Plant-soil feedbacks and the reversal of desertification with climate change

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Introduction

Desertification, the broad-scale conversion of perennial grasslands to dominance by xerophytic, unpalatable woody plants, results in persistent, dramatic consequences for ecosystem organization and dynamics, similar to dynamics in other systems (Scheffer et al., 2001). Regime shifts are persistent for decades to centuries as a result of positive feedbacks between woody plants and soil properties that maintain their dominance even if the driver that caused the shift is removed (Schlesinger et al., 1990). There is increasing evidence that climate change is pushing more ecosystems towards thresholds of change (Fagre et al., 2009). However, recent results showed that climate change manifested as a directional increase in precipitation for multiple years can increase grass production beyond that expected based on responses during drought (Peters et al., submitted). These grass responses were weakly related to annual precipitation, and accumulated through time with a series of wet years. These results suggest two processes are important to grass recovery in degraded shrublands. First, positive feedbacks between grasses and soil properties in addition to rainfall can affect water available to grasses. Second, a series of wet years can influence a sequence of processes across multiple years that are required for grass recruitment and persistence. Through time, a long-term increase in rainfall may reverse desertification, similar to effects of inter-annual variability in precipitation (Holmgren & Scheffer, 2001) and long-term herbivore exclusion (Allington & Valone, 2010). Our objective was to provide a conceptual framework for perennial grass recovery in a series of wet years, which includes both plant-soil feedbacks that increase available water to grasses and effects of precipitation on a sequence of recovery-related processes. We tested hypotheses based on this framework for grasslands and shrublands in the Chihuahuan Desert, the largest desert in North America.

Conceptual framework and hypotheses for grass recovery under directional climate change

In arid and semiarid systems, the key drivers associated with climate change are temperature, precipitation, and soil properties that influence plant available water. Although other drivers, such as livestock and land use, are also important, our focus is climatic effects. Most studies of climate change examine the direct effects of drivers on one or more processes (Fig. 1a). For example, production is related to rainfall amount or within-year variability in rainfall (Lauenroth et al., 1978; Reynolds et al., 1999; Zhou et al., 2006; Heisler-White et al., 2009). Effects of rainfall, temperature, and soil properties on seed production and seedling establishment have also been studied (Peters 2000, 2002; Peters et al., 2010).

Localized areas of higher production than predicted based on rainfall suggest that another set of processes is operating in drylands (Rango et al., 2006). Positive feedbacks between plants and dynamic soil properties, such as soil organic matter, can lead to fine-scale increases in nutrient and water availability with effects on production (Fig. 1b). These feedbacks are well-documented in many terrestrial systems (e.g., Ehrenfeld et al., 2005). Most research on feedbacks in arid and semiarid regions has focused on interactions between woody plants and soils that promote desertification (e.g., Kieft et al., 1998). These grass-soil interactions leading to grass recovery are similar to feedbacks initiated by the removal of livestock grazing where increases in water infiltration and soil nutrients influence growth of herbaceous plants (Rietkerk et al., 1997; Allington and Valone 2010).

But, plant-soil feedbacks alone are insufficient to explain grass recovery on degraded soils. Grass recovery involves a series of processes related to recruitment and growth that require consecutive wet years. Because perennial grasses in deserts often have transient, depauperate seedbanks in the soil, the first step in grass recovery is that sufficient rainfall is needed for the production of viable seeds (Peters 2002). Sufficient rainfall in the following year is then needed for these seeds to germinate followed by additional rain events in that same year for seedling establishment to occur (Peters 2000). High rainfall in a third consecutive year is needed for recruits to grow sufficiently large to persist through time (Peters et al., 2010).

High rainfall amounts alone are also insufficient to explain grass recovery. For example, individual wet years increase growth of existing plants, but they do not result in significant recruitment and persistence of herbaceous plants in interspaces between woody plants (Huenneke et al., 2002). Degraded soils with low infiltration and water-holding capacity have high rates of erosional losses by water that increase with rainfall amount (Schlesinger et al., 1989). We expect that both successive wet years AND plant-soil feedbacks are needed to reduce these erosional losses and increase effective water for grass recover (Fig. 1c). In a wet year, growth of existing herbaceous plants in interspaces between woody plants would increase with subsequent effects on litter inputs to the soil and modifications to dynamic soil properties. Seed germination and seedling establishment of new recruits would be promoted in the following wet year. Increases in herbaceous plants and litter would also increase plant available water directly through increases in interception and decreases in evaporation in the first wet year. Through time, these soil modifications from adults and seedlings would increase infiltration and water-holding capacity with feedbacks to grass establishment, growth and ultimately seed production and seedling establishment in bare soil and neighboring plant patches (Ludwig et al., 2005). Thus, growth and survival of grass seedlings to adults requires rainfall in a sequence of years combined with plant-induced changes in soil properties that act to promote grass persistence, and through time, would push the system towards a regime shift reversal in degraded systems.

On degraded soils dominated by woody plants, we hypothesized that these grass responses depend on ecosystem-specific characteristics: a resource conserving system with low rates of erosional losses to water is expected to exhibit stronger responses to multiple years of above-average precipitation than a leaky system where more resources are lost with less water and nutrients retained for plants (Ludwig et al., 1997; 2000). We expected that these responses were at least in part a result of plant-soil feedbacks that increased available water to herbaceous plants. We also hypothesized that a similar set of processes can maintain current grasslands that are susceptible to desertification without management inputs.

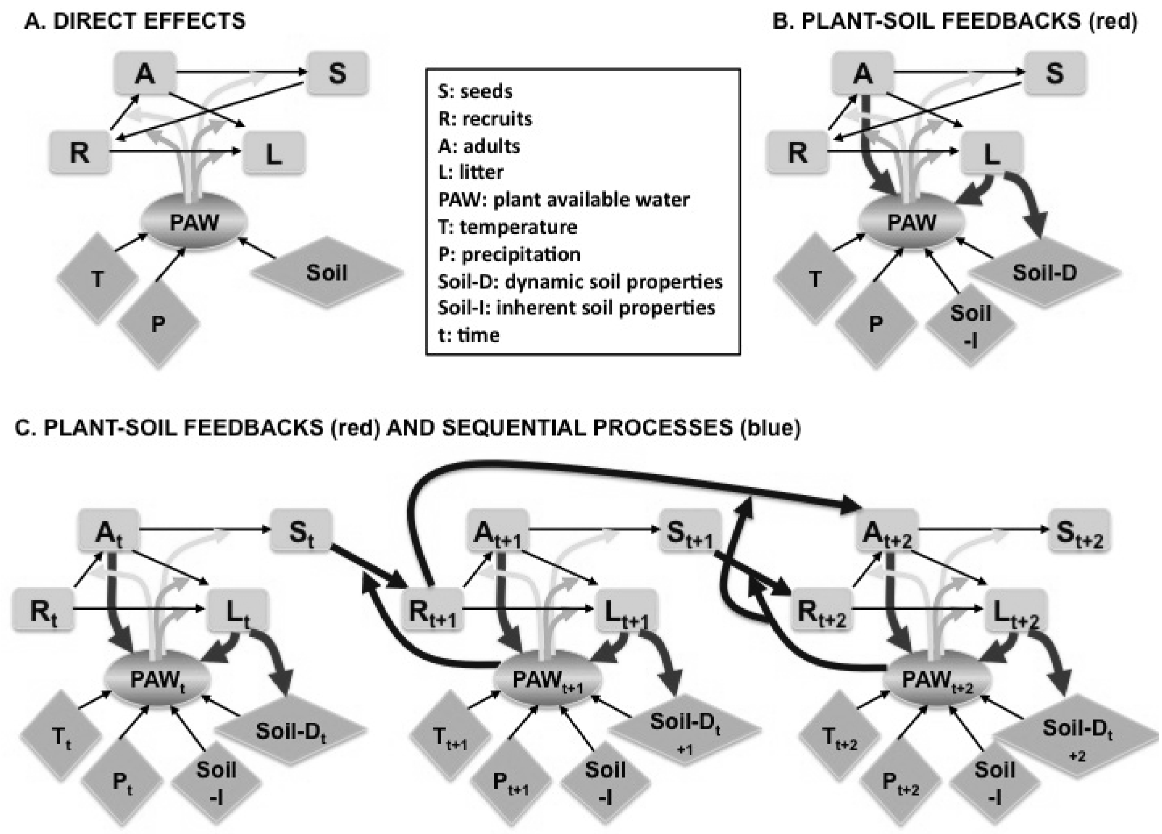

Fig. 1. Alternative conceptual frameworks for effects of directional climate change on grass recovery in drylands: (a) climate and soil drivers have direct effects on PAW and plant processes, (b) both direct effects of drivers and feedbacks from plants to soil properties (red) influence water available to grasses, and (c) direct effects, plant-soil feedbacks (red), and a sequence of processes that occur in a series of wet years (blue) affect water availability to plants. We tested hypotheses related to framework (c).

Materials & Methods

Hypotheses derived from our conceptual framework (Fig. 1c) were tested using data collected from the Jornada Basin U.S. Department of Agriculture-Long Term Ecological Research site in southern New Mexico, USA (32.5N, 106.45W). Climate is arid to semiarid with an average of 25 cm of annual precipitation over the past 80 years, occurring mostly during the monsoon period of 1 July to 1 October. Average monthly temperatures over the same time period ranged from 6 (January) to 26oC (July). Current livestock grazing intensities are maintained at low levels throughout the site (Fredrickson et al., 1998). Vegetation maps from 1858 and 1998 were used to identify the most common grassland-shrubland conversions in Chihuahuan Desert ecosystems (Gibbens et al. 2005; Peters et al., submitted). Because nearly half of the Jornada (59%) converted from upland grasslands to either creosotebush or mesquite shrublands (Table 1), analyses focused on these three ecosystem types. In addition, these types represent both resource conserving and leaky systems (Ludwig et al., 1997) based on their topography, and differ in their dominant species and soils: (1) upland grasslands dominated by black grama (*Bouteloua eriopoda*), mesa dropseed (*Sporobolus flexuosus*), and several threeawn species (*Aristida* spp.), a resourcing conserving system on level locations with loamy sand to sandy loam soils, (2) mesquite (*Prosopis glandulosa*) shrublands, a resource conserving system located on uplands with loamy sand soils, and (3) creosotebush (*Larrea tridentata*) shrublands, a resource leaky system located on upper bajadas slopes with sandy loam soils. Within each of three ungrazed locations for each type, a systematic grid of 49 1 m^2 permanent quadrats with 10 m buffers was established in 1989, and sampled for biomass and richness from 1989 spring through 2009 three times each year (dormant late winter, spring peak growth, fall peak growth). The experimental design and sampling protocols are detailed in Huenneke et al. (2001; 2002). Annual aboveground net primary production (ANPP) was measured as the increment in biomass by species in a quadrat summed for the three time periods, and averaged across quadrats. Monthly precipitation amounts from cumulative, graduated rain gauges were summed across months at each location to obtain an annual amount based on water year (Oct. 1 to Sept. 30) that corresponds with vegetation measurements used to calculate ANPP. Linear mixed model with repeated measures (SAS Proc Mixed) was used to determine the relationship between ANPP and water-year precipitation for each ecosystem type. 95% confidence intervals for the predicted values were used to identify outliers.

Table 1. Area (ha) and % of area of 1858 upland and playa grasslands converted to other ecosystem types by 1998 at the Jornada Basin Long-Term Ecological Research Site.

Ecosystem type in 1858	Ecosystem type in 1998										
	Creosotebush shrublands		Mesquite shrubland		Tarbush shrublands		Other		No change		Total
	Area	%	Area	%	Area	%	Area	%	Area	%	Area
Upland grasslands	11,227	28	23,444	59	2,134	5	1,285	4	1,430	4	39,520
Playa grasslands	757	9	3,467	41	1,679	20	650	7	1,946	23	8,499

Results & Discussion

ANPP was similar until 2003 for all three ecosystem types (ca. 100 g/m^2/y) (Fig. 2). Beginning in 2004, rainfall was above average for five years when production responses diverged among ecosystem types. Production on the two ecosystem types on sandy, level uplands increased beginning in 2005 (grasslands) and 2006 (mesquite shrublands), primarily as a result of large increases in perennial grasses and forbs that were maintained above the long-term average through 2009 even with very low annual precipitation in that year (10.5 cm) (Fig. 2b c). These ecosystem types are "resource conserving" (*sensu* Ludwig et al. 1997; 2000) in that water redistribution is localized among plants and interspaces with very little or no losses to runoff via overland flow. By contrast, the "leaky" ecosystem type (creosotebush shrublands) located on upper bajadas with frequent losses of water to runoff showed only small responses to the sequence of wet years (Fig. 2d). These results support our hypothesis that resource conserving systems have greater responses to multiple wet years compared with leaky systems.

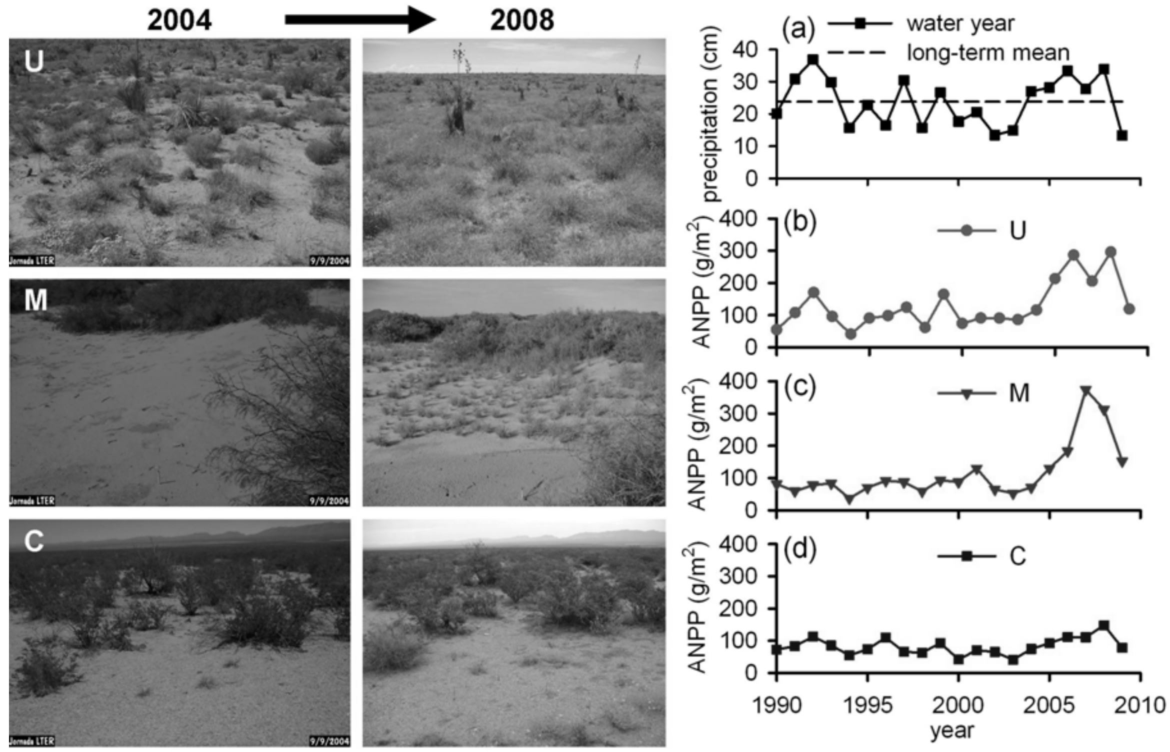

Fig. 2. Left: Photos illustrate herbaceous responses before (2004) and after 4 wet years (2008) in upland grasslands (U), mesquite shrublands (M), and creosotebush shrublands (C). Right: Precipitation and ANPP were low and variable from 1990-2003. Rainfall was above average from 2004-2008, and below average in 2009. ANPP more than doubled with multiple wet years in resource conserving systems (grasslands and mesquite), and showed little change in a leaky system with high runoff (creosotebush shrublands).

ANPP was positively related to annual precipitation for each ecosystem type from 1990-2003 (Fig. 3). For grasslands and mesquite shrublands, ANPP values in 2004-2009 were significantly larger than expected based on their respective regressions (Fig. 3a, b). These values indicate an increase in rain-use efficiency (RUE: grams production per unit rainfall) in the wet period which likely reflects the positive influence of greater effectiveness of rainfall corresponding to the influence of plants on localized water capture and PAW. These plant-soil feedbacks were not found in creosotebush shrublands where ANPP values in the sequence of wet years were predicted by rainfall amount using the long-term regression (Fig. 3c). These results provide support for our hypothesis that plant-soil feedbacks are more important in resource conserving than leaky systems.

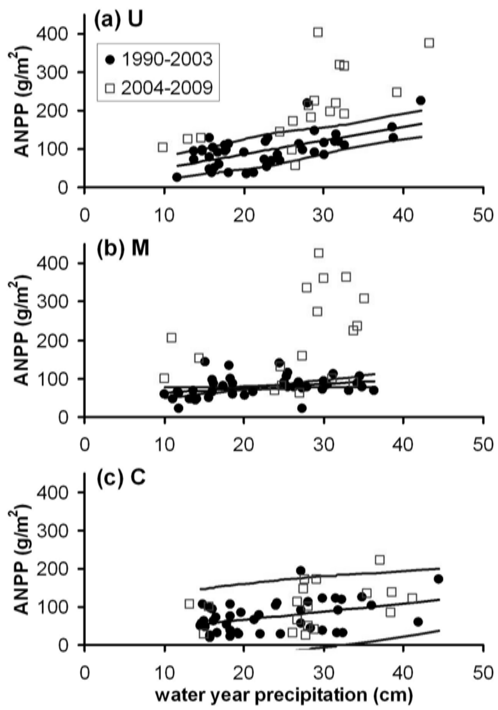

Fig. 3. Relationship between ANPP and time with 95% confidence intervals (blue lines) for 1990-2003 in (a) upland grasslands, (b) mesquite shrublands, and (c) creosotebush shrublands. ANPP in wet years (2004-2009) shown as points. The black line is the regression line.

Conclusions

A sequence of 5 wet years following 14 years of variable rainfall resulted in an increase in production in resource conserving ecosystem types that was greater than predicted based on rainfall alone. The increase in production was primarily by herbaceous plants, which captured water locally to increase plant available water to both existing plants and new recruits. The sequence of wet years allowed a series of linked plant processes to occur that resulted in the establishment and survival of perennial grasses and forbs. We predict that a continued series of wet years will maintain the herbaceous component of these systems, and may act to reverse desertification on degraded shrublands, and to maintain perennial grasslands without management inputs. Degraded shrublands located on slopes susceptible to runoff of water responded linearly to annual precipitation in multiple wet years, and are expected to be resistant to a shift back towards grasslands under a directional increase in precipitation.

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