Directional climate change and potential reversal of desertification in arid and semiarid ecosystems

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Abstract

Our objective was to determine if long-term increases in precipitation can maintain grasslands susceptible to desertification, and initiate a reversal of historic regime shifts on desertified shrublands. Perennial grass production and species richness in a multi-year wet period were hypothesized to be greater than expected based on precipitation in a sequence of dry years. These responses were expected to differ for grasslands and shrublands with different dominant species and topo-edaphic properties. Long-term trends in desertification were documented using vegetation maps beginning in 1858, 1915, 1928, and 1998). These trends were compared with herbaceous and woody species responses to a sequence of dry (1994–2003) and wet years (2004–2008) for two grassland (uplands, playas) and three desertified shrubland types (honey mesquite, creosotebush, tarbush) in the Chihuahuan Desert. Analyses showed that both types of grasslands decreased in spatial extent since 1858 whereas areas dominated by mesquite or creosotebush increased. Production of upland grasslands in the wet period was greater than expected based on responses during the dry period whereas the relationships between species richness and precipitation was the same for both periods. Precipitation was not important to responses in playa grasslands in either period. For all ecosystem types, the production response in wet years primarily was an increase in herbaceous plants, and the most pronounced responses occurred on sandy sites (upland grasslands, mesquite shrubland). Results suggest that multiple wet years are needed to initiate a sequence of grass establishment and survival processes that can maintain upland grasslands without management inputs and lead to a state change reversal in desertified shrublands. Restoration strategies need to take advantage of opportunities provided by future climates while recognizing the importance of ecosystem type.

Keywords: extreme events, grasslands, regime shift, shrublands, spatial context, wet-dry climatic periods

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Introduction

Shifts from one ecological state to another result in persistent, dramatic consequences for the organization and dynamics of many ecosystems (Scheffer *et al.*, 2001; Carpenter, 2003). These state changes (i.e., regime shifts) can persist for decades to centuries as a result of changes in the internal dynamics and feedbacks among system components that prevent a reversal even if the driver that caused the shift is removed (Scheffer *et al.*, 2001; Carpenter, 2003). There is increasing evidence that climate change is resulting in more ecosystems crossing thresholds of change (Fagre *et al.*, 2009; Bush *et al.*, 2010). It is less well recognized that directional changes in climate may provide opportunities to reverse or significantly alter historic regime shifts, similar to effects of inter-annual variability in precipitation (Holmgren & Scheffer, 2001) and long-term herbivore exclusion (Allington & Valone, 2010). A better understanding is

needed about the environmental conditions and ecological processes responsible for regime shift reversals before accurate predictions can be made about their long-term consequences to ecosystem function (Millennium Ecosystem Assessment [MEA], 2005; Solomon *et al.*, 2007). A regime shift reversal associated with non-stationary climate drivers may take several forms (Milly *et al.*, 2008). Herein, we define a reversal based on a return to dominance by a previous life form rather than to the historical species composition that may be unknown or unattainable (Jackson & Hobbs, 2009).

A historic regime shift of particular importance globally is the conversion of perennial grasslands to dominance by unpalatable, xerophytic woody plants (Reynolds & Stafford-Smith, 2002). Environmental degradation associated with this 'desertification' influences ecosystem services to over 250 million people globally (MEA, 2005; Reynolds *et al.*, 2007). The desertification process often is driven by prolonged drought interacting with livestock overgrazing that reduce cover and increase mortality of grasses compared with drought- and grazing-resistant woody plants. As

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woody plant density increases, wind and water redistribution of nutrients and organic matter occurs from bare-soil interspaces to 'islands of fertility' beneath woody plants (Schlesinger *et al.*, 1990; Okin *et al.*, 2009; Field *et al.*, 2010). These positive plant-soil feedbacks create a landscape mosaic of woody plants in high nutrient patches interspersed with degraded bare-soil interspaces where recruitment of perennial grasses occurs infrequently (Aguiar & Sala, 1997; Rango *et al.*, 2006). Woody plant-dominated systems on degraded soils are believed to be very persistent under current climatic and biotic conditions (Bestelmeyer *et al.*, 2003), and efforts to restore grasses often are unsuccessful (Herrick *et al.*, 2006).

Directional changes in climate as a result of global warming either may maintain current trends in desertification or provide opportunities to alter the course of historic regime shifts (Allen & Breshears, 1998; Easterling *et al.*, 2000; Breshears *et al.*, 2005). In arid regions, climate model projections diverge with regard to the direction and magnitude of changes in precipitation (Karl & Wright, 1998; Burke *et al.*, 2006; IPCC, 2007; Seager *et al.*, 2007). Increases in frequency and severity of drought, as predicted by some models (Seager *et al.*, 2007; Schoof *et al.*, 2010), are expected to maintain current desertified systems and increase the land susceptible to woody plant encroachment, even in the absence of livestock overgrazing (Verstraete *et al.*, 2009).

Alternatively, long-term increases in rainfall may provide opportunities for a reversal of historic regime shifts. Increases in annual rainfall amounts have occurred in some regions over the past 50 years (Karl & Wright, 1998), and are predicted to occur in arid and semiarid regions globally based on some global change models (IPCC 2007). Long-term increases in precipitation may affect ecosystems differently than individual wet years during average or dry periods of time. In drylands, individual wet years increase growth of existing plants, but they do not result in recruitment and persistence of grasses and other herbaceous plants in interspaces between woody plants (Huenneke *et al.*, 2002). A sequence of wet years may be needed for seed production and seedling establishment of herbaceous plants followed by their survival, persistence, and eventual dominance (Peters *et al.*, 2010). In addition, the presence of herbaceous plants can capture soil water with feedbacks to grass recovery (Rango *et al.*, 2006), similar to processes leading to woody plant dominance during degradation (Schlesinger *et al.*, 1990; Peters *et al.*, 2004).

A key indicator of change in ecosystem function, and potentially grass recovery, is a change in rain-use efficiency (RUE) defined as the grams of production per unit of precipitation (Le Houérou, 1984). Although RUE may not change with precipitation across biomes (Sala *et al.*, 1988), changes within systems through time are more complex (Hein & de Ridder, 2006; Bai *et al.*, 2008). In general for arid systems, within-site RUE increases with annual precipitation (Hein & de Ridder, 2006), and decreases with increases in soil degradation associated with livestock grazing (Snyman & Fouché, 1991; Verón & Paruelo, 2010). A reduction in livestock grazing can reduce degradation through the generation of feedbacks between grasses and soil water that increase water available to plants (Rietkerk *et al.*, 1997; Allington & Valone, 2010). A long-term increase in precipitation can also result in a more water conserving system where RUE increases as a result of both reductions in evaporative losses and positive feedbacks between grasses and water availability (Wood *et al.*, 1987; Angers & Caron, 1998; Ehrenfeld *et al.*, 2005).

Long-term data collected during a multi-year drought followed by an extended wet period were used to determine if a sequence of wet years can push desertified woody plant-dominated systems beyond their domain of natural variability to initiate a regime shift toward grass dominance. Aboveground net primary production (ANPP) and species richness in a multi-year wet period were hypothesized to be greater than expected based on precipitation (PPT) in a sequence of dry years. This hypothesis was tested in the Chihuahuan Desert that experienced a broad-scale shift from perennial grasslands to shrublands over the past several centuries (Humphrey, 1958; Grover & Musick, 1990; Gibbens *et al.*, 2005). This desert consists of five major ecosystem types (two grasslands, three shrublands) with different species dominance and composition, soil properties, and topography that were expected to influence their response to long-term increases or decreases in precipitation.

To test this hypothesis that system responses in a wet period are greater than expected based on precipitation in a dry period, two responses were examined that are inter-related: (1) ANPP, a major component of the carbon budget, and (2) biodiversity (i.e., species richness) that determines organismal responses driving ecosystem dynamics, including ANPP (Chapin *et al.*, 2000). Maps of dominance in 4 years (1858, 1915, 1928, and 1998) were combined with 15 years of detailed plant production and biodiversity responses for each ecosystem type. These years included a 10-year drought (1994–2003) followed by a 5-year wet period (2004–2008). Four questions were addressed: (1) What are historic trends in these ecosystems? (2) How do these ecosystems differ in production, richness, and RUE responses during drought compared to an extended wet period? (3) Does the response to increased precipitation reflect grass recruitment and expansion or

is the increase primarily due to growth of existing woody plants? (4) How are these systems expected to change under directional changes in climate?

Methods

Study site and sample locations

The study was conducted at the Jornada Basin U.S. Department of Agriculture (USDA) – Long Term Ecological Research (LTER) site in southern New Mexico, USA (32.5°N, 106.45°W). Climate is arid to semiarid with an average of 25 cm of annual precipitation over the past 95 years, occurring mostly during the summer to fall monsoon period of 1 July to 1 October. Average monthly temperatures over the same time period ranged from 6 °C in January to 26 °C in June. Livestock grazing has decreased over time with peaks in the late 1800s (Fredrickson et al., 1998). Current grazing intensities are maintained at low levels throughout the 100 000 ha site.

To focus on climatic effects on variation in ANPP and richness, three ungrazed locations were selected for each ecosystem type to represent the range of variation in vegetation, soils, and topography of Chihuahuan Desert ecosystems (Table 1): (1) upland grasslands dominated by black grama (Bouteloua eriopoda), mesa dropseed (Sporobolus flexuosus), and several threeawn species (Aristida spp.) on level locations with loamy sand to sandy loam soils (2) playa grasslands on low-lying, run-in locations with clay soils dominated by vine mesquite (Panicum obtusum), tobosa grass (Pleuraphis mutica), and alkali sacaton (Sporobolus airoides), (3) mesquite (Prosopis glandulosa) shrublands located on level uplands with loamy sand soils, (4) creosotebush (Larrea tridentata) shrublands on upper bajadas slopes with sandy loam soils, and (5) tarbush (Flourensia cernua) shrublands on level lower bajada locations with sandy loam to sandy clay loam soils.

Rainfall measured at each location and the Palmer Drought Severity Index (PDSI; Palmer, 1965) were used to distinguish wet and dry periods for the time of vegetation sampling. Monthly precipitation was summed to obtain an annual amount based on water year (October 1 to September 30) to correspond with timing of vegetation measurements. Similar long-term average rainfall was found for all locations (23 to 25 cm yr^{-1}). PDSI values for the region were obtained from an on-line source (http://www7.ncdc.noaa.gov/CDO/cdo). This index uses monthly air temperature and rainfall information as well as soil properties to estimate moisture supply and demand as a measure of departure from the mean condition at a site (Palmer, 1965; Heim, 2002). A value of 0 is normal, drought severity increases with the absolute value of the negative number (−3 is moderate drought; −4 is extreme drought), and excess rain is shown by the magnitude of the positive number (e.g., 2 is moderate rainfall).

Using both annual rainfall amounts and PDSI values, two climatic periods were identified: 1994–2003 (dry) and 2004–2008 (wet) (Fig. 1). Although individual years within each period may not reflect the average rainfall or PDSI of that period, combining the two measures of climate for each year results in the general pattern. For example, 2 years in the dry period (1997, 1999) had large amounts of rainfall, but small PDSI values. Similarly, 2 years in the wet period (2006, 2008) had negative PDSI, but high rainfall amounts. The wet period had significantly greater average rainfall (30 cm yr^{-1}) compared with the dry period (19 cm yr^{-1}). Years in the wet period had a large proportion of rainfall in the summer growing season (1 July to 30 September) (Fig. 1a). Years 2004, 2006, and 2008 had particularly wet summers reflected in the positive drought indices (Fig. 1b). Years during the dry period had negative drought indices in nearly all spring (1 April to 30 June) or summer growing seasons. No pattern in precipitation amount during the dormant season (1 October to 31 March) was observed in either time period.

Historic trends in ecosystem type

Long-term trends in vegetation dynamics were obtained from maps created in 4 years (1858, 1915, 1928, and 1998) depicting the areal extent of each ecosystem type across a 59 000 ha portion of the Jornada operated by the USDA (Gibbens et al., 2005). The original 1858 map consisted of two maps: one showing grass condition (very good, good, fair, and poor) and another showing shrub presence by dominant species. An 1858 ecosystem type map was created by assuming locations with very good and good grass were grass dominated, and fair and poor grass locations were dominated by the shrub species with largest presence. Because upland and playa grassland types are distinguished by topography that is time-invariant, the grassland type of each location in 1858 was assumed to be the same as the 1915 map. For each year, the percentage of area (% area) occupied by each ecosystem type was estimated using ArcGIS.

Comparison of responses within and across climatic periods

Within each location, a systematic grid of 48 or 49 1 m^2 permanent quadrats with 10 m buffers was established in 1989, and sampled for biomass and richness in three seasons each year [dormant late winter (February), spring peak growth (May), and fall peak growth (September to October)]. The experimental design and sampling protocols are detailed in Huenneke et al. (2001, 2002). Sample date varied among years by 2–3 weeks depending on growth patterns and weather constraints. Plant biomass was estimated by species using non-destructive measurements of individual plant dimensions (cover, height) converted to biomass using regression equations based on periodic reference harvests (Huenneke et al., 2001). Biomass was summed across individuals by species per quadrat. Annual ANPP was estimated using the positive increment in biomass by species in a quadrat summed for the three seasons. Each annual value of ANPP is the mean over 48 or 49 quadrats at a location. Yearly rain-use efficiency was calculated using ANPP divided by water year precipitation by location. Richness was obtained by counting the number of species in each quadrat in each season, summing the total number of unique species per year, and dividing it by 49 m^2 (n m^{-2}).

Table 1 Key properties of five ecosystem types in the Chihuahuan Desert

| Ecosystem type	Dominant species	Soil texture class*	Period d = dry w = wet	ANPP‡, g m⁻² yr⁻¹ Mean (SE)	Species richness†, n m⁻² Mean (SE)	RUE†,‡, (g m⁻²) cm⁻¹ Mean (SE)
Upland grasslands	*Bouteloua eriopoda* (black grama) *Sporobolus flexuosa* (mesa dropseed); *Aristida* spp. (threeawns)	Loamy sand to sandy loam	All years	136 (13.3)	11.1[A] (0.78)	5.5 (0.4)
			1994–2003 (d)	92[b] (7.3)	10.4[b] (1.01)	4.6[b] (0.3)
			2004–2008 (w)	223[a] (24.9)	12.5[a] (1.12)	7.2[A,a] (0.7)
Playa grasslands	*Panicum obtusum* (vine mesquite) *Pleuraphis mutica* (tobosa grass) *Sporobolus airoides* (alkali sacaton)	Clay	All years	200[§] (31.3)	4.9[B] (0.29)	8.9[§] (1.6)
			1994–2003 (d)	172 (35.8)	4.7 (0.35)	9.9 (2.3)
			2004–2008 (w)	255 (60.0)	5.3 (0.52)	6.6[¶] (1.3)
Mesquite shrublands	*Prosopis glandulosa* (honey mesquite)	Loamy sand	All years	123 (14.7)	4.8[B] (0.44)	5.2 (0.4)
			1994–2003 (d)	77[b] (5.4)	4.2[b] (0.48)	4.3[b] (0.3)
			2004–2008 (w)	214[a] (32.0)	6.2[a] (0.79)	7.1[A,a] (1.0)
Creosotebush shrublands	*Larrea tridentate* (creosotebush)	Sandy loam	All years	81 (7.4)	6.1[B] (0.50)	3.4 (0.3)
			1994–2003 (d)	68 (7.3)	5.4[b] (0.59)	3.4 (0.3)
			2004–2008 (w)	108 (15.0)	7.4[a] (0.85)	3.4[B] (0.5)
Tarbush shrublands	*Flourensia cernua* (tarbush) *Schleropogon brevifolius* (burrograss)	Sandy loam to sandy clay loam	All years	79 (6.2)	5.3[B] (0.31)	3.5 (0.2)
			1994–2003 (d)	60[b] (4.9)	4.7[b] (0.33)	3.3 (0.2)
			2004–2008 (w)	118[a] (10.0)	6.6[a] (0.54)	3.9[AB] (0.4)

ANPP, aboveground net primary production.

*Soil texture class based on average sand, silt, and clay (%) in top 30 cm.

†Capital letters show significance across ecosystem types. If effect of ecosystem type is the same between periods, then capital letters are noted next to all year means. If effect of ecosystem type is different between periods, then capital letters are noted next to the period means. Small letters show significance among climatic periods within each ecosystem type.

‡RUE: rain-use efficiency (ANPP/PPT).

§Playa grasslands were excluded for comparisons across ecosystem types because of very high variance.

¶Two data points from playas in 2004 were excluded because of high measurement error for precipitation.
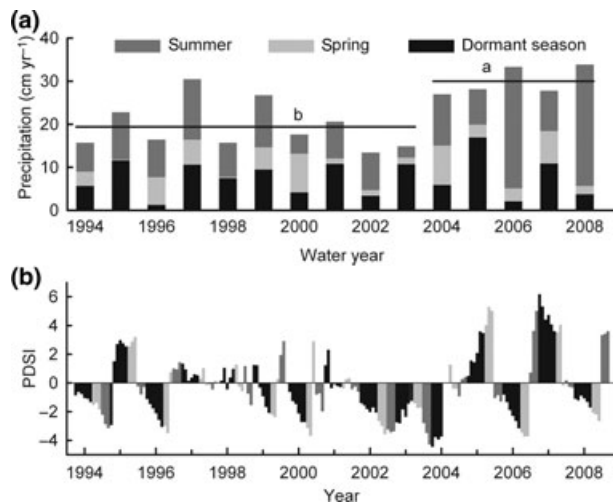
Fig. 1 (a) Water-year (October 1 – September 30) precipitation at the Jornada Basin USDA-LTER site averaged across 15 locations for the years 1990 to 2009 (average = 24 cm yr^{-1}). Annual rainfall is shown for three seasons relevant to growth of C_4 and C_3 plants: dormant season (1 October to 1 March), spring (1 April to 1 June), and summer (1 July to 1 September). (One-way anova; PROC GLM, sas, version 9.2) (b) Palmer Drought Severity Index (PDSI) calculated monthly for the National Climate Data Center region (NM 8) for the Jornada Basin (http://www7.ncdc.noaa.gov/CDO/cdo). Negative values indicate drought and positive values occur in wet months. Two climatic periods are shown in (a) based on average water-year precipitation and the PDSI index: dry (1994–2003) and wet (2004–2008). Different letters indicate significantly different means in water-year precipitation between periods.

Analyses and results for ANPP differ from previous uses of the data from 1989 to 1998 (Huenneke *et al.*, 2002) in three ways: (1) *Yucca elata* was removed in current analyses because its growth form results in large errors in biomass estimates from year to year, (2) current regressions between biomass and plant volume used an intercept equal to 0 to be consistent with a recent study in a similar system (Muldavin *et al.*, 2008), and (3) additional reference harvests obtained in extreme years since 1998 resulted in adjusted regression coefficients through time that reflect year-to-year variation in ANPP. These changes result in ANPP values that are smaller by 0 (playas) to 59% (creosotebush) compared with previous studies (Huenneke *et al.*, 2001, 2002).

Mixed model analysis of repeated measures (PROC MIXED; sas software, version 9.2; SAS Institute Inc., Cary, NC, USA) with two fixed factors and their interaction) was used to examine effects of ecosystem type and climatic period (1994–2003 dry, 2004–2008 wet) on response variables (ANPP, species richness, RUE). Log-transformed values were analyzed to meet assumptions of residual normality and homogeneity of variances, although non-transformed values are presented to aid in interpretation. Means between any two ecosystem types within a climatic period and means between climatic periods within an ecosystem type were compared using the

LSMEANS statement with the DIFF and SLICE options. Playa grasslands were excluded from the ANPP or RUE analysis across ecosystem types because the variances were much larger than other types due to flooding events that can either promote or kill plants depending on timing of water inputs. Square root-transformed ANPP or RUE values of playa grasslands were compared between climatic periods using mixed model analysis of repeated measures with one fixed factor (climatic period).

Importance of precipitation and climatic period

The relationship between PPT and each response variable (ANPP, species richness) within each ecosystem type for each time period and the entire time span was determined separately using mixed model analysis of repeated measures with PPT, climatic period, and their interaction as explanatory variables (Littell *et al.*, 2002). Under two circumstances, a 2-line model for the relationship was selected: (1) when the interaction between PPT and climatic period was significant (i.e., the slopes of a response variable against PPT were statistically different between the two periods), and (2) when the interaction was not significant, but the effect of PPT was significant (i.e., the slope of a response variable against PPT was statistically different from 0), and the effect of climatic period was significant (i.e., Y-intercepts from the two periods were statistically different). A 2-line model indicated that an ecosystem responded to PPT differently between the dry and wet periods. When both the effect of climatic period and the interaction were not significant, but the effect of PPT was significant, a 1-line model was selected, indicating that an ecosystem responded to PPT, but the response did not differ between the dry and wet periods. A significance level of $P < 0.05$ was used for all analyses.

Species and functional group responses

The contribution of four functional groups (annuals, perennial grasses, perennial forbs, shrubs) to ANPP and species richness was determined over time. The proportion of ANPP or richness attributed to a functional group calculated for each quadrat was averaged across quadrats within each year by ecosystem type. Quadrats with zero ANPP or richness were excluded from calculations of the mean.

Results

Historic trends in ecosystem types

Both upland and playa grasslands decreased in areal extent since 1858, although the rate of loss of upland grasslands was much faster (Fig. 2). In 1858, 82% of the Jornada was dominated by grasslands (67% uplands, 14% playas) compared with 8% of the area in 1998. Upland grasslands showed greatest losses in areal extent between 1858 and 1915 (24% of area) with another decrease between 1928 and 1998 (3%). Playa
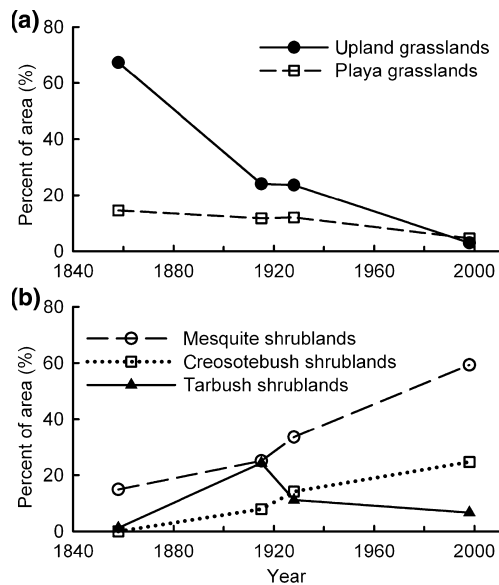
Fig. 2 Change in area of dominance (% of total area) from 1858 to 1998 for five ecosystem types in the Chihuahuan Desert: (a) grasslands and (b) shrublands.

grasslands remained similar (12% to 14%) until 1928 when there was a decrease to 1998 (5%). Area dominated by mesquite shrublands increased throughout the entire time period from 15% in 1858 to 59% in 1998. Creosotebush did not attain a large area until 1928 (14%) and increased to 25% by 1998. Tarbush reached maximum areal extent in 1915 (24%), and subsequently decreased to 7% by 1998 with a conversion of many areas to creosotebush.

Comparison of responses within and across climatic periods

Average production of upland grasslands and the three shrubland types were statistically the same, while average species richness of upland grasslands was significantly higher than other ecosystem types for all years and the two climatic periods (Table 1). Within an ecosystem type, both ANPP and richness were significantly higher in the wet than dry period for upland grasslands, mesquite shrublands, and tarbush shrublands; only species richness was significantly higher in the wet period for creosotebush shrublands, and neither variable was different between climatic periods for playa grasslands. RUE values were statistically the same between upland grasslands and the three shrubland types in the dry period (Table 1). In the wet period, RUE of upland grasslands and mesquite shrublands were significantly higher than creosotebush shrublands. Only upland grasslands and mesquite

shrublands had significantly greater RUE in the wet compared to the dry period.

Importance of precipitation and climatic period

The ANPP increased with precipitation in upland grasslands, creosotebush shrublands, and tarbush shrublands, but the relationship differed between climatic periods in two of these ecosystem types (Fig. 3 and Table 2). In upland grasslands, the slope during the wet period (10.6) was significantly larger than that during the dry period (3.9) (Fig. 3a and Table 2). In tarbush shrublands, the slopes were statistically indistinguishable in both periods (1.7), but the intercept was significantly greater in the wet (65.4) than that in the dry period (32.0) (Fig. 3e and Table 2). In creosotebush shrublands, the relationship was the same in both two periods (slope = 3.1) (Fig. 3d and Table 2). By contrast, ANPP in playa grasslands and mesquite shrubland was not related to precipitation in either time period (Fig. 3b,c and Table 2). Although the response of ANPP to PPT in mesquite shrublands did not differ between climatic periods (the effect of PPT was non-significant
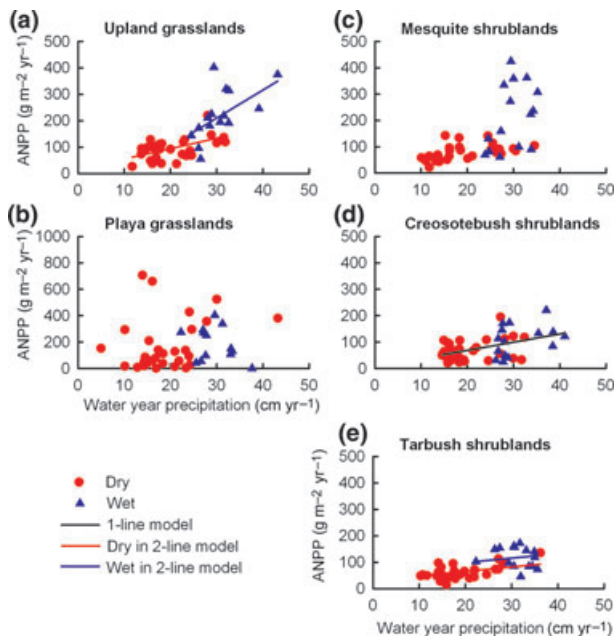
Fig. 3 Relationships between water-year precipitation (October 1 – September 30) and aboveground net primary production (ANPP) for data collected between 1994 and 2008: (a) upland grasslands, (b) playa grasslands, (c) mesquite shrublands, (d) creosotebush shrublands, and (e) tarbush shrublands. Regression lines, if significant, are shown for each of three time periods for each ecosystem type [all years, dry period (1994–2003), wet period (2004–2008)]. Regression coefficients are shown in Table 2.

Table 2 Statistics for the better model depicting the relationship between aboveground net primary production (ANPP) and water year precipitation (PPT) for three ecosystem types[*]

	Upland grasslands		Creosotebush shrublands[‡]		Tarbush shrublands	
	Estimate	P	Estimate	P	Estimate	P
1-line model[†]						
Intercept			6.6	0.828		
PPT			3.1	<0.001		
2-line model[†]						
Intercept_dry	15.1	0.656			32.0	0.037
Intercept_wet	−108.5	0.203			65.4	0.012
PPT_dry	3.9	0.020			1.7	0.026
PPT_wet	10.6	<0.001			1.7	0.026
Effect						
Period		0.173				0.046
PPT		<0.001				0.026
Period×PPT		0.037				ns[‡]

[*]None of the regressions were significant for playa grasslands or mesquite shrublands.
[†]1-line model: regression with precipitation (PPT) as the only explanatory variable. 2-line model: regression with PPT, climatic period, and their interaction as explanatory variables. Two climatic periods, a dry (1994–2003) and a wet period (2004–2008), were identified.
[‡]ns, non-significant; therefore not included in the analysis.

in either period), the ANPP values were more variable in the wet than those in the dry period. For example, ANPP in mesquite shrublands ranged from 99 to >400 g m^{-2} yr^{-1} for 30 cm rainfall (Fig. 3b).

Species richness was positively related to precipitation in all ecosystem types except for playa grasslands in both wet periods, and for tarbush shrublands in the wet period (Fig. 4). For upland grasslands and mesquite shrublands, the relationship did not differ between climatic periods (Fig. 4a,c and Table 3). For creosotebush and tarbush shrublands, the precipitation relationship differed between periods. During the dry period, species richness increased with precipitation for both types (slope = 0.3 for creosotebush, 0.1 for tarbush), but during the wet period, species richness was either not related (creosotebush; Fig. 4d and Table 3) or decreased with precipitation (tarbush, slope = −0.3; Fig. 4e and Table 3).

Species and functional group responses

Most of the increase in ANPP during the wet period in upland grasslands and all three shrubland types was associated with herbaceous plants, but the importance of functional group changed through time (Fig. 5). In upland grasslands, production of annuals increased first (2006), followed by an increase in production of the dominant perennial grass species (black grama) in 2008 (Fig. 5a). In mesquite shrublands, production
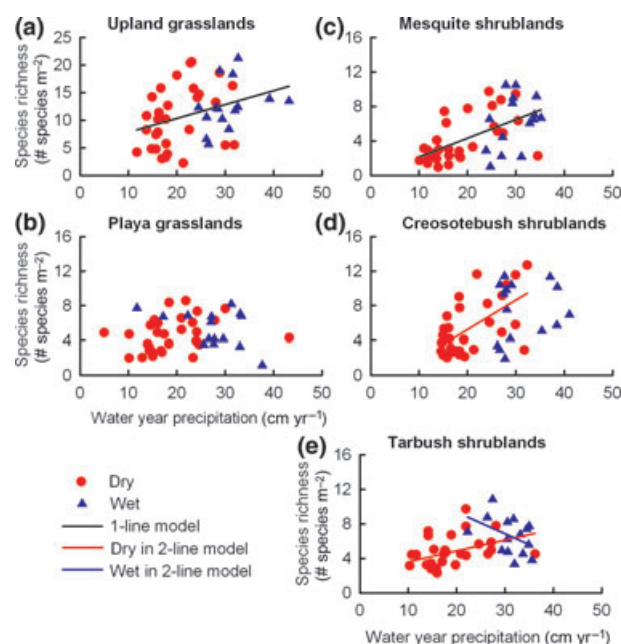
Fig. 4 Relationships between water-year precipitation (October 1 – September 30) and species richness for data collected between 1990 and 2008: (a) upland grasslands, (b) playa grasslands, (c) mesquite shrublands, (d) creosotebush shrublands, and (e) tarbush shrublands. Regression lines, if significant and slopes >0, are shown for each of three time periods for each ecosystem type [all years, dry period (1994–2003), wet period (2004–2008)]. Regression coefficients are shown in Table 3.

Table 3 Statistics for the better model depicting the relationship between species richness and water year precipitation (PPT) for four ecosystem types[*]

	Upland grasslands		Mesquite shrublands‡		Creosotebush shrublands		Tarbush shrublands	
	Estimate	P	Estimate	P	Estimate	P	Estimate	P
1-line model[†]								
Intercept	5.3	0.028	0.0	0.982				
PPT	0.3	0.008	0.2	<0.001				
2-line model[†]								
Intercept_dry					−1.5	0.457	2.3	0.061
Intercept_wet					6.3	0.123	14.4	<0.001
PPT_dry					0.3	<0.001	0.1	0.013
PPT_wet					0.0	0.768	−0.3	0.030
Effect								
Period						0.067		0.002
PPT						0.012		0.311
Period×PPT						0.041		0.004

[*]None of the regressions were significant for playa grasslands.
[†]1-line model: regression with precipitation (PPT) as the only explanatory variable. 2-line model: regression with PPT, climatic period, and their interaction as explanatory variables. Two climatic periods, a dry (1994–2003) and a wet period (2004–2008), were identified.
‡ns, non-significant; therefore not included in the analysis.
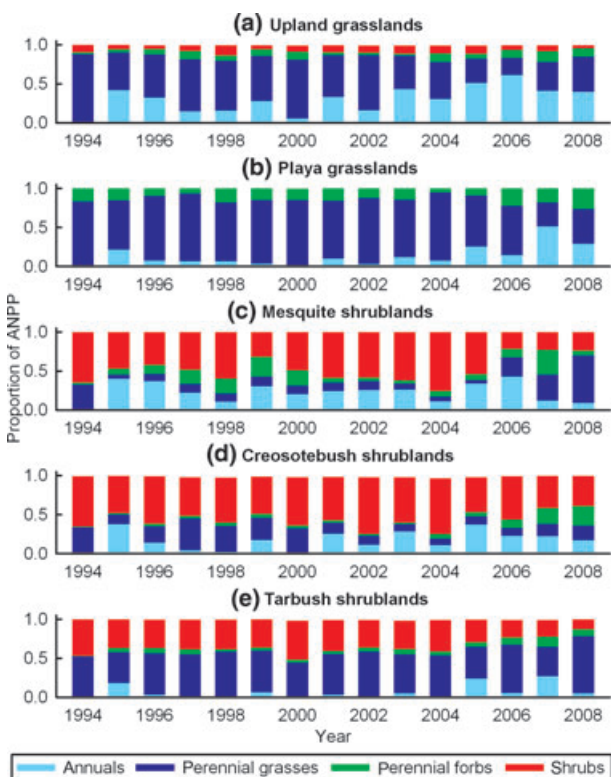
Fig. 5 Average proportion of total aboveground net primary production (ANPP) by dominant species or functional group for each ecosystem type: (a) upland grasslands, (b) playa grasslands, (c) mesquite shrublands, (d) creosotebush shrublands, and (e) tarbush shrublands.

increases were the result of annuals in 2006, perennial forbs in 2007, and perennial grasses (mostly mesa dropseed) in 2008 (Fig. 5c). In creosotebush shrublands, annuals provided the initial increase in production followed by perennial forbs (Fig. 5d). In tarbush shrublands, the production increase was mainly due to perennial grasses, in particular burrograss, tobosa, and bush muhly (*Muhlenbergia porteri*) (Fig. 5e).

Although species richness was higher during the wet compared with the dry period for upland grasslands and the three shrubland types, the increase was only ca. 2 species m^{-2} (Table 1), which was too small for patterns of functional groups to be detected (Fig. 6). However, species richness of perennial grasses in mesquite shrublands increased in 2006–2008 (Fig. 6c) and number of annual species increased in 2005–2007 in tarbush shrublands (Fig. 6e).

Discussion

Given the uncertainty in future precipitation regimes (IPCC, 2007), alternative scenarios need to be examined that account for both long-term increases and decreases in drivers. In addition, informed predictions about future ecosystem dynamics require a close match between temporal scales of key drivers with scales of the process or dynamic of interest (Weltzin *et al.*, 2003; Knapp *et al.*, 2008). For regime shifts, changes in amount of annual rainfall at the decadal scale or longer
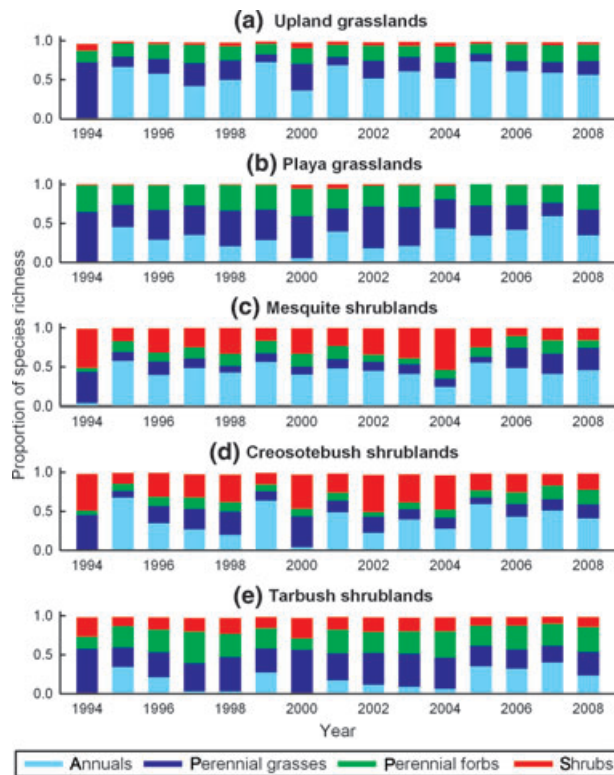
Fig. 6 Average proportion of species richness by dominant species or functional group for each ecosystem type: (a) upland grasslands, (b) playa grasslands, (c) mesquite shrublands, (d) creosotebush shrublands, and (e) tarbush shrublands.

are expected to be important because of their influence on recruitment, survival, and persistence of alternative dominant species (Swetnam & Betancourt, 1998; Jackson *et al.*, 2009). Decadal scale changes in rainfall can lead to the reorganization of communities (Schwinning & Sala, 2004) or development of novel species assemblages (Hobbs *et al.*, 2009). Results from this study support part of our hypothesis that production responses by most Chihuahuan Desert ecosystem types to a long-term drought cannot be linearly extrapolated to explain responses during an extended wet period. Above-ground net primary production was greater than expected based on precipitation in a sequence of dry years. Species richness did not follow the same pattern. A directional increase in precipitation resulted in thresholds in ANPP that are expected to either slow down or reverse the historic regime shift from upland grasslands to woody plant dominance, in particular by mesquite, that occurred in arid systems globally over the past several centuries in the presence of drought and livestock overgrazing (Buffington & Herbel, 1965; Reynolds & Stafford-Smith, 2002). This regime shift reversal is similar to effects of inter-annual variability in precipitation (Holmgren & Scheffer, 2001) and long-

term herbivore exclusion that promote grass cover and dominance in shrublands (Allington & Valone, 2010).

Although effects of livestock grazing, a common land use regionally and globally, were not studied herein, previous studies of grazing and precipitation can be used to place the results of the current study in a broader context. Based on research conducted in many locations, including the Chihuahuan Desert (e.g., Havstad *et al.*, 2006), the negative impacts of livestock overgrazing on grasses would overwhelm positive effects of wet years on grass production (Nelson, 1934). By contrast, managed grazing that attempts to match stocking rates with forage production by grasses would allow grasses to respond to increases in precipitation. For example, light to moderate grazing in the Chihuahuan reduces negative impacts on grasses that actively grow during the summer (Valentine, 1970). Nevertheless, an improved understanding of the interactive effects of directional changes in precipitation and livestock grazing on grass–shrub interactions is a critical area for future research.

Mechanistic explanations for responses

Chihuahuan Desert ecosystem types responded differently to an extended wet or dry period that likely reflects different processes governing dynamics. Ecosystem types with little topographic relief on sandy or loamy soils had an increase in either regression slope (upland grasslands), intercept (tarbush shrublands), or variability in ANPP (mesquite shrublands) in the wet compared with the dry period. These desert soils have low soil organic matter and aggregate stability that result in low water-holding capacity, but a high infiltration capacity (Gile *et al.*, 1981). Little or no directional topographic relief on coarse soils would have interacted with these soil properties to result in low losses of water to run off, increased depth of infiltration, and reduced evaporative losses relative to total losses from near-surface soils in multiple years with above-average precipitation. These processes would have led to greater increases in plant available water and observed production in wet years than expected based on precipitation in dry years.

However, this physically based explanation is insufficient to explain the larger than expected ANPP response by herbaceous plants in the wet period for these ecosystem types. An extended sequence of wet years may have led to cumulative effects of ecosystem responses as a result of the development of plant-soil feedbacks and an increase in herbaceous cover through time from existing plants as well as the establishment, growth, and survival of recruits in interspaces between adults. Feedbacks between plants and soil properties

leading to increases in nutrient and water availability to plants have been well-documented (e.g., Ehrenfeld *et al.*, 2005), and play an important role in shrub invasion (Schlesinger *et al.*, 1990). Results from this study suggest that the development of these feedbacks in shrublands has the potential to lead to grass recovery in ecosystem states that have been perceived as stable and resistant to change (Bestelmeyer *et al.*, 2003).

In creosotebush shrublands, ANPP increased with precipitation regardless of a dry or wet period, which likely reflects the importance of horizontal water redistribution. Because these shrublands are located on slopes, the same response of ANPP to precipitation between the dry and wet period suggests that losses of water to runoff were linearly related to amount of precipitation or rainfall intensity that was similar in wet and dry years. Most runoff on these sites occurs in interconnected areas between shrubs (Schlesinger *et al.*, 1989). The low species richness combined with high runoff in interspaces would limit the ability of subdominant species to respond to increases in rainfall.

In playa grasslands, production was highly variable in both climatic periods, and may have been driven by both rainfall and the amount of overland flow of water from upslope locations. Playas are 'resource-conserving' areas with concentrated runoff (Ludwig *et al.*, 1997) that can lead to either higher or lower ANPP depending on the timing and amount of water inputs (Peters *et al.*, 2006). The wettest year in the wet period (2008) had close to zero production because of flooding during the time of peak growth.

Threshold responses with changes in precipitation

For most of the dominant ecosystem types in the Chihuahuan Desert, thresholds in ecosystem responses were found across the range in naturally occurring annual precipitation over a 15-year time frame that included both an extended dry and wet period. These thresholds resulted from different relationships between production or richness with precipitation in a wet compared to a dry period that were also different from all years combined. These findings have important implications for predictions of responses under directional changes in precipitation. Extrapolation approaches based on individual wet or dry years, short-term responses to precipitation, or long-term data that combines wet and dry periods (e.g., Burke *et al.*, 1991; Fay *et al.*, 2008) will tend to minimize variation in predicted ANPP by under-estimation in wet periods and over-estimation in dry periods. Results shown herein are similar to errors associated with experimental manipulations that exceed the historic variation in rainfall to result in different magnitude and even direc-

tion of change in ecological responses compared to long-term observations (Nipper *et al.*, 2006).

Approaches to studying effects of altered rainfall on threshold behavior in ecosystem responses include long-term observations, experimental manipulations, process-based models, and cross-site comparisons (Weltzin *et al.*, 2003). Most experimental manipulations of rainfall are typically short term (<5 years) (Lauenroth *et al.*, 1978; Yahdjian & Sala, 2006; Zhou *et al.*, 2006), or if long term, they focus on drought (Reynolds *et al.*, 1999) or altered variability in rain events (e.g., Knapp *et al.*, 2002; Heisler-White *et al.*, 2009). Long-term observations provide a powerful approach that can take advantage of the full suite of naturally occurring conditions associated with extended wet or dry periods (Brown *et al.*, 2001). Although it can be challenging to disentangle the proportional effects of each driver (Weltzin *et al.*, 2003), important information can be obtained. For example, observational studies of vegetation during and following the severe, extended drought of the 1930s in the central US were instrumental in identifying plant species sensitivities to weather, and changes in species composition and dominance in response to below-average precipitation (Weaver & Albertson, 1944; Weaver, 1968). Studies that combine experimental manipulations and long-term observations under both effects of multi-year increases and decreases in total amount of rainfall and its intra-annual variability are essential to predict ecosystem dynamics in future climates.

Future trajectories under climate change

With no change in annual precipitation (average of 25 cm yr^{-1}) and well-managed livestock grazing, Chihuahuan Desert landscapes are expected to continue to be dominated by desertified shrublands with isolated patches of perennial grasslands (Gibbens *et al.*, 2005). Under a directional decrease in precipitation, the areal extent of mesquite and creosotebush shrublands are expected to increase based on our results for a recent drought combined with responses to drought in the 1950s (Yao *et al.*, 2006), the most severe drought in this region over the past 350 years (Fredrickson *et al.*, 1998). Most of the increase in mesquite and creosotebush is expected to occur at the expense of upland grasslands and tarbush shrublands, similar to historic trajectories.

However, a directional increase in precipitation would result in different dynamics for most ecosystem types than predicted based on the past 140 years. Shrublands dominated by mesquite or tarbush that were historically grasslands are expected to decrease in areal extent as herbaceous species increase in production and richness with multiple successive wet years.

Because these shrubs can live decades to centuries (Archer *et al.*, 1988; Archer, 1989), savannas co-dominated by grasses and shrubs may become the predominant ecosystem type initially followed by eventual grass dominance if the increase in precipitation persists through time.

Although not sampled herein, we also expect that historic shrublands would persist regardless of changes in climate. At the Jornada site, approximately 15% of the area was dominated by mesquite in 1858 that predates most of the colonization and large-scale introduction of domestic livestock (Fredrickson *et al.*, 1998). Because these locations have been dominated by mesquite shrubs for hundreds, if not thousands of years, we expect that edaphic controls will maintain their dominance even with changes in precipitation and temperature, or changes in stocking rates.

Upland grasslands would increase in production and potentially spatial extent with increasing rainfall such that shrub encroachment would be reduced from current rates. These results are supported by simulation modeling analyses showing shifts to perennial grass dominance with a directional increase in precipitation (Peters, 2002). However, upland grasslands presently are remnant areas of high richness located within large expanses of low richness shrublands such that few additional species are available at the landscape to regional scale to increase grassland richness even with increases in precipitation. A threshold response of production to increasing rainfall is expected when the system meets its structural and functional capacity to respond without the addition of species with novel traits (Lauenroth & Sala, 1992). In addition, careful livestock management will be needed to maintain these upland grasslands through time even in a higher precipitation regime (Havstad *et al.*, 2006).

In playa grasslands, changes in precipitation will primarily influence modifications in overland flow rather than rainfall. An increase in high intensity precipitation events associated with increases in amount would increase the frequency of flooding events through connections with upslope locations. Production would either increase or decrease depending on timing of the event relative to plant growth (Peters *et al.*, 2006). Because playas are isolated areas, the low frequency and abundance of flood-tolerant species in the regional species pool may constrain responses in wet years. A decrease in precipitation would reduce both overland flow and local rainfall, and act to reduce production, similar to the change from 1993 to 1994.

The single linear relationship between production and precipitation in creosotebush shrublands for all climatic periods reflects the primary response by dominant shrubs to rainfall with nominal increases in production, but not species richness, by perennial forbs. Because creosotebush plants can live hundreds to thousands of years (McAuliffe, 1988), these systems will have limited ability to modify species dominance or composition with long-term changes in precipitation. These results are similar to a previous study where a multi-decadal increase in winter precipitation resulted in a threefold increase in shrub density (Brown *et al.*, 1997). Thus, this ecosystem type is expected to be maintained in its current state in terms of species composition and areal extent regardless of a directional increase in precipitation.

Conclusions

Chihuahuan Desert landscapes consist of a heterogeneous suite of ecosystem types that differ in vegetation, soils, historic legacies, and connectedness with other ecosystems. Predicting future trajectories of change at the landscape scale requires a consideration of both wetter and drier conditions. Combining centuries-long patterns of ecosystem change with long-term data in response to variation in rainfall is one approach to elucidating pattern–process relationships across heterogeneous landscapes. Our results suggest that a long-term decrease in precipitation will accelerate current desertification trends with continuing loss of grasslands. On the contrary, a multi-year increase in precipitation can act to: (1) decrease the rate of grassland to shrubland conversion, and (2) convert desertified shrublands to savannas containing mixtures of shrubs and grasses, and potentially a return to grasslands in the future. Shifts between grasslands and shrublands in the American Southwest have occurred several times over the past 10 000 years (Buck & Monger, 1999); global changes in drivers that increase precipitation over a series of years may provide a mechanism for an unexpected shift in the near future. Because this regime shift reversal is not predicted based on responses to historical drivers, assumptions about ecosystem dynamics in the face of global change need to be re-examined, and new strategies need to be developed to take advantage of opportunities provided by future climates (Milly *et al.*, 2008).

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