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PULSE EVENTS AND ARID ECOSYSTEMS

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A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA

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Abstract In dryland ecosystems, the timing and magnitude of precipitation pulses drive many key ecological processes, notably soil water availability for plants and soil microbiota. Plant available water has frequently been viewed simply as incoming precipitation, yet processes at larger scales drive precipitation pulses, and the subsequent transformation of precipitation pulses to plant available water are complex. We provide an overview of the factors that influence the spatial and temporal availability of water to plants and soil biota using examples from western USA drylands. Large spatial- and temporal-scale drivers of regional precipitation patterns include the position of the jet streams and frontal boundaries, the North American Monsoon, El Niño Southern Oscillation events, and the Pacific Decadal Oscillation. Topography and orography modify the patterns set up by the larger-scale drivers, resulting in regional patterns (10^2–10^6 km^2) of precipitation magnitude, timing, and variation. Together, the large-scale and regional drivers impose important pulsed patterns on long-term precipitation trends at landscape scales, in which most site precipitation is received as small events (<5 mm) and with most of the intervals between events being short (<10 days). The drivers also influence the translation of precipitation events into available water via linkages between soil water content and components of the water budget, including interception, infiltration and runoff, soil evaporation, plant water use and hydraulic redistribution, and seepage below the rooting zone. Soil water content varies not only vertically with depth but also horizontally beneath versus between plants and/or soil crusts in ways that are ecologically important to different plant and crust types. We highlight the importance of considering larger-scale drivers, and their effects on regional patterns; small, frequent precipitation events; and spatio-temporal heterogeneity in soil water content in translating from climatology to precipitation pulses to the dryland ecohydrology of water availability for plants and soil biota.

Keywords Drought duration · El Niño Southern Oscillation · Evapotranspiration · Infiltration depth · Pacific Decadal Oscillation

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Introduction

The fluxes of water through the soil-plant-atmosphere continuum, and interactions with the planetary boundary layer, are key elements of the hydrologic cycle (Noy-Meir 1973; Beatley 1974; Ehleringer et al. 2000; Jackson et al. 2001; Weltzin et al. 2003). A study of the factors that drive the spatial and temporal patterns of precipitation pulses—and the way they drive organismal, population, community, and ecosystem functions— requires consideration at multiple scales from global-scale atmospheric and oceanic processes, to fine-scale variation at the scale of individual organisms.

Weather derives from the solar-powered cascade of mass, energy, and momentum through the atmosphere (Aguado and Burt 2004). Global-scale redistribution of solar energy forces the movement of air masses and the moisture that they carry. The patterns of poleward energy redistribution are complicated by ocean surface currents, the jet streams, and prevailing wind patterns. At smaller and smaller spatial and temporal scales, other processes and factors add additional levels of complexity to precipitation patterns. The net result is the patterns of rain and snowfall that emerge from comparisons of state climate division (based on averages of measurements made by weather stations across landscapes), and individual weather station time-series data.

Water that is functionally available for plants and soil biota has frequently been viewed simply as incoming precipitation (see Schwinning and Sala 2004 in this series of reviews for a consideration of the nature of resource pulses, including precipitation). However, processes at larger scales drive the magnitude and timing of precipitation pulses, and the subsequent transformation of precipitation pulses to soil water available for plants and other organisms can be complex. For example, soil depth, soil texture, petrocalcic layers, parent material, organic matter content, snow pack depth, snow redistribution, vegetation type, leaf area index, and soil surface characteristics (i.e., the presence, cover, and nature of soil biotic crusts) can all affect the extent to which rain or snow melt water will infiltrate a soil to some depth, or run off its surface. Moreover, these factors affect both the vertical and horizontal heterogeneity of soil water availability. In this manner, precipitation pulses are translated into soil water pulses that are available to plant roots and soil biota for uptake.

To fully understand the ecological implications of the frequency and intensity of precipitation pulses, it is necessary to begin with an examination of the macroscale physical processes that generate weather, and then consider their influence on precipitation patterns as they are modified at finer and finer spatial scales. Here we provide an overview of processes that influence the spatial and temporal availability of water to plants and soil biota using examples from western USA drylands (arid, semi-arid, and sub-tropical areas). More specifically, we (1) highlight the nature of, and relationships between, meso-, and regional-scale weather patterns of western USA drylands, and the processes that drive them; (2) quantify precipitation trends across the drylands of western USA relative to frequency of events as a function of event size, and the distribution of interval periods between precipitation events; and (3) summarize processes affecting the ways in which precipitation pulses are translated into spatio-temporal heterogeneity in soil water content that determines water availability for plants and soil biota. We focus on dryland ecosystems in the western USA, where an extensive network of weather stations provides an opportunity to highlight the bridge between larger-scale climate forcings and finer scale translation into soil water. Although our examples are drawn from western USA drylands, concepts related to multi-scale determinants of soil water pulses have relevance for other dryland regions as well.

Macro-, meso-, and regional-scale processes driving precipitation patterns of the western USA

Macro- and meso-scale patterns and processes

The drylands of the western USA west of the 100th meridian longitude exhibit considerable complexity in precipitation magnitude, timing, and variation (Rajagopalan and Lall 1998), especially in comparison to patterns in the eastern half of the country. A key characteristic is that precipitation is greatly exceeded by evaporative demand. The large-scale pressure systems and frontal patterns that affect precipitation patterns for western USA drylands result from the dynamics of Pacific basin atmospheric and oceanic conditions (Leathers et al. 1991; Lins 1997). These impart a complex interplay between the position of the jet streams and their moisture content, the Bermuda High pressure system, the subtropical High off the coast of California, and the phase of various large-scale ocean-atmosphere oscillatory systems (Mantua et al. 1997). Maritime polar fronts originating from the direction of the Gulf of Alaska dominate wintertime precipitation patterns for much of western USA, bringing rain to the west coast and low elevations further inland, and snow at higher elevations and latitudes (Jorgensen et al. 1967; Sellars and Hill 1974; Barry and Chorley 1998; Sheppard et al. 2002). Coastal geography, off-shore wind and water currents, seasonal movements of the jet streams, prevailing frontal systems and high pressure zones, the North American (also referred to as the Southwest or Arizona) monsoon, and topography all further contribute to the complexity of precipitation patterns in western drylands (Bryson and Hare 1974; Sheppard et al. 2002).

The Pacific Decadal Oscillation (PDO) imposes an inter-decadal cycle of wet and dry periods for western USA (Rajagopalan and Lall 1998). The PDO is characterized by variation in Pacific Ocean sea surface temperatures, ocean surface height, sea level pressure, and wind patterns (Cane et al. 1997). Over the past 100 years, two PDO full cycles have occurred: cool PDO conditions occurred between 1890 to 1924 and from 1947 to 1977, while warm PDO conditions occurred between 1925 to 1946 and 1977 to the mid-1990s (McCabe and Dettinger 1999). The PDO is correlated with decadal variation in northern Rocky Mountain snowpack (Selkowitz et al. 2002), and oscillations in the hydrologic balance in the Sierra Nevada and Rocky Mountains (Benson et al. 2003; Gray et al. 2003). The ecohydrologic importance of this relatively longer-term process is highlighted by a major drought in southwestern USA during the 1950s that produced landscape-scale tree mortality and associated reductions in herbaceous vegetation (Allen and Breshears 1998).

Another major determinant of interannual variation in western USA precipitation patterns is the El Niño Southern Oscillation (ENSO; Cane 1986; Cayan and Webb 1992; Kahya and Dracup 1993, 1994). ENSO has a return time of 3–5 years, and wet and dry phases that last from 6 to 18 months (Barry and Chorley 1998). The atmospheric circulation patterns during wet El Niño periods result in altered temperature and precipitation patterns across large portions of the globe, including portions of western USA drylands. In years following El Niño, the La Nina phase of ENSO results in drier conditions throughout the parts of western USA that are wetter during El Niño (Kiladis and Diaz 1989). A number of analytical, observational, and theoretical approaches suggest an interaction of the PDO and ENSO in determining the interannual variability in the magnitude of wintertime western USA precipitation (Yarnal and Diaz 1986; Dettinger et al. 1998; McCabe and Dettinger 1999; Rajagopalan and Lall 1998; Sheppard et al. 2002). The effects of ENSO cycles are evident in streamflow patterns across western USA (Cayan and Webb 1992; Kahya and Dracup 1993, 1994). Based on long-term simulations of soil water dynamics at the Jornada Long Term Ecological Research Site, in southern New Mexico, the proportion of precipitation that returns to the atmosphere as transpiration relative to total evapotranspiration is predicted to decrease

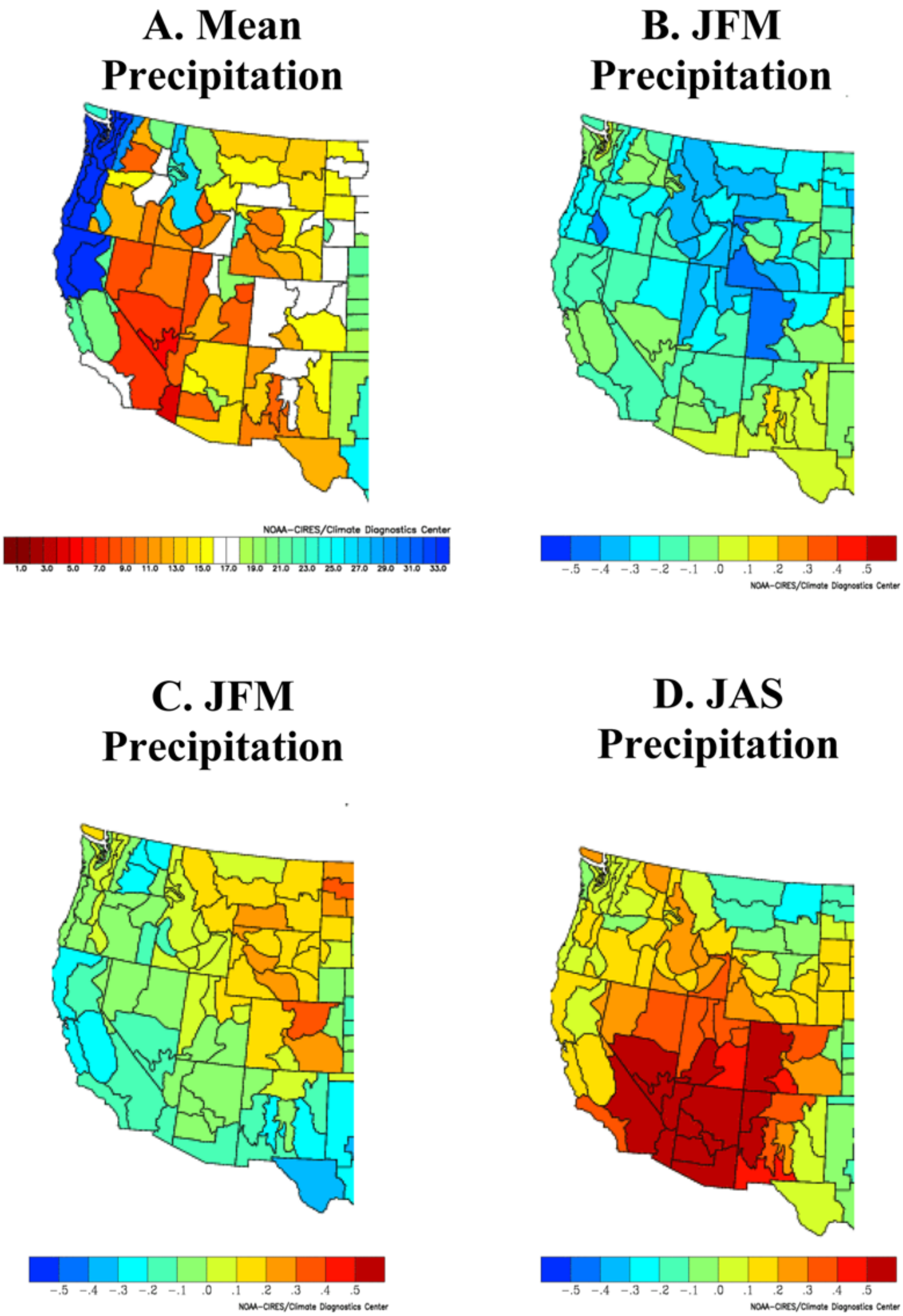


Fig. 1a–d Spatial patterns of precipitation for state climate divisions of western USA, west of 100°W longitude. **a** Average annual precipitation for 1895–2002 (NOAA-CIRES Climate Diagnostics Center). **b** Correlation of winter (January–March) total precipitation for the years 1948–2002 with the PDO Index (first principal component of Northern Hemisphere extra tropical sea surface temperatures). **c** Correlation of winter (January–March) total precipitation for the years 1948–2002 with the SOI. **d** Correlation of summer (July–September) total precipitation with a two-stage Southwest Monsoon Index (NCDC 1994). Images were provided by the NOAA-CIRES Climate Diagnostics Center, Boulder, Colorado from their Web site at http://www.cdc.noaa.gov/

substantially with decreasing precipitation (Reynolds et al. 2000). Hence, in dry La Nina years, transpiration may only comprise 10–20% of total evaportansipration, whereas in wet El Niño years this fraction may exceed 50%.

For large portions of southwestern USA, seasonal variation in precipitation occurs due to the North American monsoon (Adams and Comrie 1997), a mesoscale circulation that develops over southwestern USA and northern Mexico during the months of July through September. The northern and western extent of the summer monsoon flow generally forms an abrupt boundary from approximately east of Yuma, Arizona northeast to Rawlins, Wyoming, though there is considerable seasonal and interannual variation in the location of the boundary. The ecological importance of the North American monsoon has been highlighted by research in semiarid woodlands spanning either side of the monsoon boundary, where the proportion of annual precipitation received during the summer monsoon season ranged from 18% in northern Utah to 60% in southern Arizona (Williams and Ehleringer 1996). Use of summer precipitation for both *Pinus edulis* and *Juniperus osteosperma* increased with an increasing proportion of summer precipitation at a site, and *Quercus gambelii* did not use summer rain in most locations, except at the wettest end of the gradient. Hence, spatial patterns interact with the seasonal timing of the monsoon to affect the magnitude and timing of rainfall pulses and soil water availability on either side of the monsoon boundary and can have a significant effect on plant water uptake.

Regional patterns and relationships with larger-scale processes

Regional patterns of precipitation can be compared using state climate division historical data (NCDC 1994; we examined data for 1948–2002 which captures the late twentieth century wet period from http://www.cdc.noaa.gov). State climate divisions are based on geographic regions similar in elevation, topography, and climate patterns. Monthly averages are computed for all stations within the division that report both temperature and precipitation, and are corrected for time of observation bias (Karl et al. 1986). Historical precipitation values for contiguous climate divisions are often similar to one another, resulting in a clustering of divisions into regional spatial patterns. Average precipitation thus exhibits regional patterns across the western USA (Fig. 1a). These patterns are consistent with general descriptions of precipitation patterns for western USA: the wettest conditions occur along the Pacific Coast and higher elevations of the Rocky Mountains, decrease eastward due to the rainshadow effects of the Cascade Mountains and Sierra Nevada, and increase east of the Rocky Mountain front range. Regional precipitation patterns for clusters of climate divisions are also correlated with larger-scale spatial and temporal drivers, such as the PDO Index, the El Niño phase of ENSO, and the North American monsoon (Fig. 1b–d). For example, winter (January to March) precipitation is negatively correlated with the PDO Index for much of the northern Rocky Mountains (Fig. 1b), whereas winter precipitation for the southern half of western USA is negatively correlated with the southern oscillation index (SOI; Fig. 1c). That is, greater rainfall occurs during stronger El Niño events for California east to the Trans Pecos of Texas. Clusters of climate divisions

Table 1 Temporal patterns of precipitation variation for western USA. Data are coefficients of variation, except for 1948–2002 which are means/CV. Data are coefficients of variation computed from monthly means from 1948–2002 for selected state climate divisions, arranged in order of increasing annual mean precipitation. The cool phase of the Pacific Decadal Oscillation (*Cool PDO*) are CVs for the years 1957–1976; the warm phase of the PDO (*Warm PDO*) are CVs for 1977–1996; winter (*Winter*) CVs are for January, February and March, 1948–2002; the CVs for January, February, March for El Niño years (*El Niño Winter*) are computed for 1958, 1966, 1973, 1978, 1983, 1988, 1992, 1993, 1995, and 1998; summer monsoon (*Summer*) data are CVs for July, August and September, 1948–2002

Location	1948–2002 mean/CV	Annual		Seasonal		
		Cool PDO	Warm PDO	Winter	El Niño Winter	Summer
California, Southern Deserts	69/42	36	41	102	71	140
New Mexico, Central Valley	243/25	19	21	83	69	78
Wyoming, Green and Bear Drainages	245/23	17	26	51	43	65
Washington, Central Basin	252/22	17	23	59	57	97
Nevada, Northeast	282/22	20	23	52	46	88
Arizona, South Central	296/21	14	23	130	104	46
Texas, Trans Pecos	304/29	23	27	96	84	65
Idaho, Southwestern Highlands	312/25	22	23	61	66	102
Oregon, South Central	312/22	18	22	56	55	95
Utah, South Central	318/25	20	20	73	69	103
Montana, Central	379/18	19	19	49	57	63
Colorado, Western	404/17	8	15	4	48	59

emerge in the northern Rocky Mountains that have positive correlations of annual precipitation with the SOI, indicative of a general tendency toward lower precipitation totals during El Niño. Positive correlations occur for summer (July to September) precipitation and the North American monsoon for most of the climate divisions of the Intermountain and Southwest desert regions (Fig. 1d). These relationships at the state climate division help to resolve regional spatial patterns of precipitation and correlations with larger-scale processes such as the PDO, ENSO, and the North American monsoon.

Temporal variation in precipitation patterns emerges from analyses of precipitation data from 12 state climate divisions across western USA (Table 1). We computed coefficients of variation for January 1948 through December 2002 for annual totals at each site, and for winter and summer months, warm and cool phases of the PDO, and El Niño years, based on climate division data from the NOAA-CIRES Climate Diagnostics Center (http://www.cdc.noaa.gov/index.html). Based on the correlation matrix for the CVs from Table 1, variation in annual precipitation is positively correlated with variation in both the cool phase (r =0.91), and the warm phase (r =0.95) of the PDO. Variation in winter month precipitation totals (i.e., sums for January through March for each year 1948– 2002) is positively correlated (r =0.85) with El Niño variation. Variation in summer month precipitation (i.e. July through September totals for each year 1948–2002) is positively correlated with annual variation (r =0.69), and with variation in the warm phase of the PDO (r =0.61). Despite differences in the size of state climate divisions and our use of only 12 divisions across the topographically complex western USA, these results provide a further perspective on the temporal relationships between precipitation and drivers such as PDO, ENSO, and the North American monsoon. Moreover, these results provide a larger-scale perspective on spatial and temporal precipitation patterns in comparison to the daily patterns measured at individual weather stations, to which we turn next.

Spatial and temporal patterns of daily precipitation

The temporal distribution of daily precipitation is an important source of pulsing in arid and semiarid regions (Noy-Meir 1973). Two key characteristics of the temporal distribution are the size-class distribution of daily precipitation events and the size-class distribution of the amount of time that has elapsed since the last event. Previous analyses have been limited to a few sites, but have indicated a consistent pattern of dominance of daily precipitation events by the smallest size classes (Sala and Lauenroth 1982; Sala et al. 1992; Golluscio et al. 1998). For instance, events ≤ 5 mm account for more than 65% of all daily precipitation events at the semiarid Central Plains Experimental Range in eastern Colorado (Sala and Lauenroth 1982; Sala et al. 1992). Even fewer analyses have been conducted of the distribution of times since the last precipitation event. At the Central Plains Experimental Range, 90% of the dry periods are less than 15 days in length (Wythers et al. 1999). The objective of this section is to investigate whether a high frequency of small precipitation events and dominance of short dry intervals between events is a general characteristic of the pulsing environment of arid and semiarid sites in western USA.

We collected 30 years of daily precipitation and temperature data (1972–2002) from 316 sites in the western USA between 120° and 105°W longitude from the National Climatic Data Center web site (http://lwf.ncdc.noaa.gov/oa/ncdc.html) (Table 2). We selected sites to be representative of non-forested ecosystems, regularly distributed within the arid and semiarid portions of 11 western states, and at relatively low elevation (mean 1,308 m) over the region. Average mean annual precipitation for the sites was 288 mm and average mean annual temperature was 10.9°C.

On average, 47% of all of the precipitation events received at arid and semiarid sites in the western USA are ≤5 mm (Fig. 2) although the range is large (24–65%). Associated with this wide range of small events is, not surprisingly, a wide range of the largest size events (>30 mm) from 2–23%. Sites with a high percentage of small events have the lowest percentage of large events and vice versa. For instance, in Hanksville, Utah (38.33 N, 110.43 W) 64% of all precipitation events are ≤5 mm and only 1% are >30 mm. By contrast, small events (<5 mm) account for 26% and very large events (>30 mm) account for 20% of the precipitation events at the Santa Rita Experimental Range in southern Arizona (31.46 N, 110.51 W).

Dry periods (intervals between precipitation events) are dominated by those with the shortest duration (Fig. 2). On average 69% of the dry periods are ≤10 days and only 8% are ≥31 days. As expected, sites with a large percentage of short dry periods (<9 days) had the smallest percentages of long dry periods (>31 days). As an example, 87% of the dry periods in Rosalia, Washington (47.14 N, 117.22 W) are short and 2% are long. This contrasts with Death Valley, California (36.28 N, 116.52 W) which has an average of 38% short dry periods and 35% long dry periods.

Cluster analyses suggested no clear regional patterns of either distributions of event sizes or dry periods. However, regressions of cluster results against environmental

Table 2 Characteristics of the 316 sites used in the analysis of precipitation events and dry periods between events. *MAT* mean annual temperature, *MAP* mean annual precipitation

	Mean	Max	Min
Latitude (°N)	39.66	48.56	31.27
Longitude (°W)	−113.38	−105.12	−121.41
Elevation (m)	1,313	2,332	−59
MAT (°C)	10.86	24.61	1.04
MAP (mm)	288	588	60

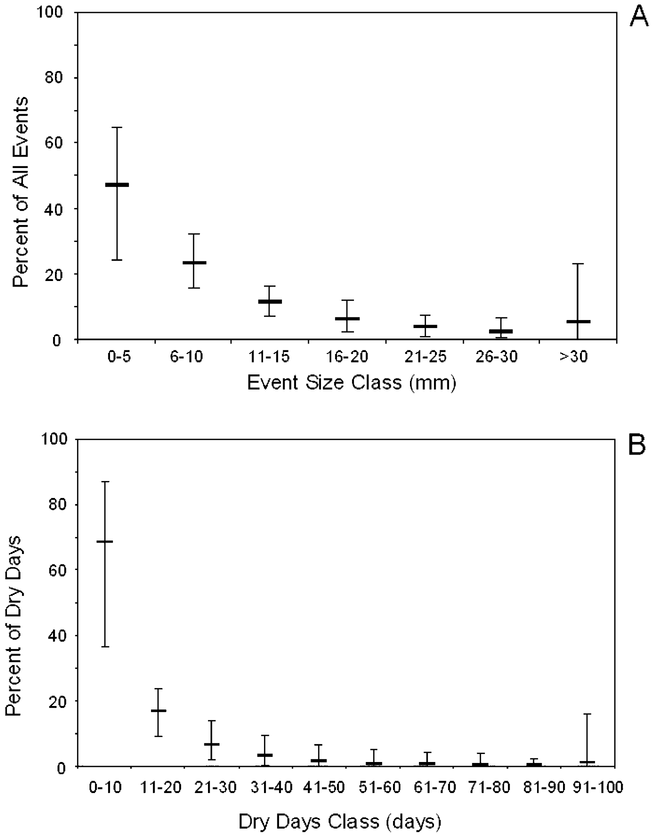


Fig. 2 **a** Frequency of daily precipitation events in seven size classes. **b** Frequency of dry days between daily precipitation events in ten size classes. Data are means and *error bars* represent ±1 SD from 316 sites in the arid and semiarid portions of western USA

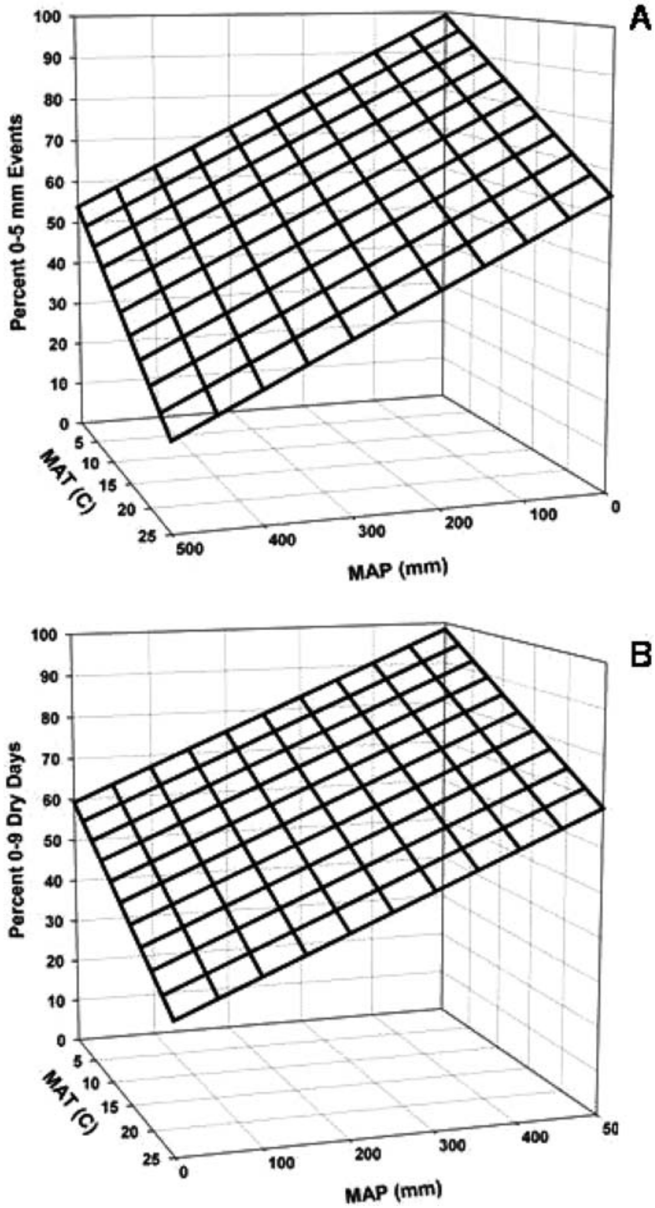


Fig. 3 **a** Percentage of all daily precipitation events that fall within the 0–5 mm size class, in relation to mean annual temperature (*MAT*, °C) and mean annual precipitation (*MAP*, mm). **b** Percentage of all dry intervals that fall within the 0–9 dry days class, in relation to MAP (°C) and MAT (mm). Data are from 316 sites in the arid and semiarid portions of western USA

variables indicated a strong relationship between the importance of small events and mean annual precipitation and temperature (r^2 =0.82). The importance of precipitation events in the smallest size class (0–5 mm) decreased as both mean annual precipitation and mean annual temperature increased (Fig. 3). Small events were of least importance at the warmest and wettest sites and the most important at the coolest and driest sites. The trend of diminished importance of small events and increased importance of large events as mean annual temperature increases is a well supported global phenomenon (Karl and Trenberth 2003). The importance of short dry periods was negatively related to mean annual precipitation and positively related to mean annual temperature (r^2 =0.99). The importance of short dry intervals between precipitation events was greatest at the coolest and wettest sites and least at the warmest and driest sites (Fig. 3b). At any particular mean annual temperature, the importance of short dry intervals increased as mean annual precipitation increased.

Why did we not find clear regional patterns in either event size distributions or dry period distributions when both are strongly related to mean annual precipitation and temperature? The answer very likely can be found in the geographic complexity of the West. Casual examination of a map of mean annual precipitation for the West confirms a corresponding regional complexity that precludes simple patterns (http://www.climatesource.com/images/ppt_ann.gif).

Relationships between environmental variables and precipitation and drought regimes suggest important differences in the pulsing environments of wet, dry, warm and cool locations within the arid and semiarid West. The coolest locations are characterized by a frequent alternation of wet and dry conditions; that is, short wet periods are followed by short dry periods. This is true regardless of mean annual precipitation. From a daily perspective, these are relatively high frequency pulsed environments. By contrast, the situation in the warmest locations is complex. In warm areas, the importance of small precipitation events increases as mean annual precipitation decreases and the importance of short dry periods increases as mean annual precipitation increases. In the warmest and driest locations, small precipitation events account for 60% of the total and short dry periods account for 45% of all dry periods. In the warmest and wettest locations, small precipitation events are less than half of total events and short dry periods make up approximately 75% of the total. Because bare soil evaporation is such an important process in warm arid and semiarid locations, the pulsing regime is largely determined by the characteristics of the dry periods. Warm dry locations, on a daily basis, are weakly pulsed with low frequency events. By contrast, warm wet locations are strongly pulsed with a high frequency.

The key finding from this analysis is that precipitation size class and dry period size class distributions cannot be simply categorized for the arid and semiarid portions of the western USA. The precipitation regime of only a portion of the region can be characterized as dominated by small events and short dry periods. In some areas, small precipitation events account for less than 30% of total events and short dry periods less than 40% of total dry periods. Since these patterns have a large influence on pulsing regimes, understanding them is of great importance in our quest to understand the importance of pulses in arid and semiarid ecosystem dynamics.

These general patterns for daily-scale precipitation and dry periods emerge even though there is a high degree of spatial and temporal variation in synoptic weather patterns in the West. Additional research will be needed to quantify how or whether variation in these daily patterns can be explained by large-scale patterns. The general patterns quantified here, however, have important implications for translating precipitation events and intervening dry periods into soil water dynamics, which are the pulses of greatest ecological relevance.

Spatial and temporal patterns of soil water pulses

Pulses of the water budget

Precipitation patterns and their synoptic weather relationships are key drivers of ecosystem processes in arid and semiarid ecosystems. However, from an ecological perspective, these factors are precursors to pulses of more direct relevance: when, where, and how much of this precipitation will be translated into soil water available to plants and soil biota. Because there are many factors that influence this process, understanding precipitation patterns is necessary, but not sufficient to evaluate the effects of a

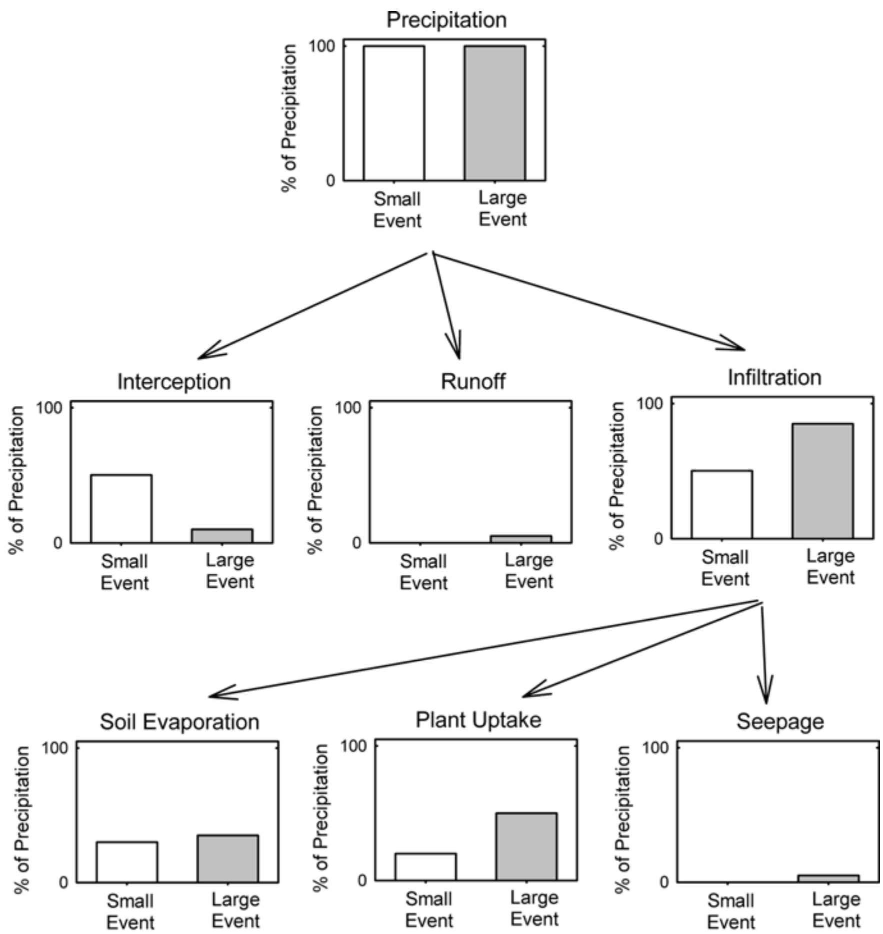


Fig. 4 General patterns of pulses for components of a water budget for small and large precipitation events. All *panels* are normalized relative to 100% of the event; hence the figure emphasizes the relative size of each component of the water budget for small versus large events, not the actual amount. Note that extreme, high intensity events are not considered here

precipitation pulse from an ecological perspective. Rather, the various components of the water budget need to be considered. These components vary in magnitude as a function of event size and are modified by the length of the interval between events, as well as by characteristics of the event (e.g., snow vs rain, and precipitation intensity). Here we evaluate the ecological implications of the precipitation characteristics described above.

The major components of the water budget usually include inputs of precipitation and losses by interception, runoff, soil evaporation, plant uptake and transpiration, and seepage (downward movement of water out of the soil zone of interest), as well as the associated changes in infiltration and soil water storage (Noy-Meir 1973; Campbell and Harris 1981; Wilcox et al. 2003b; Fig. 4). In dryland ecosystems, precipitation events on the scale of minutes are often the event of interest. How does a precipitation event get partitioned among the components of the water budget, and over what time scales does the partitioning occur? The water budget at the scale of a watershed differs from that at the scale of individual plants. We initially focus on the watershed scale, and then later evaluate finer-scale patterns.

Interception by foliage, of woody plants, herbaceous plants, plant litter, or soil biotic crusts is the first process that diminishes precipitation input to the soil. The amount of precipitation intercepted is highly variable by plant type, with reported values of 4–46% precipitation for shrubs and 11–84% for grasses (Branson et al. 1981; Reynolds et al. 2000; Wilcox et al. 2003b). Interception also varies with precipitation amount, as the foliage has a holding capacity that may intercept all water from small precipitation events and only a small fraction of very large precipitation events (Corbett and Crouse 1968; Branson et al. 1981; Waring and Running 1998). Intercepted rainfall is generally viewed as returned to the atmosphere via evaporation within a day of a precipitation event (Waring and Running 1998), unless air temperatures are sufficiently low to retard evaporation rates. Following losses associated with interception, the interrelated processes of infiltration rate and runoff determine the net input to the soil. The infiltration capacity of the soil is determined by several factors, but particularly by the permeability of the soil surface; residence time of the water; and the duration, intensity, and form of the precipitation event (Branson et al. 1981; Dingman 1994). Soil permeability increases as the size and number of soil pores increases and thus is influenced by soil texture, aggregate structure, animal burrows and ground covers (e.g., rocks, plant litter, biological crust organisms). Runoff processes generally occur rapidly, during and in the minutes following a precipitation event. Runoff at a watershed scale is generally small in dryland ecosystems, usually <5% of the annual water budget (Wilcox et al. 2003b). Runoff events tend to be associated with high intensity (e.g., summer monsoons) and high frequency (El Niño years) events. Infiltration pulses may span longer time frames of hours to days than runoff pulses as soil water moves down through the soil profile. Hydraulic redistribution by plant roots can result in a decrease in soil water content at one soil depth and an associated increase in soil water content at another, the direction of which is dependent on gradients of water potential (Caldwell et al. 1998; Ryel et al. 2003). The soil water pulse is the most interactive component of the water budget, receiving inputs via infiltration and hydraulic redistribution and losses from soil evaporation, plant water uptake, and seepage to deeper locations. These processes all have a spatial component to them, which we will consider below.

Temporally, soil water is depleted over days and weeks primarily by soil evaporation and plant uptake and transpiration. Seepage is usually a very small component of the water budget, <5%, and may occur over days following an event (Wilcox et al. 2003b). Soil evaporation occurs at shallow depths, generally <15 cm, and varies temporally largely due to available energy, as reflected in soil temperature values, which themselves lag solar radiation inputs (Ben-Asher et al. 1983). Plant water uptake is interrelated with transpiration and hence also exhibits a diurnal cycle. Because plant roots can extend below the evaporative zone, they may be able to extract water over a longer time period than that for which soil evaporation persists. The interactive effects of soil evaporation, plant uptake and transpiration, and seepage, affect the overall dry-down pattern of soil water, which can of course be modified by additional soil infiltration or hydraulic redistribution events.

Notably, the magnitudes of the pulses of the water budget are generally modified by soil texture. Soils with higher sand content allow greater infiltration (Dingman 1994). This can result in not only greater infiltration initially but also in reduced evaporation if the infiltration extends below the evaporative zone.

There are ecologically significant implications of precipitation event size in terms of how precipitation is partitioned among the water budget for small versus large precipitation events. (This excludes extreme events that have a very high rate of rainfall intensity, as a large proportion of the event can be lost from the system as runoff). Differences within the water budget between small and large events occur for all aspects of the water balance at the ecosystem scale (Fig. 4). For small events relative to large events, interception is a much larger percentage of precipitation input, and runoff at the hillslope scale is often non-existent or negligible. Consequently, a smaller proportion of water from small events infiltrates the soil. The infiltrated water is then distributed among three loss terms: soil evaporation, plant uptake and transpiration, and seepage to deeper layers below the rooting zone. Small events produce less soil water infiltration and are unlikely to produce any seepage. As most of the input in soil water from a small event is concentrated at shallow depth, this water is much more susceptible to evaporation, and hence for small events we expect a large proportion of the soil water to leave by soil evaporation than by plant uptake and transpiration. Therefore, the distribution of precipitation events as a function of size, quantified above, is ecologically important.

The number of days between precipitation events has a related influence on the distribution among the components of the water balance. When events occur in close succession to one another, they can provide an additive effect. For example, runoff is sensitive to antecedent soil water content of the surface layer and seepage generally depends on saturation of the soil layer of interest. Soil evaporation is viewed as a two-stage process, with the stages reflecting different rates of evaporation depending on whether or not the soil surface is wet; consequently the number of days between precipitation events may be particularly important for evaporation (Ritchie 1972; Dingman 1994). Further, plant root activity may be dependent on stimulation from an initial wetting event. The soil water dynamics in dryland systems, then, in which small events occur more often than larger events, is moderated by the fact that these events are more frequent (≤10 days. Fig. 3).

The magnitude of the water pulses (Fig. 4) is also affected by type of precipitation. Snowfall events generally are of much lower intensity than rainfall events, and hence have different runoff relationships (Dingman 1994; Wilcox et al. 2003a). Unlike rainfall, snow can accumulate over time, entering the soil profile in whole or part during a snowmelt event. Snowmelt can also occur during periods of reduced potential evaporation relative to rainfall events, making the resultant slow release more effective per unit of precipitation than rainfall in increasing soil water content (e.g., Sala et al. 1992; D.D. Breshears, Myers and Barnes, submitted). In effect then, snow events behave more like large events in that a larger proportion of the precipitation input is translated into plant-available water. Further, because snow can accumulate over several precipitation events and then melt during a single interval, aggregated snow events can produce particularly large pulses of input to soil moisture (Fig. 4). The overall trends in the water budget at the scale of an ecosystem or hillslope, however, also need to be evaluated in greater detail at the scale of individual plants, where small-scale heterogeneity can have important implications for plants of different functional types.

Heterogeneity of soil moisture pulses

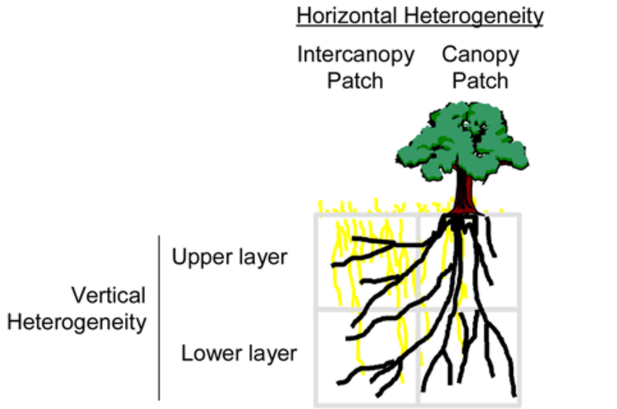
As presented above, a pulse of plant water uptake and transpiration depends most directly on the pulse of soil water, which itself is the most interactive component of the water budget. Further, soil water pulses exhibit substantial variation, both vertically with soil depth and horizontally with surface cover. Both aspects of this variation are ecologically important. Vertically, there is generally a progression of depth of water accessed from soil crust biota to herbaceous plants to shrubs to trees (Walter 1971; Jackson et al. 1996; Belnap and Lange 2001). In addition, there is an important vertical distinction between the upper zone of soil evaporation, where plants must effectively compete with that process, versus a lower zone where soil evaporation does not occur. Horizontally, trees and shrubs may access soil water in the intercanopy spaces that separate woody plants (sometimes referred to as interspaces) whereas herbaceous plants, which often occur in the intercanopy spaces, may be limited to uptake from intercanopy spaces (Belsky et al. 1989; Joffre and Rambal 1993; Dawson 1993; Breshears et al. 1997a). Hence, it is important to evaluate soil water availability in the context of both vertical and horizontal heterogeneity.

Vertical heterogeneity

Key determinants of vertical heterogeneity are factors that influence water infiltration—interception, runoff, hydraulic redistribution, and especially the magnitude and frequency of incoming precipitation pulses (Fig. 5). Given equal intensity, larger and more frequent precipitation pulses generally result in greater penetration of water into the soil profile than smaller, less frequent events. Also, a given amount of water will penetrate further into sandy soils than finer-textured soils. On a longer time scale, vertical heterogeneity with depth varies between wet versus dry years. For example, for the Central Plains Experimental Range in Colorado, predicted water availability for plants in dry years is limited to only the top 40 cm, whereas in wet years, water availability extends to below 1 m. Concurrently, water is predicted to be available at shallow depths more frequently in dry years than wet years, due to a lack of deeper infiltration in dry years (Sala et al. 1992). Within more arid sites, different plant functional types such as grasses and shrubs may utilize moisture at the same depth; differentiation among these plants may be achieved temporally rather than spatially (Reynolds et al. 2000). For example, in systems where a significant amount of precipitation occurs as snow, woody plants that are active may be able to access soil water in warm, between snow storm intervals, whereas the dormant herbaceous plants do not have this opportunity. Also, shrub roots may act as conduits that channel stemflow water to deeper soil depths than that predicted by infiltration alone (MartinezMeza and Whitford 1996; Devitt and Smith 2002).

Horizontal heterogeneity

Although the greatest focus to date has been on the role of vertical heterogeneity in soil water and associated phenological differentiation among plant functional types, there is growing evidence that horizontal heterogeneity in soil moisture, associated with variations in surface cover, are also important. Horizontal differences in soil water have been documented most frequently at the scale of the canopy patches of woody plant and the intercanopy areas that separate them (Belsky et al. 1989; Joffre and Rambal 1993; Dawson 1993; Breshears et al. 1997b). Horizontal heterogeneity is dynamic through time, as



Component of water budget	Effect on Vertical Heterogeneity (lower relative to upper layer)	Effect on Horizontal Heterogeneity (canopy relative to intercanopy patch)
Interception	+ or − −	− − −
Runoff	−	++
Hydraulic redistribution	− or +	− or +
Soil evaporation	− −	+
Plant water uptake	− or +	− or +
Seepage	−	?

Fig. 5 Spatial heterogeneity in soil moisture with respect to vertical differences with depth and horizontal differences associated with vegetation cover, and the potential effects of different components of the water budget on this heterogeneity. The canopy patches, depicted for woody plant canopies, could also apply at smaller scales to herbaceous canopies or biological soil crust cover. The *signs* indicate the expected directions of impact on soil water heterogeneity for a given process

canopy patches can be either wetter or drier than intercanopy patches, and this relationship can change through time (Breshears et al. 1997b). Similar types of differences may occur at a finer scale in the intercanopy spaces separating woody plants, among bare patches, herbaceous patches, and patches of biological soil crusts.

As with vertical heterogeneity in soil water, the different components of the water budget have differing effects on horizontal heterogeneity in soil water (Fig. 5). The interaction of precipitation size, intensity, and type with soil surface and plant characteristics is a dominant factor in determining horizontal heterogeneity. As we have noted, small precipitation events can comprise a large fraction of total annual precipitation, and they may be substantially intercepted in the canopy patches by the woody plant canopy, associated litter and/or the biological crust layer. Larger inputs from snowfall events may also be greatly modified by interception. For example, at the Mesita del Buey piñon-juniper woodland site near Los Alamos, New Mexico, soil water content was generally 20% greater in intercanopy than canopy locations following snowmelt (Breshears et al. 1997b). Runoff and the associated redistribution of water is also an important determinant of horizontal heterogeneity in soil water. The spatial scale and amount of runoff that is redistributed varies with precipitation event size (Wilcox et al. 2003a). Notably, even small precipitation events frequently generated runoff that is redistributed to down-slope vegetated patches, particularly herbaceous patches (Wilcox et al. 2003a). Similarly, water is often blocked by biological crust mounds that can be up to 15 cm high. These mounds decrease water velocity and increase water residence time, allowing for little, if any runoff during small events. Water that does run off is channeled into adjacent lower areas or to nearby plants, with the height, absorptivity, and orientation of the mounds determining the amount and pathway of the water flow (Belnap and Lange 2001).

Evaporation can also contribute to horizontal heterogeneity in soil moisture. For example, in a semiarid piñon-juniper woodland, soil temperatures beneath trees can be more than 10°C lower than for intercanopy patches in the summer, substantially reducing soil evaporation rates (Breshears et al. 1998). At a finer scale, patches of well-developed biological soil crust can be 14°C warmer than adjacent bare soils (Belnap and Lange 2001), although these same organisms also “cap” the soil surface, hence retarding evaporation. Although less clearly quantified, plant water use and hydraulic redistribution can also affect horizontal heterogeneity in soil moisture (e.g., Breshears et al. 1997a), and this can likely occur in ways that increase or decrease the ratio of soil water under canopies versus that in intercanopies.

Horizontal heterogeneity is often ignored in models of ecosystem dynamics or considered in isolation of vertical heterogeneity. However, it is important to consider these factors simultaneously (Breshears and Barnes 1999). Many interactions among woody and herbaceous plants occur within shallow intercanopy areas, a horizontal rather than vertical interaction (Breshears et al. 1997a). Establishing the controls on horizontal heterogeneity is particularly challenging, as nearly every component of the water budget and ground surface cover contributes to it. Indeed, in some cases differences associated with horizontal heterogeneity are of similar magnitude to those associated with vertical heterogeneity (D.D. Breshears, Myers, and Barnes, submitted), and therefore may be of particular ecological importance among different life forms within the same ecosystem.

Emerging multi-scale issues for precipitation pulses in dryland ecosystems

It has been 30 years since Noy-Meir, in a seminal paper on desert ecology, drew our attention to the centrality of water, water budgets and the importance of pulses for understanding the dynamics of desert ecosystems and other drylands (Noy-Meir 1973). Despite the substantial progress that has been made in understanding the role of water in desert ecosystem ecology over the past 30 years, several issues associated with the fate of water after it has entered the soil are still in need of urgent consideration. Our most elementary need is for long-term data sets of soil water by depth. It is astonishing that despite the fundamental importance of soil water, that there are hardly any data sets across wide regions (save that presented above) that exceed a few (5) years in length. This short duration is of concern because of large interannual variation in precipitation in arid and semiarid ecosystems that translates into associated variation in water budgets and soil water. Because of the probabilistic nature of inputs, the most useful data sets are those collected using nondestructive continuous sampling. By continuous sampling we mean regular samples at short (minutes) intervals. The majority of the few extant long-term data sets were collected using discrete sampling intervals (weeks to a month). The fact that precipitation occurs on only a few days in dryland areas and soils are wet for a small fraction of the days in a year, guarantees that most of the data collected under a discrete sampling strategy will represent dry soil and that many wet soil events will be missed. It has only been over the past decade or so that reliable continuous sampling systems have become available (Jackson et al. 2000). Our key need now is to accumulate sufficient data to allow us to reliably evaluate the relationships between pulse inputs and pulses in soil water. Also lacking, as a result of methodological constraints, are nondestructive continuous measurements at the very shallow intervals (0–0.5 cm) relevant to soil microbiological activity, especially biotic crusts. Our data needs are not limited to the vertical distribution of soil water and how it varies over time, but also variation in soil water horizontally at hierarchical scales from woody canopy/intercanopy to herbaceous canopy/intercanopy to crust/bare soil types.

In dryland ecosystems the two processes that dominate the fate of water after it has entered the soil are bare soil evaporation and transpiration. Our understanding of the partitioning of soil water between these two processes is very limited. Because of the high potential evotranspiration in drylands, these two processes compete, and a reduction in one is almost guaranteed to result in an increase in the other. This has important implications for any surface manipulations in dryland ecosystems such as land use change as well as for climate change. Understanding how water is partitioned under current conditions will help ecologists make predictions about the changes we should expect with land use and/or climate change. At the same time, greater understanding of effects of climate change on evapotranspiration for different vegetation types will be important for improved ground-water hydrology models.

To address emerging issues associated with climate change and intensification of land use, we will need to not only improve our understanding of site-specific water budgets, but will also need to develop improved understanding of the linkages of site water dynamics with large-scale processes such as El Niño and the Pacific Decadal Oscilllation. General Circulation Model (GCM) predictions of potential future precipitation regimes suggest that the amount and seasonality of precipitation will change across the western USA within the next 50–100 years. However, patterns of precipitation change will not be consistent across the entire region (Arritt et al. 2000). The considerable variation and hence, uncertainty, in the predictions of general circulation models, and their inability to make predictions as to how the timing or amount of precipitation will change across the topographically complex western USA suggest the need for Regional Climate Models (e.g., Snyder et al. 2002) with greater spatial and temporal resolution. There is also a need for better understanding of how changes in precipitation type (i.e., snow to rain shifts due to anthropogenic climate change), will affect organismal, population, community, and ecosystem functions. For example, forcing of snow melt to earlier dates due to climate change will affect soil and plant water relations and photosynthesis (Loik and Harte 1996, 1997; Loik et al. 2000) that underlie patterns of aboveground biomass accumulation and reproductive effort in response to climate change (Harte and Shaw 1995). Snowmelt timing is a critical signal for animal behavior, and altered climate patterns may impact the timing of migration and emergence from hibernation (Inouye et al. 2000). The importance of elevation on precipitation magnitude is evident in the greater biomass and diversity at higher elevations in comparison to adjacent lower elevation ecosystems. As a result, the many mountain systems of the arid and semiarid western USA support diverse meadow and forest communities at altitudes above shrub- or grassland-dominated valley systems. For certain regions (e.g., the Basin and Range province of the Great Basin Desert in Nevada), the high elevation communities represent resource islands that are important for migrating species; changes in precipitation and temperature patterns resulting from anthropogenic activities could significantly impact the population dynamics of plants and other organisms in this region (Murphy and Weiss 1992).

In summary, we wish to stress that evaluation of resource pulses in dryland ecosystems is more complex than the evaluation of individual precipitation events. Ecologists are just beginning to understand how larger-scale meteorological forcing drives precipitation patterns; an increasing awareness of mechanistic climatological relationships will help us further understand long-term and short-term changes in ecosystem attributes. The impact of these forcings needs to be further evaluated with respect to ways in which the general patterns of precipitation events will be expected to vary with climatic fluctuation and climate change. Those general patterns include a dominance of small, frequent precipitation events across systems, with the hottest and driest locations in western USA having precipitation regimes dominated by small precipitation events and intra-seasonal drought regimes dominated by long dry periods and the coolest and wettest locations having the opposite conditions. Precipitation events are often assumed a proxy for water available to plants and microorganisms, but here we point out the important impacts of different aspects of the water budget on available water and the importance of horizontal as well as vertical heterogeneity in soil water in determining that amount. Accounting for the complex, multi-scale factors we present here will be required to improve our understanding and ability to predict how ecosystems respond to water pulses in dryland ecosystems.

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