

Shrubland carbon sink depends upon winter water availability in the warm deserts of North America

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ABSTRACT

Global-scale studies suggest that dryland ecosystems dominate an increasing trend in the magnitude and interannual variability of the land CO₂ sink. However, such model-based analyses are poorly constrained by measured CO₂ exchange in open shrublands, which is the most common global land cover type, covering ~14% of Earth's surface. Here we evaluate how the amount and seasonal timing of water availability regulate CO₂ exchange between shrublands and the atmosphere. We use eddy covariance data from six US sites across the three warm deserts of North America with observed ranges in annual precipitation of ~100–400mm, annual temperatures of 13–18°C, and records of 2–8 years (33 site-years in total). The Chihuahuan, Sonoran and Mojave Deserts present gradients in both mean annual precipitation and its seasonal distribution between the wet-winter Mojave Desert and the wet-summer Chihuahuan Desert. We found that due to hydrologic losses during the wettest summers in the Sonoran and Chihuahuan Deserts, evapotranspiration (ET) was a better metric than precipitation of water available to drive dryland CO₂ exchange. In contrast with recent synthesis studies across diverse dryland biomes, we found that NEP could not be directly predicted from ET due to wintertime decoupling of the relationship between ecosystem respiration (R_{eco}) and gross ecosystem productivity (GEP). Ecosystem water use efficiency (WUE = GEP/ET) did not differ between winter and summer. Carbon use efficiency (CUE = NEP/GEP), however, was greater in winter because R_{eco} returned a smaller fraction of carbon to the atmosphere (23% of GEP) than in summer (77%). Combining the water-carbon relations found here with historical precipitation since 1980, we estimate that lower average winter precipitation during the 21st century reduced the net carbon sink of the three deserts by an average of 6.8TgC yr⁻¹. Our results highlight that winter precipitation is critical to the annual carbon balance of these warm desert shrublands.

1. Introduction

Dryland ecosystems, defined as those in which water is the main limiting resource (Noy-Meir, 1973), occupy 30–40% of the terrestrial surface (Bastin et al., 2017; Reynolds et al., 2007), and model-based studies suggest they strongly influence the global carbon cycle due to the inherent variability of water status (Ahlström et al., 2015; Jung et al., 2011; , 2017; Middleton and Thomas, 1992; Poulter et al., 2014).

Ground-based flux measurements in drylands show even greater temporal variability than these model results (Biederman et al., 2017). Unfortunately, the availability of continuous, long-term CO₂ exchange measurements has lagged in drylands as compared to mesic and humid regions in datasets such as AmeriFlux (Novick et al., 2017; Scott et al., 2015, Supplementary Information Fig. S1) and FLUXNET 2015 (<http://fluxnet.fluxdata.org/sites/site-list-and-pages/?view=map>). Therefore, current understanding of land-atmosphere exchange in drylands relies

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substantially upon local, site-based measurements of limited spatial and temporal scales (Huenneke et al., 2002; Huxman et al., 2004; Knapp and Smith, 2001; Muldavin et al., 2008; Sala et al., 2012). Meanwhile, biospheric models (Ahlström et al., 2015; Poulter et al., 2014), remote sensing observations and related models (Forzieri et al., 2014; Ma et al., 2015; Verma et al., 2014), and empirical upscaling of sparse flux measurements (Jung et al., 2011, 2017) are highly extrapolated and poorly constrained due to the limited spatiotemporal coverage of dryland ecosystem flux observations. While recent work has quantified carbon dioxide flux measurements for an expanded number of dryland ecosystems (Biederman et al., 2016, 2017; Anderson-Teixeira et al., 2011; Haverd et al., 2016; Ma et al., 2016), these synthesis studies are dominated by grasslands, savannas, woodlands, and seasonally dry forests. Meanwhile, less is known about carbon dioxide fluxes in open shrublands, which are of global importance.

Open shrubland ecosystems are the most widespread vegetation type globally, occupying an estimated 14% of the terrestrial surface (Broxton et al., 2014). They inhabit both arid and semiarid regions, and their biological activity (e.g., CO_2 uptake and release) is largely controlled by water availability at the annual scale, although the timing of CO_2 exchange may also be limited by temperature and phenology (Muldavin et al., 2008; Naumburg et al., 2004; Reynolds et al., 2004). Across the warm deserts of North America considered in this paper, 84% of the land area is classified as open shrublands in the MODIS land cover dataset (Channan et al., 2014). In North America and elsewhere, significant research and land management efforts are focused on ecosystem transitions from historical grasslands to shrublands and related impacts on ecosystem services including habitat, grazing, fire regime, soil erosion, water resources and carbon storage (Archer, 1994; Huxman et al., 2005; Petrie et al., 2015; Schlesinger et al., 1990; Scott et al., 2014; Van Auken, 2009; Wilcox and Huang, 2010).

Precipitation has declined across the Southwest (southwestern U.S. and northwestern Mexico) during the 21st century, particularly during winter, and is expected to decline further in the future (Cayan et al., 2010; Cook et al., 2015; Seager and Vecchi, 2010) with unknown impacts on the region's carbon balance. Although a recent synthesis of eddy covariance data from diverse Southwest ecosystems showed annual net ecosystem production (NEP) of CO_2 could be predicted directly from annual water availability (Biederman et al., 2016), many shrublands have bimodal winter/summer growth patterns distinguishing them from other summer-dominated dryland ecosystems (Reynolds et al., 1999). Prior work has shown that in shrublands, winter moisture plays a dominant role in annual net carbon uptake quantified by aboveground net primary productivity (ANPP) (Huenneke et al., 2002; Muldavin et al., 2008) and ecosystem fluxes (Jia et al., 2016; Petrie et al., 2015). Shrublands often have greater carbon uptake in winter than grasslands due to dominance by evergreen C3 shrubs which can photosynthesize year-round (Huxman et al., 2004; Kurc and Small, 2004; Reynolds et al., 2004; Wohlfahrt et al., 2008). Furthermore, the root structure of shrubs (i.e. > 30cm) allows them to access soil moisture in deeper layers which tend to be wetted predominantly in winter (Kurc and Benton, 2010; Kurc and Small, 2004; Ogle and Reynolds, 2004; Scott et al., 2000).

The main objective of our study was to evaluate how the amount and seasonal timing of water availability regulates CO_2 exchange between shrublands and the atmosphere. We adopt the approach of Huxman et al. (2004) in leveraging the distinct rainfall patterns of the three warm deserts: Chihuahuan, Sonoran and Mojave, of the Southwest region in North America. Specifically, we evaluated NEP and its component gross fluxes gross ecosystem production (GEP) and ecosystem respiration (R_{eco}), where $\text{NEP} = \text{GEP} - R_{\text{eco}}$. These deserts present significant gradients in the amount and seasonal timing of water availability, the primary driver of dryland carbon exchange (Biederman et al., 2017; Briggs and Shantz, 1913; Noy-Meir, 1973; Scott et al., 2015). Mean annual precipitation (1980–2016) increases from ~150mm in the Mojave Desert to ~200mm in the Sonoran Desert to

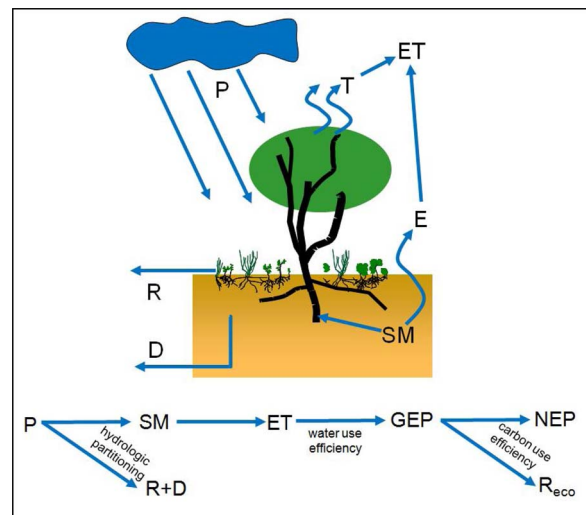


Fig. 1. Conceptual model of how water availability drives ecosystem-scale carbon dioxide exchange in drylands, based on Biederman et al. (2016). After some precipitation (P) is lost to runoff (R) and drainage (D), remaining water recharges soil moisture (SM). Soil moisture is depleted by evaporation (E) and transpiration (T), measured together as ecosystem ET. Therefore ET is a proxy of the water available to drive gross ecosystem productivity (GEP), ecosystem respiration (R_{eco}), and their difference, net ecosystem productivity (NEP).

~300 mm in the Chihuahuan Desert (using Daymet, Thornton et al., 2017). All three deserts experience some combination of frontal winter precipitation and summer rainfall influenced by the North American Monsoon (Douglas et al., 1993; Muldavin et al., 2008), while late spring (May/June) and autumn (October/November) are generally dry. However, the Mojave Desert receives the majority of its precipitation during the winter, while the Chihuahuan Desert is dominated by summer precipitation, and the Sonoran Desert has a more seasonally balanced precipitation regime.

Although precipitation (P) is the common proxy for ecosystem water availability (Sala et al., 2012), some P is lost to runoff (R) or drainage beyond the rooting zone (D) and is therefore not available to drive CO_2 exchange (Fig. 1) (Biederman et al., 2016; Briggs and Shantz, 1913; Noy-Meir, 1973). After these hydrologic losses, most remaining precipitation recharges soil moisture (SM) and becomes ecosystem-available, excepting the amount evaporated from wet surfaces (i.e. interception) (Noy-Meir, 1973). Soil moisture is subsequently depleted by evapotranspiration (ET) (Biederman et al., 2016, 2017). While short-term (e.g. diurnal) ET rates are controlled by several factors including available energy, root density, leaf area, and soil properties, ET integrated over periods during which dryland SM is recharged and fully depleted (i.e. seasonal, annual) approximates the SM that was available to drive carbon cycling. At eddy covariance sites, ET is measured using the same instruments and spatial scale integration as those used to measure CO_2 exchange, whereas direct SM measurements integrate much smaller spatial scales, use different methodology, and are generally less available and less comparable across sites (e.g. due to differences in soils, calibration and depth distribution). We previously found that across 21 Southwest sites of diverse functional types, annual ET directly predicted 60% of annual NEP variability (Biederman et al., 2016) due to relatively constant cross-biome water use efficiency ($\text{WUE} = \text{GEP}/\text{ET}$) and carbon use efficiency ($\text{CUE} = \text{NEP}/\text{GEP}$) (Fig. 1), consistent with prior CUE results in forests (Litton et al., 2007; Waring et al., 1998). However, it remains unknown how seasonal differences in hydrologic partitioning, WUE and CUE will regulate shrubland NEP.

Higher VPD is expected to reduce WUE during summer due to increased abiotic evaporation (Hu et al., 2008; Scott and Biederman, 2017). However, the detrimental effects of higher summer VPD on GEP may be partially counteracted at the leaf level by different responses of

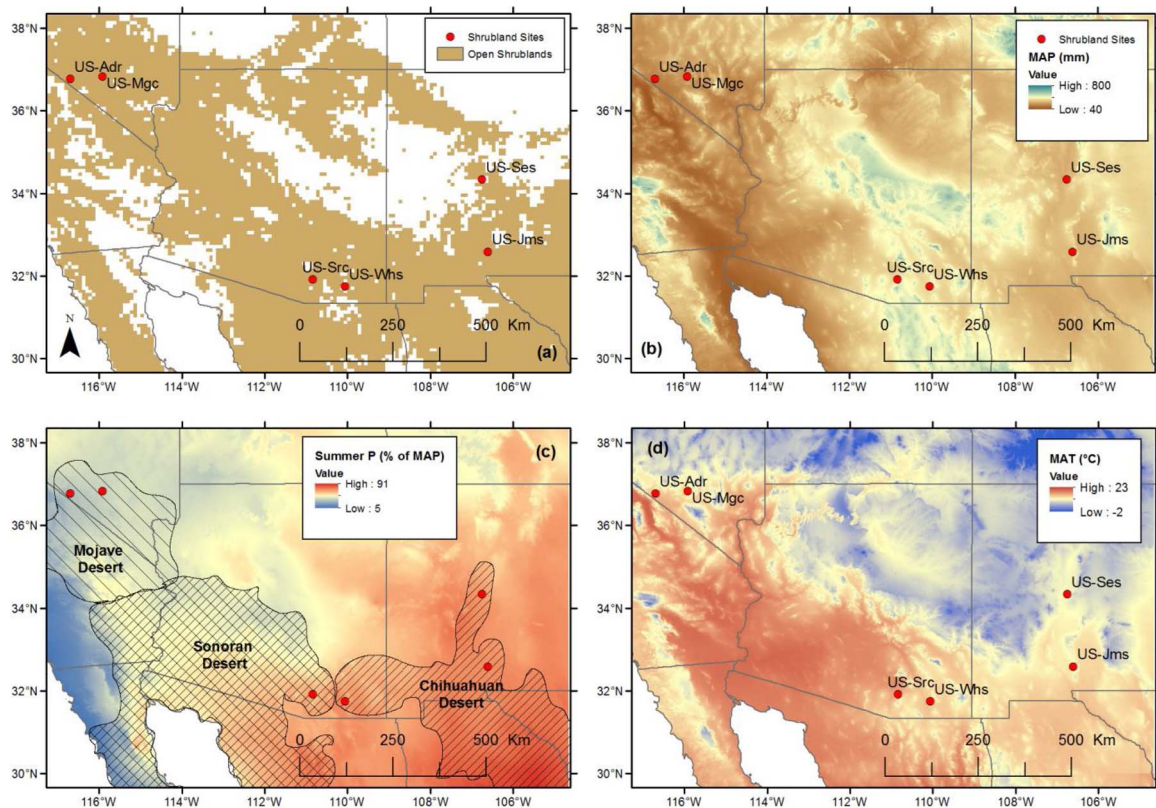


Fig. 2. Map of flux tower sites in Southwest shrublands. Background maps show (a) extent of open shrublands based on the 2012 MODIS land cover dataset, (b) mean annual precipitation (MAP), (c) percentage of MAP falling in summer, and (d) mean annual temperature (MAT). Panel (c) also shows outlines of the three North American warm deserts (Hunter et al., 2001). Climate data are normals for 1950–2000 from the WorldClim 1-km dataset [www.worldclim.org].

carbon assimilation and stomatal conductance, which may be assessed with metrics such as inherent or underlying WUE (Beer et al., 2009; Zhou et al., 2015). In this paper we focus on ecosystem-scale WUE, a functional metric critical to understanding large-scale interactions between water availability and dryland carbon uptake. WUE integrates biotic and abiotic factors including ecosystem structure, C3/C4 photosynthetic pathway (Emmerich, 2007), stomatal response to gradients of water vapor and CO₂ (Beer et al., 2009; Keenan et al., 2013; Zhou et al., 2015), temporal sequencing of precipitation (Cavanaugh et al., 2011; Liu et al., 2017), and partitioning of ET between transpiration and abiotic evaporation (Scott and Biederman, 2017).

The gradients in the magnitude and seasonal distribution of precipitation across the three deserts offer the possibility to test several hypotheses. First, the Mojave Desert is initially expected to have the lowest GEP and NEP due to its low precipitation magnitude. However, the high-intensity (convective) precipitation common in the summer-dominant Sonoran and Chihuahuan Deserts results in significant hydrologic losses, reducing the fraction of precipitation recharging soil moisture and supporting biological activity (Fig. 1). Second, greater WUE is expected during winter due to lower surface evaporation as a result of deeper infiltration of water into the rooting zone, where it is less likely to evaporate than at the surface (Andraski, 1997; Ogle and Reynolds, 2004; Scott et al., 2000; Wohlfahrt et al., 2008) and lower vapor pressure deficit (VPD), both of which can increase the fraction of available water that is transpired through plants (T/ET) (Hu et al., 2008). Third, prior results showing greater ANPP during winter/spring than summer (Huenneke et al., 2002; Muldavin et al., 2008) imply greater CUE is expected for sites/seasons with significant winter activity (i.e., a smaller fraction of GEP returned to the atmosphere by R_{eco}). With sufficient soil moisture, soil respiration is controlled by cooler winter temperatures (Wang et al., 2014), while evergreen shrubs may continue to photosynthesize (Huxman et al., 2004). When surface

soils dry but deeper soil moisture persists, which occurs most frequently during winter (Scott et al., 2000), photosynthesis may persist on moisture accessible to deep-rooted shrubs, while heterotrophic respiration may be controlled by low moisture in the litter and upper soil layers (Reichstein et al., 2002; Yang and Zhou, 2013). Meanwhile summer moisture often triggers R_{eco} pulses exceeding GEP, reducing net productivity during summer (Huenneke et al., 2002; Scott et al., 2009; Verduzco et al., 2015; Wohlfahrt et al., 2008).

In order to address these gaps in understanding how shrubland fluxes respond to the different amounts and seasonal timing of rainfall we sought to address, for shrublands of the warm North American deserts: 1) How do hydrologic losses to runoff and drainage affect the amount of precipitation that is available to drive ecosystem carbon exchange?, 2) Is annual water availability sufficient to directly predict annual NEP, or is it necessary to consider seasonal differences in WUE and CUE? 3) How have reduced annual and winter precipitation during the 21st-century impacted CO₂ exchange across the three deserts?

2. Methods and materials

2.1. Shrubland study sites across three deserts of Southwestern North America

We assembled 33 years of flux and meteorological measurements from six sites in the Mojave, Sonoran, and Chihuahuan Deserts as well as precipitation data for 1980–2016 at these six sites and across the three deserts. Available eddy covariance sites had 2–9 years of measurements (Fig. 2, Table 1). Observations were made between 2005 and 2015, though measurement periods vary by site. Sites were classified by Köppen climate (<http://koeppen-geiger.vu-wien.ac.at/present.htm>). Vegetation cover ranged from 8 to 42% consisting of one or more perennial, low-statured shrubs (Table 1). Creosotebush (*Larrea*

Table 1
Site descriptions and reference information.

Desert	Site ID	Description	Dominant Species	Veg. Cover (%)	Köppen Climate	Elevation (m)	MAP (mm) Summer ^a	MAT (°C)	Obs. Years	Site Reference and DOI
Chihuahuan	Whs	Walnut Gulch Lucky Hills shrubland	<i>Parthenium incanum</i> , <i>Acacia constricta</i> , <i>Larrea tridentata</i> , <i>Rhus microphylla</i>	42	BSk	1376	352 70%	16.8	2007–2015	(Scott, 2010) 10.17190/AMF/1246113
	Ses	Sevilleta creosotebush shrubland	<i>Larrea tridentata</i> , <i>G. sarothrae</i>	30	BSk	1610	252 68%	12.6	2007–2014	(Petrie et al., 2015) 10.17190/AMF/1246125
	Jms	Jornada mixed shrubland	<i>Prosopis glandulosa</i> , <i>Larrea tridentata</i> , <i>Parthenium incanum</i>	34	BSk	1470	270 70%	14.4	2010–2014	(Schreiner-McGraw et al., 2016; Templeton et al., 2014) ^a
	Src	Santa Rita creosotebush shrubland	<i>Larrea tridentata</i>	24	BSk	1000	378 63%	18.4	2007–2012	(Kure and Benton, 2010) 10.17190/AMF/1246127
Mojave	Mgc	Mojave Global Change	<i>Larrea tridentata</i> , <i>Lycium andersonii</i> , <i>Ambrosia dumosa</i>	18	BWk	943	131 35%	16.7	2005–2009	(Wohlfahrt et al., 2008) ^a
	Adr	Amargosa Desert Research	<i>Larrea tridentata</i>	8	BWk	850	108 30%	17.6	2011–2013	(Arthur et al., 2012) ^a

^a Jms and Mgc do not have data submitted to AmeriFlux, while ADR data have been submitted (6/2017) but not yet assigned a DOI. Data may be obtained from the corresponding author. Mean annual precipitation (MAP) and temperature (MAT) 1950–2000 from the WorldClim 1-km dataset (www.worldclim.org).

tridentata) was important at all sites (Table 1) and was the dominant shrub at four sites. The Jornada Mixed Shrubland (Jms) site had slightly more mesquite (*Prosopis glandulosa*), while mariola (*Parthenium incanum*) was most common at Lucky Hills Shrubland (Whs). Data for Whs, Santa Rita Creosotebush (Src), Sevilleta Shrubland (Ses), and Amargosa Desert Research Shrubland (Adr) are available through AmeriFlux (<https://ameriflux.lbl.gov>) while the remaining data can be obtained from the corresponding author.

Precipitation falling late in the calendar year (November/December) is often stored as soil moisture and should be associated with biological activity in the following growing season (Biederman et al., 2016; Jia et al., 2016; Ma et al., 2007; Pereira et al., 2007; Scott et al., 2000; Thomas et al., 2009; Verduzco et al., 2015). Therefore, annual CO₂ and water vapor (ET) flux sums and meteorological driving variables were calculated using an ecohydrologic year spanning November 1–October 31. (Biederman et al., 2017; Thomas et al., 2009). We further divided the ecohydrologic year into winter (Nov. May) and summer (Jun. Oct.). This partition was selected because May and June tend to be sufficiently hot and dry to reliably deplete soil moisture, minimizing seasonal carry-over and improving the accuracy of ET as a metric of water availability.

The Chihuahuan, Sonoran and Mojave Deserts are predominantly covered by open shrublands (respectively 93%, 75%, and 79%; Fig. 2a). The gradients in the amount and timing of water availability are shown by historical mean climatology for 1950–2000 (Fig. 2b, c) and the mean seasonal cycles measured at each flux site (Fig. 3, years indicated in Table 1). Because annual rainfall totals are low in the Mojave, sporadic summer rainstorms can significantly affect annual totals (and seasonal distribution) in some years. The deserts have mean annual temperatures between about 12 and 19°C. Mean seasonal cycles of temperature are similar, although in the Mojave, winter temperatures are lower, and peak temperature occurs one month later (July) than in the other two deserts, where summer monsoon storms reduce maximum temperatures beginning in July (Fig. 3). In all three deserts, there is evidence that some winter moisture can be stored in the soil until warming temperatures drive ET (Andraski, 1997; Kure and Small, 2007; Scanlon et al., 2005; Scott et al., 2000). Accordingly, MODIS EVI (Huete et al., 2002) at the study sites usually shows greening beginning in late winter (March–May) though the major greening season occurs in the summer (July–September) at the Sonoran and Chihuahuan sites (Fig. 3). At the Mojave sites, where vegetation cover is less than 20% (Table 1), EVI peaks in April and May, although the seasonal EVI signal amplitude is low (Fig. 3). Elevations (mean $\pm$ 1 standard deviation using a 1-km DEM) are 950 $\pm$ 440, 450 $\pm$ 370, and 1370 $\pm$ 250m for the Mojave, Sonoran, and Chihuahuan, respectively.

2.2. Data collection and processing

Measurements of terrestrial-atmosphere gas exchange were made at the ecosystem scale using the eddy covariance technique (Goulden et al., 1996). Data collection and regular calibrations of eddy covariance flux measurement systems followed common practices (Lee et al., 2006). We assembled 30-min measurements of precipitation, temperature, ET, VPD, NEP, and GEP and R_{eco} derived from NEP using consistent methods for all sites. We partitioned NEP into GEP and by first eliminating NEP data when the friction velocity, u^* , was less than 0.15 m s⁻¹ (Scott et al., 2009; Scott, 2010). We then fit an exponential function of air temperature to the remaining nighttime NEP data over a moving $\sim$ 5 day window (Reichstein et al., 2005), with varying window sizes to prevent grouping data across precipitation events, which 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_{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. We compared annual

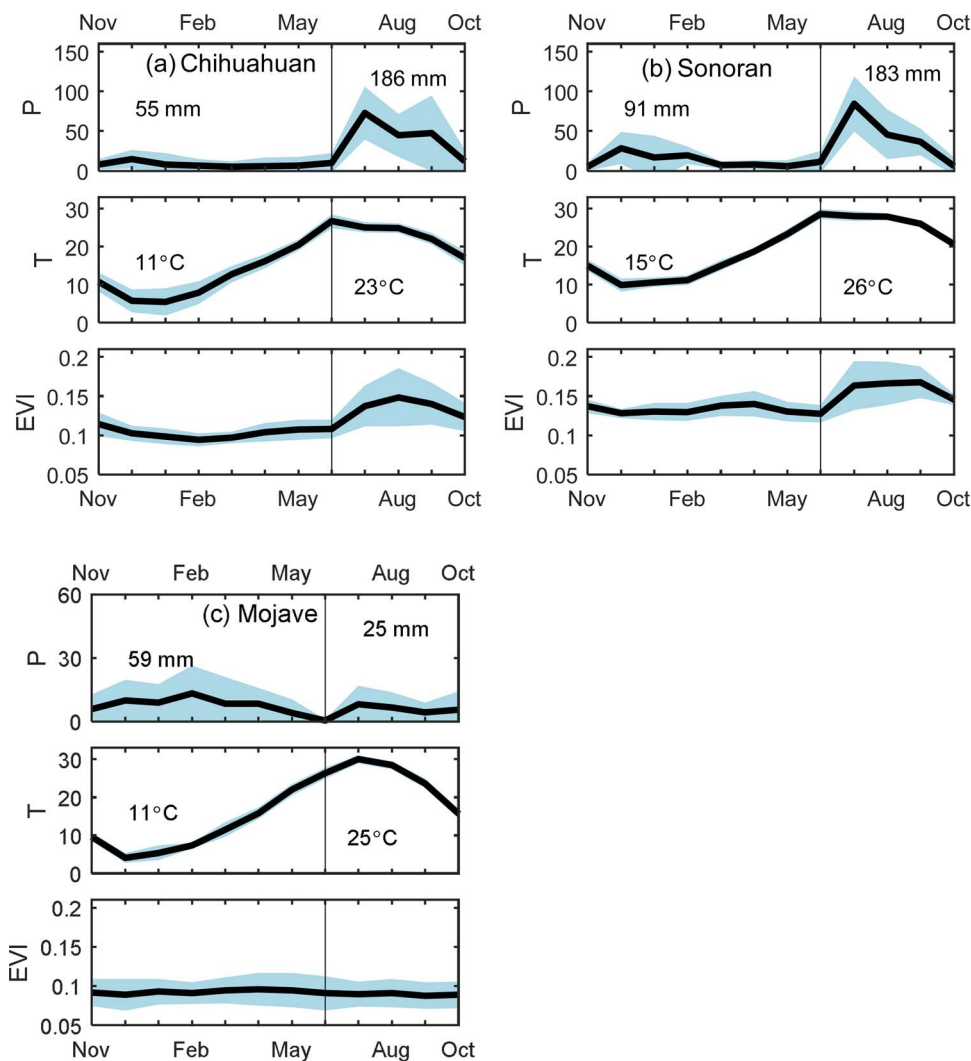


Fig. 3. Mean monthly precipitation (P, mm), temperature (T, °C), and MODIS enhanced vegetation index (EVI) for the combined sites in the (a) Chihuahuan, (b) Sonoran, and (c) Mojave Deserts (Table 1). Vertical lines show demarcation between winter and summer (1–June) according to the definition used here. Shading indicates standard deviations of monthly values. Values shown are mean seasonal precipitation and temperature.

NEP sums produced by the above methods with those provided in the FLUXNET2015 database (<http://fluxnet.fluxdata.org/data/fluxnet-2015-dataset/data-processing/>) for the two sites present in both datasets (Whs and Src). The average uncertainty in annual NEP related to u^* threshold filtering and gap-filling ranged from 5 to 16 gC m², which is much smaller than the NEP variability between the sites or among the years at a given site (Fig. S1). Finally, we calculated GEP as $GEP = R_{eco} + NEP$. GEP and R_{eco} are always positive with this sign convention. Previous studies have compared this method with a daytime partitioning approach based on light-response curves and found good agreement at the annual scale (differences < 10%), although best practices suggest that a common approach should be used across all sites in multi-site data synthesis studies (Desai et al., 2008; Lasslop et al., 2010).

Because multi-year records at the Ses site commenced with calendar year 2007, the first two months of this record (November and December 2006) were filled using mean monthly fluxes of 2007–2014 (Biederman et al., 2016), representing 2% of data for this site. November and December are usually dry, inactive months at this Chihuahuan Desert site (Fig. 3a), with each contributing, on average, 3–5% of annual fluxes (P, ET, GEP, R_{eco}).

2.3. Remote sensing of vegetation greenness

We used the enhanced vegetation index (EVI) from the Moderate Resolution Imaging Spectroradiometer (MODIS) Collection 5 to explore

seasonal similarities between greenness and fluxes of CO₂ and water. This index is distributed as the MOD13Q1 data product with 16 day temporal resolution (Google Earth Engine Team, 2015). We used the single ~250 m pixel containing each flux tower. Mean monthly EVI values were computed using data classified as best-quality to reduced contamination associated with clouds, shadows, and snow/ice.

2.4. Hydrometeorological datasets

We used two sources of long-term climate data. Climate normals for the North American deserts were characterized by the mean annual temperature, mean annual precipitation, and summer precipitation for 1950–2000 using the 1 km WorldClim dataset (www.worldclim.org). To assess the impacts of 21st-century changes in hydroclimate on carbon dioxide fluxes, we assembled monthly precipitation for 1980–2016 from the Daymet gridded dataset (Google Earth Engine Team, 2015; Thornton et al., 2017), which provides full North American coverage and has high accuracy for the Southwest region (Behnke et al., 2016). We calculated spatially averaged precipitation for each desert and season (winter/summer) using the mean of all 1-km pixels contained within each desert. WorldClim was considered the best source of long-term mean climate (average of 50 years), while Daymet data best supported our analysis of precipitation for each season and year since 1980.

One site (Whs) was co-located with runoff measurements for a subwatershed within the Walnut Gulch Experimental Watershed (Stone

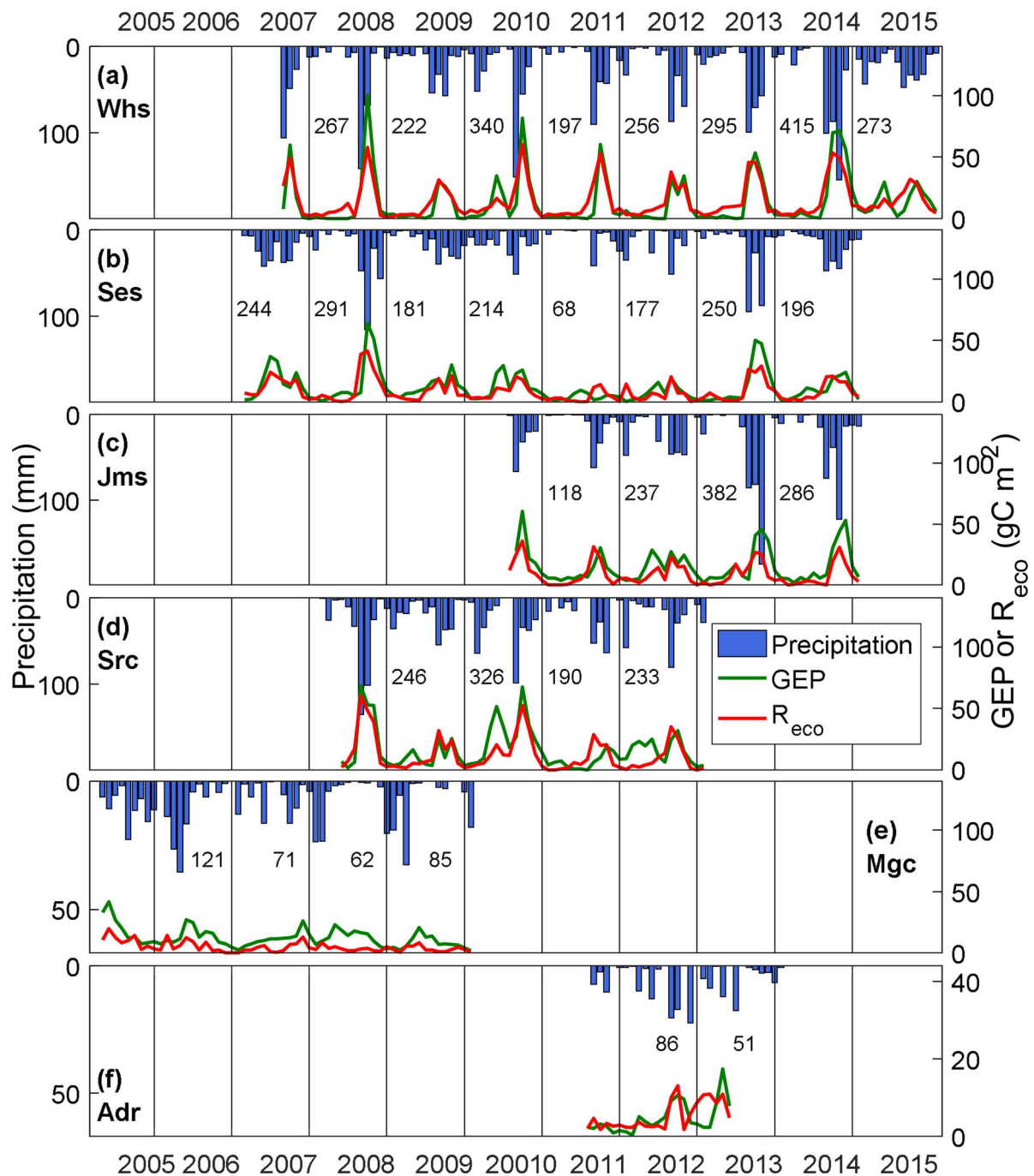


Fig. 4. Monthly precipitation, gross ecosystem productivity (GEP) and ecosystem respiration (R_{eco}) for each shrubland eddy covariance site. Vertical lines denote 1-Nov, the start of the ecohydrologic year. Numbers shown are precipitation (mm) for each complete ecohydrologic year available. Panels (a-c) represent the Chihuahuan Desert, panel (d) shows a Sonoran Desert Site, and panels (e-f) represent the Mojave Desert.

et al., 2008). Runoff was divided by watershed area (0.34 ha) to produce a linear measure comparable to precipitation and ET. Area-normalized streamflow data were obtained from <http://www.tucson.ars.ag.gov/dap/digital/aggregate.asp> (Flume 106). At Jms, the flux tower was located in a 4.7-ha subwatershed where significant deep drainage occurred in the channel before runoff was measured with a weir. Here we present integrated drainage and runoff values from a water balance analysis of this watershed (Schreiner-McGraw and Vivoni, 2017).

3. Results

3.1. Time series of precipitation, productivity, and ET

Monthly time series of precipitation, GEP and R_{eco} illustrate the availability of records at each site and for each desert (Fig. 4). The greatest number of data years was available for the Chihuahuan Desert (3 sites and 21 years), while the Sonoran Desert had one site with 5 years and the Mojave had two sites comprising 7 years. All sites had rainfall grouped into winter and/or summer with dry spring and autumn (Fig. 4), consistent with the mean seasonal cycles (Fig. 3). However, there is large year-to-year variability in both the amount and seasonality of precipitation. For example, there was below-average

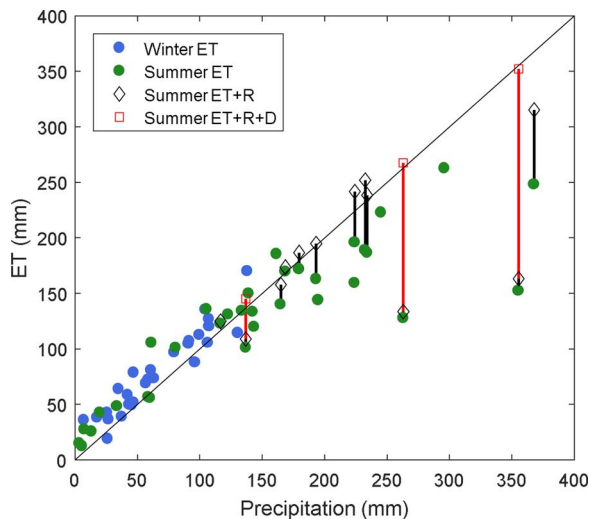


Fig. 5. The relationship of evapotranspiration (ET) with precipitation for the winter and summer seasons at the six shrubland sites combined. Each point represents one season at one site. Black diamond symbols indicate the sum of ET and independently measured runoff (R) available for the Whs and Jms sites, where the flux towers are co-located with a flow-measurement flume. Red square symbols indicate the sum of ET, R and deep drainage (D), which was estimated in a separate water balance analysis at Jms. No runoff occurred during winters. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

precipitation across the Chihuahuan (Fig. 4a–c) and Sonoran sites (Fig. 4d) during winter 2011, while the available sites all received above-average precipitation during summer 2008. At the Mojave sites (Fig. 4e, f), monthly precipitation totals are lower than for the other deserts (note the different scales). CO₂ fluxes responded to precipitation at all sites, while both fluxes were low, including negligible GEP, during dry periods. With sufficient winter precipitation, GEP usually exceeded R_{eco} (e.g., winter 2010 at Whs, Ses, Src and most winters at Mojave Global Change Shrubland (Mgc)). Summer precipitation, however, often triggered a rapid rise in R_{eco} , followed by a lagged rise in GEP, particularly following a dry winter (e.g., Whs, Ses, Jms, Src in summer 2011).

3.2. Quantifying ecosystem-available water

We investigated the relationship between water availability and vegetation cover across the six sites using simple linear models. Although cover was significantly ($p < 0.05$) predicted by mean annual precipitation ($R^2 = 0.58$), mean annual evapotranspiration was a stronger predictor ($R^2 = 0.78$). Seasonal ET was a weaker predictor of cover than the annual sums (data not shown). To investigate why vegetation cover was better predicted by ET than precipitation, we examined the relationship between ET and P (Fig. 5). Seasonal precipitation sums up to ~ 150 mm were matched to or slightly exceeded seasonal ET (close to 1:1 line). In 12 of the 14 summer seasons when precipitation exceeded ~ 150 mm, which occurred only in the Sonoran and Chihuahuan Deserts, $ET < P$, suggesting hydrologic losses to runoff and drainage (Fig. 1). Adding measured R and D in small watersheds co-located with two of the flux towers (Whs, Jms) closed most of this discrepancy in the seasonal water balance ($P \sim ET + R + D$) (Fig. 5). This supports the idea that ET is a better metric of soil water available to drive ecosystem carbon cycling after hydrologic losses (Fig. 1), and we use ET as the water availability metric hereafter.

3.3. Magnitude and variability of water and carbon fluxes across sites

Cross-site patterns in seasonal and annual water availability (ET) reflect the climatology of the three deserts (Fig. 6), with the lowest ET totals at the Mojave sites (Mgc and Adr). Seasonal distributions of ET

between winter and summer (Fig. 6) are similar to those of precipitation (Table 1, Fig. 3), suggesting there is negligible moisture storage across summer/winter seasons at these sites (i.e., precipitation recharges root-zone soil moisture, which is depleted by ET each season). Across sites, mean seasonal photosynthesis (GEP) and water availability (ET) are well-correlated, with Pearson's correlation coefficients of $R = 0.73$ in winter and $R = 0.89$ in summer, suggesting similar seasonal water use efficiency ($WUE = GEP/ET$). The correlation between R_{eco} and ET was even stronger: $R = 0.75$ in winter and $R = 0.96$ in summer. In contrast, there is little evidence that spatial patterns in mean net productivity (NEP) could be predicted directly from water availability (Fig. 6a,d). On average, the Whs site was a carbon source ($NEP < 0$) in winter and annually, with $NEP \sim 0$ for summer, although the standard deviations exceed the mean NEP magnitudes. The Whs site switched between a carbon source and sink in dry and wet years, respectively. The Ses, Jms and Mgc sites were consistently carbon sinks seasonally and annually. The Sonoran Src site had, like Whs, mean $NEP \sim 0$ in summer but took up CO₂ consistently in winter, driving a positive mean annual NEP (net carbon sink). The Mojave Adr site had NEP very close to zero ($|NEP| < 10 \text{ gCm}^{-2}$) in the one winter and two summers for which data are available.

3.4. Relating water availability to gross and net ecosystem productivity

To address our second research question, we aggregated the 33 site-years to evaluate whether water availability could *directly* predict NEP across the shrublands, as was previously demonstrated for a broader regional dataset (Biederman et al., 2016). In these shrublands, we found no direct relationship between ET and NEP for annual, winter, or summer sums (Supplementary Information Fig. S2a). Likewise, there was no direct relationship of NEP with mean seasonal temperature (Fig. S2b). To understand why the direct ET-NEP relationship did not hold for this shrubland dataset, we next investigated the linkages between ET and NEP shown in Fig. 1: the linkage of ET with GEP (i.e. water use efficiency); and the partitioning of GEP into R_{eco} and NEP (carbon use efficiency). We also addressed the impacts of VPD on ecosystem-scale WUE using the concept of underlying WUE, where $uWUE = -GEP \cdot VPD_{0.5} / ET$ (Zhou et al., 2015).

Across all site years, there was no difference between winter and summer in the slope of the relationship of ET with $GEP \cdot VPD_{0.5}$ (ANCOVA, $p > 0.05$), although the intercept was greater for summer (Fig. 7a). There were no differences in the relationship of ET with GEP, and a single linear model fit the combined dataset (Fig. 7b, $GEP = 0.66ET + 5.6$; $R^2 = 0.62$; $n = 66$ seasons). Because the intercept was not significantly different from the origin, the slope of this line may be interpreted as the WUE ($\text{gCm}^{-2} \text{mm}^{-1} \text{H}_2\text{O}$, equivalent to $1 \text{H}_2\text{O}$), which did not differ between winter and summer (Fig. 7b) (Fig. 8). Furthermore, we found no relationship between WUE and mean seasonal temperature (T) or vapor pressure deficit (VPD, Fig. S4). In contrast, the slope between ET and R_{eco} was 45% lower in winter than summer (Fig. 7c), suggesting that an increase of 100 mm of water availability in summer was associated with a 67 ± 5 (std. err.) gC m^{-2} increase in R_{eco} , compared with only $37 \pm 5 \text{ gC m}^{-2}$ in winter. Although mean R_{eco} was, on average, greater in summer, when temperatures were warmer, than in winter (i.e. different means, $p < 0.05$), we found no significant relationships between R_{eco} and temperature *within* either season (Fig. S5).

The different winter/summer relationship of water availability with R_{eco} resulted in significant seasonal differences in the CUE relationship between R_{eco} and GEP, which defines NEP (Fig. 7d). The slopes suggest that in summer, an incremental increase in GEP of 100 gC m^{-2} would be counteracted by an average of $77 \pm 9 \text{ gC m}^{-2}$ of R_{eco} , leaving a residual 23 gC m^{-2} allocated to NEP. In winter, however, an incremental increase in GEP of 100 gC m^{-2} would be counteracted by an average of only $23 \pm 7 \text{ gC m}^{-2}$ of R_{eco} , leaving 77 gC m^{-2} allocated to NEP.

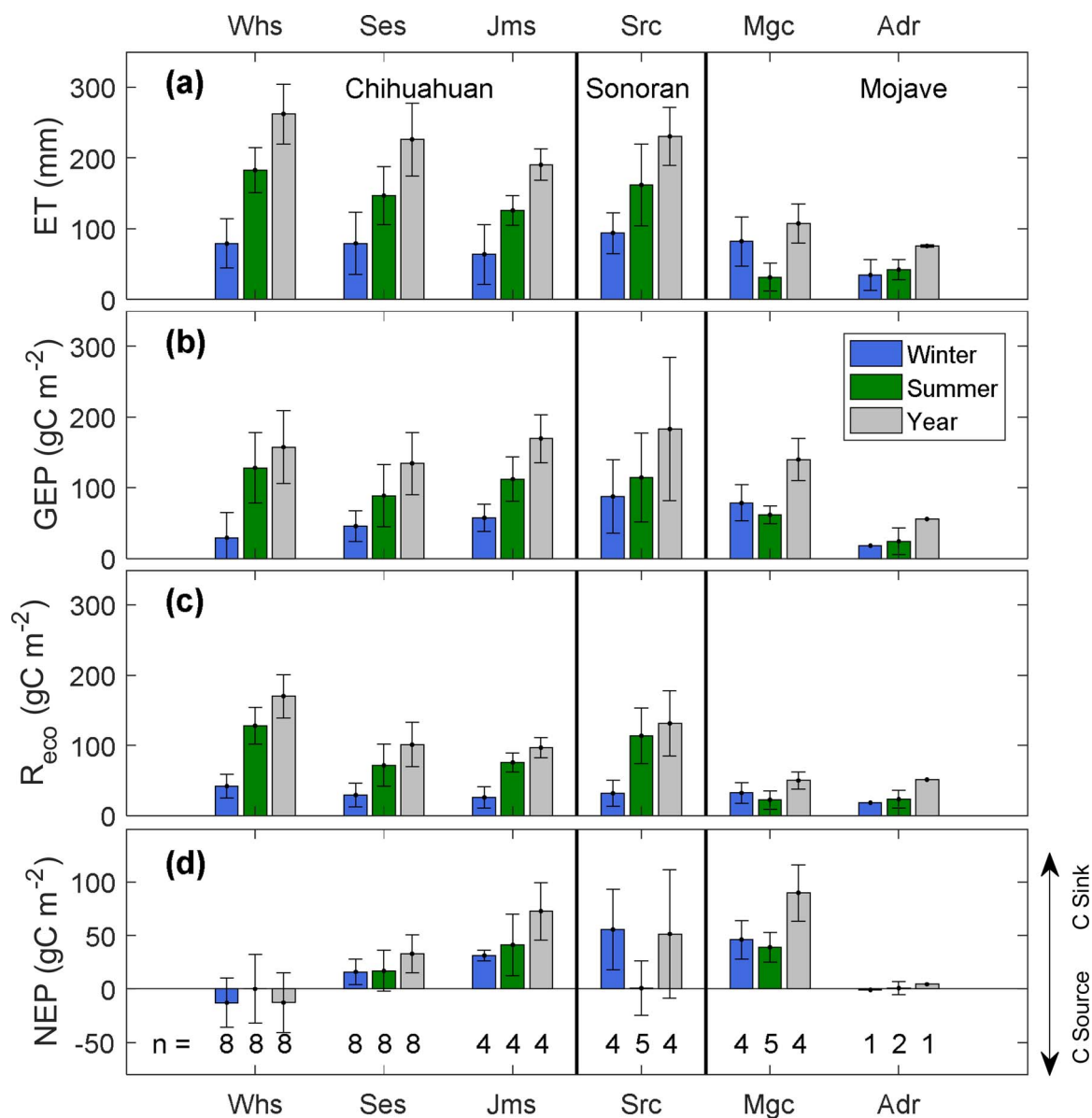


Fig. 6. Spatial patterns across the six sites in mean seasonal and annual sums of (a) ET, (b) GEP, (c) R_{eco} and (d) NEP. In the lower portion of (d), the numbers of measurement years (n) per site are shown. Error bars represent one standard deviation of the mean (not calculated for site ADR winter or year where $n = 1$). Mean seasonal values may not sum to mean annual values where the number of measurement years is unequal for winter and summer.

4. Discussion

4.1. Low respiration makes winters critical for net carbon uptake

Here we assembled a regional synthesis of six eddy covariance sites (33 site-years of measurements) in shrublands of the three warm North American deserts, which present gradients in both average annual precipitation and its seasonal distribution between winter and summer growing seasons (Table 1, Fig. 2). We found that ET is a more accurate measure of ecosystem-available water than precipitation (Fig. 5). ET and GEP were positively related across sites (spatially), but NEP did not show a spatial relationship with ET or with the desert in which a site was located (Fig. 6). Ecosystem-scale water use efficiency ($WUE = GEP/ET$) did not differ between winter and summer (Fig. 7b). However, the slopes of R_{eco} with ET and R_{eco} with GEP were lower in winter than summer (Fig. 7c), resulting more carbon sequestration in winters than summers, on average (Fig. 7d). Below we discuss how this work improves understanding of water-carbon relations in desert shrublands and use our results to make a simple estimate of how

reduced precipitation in the Southwest has shifted the regional carbon balance during the 21st century.

4.2. Hydrologic partitioning and use of ET as a proxy for water availability

Here, we found several lines of evidence suggesting ET was a better proxy of water availability than precipitation (P), some of which is lost to runoff (R) and drainage (D) before it becomes available to the ecosystem (Fig. 1). ET reflects when SM is available to the ecosystem and has the added benefit of being measured on a commensurate scale and with the same methodology as the carbon fluxes. An important implication is that ET measurements may be used as an independent check of various methods used to assess soil moisture including direct measurements, models, and remote sensing. While dryland shrub cover has previously been related to precipitation (Fensham et al., 2005), we found that mean annual ET was a better predictor of cover. Between 0–150 mm of seasonal precipitation, ET was approximately equal to P (Fig. 5). Instances in which ET slightly exceeded P could be due to precipitation undercatch, which is likely to be 5–10% of P (Scott, 2010;

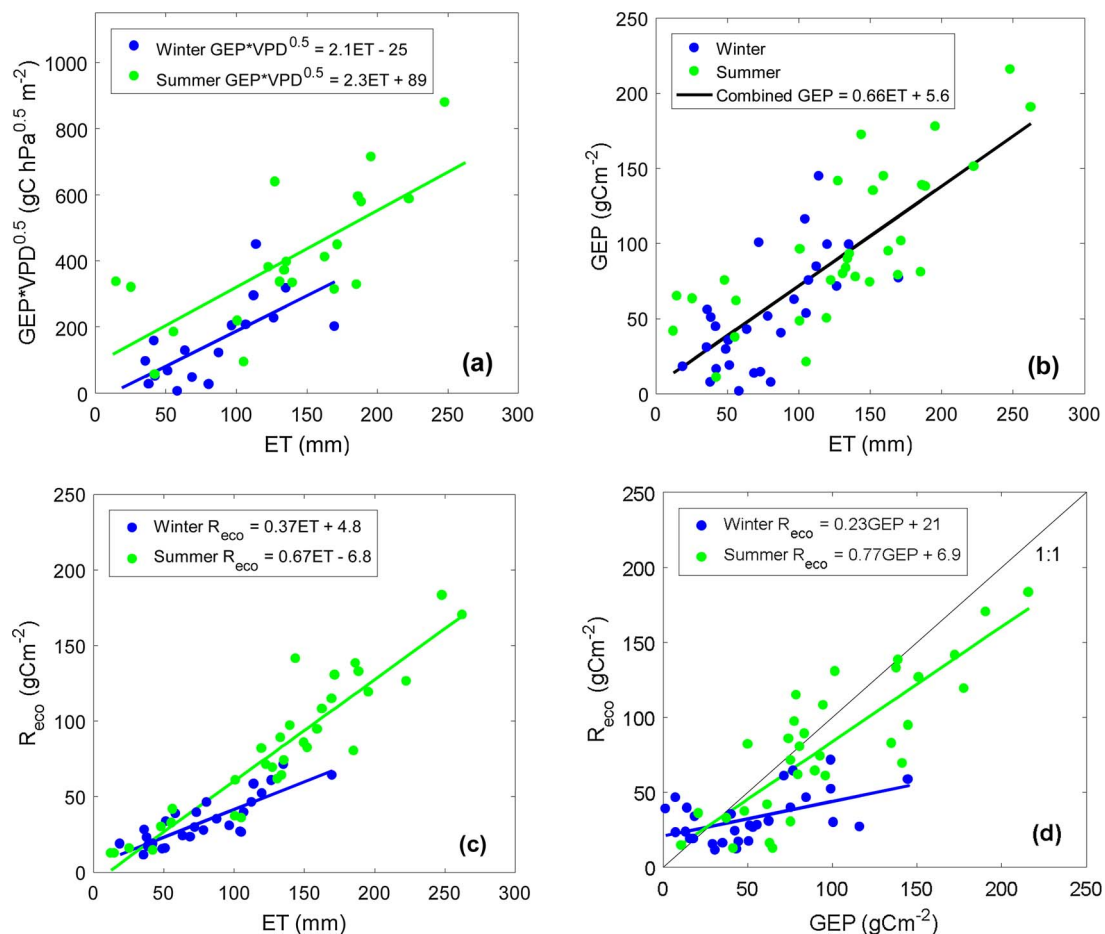


Fig. 7. The seasonal relationship of (a) ET with $GEP \cdot VPD^{0.5}$, (b) ET with GEP, (c) ET with R_{eco} , and (d) the carbon balance between GEP and R_{eco} , which determines NEP. Each point represents one site-season. In (a) the slopes were not significantly different, but different intercepts suggest a higher underlying water use efficiency (uWUE) in summer than winter (ANCOVA, $p < 0.05$). In (b) there was no seasonal difference in the linear relationships, so the data were fit with a combined model. In (c) and (d), the slopes were lower in winter than summer, so separate models were used. In (d), points above the 1:1 line indicate seasons when an ecosystem functioned as a net carbon source to the atmosphere ($R_{eco} > GEP$), while points below the line indicate net carbon uptake. All linear models shown are significant versus a constant model ($p < 0.05$).

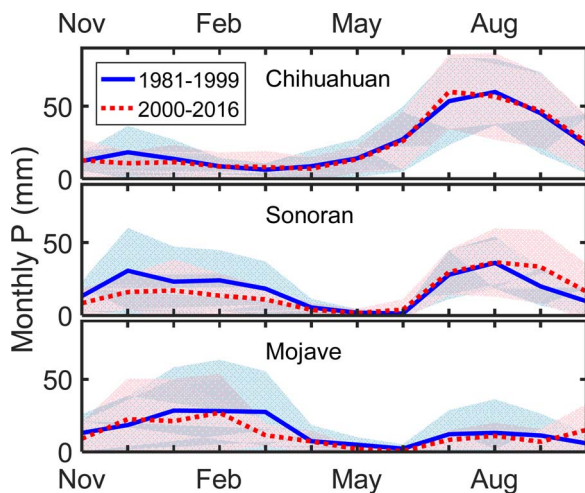


Fig. 8. Mean monthly precipitation for each desert before and after the year 2000. Shading shows temporal standard deviations among years.

Shuttleworth, 2012), small inter-seasonal carry-over of soil moisture (Andraski, 1997; Templeton et al., 2014) or errors in measurements and processing (Moreo et al., 2017). These results imply that representing local water balance at these sites does not necessarily require adjusting ET upward to force energy balance closure (Scott, 2010). This may be

due to a failure to properly account for energy storage terms in typical closure assessments performed with sub-daily fluxes (Leuning et al., 2012). It has previously been assumed that in dryland environments, $ET \approx P$ at seasonal or longer timescales (Kurt and Small, 2004; Reynolds et al., 2000). However, during the wettest summers in the Chihuahuan and Sonoran Deserts, when precipitation exceeded ~ 150 mm, $ET < P$. Because potential evapotranspiration (PET) $> P$ during summer at these desert sites, $ET < P$ likely occurred as a result of hydrologic losses to R and D , which occurs primarily along ephemeral runoff channels (Goodrich et al., 2004; Templeton et al., 2014) as supported by independent watershed measurements at two sites (Fig. 5). Controls on hydrologic losses may include precipitation intensity, vegetation, soils, and channel morphology (Polyakov et al., 2010; Turnbull et al., 2013). Collectively, our results support the idea that precipitation likely overestimates water available to drive CO_2 exchange (Biederman et al., 2016; Ponce-Campos et al., 2013; Villarreal et al., 2016), particularly in the Sonoran and Chihuahuan Deserts, where precipitation is dominated by high-intensity summer rainfall.

4.3. CO_2 exchange in warm desert shrublands of North America

It is not surprising that GEP was positively linked with water availability (Fig. 6, Fig. 7), as has been demonstrated many times for dryland ecosystems (e.g. Biederman et al., 2016; Huxman et al., 2004; Muldavin et al., 2008; Noy-Meir, 1973; Scott et al., 2015). However, our results did not support our expectation that WUE would be greater

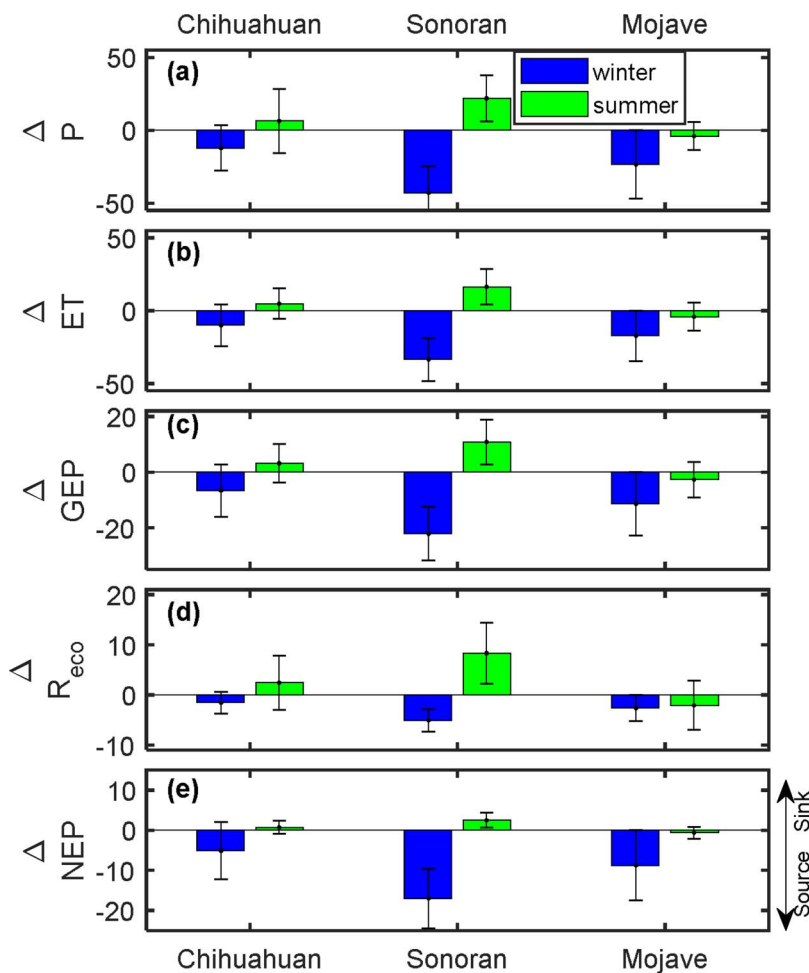


Fig. 9. Differences between seasonal water and CO₂ exchanges from 2000 to 2016 as compared with 1981–1999. Shown are mean and standard deviation of the differences. In (a) and (b), water fluxes are in mm. In (c–e) CO₂ fluxes are in gC m².

in winter due to reduced evaporative losses (i.e. increased T/ET) resulting from deeper soil infiltration and lower winter VPD. Greater underlying water use efficiency (Fig. 7a) in summer suggests that stomatal response may have partially compensated for the detrimental effects of VPD at the ecosystem scale (Beer et al., 2009; Reichstein et al., 2007). It should be noted that partitioning of available water between transpiration and evaporation may be a dominant control of WUE in open shrublands, where the ratio of T/ET may vary widely (i.e. 30–70%) depending on bare soil fraction, precipitation sequencing and phenology (Scott and Biederman, 2017). This large and variable role of abiotic evaporation in desert ecosystems challenges our ability to link process-level responses of vascular plants with the functional relationships between water and carbon at the ecosystem scale (Medlyn et al., 2017).

An absence of seasonal differences in WUE suggests that greater net productivity during winter in shrublands (Huenneke et al., 2002; Jia et al., 2016; Muldavin et al., 2008; Petrie et al., 2015) is related to carbon use efficiency (CUE). Greater winter CUE is supported by our finding of, on average, more than three times as much R_{eco} per unit of GEP during summer than winter, making winter a much more effective season for net productivity in shrublands (Fig. 7d). Although photosynthate production (GEP) is a first-order control of respiration across a range of temporal scales (Litton et al., 2007; Vargas et al., 2011; Waring et al., 1998), the critical result here is a weaker coupling of this relationship during winter. R_{eco} may be partially decoupled from GEP during winter because lower winter temperatures (Fig. S5) may reduce ecosystem respiration relative to ongoing photosynthesis by evergreen shrubs (Wang et al., 2014), or because deeper soil moisture infiltration in winter may support activity of deep-rooted shrubs while rapid drying

limits heterotrophic respiration in the litter and upper soil layers (Reichstein et al., 2002; Yang and Zhou, 2013).

Desert ecosystem fluxes are small in magnitude and inherently variable (Biederman et al., 2017; Evans et al., 2014; Noy-Meir, 1973). Measurement uncertainty is likely comparable to these small net exchanges. However, many sources of uncertainty are small (Fig. S1), and systematic errors affect absolute flux magnitudes more than the relationships among variables, which are comparatively robust (Baldocchi, 2008; Desai et al., 2008; Lasslop et al., 2010). We therefore emphasize the value of long-term, multi-site synthesis enabled by observation networks such as AmeriFlux (Novick et al., 2017). We require a greater number of observations to adequately characterize desert ecosystem function (Chu et al., 2017), in contrast to their poor representation in currently available datasets such as FluxNet 2015 (<http://fluxnet.fluxdata.org/data/fluxnet2015-dataset/>). Here, combining six sites and 33 site-years enabled identification of relationships among mechanistically linked fluxes (Fig. 1) despite the small magnitude and narrow range of flux values. More observations are particularly needed for the Mojave Desert due to its low and episodic water availability and the importance of winter flux seasonality demonstrated by our results.

4.4. Implications for north american desert carbon balance in the 21st century

We combined our results with historical precipitation data for 1981–2016 across each desert to estimate the impacts of reduced annual and winter precipitation on CO₂ exchanges (Cook et al., 2015; Seager and Vecchi, 2010). Mean monthly precipitation was lower in the

21st century for some winter months in the Chihuahuan and Mojave Deserts and was lower for all winter months in the Sonoran Desert (Fig. 9).

From the precipitation values in each year, we predicted each flux in Fig. 1 including ET (based on Fig. S6), GEP (Fig. 7b), R_{eco} (Fig. 7d), and $NEP = GEP - R_{eco}$ (Fig. 9). While any changes in summer GEP were largely counteracted by summer R_{eco} changes (Fig. 7c, d), the lower R_{eco} response to winter moisture resulted in winter declines in net carbon uptake across the three deserts (Fig. 9e). When multiplied by the shrubland area of each desert, these changes suggest an annual decline in net carbon uptake of 6.8 Tg C for the years 2000–2016 as compared with 1981–1999. While there are many sources of uncertainty in this estimate including spatial extrapolation from limited sites up to the three deserts with their inherent variabilities in climate and land cover, we suggest this analysis provides a valuable first-order estimate based on direct observations.

5. Conclusions

This study highlighted the importance of efforts to understand ecologically available water including measurements (e.g. runoff, soil moisture, and drainage) as well as efforts to define and predict water availability as a function of variables such as climate, topography, soils, and vegetation. Although we found relationships linking water availability (ET) to GEP and GEP to R_{eco} (Fig. 7), and therefore to NEP (Fig. 1), we did not find a *direct* relationship between ET and NEP (Fig. S2a) as expected based on prior synthesis results in dryland ecosystems of the Southwest (Biederman et al., 2016). Instead, we found that the relationship between respiration and gross productivity was partially decoupled in winter and that declining winter precipitation during the 21st century has already reduced the carbon sink strength of the Southwest.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agrformet.2017.11.005>.

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