

Grassland to shrubland state transitions enhance carbon sequestration in the northern Chihuahuan Desert

M. D. PETRIE¹, S. L. COLLINS¹, A. M. SWANN², P. L. FORD³ and M. E. LITVAK¹

¹Department of Biology, University of New Mexico, Albuquerque, New Mexico, USA, ²Department of Biology, Sevilleta LTER, University of New Mexico, Albuquerque, New Mexico, USA, ³USDA Forest Service, Rocky Mountain Research Station, Albuquerque, New Mexico, USA

Abstract

The replacement of native C₄-dominated grassland by C₃-dominated shrubland is considered an ecological state transition where different ecological communities can exist under similar environmental conditions. These state transitions are occurring globally, and may be exacerbated by climate change. One consequence of the global increase in woody vegetation may be enhanced ecosystem carbon sequestration, although the responses of arid and semiarid ecosystems may be highly variable. During a drier than average period from 2007 to 2011 in the northern Chihuahuan Desert, we found established shrubland to sequester 49 g C m⁻² yr⁻¹ on average, while nearby native C₄ grassland was a net source of 31 g C m⁻² yr⁻¹ over this same period. Differences in C exchange between these ecosystems were pronounced – grassland had similar productivity compared to shrubland but experienced higher C efflux via ecosystem respiration, while shrubland was a consistent C sink because of a longer growing season and lower ecosystem respiration. At daily timescales, rates of carbon exchange were more sensitive to soil moisture variation in grassland than shrubland, such that grassland had a net uptake of C when wet but lost C when dry. Thus, even under unfavorable, drier than average climate conditions, the state transition from grassland to shrubland resulted in a substantial increase in terrestrial C sequestration. These results illustrate the inherent tradeoffs in quantifying ecosystem services that result from ecological state transitions, such as shrub encroachment. In this case, the deleterious changes to ecosystem services often linked to grassland to shrubland state transitions may at least be partially offset by increased ecosystem carbon sequestration.

Keywords: carbon sequestration, Chihuahuan Desert, creosotebush shrubland, desert grassland, ecological state transition, ecosystem services

Received 30 April 2014 and accepted 24 August 2014

Introduction

The replacement of dominant vegetation communities via ecological state transitions is occurring worldwide as a consequence of global environmental change (Scheffer & Carpenter, 2003), and these transitions may alter the quality and timing of key ecosystem services (Schlesinger *et al.*, 1990; Maestre *et al.*, 2012). Ecological state transitions are especially common in aridland ecoregions in response to multiple anthropogenic drivers, and the potential for climate-induced state transitions may be increasing (Reynolds *et al.*, 2007; Diffenbaugh *et al.*, 2008; D'Odorico *et al.*, 2012). Climate model simulations for the southwestern United States predict greater aridity in the coming decades because of warmer temperatures and more variable precipitation regimes (Seager *et al.*, 2007; Gutzler & Robbins, 2011), and additional projections suggest that the summer monsoon may occur later in the growing season (Seth

et al., 2011). In addition to long-term change, extreme drought events in the southwestern US have had profound effects on vegetation communities regionally and locally in the past 60 years (Breshears *et al.*, 2005). It follows that the greater aridity produced by a changing climate is likely to increase the frequency and extent of ecosystem state transitions.

One widespread ecological state transition in arid and semiarid ecosystems is from C₄-dominated grassland to C₃-dominated shrubland (Eldridge *et al.*, 2011). As a state transition, shrub encroachment often results in permanent and measurable changes to ecosystem functioning and includes reduced plant species diversity (Baez & Collins, 2008; Knapp *et al.*, 2008; Ratajczak *et al.*, 2012), increased spatial heterogeneity in resource availability (Bhark & Small, 2003; Turnbull *et al.*, 2010), increased surface temperatures (D'Odorico *et al.*, 2010, 2012), and altered timing of ecosystem mass and energy exchange (Kurc & Small, 2007; Brunsell *et al.*, 2011). These changes may in turn feed back to promote further state transition (D'Odorico *et al.*, 2013). As a beneficial change in services, some studies have shown an

Correspondence: M.D. Petrie, tel. +1-505-453-4706, fax +1-505-277-0304, e-mail: matt@sevilleta.unm.edu

increase in above- or belowground ecosystem carbon sequestration as a result of grassland to shrubland state transitions (Jackson *et al.*, 2002; Emmerich, 2007; Knapp *et al.*, 2008). In the Chihuahuan Desert, the conditions under which grassland and shrubland may outperform each other remain unclear; Kurc & Small (2004, 2007) found grassland to be more productive than creosotebush-dominated shrubland during relatively wet growing seasons, whereas Throop *et al.* (2012) found that mesquite-dominated shrubland was more productive than grassland in a water-manipulation experiment. In other aridland systems, variables including groundwater depth (Scott *et al.*, 2014) and soil inorganic carbon content (Emmerich, 2003) may additionally influence grassland and shrubland productivity and ecosystem C sequestration.

Understanding how carbon exchange is altered by changing ecological states is of primary importance for modeling land surface processes in GCMs (Schimel, 2010). Arid and semiarid ecoregions cover 40% of the terrestrial land surface and may have an important influence on patterns of global carbon sequestration during years of above average precipitation (Reynolds *et al.*, 2007; Poulter *et al.*, 2014). Although arid ecosystems exhibit relatively low net primary production, increasing lignification and aboveground carbon storage as a result of shrub encroachment may increase above- and belowground carbon sequestration (Jackson *et al.*, 2002; Emmerich, 2007). It is unclear, however, if C sequestration is consistent through time, or can be maintained under likely scenarios of increased aridity due to global climate change (Poulter *et al.*, 2014). By quantifying the carbon sequestration dynamics of established grassland and shrubland communities, we can elucidate the degree to which grassland to shrubland transitions impact ecosystem carbon sequestration potential.

We measured differences in production and ecosystem carbon exchange dynamics between established Chihuahuan Desert grassland and nearby creosotebush shrubland in response to interannual availability in moisture, to determine if the state transition from C₄-dominated grassland to C₃-dominated shrubland resulted in increased C sequestration. During our 5-year study, total annual precipitation was at or below average, providing an analog to the type of drier conditions that are likely to occur in coming decades (Gutzler & Robbins, 2011). We measured precipitation, soil moisture, aboveground and belowground net primary production, and ecosystem carbon and energy exchange to: (i) compare the annual production and carbon sink strength of grassland and shrubland communities; (ii) characterize grassland and shrubland carbon exchange dynamics at daily, seasonal and interannual timescales; and (iii) determine the sensitiv-

ity of grassland and shrubland productivity to soil moisture availability and energy partitioning during their active growing seasons. By doing so, we identified the carbon sequestration potentials of arid grassland and shrubland, and identified the biotic and abiotic variables that shaped carbon exchange in these ecosystems over multiple temporal scales.

Site

Our research was conducted at the Sevilleta National Wildlife Refuge (SNWR), New Mexico, USA (34.3° N latitude, 106.8° W longitude). At the SNWR, temperature and precipitation interact to drive a bimodal growing season that is punctuated by two periods of vegetation production (Notaro *et al.*, 2010). The spring growing season is driven by increasing temperature and soil moisture derived from winter rainfall, and the summer growing season is driven by monsoon rainfall (Pennington & Collins, 2007; Muldavin *et al.*, 2008). The period between these seasons (approximately May–June) is typically water-limited. Mean annual precipitation for the grassland and shrubland sites was 244 mm from 1996 to 2011, and 125 mm of this (51%) occurred during the summer monsoon from July to September. During our study from 2007 to 2011, precipitation at the grassland site averaged 208 mm annually and 93 mm during the summer monsoon (−14.8% and −25.6% compared to 1996–2011, respectively), and the shrubland site averaged 226 mm annually and 100 mm during the summer monsoon (−7.4% and −20.0%, respectively; Fig. 1).

The northern boundary of creosotebush shrubland and the southern boundary of mixed blue and black-grama grassland coexist at the SNWR, and northward expansion of creosotebush into desert grassland is ongoing in the Chihuahuan Desert region (Peters *et al.*, 2006). We used long-term data from an eddy covariance tower in black grama (*Bouteloua eriopoda*)-dominated desert grassland (34.362° N, 106.702° W) and another tower 5 km south in creosotebush (*Larrea tridentata*)-dominated shrubland (34.335° N, 106.744° W). Elevation at both sites is approximately 1615 m. After a 2009 fire (DOY 217), a new tower was installed in a nearby unburned grassland location approximately 1.5 km away (34.355° N, 106.675° W), and we used data from this tower in 2010 and 2011. Therefore, we did not have data from 4 August 2009 to 1 January 2010 in grassland.

Materials and methods

Aboveground production (ANPP: g C m^{−2} yr^{−1}) was measured in spring (May) and fall (September–October) each year from 2007 to 2011 at the creosote shrubland and at the mixed grassland sites. Between 22 and 40, 1 m² permanent quadrats

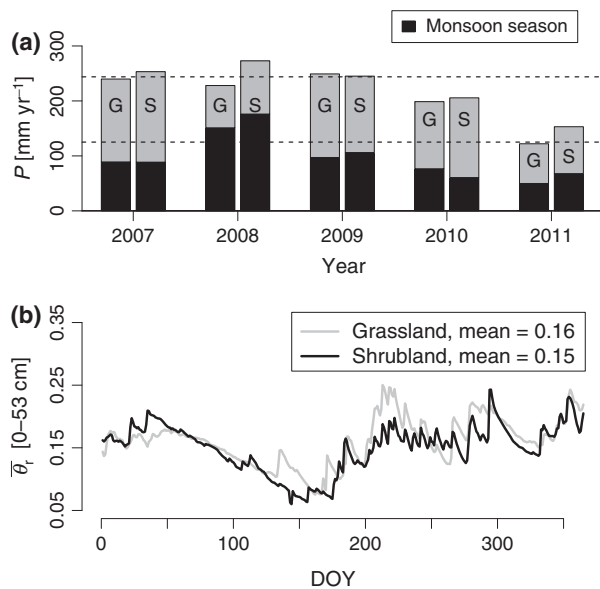


Fig. 1 Total annual and monsoon precipitation at the creosotebush shrubland (S) and mixed grassland (G) site in 2007–2011 (Panel a) and mean daily relative extractable soil moisture (θ_r) (Panel b). Mean monsoon precipitation and mean annual precipitation from 1996 to 2011 are indicated by horizontal lines in Panel a. θ_r was greater on average at the grassland site ($P < 0.001$).

were located at each grassland and shrubland site for measuring ANPP using a nondestructive allometric sampling method and linear regression based on measured species volume units developed from total standing biomass measurements (Hunneke *et al.*, 2001; Muldavin *et al.*, 2008). Belowground production (BNPP: $\text{g C m}^{-2} \text{ yr}^{-1}$) was measured each year using root ingrowth 'donuts' (Milchunas *et al.*, 2005). During this period, 10 replicate ingrowth structures in mixed grassland and creosotebush shrubland were harvested annually in November at 0–15 cm and 15–30 cm depth. The majority of grassland root biomass occurs in the upper 30 cm of soil whereas shrub roots can penetrate much deeper (Kurc & Small, 2007). Soil were sieved (2 mm) to remove roots, which were then dried at 60 °C and weighed to estimate belowground biomass ($\text{g m}^{-2} \text{ yr}^{-1}$). Data presented here are the combined production estimates from 0 to 30 cm.

Fluxes of surface carbon dioxide, water and energy were measured continuously from identical, tripod-based eddy covariance instruments at the mixed grassland and creosotebush shrubland sites from 2007 to 2011 (Anderson-Teixeira *et al.*, 2011). In both sites, a three-axis sonic anemometer (Campbell Scientific CSAT-3, Logan, UT, USA) measured vertical wind speed, and an open-path gas analyzer (LiCor LI-7500, Lincoln, NE, USA) measured carbon and water vapor concentrations. We compiled covariances to 30 min averages, corrected for temperature and water vapor influences (Webb *et al.*, 1980), and sensor separation and frequency responses (Massman, 2000). We used a planar fit coordinate system to account for anemometer tilt (Anderson-Teixeira *et al.*, 2011). We removed data in the case of instrument malfunction, when winds were

coming from behind the tower, when wind speed was too low (low friction velocity), and during rainfall events. This resulted in very few data gaps and did not limit our gapfilling procedure. We gapfilled NEE, latent and sensible energy fluxes and estimated ecosystem respiration (RE) using the Max Planck Institute (Open MPI) procedure (Falge *et al.*, 2001; Reichstein *et al.*, 2005) (<http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/index.php>). We calculated gross primary production as $\text{NEE} + \text{RE}$. Carbon flux data of net ecosystem exchange (NEE), gross primary production (GPP), and ecosystem respiration (RE) are presented in this study as $\text{g C m}^{-2} \text{ time}^{-1}$.

We used daily GPP to estimate the growing season onset and vegetation senescence in grassland and shrubland, where onset was the first day of 10 consecutive days where $\text{GPP} > 0.25 \text{ g C d}^{-1}$ in spring or summer, and senescence was the last day of 10 consecutive days where $\text{GPP} < 0.25 \text{ g C d}^{-1}$ in fall or winter. This basic threshold technique was sensitive to the abrupt changes in vegetation production that occur at the beginning and end of the growing season in the Chihuahuan Desert (Kurc & Small, 2007; Collins *et al.*, 2008).

Soils at the grassland site are classified as Turney loamy sand and soils at the shrubland site are classified as a mix between Turney loam and Nickel-Caliza very gravelly sandy loam. Differences in soil texture result in a saturated hydraulic conductivity (K_{sat}) of 1.5–5.0 cm h^{-1} at the grassland site and a K_{sat} of 2.5–8.5 cm h^{-1} at the shrubland site (United States Department of Agriculture NRCS, 2013).

Volumetric soil moisture was measured from 2007 to 2011 at grassland and shrubland eddy covariance tower sites using soil water content probes (Campbell Scientific CS 616) buried horizontally at 2.5 cm, 12.5 cm, 22.5 cm, 37.5 cm and 52.5 cm depth in 6 pits at each site, 3 under vegetation and 3 in vegetation interspaces. These probes measure volumetric soil moisture using a time-domain technique, and are accurate at the low θ values that often occur in aridland soils. At the mixed grassland sites, data were available beginning on DOY 163 in 2007, for all of 2008, were not available in 2009, and were available beginning on DOY 56 in 2010 and for all of 2011. At the shrubland site, data were available beginning on DOY 157 in 2007, for all of 2008, beginning on DOY 176 in 2009 and for all of 2010–2011. Soil moisture was recorded as 30 min averages and converted to mean daily soil moisture for all analyses. To account for differences in water-holding capacity in soils at the grassland and shrubland sites, we normalized soil moisture as relative extractable soil moisture (θ_r), calculated as:

$$\theta_r = \frac{\theta - \theta_w}{\theta_{\text{fc}} - \theta_w} \quad (1)$$

where θ_w is soil moisture at vegetation wilting point and θ_{fc} is soil moisture at soil field capacity. Due to the depth of the soil moisture profile data, we estimated θ_w to be the lowest observed θ value from 2007 to 2011 ($\theta_w = 0.065$ shrubland; 0.061 grassland), and estimated θ_{fc} from soil water holding capacity and profile depth ($\theta_{\text{fc}} = 0.35$ shrubland; 0.31 grassland) (United States Department of Agriculture NRCS, 2013). These values corroborated with soil moisture release curves obtained for soils at the grassland and shrubland eddy covariance tower sites. All statistics, analyses and figures were produced using R (R Development Core Team, 2011).

Results

Our study period was slightly drier than average [208 mm annually (14.8% lower than 1996–2011 mean), 93 mm monsoon (25.6% lower than 1996–2011 mean)]. The year 2011 was very dry, 2006 (the year prior to our study) had an especially strong monsoon season, and 2009 had high October rainfall. From 2007 to 2011, total annual precipitation was similar between grassland and shrubland ($P > 0.05$), although mean daily θ_r was 6.6% higher in grassland ($P < 0.001$) (Fig. 1). Mean daily Bowen Ratio (β) did not differ between sites ($P > 0.97$), however, indicating that grassland and shrubland experienced similar turbulent energy flux partitioning during our study.

Despite having higher average annual net primary production than shrubland from 2007 to 2011, desert grassland was a net carbon source (annual positive NEE) while the adjacent shrubland was a net carbon sink (annual negative NEE; Figs 2 and 3). In general, NPP (above- plus belowground) and NEE in grassland were more variable than shrubland, resulting in a net carbon loss from grassland of $31.1 \text{ g C m}^{-2} \text{ yr}^{-1}$ on average, while the less variable, lower production shrubland had a net C uptake of $49.0 \text{ g C m}^{-2} \text{ yr}^{-1}$. Despite measured above- and belowground plant growth, grassland was a net source of carbon in four of the 5 years of our study (Fig. 2b). This pattern was particularly notable in 2007 and 2008, where grassland NPP was larger than shrubland NPP, yet grassland NEE indicated annual net carbon loss (Figs 2 and 3). NPP data from grassland and shrubland in 2005 and 2006 (2 years prior to our study) were not anomalous from those of 2007–2011 (Figs 2a and 3a), suggesting that the pattern of grassland and shrubland carbon sequestration were likely similar over the 7 year period.

Although grassland net primary production was higher and more variable on average than shrubland ($105 \pm 67 \text{ g}$ and $77 \pm 26 \text{ g C m}^{-2} \text{ yr}^{-1}$, respectively, Figs 2a and 3a), annual shrubland GPP was 5% higher than grassland GPP (GPP = 159 g C and $152 \text{ g C m}^{-2} \text{ yr}^{-1}$, respectively, Figs 2c and 3c). The timing of maximum GPP differed seasonally between grassland and shrubland. Based on GPP, grassland was most active in spring and summer, whereas shrubland was most active in spring and fall (Table 1). Average shrubland growing season was 27 days longer than that of grassland (Fig. 4), with shrubland notably more active later in the growing season than grassland. Therefore, ground measurements of NPP did not corroborate with eddy covariance measurements of GPP. NPP by definition cannot be negative, whereas eddy covariance measurements include total ecosystem C exchange. Some

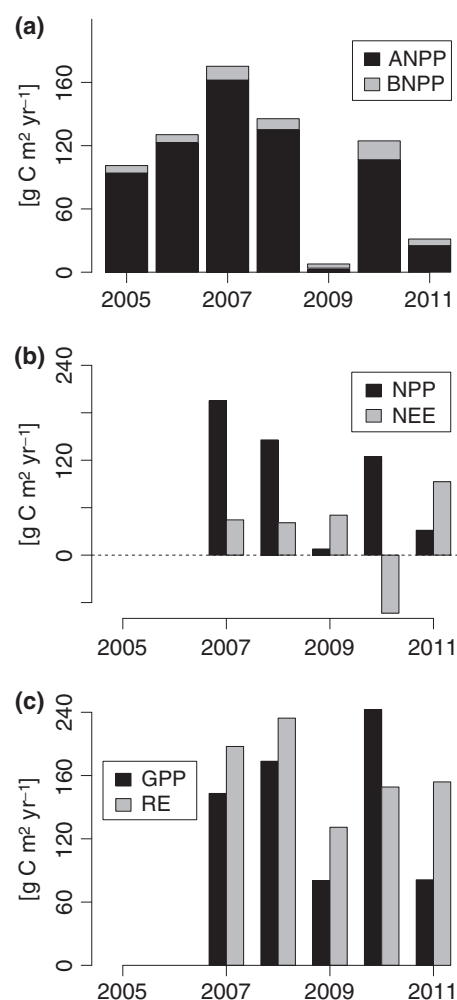


Fig. 2 Annual aboveground (ANPP) and belowground (BNPP) production from 2005 to 2011 (Panel a), net primary production (NPP) and net ecosystem exchange (NEE: $\text{g C m}^{-2} \text{ yr}^{-1}$) from 2007 to 2011 (Panel b) and gross primary production (GPP) and ecosystem respiration (RE) from 2007 to 2011 (Panel c) in desert grassland and creosotebush shrubland.

differences may also result from root production below the 30 cm threshold in shrubland (Jackson *et al.*, 2002). The ratio of RE to GPP shows that RE was 20% higher than GPP in grassland ($\text{RE}/\text{GPP} = 1.2$), whereas this ratio in shrubland shows that RE was 30% lower than GPP in shrubland ($\text{RE}/\text{GPP} = 0.7$). Grassland RE was 66% higher than shrubland RE ($\text{RE} = 183 \text{ g C}$ and $110 \text{ g C m}^{-2} \text{ yr}^{-1}$, respectively). Annually, slightly higher GPP in shrubland and much higher RE in grassland resulted in an average difference in carbon assimilation of $80.1 \text{ g C m}^{-2} \text{ yr}^{-1}$ between grassland and shrubland during our study.

The difference in daily values of NEE between grassland and shrubland was largest during dry days (Bowen Ratio: $\beta > 5$). Bowen Ratio (β : H/LE) measure-

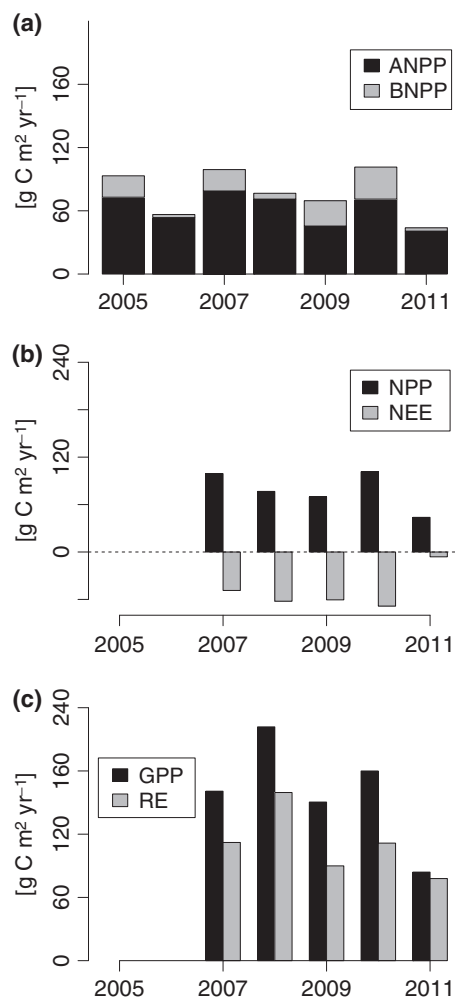


Fig. 3 Annual aboveground (ANPP) and belowground (BNPP) production from 2005 to 2011 (Panel a), net primary production (NPP) and net ecosystem exchange (NEE: $\text{g C m}^{-2} \text{yr}^{-1}$) from 2007 to 2011 (Panel b) and gross primary production (GPP) and ecosystem respiration (RE) from 2007 to 2011 (Panel c) in desert grassland and creosotebush shrubland.

ments from eddy covariance data are the ratio of partitioning between sensible energy (H) and latent energy (LE) (Bowen, 1926). We observed daily mean Bowen Ratio in this system to be more frequently influenced by the availability of water than the availability of energy, and higher β values indicate drier conditions usually caused by low LE . Average GPP in grassland and shrubland was similar at daily timescales (Fig. 5b), but grassland RE was $0.2 \text{ g C m}^{-2} \text{day}^{-1}$ (68%) higher than shrubland RE on average, and this difference was largest at high β values (Fig. 5c). During the growing season, carbon exchange in grassland was more sensitive to soil moisture variation than in shrubland, and grassland often displayed higher daily GPP and lower NEE than shrubland when soil moisture was available.

Table 1 Seasonal NEE and GPP

	Spring	Summer	Fall	Winter	Total
Grassland NEE (g)	7	9.5	4.5	10.1	31.1
Grassland GPP (g)	42.8	65.6	28.2	15.5	152.1
Grassland RE (g)	49.8	75.1	32.7	25.6	183.2
Grassland NEE [%]	23	31	14	32	100
Grassland GPP [%]	37	41	17	5	100
Grassland RE [%]	27	41	18	14	100
Shrubland NEE (g)	-21.9	-2.3	-19.4	-5.4	-49
Shrubland GPP (g)	39.9	55.5	46.4	17.6	159.4
Shrubland RE (g)	18	53.2	27	12.2	110.4
Shrubland NEE (%)	45	5	39	11	100
Shrubland GPP (%)	25	35	29	11	100
Shrubland RE (%)	16	48	25	11	100

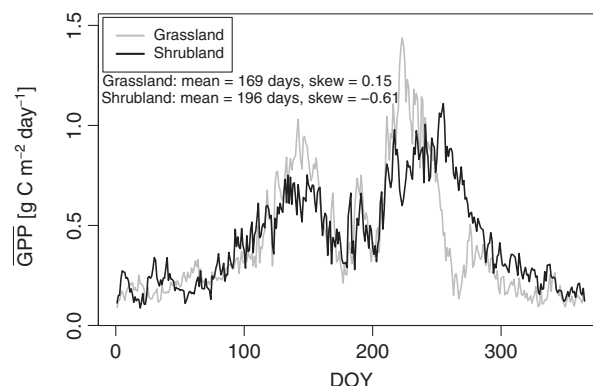


Fig. 4 Mean daily gross primary production (GPP) from 2007 to 2011 shows that creosotebush shrubland had a longer growing season than desert grassland by 27 days on average, and was notably more active late in the year.

As θ_r increased from 10% to 20%, increasing GPP dominated the grassland carbon balance, and grassland became a net carbon sink where $\theta_r \sim 14.5\%$ (Fig. 6b). Grassland GPP also increased at a higher rate than RE over this interval (Fig. 6c and d). Although shrubland was a net carbon sink on average at every θ_r value, it was a notably smaller sink than grassland at $\theta_r \geq 15\%$ (Fig. 6b).

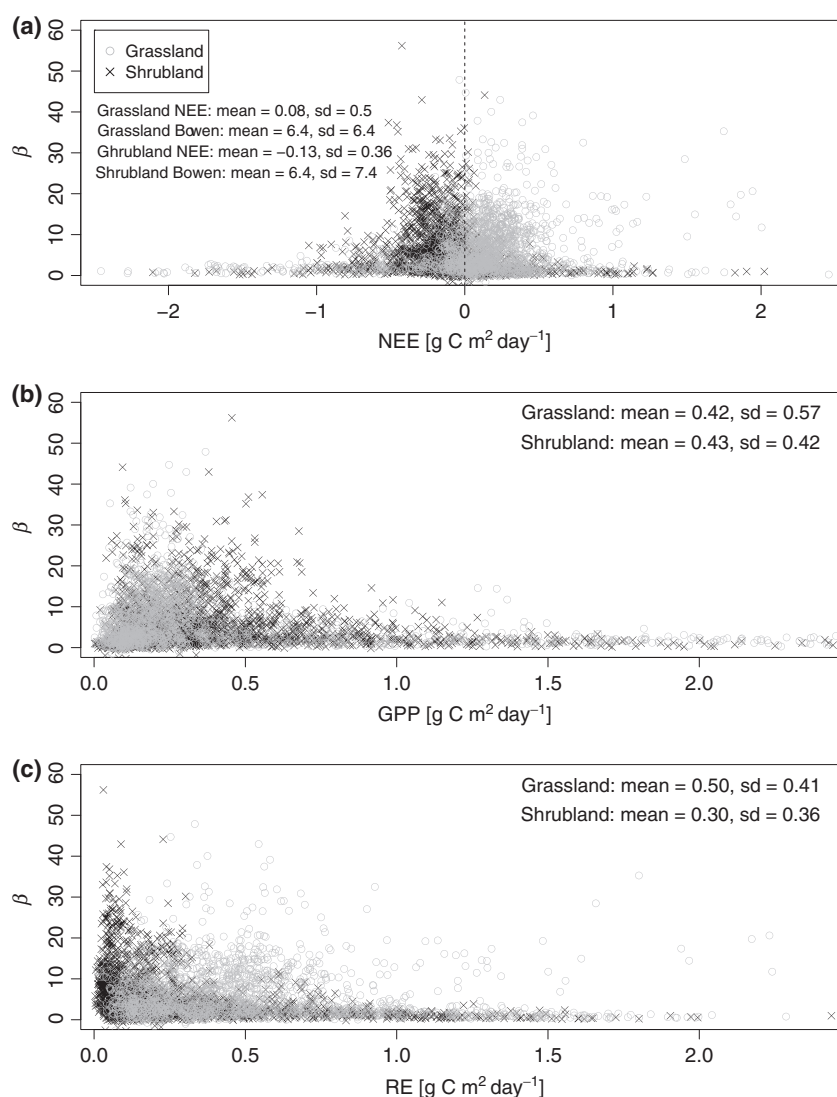


Fig. 5 Relationship among daily Bowen Ratio (β :H\LE) to daily net ecosystem exchange (NEE) (Panel a), daily gross primary production (GPP) (Panel b) and daily ecosystem respiration (RE) (Panel c) in desert grasslands and creosotebush shrublands from 2007 to 2011. Summary statistics are included (mean and standard deviation) and carbon flux units are in $\text{g C m}^{-2} \text{ day}^{-1}$.

Discussion

Grassland and shrubland production and carbon sequestration

The high variability in annual grassland production observed in our study (Fig. 2) and by others (Kurc & Small, 2007; Muldavin *et al.*, 2008; Robertson *et al.*, 2009) illustrates the ability of grassland vegetation to capitalize on wet years at the cost of reduced sequestration during dry years. Kurc & Small (2007) found that from 2000 to 2002, this grassland was a net C sink, but this occurred under a precipitation regime that was 28% higher (123 mm) than the monsoon average (96 mm) of

our study (2007–2011). During the growing season, soil water availability strongly influenced grassland net carbon balance by preferentially increasing GPP compared to RE (Fig. 6). Therefore, during relatively dry years, we found grassland RE to be greater than GPP (Figs 2 and 5; Table 1). Grassland was a small net carbon sink only in 2010 (Fig. 2b), possibly because spring production was increased by rainfall during the prior October after grassland plants had senesced. Conversely, this grassland was a large C sink during the relatively wetter years of Kurc & Small (2004, 2007), and maximum GPP may be up to two times higher in grassland than shrubland during periods of high soil moisture availability (Kurc & Small, 2007; Robertson *et al.*, 2009).

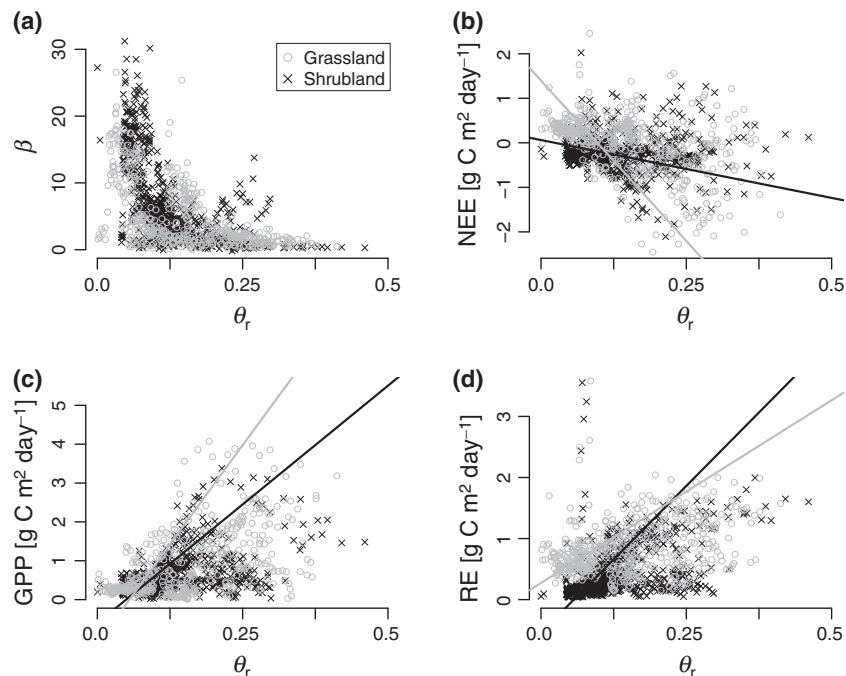


Fig. 6 Relationship between relative extractable soil moisture (θ_r) and Bowen Ratio (β) (Panel a), Net Ecosystem Exchange (NEE) (Panel b, grassland $R^2 = 0.18$, shrubland $R^2 = 0.01$), Gross Primary Production (GPP) (Panel c, grassland $R^2 = 0.29$, shrubland $R^2 = 0.22$) and ecosystem respiration (RE) (Panel d, grassland $R^2 = 0.07$, shrubland $R^2 = 0.17$) for desert grasslands and creosotebush shrublands during their active growing seasons. All carbon flux units are in $\text{g C m}^{-2} \text{ day}^{-1}$.

In contrast to grassland, shrubland displayed lower and less variable annual production (Fig. 3), and was a small carbon sink in every year of our study. Shrubland had a longer growing season than grassland, and assimilated the majority of annual carbon during spring and fall (84%), minimizing the effect of drier than average summer conditions (Fig. 1). The shrubland carbon sink in fall was nearly as large as in spring (Table 1), which has formerly been identified as the most productive period for creosotebush (Pennington & Collins, 2007; Muldavin *et al.*, 2008). Although Sponseller *et al.* (2012) found that creosotebush production may be highest in response to wet summers, our results suggest that dry conditions may alternately favor spring and fall production (Table 1). During the dry years of our study, shrubland was a small carbon sink at every time-scale of analysis, and the characteristics of shrubland carbon sequestration suggest this sink will persist in a more arid future climate.

Soil respiration in semiarid ecosystems is often dominated by heterotrophic respiration from soil biota (Belnap, 2002; Collins *et al.*, 2014), with precipitation and θ pulses having a large influence on RE during the growing season (Belnap *et al.*, 2004; Jenerette *et al.*, 2008). In addition to this, we also observed RE $\sim 0.6 \text{ g C m}^{-2} \text{ day}^{-1}$ during the growing season in grassland at $\theta_r \sim 5.0\%$, when biotic activity is expected to be limited

by low water availability (Fig. 6d). This efflux was not observed in shrubland. Although inorganic C exchange may be a large component of carbon balance in many arid and semiarid ecosystems (Emmerich, 2003; Stone, 2008), the potential for emissions from belowground petrocalcic soil horizons, determined from carbon isotope analysis, is low in the northern Chihuahuan Desert and not a significant source of carbon at the SNWR (Serna-Perez *et al.*, 2006; Breecker *et al.*, 2012). Instead, this carbon loss is likely a result of photodegradation of senesced aboveground plant biomass, which adds an additional, abiotic C flux out of the system (Rutledge *et al.*, 2010; Lee *et al.*, 2012). Abiotic C efflux is therefore an important component of carbon balance in this arid grassland, measurably contributing to annual grassland carbon loss.

Climate change and ecological state transitions

Carbon sequestration is likely to occur as a consequence of shrub encroachment in the northern Chihuahuan Desert. Over the past 100 years, monsoon season precipitation events have increased in frequency but decreased in magnitude, and the longest wet and dry periods have increased in length (Petrie *et al.*, 2013). Furthermore, projected later monsoon onset in the southwestern US will reduce precipitation in July and

increase it in October, when shrubs remain active but grasses do not (Table 1; Fig. 4) (Seth *et al.*, 2011; Cook & Seager, 2013). At the SNWR, grassland was especially sensitive to dryness during summer. In the driest year of our study (2011), the grassland growing season was only 14 days long based on GPP, whereas that of shrubland was 48 days long. If future climate induces greater aridity in summer, and monsoon precipitation extends later into the fall, grassland will become increasingly vulnerable to further shrub encroachment.

Although the specific mechanisms that induce grassland to shrubland state transitions in the southwestern US are complex, our results indicate that shrub encroachment will lead to increased carbon sequestration relative to grassland. If the shrubland carbon sink strength averages $49 \text{ g C m}^{-2} \text{ yr}^{-1}$, as seen in our study (Table 1), large-scale state transitions may increase the regional carbon sink by as much as $490 \text{ kg C ha}^{-1} \text{ yr}^{-1}$ in the southwestern US. The potential for grassland to shrubland land class change is also substantial; the Southwest Regional Gap Analysis Project (SWReGAP) estimates that there are 14.9 M hectares of blue and black-grama dominated desert grassland in New Mexico alone (USGS National Gap Analysis Program, 2014). The sink potential of shrubland is produced by growth of existing individuals as well as infill, which continues to occur in areas undergoing encroachment. Indeed, creosotebush density (by sapwood area) at this site, which has been dominated by creosotebush for longer than 40 years, actually increased from 2001 to 2013 (Fig. 7). Furthermore, Evans *et al.* (2014) found increases in ecosystem C sequestration over 10 years in a CO_2 enrichment experiment in the Mojave Desert, and Barron-Gafford *et al.* (2012) found higher C sequestration in mesquite woodland compared to grassland in

the Sonoran Desert. Due to these characteristics, the shrubland carbon pool is likely to both persist and increase in coming decades. Semiarid ecosystems have a strong influence on interannual variability in terrestrial carbon sequestration globally (Poulter *et al.*, 2014), and the patterns that we observed in our study suggest that grassland carbon sequestration that occurs during wet periods (Kurc & Small, 2004, 2007) is vulnerable to decomposition during subsequent drier periods. Conversely, semiarid shrubland is notably less vulnerable to carbon losses, and our results suggest that the state transition of grassland to shrubland over large areas ($>1000 \text{ km}^2$) would promote lower interannual variability in terrestrial carbon sequestration.

Gains in C sequestration come at a cost to other ecosystem services provided by these desert grasslands. In addition to ecological impacts, surface soil losses that accompany land class change are a significant source of dust and pollution in the southwestern US (Yin *et al.*, 2005; Field *et al.*, 2010), and shrub encroachment will lead to warmer winters in nearby urban areas as well (D'Odorico *et al.*, 2010, 2012). Land class change has been shown to influence soil moisture-precipitation feedbacks and precipitation patterns in the US Great Plains (Brunsell *et al.*, 2011), and state transitions in the Chihuahuan Desert may alter land-atmosphere interactions that are instrumental in driving vegetation activity during the summer monsoon (Dominguez *et al.*, 2008; Mendez-Barroso & Vivoni, 2010). In a future climate scenario where positive feedbacks may lengthen and intensify regional drought periods (Gutzler & Robbins, 2011), carbon sequestration, evaporation and changing ecosystem services will all be important components of climate change in the southwestern US.

Acknowledgements

This research was conducted using four datasets collected through the Sevilleta LTER. This research was partially funded by a National Science Foundation grant to the University of New Mexico for Long Term Ecological Research, by a grant from the USDA Forest Service, Western Wildland Environmental Threat Assessment Center, by NASA grant award NNX11AG91G to Litvak, and through an NSF-EPSCoR award for Hydrology to the University of New Mexico.

References

- Anderson-Teixeira K, DeLong J, Fox A, Brese DA, Litvak M (2011) Differential responses of production and respiration to temperature and moisture drive the carbon balance across a climatic gradient in New Mexico. *Global Change Biology*, 17, 410–424, doi: 10.1111/j.1365-2486.2010.02269.x.
- Baez S, Collins S (2008) Shrub invasion decreases diversity and alters community stability in northern Chihuahuan Desert plant communities. *PLoS ONE*, 3, doi: 10.1371/journal.pone.0002332.
- Barron-Gafford GA, Scott RL, Jenerette GD, Hamerlynck EP, Huxman TE (2012) Temperature and precipitation controls over leaf- and ecosystem-level CO_2 flux along

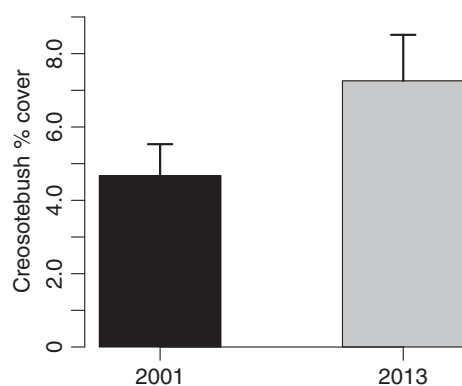


Fig. 7 Creosotebush percent cover across two 325 m transects in creosotebush-dominated shrubland at the SNWR. Creosotebush cover (%) in 2013 was higher than in 2001 (4.7% in 2001, 7.3% in 2013, $p < 0.05$). Across two longer 1000 m transects (into blue and black-grama grassland), creosotebush cover was not significantly higher in 2013 ($P > 0.13$, not shown).

- a woody plant encroachment gradient. *Global Change Biology*, **18**, 1389–1400, doi: 10.1111/j.1365-2486.2011.02599.x.
- Belnap J (2002) Nitrogen fixation in biological soil crusts from southeast Utah, USA. *Biology and Fertility of Soils*, **35**, 0178–2762, doi: 10.1007/s00374-002-0452-x.
- Belnap J, Phillips S, Miller M (2004) Response of desert biological soil crusts to alterations in precipitation frequency. *Oecologia*, **141**, 306–316, doi: 10.1007/s00442-003-1438-6.
- Bhark E, Small E (2003) Association between plant canopies and the spatial patterns of infiltration in shrubland and grassland of the Chihuahuan Desert, New Mexico. *Ecosystems*, **6**, 185–196, doi: 10.1007/s10021-002-0210-9.
- Bowen I (1926) The ratio of heat losses by conduction and by evaporation from any water surface. *Physical Review*, **27**, 779–787.
- Breecker DO, McFadden LD, Sharp ZD, Martinez M, Litvak ME (2012) Deep autotrophic soil respiration in shrubland and woodland ecosystems in central New Mexico. *Ecosystems*, **15**, 83–96, doi: 10.1007/s10021-011-9495-x.
- Breshears DD, Cobb NS, Rich PM *et al.* (2005) Regional vegetation die-off in response to global-change-type drought. *PNAS*, **102**, 15144–15148, doi: 10.1073/pnas.0505734102.
- Brunsell NA, Mechem DB, Anderson MC (2011) Surface heterogeneity impacts on boundary layer dynamics via energy balance partitioning. *Atmospheric Chemistry and Physics*, **11**, 3403–3416, doi: 10.5194/acp-11-3403-2011.
- Collins SL, Sinsabaugh RL, Crenshaw C, Green L, Porras-Alfaro A, Stursova M, Zeglin LH (2008) Pulse dynamics and microbial processes in aridland ecosystems. *Journal of Ecology*, **96**, 413–420, doi: 10.1111/j.1365-2745.2008.01362.x.
- Collins SL, Belnap J, Grimm NB *et al.* (2014) A multi-scale, hierarchical model of pulse dynamics in aridland ecosystems. *Annual Review of Ecology, Evolution and Systematics*, **45**, 397–419, doi: 10.1146/annurev-ecolsys-120213-091650.
- Cook B, Seager R (2013) The response of the North American Monsoon to increased greenhouse gas forcing. *Journal of Geophysical Research: Atmospheres*, **118**, 1690–1699, doi: 10.1002/jgrd.50111.
- Diffenbaugh NS, Giorgi F, Pal JS (2008) Climate change hotspots in the United States. *Geophysical Research Letters*, **35**, L16709, doi: 10.1007/s00704-011-0484-y.
- D'Odonorico P, Fuentes JD, Pockman WT *et al.* (2010) Positive feedback between microclimate and shrub encroachment in the northern Chihuahuan Desert. *Ecosphere*, **1**, 1–11.
- D'Odonorico P, Okin GS, Bestelmeyer BT (2012) A synthetic review of feedbacks and drivers of shrub encroachment in arid grasslands. *Ecology*, **5**, 520–530, doi: 10.1002/eco.259.
- D'Odonorico P, He Y, Collins SL, deWekker SFJ, Engel V, Fuentes JD (2013) Vegetation-microclimate feedbacks in woodland-grassland ecotones. *Global Ecology and Biogeography*, **22**, 364–379, doi: 10.1111/geb.12000.
- Dominguez F, Kumar P, Vivoni E (2008) Precipitation recycling variability and ecoclimatological stability - a study using NARR data. Part II: North American Monsoon Region. *Journal of Climate*, **21**, 5187–5203, doi: 10.1175/2008JCLI1760.
- Eldridge DJ, Bowker MA, Maestre FT, Roger E, Reynolds JF, Whitford WG (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters*, **14**, 709–722, doi: 10.1111/j.1461-0248.2011.01630.x.
- Emmerich W (2003) Carbon dioxide fluxes in a semiarid environment with high carbonate soils. *Agricultural and Forest Meteorology*, **116**, 91–102, doi: 10.1016/S0168-1923(02)00231-9.
- Emmerich W (2007) Ecosystem water use efficiency in a semiarid shrubland and grassland community. *Rangeland Ecology and Management*, **60**, 464–470, doi: 10.2111/1551-5028(2007)60[464:EWUEIA]2.0.CO;2.
- Evans L, Maio GR, Corner A, Hodgetts CJ, Ahmed S, Hahn U (2014) Self-interest and pro-environmental behaviour. *Nature Climate Change*, **3**, 122–125, doi: 10.1038/NCLIMATE1662.
- Falge E, Baldocchi D, Olson R *et al.* (2001) Gap filling strategies for long term energy flux data sets. *Agricultural and Forest Meteorology*, **107**, 71–77, doi: 10.1016/S0168-1923(00)00235-5.
- Field JP, Belnap J, Breshears DD *et al.* (2010) The ecology of dust. *Frontiers in Ecology and the Environment*, **8**, 423–430, doi: 10.1890/090050.
- Gutzler D, Robbins T (2011) Climate variability and projected change in the western United States: regional downscaling and drought statistics. *Climate Dynamics*, **37**, 835–849, doi: 10.1007/s00382-010-0838-7.
- Huenneke L, Clason D, Muldavin E (2001) Spatial heterogeneity in Chihuahuan Desert vegetation: implications for sampling methods in semi-arid ecosystems. *Journal of Arid Environments*, **47**, 257–270, doi: 10.1006/jare.2000.0678.
- Jackson R, Banner J, Jobbagy E, Pockman W, Wall D (2002) Ecosystem carbon loss with woody plant invasion of grasslands. *Nature*, **418**, 623–626, doi: 10.1038/nature00952.
- Jenerette GD, Scott RL, Huxman TE (2008) Whole ecosystem metabolic pulses following precipitation events. *Functional Ecology*, **22**, 924–930, doi: 10.1111/j.1365-2435.2008.01450.x.
- Knapp AK, Briggs JM, Collins SL *et al.* (2008) Shrub encroachment in North American grasslands: shifts in growth from dominance rapidly alters control of ecosystem carbon inputs. *Global Change Biology*, **14**, 615–623, doi: 10.1111/j.1365-2486.2007.01512.x.
- Kurc S, Small E (2004) Dynamics of evapotranspiration in semiarid grassland and shrubland ecosystems during the summer monsoon season, central New Mexico. *Water Resources Research*, **40**, W09305, doi: 10.1029/2004WR003068.
- Kurc SA, Small EE (2007) Soil moisture variations and ecosystem-scale fluxes of water and carbon in semiarid grassland and shrubland. *Water Resources Research*, **43**, W06416, doi: 10.1029/2006WR005011.
- Lee H, Rahn T, Throop HL (2012) An accounting of C-based trace gas release during abiotic plant litter degradation. *Global Change Biology*, **18**, 1185–1195, doi: 10.1111/j.1365-2486.2011.02579.x.
- Maestre FT, Salguero-Gomez R, Quero JL (2012) It is getting hotter in here: determining and projecting the impacts of global environmental change on drylands. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 3062–3075, doi: 10.1098/rstb.2011.0323.
- Massman W (2000) A simple method for estimating frequency response corrections for eddy covariance systems. *Agricultural and Forest Meteorology*, **104**, 185–198.
- Mendez-Barroso LA, Vivoni ER (2010) Observed shifts in land surface conditions during the North American Monsoon: implications for a vegetation-rainfall feedback mechanism. *Journal of Arid Environments*, **74**, 549–555, doi: 10.1016/j.jaridenv.2009.09.026.
- Milchunas D, Mosier A, Morgan J, LeCain D, King J, Nelson J (2005) Root production and tissue quality in a shortgrass steppe exposed to elevated CO₂: using a new ingrowth method. *Plant and Soil*, **268**, 111–122, doi: 10.1007/s11104-004-0230-7.
- Muldavin EH, Moore DI, Collins SL, Wetherill KR, Lightfoot DC (2008) Aboveground net primary production dynamics in a northern Chihuahuan Desert ecosystem. *Oecologia*, **155**, 123–132, doi: 10.1007/s00442-007-0880-2.
- Notaro M, Liu Z, Gallimore RG, Williams JW, Gutzler DS, Collins SL (2010) Complex seasonal cycle of ecohydrology in the Southwest United States. *Journal of Geophysical Research: Biogeosciences*, **115**, G04034, doi: 10.1029/2010JG001382.
- Pennington DD, Collins SL (2007) Response of an aridland ecosystem to interannual climate variability and prolonged drought. *Landscape Ecology*, **22**, 897–910, doi: 10.1007/s10980-006-9071-5.
- Peters D, Yao J, Gosz J (2006) Woody plant invasion at a semi-arid/arid transition zone: importance of ecosystem type to colonization and patch expansion. *Journal of Vegetation Science*, **17**, 389–396.
- Petrie M, Collins S, Gutzler D, Moore D (2013) Regional trends and local variability in monsoon precipitation in the northern Chihuahuan Desert, USA. *Journal of Arid Environments*, **103**, 63–70, doi: 10.1016/j.jaridenv.2014.01.005.
- Poulter B, Frank D, Ciais P *et al.* (2014) Contribution of semi-arid ecosystems to inter-annual variability of the global carbon cycle. *Nature*, **509**, 600–604, doi: 10.1038/nature13376.
- R Development Core Team (2011) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Ratajczak Z, Nippert JB, Collins SL (2012) Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology*, **93**, 697–703.
- Reichstein M, Falge E, Baldocchi D *et al.* (2005) On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global Change Biology*, **11**, 1424–1439, doi: 10.1111/j.1365-2486.2005.001002.x.
- Reynolds J, Stafford Smith D, Lambin E *et al.* (2007) Global desertification: building a science for dryland development. *Science*, **316**, 847–851, doi: 10.1126/science.1131634.
- Robertson T, Bell C, Zak J, Tissue D (2009) Precipitation timing and magnitude differentially affect aboveground annual net primary productivity in three perennial species in a Chihuahuan Desert grassland. *New Phytologist*, **181**, 230–242, doi: 10.1111/j.1469-8137.2008.02643.x.
- Rutledge S, Campbell DI, Baldocchi D, Schipper LA (2010) Photodegradation leads to increased carbon dioxide losses from terrestrial organic matter. *Global Change Biology*, **16**, 3065–3074, doi: 10.1111/j.1365-2486.2009.02149.x.
- Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology & Evolution*, **18**, 648–656, doi: 10.1016/j.tree.2003.09.002.
- Schimel DS (2010) Drylands in the earth system. *Science*, **327**, 418–419, doi: 10.1126/science.1184946.

- Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG (1990) Biological feedbacks in global desertification. *Science*, **247**, 1043–1048, doi: 10.1126/science.247.4946.1043.
- Scott RL, Huxman TE, Barron-Gafford GA, Jenerette GD, Young JM, Hamerlynck EP (2014) When vegetation change alters ecosystem water availability. *Global Change Biology*, **20**, 2198–2210, doi: 10.1111/gcb.12511.
- Seager R, Ting M, Held I *et al.* (2007) Model projections of an imminent transition to a more arid climate in southwestern North America. *Science*, **316**, 1181–1184, doi: 10.1126/science.1139601.
- Serna-Perez A, Monger H, Herrick J, Murray L (2006) Carbon dioxide emissions from exhumed petrocalcic horizons. *Soil Science Society of America Journal*, **70**, 795–805, doi: 10.2136/sssaj2005.0099.
- Seth A, Rauscher S, Rojas M, Giannini A, Camargo S (2011) Enhanced spring convective barrier for monsoons in a warmer world? *Climatic Change*, **104**, 403–414, doi: 10.1007/s10584-010-9973-8.
- Sponseller RA, Hall SJ, Huber DP, Grimm NB, Kaye JP, Clark CM, Collins SL (2012) Variation in monsoon precipitation drives spatial and temporal patterns of *Larrea tridentata* growth in the Sonoran Desert. *Functional Ecology*, **26**, 750–758, doi: 10.1111/j.1365-2435.2012.01979.x.
- Stone R (2008) Ecosystems - Have desert researchers discovered a hidden loop in the carbon cycle? *Science*, **320**, 1409–1410, doi: 10.1126/science.320.5882.1409.
- Throop HL, Reichmann LG, Sala OE, Archer SR (2012) Response of dominant grass and shrub species to water manipulation: an ecophysiological basis for shrub invasion in a Chihuahuan Desert grassland. *Oecologia*, **169**, 373–383, doi: 10.1007/s00442-011-2217-4.
- Turnbull L, Wainwright J, Brazier R (2010) Hydrology, erosion and nutrient transfers over a transition from semi-arid grassland to shrubland in the South-Western USA: a modelling assessment. *Journal of Hydrology*, **388**, 258–272, doi: 10.1016/j.jhydrol.2010.05.005.
- United States Department of Agriculture NRCS (2013) Web soil survey. <http://websoilsurvey.sc.egov.usda.gov/App/HomePage.htm>.
- USGS National Gap Analysis Program (2014) Southwest regional GAP analysis project. <http://swregap.nmsu.edu/default.htm>.
- Webb E, Pearman G, Leuning R (1980) Correction of flux measurements for density effects due to heat and water vapour transfer. *Quarterly Journal of the Royal Meteorological Society*, **106**, 85–100.
- Yin D, Nickovic S, Barbaris B, Chandy B, Sprigg WA (2005) Modeling wind-blown desert dust in the southwestern United States for public health warning: a case study. *Atmospheric Environment*, **39**, 6243–6254, doi: 10.1016/j.atmosenv.2005.07.009.