less than site-level cross-year NEP ($\sigma = 17$ and $50 \text{ g C m}^{-2} \text{ yr}^{-1}$, respectively). Annual NEP averages and standard deviations were shb-w = $-19 \pm 27$, gra-w = $18 \pm 52$, sav-s = $13 \pm 53$, and gra-s = $13 \pm 69 \text{ g C m}^{-2} \text{ yr}^{-1}$. These differences in means were not statistically significant.

### 3.2. Ecosystem Carbon Balance and Precipitation

We defined the precipitation pivot point ($P_p$) for net carbon exchange as the precipitation amount where the predicted NEP of an ecosystem is zero (open circles, Figure 4). This $P_p$ was closer to the mean precipitation of the study period ($P_{study}$) and well below the previous 30 year average ($P_{hist}$) for all but the shrubland site, shb-w, which had no grass cover. The relative positions of $P_{study}$ and $P_p$ indicate that in a year with a precipitation amount equal to the average precipitation of 21st century drought, we would predict that
shb-w would be a carbon source (i.e., NEP < 0), while the other three sites would be carbon sinks. The pivot point offset ($P_{\text{study}} - P_p$) was negative at shb-w and similarly positive at the other three sites. Grass-free shb-w was the only site with a negative offset (Figure 5).

### 3.3. Functional Relationships

In order to better understand how differences in water availability and ecosystem structure may have impacted NEP, we examined the functional relationships between ET and GEP and $R_{\text{eco}}$. Annual ET was closely coupled with GEP (Figures 6a and 6c). Site relationships were linear, and ET as a predictor explained a significant amount of the temporal variance. Compared to ET, precipitation explained about 23% less of the variance in GEP, most likely due to variable hydrologic losses (data not shown). Likewise, GEP was closely coupled with $R_{\text{eco}}$ (Figures 6b and 6d). Slopes were around 0.5, indicating that GEP was much more sensitive than $R_{\text{eco}}$ to fluctuations in annual water availability. Pooling all data together, $R^2 = 0.92$ ($p < 0.001$) for ET:GEP and 0.85 ($p < 0.001$) for GEP: $R_{\text{eco}}$. Individual site slopes and intercepts for both relationships shown in Figure 6 did not significantly differ, but there were two notable differences in the paired-site comparison. First, differences in mean NEP at the Walnut Gulch sites between gra-w (18 g C m$^{-2}$ yr$^{-1}$) and shb-w (−19 g C m$^{-2}$ yr$^{-1}$) appear due to a higher productivity for a given water availability rather than more $R_{\text{eco}}$ for a given GEP. Second, even though there was more $R_{\text{eco}}$ for a given GEP at gra-s than sav-s for the Santa Rita pair, there was no net effect on mean NEP (which is equivalent at these sites) because gra-s had higher water availability, which increased GEP.

---

**Figure 4.** Hydrological year precipitation (x axis) and NEP (y axis) for all four sites. The ecosystem carbon balance pivot point (open circle, ±95% CI thick line), average precipitation ($P_{\text{study}}$) for the measurement period, and precipitation for the preceding 30 year period ($P_{\text{hist}}$) are also indicated.

**Figure 5.** Total woody and perennial grass cover (bars) and pivot point offset ($P_{\text{study}} - P_p$ line) at the study sites. Grass cover at shb-w is zero.
All sites had large positive x-axis intercepts for ET:GEP, indicating a substantial amount of ET does not support plant photosynthesis (Figures 6a and 6c). We interpreted this as an estimate of a site’s average abiotic evaporation, $E$, via bare soil or canopy interception. Average $E$, estimated by this method, was similar across the sites ($E = 117 \pm 48$ to $155 \pm 64$ mm yr$^{-1}$, 95% confidence interval (CI)) despite the larger ET differences, indicating a greater proportion of $E$ at the drier sites. By subtracting a site’s estimated $E$ from mean ET, we calculated an average transpiration efficiency, $T/ET$, of 0.46 for shb-w, 0.55 for gra-w, 0.62 for sav, and 0.58 for gra-s. These differences were not significantly different from each other given the uncertainty in the estimates of $E$. We found significant differences in mean annual ecosystem water use efficiency ($WUEe = GEP/ET$) between the sites with shb-w = 0.59$^a$, gra-w = 0.85$^b$, sav-s = 1.01$^{bc}$, and gra-s = 1.11$^c$ (nondiffering site means share the same superscript, analysis of variance, Tukey’s honestly significant difference criterion, $\alpha = 0.05$). Annual WUEe was positively related to both ET and LAI (Figure 7, $R^2 = 0.66$ and 0.86, respectively). WUEe decreased in drier years and at drier sites, with gra-w having a higher WUEe for a given ET than shb-w (Figure 7a). As the grassland had a higher LAI for a given water availability, LAI resulted in a better predictor of WUEe than ET (Figure 7b).

4. Discussion

4.1. Pivot Point of Ecosystem Carbon Balance in Relation to Current and Past Rainfall

The current widespread drought conditions over the Southwest began for southern Arizona in the mid-1990s (Figure 1). For the four study sites this has meant a 10–20% reduction in precipitation in comparison with the previous 30 year period, which was wetter than average compared to the long-term mean. Over the last decade, mean annual NEP was small but consistently varied at all sites between positive and negative totals (Figure 3). This switching between source and sink behavior, respectively, related to annual water availability is quite unusual compared to the more frequently measured forest sites [Luyssaert et al., 2007]. The prevalence of more consistent sink behavior from one year to the next in many parts of the world, especially temperate, North American and European forests, has been attributed to a lack of water limitation and disturbance history, which maintain the forest in a more active, early successional growth stage. Because drylands experience such large interannual variability in total precipitation, even within extended dry periods, they may be more responsive to changes in water availability by rapid adjustments of surface conductance via changes in LAI, altered leaf-level stomatal opening, and/or the degree of activity and
abundance by annual plant species, which in turn modifies carbon, and other important nutrient pools [Chesson et al., 2004; Schwinning and Sala, 2004].

Our expectations were that 21st century drought would result in a tendency for southwestern U.S. ecosystems to be losing the carbon that likely accumulated in the wetter previous multidecade period. Instead, we found both positive and negative annual NEP amounts at all sites (Figure 3) and that three of our four sites could be expected to function as net carbon sinks when annual precipitation equals the current drought period average (Figure 4). There are many other confounding environmental factors like the seasonal distribution of precipitation and variations in climate forcing that influence the GEP and $R_{eco}$ that determine NEP [Hamerlynck et al., 2013; Scott et al., 2009]. Nevertheless, annual $P$ explained from 48 to 88% of the variability in annual NEP at our sites. We also hypothesized that ecosystems with greater amounts of herbaceous and less woody biomass would tend to have higher NEP due to a faster adjustment of carbon pools to drought. On this we found only limited support. For the case of the Walnut Gulch sites, the pivot point offset, defined as the difference between the current mean precipitation, $P_{study}$ and carbon balance pivot point, $P_p$, was positive at gra-w and negative at shb-w with big differences in woody and grass cover between them. For the Santa Rita sites, there was little difference in the pivot point offset, but both of these sites were more structurally similar and have a significant herbaceous component.

We propose that the pivot point offset tells us about adjustments of ecosystem carbon stocks to the current long-term drought, such that positive offsets indicate that an adjustment has already occurred and negative offsets indicate a lack of adjustment. An adjustment could be described as a two stage processes [van der Molen et al., 2011]. First, a decrease in mean annual precipitation would cause plants to die or shed organs, reducing photosynthetic capacity and increasing dead biomass. Second, dead biomass would serve as substrate for a pulse of elevated $R_{eco}$ (relative to GEP) that could last years to decades. When the carbon stocks supporting the respiration pulse have diminished, NEP returns to a new quasi-equilibrium between precipitation, GEP, and $R_{eco}$.

Every biome is expected to have its characteristic drought response timescale over which these two adjustment steps occur, depending on factors like climate, vegetation structure, and edaphic conditions [Vicente-Serrano et al., 2013]. Although we cannot resolve the exact speed, we can infer that for all sites except the shrubland such adjustment of carbon pools occurred in less than 10 years, the time between the onset of the current drought and the measurement period for this study. There are many reasons that would support the shrubland, with very little perennial grass or annual forb and herbaceous production, adjusting more slowly to the drought (Figure 5). First, the plant carbon stocks are much greater and more recalcitrant in the shrubland. Cox et al. [1986] compared the shb-w and gra-w sites and found that the shrubland had seventeenfold and fivefold higher aboveground and belowground biomass, respectively, and that 80% of the belowground biomass was coarse roots in the shrubland compared to 5% in the grassland. These differences in above and belowground biomass do not result from a difference in gross productivity but rather a much slower turnover of the more recalcitrant plant C pools. Second, shrub cover changes much more slowly in response to precipitation variations and disturbance compared to perennial bunchgrasses and annuals [Bonet and Pausas, 2004; Munson et al., 2013]. Gross carbon fluxes for a shrubland site in New Mexico were much less variable across a wet to dry transition than a neighboring grassland site indicating a less rapid adjustment.
to precipitation changes [Kurc and Small, 2007; Petrie et al., 2014]. Finally, the current drought has been characterized by cool season precipitation deficits that likely are more detrimental to woody plants than grasses and could prolong either one, or both, of the adjustment processes [McAuliffe and Hamerlynck, 2010; Munson et al., 2013; Petrie et al., 2014].

4.2. Water Availability Drives Ecosystem Functional Responses

Annual ET explained 82–96% of the variability GEP (Figures 6a and 6c), suggesting that current-year water availability is a strong predictor of annual productivity. Other environmental drivers like precipitation/productivity legacies [Sala et al., 2012] and precipitation event size and distribution [Fay et al., 2003; Knapp et al., 2008] have also been shown to affect plant productivity in semiarid regions, but our results suggest that these are considerably less important at the annual scale. One reason for this is our use of ET as a proxy for water availability rather than the commonly used variable $P$ which neglects hydrologic losses. However, real lags between precipitation and productivity that may impart legacy effects may also be partially masked by using ET as ET more carefully tracks when soil moisture storage is accessed and becomes available to support plant growth.

Slopes of GEP:Reco indicated that in wetter years, about 50% of increased GEP was offset by Reco, and the rest augmented NEP (and vice versa for drier years, Figures 6b and 6d). This explains the strong sensitivity of annual NEP to $P$ (Figure 4) and mirrors the stronger sensitivity of ecosystem photosynthetic assimilation than respiration to drought found in many regions of the world [e.g., Schwalm et al., 2010]. Baldocchi et al. [2015] found a similar strong correlation for the annual GEP:Reco relationship across a global FLUXNET database ($R_{\text{eco}} = 0.71\text{GEP + 153}, R^2 = 0.76$) and showed that most of this correlation was not spurious created when partitioning NEP, especially if annual sums are used. We found considerably smaller slopes with both smaller and larger intercepts for our site-based relationships (Figures 6a and 6c), but pooling all the data yielded a good agreement with the slope but not the offset ($R_{\text{eco}} = 0.73\text{GEP + 67}, R^2 = 0.85$) compared to the more global relationship. More work is needed to examine these across time and space relationships using longer (>5 year per site) and bigger data sets.

While the similar slopes of the ET:GEP lines suggest a similar sensitivity of productivity to changes in water availability (Figures 6a and 6c), annual ecosystem water use efficiency (WUEe = GEP/ET) differed between the sites. As the fitted relationships had nonzero y intercepts, the ET:GEP slope and WUEe are not equivalent [Verón et al., 2005]. Annual and mean WUEe increased with water availability, implying a more efficient ecosystem use of water in wetter years and at wetter sites (Figure 7). We propose that these differences were due in part to the differences the relative proportion of ET not accessible by plants (i.e., bare soil and interception evaporation), as estimated by x intercept in the ET:GEP regression. As ET increased, the transpiration efficiency, $T/ET$, increased, resulting in more transpiration and photosynthesis. These across site and year results are consistent with a growing season study that quantified evapotranspiration partitioning at the shrubland site (shb-w), where Scott et al. [2006] found increasing monthly WUEe and $T/ET$ as the rainy season progressed. However, while we found the WUEe increased with water availability, Huxman et al. [2004] using aboveground net primary production data (ANPP) and precipitation ($P$) showed a decrease in rain use efficiency (ANPP/$P$) in wetter years and at wetter sites across a broader water availability gradient. Again, our results may differ, since using precipitation as a measure of water availability neglects hydrologic losses ($P$-$ET$) which increased with $P$ at our sites.

Annual average LAI explained much of the variation in WUEe (Figure 7b, $R^2 = 0.86$). At the two nearby sites in Walnut Gulch, the grassland supported a higher LAI than the shrubland at a given water availability. This resulted in a higher WUEe for a given ET (Figure 7a). This again points to the importance of ecosystem structure modulating a site’s water balance, in this case, by affecting the transpiration efficiency ($T/ET$). With the exception of the shrubland, the other sites had perennial grass cover and bare soil patches that readily fill in with annuals during the rainy season. This likely leads to less abiotic bare soil evaporation losses and more water available for photosynthesis. Sites and years with higher water availability have higher LAI and transpiration efficiencies that lead to increased WUEe [Hu et al., 2008]. The range of our estimates of $T/ET$ (0.46 for shb-w, 0.55 for gra-w, 0.62 for sav-s, and 0.58 for gra-s) agrees well with measured rates at the shrubland site [Cavanaugh et al., 2011] and differences between the grassland (gra-w) and shrubland (shb-w) $T/ET$ [Moran et al., 2009]. Likewise, as conceptualized by Huxman et al. [2005], $T/ET$ can be expected to increase with mean water availability, and grass-dominated sites are expected to have higher $T/ET$ than woody plant-dominated sites in semiarid regions. At all of the sites, evaporation was a substantial part of annual

4.2. Water Availability Drives Ecosystem Functional Responses

Annual ET explained 82–96% of the variability GEP (Figures 6a and 6c), suggesting that current-year water availability is a strong predictor of annual productivity. Other environmental drivers like precipitation/productivity legacies [Sala et al., 2012] and precipitation event size and distribution [Fay et al., 2003; Knapp et al., 2008] have also been shown to affect plant productivity in semiarid regions, but our results suggest that these are considerably less important at the annual scale. One reason for this is our use of ET as a proxy for water availability rather than the commonly used variable $P$ which neglects hydrologic losses. However, real lags between precipitation and productivity that may impart legacy effects may also be partially masked by using ET as ET more carefully tracks when soil moisture storage is accessed and becomes available to support plant growth.

Slopes of GEP:Reco indicated that in wetter years, about 50% of increased GEP was offset by Reco, and the rest augmented NEP (and vice versa for drier years, Figures 6b and 6d). This explains the strong sensitivity of annual NEP to $P$ (Figure 4) and mirrors the stronger sensitivity of ecosystem photosynthetic assimilation than respiration to drought found in many regions of the world [e.g., Schwalm et al., 2010]. Baldocchi et al. [2015] found a similar strong correlation for the annual GEP:Reco relationship across a global FLUXNET database ($R_{\text{eco}} = 0.71\text{GEP + 153}, R^2 = 0.76$) and showed that most of this correlation was not spurious created when partitioning NEP, especially if annual sums are used. We found considerably smaller slopes with both smaller and larger intercepts for our site-based relationships (Figures 6a and 6c), but pooling all the data yielded a good agreement with the slope but not the offset ($R_{\text{eco}} = 0.73\text{GEP + 67}, R^2 = 0.85$) compared to the more global relationship. More work is needed to examine these across time and space relationships using longer (>5 year per site) and bigger data sets.

While the similar slopes of the ET:GEP lines suggest a similar sensitivity of productivity to changes in water availability (Figures 6a and 6c), annual ecosystem water use efficiency (WUEe = GEP/ET) differed between the sites. As the fitted relationships had nonzero y intercepts, the ET:GEP slope and WUEe are not equivalent [Verón et al., 2005]. Annual and mean WUEe increased with water availability, implying a more efficient ecosystem use of water in wetter years and at wetter sites (Figure 7). We propose that these differences were due in part to the differences the relative proportion of ET not accessible by plants (i.e., bare soil and interception evaporation), as estimated by x intercept in the ET:GEP regression. As ET increased, the transpiration efficiency, $T/ET$, increased, resulting in more transpiration and photosynthesis. These across site and year results are consistent with a growing season study that quantified evapotranspiration partitioning at the shrubland site (shb-w), where Scott et al. [2006] found increasing monthly WUEe and $T/ET$ as the rainy season progressed. However, while we found the WUEe increased with water availability, Huxman et al. [2004] using aboveground net primary production data (ANPP) and precipitation ($P$) showed a decrease in rain use efficiency (ANPP/$P$) in wetter years and at wetter sites across a broader water availability gradient. Again, our results may differ, since using precipitation as a measure of water availability neglects hydrologic losses ($P$-$ET$) which increased with $P$ at our sites.

Annual average LAI explained much of the variation in WUEe (Figure 7b, $R^2 = 0.86$). At the two nearby sites in Walnut Gulch, the grassland supported a higher LAI than the shrubland at a given water availability. This resulted in a higher WUEe for a given ET (Figure 7a). This again points to the importance of ecosystem structure modulating a site’s water balance, in this case, by affecting the transpiration efficiency ($T/ET$). With the exception of the shrubland, the other sites had perennial grass cover and bare soil patches that readily fill in with annuals during the rainy season. This likely leads to less abiotic bare soil evaporation losses and more water available for photosynthesis. Sites and years with higher water availability have higher LAI and transpiration efficiencies that lead to increased WUEe [Hu et al., 2008]. The range of our estimates of $T/ET$ (0.46 for shb-w, 0.55 for gra-w, 0.62 for sav-s, and 0.58 for gra-s) agrees well with measured rates at the shrubland site [Cavanaugh et al., 2011] and differences between the grassland (gra-w) and shrubland (shb-w) $T/ET$ [Moran et al., 2009]. Likewise, as conceptualized by Huxman et al. [2005], $T/ET$ can be expected to increase with mean water availability, and grass-dominated sites are expected to have higher $T/ET$ than woody plant-dominated sites in semiarid regions. At all of the sites, evaporation was a substantial part of annual
ET which highlights the need for improved measurements [Kool et al., 2014] and understanding of T/ET to further untangle integrated ecosystem fluxes, especially in water-limited systems [Newman et al., 2006].

5. Conclusions

Determining the link between water availability and ecosystem carbon cycling is crucial to understanding the implications of current and future droughts on ecosystem function [Jenerette et al., 2012; van der Molen et al., 2011]. We examined the functional responses between carbon and water fluxes for semiarid ecosystems and were able to show that water availability and ecosystem structure (relative grass versus woody cover) likely influences an ecosystem’s average NEP response to drought. As semiarid lands have been shown to play a large role in the variability and trend in the global land carbon sink [Ahlström et al., 2015] these findings on the sensitivities of GEP and $R_{eco}$ to interannual fluctuations in water availability illustrate the overriding importance of water in the annual source/sink function of these ecosystems. Additionally, differences in ecosystem structure and their associated carbon pool size and turnover rates likely contribute to the speed at which NEP can adjust to climatic shifts (i.e., their acclimation potential).

Semi-arid regions have high interannual precipitation variability, and many of these regions worldwide are expected to get drier due to climate change [Schwalm et al., 2012; Seidel et al., 2008]. These regions have also experienced rapid changes in vegetation structure and land use [Asner et al., 2004; Poulter et al., 2014]. This study illustrates that semiarid ecosystem’s photosynthesis and respiration responses to fluctuations in annual water availability will likely be insensitive to these changes in climate and plant composition. However, longer-term alterations in precipitation can be expected to alter ecosystem water use efficiency in part due to the partitioning of ET between abiotic and biotic pathways, and the rate of adjustment of ecosystem structure and carbon pools likely depends on the community plant composition, with faster adjustments in nonwoody dominated systems.

Acknowledgments

Data used in this paper are available at the Ameriflux Data Repository (http://ameriflux.lbl.gov/) or upon request to the corresponding author. This work was supported by USDA-ARS and funding for these Ameriflux Core Sites was provided by the U.S. Department of Energy Berkeley National Labs. Funding for these data sets and maintaining the eddy covariance measurement systems, especially in water-limited systems, was provided by the USDA-ARS and the University of Arizona. We thank R. Bryant for his expert technical assistance in maintaining the eddy covariance sites. USDA-ARS is an equal opportunity employer.

References


Oak Ridge National Laboratory Distributed Active Archive Center (2015), MODIS Subsetted Land Products, Collection 5, Oak Ridge, Tenn.


