Multi-scale temporal variation in water availability: Implications for vegetation dynamics in arid and semi-arid ecosystems

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Abstract

The objective of this paper is to illustrate the importance of variation in water availability to temporal variation in vegetation dynamics in arid and semi-arid ecosystems. We hypothesize that fine-scale pulses of precipitation interact with longer scale variation in climate and weather to generate temporal variation in plant community composition. Arid and semi-arid regions exhibit great temporal variability in water availability as a result of variation in climate and weather at multiple scales and vegetation-soil water feedbacks. The scales of variation include: shifting climate regimes over centuries and decades, inter-annual variation in weather patterns, seasonal differences in winter and summer precipitation, and within-season variability in precipitation frequency and magnitude. In arid and semi-arid regions, pulses of rainfall are separated by intervening dry periods of variable lengths. This situation results in fluctuating availability of water that limits plant production and controls other ecological processes, such as rates of nutrient cycling. In some semi-arid and arid systems, temporal variation in water availability may create positive feedbacks that facilitate encroachment of C3 woody plant species into areas formerly dominated by C4 grasses. Our ability to predict these

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complex shifts in vegetation composition may be improved by including temporal variation in climate, weather, and ecosystem processes.

1. Introduction

Semi-arid and arid areas exhibit great temporal variability both in water availability and vegetation dynamics. In some of these regions, rainfall is delivered in discrete "pulses" followed by intervening dry periods of variable length (i.e., "interpulses"). Although many systems are characterized by wet and dry periods, the distinction is that these pulse/interpulse periods differ so dramatically in soil moisture that the biotic and abiotic function associated with these periods also differs substantially, especially during the summer growing season (Austin et al., 2004; Huxman et al., 2004; Schwinning et al., 2004). Rainfall pulses can be large or small in magnitude and, in conjunction with temperature, wind, infiltration, surface flow, and evapotranspiration, determine the length of time that the soil is wet or dry.

Patterns of wet and dry periods that occur at longer temporal scales interact with these finer scale pulse dynamics to influence water availability (Loik et al., 2004). For example, frequent small pulses may have different effects on water availability than one large pulse, depending upon whether these pulses occur during a decadal drought or during a wet period (Ni et al., 2002). We review evidence that the oscillation between pulse/interpulse periods, interacting with decadal and longer variation in climate and weather, is a primary driver of variation in plant community composition across a range of temporal scales. This temporal variation interacts with spatial variation in drivers and processes to generate the complex patterns and dynamics observed at multiple spatial and temporal scales (Weltzin et al., 2003; Peters and Havstad, 2006), and may play a role in the observed shift from grassland to shrubland in the Chihuahuan Desert (Neilson, 1986). Our objectives are: (1) to develop a conceptual framework of cross-scale interactions for temporal variation; (2) to demonstrate the utility of this framework for understanding grass–shrub vegetation changes using data from the Jornada Basin in the northern Chihuahuan Desert; and (3) to present an experimental design that examines the effects of fine-scale variation in precipitation pulses on the responses of shrubs and grasses.

2. Conceptual framework for temporal variation and cross-scale interactions

Variations in water availability considered in this manuscript are a result of climate and weather patterns interacting at multiple scales. Directional change in climate or vegetation at shorter time scales may be mere variation at longer time

scales. Climatic oscillation or variation can result from natural changes in broad scale solar or atmospheric drivers and have important effects on shifts between grasslands and shrublands (Neilson, 1986; Van Devender, 1995; Buck and Monger, 1999). Directional changes in global climate as a result of elevated concentrations of atmospheric carbon dioxide are an additional source of variation at large temporal scales that can influence broad scale patterns in vegetation through effects on plant phenology and physiology (Parmesan and Galbraith, 2004). At decadal scales, alternations between dry and wet cycles interact with longer-term climate patterns. For example, changes in the Pacific Decadal Oscillation (PDO) index have been reported to last 20–30 years and may produce fluctuations in sea surface temperatures that result in abnormally wet or dry precipitation patterns (Zhang et al., 1997). Variation exists in total amount of rainfall received within a year (wet years vs. dry years), which may be a result of El Niño/Southern Oscillation (ENSO) that generates El Niño/La Niña events at 3–7 year cycles (Gutzler and Preston, 1997). Additionally, there is variation due to the seasonal patterns of rainfall in the southwestern United States. In the Chihuahuan Desert, the majority of rain (>53%) falls during the summer growing season (July–September) as monsoonal rainfall. This rainfall is derived from local convective processes acting on air drawn from the Gulf of Mexico and Pacific Ocean and usually occurs as short duration, high intensity storms that penetrate only shallow soil depths before creating run-off events. These convective storms are spatially variable and occur over localized parts of the landscape. Generation and redistribution of runoff lead to further spatial variability in water availability (Rango et al., 2006). The remainder of the rainfall occurs mainly during winter months (November–February). Winter storms are generally frontal storms, which produce longer duration, less intense rainfall that percolates to greater soil depths. Lastly, within a growing season, the "pulse-pattern" of rainfall can vary in terms of the frequency, magnitude, and intensity of rain events.

In our conceptual framework, these different scales of temporal variability in climate and weather have different ecological impacts with interactions occurring across temporal scales (Fig. 1). At the scale of centuries, variation in the magnitude and proportion of summer vs. winter rainfall may interact with the photosynthetic pathway of plants to determine the suite of plant functional types that are possible on a landscape. Over decadal time scales, variation in the magnitude and proportional amount of seasonal precipitation interacts with these functional types on the landscape. Periods of decadal drought or above average rainfall may also interact with broad scale centurial scale variability to promote episodic recruitment events that change demographic structure and species composition. Species composition affects the way the system can respond to fine-scale (i.e., yearly and seasonal variation in water availability) precipitation pulses. On finer time scales, precipitation from the previous season and species phenology, determined by the interactions at decadal and centurial scales, may influence carbon metabolism in plants and microbes, and determine patterns of individual plant production. Thus, temporal variation in functional group composition, species composition, and production by individual plants at a

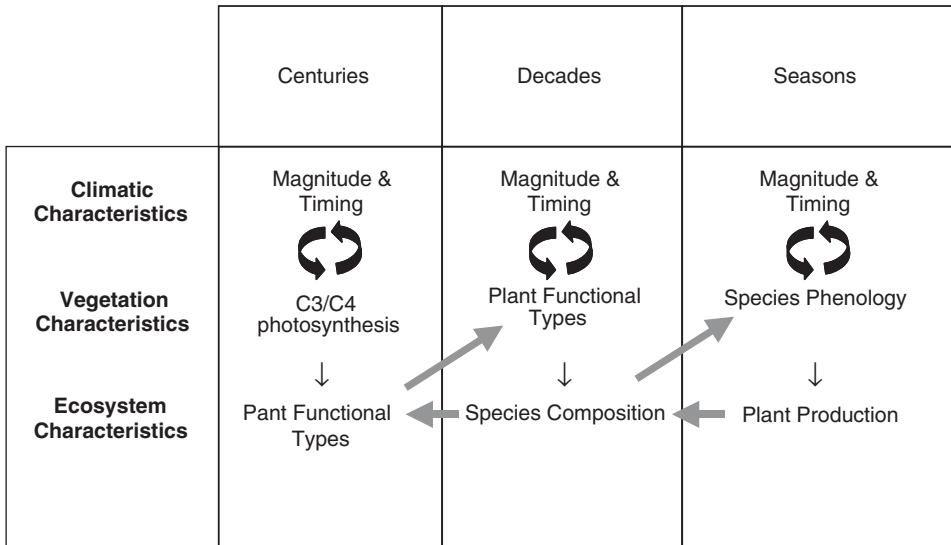|	Centuries	Decades	Seasons
Climatic Characteristics	Magnitude & Timing ⟲	Magnitude & Timing ⟲	Magnitude & Timing ⟲
Vegetation Characteristics	C3/C4 photosynthesis	Plant Functional Types	Species Phenology
Ecosystem Characteristics	Pant Functional Types	Species Composition	Plant Production

Fig. 1. Conceptual diagram illustrating the different scales of temporal variation in water availability and the interactions between precipitation characteristics and vegetation characteristics that produce ecosystem characteristics (black arrows). Gray arrows illustrate how temporal variation in functional group composition, species composition, and production by individual plants is determined by cross-scale interactions between climatic drivers and vegetation characteristics.

particular location is determined by cross-scale interactions between climatic drivers and vegetation characteristics.

In addition to the long-term feedbacks between vegetation and climate, feedbacks between plants and hydrologic processes can accentuate short-term temporal variability in water availability. Conversion of grasslands to shrublands in the Chihuahuan Desert results in larger bare spaces between plants (Schlesinger et al., 1990). These changes in land surface cover may result in altered surface energy budget components (Dugas et al., 1996). Open interspaces often have higher temperatures and consequently, evaporative loss of surface soil water is greater than for vegetated areas. This relationship has been documented in semiarid pinyon-juniper woodlands (Breshears et al., 1997, 1998). Thus, interspaces and vegetated areas may differ in duration of soil wetting as well as amount of water lost via plant transpiration or evaporation. These processes are accentuated because changes in land surface cover also affect distribution of overland flow, with runoff generally greater from intershrub spaces (Wainwright et al., 2000; Abrahams et al., 2003). The physical structure of shrub canopies also affects interception, infiltration (Bhark and Small, 2003), and stemflow (Whitford et al., 1997). These structural effects impact water distribution, and therefore may change soil water availability under shrubs and in interspaces (Hennessy et al., 1985). Additionally, many woody shrubs have been found to redistribute water (i.e., hydraulic redistribution) via their root systems in response to soil water potential gradients. This passive behavior by deep-rooted

shrubs can lift water from lower depths during dry interpulse periods when the surface soil is dry; thus, changing the temporal dynamics of soil moisture (Caldwell et al., 1998). During wet pulse periods when soil water potentials are reversed, both *Prosopis velutina* (velvet mesquite) and *Artemisia tridentata* (big sagebrush) have been shown to redistribute shallow soil water to lower depths within the soil profile (Ryel et al., 2002; Hultine et al., 2003), potentially drying shallow soil at a faster rate. These feedbacks between plants and the water cycle affect the temporal and spatial patterns of water availability.

3. Temporal variation in climate and vegetation in the Chihuahuan Desert

We illustrate the utility of our temporal framework for understanding grass to shrub conversion, patterns of plant productivity, and plant physiological responses using multi-scale data from the Jornada ARS-LTER site in southern New Mexico, USA (32°37N, 106°44W). We examine variations in water availability at five major scales that are expected to influence vegetation dynamics: centennial, decadal, yearly, within year, and within season (Fig. 2).

3.1. Century scale

During the past 20,000 years, paleoecological records indicate that vegetation in the Northern Chihuahuan Desert has shifted between C3 shrublands in more arid periods, C4 grasslands under more mesic conditions, and C3 woodlands during the wettest periods (Van Devender, 1995; Monger, 2003). Multi-proxy records of the isotopic composition of soil carbonates, fossil pollen records, packrat middens, changes in lake levels, and erosion indicate that an increased period of aridity existed about 2200 years ago that reduced the amount of C4 grasses and increased the abundance of C3 shrubs (Van Devender and Spaulding, 1979; Monger et al., 1998; Buck and Monger, 1999; Monger, 2003). During the past 1000 years, winter precipitation as reconstructed by tree ring analyses for the region has varied around the long-term mean of 95 mm with a standard deviation of 32 mm (Ni et al., 2002; Fig. 2a). During the past century (1914–1996), regression and auto-correlation analyses of precipitation data collected at the Jornada revealed that precipitation has increased slightly as a result of a small increase in mean summer rainfall and a more noticeable increase in mean winter rainfall (Conley et al., 1992; Wainwright, in press).

These patterns of climatic change may be partly responsible for the recent increase in cover and abundance of woody plants and associated decrease in perennial grasses at the Jornada (Fig. 3), as well as throughout the southwestern United States (Grover and Musick, 1990; Gibbens et al., 2005). At the Jornada, much of the former C4 perennial grasslands have been replaced by C3 desert shrublands dominated by *Larrea tridentata* (creosotebush) and *Prosopis glandulosa* (honey mesquite) over the past 150 years. Vegetation data redrawn from Peters et al. (2004a) depict the change in coverage of grass and shrubs through time (Fig. 3). Data were
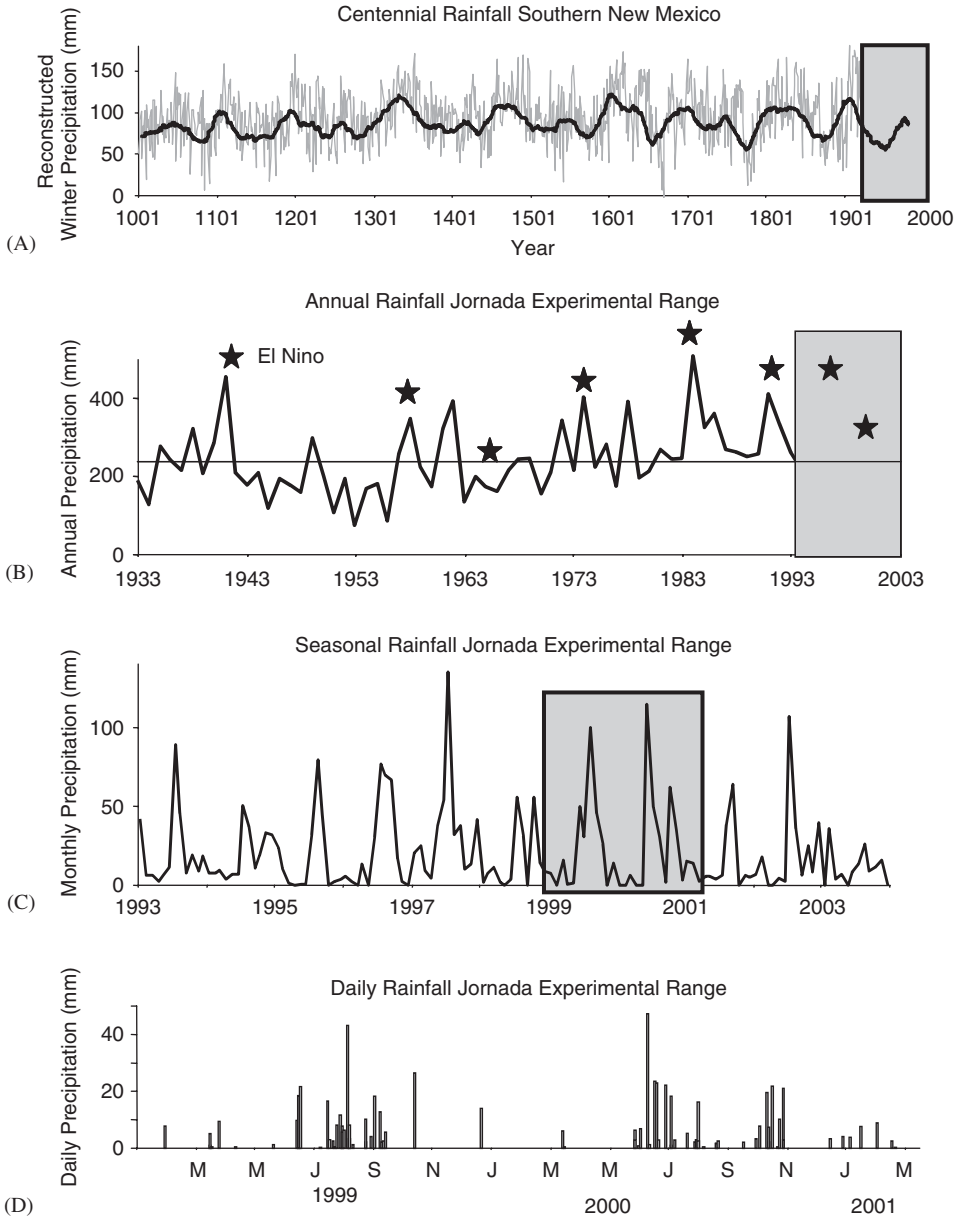
Fig. 2. Scales of temporal variability in precipitation. Panels illustrate the different scales of variation: (A) century, (B) decade/annual, stars indicate El Nino events and solid black line represents mean annual precipitation (237 mm) from 1914 to 2003, (C) season, (D) daily precipitation at the Jornada Experimental Range. The centennial winter rainfall pattern (panel a) is modified from the reconstruction for Division 8, Southern New Mexico in Ni et al. (2002) and the trend line (solid black line) shows a 25-year moving average of annual precipitation.
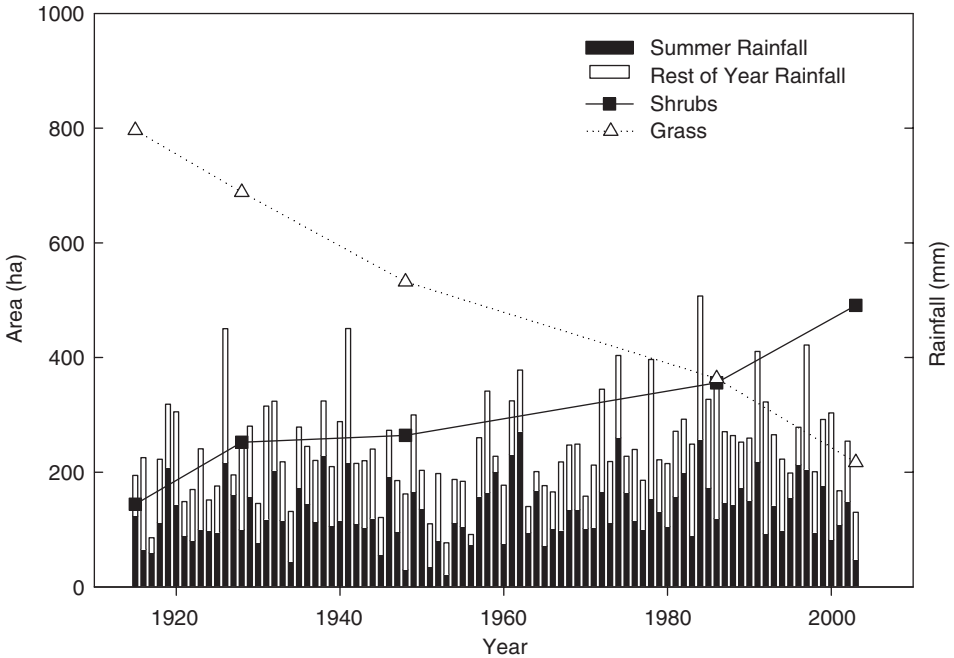
Fig. 3. Vegetation data redrawn from Peters et al. (2004a) depict the change in coverage of grass and shrubs through time. Rainfall data are also plotted through time to illustrate patterns of summer rainfall (July–September) and for the remainder of the year. A slight increase in summer rainfall and a more noticeable increase in winter precipitation have been documented over the last century (see Wainwright, in press).

derived from historic and current vegetation maps of the Jornada site. A modeling study by Gao and Reynolds (2003), supports the idea that wetter winters and drier summers during the last century facilitated the grass to shrub conversion, especially in the context of an extreme drought in the 1950s. However, temporal variation in rainfall failed to reproduce vegetation shifts in the earlier part of the century, suggesting multiple causal factors such as grazing are likely to be involved (Gao and Reynolds, 2003). On geologic time scales, increased shrub cover was associated with greater aridity (see above), yet within the last 150 years it appears that a slight increase in total precipitation has favored shrubs over grasses, largely due to increased winter precipitation. Because of their ability to access deeper soil moisture, the relative advantage of shrubs over grasses is enhanced both when competition for shallow water is increased due to greater aridity (as in the long-term climate record) and when availability of deep soil water is greater due to increased winter precipitation (as in the last 150 years). Additionally, changes in aridity over the geologic record were potentially of larger magnitude than those during the past 150 years (Monger, 2003).

3.2. Decadal scales

Decadal patterns can be observed by examining annual rainfall totals from 1914 to 2003 (Fig. 2b). The Chihuahuan Desert has experienced several periods with below average rainfall for consecutive years, including an extreme, prolonged drought during the 1950s. Data from long-term permanent quadrats at the Jornada showed that the 1950s drought resulted in a loss of grass cover (Herbel et al., 1972) and an increase in honey mesquite and other shrubs (Gibbens and Beck, 1987). The drought reduced grass species frequency and cover on most parts of the landscape. A return to average rainfall patterns in subsequent years restored grass cover and species composition in lowland quadrats, but did not restore grass cover in many quadrats located in upland communities. Black grama (*Bouteloua eriopoda*) became locally extinct in 39% of the upland quadrats during this drought (Peters et al., 2004b). Lowland sites typically have heavier textured soil and receive additional water from overland flow because of landscape position; thus, lowland quadrats may have more water available to plants.

3.3. Annual scales

At annual scales, variance in rainfall among years is high in arid and semi-arid systems such as the Jornada (CV = 37%) (Wainwright, in press). Nine El Nino events have occurred at the Jornada over the past 70 years (Fig. 2b). Simulation modeling has illustrated that ENSO events may promote changes in community structure through differential seedling establishment. Modeling results indicated the probability of establishment in El Nino vs. La Nina years varied by species for perennial grasses (Peters, 2000). The large temporal variation in rainfall in semi-arid and arid regions is often correlated with annual patterns in vegetation productivity, but variability in vegetation productivity can exceed that of rainfall variability (Ludwig, 1987; Le Houérou et al., 1988; Lauenroth and Sala, 1992). At the Jornada, above-ground net primary productivity (ANPP) has been measured three times per year for 10 years in five dominant plant community types (creosotebush, mesquite, tarbush [*Flourensia cernua*], upland grasses, and playas) at three sites in each community type. Correlations between precipitation records and ANPP on a site-by-site basis were not significant (Huenneke et al., 2002). This lack of predictive power is likely due to complex relationships among factors that determine soil water availability (e.g., soil type and texture, feedbacks between vegetation and hydrologic processes, landscape position and topography) as well as lack of sampling for belowground net primary production.

3.4. Seasonal scales

Seasonal distribution of total monthly rainfall at the Jornada during a 10-year interval is shown in Fig. 2c. The Jornada is characterized by a peak in monthly precipitation in the summer (July–September) and a less pronounced peak in the winter (December–February). The seasonal distribution of rainfall appeared to

influence ANPP in the different community types described above (Huenneke et al., 2002). Grassland ANPP was typically greatest after wet summer growing seasons, whereas communities dominated by creosotebush and mesquite had increased ANPP following wet winter/spring conditions. Thus, ANPP appears to depend in part on the interaction of within year seasonal precipitation patterns and plant phenology. It has been suggested that temporal partitioning of water resources by species with different phenologies is a mechanism to reduce competition in water-limited environments (Reynolds et al., 1999, 2000). However, in the Jornada Basin, the duration of phenological activity is generally longer for shrubs than grasses and may overlap with grass species phenological activity, especially in the case of mesquite. Additionally, species such as mesquite may use water from small and large rainfall events and appear to be highly flexible in their ability to use water from different soil depths (Snyder and Williams, 2003; Snyder et al., 2004). Consequently, there may be little realized phenological partitioning for grasses when mesquite shrubs are present.

3.5. Within season scales

Precipitation pulses within season on the Jornada are shown for a 3-year interval (Fig. 2d). In general, all three warm deserts (Mojave, Sonoran, and Chihuahuan) in the southwestern United States and northern Mexico are characterized by a high frequency of small storm sizes ($<10\,mm$) and a low frequency of large events, and time intervals between rain events are generally between 5 and 10 days (Reynolds et al., 2004). Rainfall data (1920–2000) from the Jornada were used to determine the frequency distribution of summer (June–September) rainfall event size classes in 5-mm increments (data not shown). The mean number of rainfall events below 5 mm and between 5 and 10 mm was 14 and 5, respectively. Rainfall events in 5-mm size intervals between 10 and 30 mm occurred on average between 2.5 and 1.5 times per summer.

Although global climate models predict changes in the amount and seasonality of precipitation, little is known about the ecological effects of changes in frequency and size of rainfall events within season (but see Knapp et al., 2002; Fay et al., 2003). Changes in frequency and size of rainfall events may alter water availability in shallow soil layers and produce differential patterns in the depth and duration of soil wetting. Because various ecosystem components (grass roots, shrub roots, biological soil crust, and the majority of soil microbes) vary with depth in the soil profile, these changes in wetting patterns may have important effects on plant production and biogeochemical cycles (Austin et al., 2004; Huxman et al., 2004). Small frequent pulses likely favor shallow rooted, fast responding plant species that can take advantage of these rain events (Sala and Lauenroth, 1982). Photosynthetic activity of biological soil crusts (Belnap et al., 2004) and shallow soil microbial respiration may also be affected by within-season temporal variability of rainfall (Austin et al., 2004). Larger storm events and longer interpulse periods of no rainfall may favor production by slow responding deep-rooted shrub species that access deep stored water (Ogle and Reynolds, 2004). We are testing these ideas with a precipitation manipulation experiment (described below).

3.6. Cross-scale interactions

Coexistence between different functional groups (i.e., herbaceous and woody plants) in semi-arid and arid regions has been suggested to occur as a result of partitioning of soil water resources between deep and shallow layers (Walter, 1971). Walter's two-layer hypothesis suggests functional groups vertically partition resources according to their growth strategy: shallow-rooted herbaceous plants primarily use shallow soil water derived from growing season precipitation whereas deep-rooted, woody perennials primarily use more consistently available deep soil moisture derived from winter precipitation. In contrast to this hypothesis and as illustrated in this paper, there is mounting evidence to suggest that many shrub species have both shallow and deep roots and are capable of using shallow soil water following rainfall events, while relying on deeper water during dry periods (Flanagan et al., 1992; Donovan and Ehleringer, 1994; Lin et al., 1996; Weltzin and McPherson, 1997; Dodd et al., 1998; Williams and Ehleringer, 2000; Gibbens and Lenz, 2001; Gebauer et al., 2002; Schwinning et al., 2002; Snyder and Williams, 2003). The reliance of woody plants on deep soil water during dry periods, in conjunction with evidence of climate change within the last century, suggests that a greater reservoir of stored deep soil water may have favored the survival of woody plants in areas formerly dominated by perennial grasses. The importance of winter precipitation for woody shrubs is supported by an analysis showing greater woody plant abundance in sites with lower mean annual precipitation (MAP) and a greater proportion of winter rainfall (Paruelo and Lauenroth, 1996). Although Ogle and Reynolds (2004) did not observe a relationship between winter precipitation and shrub abundance, they did report a positive relationship between MAP and grass abundance. The prevailing climate pattern, perhaps expressed at the scale of centuries or beyond, dictates that shrubs and grasses both can exist at the Jornada. However, it is the amount and seasonality of precipitation that varies at the scale of decades that may determine which of the two functional plant types predominate. Whereas, annual or within-season variation in precipitation influences the relative productivities of the two functional types.

4. A fine-scale precipitation experiment

We are currently examining the effects of fine-scale temporal patterns in precipitation on plant performance and ecosystem processes at the Jornada by manipulating annual, seasonal, and within-season rainfall pattern. We applied a 60-mm increase in summer precipitation (46% increase relative to mean summer rainfall) at two different frequencies and magnitudes over 12 weeks during the summer growing season to replicated plots containing both honey mesquite and black grama grass. Plots received either: ambient precipitation (controls), ambient plus frequent small (5–6 mm) rainfall events applied weekly, or ambient plus infrequent large (20–24 mm) events applied monthly. The hypothesized response to these rainfall treatments is that increased shallow soil moisture (measured in the

upper 12 cm of the soil profile) will increase the relative photosynthetic contribution of black grama grass. At the extreme ends of the continuum (Fig. 4), shallow soil moisture may have little effect on photosynthetic rates of shallow rooted species, but for different reasons. At the dry end of the continuum, water is unavailable to plants. At the wet extreme, there is likely a threshold level of soil water beyond which additional soil moisture does not confer a physiological improvement due to other plant constraints (e.g., active root area, plant density, secondary limitation by other resources such as nitrogen).

Preliminary results from an isolated watering event in August 2004 on a sandy loam soil are plotted with a predicted response curve (Fig. 4). These data demonstrate that the different rainfall treatments, as reflected by differences in soil water content at 0 to 12 cm depth, influenced the degree to which grasses responded with increased photosynthesis (Fig. 4). Similar to our predicted response, there was an increase in black grama photosynthesis between 6% and 8% volumetric soil moisture, indicating that there is a potential threshold level of soil moisture that causes the leaf-level photosynthesis ratio to shift to greater influence of black grama. The field data indicate the maximum threshold of black grama response may have been reached at
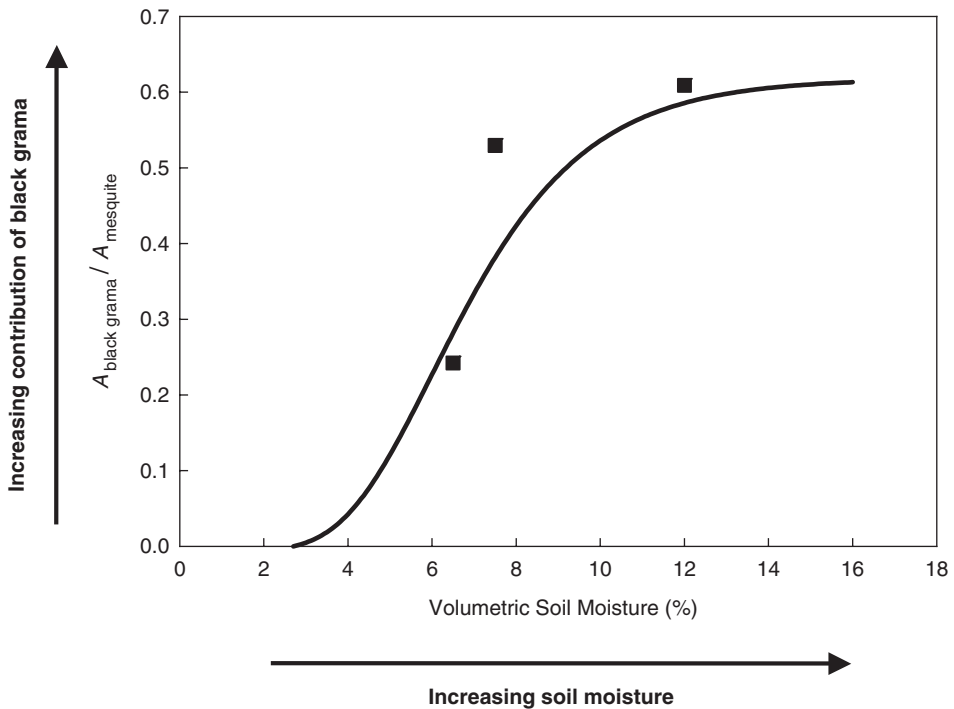

Fig. 4. Conceptual response curve (solid sigmodial line) illustrating the effect of rainfall magnitude on the relative contribution of black grama photosynthesis (A) to mesquite photosynthesis (A). Field data on leaf-level gas exchange rate ratios of black grama:mesquite (■) and volumetric soil moisture in the upper 12 cm of soil after simulated storms of different sizes in August 2004 are plotted for reference.

12% soil moisture, the approximate field capacity for sandy loam soils. Mesquite photosynthesis for this sampling day was relatively insensitive to shallow soil moisture (approximately $22 \, \mu mol \, m^{-2} \, s^{-1}$) regardless of watering treatment. Therefore, the change in the ratio is a function of increased black grama photosynthetic rates. These preliminary data support the hypothesis that oscillations between pulse and interpulse can potentially "shift" the biological dominance of this system. Magnitude of the rainfall events influences immediate photosynthetic response, but temporal variation, or the integration of soil water over time due to storm frequency and magnitude, will determine the length of time that the photosynthetic contribution of these different plant functional types persists and the magnitude of this response through time. This integration through time, in conjunction with temperature, should explain much of the seasonal patterns of plant productivity.

5. Conclusions

Just as islands of fertility under shrubs concentrate biological activity in space, rainfall pulses concentrate biological activity in time. As Holling (1992) suggested, the dominant pulses can entrain many other ecosystem processes, including the dynamics of nitrogen cycling and the population dynamics of plants and herbivores (see also Schwinning and Sala, 2004). The impacts of climatic events at different temporal scales propagate through this ecosystem via direct trophic relations and also through indirect or non-trophic relationships and feedbacks. The pulse pattern leaves an ecological legacy, which influences subsequent responses to rain and drought.

Temporal variation in water availability is important for explaining complex patterns in these heterogeneous desert landscape systems and is specifically related to several key elements discussed by Peters and Havstad (2006; i.e., context, transport processes, feedbacks, and resource redistribution). As with spatial variability, the temporal variation in water availability and plant response are nonlinearly related and exhibit threshold behaviors. Our conceptual framework of cross-scale temporal variation provides a dynamic view of landscapes that complements the spatial model of landscape heterogeneity. Arid and semi-arid systems are characterized by pulses of high and low biotic activity driven by temporal variation in water availability. Understanding this variation will help to identify thresholds of resource availability that determine species-specific responses, integrate species responses through time as a function of resource availability, and predict dramatic shifts in community composition from episodic recruitment events generated by complex cross-scale temporal interactions in water availability. This understanding is essential for predicting the effects of directional climate change on ecosystem structure and function.

5.1. Management opportunities

The fluctuations inherent to pulsed ecosystems are usually disruptive, or at least inconvenient, to human societies based upon predictable "average" conditions. Any

sustainable management plan must treat these recurrent pulses as an inherent feature of the ecosystem, rather than as an unpredictable boon or disaster. Pulsed ecosystems allow managers to focus management activity at critical times. The same pulses that complicate and threaten static management plans also offer a valuable management opportunity. Obviously, management activities change in response to the arrival or failure of rain pulses, but it is not so obvious that management during wet periods should be preparing the ecosystem for the next drought and that management during drought influences the post-drought recovery. Droughts, floods, and other ecologically important pulses are, in a sense, predictable. We do not know exactly *when* they will occur, but we know that they *will* occur. We can predict and use the changes in ecosystem function that accompany the pulse to multiply the effectiveness of management actions. By understanding and capitalizing on the interactions across temporal scales, managers can be prepared to take advantage of rare combinations of conditions to restructure or rehabilitate ecosystems.

Acknowledgments

References

Abrahams, A.D., Parsons, A.J., Wainwright, J., 2003. Disposition of rainwater under creosotebush. Hydrological Processes 17, 2555–2566.

Austin, A.T., Yahdjian, L., Stark, J.M., Belnap, J., Porporato, A., Norton, U., Ravetta, D.A., Schaeffer, S.M., 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141, 221–235.

Belnap, J., Phillips, S.L., Miller, M.E., 2004. Response of desert biological soil crusts to alterations in precipitation frequency. Oecologia 141, 306–316.

Bhark, E.W., Small, E.E., 2003. Association between plant canopies and the spatial patterns of infiltration in shrubland and grassland of the Chihuahuan Desert, New Mexico. Ecosystems 6, 185–196.

Breshears, D.D., Rich, P.M., Barnes, F.J., Campbell, K., 1997. Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. Ecological Applications 7, 1201–1215.

Breshears, D.D., Nyhan, J.W., Heil, C.E., Wilcox, B.P., 1998. Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and intercanopy patches. International Journal of Plant Sciences 159, 1010–1017.

Buck, B.J., Monger, H.C., 1999. Stable isotopes and soil-geomorphology as indicators of Holocene climate change, northern Chihuahuan Desert. Journal of Arid Environments 43, 357–373.

Caldwell, M.M., Dawson, T.E., Richards, J.H., 1998. Hydraulic lift: consequences of water efflux from the roots of plants. Oecologia 113, 151–161.

Conley, W., Conley, M.R., Karl, T.R., 1992. A computational study of episodic events and historical context in long-term ecological processes: climate and grazing in the northern Chihuahuan Desert. Coenoses 7, 55–60.

Dodd, M.B., Lauenroth, W.K., Welker, J.M., 1998. Differential water resource use by herbaceous and woody plant life-forms in a shortgrass steppe community. Oecologia 117, 504–512.

Donovan, L.A., Ehleringer, J.R., 1994. Water stress and use of summer precipitation in a Great Basin shrub community. Functional Ecology 8, 289–297.

Dugas, W.A., Hicks, R.A., Gibbens, R.P., 1996. Structure and function of C-3 and C-4 Chihuahuan Desert plant communities. Energy balance components. Journal of Arid Environments 34, 63–79.

Fay, P.A., Carlisle, J.D., Knapp, A.K., Blair, J.M., Collins, S.L., 2003. Productivity responses to altered rainfall patterns in a C-4 dominated grassland. Oecologia 137, 245–251.

Flanagan, L.B., Ehleringer, J.R., Marshall, J.D., 1992. Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon-juniper woodland. Plant Cell and Environment 15, 831–836.

Gao, Q., Reynolds, F.F., 2003. Historical shrub–grass transitions in the northern Chihuahuan Desert: modeling the effects of shifting rainfall seasonality and event size over a landscape gradient. Global Change Biology 9, 1475–1793.

Gebauer, R.L.E., Schwinning, S., Ehleringer, J.R., 2002. Interspecific competition and resource pulse utilization in a cold desert community. Ecology 83, 2602–2616.

Gibbens, R.P., Beck, R.F., 1987. Increase in number of dominant plants and dominance classes on a grassland in the northern Chihuahuan Desert. Journal of Range Management 40, 136–139.

Gibbens, R.P., Lenz, J.M., 2001. Root systems of some Chihuahuan Desert plants. Journal of Arid Environments 49, 221–263.

Gibbens, R.P., McNeely, R.P., Havstad, K.M., Beck, R.F., Nolen, B., 2005. Vegetation change in the Jornada Basin from 1858 to 1998. Journal of Arid Environments 61, 651–668.

Grover, H.D., Musick, H.B., 1990. Shrubland encroachment in southern New Mexico, USA: an analysis of desertification processes in the American Southwest. Climatic Change 17, 305–330.

Gutzler, D.S., Preston, J.W., 1997. Evidence for a relationship between spring snow cover in North America and summer rainfall in New Mexico. Geophysical Research Letters 24, 2207–2210.

Hennessy, J.T., Gibbens, R.P., Tromble, J.M., Cardenas, M., 1985. Mesquite (Prosopis-Glandulosa-Torr) dunes and interdunes in southern New Mexico—a study of soil properties and soil–water relations. Journal of Arid Environments 9, 27–38.

Herbel, C.H., Ares, F.N., Wright, R.A., 1972. Drought effects on a semidesert grassland range. Ecology 53, 1084–1093.

Holling, C.S., 1992. Cross-scale morphology, geometry and dynamics of ecosystems. Ecological Monographs 62, 447–502.

Huenneke, L.F., Anderson, J.P., Remmenga, M.D., Schlesinger, W.H., 2002. Desertification alters patterns of aboveground net primary production in Chihuahuan ecosystems. Global Change Biology 8, 247–264.

Hultine, K.R., Cable, W.L., Burgess, S.S.O., Williams, D.G., 2003. Hydraulic redistribution by deep roots of a Chihuahuan Desert phreatophyte. Tree Physiology 23, 353–360.

Huxman, T.E., Snyder, K.A., Tissue, D., Leffler, A.J., Ogle, K., Pockman, W.T., Sandquist, D.R., Potts, D.L., Schwinning, S., 2004. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. Oecologia 141, 254–268.

Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D., Harper, C.W., Danner, B.T., Lett, M.S., McCarron, J.K., 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. Science 298, 481–484.

Lauenroth, W.K., Sala, O.E., 1992. Long-term forage production of North American shortgrass steppe. Ecological Applications 2, 397–403.

Le Houérou, H.N., Bingham, R.L., Skerbek, W., 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. Journal of Arid Environments 15, 1–18.

Lin, G.H., Phillips, S.L., Ehleringer, J.R., 1996. Monsoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau. Oecologia 106, 8–17.

Loik, M.E., Breshears, D.D., Lauenroth, W.K., Belnap, J., 2004. A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. Oecologia 141, 269–281.

Ludwig, J.A., 1987. Primary productivity in arid lands: myth and realities. Journal of Arid Environments 13, 1–7.

Monger, H.C., 2003. Millennial-scale climate variability and ecosystem response at the Jornada LTER site. In: Greenland, D., Goodin, D.G., Smith, R.C. (Eds.), Climate Variability and Ecosystem Response at Long-Term Ecological Research Sites. Oxford University Press, London, pp. 341–369.

Monger, H.C., Cole, D.R., Gish, J.W., Giordano, T.H., 1998. Stable carbon and oxygen isotopes in Quaternary soil carbonates as indicators of ecogeomorphic changes in the northern Chihuahuan Desert, USA. Geoderma 82, 137–172.

Neilson, R.P., 1986. High-resolution climatic analysis and southwest biogeography. Science 232, 27–34.

Ni, F., Cavazos, T., Hughes, M.K., Comrie, A.C., Funkhouser, G., 2002. Cool-season precipitation in the southwestern USA since AD 1000: comparison of linear and nonlinear techniques for reconstruction. International Journal of Climatology 22, 1645–1662.

Ogle, K., Reynolds, J.F., 2004. Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays. Oecologia 141, 282–294.

Parmesan, C., Galbraith, H., 2004. Observed impacts of global climate change in the US, Pew Center on Global Climate Change. http://www.pewclimate.org/global-warming-in-depth/all_reports/observe-dimpacts/.

Paruelo, J.M., Lauenroth, W.K., 1996. Relative abundance of plant functional types in grasslands and shrublands of North America. Ecological Applications 6, 1212–1224.

Peters, D.P.C., 2000. Climatic variation and simulated patterns in seedling establishment of two dominant grasses at a semiarid–arid grassland ecotone. Journal of Vegetation Science 11, 493–504.

Peters, D.P.C., Havstad, K.M., 2006. Nonlinear dynamics in arid and semiarid systems: interactions among drivers and processes across scales. Journal of Arid Environments 65, 196–206.

Peters, D.P.C., Pielke Sr., R.A., Bestelmeyer, B.T., Allen, C.D., Munson-McGee, S., Havstad, K.M., 2004a. Cross-scale interaction, nonlinearities, and forecasting catastrophic events. Proceeding of the National Academy of Science 101, 15130–15135.

Peters, D.P.C., Yao, J., Havstad, K.M., 2004b. Insights to invasive species dynamics from desertification studies. Weed Technology 18, 1221–1225.

Rango, R., Tartowski, S.L., Laliberte, A., Wainwright, J., Parsons, A.J., 2006. Islands of hydrologically enhanced biotic productivity in natural and managed arid ecosystems. Journal of Arid Environments 65, 235–252.

Reynolds, J.F., Virginia, R.A., Kemp, P.R., de Soyza, A.G., Tremmel, D.C., 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. Ecological Monographs 69, 69–106.

Reynolds, J.F., Kemp, P.R., Tenhunen, J.D., 2000. Effects of long-term rainfall variability on evapotranspiration and soil water distribution in the Chihuahuan Desert: a modeling analysis. Plant Ecology 150, 145–159.

Reynolds, J.F., Kemp, P.R., Ogle, K., Fernandez, R.J., 2004. Modifying the pulse-reserve paradigm for deserts of North America: precipitation pulses, soil water and plant responses. Oecologia 141, 194–210.

Ryel, R.J., Caldwell, M.M., Yoder, C.K., Or, D., Leffler, A.J., 2002. Hydraulic redistribution in a stand of *Artemisia tridentata*: evaluation of benefits to transpiration assessed with a simulation model. Oecologia 130, 173–184.

Sala, O.E., Lauenroth, W.K., 1982. Small rainfall events: an ecological role in semiarid regions. Oecologia 53, 301–304.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A., Whitford, W.G., 1990. Biological feedbacks in global desertification. Science 247, 1043–1048.

Schwinning, S., Sala, O.E., 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141, 211–220.

Schwinning, S., Davis, K., Richardson, L., Ehleringer, J.R., 2002. Deuterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado Plateau. Oecologia 130, 345–355.

Schwinning, S., Sala, O.E., Loik, M.E., Ehleringer, J.R., 2004. Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. Oecologia 141, 191–193.

Snyder, K.A., Williams, D.G., 2003. Defoliation alters water uptake by deep and shallow roots of *Prosopis velutina* (Velvet Mesquite). Functional Ecology 17, 363–374.

Snyder, K.A., Cable, J.M., Huxman, T.E., Tartowski, S.L., 2004. Arid ecosystem responses to variations in the frequency and magnitude of growing season precipitation. 89th Annual Meeting, Ecological Society of America, p. 476.

Van Devender, T.R., 1995. Desert grassland history: changing climates, evolution, biogeography and community dynamics. In: McClaran, M.P., Van Devender, T.R. (Eds.), The Desert Grassland. University of Arizona Press, Tucson, AZ, USA, pp. 68–99.

Van Devender, T.R., Spaulding, W.G., 1979. Development of vegetation and climate in the Southwestern United States. Science 204, 701–710.

Wainwright, J.A., in press. Climate and climatological variations in the Jornada Basin. In: Havstad, K.M., Huenneke, L.F., Schlesinger, W.H. (Eds.), Structure and Function of a Chihuahuan Desert Ecosystem: the Jornada Basin LTER. Oxford University Press, Oxford.

Wainwright, J., Parsons, A.J., Abrahams, A.D., 2000. Plot-scale studies of vegetation, overland flow, and erosion interactions: case studies from Arizona and New Mexico. Hydrological Processes 14, 2921–2943.

Walter, H., 1971. Natural savannahs as a transition to the arid zone. In: Burnett, J.H. (Ed.), Ecology of Tropical and Subtropical Vegetation. Oliver & Boyd, Edinburgh, pp. 238–265.

Weltzin, J.F., McPherson, G.R., 1997. Spatial and temporal soil moisture resource partitioning by trees and grasses in a temperate savanna, Arizona, USA. Oecologia 112, 156–164.

Weltzin, J.F., Loik, M.E., Schwinning, S., Williams, D.G., Fay, P.A., Haddad, B.M., Harte, J., Huxman, T.E., Knapp, A.K., Lin, G., Pockman, W.T., Shaw, M.R., Small, E.E., Smith, M.D., Smith, S.D., Tissue, D.T., Zak, J.C., 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. Bioscience 53, 941–952.

Whitford, W.G., Anderson, J., Rice, P.M., 1997. Stemflow contributions to the "fertile island" effect in creosotebush, *Larrea tridentata*. Journal of Arid Environments 35, 451–457.

Williams, D.G., Ehleringer, J.R., 2000. Intra- and interspecific variation for summer precipitation use in pinyon-juniper woodlands. Ecological Monographs 70, 517–537.

Zhang, Y., Wallace, J.M., Battisti, D.S., 1997. ENSO-like interdecadal variability: 1900–1993. Journal of Climate 10, 1004–1020.