

Mechanisms of grass response in grasslands and shrublands during dry or wet periods

Debra P. C. Peters · Jin Yao · Dawn Browning · Albert Rango

Received: 25 April 2013 / Accepted: 8 November 2013 / Published online: 22 November 2013
© Springer-Verlag Berlin Heidelberg (outside the USA) 2013

Abstract Multi-year climatic periods are expected to increase with global change, yet long-term data are often insufficient to document factors leading to ecological responses. We used a suite of long-term datasets (1993–2010) to examine the processes underlying different relationships between aboveground net primary production (ANPP) and precipitation in wet and dry rainfall periods in shrublands and grasslands in the Chihuahuan Desert. We hypothesized that trends in ANPP can be explained by different processes associated with their dominant grasses [*Bouteloua eriopoda* (grasslands); *Sporobolus flexuosus* (shrublands)] and with ecosystem properties that influence soil water dynamics with feedbacks to ANPP. We compared datasets on recruitment and growth for 7 years with no trend in precipitation followed by a 4-year drought and 5 consecutive wet years. We integrated these data in a simulation model to examine the importance of positive feedbacks. In grasslands, ANPP was linearly related to precipitation regardless of rainfall period, primarily as a result of stolon recruitment by *B. eriopoda*. A lag in responses suggests the importance of legacies associated with stolon density. In shrublands, ANPP was only related to rainfall in the wet period when it increased nonlinearly as the number of wet years increased. Seed availability increased

in the first wet year, and seedling establishment occurred 2–4 years later. Increases in biomass, litter and simulated transpiration beginning in the third year corresponded with increases in ANPP. Understanding the processes underlying ecosystem dynamics in multi-year dry or wet periods is expected to improve predictions under directional increases or decreases in rainfall.

Keywords *Bouteloua eriopoda* · Demographic processes · Grasslands · Plant–soil water feedbacks · *Sporobolus flexuosus*

Introduction

Extreme climatic events are changing in frequency, magnitude, timing, and duration to influence ecosystems globally (Karl et al. 1995; Easterling et al. 2000). Effects of extreme events on ecosystems include shifts in species and functional group composition and changes in plant production (Kreyling et al. 2008; Ponce Campos et al. 2013) that can lead to state changes (Bestelmeyer et al. 2011). Climatic periods that consist of events occurring over consecutive years, such as multi-year drought, are particularly important to ecosystem dynamics because their effects can accumulate nonlinearly through time with threshold behavior that cannot be predicted from single-year events (Weaver and Albertson 1939). Understanding ecosystem responses to these climatic periods can provide insights into effects of directional changes in rainfall associated with global change (IPCC 2007). However, long-term data are often insufficient to document ecosystem responses to these events and, more importantly, to determine the underlying processes needed for reliable predictions (Jentsch et al. 2007).

Communicated by Truman Young.

D. P. C. Peters (✉) · J. Yao · D. Browning · A. Rango
Jornada Basin Long Term Ecological Research Program, New Mexico State University, Las Cruces, NM 88003-0003, USA
e-mail: debpeter@nmsu.edu

D. P. C. Peters · D. Browning · A. Rango
United States Department of Agriculture–Agricultural Research Service, Jornada Experimental Range, Las Cruces, NM 88003-0003, USA

Recent analyses of long-term data in the Chihuahuan Desert show that grasslands and desertified shrublands respond differently to a series of dry or wet years and that these responses may have important consequences for state changes (Peters et al. 2012). Similar to grasslands within the region and globally (e.g., Lauenroth and Sala 1992; Huxman et al. 2004; Muldavin et al. 2008), total above-ground net primary production (ANPP) in upland grasslands is linearly related to annual rainfall in both climatic periods. In contrast, total ANPP in shrublands dominated by honey mesquite (*Prosopis glandulosa*) is similar each year in a multi-year dry period, but ANPP in a sequence of wet years is either similar to a year with a similar rainfall amount or it is 1.5- to twofold larger, primarily from perennial grasses (Peters et al. 2012). The mechanistic basis for these ecosystem-specific relationships in different climatic periods is not well understood, and the different relationships between grass ANPP and precipitation in these periods have not been examined. This information is needed before predictions can be made about the response of these alternative states to directional increases or decreases in rainfall as environmental drivers continue to change in the future (IPCC 2007).

We expect that the effects of consecutive dry or wet years play out differently in these grasslands and shrublands as a result of the processes governing the dynamics of their dominant grass species and their site-specific ecosystem properties that influence soil water dynamics. In these upland grasslands, most of the response is by the stoloniferous, C₄ grass, *Bouteloua eriopoda* (black grama), which dominates herbaceous production in most years. *B. eriopoda* plants respond to rainfall primarily by expanding vegetatively via the production of stolons into small bare soil gaps (diameter <25 cm) that are characteristic of grasslands (Nelson 1934; Okin et al. 2009). Recruitment of this species by seed occurs infrequently in the Chihuahuan Desert as a result of low seed production, few germinable seeds in the soil, and restrictive microenvironmental conditions required for establishment (Nelson 1934; Neilson 1986; Peters 2000, 2002; Peters et al. 2010). Thus, we hypothesized that *B. eriopoda* recruitment by stolons and production of biomass exhibit a linear positive relationship with rainfall, with no cumulative effects through time regardless of the rainfall period, in response to a linear increase in soil water in small gaps (Duniway et al. 2010).

In mesquite shrublands, increases in ANPP are primarily from the C₄ bunchgrass, *Sporobolus flexuosus* (mesa dropseed), a species that recruits by seed and which has low cover and an abundance of adult plants in most years (Gibbens 1991; Gibbens et al. 2005). Although shrublands have similar total vegetative cover as grasslands, the spatial distribution of that vegetative cover is different in that there are fewer, large bare soil gaps (diameter >50 cm)

(Okin et al. 2009). *S. flexuosus* responses in non-wet periods are expected to be negligible as a result of low and variable seed production, few seeds stored in the soil, and insufficient water for recruitment in bare interspaces with high evaporative losses (Gibbens 1991; Guo et al. 1999; Wythers et al. 1999). A period of wet years is expected to facilitate a sequence of processes leading to a positive response in recruitment and biomass production through time. High rainfall in 1 year would result in the production of viable *S. flexuosus* seeds capable of germinating and becoming established in interspaces between shrubs in subsequent wet years. Individual wet years followed by dry years would lead to seedling mortality, whereas high rainfall in a third, fourth, and/or fifth consecutive year would allow recruits to grow sufficiently large to persist and produce seed. Canopies of bunchgrasses and other herbaceous plants would increase in areal extent and biomass through tillering, leading to increases in litter on the soil surface that in turn would reduce evaporative losses and increase water available for transpiration in interspaces (Tielbörger and Kadmon 2000; Butterfield et al. 2010). This increase in water combined with an increase in seed availability would lead to additional seedling establishment events through time. These plant–soil water feedback effects would accumulate through time as biomass and litter accumulate to result in water-conserving systems with greater rain-use efficiency (RUE) and ANPP than expected based on rainfall alone (Angers and Caron 1998). Thus, grass ANPP in a sequence of wet years is expected to be related to the number of consecutive wet years rather than to rainfall amount in any given year. This relationship through time would be nonlinear if positive feedbacks among herbaceous biomass, litter, and soil water were important to grass persistence. These positive feedbacks may also occur in grasslands, but their effects would be less pronounced because the bare soil gaps are smaller.

To test our hypotheses, we took advantage of a suite of co-located long-term datasets on grass recruitment and growth collected during a natural rainfall variation “experiment” over an 18-year period in the Chihuahuan Desert. The study is ongoing and consists of 7 years of rainfall with no year-to-year trend (1993–1999) followed by a 4-year drought (2000–2003) and a 5-year wet period (2004–2008). Because the two most recent years have been dry (2009) followed by wet (2010), they were used to examine the persistence of patterns developed during the wet period. We examined seed production, establishment, and growth of *B. eriopoda* in upland grasslands that have historically dominated much of the northern Chihuahuan Desert and of *S. flexuosus* in mesquite shrublands that currently dominate many upland locations (Gibbens et al. 2005). We addressed the following questions for each species in the ecosystem type of response: (1) what is the timing of seed availability

and successful recruitment in the three rainfall periods (no trend, dry, wet)? (2) What characteristics of precipitation (seasonality, total) are related to each recruitment process? (3) What is the relationship between each ecosystem response (grass ANPP, RUE, herbaceous biomass, litter) and precipitation or number of sequential wet years? Finally, we used simulation model analyses to examine the effects of herbaceous biomass and litter on water transpired by grasses to determine if plant–soil water feedbacks could explain grass ANPP responses in the 2004–2008 wet period.

Materials and methods

Study site and sample locations

The study was conducted at the Jornada Basin Long Term Ecological Research (JRN) site in southern New Mexico, USA (32.5N, 106.45W). Climate is arid to semiarid with a mean annual precipitation of 25 cm over the past 30 years, mostly occurring between 1 July and 1 October. Mean monthly temperatures over the same time period ranged from 6 °C in January to 26 °C in June, with an annual mean of 15 °C. Livestock grazing has decreased over time since peaks in the late 1800s up to around 1910 (Fredrickson et al. 1998). Current grazing densities are maintained at low levels throughout the 100,000-ha site. To focus on climatic and biotic effects on grass responses, we selected three upland grassland and three mesquite shrubland ungrazed locations with similar soils in the top 30 cm [loamy sand (>80 % sand) to sandy loam (65 % sand); see Peters et al. (2012) for soil profile details]. Locations were selected to represent spatial variation in each ecosystem type at the JRN site (Huenneke et al. 2001). Details on the experimental design are described below for each study and dataset.

Rainfall measured monthly at each location was summed to obtain water year (1 October to 30 September) precipitation (WPPT) data. Similar long-term mean rainfall was found for all locations (24–27 cm year⁻¹). Three time periods were identified based on year-to-year patterns in the amount of precipitation compared with the 30-year mean (1981–2010). Rainfall in each year in the wet period (2004–2008) was greater than the long-term mean, rainfall in each year in the dry period was lower than the long-term mean (Table 1). The wet period had significantly greater mean rainfall (30.2 cm year⁻¹) than the no-trend period (22.1 cm year⁻¹; 1993–1999) which in turn was significantly greater than that in the dry period (17.5 cm year⁻¹; 2000–2003). Analysis of variance for nested classifications (PROC GLM in SAS ver. 9.2; Littell et al. 2002) was used with rainfall period and ecosystem type as fixed effects and three locations nested within each ecosystem

Table 1 Mean annual air temperature and precipitation for each water year (1 October–30 September) from 1993 to 2010 at the Jornada Basin USDA–LTER site

Year	Temperature (°C year ⁻¹) ^a	Precipitation (cm year ⁻¹) ^a	Climate period
1993	15.0 –	30 +	No trend
1994	15.7 +	15 –	No trend
1995	15.8 +	23 –	No trend
1996	16.2 +	21 –	No trend
1997	15.5 +	26 +	No trend
1998	15.0 –	15 –	No trend
1999	15.8 +	26 +	No trend
2000	16.2 +	20 –	Dry
2001	15.3 +	22 –	Dry
2002	15.8 +	15 –	Dry
2003	15.6 +	15 –	Dry
2004	15.5 +	27 +	Wet
2005	15.5 +	28 +	Wet
2006	15.6 +	34 +	Wet
2007	15.0 –	29 +	Wet
2008	14.8 –	33 +	Wet
2009	15.2 +	12 –	
2010	14.2 –	29 +	
30-year mean	15.1	25	

USDA–LTER, United States Department of Agriculture–Long Term Ecological Research site

Data are averaged across six locations (three grasslands, three shrublands). The 30-year mean (1981–2010) was used to identify three climate periods (no trend, dry, wet)

^a “+”, “–” indicates annual value was greater/less than the 30-year mean

type. The only pattern in temperature was that the dry period had greater mean daily temperature than the long-term mean (Table 1).

Seed availability by species

Monthly observations of plant phenology from 1993–2010 included production of seeds (i.e., caryopses) by *B. eriopoda* at all three upland grasslands and by *S. flexuosus* at two of the mesquite shrublands for which data were available. We recorded the number of individual grasses with developing or mature seeds that intersected each of two 75-m line transects located approximately 5 m from the grid of quadrats sampled for recruits. Belt transects were walked monthly with observers counting the number of grass patches producing seed; these data provide information on the abundance of seed-producing grasses as well as on the timing of seed production. Methods to quantify seed productivity vary widely (e.g., Russell and Schupp 1998; Fox 2011). To characterize patterns in the

timing and abundance of seed production, we developed a seed availability index (SAI). The SAI was calculated annually for each species–site combination as the mean of two relativized metrics: the maximum number of grasses producing seeds and the number of months of peak seed production. Relativized values (0–1) were determined using data for all 18 years for both the abundance and timing values. A value of 0 denotes that no seeds were produced in a given year while a high value could denote either that many individuals produced seed, seed was produced early in the year and retained on the plant longer, or both. Interpretations of the SAI index assume that the availability of germinable seeds increases with increases in both the number of plants producing seeds and the length of time seeds are allowed to develop to maturity on a plant.

Establishment of recruits by species

Within each of the five locations sampled for seed availability, we sampled a systematic grid of forty-nine 1-m² permanent quadrats for height and percentage cover of each plant in three seasons in each year [dormant (February) and spring (May) and fall peak growth (September to October)] from 1993 to 2010. We defined a recruit as an individual with height ≤ 20 cm and area ≤ 10 cm² (i.e., cover = 0.1 %). Field observations through time confirmed that *B. eriopoda* recruits (i.e., ramets) were primarily from stolons. The annual number of recruits per location was the sum of spring and fall counts.

Ecosystem responses (biomass, ANPP, RUE, litter)

Herbaceous biomass was calculated from species-specific allometric equations using data on height and percentage cover by each herbaceous plant in each quadrat sampled for recruits and then summing the data by species. Maximum live herbaceous biomass in a year was the largest biomass on each quadrat among the three seasons. ANPP was estimated using the positive increment in biomass-by-grass species in a quadrat summed across seasons. Each value of ANPP is the mean of 49 quadrats at a location. The experimental design and sampling protocols are detailed in Huenneke et al. (2001) as modified by Peters et al. (2012). To improve estimates of ANPP-related variables and to be consistent with previous analyses (Peters et al. 2012), we included a third mesquite shrubland location with similar vegetation and soils as the shrubland locations used for recruitment and sampled at this location for biomass and ANPP with the same design and methods as at the other five locations. We calculated RUE as grams of ANPP per unit of water year precipitation for each location

(Le Houérou 1984). Because litter was not estimated on the quadrats, we used a long-term dataset with litter measurements from neighboring upland grassland and mesquite shrubland locations with similar soils within 8 km of the quadrats. Litter (defined as detached dead plant material) was estimated each autumn from 2001 to 2010 using 10-cm resolution data from three 30-m lines as a subset of a continuous 150-m transect at each location (Rango et al. 1998). Litter (% cover) was calculated using the length of each line covered by litter (m) divided by the total length sampled (90 m) and then multiplied by 100.

Statistical analyses of field data

Multiple regression analyses with stepwise selection were used to examine relationships between SAI or recruitment and potential explanatory variables using data for the entire time span and by period (no trend, dry, wet). For SAI, the potential explanatory variables were amount of seasonal precipitation (dormant: October–March; spring: April–June; summer: July–September) and year. For recruitment, potential explanatory variables were seasonal precipitation, year, and SAI values from the current year and from the previous 1, 2, 3, or 4 years. Square root transformations of variables were performed when appropriate to meet assumptions associated with homogeneity of variance and normality of residuals. When two or three seasons of precipitation variables were selected in a model and the regression slopes were similar, we summed the selected seasonal precipitation values into one variable and repeated the analysis.

The relationship between grass ANPP (or RUE or biomass) and WPPT (or year) within each ecosystem type was compared among periods using repeated-measures analysis of variance (PROC MIXED in SAS ver. 9.2). In this analysis, grass ANPP (or RUE or biomass) was the dependent variable, period was the fixed factor, WPPT (or year) was the covariate, and annual measures at each location were repeated measures. If the regression slopes were not significantly different among periods, then the *Y*-intercepts were compared given the same slope. If the *Y*-intercepts were also similar, then one regression line was fit to all data. The dependent variable was log-transformed when necessary to meet assumptions of the analysis.

The wet period was the only one in which ANPP or RUE was related to year, and repeated-measures analysis indicated that the within-subject errors were not significantly correlated to each other (*p* values of likelihood ratio test of fitness of covariance models ranged from 0.06 to 0.92). Thus, we used simple regression to select the best-fit model for the relationship between ANPP (or RUE) and year by comparing the *r*² values from a linear model [$Y = a + b$

(year 2003)] with an exponential model [$Y = a + b \times \exp(\text{year } 2003)$]. 2003 (the year prior to the start of the wet period) was subtracted from year to keep the values of the exponent within a reasonable range. This scalar transformation of year that denoted the number of sequential wet years did not alter the interpretation of the variable “year” in the model.

To compare maximum live herbaceous biomass (or litter) in the wet period to the other periods, we calculated the 95 % confidence interval for each variable during the no-trend and dry periods. The confidence interval for biomass was calculated using a repeated measures analysis with each location’s yearly values as the repeated measures and that for litter was calculated by assuming the three data points (2001–2003) were normally distributed and independent.

Simulation of plant-soil water feedbacks

Model description We used a simulation model of soil water dynamics (SOILWAT; Parton 1978) to determine if positive feedbacks between grasses and soil water could account for trends in grass ANPP during the wet period. SOILWAT is a multi-layer, daily timestep model that has been tested for arid and semiarid ecosystems in the western USA, including the Jornada site (Lauenroth et al. 1994; Peters et al. 2010; Sala et al. 2012). Input parameters include daily temperature and precipitation and monthly wind speed, relative humidity, cloud cover, aboveground biomass, and litter. Soil texture (percentage sand, silt, clay), percentage rocks by volume, and root biomass are input parameters by depth in the soil profile. Processes simulated daily include bare soil evaporation, transpiration by plants, interception by the plant canopy, and infiltration in the soil profile. Loss of water to deep drainage occurs infrequently in dry ecosystems and was not included here.

The model first partitions a daily rain amount into canopy interception, evaporation, or transpiration. On these sandy soils (loamy sands, sandy loams) with little topographic relief, infiltration rates are high (Snyder et al. 2006); thus we assumed that horizontal run-on and run-off processes were negligible such that all of the water available for transpiration infiltrates to the top soil layer (sensu Peters et al. 2010). Plant available water (PAW) in a layer depends on soil texture and is calculated as the difference in soil water content between field capacity and permanent wilting point. Root biomass is used to calculate the amount of PAW that is transpired each day from a soil layer. The rest of the water remains in the soil. When the top layer reaches field capacity, the extra water infiltrates to

the second layer where it is either used for transpiration or accumulates in the soil. This “tipping bucket” process continues until all layers are simulated each day. Interception and evaporation are affected by aboveground biomass and litter, although with opposite effects on transpiration: losses to interception increase and water available for transpiration decreases as biomass increases, but increases in litter act to decrease evaporation and increase water available for transpiration. The net effect on transpiration depends on the amount of biomass and litter, the size of a rain event, soil texture, and the initial water content of the soil. These tradeoffs and interactions lead to complex patterns in soil water dynamics and transpiration because precipitation, soils, plant biomass, and litter change in time and space.

Model parameterization The model was parameterized using precipitation and soils from the same six locations where ANPP, biomass, phenology, and establishment data were collected. Precipitation was collected monthly using collectors at each location during the entire study period. Daily precipitation was collected at each location starting in 2000, but daily data before 2000 are available from weather stations within 5 km of each location. We used the temporal pattern in daily precipitation events either from each location (when available) or from the nearest weather station to distribute the monthly amount across each day. Daily temperature was obtained from the nearest weather station with similar elevation. Monthly wind speed, cloud cover, and relative humidity, and percentage of evaporation and transpiration by depth were obtained from previous simulations for the Jornada site (Peters et al. 2010); these parameters remained the same for all runs. Soils were collected by horizon from pits located adjacent to each location. Air-dried soils were analyzed for particle size distribution using standard methods in the laboratory (Monger 2006). We created the same depth structure for each location (0–5, 5–10, 10–15, 15–20, 20–30, 30–50, 50–75, 75–100 cm; Peters et al. 2010) by either combining or linearly extrapolating texture values across depths. Maximum aboveground herbaceous biomass values for each year were obtained from the same samples used to calculate the ANPP. The same amount of herbaceous biomass was assumed to occur in each month, and monthly litter was assumed to be the same as biomass. Percentage live biomass by month was based on phenological patterns of the vegetation, and the same values were used for all locations. Maximum live biomass occurs during the months of maximum precipitation (July–August); no live perennial biomass is found during the winter (November–February).

Experimental simulations We conducted two sets of simulations for each location where the only values that

changed were monthly biomass and litter during 2004–2008. First, we used a linear relationship between herbaceous biomass and annual precipitation from 1993 to 2003 for each ecosystem type to calculate yearly biomass from 2004 to 2008 as inputs to the model. This relationship assumes that no plant–soil water feedbacks are operating since biomass is related to the amount of precipitation. Second, we used field estimates of biomass from 2004 to 2008 as model inputs to determine the effects of biomass on the amount of water available for transpiration as a measure of plant–soil water feedbacks. In both runs, we summed daily transpiration values in each layer across all days at the end of each water year to obtain an annual amount of water transpired ($\text{cm layer}^{-1} \text{ year}^{-1}$). Because roots of perennial grasses in arid and semiarid ecosystems are concentrated in the top 30 cm (Gibbens and Lenz 2001), we summed transpiration values in the 0- to 30-cm layers to determine the amount of water available to grasses in each year at each location (cm year^{-1}). We used repeated-measures analysis of covariance (PROC MIXED in SAS ver. 9.2) to compare the relationship of transpiration and time between the two sets of simulations within each ecosystem type, with simulation type (set) as the fixed factor and number of consecutive wet years (time) as the covariate.

Results

Seed availability and establishment of recruits by species

Seed availability and number of recruits exhibited different patterns through time for *B. eriopoda* in upland grasslands than for *S. flexuosus* in mesquite shrublands (Figs. 1, 2). The factors related to these recruitment processes also differed within species over time and between species within a given year and across years.

For *B. eriopoda*, there was no clear relationship between timing of the two recruitment processes (i.e., seed production, establishment of recruits) (Fig. 1). This species produced seeds and recruited ramets every year with high variability across years. *B. eriopoda* did not produce seed at the end of the drought (2003), resulting in the lowest SAI value of all 18 years (Fig. 1a). Seed availability peaked at the start of the wet period (2004) as a result of both an early onset of seed production (June) and a large number of individuals producing seeds. Decreases in SAI the following years (2005, 2006) were due to late onset (November) and a decrease in the number of seeds producing individuals. SAI values increased through time over the wet period (2005–2008) with a modest decrease in the following dry year (2009). Seed availability was positively related to growing season precipitation (spring + summer) ($R^2 = 0.52$,

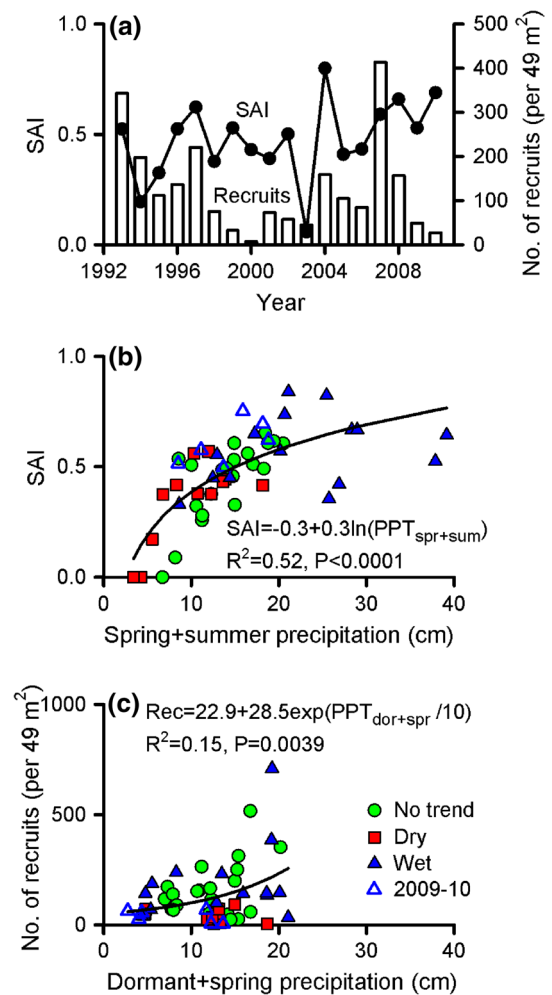


Fig. 1 Recruitment of *Bouteloua eriopoda* (black grama) in grasslands. **a** Temporal variation in recruitment is based on seed availability [SAI seed availability index; unitless] and from counts of stolons (number 49 m^{-2}). **b, c** The relationship between SAI and spring and summer precipitation combined ($PPT_{spr+sum}$; $N = 54$) (**b**) and number of recruits and dormant and spring precipitation combined ($PPT_{dor+spr}$; $N = 54$) (**c**). No-trend years (circles 1993–1999), dry years (rectangles 2000–2003), and wet years (triangles; 2004–2008) are indicated

$P < 0.0001$) (Fig. 1b). Numbers of *B. eriopoda* recruits were variable throughout the 18-year time span, with a peak in the middle of the wet period (2007) (Fig. 1a). Number of recruits in all years was weakly related to precipitation from October to July (dormant + spring) ($R^2 = 0.15$, $P = 0.004$); the nonlinear form of the relationship was governed by a few large values in wet years (Fig. 1c).

In contrast, for *S. flexuosus*, there were two pulses in successful recruitment events based on number of seedlings (1995–1996; 2006–2009) that were preceded by years with the production of seeds (1993; 2004–2010) (Fig. 2a). Although seeds were produced in the intervening years (1999–2001), conditions were insufficient for seedling

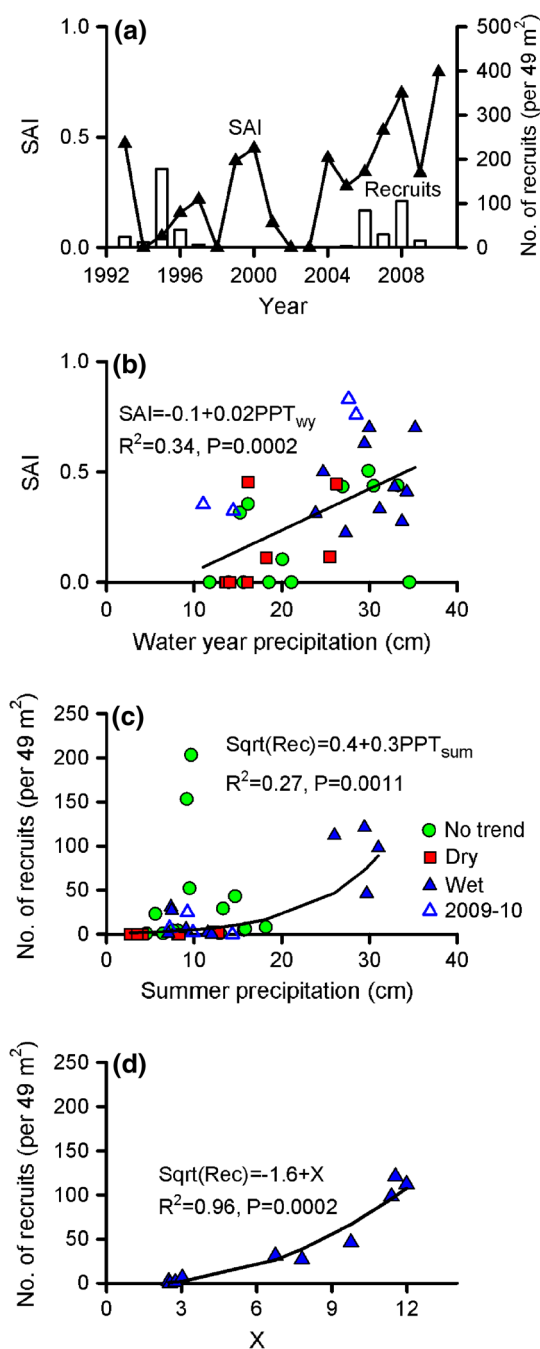


Fig. 2 Recruitment of *Sporobolus flexuosus* in shrublands. **a** Mean seed availability (SAI; unitless) and mean number of recruits by seedlings (number 49 m⁻²) through time for two locations, **b** SAI is positively related to water year precipitation (PPT_{wy} ; $N = 36$), **c** number of seedlings is positively related to summer precipitation (PPT_{sum} ; $N = 36$), **d** in the wet period, the number of seedlings is related to PPT_{sum} , seed availability 2 years previously (t_2), and number of consecutive wet years: square root (recruitment) [$Sqrt(Rec)$] = $-1.6 + 0.1 \times PPT_{sum} + 9.6 \times SAI_{t-2} + 0.9 \times$ no. consecutive wet years ($N = 10$). **c**, **d** Regressions were conducted using square-root transformed Y , but the regression lines are shown using back-transformed predicted values. No-trend years (circles; 1993–1999), dry years (rectangles; 2000–2003), and wet years (triangles; 2004–2008) are indicated

establishment for a 7-year period that included individual wet years and an extended drought (1997–2003). For all years, SAI was positively related to water year precipitation ($R^2 = 0.34$, $P = 0.0002$) (Fig. 2b), and seedling establishment was related to summer precipitation ($R^2 = 0.27$, $P = 0.001$) (Fig. 2c). For analyses confined to the wet period (2004–2008), establishment was positively related to summer precipitation, number of seeds produced 2 years prior, and the number of sequential wet years ($R^2 = 0.96$, $P = 0.0002$) (Fig. 2d).

Relationships between ecosystem variables and precipitation or time

Perennial grass ANPP, which was 82 % *B. eriopoda* production, had a different relationship with WPPT in the two ecosystem types (not shown). In upland grasslands, one regression line explained variation in ANPP for all three periods (ANPP = $2.3 \times WPPT$; $P = 0.0005$). For shrublands, *S. flexuosus* comprised 46 % of perennial grass ANPP, which was not related to WPPT in any time period because very small ANPP (<21 g m⁻² year⁻¹) occurred regardless of rainfall amount in dry and mean years, whereas very high variability occurred in wet years (0–233 g m⁻² year⁻¹) for the same rainfall amount. ANPP in the wet period showed exponential increases through time in both grasslands (ANPP = $36.1 + 0.6 \times \exp$ (year 2003); $R^2 = 0.6$; $P = 0.0007$) and shrublands (ANPP = $-0.2 + 1.2 \times \exp$ (year 2003); $R^2 = 0.89$; $P < 0.0001$), with the largest increases starting in 2006, the third sequential wet year (Fig. 3a, b). RUE was not related to WPPT in grasslands or shrublands (not shown). RUE in the wet period showed nonlinear increases through time in both ecosystem types (Fig. 3c, d). In grasslands, large ANPP and RUE values were maintained in 2009 and 2010 with small variation across locations (Fig. 3a, c). In shrublands, ANPP and RUE values in these years were variable across locations, yet values were larger than before 2006 (Fig. 3b, d).

In grasslands, herbaceous biomass prior to the wet period was significantly related to WPPT (biomass = $23.2 + 3.2 \times WPPT$; $P = 0.003$), but the relationship was not significant in the wet period or for any periods in shrublands (not shown). Biomass showed a time lag in that values were significantly larger in the third and additional wet years (grasslands: 2006, 2008; shrublands: 2006–2008) compared with the 95 % confidence interval for the 1993–2003 data. Litter also showed a time lag in the wet period, with increases in 2006 (grasslands) or 2007 (shrublands) (Fig. 4c, d). For both biomass and litter, these large values were maintained in the wet year (2010) following a dry year (2009) in both ecosystem types.

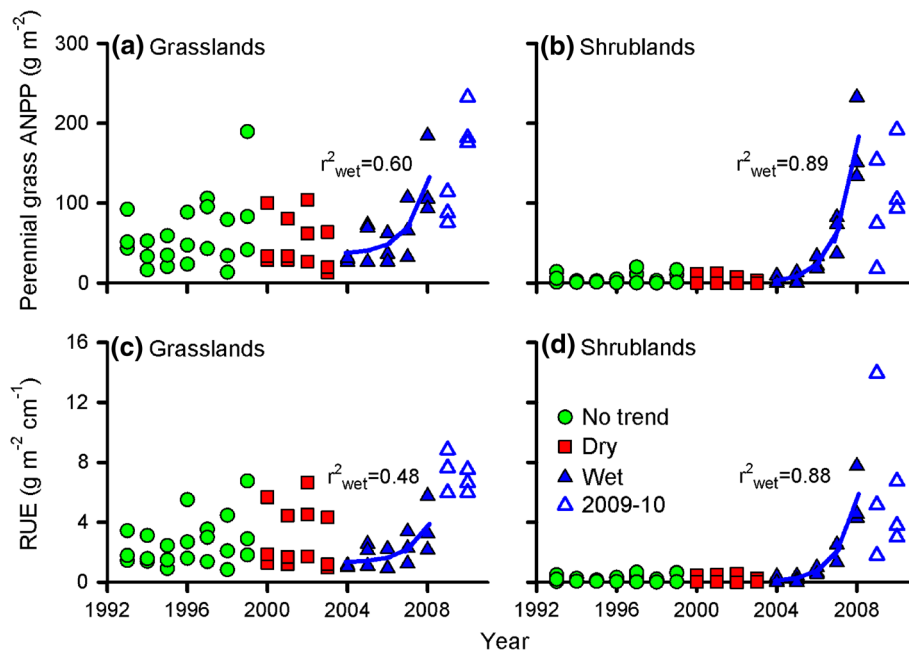
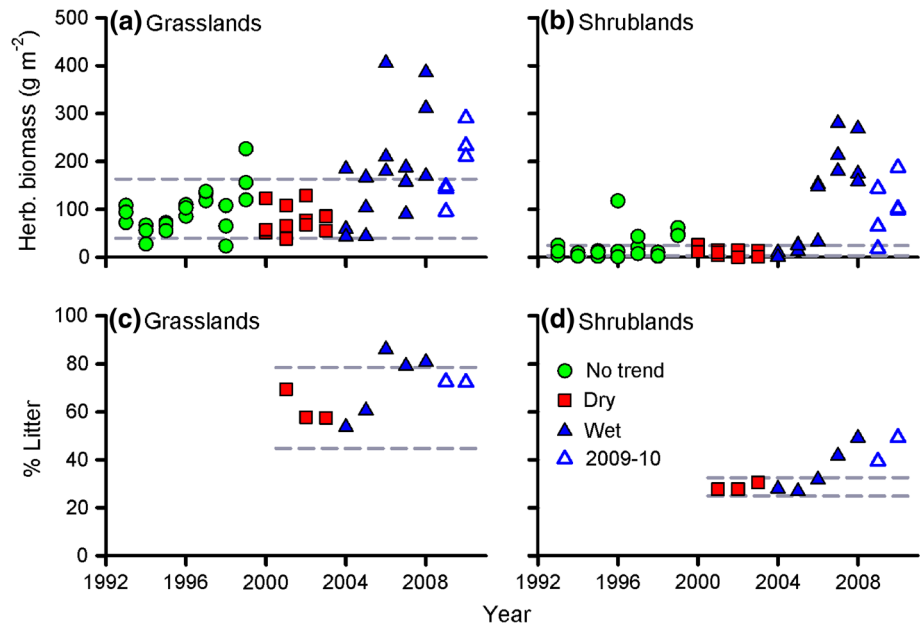


Fig. 3 **a, b** Perennial grass production (ANPP) through time in grasslands (**a**) and shrublands (**b**). An exponential relationship in the wet period in each ecosystem type was a better fit to the data based on a larger R^2 value [grasslands: ANPP = $36.1 + 0.6 \exp$ (no. consecutive wet years), $R^2 = 0.60$, $P = 0.00007$, $N = 15$; shrublands: ANPP = $-0.2 + 1.2 \exp$ (no. consecutive wet years), $R^2 = 0.89$, $P < 0.0001$, $N = 15$]. No-trend years (circles; 1993–1999), dry years (rectangles; 2000–2003), and wet years (triangles; 2004–2008) are indicated. Data in a subsequent dry (2009) and wet (2010) year are shown as open triangles. **c, d** Rain use efficiency (RUE; g m^{-2} ANPP

cm^{-1} precipitation) through time in grasslands (**c**) and shrublands (**d**). An exponential relationship was a better fit to the data during the wet period in each ecosystem type based on a larger R^2 value [grasslands: RUE = $1.3 + 0.02 \exp$ (no. consecutive wet years), $R^2 = 0.48$, $P = 0.0041$, $N = 15$; shrublands: RUE = $-0.001 + 0.04 \exp$ (no. consecutive wet years), $R^2 = 0.88$, $P < 0.0001$, $N = 15$]. No-trend years (circles; 1993–1999), dry years (rectangles; 2000–2003), and wet years (triangles; 2004–2008) are indicated. Open triangles Data in a subsequent dry (2009) and wet (2010) year. Regression lines are only shown when correlations are significant

Fig. 4 Maximum live herbaceous biomass (**a, b**) and litter (**c, d**) in grasslands or shrublands. The 95 % confidence intervals for the 1993–2003 data are shown. Years within period are shown by circles (no-trend years), rectangles (dry years), and filled triangles (wet years). Open triangles Data in a dry (2009) and wet (2010) rainfall year



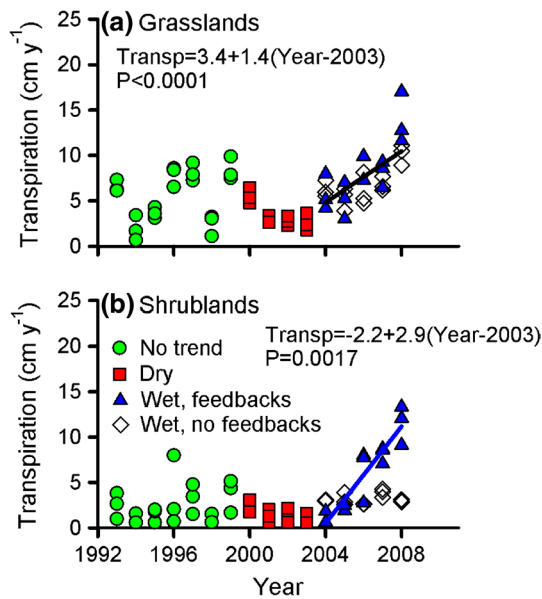


Fig. 5 Total amount of simulated water transpired (cm year^{-1}) in the upper 30 cm of the soil profile for linear estimates of ANPP (without plant–soil water feedbacks; *filled triangles*) compared with field estimates of ANPP (with plant–soil water feedbacks; *open diamonds*) in grasslands (a) and shrublands (b). Significant relationships between transpiration and year were found in grasslands where slopes of the lines with and without feedbacks were similar (shown by one *black line* for all data from 2004 to 2008) and in shrublands for runs with feedbacks (shown by one *blue line* for filled *blue triangles* only). Years within period are shown by *circles* (no-trend years) or *rectangles* (dry years). *Regression lines* are only shown when correlations are significant. Color figure is available online

Plant–soil water feedbacks

In grasslands, the simulated temporal patterns of transpiration during the wet period were the same between the simulations with and without plant–soil water feedbacks, but in shrublands the simulated temporal patterns were significantly different (Fig. 5a, b). In grasslands, simulated transpiration linearly increased with time ($P < 0.0001$ for the slope), and the linear trends were statistically the same in both simulations (Fig. 5a). The interaction of time and simulation type was not significant ($P = 0.06$). The Y -intercepts were statistically the same ($P = 0.06$) when we fit two regression lines with the same slope. In shrublands, the modeled relationships between transpiration and time were significantly different between the two simulations ($P < 0.0001$ for the interaction of time and simulation type) (Fig. 5b). Simulated transpiration linearly increased with time ($P = 0.002$ for the slope) in the simulation with feedbacks where field estimates of ANPP were used, but it had no relationship with time in the scenario without feedbacks where ANPP was calculated from annual precipitation ($P = 0.72$ for the slope). Although modeled ANPP increased linearly in shrublands, the rate of increase was

twice as fast as in grasslands and was a better approximation to the exponential increase in field-based estimates of ANPP than simulations without plant–soil feedbacks.

Discussion

Extreme climatic events that span multiple years are characteristic of many ecosystem types, yet the processes underlying ecological responses through time are often poorly understood. We used a suite of co-located long-term datasets from a natural rainfall variation “experiment” over an 18-year period in the Chihuahuan Desert to provide a process-based explanation for observed differences in grass ANPP in dry and wet periods in decertified shrublands and neighboring grasslands. Our results support the hypothesis that trends in ANPP can be explained by different processes associated with the dominant grasses [*Bouteloua eriopoda* (grasslands); *Sporobolus flexuosus* (shrublands)] and, for desertified shrublands, with ecosystem properties that influence soil water dynamics with feedbacks to recruitment and ANPP. Understanding the processes governing dynamics in multi-year dry or wet periods is expected to improve predictions of ecosystem dynamics under directional increases or decreases in rainfall expected with climate change (IPCC 2007).

Species and ecosystem differences

In grasslands, our results support the hypothesis that *B. eriopoda* recruitment by stolons and production of biomass have positive relationships with rainfall regardless of the rainfall period. This species expands or contracts through stolon production or loss to result in changes in ANPP with changes in rainfall (Nelson 1934). Vegetative expansion occurs in the small bare gaps (diameter < 25 cm) commonly found between plants in grasslands (Okin et al. 2009). Although the linear ANPP–PPT relationship was not significantly different across rainfall periods, large variance in ANPP for years with a similar rainfall amount was explained by examining trends through time, in particular for the wet period. Because our modeling exercise did not show feedbacks between the vegetation and soil water dynamics in these grasslands, alternative explanations for relationships through time are needed. The 2-year time lag in response by *B. eriopoda* at the start of the wet period (2004–2005) may result from constraints on stolon or tiller density following dry years that limit recruitment of new propagules even under conditions of high rainfall (Sala et al. 2012). Existing stolon or tiller density can enhance ANPP (Reichmann et al. 2013) such that continued high rainfall conditions would increase stolon or tiller density and lead to the nonlinear increase in ANPP with increasing

number of consecutive wet years. High stolon density at the end of the wet period would also result in the observed relatively high ANPP (and RUE) in the subsequent dry (2009) and wet (2010) years.

In decertified shrublands, our results support the hypothesis that grass ANPP is not linearly related to precipitation in any time period as a result of the sequential processes required for the bunchgrass, *S. flexuosus*, to increase in density and cover. Recruits of this species primarily occur in large interspaces (diameter >50 cm) between shrubs where evaporative losses are high and soil moisture is lower than under shrub canopies (Bhark and Small 2003). In periods with no trend in rainfall or in a sequence of dry years, soil moisture in interspaces would be variable or low from year-to-year. Under these conditions, seeds that are produced or stored in the soil or seedlings that become established in one or two consecutive wet years would not have sufficient water in subsequent years for growth and survival through time. However, a series of wet years would allow a sequence of processes to occur: an increase in seed availability in the first wet year after a drought followed by seedling establishment 2–4 years later would allow new recruits to survive. In the third wet year, increases in biomass and litter would result in the capture of water under grass canopies, leading to increases in water available for transpiration and thereby promoting growth of these recruits as well as the production of seeds to continue the grass recovery process through time. The role of plant–soil feedbacks in forming islands of fertility that promote shrub expansion into desertification of grasslands has been well studied in arid regions globally (e.g., Schlesinger and Pilmanis 1998). Our results provide support for similar processes operating to promote grass recruitment and recovery through increases in soil water, although more direct tests are needed.

In shrublands, bunchgrasses would also increase in cover as new tillers are produced and they would also experience legacies in the wet period (Sala et al. 2012), similar to *B. eriopoda* in grasslands (described above). Although we are unable to distinguish the relative importance of plant–soil water feedbacks compared with tiller legacies to trends in ANPP by bunchgrasses in the wet period, both processes are likely operating to generate the exponential increase in ANPP through time and, therefore, they require further investigation.

Sequential processes and strategies for restoration

The sequence of demographic processes required for grass recovery in desertified shrublands is similar to processes needed for range expansion (Gray et al. 2006) and restoration when propagules are not available on-site (Young et al. 2005). For species lacking a persistent seed bank in the soil, seed additions are often used to “jump start” the recovery process, although successful establishment of perennial

species may depend on temporal contingency (Vaughn and Young 2010). Repeated seed additions may be needed to capture the conditions required for germination and establishment, particularly in arid systems where rainfall is low and variable and is the only source of water to plants (Wilson 2002). In our study, a naturally occurring sequence of wet years that led to a broad-scale establishment of perennial grasses in decertified shrublands was an effective alternative to seeding trials complemented with water additions that have mixed rates of success (Herrick et al. 2006).

S. flexuosus is an important forage species in the Chihuahuan Desert with restoration potential in the southwestern USA (Gibbens 1991). In our study, recruitment of this species was only partly explained by rainfall; the inclusion of seed availability at a 2-year lag and number of consecutive wet years resulted in a very high R^2 (0.96). A comprehensive study of patterns of reproductive phenology is needed to determine the environmental conditions conducive to establishment and persistence; however, our studies provide insights to these conditions. The lag between seed production and establishment may be explained by the physical abrasion needed to break seed dormancy of this species (Toole 1941). The number of consecutive wet years is likely related to the accumulation of biomass and litter through time that provided safe sites as protection from granivores and created microhabitats with low evaporation and increased water available for germination and establishment (Whitford 2002; Butterfield et al. 2010). These explanatory variables (seed availability, precipitation, number of wet years, biomass, litter) can be used to develop effective restoration strategies for this species, in particular in persistent sandy mesquite shrublands where perennial grass establishment occurs infrequently under dry or mean rainfall conditions.

Restoration strategies for stoloniferous grasses, such as *B. eriopoda*, need a different approach. Seedling establishment occurs infrequently in these species and, therefore, maintaining remnant grass plants is critical to their ability to recover, both to extreme climatic events and land-use practices that reduce grass cover and abundance (i.e., drought, fire, livestock grazing) (Bestelmeyer et al. 2012). Remnant grasses are particularly important for perennial grasses that recruit very infrequently by seed, such as *B. eriopoda* (Neilson 1986). Recent studies show that remnant *B. eriopoda* plants can be found in isolated microsites even in ecosystems that appear to be overwhelmingly dominated by shrubs (Peters et al. 2006).

Conclusions

Our results showing different processes underlying similar trends in ANPP and RUE with time during a 5-year

wet period for grasslands and decertified shrublands indicate the importance of understanding the role of underlying processes to ecosystem dynamics and to restoration strategies. These alternative states in the Chihuahuan Desert occur on neighboring locations with similar topographic conditions, yet they have diverged in lifeform dominance over the past 150 years (Gibbens et al. 2005). These shifts in dominance and composition have resulted in current states of different processes governing responses to climate. Our findings that dynamics under directional increases in rainfall cannot be predicted from responses in individual wet years or from relationships developed from years with no trend or in a dry period have important implications for climate change research. Time lags in responses to wet periods that may result either from stolon densities or plant–soil water feedbacks in multi-year wet periods need to be accounted for.

Acknowledgments We thank Laura Huenneke for designing the long-term studies on plant ANPP and phenology, and John Anderson and the Jornada Basin LTER technicians for collecting the data through time. Kris Havstad provided constructive comments on the manuscript. Funding was provided by the National Science Foundation to New Mexico State University as part of the Jornada Basin Long Term Ecological Research Program (DEB-1235828) and by related awards to New Mexico State University (DEB-0917668, EF-1065699). The Jornada Basin site consists of the Jornada Experimental Range administered by the U.S. Department of Agriculture–Agricultural Research Service, and the Chihuahuan Desert Rangeland Research Center administered by New Mexico State University. The NPP and Phenology studies are funded by the Jornada LTER Program, and the JORNEX Project is jointly funded by the LTER and USDA–ARS. The experiments comply with the current laws of the USA in which the experiments were performed.

References

- Angers D, Caron J (1998) Plant-induced changes in soil structure: processes and feedbacks. *Biogeochemistry* 42:55–72
- Bestelmeyer BT, Ellison AM, Fraser WR, Gorman KB, Holbrook SJ, Laney CM, Ohman MD, Peters DPC, Pillsbury FC, Rassweiler A, Schmitt RJ, Sharma S (2011) Analysis of abrupt transitions in ecological systems. *Ecosphere* 2:129. doi:10.1890/ES11-00216.1
- Bestelmeyer BT, Duniway MC, James DK, Burkett LM, Havstad KM (2012) A test of critical thresholds and early warning indicators in a desertification-prone ecosystem: more resilience than we thought. *Ecol Lett*. doi:10.1111/ele.12045
- Bhark EW, Small EE (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
- Butterfield BJ, Betancourt JL, Turner RM, Briggs JM (2010) Facilitation drives 65 years of vegetation change in the Sonoran Desert. *Ecology* 91:1132–1139
- Duniway MC, Snyder KA, Herrick JE (2010) Spatial and temporal patterns of water availability in a grass-shrub ecotone and implications for grassland recovery in arid environments. *Ecophysiology* 3:55–67
- Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000) Climate extremes: observations, modeling, and impacts. *Science* 289:2068–2074
- Fox BJ (2011) Review of small mammal trophic structure in drylands: resource availability, use, and disturbance. *J Mammal* 92:1179–1192
- Fredrickson E, Havstad KM, Estell R, Hyder P (1998) Perspectives on desertification: south-western United States. *J Arid Environ* 39:191–207
- Gibbens RP (1991) Some effects of precipitation patterns on mesa dropseed phenology. *J Range Manage* 44:86–90
- Gibbens RP, Lenz JM (2001) Root systems of some Chihuahuan Desert plants. *J Arid Environ* 49:221–263
- Gibbens RP, McNeely RP, Havstad KM, Beck RF, Nolen B (2005) Vegetation change in the Jornada Basin from 1858 to 1998. *J Arid Environ* 61:651–668
- Gray ST, Betancourt JL, Jackson ST, Eddy RG (2006) Role of multi-decadal climate variability in a range extension of pinyon pine. *Ecology* 87:1124–1130
- Guo Q, Rundel PW, Goodall DW (1999) Structure of desert seed banks: comparisons across four North American desert sites. *J Arid Environ* 42:1–14
- Herrick JE, Havstad KM, Rango A (2006) Remediation research in the Jornada Basin: past and future. In: Havstad KM, Huenneke LF, Schlesinger WH (eds) Structure and function of a Chihuahuan Desert ecosystem. Oxford University Press, New York, pp 278–304
- Huenneke LF, Clason D, Muldavin E (2001) Spatial heterogeneity in Chihuahuan Desert vegetation: implications for sampling methods in semi-arid ecosystems. *J Arid Environ* 47:257–270
- Huxman TE, Smith MD, Fay PA, Knapp AK, Shaw MR, Loik ME, Smith SD, Tissue DT, Zak JC, Weltzin JF, Pockman WT, Sala OE, Haddad BM, Harte J, Koch GW, Schwinning S, Small EE, Williams DG (2004) Convergence across biomes to a common rain-use efficiency. *Nature* 429:651–654
- IPCC (Intergovernmental Panel on Climate Change) (2007) Climate change 2007: synthesis report. IPCC, Geneva
- Jentsch A, Kreyling J, Beierkuhnlein C (2007) A new generation of climate change experiments: events, not trends. *Front Ecol Environ* 5:315–324
- Karl TR, Knight RW, Plummer N (1995) Trends in high-frequency climate variability in the 20th century. *Nature* 377:217–220
- Kreyling J, Wenigmann M, Beierkuhnlein C, Jentsch A (2008) Effects of extreme weather events on plant productivity and tissue die-off are modified by community composition. *Ecosystems* 11:752–763
- Lauenroth WK, Sala OE (1992) Long-term forage production of North American shortgrass steppe. *Ecol Appl* 2:397–403
- Lauenroth WK, Sala OE, Coffin DP, Kirchner TB (1994) The importance of soil water in the recruitment of *Bouteloua gracilis* in the Shortgrass Steppe. *Ecol Applic* 4:741–749
- Le Houérou HN (1984) Rain-use efficiency: a unifying concept in arid land ecology. *J Arid Environ* 7:213–247
- Littell RC, Stroup WW, Freund RJ (2002) SAS for linear models, 4th edn. SAS Institute, Cary
- Monger HC (2006) Soil development in the Jornada Basin. In: Havstad KM, Huenneke LF, Schlesinger WH (eds) Structure and function of a Chihuahuan Desert ecosystem: The Jornada basin long-term ecological research site. Oxford University Press, New York, pp 81–106
- Muldavin E, Moore D, Collins SL, Wetherill KR, Lightfoot DC (2008) Aboveground net primary production dynamics in a northern Chihuahuan Desert ecosystem. *Oecologia* 155:123–132
- Neilson RP (1986) High resolution climatic analysis and Southwest biogeography. *Science* 232:27–34
- Nelson EW (1934) The influence of precipitation and grazing on black grama grass range. U.S. Department of Agriculture Technical Bulletin 409. U.S. Department of Agriculture, Washington, DC

- Okin GS, Parsons AJ, Wainwright J, Herrick JE, Bestelmeyer BT, Peters DPC, Fredrickson EL (2009) Do changes in connectivity explain desertification? *Bioscience* 59:237–244
- Parton WJ (1978) Abiotic section of ELM. In: Innis GS (ed) Grassland simulation model. Ecological studies vol 26. Springer, New York, pp 31–53
- Peters DPC (2000) Climatic variation and simulated patterns in seedling establishment of two dominant grasses at an ecotone. *J Veg Sci* 11:493–504
- Peters DPC (2002) Recruitment potential of two perennial grasses with different growth forms at a semiarid-arid transition zone. *Amer J Bot* 89:1616–1623
- Peters DPC, Mariotto I, Havstad KM, Murray LW (2006) Spatial variation in remnant grasses after a grassland to shrubland state change: implications for restoration. *Rangeland Ecol Manage* 59:343–350
- Peters DPC, Herrick JE, Monger HC, Huang H (2010) Soil-vegetation-climate interactions in arid landscapes: effects of the North American monsoon on grass recruitment. *J Arid Environ* 74:618–623
- Peters DPC, Yao J, Sala OE, Anderson J (2012) Directional climate change and potential reversal of desertification in arid ecosystems. *Global Change Biol* 18:151–163
- Ponce Campos GE, Moran MS, Huete A, Zhang Y, Bresloff C, Huxman TE, Eamus D, Bosch DD, Buda AR, Gunter SA, Heartsill Scalley T, Kitchen SG, McClaran MP, McNab WH, Montoya DS, Morgan JA, Peters DPC, Sadler EJ, Seyfried MS, Starks PJ (2013) Ecosystem resilience despite large-scale altered hydroclimatic conditions. *Nature* 494:349–352
- Rango A, Ritchie JC, Schmugge TJ, Humes KS, Hipps LE, Prueger JH, Havstad KM (1998) JORNEX: A multidisciplinary remote sensing campaign to quantify plant community/atmospheric interactions in the northern Chihuahuan Desert of New Mexico. In: Wheeler H, Kirby C (eds) *Hydrology in a changing environment*. John Wiley, London, pp 585–590
- Reichmann LG, Sala OE, Peters DPC (2013) Precipitation legacies in desert grassland primary production occur through previous-year tiller density. *Ecology* 94:435–443
- Russell SK, Schupp EW (1998) Effects of microhabitat patchiness on patterns of seed dispersal and seed predation of *Cercocarpus ledifolius* (Rosaceae). *Oikos* 81:434–443
- Sala OE, Gherardi LA, Peters DPC (2012) Effects of interannual precipitation variability on ecosystem water balance and its consequences for aboveground net primary production. *Ecol Soc Am Annu Meet Abstracts OOS* 12–6:p66
- Schlesinger WH, Pilmanis AM (1998) Plant–soil interactions in deserts. *Biogeochemistry* 42:169–187
- Snyder KA, Mitchell KA, Herrick JE (2006) Patterns and controls of soil water in the Jornada Basin. In: Havstad KM, Huenneke LF, Schlesinger WH (eds) *Structure and function of a Chihuahuan Desert ecosystem: The Jornada basin long-term ecological research site*. Oxford University Press, New York, pp 107–132
- Tielbörger K, Kadmon R (2000) Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology* 81:1544–1553
- Toole VK (1941) Factors affecting the germination of various drop-seed grasses (*Sporobolus* spp.). *J Agric Res* 62:691–715
- Vaughn KJ, Young TP (2010) Contingent conclusions: year effects influence the results of ecological field experiments, but temporal replication is rare. *Restor Ecol* 18(S1):59–64
- Weaver JE, Albertson FW (1939) Major changes in grassland as a result of continued drought. *Bot Gaz* 100:576–591
- Whitford WG (2002) *Ecology of desert systems*. Academic Press, San Diego
- Wilson S (2002) Prairies. In: Perrow MR, Davy AJ (eds) *Handbook of ecological restoration: restoration in practice*, vol 2. Cambridge University Press, New York, pp 443–465
- Wythers KR, Lauenroth WK, Paruelo JM (1999) Bare-soil evaporation under semiarid field conditions. *Soil Sci Soc Am J* 63:1341–1349
- Young TP, Petersen DA, Clary JJ (2005) The ecology of restoration: historical links, emerging issues, and unexpected realms. *Ecol Lett* 8:662–672