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

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A B S T R A C T

Global-scale studies suggest that dryland ecosystems dominate an increasing trend in the magnitude and interannual variability of the land CO_2 sink. However, such model-based analyses are poorly constrained by measured CO_2 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 CO_2 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 CO_2 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 CO_2 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 NEP = GEP R_{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

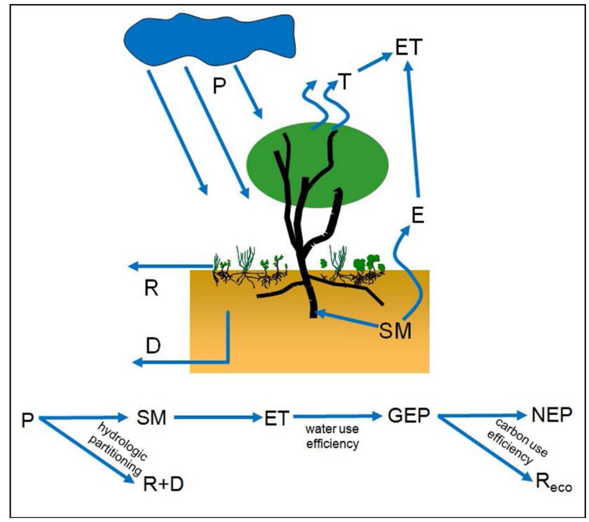

Fig. 1. Conceptual model of how water availability drives ecosystem-scale carbon dioxide exchange in drylands, based on Biederman et al. (2016). After some precipitation (P) is lost to runoff (R) and drainage (D), remaining water recharges soil moisture (SM). Soil moisture is depleted by evaporation (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 (WUE = GEP/ET) and carbon use efficiency (CUE = NEP/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