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Title: Ecosystem consequences of precipitation variability and extremes in semiarid grassland and shrubland.

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Abstract:

1) Objective: To understand changes in ecosystem structure and function of semiarid grassland and shrubland caused by **a)** extended periods of severe drought or above-normal precipitation and **b)** precipitation variability. These forcings alter the pulses of soil moisture that drive biotic activity, such as primary productivity, community composition and ecosystem function. Using existing infrastructure, this work assesses the long-term consequences of disparate precipitation forcings.

2) Hypotheses:

Multi-year precipitation extremes: Grass cover will be more responsive to precipitation forcing than creosotebush and grass cover changes will alter the horizontal redistribution of precipitation by changing connectivity among bare soil patches. Prolonged drought will accelerate the conversion of mixed grass-shrub to shrubland while abundant water will increase grass cover.

Within-season precipitation variability: Ecosystem C fluxes and the rate of shrub encroachment into grassland will change with event size and frequency. Frequent small rain events will (1) increase soil CO₂ fluxes without affecting grass growth rates, and (2) stimulate *Larrea* seed germination but not provide sufficient soil moisture for survival. Infrequent large events will (1) increase CO₂ fluxes and stimulate grass growth, and (2) enhance *Larrea* seedling germination and establishment. The net result may be enhanced rate of shrub encroachment.

3) Location: Grass, mixed grass-shrub and shrub communities at the Sevilleta LTER in central New Mexico. The research directly funded by this proposal will be compared with data from two additional rainfall manipulation experiments at Sevilleta (winter addition in grassland, annual rainfall in piñon-juniper woodland), building a unique long term database of different rainfall manipulations.

4) Approaches/Methods: Long term extremes are imposed by excluding ambient precipitation with moveable shelters to impose drought or supplementing it using overhead irrigation. NICCR funds would support monitoring recovery after five years of drought treatment, the final two years of water addition treatment (now in year 3) and three years of monsoon manipulations. Long term mesic conditions are imposed by adding six large storms (20 mm each) per year. Monsoon precipitation variability is manipulated in separate plots by adding either one large (20 mm) or four small (5 mm) events monthly during July - September. Both studies measure plant water relations, NPP, and species composition and abundance to document changes in ecosystem structure and function caused by the treatment.

5) Deliverables: This long-term project will contribute to a detailed understanding of the ecosystem responses to precipitation extremes and variability. Deliverables include presentations and peer-reviewed publications as well as treated plots suitable for new manipulations after multi-year precipitation forcing.

Narrative:

Introduction

In semi-arid environments, precipitation-driven spatial and temporal patterns of soil water content are a key control on plant and ecosystem function (Noy-Meir 1973, Reynolds et al. 2004). In the absence of accessible groundwater, temporal variation in water availability results from discrete storms, each providing a pulse of soil water that drives biotic activity until available water is depleted (Fig. 1, Schwinning and Sala 2004). The spatial pattern (1 m scale) of soil water is determined by the amount of water reaching the soil surface and the effects of lateral redistribution, infiltration and runoff. The short-term responses of plant, plot and ecosystem to an individual pulse are controlled by this spatial pattern of soil water, the pre-storm physiological state of vegetation and prevailing environmental conditions (Huxman et al. 2004, Ogle and Reynolds 2004, Kurc and Small 2007). Climate variability and change, on time scales from seasons to decades and longer, are likely to alter the long-term sequence of precipitation pulses in aridland ecosystems worldwide. Moreover, ecosystem structure and function may be altered by deviations in pulse regime such as increased frequency and/or duration of extreme events (prolonged drought or above-average precipitation), changes in the frequency of rainfall events of different sizes, or a change in the seasonal distribution of precipitation (Loik et al. 2004). Rising levels of CO₂ and other greenhouse gases are widely expected to influence precipitation and hence soil moisture but the specific predictions of climate models vary widely (e.g. Canadian and Hadley models Allen et al. 2000, Cook et al. 2004, Seager et al. 2007, Wentz et al. 2007, Zhang et al. 2007).

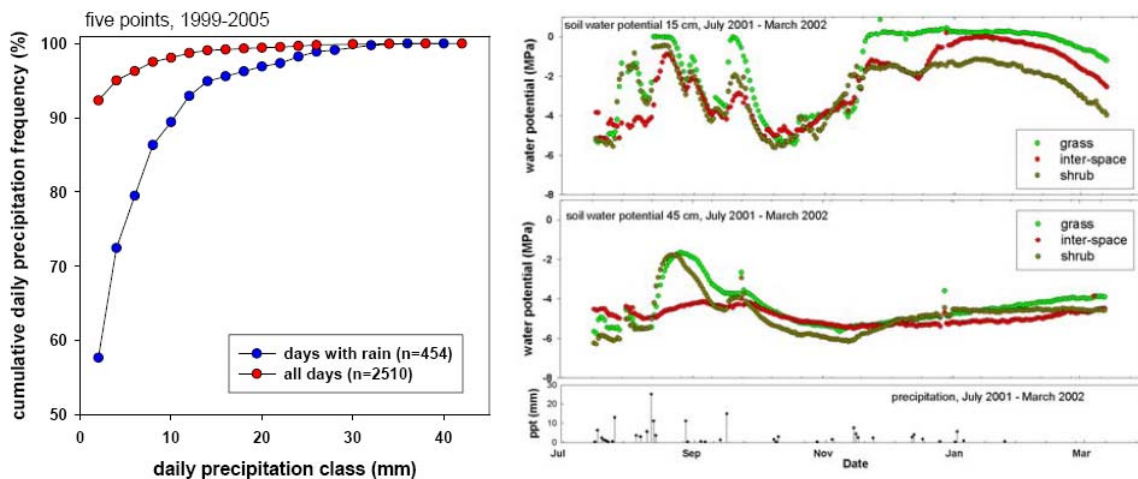


Figure 1 Right: Response of soil water potential to rainfall pulses of different sizes from July – Mar. Measurements were made in the ecotone plots at LPEX and symbols denote, grass, shrub and bare soil cover types. Note differences with pulse size and cover type. Left: pulse size frequency from the five points meteorological station at the Sevilleta LTER showing all days (red) and rainy days (blue). Note that nearly 60% of rainy days have less than 2 mm rainfall.

In addition to climate change, aridland ecosystems in the American Southwest and in other regions of the world are undergoing a state transition from dominance by grasses to dominance by woody vegetation. For example, in the southwestern US, creosotebush (*Larrea tridentata*) now dominates nearly 19 million ha of former grassland (van Auken 2000). The replacement of dominant C₄ grasses by native C₃ shrubs alters carbon storage and net primary production (Jackson et al. 2002, Hughes et al. 2006)(Knapp et al. 2007), modifies hydrological functioning (Jackson et al. 2002, Bhark and Small 2003), and enhances loss of biodiversity (Báez et al. 2006, Báez and Collins 2007) and soil fertility of arid and semiarid systems (Van Auken 2000, Huenneke et al. 2002). Although shrub encroachment likely results from multiple interacting factors, one potential driver of this state transition is climate variability.

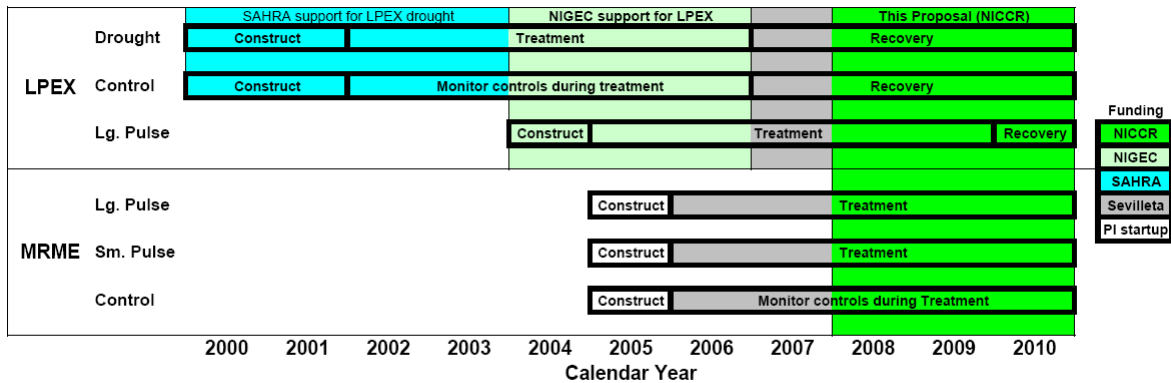


Figure 2. Timeline of construction and implementation of LPEX and MRME experiments at the Sevilleta LTER, including the past, present and proposed funding sources.

Understanding semi-arid systems under current climate and anticipating their response to potential shifts in climate resulting from human activities or other factors requires information about species and ecosystem responses to a variety of precipitation forcings. To address this problem, this proposal brings together a plant physiological ecologist (Pockman), a plant community ecologist (Collins) and a surface water hydrologist (Small) to continue two precipitation manipulation experiments at the Sevilleta LTER. Our objectives are to understand the effects of 1) extreme events (drought and above average precipitation) and 2) a change in summer rainfall that occurs with different storm sizes. We will address **NICCR focus 1** by continuing two established long-term experiments at the Sevilleta LTER (SEV) that examine the potential effects of precipitation change (see timeline in Fig. 2): **1)** the Long-term Precipitation Extremes experiment (LPEX) is a collaborative project (Pockman and Small) previously funded by NIGEC and NSF-SAHRA, and **2)** the Monsoon Rainfall Manipulation Experiment (MRME) established by Collins with UNM start-up funds. Providing a rich set of comparisons with this work are two separately-funded experiments at SEV that include a precipitation manipulation component: **3)** an NSF funded factorial global change manipulation of winter (El Nino) rainfall, nighttime warming and N

Table 1. Comparison of the treatment regimes and treatment period for each treatment in the Long Term Precipitation Extremes and Monsoon Rainfall Manipulation Experiments.

	Treatments					
	Long term Precipitation. Extremes Expt. (LPEX)			Monsoon Rainfall Manipulation Expt. (MRME)		
	Rainout	Control	Lg. pulse	Lg. pulse	Sm. Pulse	Control
Community type	Grassland, Shrubland & Mixed	Grassland, Shrubland & Mixed	Grassland, Shrubland & Mixed	Grassland	Grassland	Grassland
plots	3 x 3	3 x 3	3 x 3	5	5	3
Precip (mm)	140	250	370	310	310	250
Events Added	-6	0	+6	+3	+12	0
Event size (mm)	n/a	n/a	20 mm	20 mm	5 mm	n/a
Trt. Period	Apr – Nov	n/a	Apr – Nov	Jul – Sept	Jul - Sept	n/a
Trt. Start	2002	n/a	2005	2006	2006	n/a
Trt. End	2006	n/a	2009	2010	2010	n/a
NICCR funds	Drought recovery		2 yrs of treatment	3 years of treatment	3 years of treatment	

deposition, and 4) a DOE-PER funded ecosystem study of mechanistic responses to precipitation extremes in piñon-juniper woodland. Taken together, these studies offer the opportunity to synthesize data from treatments that span the range listed above (wet and dry extreme events, summer and winter water addition and changes in event size). This proposal requests NICCR funds to continue the treatments and measurements at the LPEX and MRME experiments for the next three years.



Fig. 3. Left: Irrigation system at MRME plots (with grassland rainout structure in background). Right: Irrigation system in operation at a MRME plot during the summer monsoon of 2006.

Results of

Related NIGEC Research – The Long-term Precipitation Extremes (LPEX) project was initiated by Pockman and Small in 2000 with seed money from SAHRA, NSF’s hydrology STC at the University of Arizona. Taking an ecohydrological approach to understanding the role of climate extremes in shrub invasion, we deployed 18 plots (9 m x 12 m, see summary in Table 1) comprising 3 rainout shelters (Fig. 3) and 3 untreated controls in black grama grassland, creosotebush shrubland, and mixed grass-shrub communities within 2 km at SEV. Treatments were based on the long term extreme drought (ca. 5 years during 1950’s). The driving hypotheses included 1) that the dominant C₄ shallow rooted grass (black grama, *Bouteloua eriopoda*) would be more sensitive to extreme drought than more deeply rooted C₃ evergreen shrub (Creosotebush, *Larrea tridentata*) and 2) that changes in cover associated with mortality of grasses would alter the distribution of soil moisture such that post-drought water availability would be diminished under grass canopies thereby reinforcing the establishment of shrubs. NIGEC support (2003-2006) completed the rainout treatments started with SAHRA funding (-50% of ambient) and added 3 water addition plots (several years of +50% of long-term average, e.g. 1990’s) in each vegetation community (total experiment is 27 plots across three communities). Rainout treatments ended in spring 2006 after five years and these plots are now being monitored to determine the response of the vegetation and hydrology after extended precipitation forcing. NIGEC funding

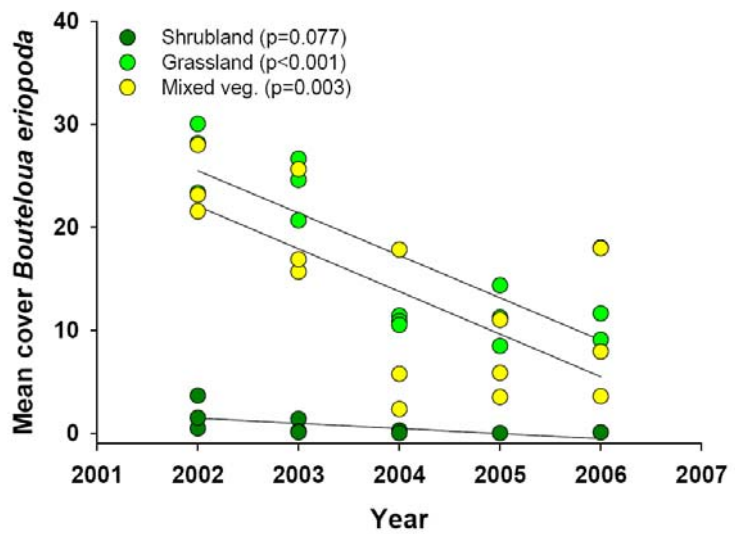


Fig. 4. Annual surveys of mean cover of black grama grass in grassland, mixed grass shrub and shrubland (sparse cover) over the course of four years of drought imposed by rainout shelters (year 1 data not shown). Rainout treatments ended in June 2006 so these data do not reflect continuous treatment.

completed 2 of 5 years of water addition treatments but additional funding is required to extend treatments to the planned five year mark. The Sevilleta LTER has maintained the treatments to provide an opportunity to secure continuing funding but this support is temporary and can not provide the full range of measurements for the remaining 2 years of the five year treatment.

The long term dataset from the LPEX drought treatments shows the following key results:

1. **Grass productivity under drought treatment was ~50% less than in controls;** while shrub productivity did not change. The grass response occurred in all five years of drought, in both the grassland and ecotone plots (Fig. 4). Continued study will reveal whether these changes are completely reversible or whether grass mortality will lead to lasting changes in surface hydrology and vegetation structure that produce a state change in the grassland and/or the mixed vegetation community. (drought hypothesis 1).
2. ***Bouteloua* responded more to water-addition treatment than did *Larrea*.** Grass productivity increased significantly compared to the control during the first two years of treatment while shrub responses have been smaller. This likely occurs because a greater proportion of grass root volume occurs in the top 30 cm of soil (Kurc and Small 2007) where soil water potential is highest following our water additions. The peak of the shrub rooting distribution occurs below 30 cm where the change in soil water potential is smaller (and the change in water content is much smaller).
3. **As a result of the decreased grass productivity, the standing biomass of grass and percent of ground area covered by grass declined throughout the experiment.** Accordingly, the percent cover of bare soil increased.
4. **Under drought treatment, the fraction of precipitation that was transported off the plots via overland flow increased (Fig. 5),** most likely due to the decrease in grass ground cover. We also suspect that the fine sediment and nutrient flux increased with runoff (Small and Pockman, *in prep*). The differential response in plant water relations and productivity exhibited a large effect early in the drought treatment. Grass productivity remained low throughout the remainder of the treatment and grass cover decreased. We are currently analyzing the soil water potential data to determine whether there were shifts in the pattern of soil moisture following storms of similar size as the treatments progressed.
5. In addition to these results from LPEX, the newly established MRME experiment (prototyped in 2006) came on-line in July 2007. This experiment is unique in that it includes 42 sensors for continuous monitoring of soil CO₂ and calculations of CO₂ fluxes. **Results to date suggest that precipitation variability (one large vs. several small events) alters *Bouteloua* photosynthesis, soil respiration (Fig. 6), and net ecosystem exchange.**

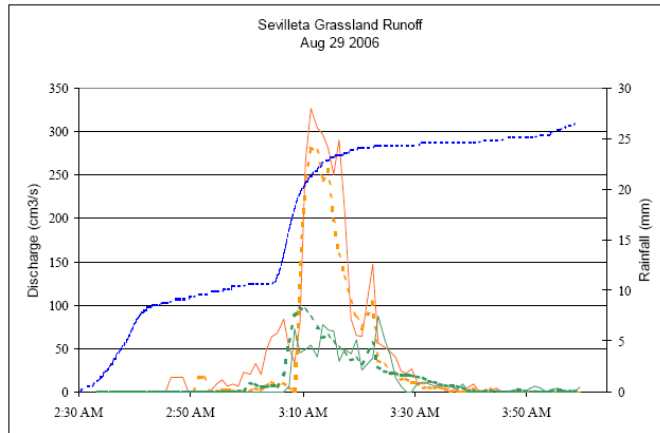


Fig. 5. Runoff following a single 25 mm storm at the grassland LPEX plots during summer 2006. Green lines are control plots, orange lines are rainout plots and the blue line shows cumulative rainfall. Note the large difference in discharge between control and rainout plots (solid and broken lines of each color are different plots).

The research proposed here is focused on the effects of annual precipitation extremes and seasonal precipitation variability on ecosystem structure (species composition) and function (plant water

relations, soil CO₂ fluxes, NPP) at the ecotone between semiarid grass- and shrub-dominated communities. These manipulations are less common among experimental approaches because of the time required and the difficulty of manipulating variability (e.g., Knapp et al. 2002). Overarching hypotheses for the LPEX and MRME components are:

LPEX: Grasses will be more responsive to both drought and water addition reflecting their shallower rooting depth and limited period of activity and the relative insensitivity of *Larrea* to summer precipitation. Because infiltration and post-rainfall soil moisture are highest under plant canopies, changes in canopy cover in grassland may feedback on spatial patterns of soil moisture. Under drought this would mean less soil moisture where grass canopies have been lost during drought and increased water where grass canopies have expanded under water addition. If the decrease in soil moisture under drought is sufficient to diminish grass productivity then extended drought in the mixed grass-shrub community could push the system toward shrub domination.

MRME: Changes in event size and variability will have differential effects on creosote invasion of desert grassland. Essentially, changes in rainfall variability will increase seed germination and seedling establishment of *Larrea* in desert grassland. Increased frequency of smaller rainfall events will increase seed germination but not necessarily seedling establishment, whereas a small number of larger events will increase establishment but not necessarily seed germination. Changes in rainfall variability will alter soil C and N dynamics, as well. Specifically, a larger number of small events will increase soil CO₂ effluxes by stimulating microbial but not plant growth, whereas a small number of large events will increase aboveground NPP by providing sufficient deep soil moisture to sustain plant growth for longer periods of time during the monsoon season depending on soil N availability.

We wish to emphasize that our rainfall manipulation experiments (LPEX, MRME, Nighttime Warming, PJ Rainout) have already been established using other funding sources. External support for Nighttime Warming and PJ Rainout continues. Here, we are requesting NICCR funding to maintain infrastructure and intensively measure LPEX and MRME over the next three years. Because the experimental infrastructure exists, this represents an important opportunity to leverage NICCR funding.. More importantly by continuing these two long term projects, NICCR funds will facilitate synthesis and inter-comparison among all of our rainfall manipulation studies. The 27 experimental plots of LPEX span the ecotone between creosotebush shrubland and black grama grassland. As shown in the timeline (Fig. 2), it consists of independent five year drought (2001-2006) and water addition treatments (2004-2009). Although drought treatment ended in 2006, measurements will continue through the post-drought recovery. The water-addition treatment is completing its third of five years of treatment (NIGEC funding expired August, 2006). The second component of this proposal, the just-established Monsoon Rainfall Manipulation Experiment (MRME), comprises a second set of 13 plots, co-located with and the same size as the grassland component of LPEX, that are devoted to understanding the consequences of precipitation variability on ecosystem processes in black grama grassland. Water addition is used to alter the pulse size

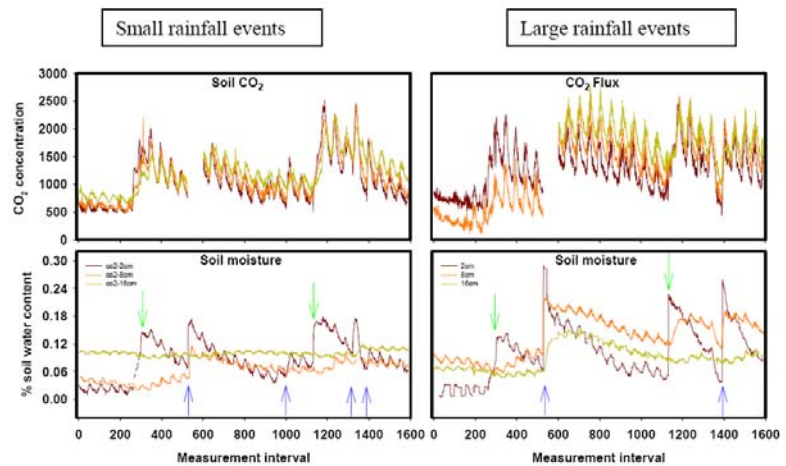


Fig. 6. Initial data from MRME during summer 2007 showing soil water content and soil CO₂ concentration (ppm) at three depths (2, 8, and 16 cm) through the course of natural storms (blue arrows) and treatment events (green arrows).

and timing during the summer monsoon (July through September, Table 1) and to identify the effects of such variability on above- and belowground production, community composition and diversity, and soil carbon and nitrogen dynamics. With NICCR funding, we would also include a new *Larrea* seed and seedling addition experiment to MRME. Taken together, these two ongoing long term experiments will enhance our understanding of how semi-arid systems are likely to respond to climate forcing in the future. Below, we describe each component in detail and discuss the integration of these two projects and their comparison with other projects at SEV.

Conceptual background

Semiarid ecosystems are pulse driven. Plant and ecosystem exchange of carbon and water in arid and semi-arid environments are complex because they reflect the integrated responses of plant, microbial and physical processes to precipitation pulses of different size and duration (Fig 1. Huxman et al 2004a, 2005 Ogle and Reynolds 2004, Reynolds *et al.* 2004, Schwinning et al 2004, Schwinning & Sala 2004, Belnap *et al.* 2005). Furthermore, ecosystem hydrology strongly influences the vertical and horizontal distribution of soil moisture that drives subsequent ecosystem responses (Loik et al 2004). Surface micro-topography, organic matter content and root channels associated with vegetation and soil texture, and pre-conditioning are among the factors that control the horizontal redistribution of rain water. For many rain events at the SEV, where vegetation cover averages around 54% in grassland and 28% in shrubland, this redistribution leads to greater infiltration under grass and shrub canopies than under bare soil (Bhark and Small 2003). Not only is soil moisture infiltration greater under plant canopies, but carbon and nitrogen availability are also higher beneath plants compared to bare soil (Schlesinger et al. 1990, Kieft et al. 1998). Thus, biotic activity is driven by the interaction between soil nutrient availability and complex and dynamic vertical and horizontal patterns of soil moisture (Rodriguez-Iturbe 2000).

Biotic pulse response is determined by horizontal and vertical soil moisture distribution. Following precipitation, the vertical profile of soil moisture under different cover types (bare soil, grass, and shrub) triggers biotic activity in the form of grass and shrub gas exchange, nutrient uptake, and microbial metabolism as well as water dependent physical processes in the soil. Each of these groups has a different characteristic response curve to soil moisture and integrates soil water content over a different range of depths. Because plants exhibit species-specific variation in drought tolerance and rooting depth, plant responses are species- and functional type-specific (Ogle and Reynolds 2004, Reynolds et al. 2004).

Microbial functional type responses (bacteria vs. fungi) occur throughout the soil profile but are strongly biased toward shallow soils with the result that their activity is triggered by precipitation events that are too small to stimulate plant responses (Austin et al. 2004, Cable and Huxman 2004, Kurc and Small 2007). Yet microbial activity following the many small rain events (at SEV nearly 60% of rain events are < 2 mm, Fig. 1) feeds back on plant activity through its effect on soil nutrient cycling (White et al. 2004, Welter et al. 2005, Collins et al. 2007). Indeed, N₂O fluxes from SEV soils increased with increasing soil water content (Crenshaw et al. 2007) demonstrating the dependence of N cycling on soil water in this grassland ecosystem. Isotopomer analyses indicate that the majority of this flux is from nitrification by fungi (Peggy Ostrom, unpublished data). If nutrient release occurs primarily when plants are inactive, nutrient retention processes (e.g., plant uptake) are diminished and N losses via denitrification may increase ultimately decreasing NPP. Such changes would vary with the size, frequency and intensity of precipitation events. Alternatively, atmospheric N deposition, which is increasing in arid regions like the Sevilleta (Fenn et al. 2003, Baez et al. 2007), may counteract N losses via leaching and denitrification. It is unclear, however, how climate change interacts with N availability to affect rates of shrub encroachment into grassland.

Physiological state of vegetation also influences pulse response: The physiological state of vegetation can significantly affect the response to precipitation pulses. In C₄ grasslands at SEV, small events early in the growing season lead to CO₂ release of short duration. Following the first significant pulse of the summer monsoon, C₄ grassland exhibits large efflux of CO₂ because even though the rooting zone exhibited large increases in soil water potential the grasses are inactive (Kurc and Small 2004, 2007) and microbial and physical processes dominate the response. A second significant pulse during the

monsoon, even of the same size, initiates significant carbon uptake by the now-active grass canopy, resulting in net carbon uptake by the ecosystem. In other words, early precipitation events “prime the pump” by stimulating decomposition prior to plant growth. In these systems, subsequent pulse responses depend on C limitation of microbes (Sponseller 2007) and whether precipitation patterns maintain enough soil moisture to support continued grass activity. Small rainfall events (<2 mm) at the Sevilleta wet only surface soil (Fig.1) and stimulate microbial activity which increases carbon fluxes from soils (Kurc and Small 2007) but larger events (>5 mm) are required to stimulate plant growth and net carbon uptake (Sala and Lauenroth 1982, Kurc and Small 2007).

Different responses to precipitation changes among functional types: Semiarid shrubland and grassland ecosystems should respond differently to precipitation variability because of contrasting plant characteristics, nutrient cycling, and surface hydrology. Grasses and shrubs differ in many ways: deeper-rooted, C₃ woody shrubs draw upon a larger soil volume and are less dependent on water availability during a specific time period than grasses (Walter 1971, Jackson et al. 1996). In shrubland, available N and other nutrients are concentrated in widely spaced “islands of fertility” located beneath shrub canopies (Schlesinger et al. 1990, Kieft et al. 1998). In contrast, soil resources in C₄-dominated grassland are more uniformly distributed in time and space. Surface and vadose zone water cycling also differ in grassland and shrubland. In shrubland, a larger fraction of rainfall runs off (Abrahams et al. 1995) and infiltration is more spatially heterogeneous, focused beneath shrub canopies (Bhark and Small 2003).

The role of precipitation extremes and variability in vegetation change: In the Southwestern U.S., and semiarid environments worldwide, extensive areas of grassland have been replaced by shrubland over the past century (van Vegten 1983, Pelaez et al. 1994, Archer et al. 1995, Gill and Burke 1999). The environmental changes resulting from this vegetation transition are dramatic (Schlesinger et al. 1990) and can strongly influence regional and global carbon budgets through increased carbon storage in woody biomass (Pacala et al. 2001, Schimel et al. 2001). Climatic variability and change, grazing practices, and fire management have all been implicated in the transition from grassland to shrubland (Neilson 1986, Bahre and Shelton 1993, Archer et al. 1995) but climatic variability is only a reasonable cause of change if shrubs and grasses respond differentially to fluctuations or directional changes in precipitation regime. One such predicted change is an increase in winter precipitation which would favor C₃ shrubs over C₄ grasses that depend primarily on summer rainfall (Peters 2002).

Plant and ecosystem responses to precipitation extremes: Many experiments have been conducted to examine the response of semiarid ecosystems to drought with particular emphasis on seasonal drought (Schwinning et al. 2005, Bates et al. 2006, Potts et al. 2006). In our region, Reynolds et al. (1999) and Whitford et al. (1995) subjected *Larrea* to seasonal drought (summer or winter) for several years, with stronger responses to winter precipitation than summer. Sharifi et al. (1988), Lajtha and Whitford (1989), Fisher and Whitford (1988) and others have examined the response of *Larrea* to water and N addition for one or two seasons. Water treatment studies on desert grasses have not been as extensive. Stephens and Whitford (1993) amended black grama plots with water and N and combined water and N. Lane (2000) found increased grass LAI across a precipitation gradient. The primary, cross-cutting conclusions that can be drawn from these studies are: **1)** Shrubs survive multi-year *seasonal* drought, partly via their ability to fix carbon during favorable conditions throughout the year. **2)** More water yields more growth, and vice versa, for grasses and shrubs. **3)** The relative response to water, N, and water + N is variable. In some locations, N amendments stimulate growth, suggesting nitrogen limitation, whereas in others, such as the Sevilleta, the absence of response to N addition suggests N is not limiting to black grama (Báez et al. 2007).

The role of N availability in ecosystem processes in aridlands: Although water is considered to be the main driver of ecosystem processes in arid areas, N availability may also limit NPP when moisture is available following summer rainfall events (Austin et al. 2004). Indeed, data from a long-term N-fertilization experiment at the Sevilleta show that aboveground NPP is limited by N during years of above average monsoon precipitation (Collins et al. unpublished). Moreover, the N cycle in arid lands is dominated by fungal rather than bacterial processes (McLain and Martens 2005, McLain and Martens 2006). This appears to be true at the Sevilleta where high soil temperatures and low ambient soil moisture

favor fungi over bacteria (Stursova et al. 2006, Crenshaw et al. 2007, Zeglin et al. 2007). N fertilization, however, has been found to reduce abundance of mycorrhizal fungi (Johnson et al. 2003) and increase fungal species diversity at SEV (Porrás-Alfaro et al. 2007). Given that N deposition in arid ecosystems has increased more than five-fold during the last few decades (Vitousek et al. 1997, Holland et al. 1999, Nilles and Conley 2001), increased N availability along with changes in the amount and variability of precipitation are likely to significantly impact microbial and plant community structure and ecosystem processes in aridland ecosystems.

Ecosystem responses to increased precipitation variability: There is strong evidence that variation in precipitation regime can alter key ecosystem properties in grasslands (Knapp & Smith 2001, Knapp et al. 2002, Fay et al. 2003). Ecosystem response to increased variability depends on changes in resource availability (water, N) along with responses in photosynthesis, growth, and abundance of dominant species. Global change models predict that precipitation patterns in the future will become more variable (Houghton et al. 2001, Weltzin et al. 2003). This is of particular concern in arid areas where seasonal and annual precipitation are highly variable to begin with (Gosz et al. 1995, Pennington and Collins 2007). Nevertheless, evidence suggests that variation in the daily size of precipitation events during the summer monsoon, the period of maximum NPP, is increasing at SEV. In some scenarios, precipitation pattern is predicted to change from one dominated by many small events to one in which rainfall comes in less frequent but larger events. In tallgrass prairie, for example, a smaller number of larger precipitation events led to lower aboveground NPP and soil CO₂ fluxes, and an increase in plant species diversity (Knapp et al. 2002). Such changes in precipitation and soil water dynamics will likely interact with availability of limiting resources (e.g., soil N) to affect ecosystem processes and dynamics in arid and semiarid regions as well.

Pulse dynamics occur at multiple temporal scales. Although the pulse-reserve paradigm for aridland ecosystems was primarily developed around individual rainfall events, precipitation in aridland ecosystems can exhibit pulses at multiple time scales from events to decades (Fig. 7). Many measures of system response, such as annual NPP, integrate physiological responses to pulse events over the growing season. The LPEX and MRME experiments represent two endpoints in this continuum of pulse dynamics in aridlands, chronic multiyear drought or above average rainfall at one extreme (LPEX), to changes in the timing and frequency of pulse

events within a growing season (MRME). Common measurements in each experiment (plant water status, photosynthesis, NPP) allow us to integrate our results across these and other rainfall manipulation experiments to better understand how climate change will affect aridland ecosystem structure and function.

Project description and justification

The consequences of precipitation extremes – LPEX addresses the ecosystem response to precipitation extremes (Fig. 4) and their possible role in driving vegetation change in semiarid ecosystems. The design, described above, allows comparison of the responses of the mixed grass-shrub community in the ecotone with the responses of the adjacent ‘pure’

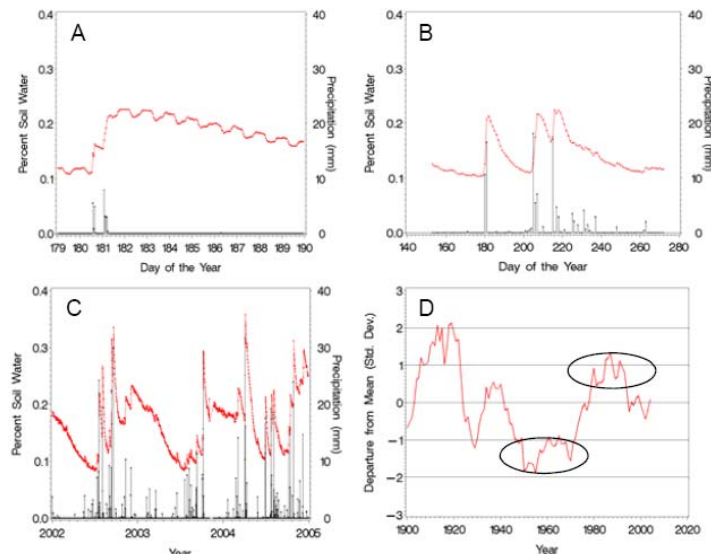


Fig. 7. Pulse rainfall events and soil-water dynamics at multiple temporal scales at Deep Well met. station, Sevilleta LTER: (A) single event, (B) multiple events during the summer monsoon, (C) interannual variation over multiple years and (D) decadal precipitation dynamics.

grassland and shrubland ecosystems located within 1 km. Plot size was chosen to allow reasonable plot scale measurements of runoff and to measure whether the differential responses of C₄ summer-active grasses and C₃ evergreen shrubs lead to shifts in the spatial pattern of soil moisture following storms (Small and Pockman, in prep). The differential responses of grasses and shrubs are supported by numerous detailed studies of grass and shrub physiology, by long term measurements of grassland and shrubland ANPP (Smith et al. 2000, Van Auken 2000, Huenneke et al. 2002, Muldavin et al. 2007) and by manipulative studies of a single vegetation type at a time (Fisher and Whitford 1995, Reynolds et al. 1999). However, comparisons of shrubland and grassland responses from independent studies are difficult, given study-to-study differences in experimental design, location, target species and prevailing climate conditions. This ongoing project addresses how the extremes of precipitation variability (extended drought and wet periods) on timescales of 1 to several years influence semiarid grassland and shrubland ecosystems, including the structure and processes acting when the distribution of shrub species has expanded into grassland.

During the project period, NICCR funding will be used to monitor the recovery of the drought treatment and maintain the water addition treatment to complete 5 years of LPEX treatment. During drought recovery, we hypothesize that the following will occur:

1. ***Grass productivity (g/m²) will increase in the drought plots (as a percent of control productivity) compared to that measured during the 5-year drought treatment. However, it will remain lower than in the control plots throughout the recovery period (low resilience).*** There are several reasons why the productivity in the drought plots may not fully recover, including (a) limitations imposed by soil nutrients; (b) limitations on soil water associated with the reduced infiltration currently observed in the drought plots; and (c) the lower amounts of below- and above-ground biomass that exist at the end of the drought. If this hypothesis is correct, it suggests that complete recovery from drought is a process that is prolonged by the changes in ecosystem state that accumulated during the drought.
2. ***The fraction of the ground surface covered by standing grass will increase during the recovery. However, this increase will lag the productivity response.*** We expect that the initial re-growth during recovery will be focused in the largest and healthiest grass clumps, yielding a limited change in grass-covered area. This will be followed by re-growth at the margins of current clumps and in areas where clumps disappeared during the drought. The pattern and timing of regrowth are important controls on runoff generation, so they will be observed carefully.
3. ***Initially, runoff from drought plots will exceed runoff from control plots, as was the case at the end of the drought treatment. Runoff from the drought plots will decrease and approach that observed from the control plots, although this change will lag the recovery observed in productivity and plant cover.*** The runoff response should lag the recovery in plant growth because the pattern and extent of vegetation on the ground influences runoff generation and infiltration. These responses will be greatest in the grassland and ecotone plots where the effect of drought on runoff was greatest.

During the continuation of our long term water addition treatment, we will test the following hypotheses.

1. ***Grass productivity will continue to increase compared to controls as the physiological effects of high water availability are reinforced over time by accumulation of belowground biomass, expanding grass cover and strong infiltration under the canopies.*** Shrub productivity will also increase but our drought treatment and the work of others reinforce the limited response of *Larrea* to summer precipitation forcing.
2. ***Grass cover will increase in response to continuing water addition while shrub cover will remain constant with little or no grass establishment in bare soil areas.*** Cover of herbaceous species will also increase, particularly in grassland and ecotone plots but in shrub plots the slow infiltration in the large bare soil patches will limit the establishment of herbs.
3. ***Just as runoff increased in the drought treatment, runoff in grassland and perhaps ecotone plots will decrease as high grass productivity and cover decreases the connectivity among bare soil interspaces.*** The response of ecotone plots will depend on the relative effects of the disconnected bare

soil of grass areas compared to the highly connected bare soil surrounding shrubs. In the shrubland, runoff and the pattern of infiltration are unlikely to change significantly in this self-reinforcing community structure.

Monsoon Rainfall Manipulation Experiment (MRME): The overarching hypothesis to be tested with NICCR funding is that precipitation variability will alter ecosystem C fluxes, NPP and the rate of shrub encroachment into grassland. Our specific hypotheses address both the germination and establishment phases of *Larrea* in relation to grass NPP. In general, *Larrea* seedlings germinate in or near grass clumps but rarely in bare soil (Peters et al. 2007). We hypothesize that germination rate of *Larrea* seeds will increase in plots with more small rainfall events relative to ambient and large rainfall treatments. This will occur because of higher amounts of shallow soil moisture during the monsoon when *Larrea* seeds normally germinate. However, we hypothesize that *Larrea* establishment will be lower with more small rainfall events because of insufficient soil moisture in deeper layers to sustain growth. Further, we hypothesize that small rainfall events will not stimulate grass production because of limited water infiltration. In addition, we hypothesize that germination and establishment will be higher in plots with a small number of large rain events because such storms result in deeper infiltration and longer intervals during which soil water is available (Bhark and Small 2003). Alternatively, *Larrea* establishment may decrease in the large event treatments because of competition with black grama. We also hypothesize that frequent small events will increase C losses from soil relative to controls via increased microbial processes which are decoupled from plant uptake. Finally, we hypothesize that a precipitation regime dominated by a small number of large events will increase aboveground NPP of black grama by providing sufficient periods of soil moisture for plant growth.

We will test these hypotheses by monitoring NPP, and creosote seed germination and seedling establishment in ambient, small and large rainfall treatments. In addition, we will measure leaf tissue chemistry (plant nutrient status), leaf water potential and photosynthetic responses (water stress) of black grama and *Larrea* at weekly intervals in all precipitation treatments. Soil CO₂ fluxes (Vaisala GM222 CO₂ probes), soil moisture and soil temperature (Decagon Ech2o-TM probes) at 3 depths are measured every 30 minutes in each plot. Soil N availability is measured seasonally with ion exchange resins in fertilized (5 g Nm⁻²) and control subplots. Detailed methods are given below.

Impact of NICCR funding: Global environmental change is likely to have significant negative consequences on aridland ecosystem structure and function. Increased climate variability and severity will also have significant economic impacts in this region of rapid population growth and expansion. Although the funding we are requesting will be used to maintain LPEX and enhance MRME, these two projects are part of a more comprehensive set of global change experiments in grass-, shrub- and tree-dominated ecosystems at the Sevilleta LTER site. Moreover, all experiments address the effects of potential changes in climate regime on Chihuahuan Desert and Piñon-Juniper ecosystems. All of these experiments were established and in some cases remain supported by non-LTER funding (NSF-Ecology, UNM Start-up, DoE-NIGEC, DoE-PER). Together, however, these experiments include the breadth of potential seasonal and annual changes in rainfall and how those changes will interact with other global changes, such as warming or atmospheric N deposition. As a consequence, NICCR funding would not only allow us to continue and expand upon existing experiments but would also all us to synthesize results across these experiments. Doing so will yield a more general understanding of how global environmental change will likely impact aridland community structure and ecosystem processes.

Detailed methods

This project will support the continuing operation of two existing long-term experimental systems that 1) assess the effects of extended drought and increased precipitation on ecosystem function across the ecotone from shrubland to grassland and 2) determine the ecosystem consequences of precipitation variability by altering the size and frequency of monsoon rainfall events. This project will make all data

and derived data products available to the public via the Sevilleta LTER on-line database no more than 1 year after completion of the project (including detailed metadata according the standard LTER protocols).

Current pulse regime at SEV and the effect of possible changes: Mean annual precipitation at the grassland-shrubland transition is approximately 250 mm/yr with almost 60% of rainfall events smaller than 2 mm (Fig 1). Like most semiarid systems, there is substantial year-to-year variability; the range since 1988 is 103 – 327 mm. Historically, the system experienced periodic prolonged and severe drought as well as extended periods of above average precipitation (Milne et al. 2003). Precipitation anomalies that persist for a single season are important, as are multi-year anomalies that are restricted to a single season. However, the most dramatic ecosystem impacts result from year-round climate forcing, such as observed during the 1950's drought (Swetnam and Betancourt 1998). This type of forcing precludes relief from drought stress via persistence of accumulated soil moisture from the non-treatment season or plasticity of plant response.

It is unclear how rainfall patterns will change in our region in the future (Seager et al. 2007, Wentz et al. 2007, Zhang et al. 2007), although models do predict that precipitation events will become more variable (SRAG 2000, Han and Roads 2004, Leung et al. 2004). The current consensus (IPCC), based on climate modeling, is that intensification of the hydrologic cycle is expected, with more variable rainfall events and possibly more extreme summer droughts (Seager et al. 2007). In addition, climate models also predict more frequent El Nino events in winter (Houghton et al. 2001). We used the historical record to constrain the approximate intensity of multiyear dry/wet intervals. However, the details of future changes are unknown, particularly at the sub-continental scale. Potential shifts include a decrease in annual precipitation that, based on current rainfall patterns, could mean fewer small rainfall events. Alternatively, climate change may not increase annual rainfall but instead would lead to a smaller number of larger events punctuated by longer intervals between events. A third alternative is an increase in winter versus summer precipitation. All of these scenarios, represented in our work at SEV, would result in altered community structure and ecosystem processes.

Vegetation and Cover Types: The dominant grass is *Bouteloua eriopoda* (black grama) and the dominant shrub is *Larrea tridentata* (creosotebush). Secondary species (cover < 5% of plot area) include: *Bouteloua gracilis* (blue grama), *Hilaria sp.*, *Sporobolus sp.*, and *Gutierrezia sarothrae*. Mixed grass-shrub plots contain five or six mature shrubs, ~40% black grama cover, and ~40% bare interspace. Black grama cover is ~50% in grassland with about 50% bare interspace. In shrubland, shrub canopy cover is only ~30% and bare interspace is about 70%.

Experimental plots: All experimental plots for LPEX and MRME are 9 x 14 m and are instrumented as described below. All 27 LPEX plots were prepared as follows: (1) the perimeter was trenched to 1.2 m with a Ditch Witch, lined with 2 sheets of thick plastic, and backfilled; (2) 28 cm sheet metal was inserted along each trench to limit exchange of water between plot and off-plot surfaces; (3) portable canopy walkways held 50 cm above the plot allow access to the entire plot without trampling soil and vegetation, which are easily affected by even minimal foot traffic; and (4) shelters over the three drought plots utilized retractable tops 2 m high at center and extending 1.7 m beyond the plot edge. MRME plots were not trenched or edged because water addition treatments are less sensitive to the effects of water crossing the plot boundary than drought manipulations.

Experimental Treatments: The manner in which rainfall manipulation treatments are applied can strongly influence the outcome of this type of experiment (Hanson 2000). Our drought treatment, now complete but described here because we propose to follow the recovery of these plots, was a ~50% reduction in ambient rainfall, achieved primarily by excluding large storms. This is consistent with the extreme magnitude and duration of drought in the historical rainfall record (1915-present) represented by the 1950's drought in central NM, an event associated with widespread woody plant mortality. It is also consistent with the observation that drought in our region is the result of longer dry periods (not simply smaller storms, the 10 driest years had 17 ± 4 days with > 2 mm rain while 10 wettest years had 31 ± 5 days with > 2 mm rain) and a reduced number of large events. The distribution of total daily rainfall differs in dry and wet years: a higher percentage of storms are large (>20 mm) in wet than in dry years, 6% and < 0.5%, respectively. By modifying ambient rainfall, our treatment also maintained natural

rainfall variability influencing our control plots (Fay et al. 2000). Our water-addition treatments represent a similar increase in precipitation above MAP, corresponding to a prolonged wet period during the late 1980's and early 1990's. The water addition treatment is exposed to all ambient rainfall experienced by the control plots plus 6 large 'storms' added using our overhead irrigation system (Fig 3).

Water addition regime: The LPEX water addition plots receive six additional large events per year. Additions are distributed throughout the year according to the seasonal rainfall cycle, but the actual days are chosen at random. Because freezing temperatures can damage water storage tanks and our distribution system, there is some bias away from additions during November – February. At each event, the rainfall amount for each storm is the same for all 9 water addition plots. It is calculated to maintain a 50% increase per year while maintaining each event in the range 10 - 35 mm to ensure that it is feasible to transport the required volume of water. This treatment yields a realistic wet interval, as shown by simulated 4-year experiments based on the historical rainfall record. The rainfall total is $150 \pm 1.5\%$ of the control; the number of rainy days per year increases by 6; and there is a higher percentage of large storms.

The MRME plots receive either a large storm treatment or a small storm treatment to produce the same total addition of water during the monsoon season (Fig 8). This has the effect of increasing the amount of monsoon precipitation and imposing differences in precipitation variability at the same time. The large storm treatment (n=5 plots) consists of a single 20 mm water addition during each month of the monsoon period (July-September) while the small storm treatment requires the application of four 5 mm storms, separated by 7-10 days, during the same period.

Water addition methods: Water addition to LPEX and MRME plots uses a sprinkler system that consists of three square-pattern nozzles mounted on PVC piping and suspended 3 m above each plot (Fig. 3). Two arms are spaced to achieve even coverage over the entire plot with a small area outside the plot receiving water as well. We use application rates of 50 mm/hour, a reasonable intensity for NM storms that yields a spatially homogenous pattern with realistic drop sizes. To control key water chemistry, we produce all treatment water using a dedicated reverse-osmosis (RO) system that was purchased for this project and co-located at a UNM facility

with 9000 gallons of storage. A commercial trucker transports 8000 gallons of water from Albuquerque to storage tanks located at all water-addition plots. This system yields water with chemistry (electrical conductivity = 7.7 $\mu\text{S}/\text{cm}$) similar to Sevilleta rainwater. For example, nitrate in rainwater and the RO water is 0.4 ppm and 0.6 ppm, respectively. The Cl^- concentration of the RO water is somewhat higher than rainwater however because the Cl^- inventory is large (Phillips 1994), the treatment effect is less than

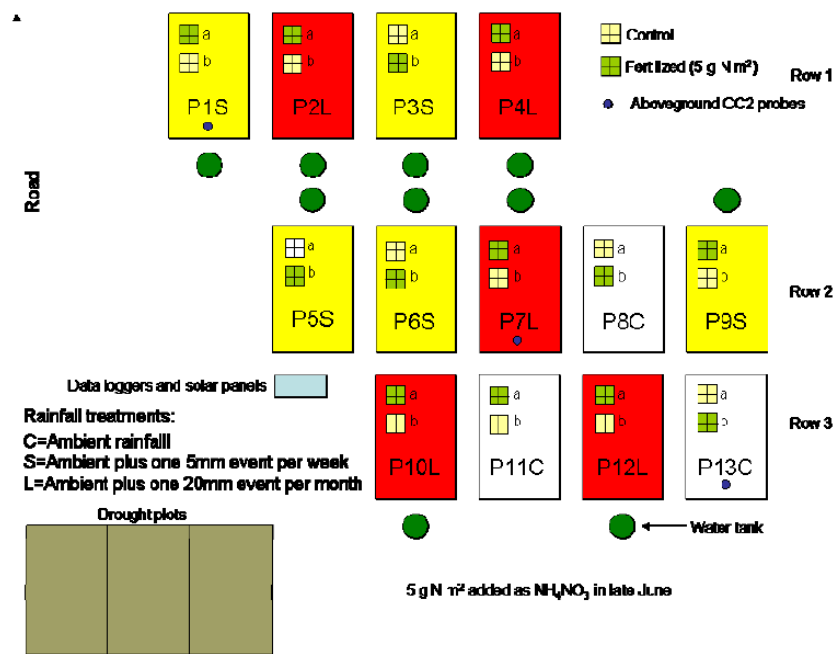


Fig. 8. Plot layout of the MRME experiment in grassland at the Sevilleta LTER. Plots receiving a single large addition (20 mm) per month are red, small addition plots (4 x 5 mm) are yellow and control plots are white. Water tanks store water at each plot prior to treatment, so that all treatments can be applied in a short period of time.

2% of total Cl⁻ of the root zone.

Plant water relations and gas exchange: Because of the effort required to make detailed physiological measurements across 27 plots in three communities across 2 km, we do not plan intensive measurements of this kind. We will periodically measure grass and shrub pre-dawn and midday water potential across LPEX and MRME plots, timing our measurements to document the magnitude and duration of our treatment effects. Likewise, we will subsample plots with a LI-Cor LI-6400 to measure transpiration, photosynthesis and stomatal conductance to confirm the treatment differences that exist. In the first and third year we will make intensive measurements following one summer monsoon storm in the LPEX plots to document the differential responses to soil moisture pulses.

Volumetric soil moisture and soil water potential (Ψ_s): On the LPEX plots we measure soil water potential (Ψ_s) with heat dissipation sensors (HDS; (Bristow et al. 1993, Reece 1996)) and thermocouple psychrometers (TCP; (Koide et al. 1991)). We chose these methods because small changes in the water content of dry soils result in easily detectable changes in soil water potential. Lab moisture release curves are available for conversion to volumetric soil water content. Vertical profiles of HDS (5, 15 cm) and TCP (15, 30, 45, 60 cm, and 80 cm in grassland and shrubland only) are deployed under grass, shrub, and bare soil cover types (one profile per cover per plot). All probes are measured hourly and the data stored by dataloggers.

Surface water redistribution: Plot scale runoff is diverted into buried stock tanks with continuously monitored floats permitting calculation of the runoff fraction for each rainfall event. Surface water redistribution within plots can be inferred from spatial infiltration patterns recorded by the horizontal array of soil moisture probes.

Connectivity: We will use the aerial photo mosaics to quantify connectivity of the surface drainage network (Davenport et al. 1998) by calculating (1) the percentage of interspaces that are connected to the lower end of the plot, and therefore contribute to plot scale runoff and (2) connectivity functions that show the probability distribution of clusters of different dimensions (Western et al. 2001).

Vegetation methods: LPEX Grass and shrub ANPP are measured annually via harvest methods for black grama, estimates of plant species cover (all species) and stem growth increments for shrubs. For herbaceous species (all plots) cover is measured in late spring and early fall in five permanently located 1 m² quadrats in each treatment plot. In addition, standing crop of black grama is measured annually by clipping five 10 x 10 cm subplots per plot, sorting by current years production and previous years dead, drying at 60C to constant weight. These samples will allow us to calculate LAI for grasses and to determine composition and abundance responses of all herbaceous species.

Shrub ANPP is measured on 5 creosotebush plants (mixed and shrub communities only) per replicate plot in March, late June and October using allometric methods based on first order twigs (Allen et al. In Prep). This method has greater sensitivity for measuring growth over shorter periods than whole plant estimates. Twigs to be measured are marked with paint and the basal diameter and length are measured. Then regressions are used to convert twig dimensions into biomass. A second set of regressions relating the number of first order twigs per plant to plant volume is used to obtain whole plant biomass. Incremental changes in whole plant biomass can then be estimated by repeated sampling. These measurements have already commenced and will provide the basis for measuring changes in community composition and diversity in response to our experimental treatments over time. With NICCR funding we would add measurement of seed production using twigs marked for growth measurement and seed biomass will be estimated before dehiscence by sub-sampling.

The newly established Monsoon Rainfall Manipulation Experiment (MRME) will permit us to test how variation in summer precipitation pattern affects community structure and ecosystem processes in desert grassland. MRME includes five replicates of two altered rainfall treatments: weekly addition of 5 mm rainfall, and monthly addition of 20 mm of rainfall in July, August and September. These treatments are compared with three replicates receiving only ambient rainfall. Although the design increases rainfall above the long-term average, the treatments also alter rainfall *variability*, which is the primary goal of the experiment. Rainfall is added by an overhead (7 m) sprinkler system fitted with

sprinkler heads that deliver rainfall quality droplets. The system can create a 20 mm rainfall event in 17 min, which simulates the intensity and duration of a monsoon event. At the end of the monsoon season, each variability treatment will have received the same total amount of precipitation (ambient plus 60 mm), but that precipitation is delivered in different sized events and with different intervals between events. The ambient rainfall plots provide a measure against which treatment effects can be compared to interannual variations in precipitation.

Each plot (9x14 m) includes subplots (2x2 m) that receive 50 kg N ha⁻¹ y⁻¹. The following are measured in this experiment: (1) seasonal (July-September and October-June) soil N availability using Western Ag Innovations ion-exchange resin membrane root simulation probes in fertilized and control subplots (Drohan et al. 2005), (2) plant species composition and ANPP (allometrically using standard SEV LTER protocols Muldavin et al. 2007), (3) seasonal root and fungal dynamics in minirhizotrons, and (4) soil temperature, moisture (Ech₂O Probes), and CO₂ fluxes (GMT222 Vaisala CO₂ sensors, Tang et al. 2003) under grass canopies at three depths (2, 8 and 16cm) every 30 min. In addition, predawn and mid-day (10-noon) water potential and mid-day leaf photosynthetic gas exchange and stomatal conductance of black grama are measured prior to and up to 5 days after scheduled precipitation events. Data streams from MRME indicate that the treatment effects are working (Fig 6). For example, soil water volume was higher and declined more slowly following a single large event relative to several small events.

To test hypotheses regarding the effects of monsoon precipitation variability on shrub encroachment into desert grassland, we propose a *Larrea* seed and seedling addition experiment to MRME with NICCR funding. The environmental filter for plants includes seed germination and seedling establishment phases (Grubb 1977, Harper 1977). In aridland systems, these phases depend heavily on soil water availability. In 2006, a year of high monsoon precipitation, we found abundant *Larrea* seedlings in our long-term vegetation monitoring plots. Widespread germination of *Larrea* has not been observed at our site since 1996, another year with above average monsoon rainfall following an extended dry period. Thus, large rainfall events, particularly after dry periods, may stimulate *Larrea* seed germination. Establishment will then be based on soil moisture dynamics in the upper soil layers whereas persistence will depend on deeper soil moisture derived primarily from winter rains.

Creosote seed germination and seedling survival: To assess the effect of our treatments on the ability of creosote to establish in grassland, we will measure the germination of seeds placed in our experimental plots as well as the survival of greenhouse-germinated seedlings planted in a 1.2 x 0.25 m sub-plot in replicate treatments plots. Seed addition treatments are used because natural seed germination is rarely observed, *Larrea* invasion is likely dispersal limited and we can control the number and location of seed addition plots. Creosote seed will be added at a rate estimated to produce 200 germinated seeds per subplot. Seed will be collected from multiple maternal plants in a population near the LPEX and MRME experiments at the Sevilleta and each seed germination plot will receive equal numbers of seeds from each maternal line. Fresh seed will be used because it has significantly higher germination success (McGee and Marshall 1993). In the creosote seed addition subplots we will measure germination success weekly over the monsoon season, mortality monthly over the first year, and growth of all surviving individuals bi-annually (at peak biomass for each growing season). This will allow us to test the hypothesis that germination and establishment of *Larrea* are differentially effected by the size and frequency of rainfall events. We are using similar *Larrea* seed addition protocols in our nighttime warming experiment which will allow us to synthesize results from these two experiments. Longer-term responses by *Larrea* to precipitation variability are currently measured in LPEX, giving us a range of precipitation treatments and life stage responses of *Larrea* to potential changes in precipitation regimes.

Timeline

All research infrastructure is in place at LPEX and MRME via other funding sources, providing significant leveraging of NICCR funds. Because there is no implementation delay, we will be collecting data throughout the project period. Furthermore, we will continue analyzing the large database accumulated during existing long term treatments and will be able to submit manuscripts in all three years of the project.

Relationship of this project to other DOE funding

PI Pockman and Nate McDowell (Los Alamos National Lab) are currently supported by DOE-PER for an ecosystem rainfall manipulation in piñon-juniper (PJ) woodland designed to understand the mechanisms associated with differential mortality during drought. The project (completing its first year) is building 3 replicates of rainout shelters (60% exclusion), rainout shelter controls (structure in place but no rain diverted), water addition (50% of MAP) and untreated control on 40 x 40 m plots at the Sevilleta LTER. Intensive physiological measurements (sap flow, soil moisture, plant water status, plant productivity and carbon balance) on one block will be used to monitor piñon and juniper responses to long term treatments and to parameterize a hydraulic model (Sperry et al 1998, 2002). The model will be used to assess plant responses in the context of hydraulic limits on water transport in the soil and xylem. This project differs from the proposed research because it focuses on piñon-juniper woodland rather than semiarid grassland and shrubland, and it is highly mechanistic, measuring the detailed water relations and carbon balance parameters in each target species.

Deliverables and schedule for research.

Treatments have already been established under other funding and will be maintained for the full three year funding period. We anticipate publications based on initial vegetation responses to be prepared after the first year of treatment. The long term nature of the treatments means that synthetic publications describing the responses to the entire period of forcing will be produced at the end of the third year. Additional publications will document system resilience from the extended climate forcings we are imposing during this funding period.

The findings of this study will help improve the functioning of terrestrial ecosystem models and their linkage to precipitation scenarios driven by global and regional climate models. In particular, our data on several different manipulations in the same ecosystem will provide detailed information about the effect of different precipitation forcings on ecosystem function.

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