

Ecohydrology of Dry Regions: Storage versus Pulse Soil Water Dynamics

W. K. Lauenroth,^{1*} D. R. Schlaepfer,¹ and J. B. Bradford²

¹Department of Botany, University of Wyoming, 1000 E. University Avenue, Laramie, Wyoming 82070, USA; ²US. Geological Survey, Southwest Biological Science Center, 2255 N. Gemini Dr., Flagstaff, Arizona 86001, USA

ABSTRACT

Although arid and semiarid regions are defined by low precipitation, the seasonal timing of temperature and precipitation can influence net primary production and plant functional type composition. The importance of precipitation seasonality is evident in semiarid areas of the western U.S., which comprise the Intermountain (IM) zone, a region that receives important winter precipitation and is dominated by woody plants and the Great Plains (GP), a region that receives primarily summer precipitation and is dominated by perennial grasses. Although these general relationships are well recognized, specific differences in water cycling between these regions have not been well characterized. We used a daily time step soil water simulation model and twenty sites from each region to analyze differences in soil water dynamics and ecosystem water balance. IM soil water patterns are characterized by storage of water during fall, winter, and spring resulting in relatively reliable available water during spring and early summer, particularly in deep soil layers. By contrast, GP soil water patterns are driven by pulse precipitation events during the warm season, resulting in fluctuating water availability in all

soil layers. These contrasting patterns of soil water—storage versus pulse dynamics—explain important differences between the two regions. Notably, the storage dynamics of the IM sites increases water availability in deep soil layers, favoring the deeper rooted woody plants in that region, whereas the pulse dynamics of the Great Plains sites provide water primarily in surface layers, favoring the shallow-rooted grasses in that region. In addition, because water received when plants are either not active or only partially so is more vulnerable to evaporation and sublimation than water delivered during the growing season, IM ecosystems use a smaller fraction of precipitation for transpiration (47%) than GP ecosystems (49%). Recognizing the pulse-storage dichotomy in soil water regimes between the IM and GP regions may be useful for understanding the potential influence of climate changes on soil water patterns and resulting dominant plant functional groups in both regions.

Key words: semiarid; water balance; grassland; shrubland; storage; pulse.

Received 27 March 2014; accepted 6 August 2014;
published online 1 October 2014

Electronic supplementary material: The online version of this article (doi:10.1007/s10021-014-9808-y) contains supplementary material, which is available to authorized users.

Author contributions WL, DS, and JB conceived of and designed the study; WL and DS performed research and analyzed the data; WL, DS, and JB wrote the paper.

*Corresponding author; e-mail: wlauenro@uwyo.edu

INTRODUCTION

Temperate arid and semiarid North America consists of two large regions that superficially, because of their low precipitation, seem quite similar. The intermountain (IM) zone is between the Rocky Mountains

Table 1. Key Features for 20 Intermountain and 20 Great Plains Sites

	Lat (degN)	Long (degW)	Elevation (m)	MAT °C	MAP mm	Snow/MAP (%)	PET (mm)	Corr ^a (Temp, PPT)
Intermountain								
Mean	41.31	-112.83	1,348	9.33	344	19	1,194	-0.24
Minimum	35.33	-120.79	72	5.42	260	5	978	-0.71
Maximum	46.47	-103.05	2,137	15.95	472	42	1,813	0.25
Great Plains								
Mean	42.45	-105.07	1,163	9.13	378	13	1,249	0.52
Minimum	35.07	-112.79	640	4.13	303	7	938	0.40
Maximum	49	-101.47	1,829	15.07	471	20	1,616	0.61

MAT mean annual temperature, MAP mean annual precipitation, Snow/MAP mean annual snowfall divided by MAP, PET potential evapotranspiration
^aMean of the annual correlation coefficients of monthly temperature and monthly precipitation (Sala 1997)

and the Sierra Nevada and Cascade Ranges, whereas the Great Plains is east of the Rocky Mountains (Lauenroth and Bradford 2009, 2011). Despite similar dryness, these regions have important differences in climate and vegetation.

Both regions span similar ranges of latitude in the U.S. (approximately 35°–50°N) and therefore have comparable seasonal and annual temperatures (Lauenroth and Bradford 2009). The key differences in climate between the Great Plains and the IM zone are related to the seasonality of precipitation and therefore the seasonality of their dry seasons (Bailey 1979; Paruelo and Lauenroth 1996). In the IM zone, precipitation is approximately evenly distributed throughout the year, whereas in the Great Plains a majority of annual precipitation occurs in the summer. The relatively even seasonal distribution of precipitation in the IM zone combined with a peak in temperature in the summer results in a summer dry season (Bailey 1981). By contrast, summer is the wet season in the Great Plains (Lauenroth and Burke 1995).

Differences in the overlap between seasonality of precipitation and seasonality of temperature, and thus the dry season, have important consequences for plant functional type abundance (Sala 1997). Two key characteristics that are influenced by this overlap in dry regions are the balance between C₃ and C₄ species and the relative importance of shrubs versus herbaceous functional types (Paruelo and Lauenroth 1996; Sala 1997). The seasonality of wet soil during the period when temperatures are favorable for plant growth is an important control on the balance between C₃ and C₄ species (Epstein and others 1997; Teeri and Stowe 1976). By contrast, the amount of precipitation that is received during the period when temperature, and therefore potential evapotranspiration, is low influences the balance between shrubs and herbaceous functional types by

impacting the amount of water that gets stored in the deepest soil layers (Dodd and Lauenroth 1997; Sala 1997). Shrubs have an advantage in using this deep soil water (Sala 1997; Walter 1973).

The natural vegetation of the arid and semiarid portions of the IM zone is a mixture of C₃ grasses and shrubs or small trees with very few C₄ grasses (Paruelo and Lauenroth 1996; West 2000). By contrast, the vegetation of the Great Plains is best described as mixed C₄ and C₃ grasslands with a small component of woody plants (Lauenroth and Burke 1995). C₄ grasses dominate the southern two-thirds of the U.S. portion of the Great Plains and C₃ grasses dominate the northern one-third (Epstein and others 1997).

The differences in climate and vegetation between these two dry regions suggest that there should be important differences in the temporal and spatial distribution of soil water availability and ecosystem water balance. However, differences in ecosystem water balance between these regions have not been well characterized, despite the recognized importance of water availability in dryland ecosystems. The objective of this manuscript is to evaluate these differences by focusing on forty sites, twenty in the IM zone and twenty in the Great Plains. We conducted our evaluation using SOILWAT a daily time step soil water simulation model (Lauenroth and Bradford 2006, 2011; Schlaepfer and others 2012a). Our sites were chosen to have similar ranges of mean annual temperatures and precipitation (Table 1, Tables A1, and A2). Our specific questions for this analysis were

- (1) How do the long-term average dynamics of soil water potential differ between IM shrublands and Great Plains grasslands?
- (2) Are the regional patterns of soil water potential sufficiently distinct that they can be used to categorize sites?

- (3) How do these differences in soil water dynamics translate into differences in the temporal and spatial (depth) patterns of water that contributes to actual evapotranspiration?
- (4) What are the major differences in ecosystem water balance between the IM shrublands and Great Plains grasslands?

METHODS

We chose 20 weather stations from each of the IM and the Great Plains regions used by Lauenroth and Bradford (2009) (Table 1, Tables A1, and A2). The stations were selected from the arid and semiarid, low elevation, portions of each region and to represent similar ranges of annual temperature and precipitation in each region. We collected 41 years of daily precipitation and temperature data (1970–2010) from each weather station from NOAA National Climatic Data Center (<http://www.ncdc.noaa.gov/>). For each station, we excluded those years with more than 90 missing days for either daily precipitation or minimum or maximum temperature. From among the remaining years, we selected the most recent 30 years for use in the simulation model. We estimated remaining missing minimum and maximum temperature values as the mean value among years for each missing day. Missing precipitation values were estimated with a random draw for the same days of the year of another year without missing data during the desired period.

SOILWAT is a daily time step, multiple-layer soil water model developed for semiarid grasslands (Parton 1978), which we recently adapted for semiarid shrublands (Schlaepfer and others 2012a; Bradford and others 2014b). SOILWAT requires input information about weather, vegetation, and soil properties. Weather inputs include daily precipitation, daily maximum and minimum air temperatures, mean monthly relative humidity, mean monthly wind speed, and mean monthly cloud cover.

Vegetation in SOILWAT consists of monthly aboveground plant biomass (total and live), aboveground litter biomass, and root water uptake capacity by depth implemented as transpiration coefficients for each soil layer (Appendix in Supplementary material). We calculated the composition of plant functional types (shrubs, C₃ grasses, and C₄ grasses) for each site in each region from climatic variables and equations in Puelo and Lauenroth (1996). Plant functional type biomass was calculated from a relationship between

precipitation and biomass amount. The growing season length for each functional type (the period of green biomass) was calculated from temperature. Transpiration coefficients, scaled to total soil depth, were estimated from root depth distributions (Schenk and Jackson 2003). Additional detail about the vegetation in SOILWAT can be found in Bradford and others (2014a, b).

We simulated soil water in eight layers (0–5, 5–10, 10–20, 20–30, 30–40, 40–60, 60–80, 80–100 cm). We later aggregated them into 0–30 cm, 30–60 cm, and 60–100 cm layers to simplify presentation. Properties for each soil layer consist of texture (percentage sand, silt, and clay), bulk density, field capacity, and minimum water content. The soil water potential that can no longer sustain transpiration was –3.5 MPa for grasses and –3.9 MPa for shrubs (Sala 1981; Kolb and Sperry 1999). We simulated the water balance in a soil profile in which each layer had a sandy loam texture (58 % sand, 10 % clay, and 32 % silt).

SOILWAT simulates interception by and evaporation from the canopy and litter layer, infiltration into the soil, distribution of infiltrated water among soil layers, and losses by bare-soil evaporation from the upper soil layers and transpiration from each layer. We estimate snowfall, snow accumulation, melt, loss (sublimation and wind redistribution), and snowpack temperature based on the SWAT2K snow module (Neitsch and others 2005; Debele and others 2010). We included hydraulic redistribution, based on the Ryel and others (2002) model. A description of SOILWAT is presented in Parton (1978) and examples of applications can be found in Lauenroth and others (1993), Lauenroth and others (1994), Coffin and Lauenroth (1993), Lauenroth and Bradford (2006, 2011), Schlaepfer and others (2012a, 2012b), and Bradford and others (2014a, 2014b). A corroboration test for the grassland version comparing modeled to observed soil water ($r^2 = 0.66$) can be found in Lauenroth and others (1994). Schlaepfer and others (2012a) have a corroboration test of SOILWAT estimation of seasonal total evapotranspiration and transpiration against field-measured values for a sagebrush ecosystem and a test of the representation of hydraulic redistribution in sagebrush ($r^2 = 0.80$) and daily snow water equivalents at 10 SNOTEL stations (r^2 ranged from 0.12 to 0.89) in SOILWAT. Bradford and others (2014a) contain a corroboration of SOILWAT estimates of daily soil water dynamics at multiple depths compared against field-measured values for a sagebrush ecosystem.

RESULTS

Climates of the Sites

Mean annual precipitation ranged from 260 to 472 mm for the IM sites and from 303 to 471 mm for the Great Plains (GP) (Table 1, Tables A1, A2 in Supplementary material). The percentage of snow to total precipitation varied from 5 to 42 % for the IM sites and from 7 to 20 % for the GP. Mean annual temperatures were almost identical for the two regions, although the coldest site in the GP was almost 1.5 °C below the coldest IM site. Average potential evapotranspiration (PET) was higher for the GP sites than for the IM sites, but the site with the highest PET was in the IM (Table 1, Tables A1, A2 in Supplementary material). The correlation coefficient between monthly precipitation and monthly temperature averaged -0.24 (range -0.71 to 0.25) for the IM sites compared to an average of 0.52 (range 0.40 to 0.61) for the GP sites. The concentration of precipitation in the winter increased with longitude across the IM region ($r = -0.69$; data not shown).

Daily average PET was the lowest in the winter and highest in the summer for sites in both regions and maximum values occurred on approximately July 1 (Figure 1). Average daily precipitation was slightly higher in the winter than the summer for

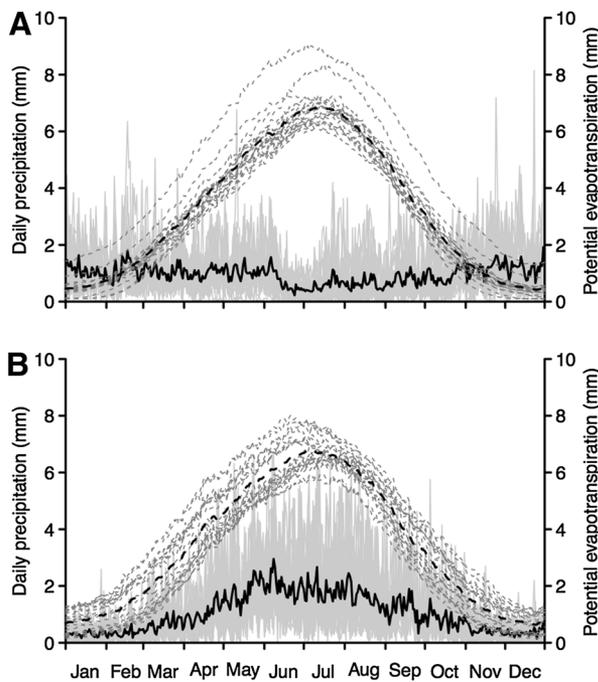


Figure 1. Long-term (30 year) mean daily precipitation and potential evapotranspiration for 20 Intermountain sites (A) and 20 Great Plains sites (B). The *bold black lines* are the means of the sites.

the IM sites. The wettest days occurred between November and April and the driest days were in June (Figure 1A). The GP sites had an opposite pattern (Figure 1B). The wettest days occurred between April and November and the driest days in December and January. Combining the PET and precipitation data illustrated that late fall, winter, and early spring are the wet season for the IM region and late spring, summer, and early fall are the wet season in the GP.

The snow seasons are the same for both regions (November–April), but the amounts of water stored in the snowpack were very different (Figure 2). Snowpack in the IM was greater and much more variable among sites than in the GP. Seasonal maximum snow water equivalent in the IM ranged from near zero to almost 120 mm compared to a range of zero to slightly greater than 20 mm in the GP.

Temporal Dynamics of Soil Water Potential

The simulated temporal pattern of daily average soil water potential in the IM region was a smooth curve with a plateau of high values during the wet season (soil water potential > -1.5 MPa) and a June–October dry period (soil water potential < -1.5 MPa) (Figure 3). The wet period had few fluctuations in soil water potential from day-to-day and the dry period had substantial daily variability especially in the 0–30 cm layer. Much of the dry season daily variability was associated with the North American monsoon. On average, the wet soil period lasted 155 days before and 60 days after the dry season. The dry season was, on average, 150 days.

Daily average soil water potential in the GP peaked in spring and late fall with both a winter and summer dry period (Figure 4). Daily fluctuations were characteristic of all seasons and all depths, although they were less pronounced in the 60–100 cm layer. Although some of the GP sites were influenced by the monsoon, any additional day-to-day fluctuations were lost in those associated with the warm season peak in precipitation experienced by all sites (Figure 1). Because of the high degree of daily fluctuations, the wet and dry soil periods were more difficult to define for the GP sites than they were for the IM sites. In the 0–30 cm layer, the period of wet conditions lasted approximately 100 days in the spring and 50 days in the fall, although the variability among sites was large. It was different for the deeper layers, but the dry periods were equally difficult to identify.

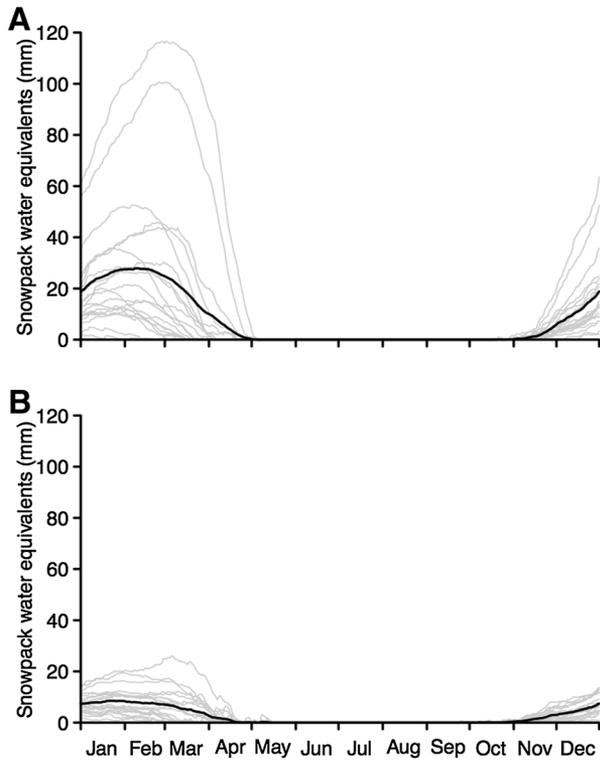


Figure 2. Long-term (30 years) simulated mean daily snow water equivalent in the snowpack for 20 Intermountain sites (A) and 20 Great Plains sites (B). The bold black lines are the means of the sites.

On average, dry soil conditions for the 0-30 cm layer lasted more than 100 days in the summer, but again with huge variability.

We evaluated the distinctiveness of annual patterns of soil water potential by analyzing peaks in the 0-30 cm soil layer. We first converted all soil water potentials to positive numbers and calculated average daily values for each region. We then calculated the first differences ($day_n - day_{n+1}$) for the regional averages (Figure 5). Average daily fluctuations in soil water potential for the IM region were low from November through May and high during the season of low soil water potential (Figures 3, 5). The largest daily differences were caused by drying (negative). By contrast, the average daily differences for the GP region were low only from November through February and high for the remainder of the annual cycle. The differences were evenly divided between drying and wetting.

We also calculated the first differences on a site basis and counted the number of increases. On average, the IM had 74 (SD = 9) and the GP 89 (SD = 14) positive peaks in average daily soil water potential. We used a maximum likelihood model to answer the question: Are the number of peaks that

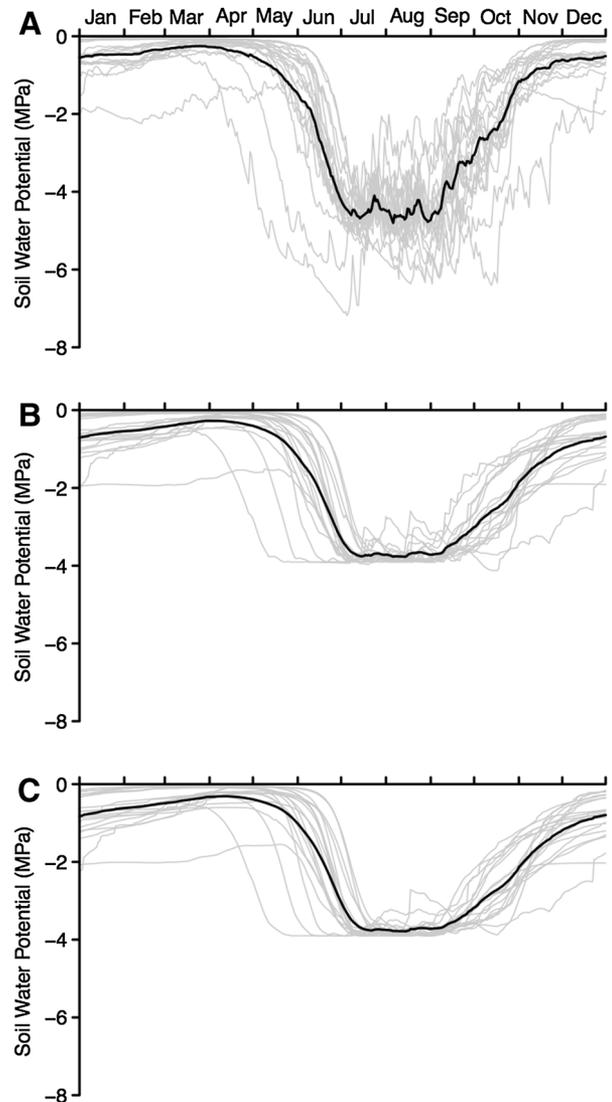


Figure 3. Long-term (30 years) simulated mean daily soil water potential in the 0-30 cm layer (A), 30-60 cm layer (B), and 60-100 cm layer (C) for 20 Intermountain sites. The bold black lines are the means of the sites.

exceeded one standard deviation different between the two regions and can this be used to classify a site correctly into its region? This criterion correctly classified 70 % of the IM sites and 75 % of the GP sites. These results indicated that the GP is a more pulse-dominated soil water potential environment than the IM. This result is further emphasized by examining site and regional averages of total soil water content in the 0-30 cm layer (Figure A1 in Supplementary material).

Evapotranspiration

Maximum average daily evapotranspiration (AET) rates were approximately 4 mm per day in both

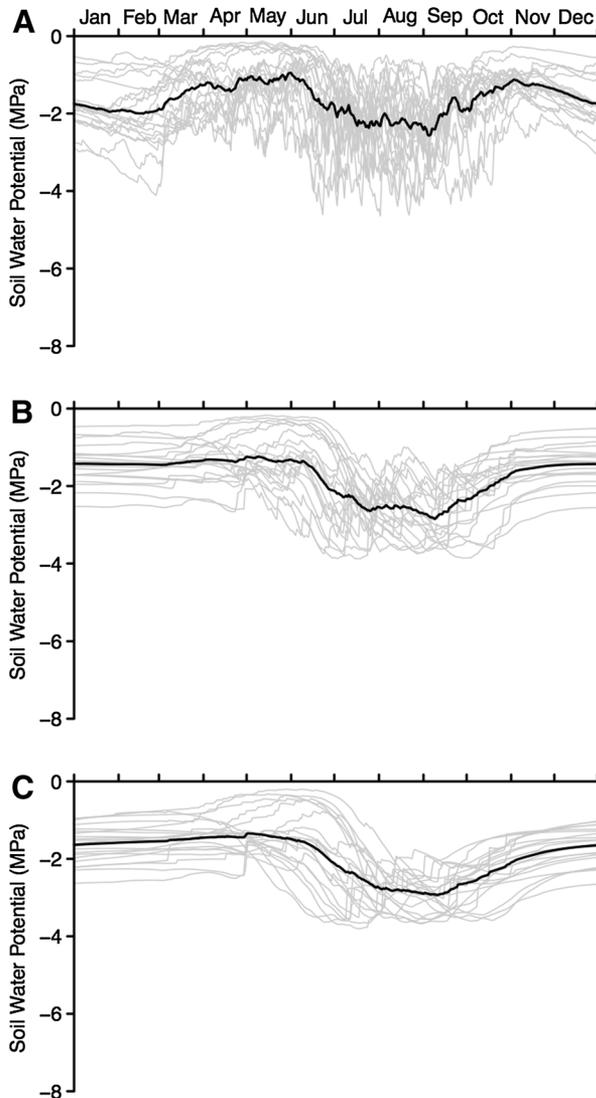


Figure 4. Long-term (30 years) simulated mean daily soil water potential in the 0–30 cm layer (A), 30–60 cm layer (B), and 60–100 cm layer (C) for 20 Great Plains sites. The *bold black lines* are the means of the sites.

regions (Figure 6). AET in the IM region peaked in late May and early June, reaching minimum values in the winter. Greatest site-to-site variability was at the time of peak values with a secondary peak in variability associated with the monsoon. Peak AET rates occurred throughout the summer wet period for the GP, although the absolute peak occurred during the month of June. Minimum values occurred in the winter.

The regional average daily percentage contribution of transpiration to evapotranspiration (T/AET) ranged from 5 to 75 % in the IM and from less than 5 to almost 70 % in the GP (Figure 7). Maximum values were in late May and early June for the IM

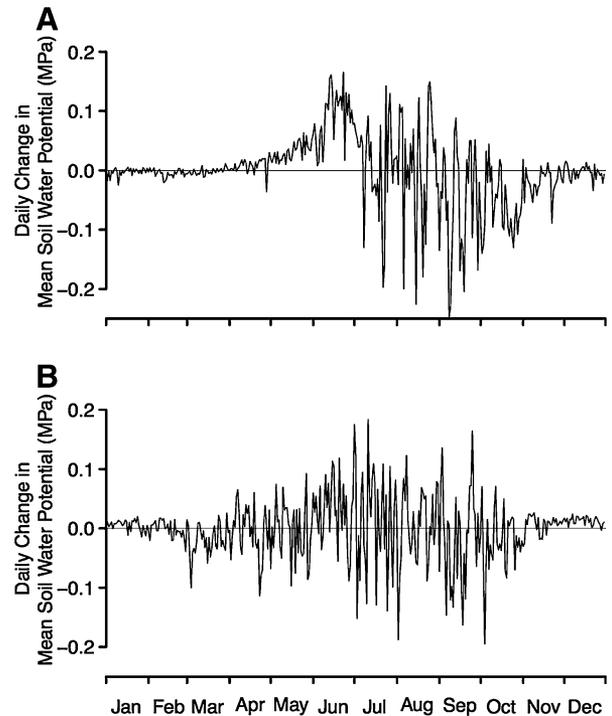


Figure 5. Long-term (30 years) mean daily changes in simulated soil water potential for the 0–30 cm layer for the mean of 20 Intermountain sites (A) and the mean of 20 Great Plains sites (B).

and late June and early July for the GP. As with most of the other water balance components, there was considerable variability within regions.

Water Balance

The percentage of mean annual precipitation that was returned to the atmosphere as AET ranged from 69 to 96 with a mean of 88 for the IM region and from 93 to 98 with a mean of 96 for the GP region (Table 2, Tables A3, A4 in Supplementary material). The lower values for the IM region were related to the amount of cold season precipitation they received and the site with the minimum value (69 %) had a near Mediterranean climate type. Transpiration accounted for an average of 47 % of AET for the IM region and 49 % for the GP, whereas an average of 53 and 51 % of AET was lost to evaporation by sites in the IM and GP, respectively. Average snow water loss was similar between the two regions, but the IM had the widest range of loss values (Table 2, Tables A3, A4 in Supplementary material). The greatest differences between the regions were in the amount of water lost annually to deep drainage beyond the rooting zone (Table 2, Tables A3, A4 in Supplementary

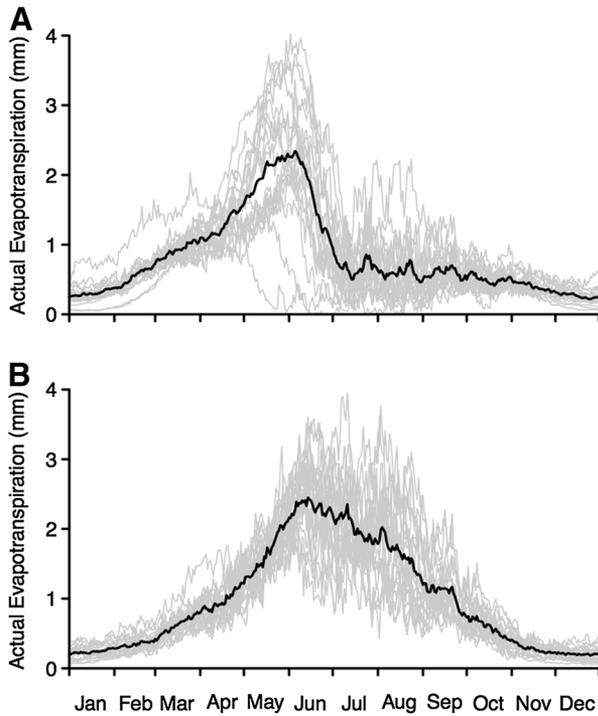


Figure 6. Long-term (30 years) simulated mean daily actual evapotranspiration for 20 Intermountain sites (A) and 20 Great Plains sites (B). The *bold black lines* are the means of the sites.

material). The minimum values for the regions were similar, but the mean and maximum were substantially larger for the IM. The amount of water lost to deep drainage in the IM region was an exponential function of non-growing season (cold season) precipitation ($r^2 = 0.92$; Figure 8). No such strong relationship held for the GP sites ($r^2 = 0.10$).

DISCUSSION

Noy-Meir (1973) conceptualized dry regions as being characterized by pulse water availability of short duration. The dominance of pulse water inputs in arid and semiarid regions has been widely recognized (Sala and Lauenroth 1982; Sala and others 1992; Lauenroth and Bradford 2006; Nagler and others 2007; Reynolds and others 2000; Williams and others 2009). Our results of storage-dominated soil water dynamics in the IM region show clearly that understanding the pulse nature of inputs is not sufficient to accurately represent the temporal patterns of soil water and subsequent ecosystem-scale water balance in all semiarid areas. This result has important implications for vegetation structure and ecosystem processes.

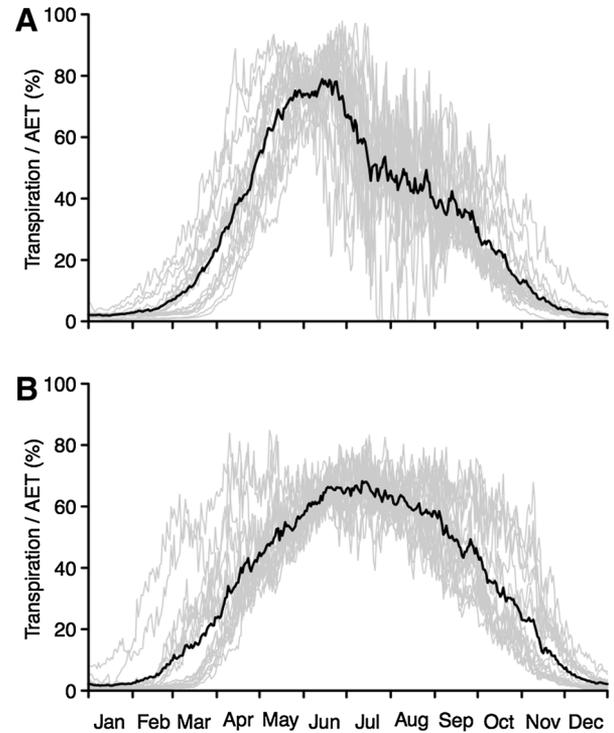


Figure 7. Long-term (30 years) simulated mean daily transpiration/actual evapotranspiration for 20 Intermountain sites (A) and 20 Great Plains sites (B). The *bold black lines* are the means of the sites.

Climates of the Sites

Climatic differences between the IM and GP regions are the driving force for the important ecosystem-scale ecohydrological differences. The key climatic differences are reflected in the correlation between monthly temperature and precipitation (Table 1, Tables A1, A2 in Supplementary material), a measure of the degree of overlap between the warm and the wet seasons (Sala 1997). When overlap is high, as in continental climates such as the Great Plains, precipitation is received when temperature is not only warm and favorable for plant growth but also when evaporative demand of the atmosphere (PET) is highest (Figure 1). If all of the precipitations are received during the warm season, the correlation coefficient approaches 1. The opposite occurs in Mediterranean climates in which the cold season is wet and almost none of the precipitation falls in the warm season. The climates of our IM sites were intermediate between continental and Mediterranean types. Precipitation is received in both the cold and warm seasons with a slight bias toward the cold season (Figure 1). The average correlation coefficient for our IM sites was -0.24. The GP correlation coefficients were all

Table 2. Annual Water Balance for 20 Intermountain and 20 Great Plains Sites

	AET (mm)	$\frac{AET}{MAP}$ (%)	T (mm)	$\frac{T}{AET}$ (%)	E (mm)	$\frac{E}{AET}$ (%)	Snow loss (mm)	Deep loss (mm)
Intermountain								
Mean	300	88	143	47	157	53	31	43
Minimum	242	69	77	29	88	36	4	11
Maximum	417	96	223	64	194	71	60	124
Great Plains								
Mean	364	96	183	49	181	51	30	15
Minimum	291	93	120	40	157	41	15	10
Maximum	453	98	273	59	214	60	45	34

AET annual evapotranspiration, T transpiration, E evaporation

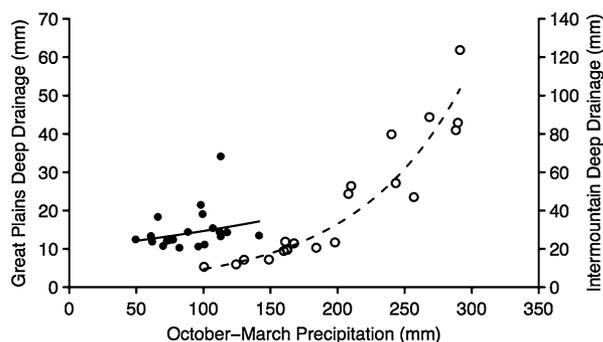


Figure 8. Regression relationships between long-term (30 years) simulated mean daily deep drainage and October–March precipitation for 20 Intermountain sites (dotted line and white points; $r^2 = 0.92$) and 20 Great Plains sites (continuous line and black points; $r^2 = 0.10$).

positive and the average across sites was 0.52. One of the significant effects of the sign and the magnitude of the correlation coefficient is related to the probability of deep soil water storage; this probability increases as the correlation coefficient decreases from 1 to -1 (Dodd and Lauenroth 1997). The correlation coefficient tends to be positive and large in the Great Plains and changes sign and decreases westward through the IM zone (Schlaepfer and others 2012a). Our sites are excellent examples of the relationship between these correlation coefficients and deep-water storage. Our IM sites have a clear annual pattern of soil water storage throughout the profile in the cool season and loss during the warm season, whereas our GP sites have minimal deep soil water storage. We refer to the IM sites as having a storage-dominated soil water regime and the GP sites as having a pulse-dominated regime.

Snowpack reinforces the influence of cool season precipitation on deep soil water storage. Our sites again provide contrasting examples, substantial

snow accumulation, and associated spring soil water recharge in the IM sites and less snow accumulation in the GP (Figure 2). The end of the snow season coincides with a period of rapidly increasing transpiration and evaporation (AET) losses at both sites (Figure 5). In the IM, the end of the snow season also corresponds with the period of the highest soil water potential throughout the profile (Figure 4), which has been documented for other sites in the IM (Sridhar and Nayak 2010; Seager and Vecchi 2010).

Temporal Dynamics of Soil Water Potential

One of the most striking differences between the regions is in the temporal dynamics of soil water potential (Figures 3, 4, and 5). In the storage-dominated IM sites, soil water potential increases in the fall, reaches a peak immediately following snow melt, and dries to a summer minimum of approximately -4 MPa (Figure 3). By contrast, the GP sites have pulse-dominated soil water dynamics throughout most of the annual cycle with soil water potential minima greater than -3 MPa (Figure 4). Day-to-day changes in soil water potential are the result of the interactions between inputs and PET, the force driving outputs back to the atmosphere. The distributions of sizes of inputs are similar for the two regions (Lauenroth and Bradford 2009). The explanation for the differences in the smoothness of the soil water potential curves resides in the strength of the atmospheric demand driving outputs. Because the distribution of IM precipitation is almost without seasonality, the IM wet season is defined by the period when PET is low relative to precipitation inputs (Figures 1A, 3, and Figure A2 in Supplementary material). PET is less than precipitation from November through February. By contrast, at the

regional scale, GP PET is always greater than precipitation and the wet season is at least partially explained by increasing precipitation in the spring (Figures 1B, 4). Drier minimum soil water potentials in the IM compared to the GP can be explained by smaller ratios of precipitation to potential evapotranspiration in the IM during midsummer compared to the GP (Figure A1).

Patterns of Evapotranspiration

Transpiration is constrained to periods with favorable temperature, green biomass, and available water in a soil layer with active roots. Evaporation is limited by the presence of water to be evaporated on plant or litter surfaces, or in the shallowest layers of the soil. Under most conditions, the energy required to change the state of water (indexed by PET) is available in abundance in arid and semiarid regions. Although this is true for both the IM and GP, the distribution through time is constrained by the seasonality of energy inputs, which causes the seasonality in PET (Figure 1). In both regions, PET is low in winter and maximum in summer and AET follows that pattern. In the IM, water available to be lost to the atmosphere is high in the winter and spring, but low winter AET is constrained by snow cover and low PET (Figures 1, 2, 3, 6). When the surface is covered with snow, evaporation is replaced by sublimation.

Insights into the amount of water lost by evapotranspiration, except for a few short-term field results and a few flux tower results, are limited to modeling studies such as ours. Our seasonal patterns of evaporation and transpiration are constrained by available water, energy, and green biomass. Wight and others (1986) used three different models to evaluate AET and produced similar patterns to those we show for the IM. Further, we ran SOILWAT using their input data and produced essentially identical results (not shown). The only results for the GP, besides ours, were produced using SOILWAT and are identical to our results (Sala and others 1992; Lauenroth and Bradford 2006).

The relative contributions of transpiration (T) and evaporation (E) to AET are two of the most important unknowns in dryland and global ecohydrology (Schlaepfer and others 2014). Our results suggest daily average T/AET ratios ranging from 5 to 75 % and annual averages of 47 and 49 % for the IM and GP, respectively. Evaporation accounted for a larger percentage of annual water loss than transpiration with average E/AET ratios for the IM sites of 53 and 51 % for the GP sites (Table 2, Tables A3, A4 in Supplementary

material). Paruelo and Sala (1995) modeled T and E in the Patagonian Steppe, which has many similarities to the IM (Paruelo and others 1995), and found long-term averages of 34 % for T and 56 % for E. Wight and others (1986) modeled growing season (April–September) T and E for 3 years using 3 models for an IM site and reported average T/AET ratios ranging from 42 to 52 %. Prior to this work, no comparisons existed for the GP. Despite their many important differences in seasonality of water inputs and vegetation structure, these two regions have effectively identical partitioning of water loss between transpiration and evaporation.

Water Balance

Our simulation model constrains AET and deep drainage to account for 100 % of the annual precipitation in both the IM and GP (Table 2, Tables A3, A4 in Supplementary material). SOILWAT's exclusion of runoff relies on the assumption that we are representing level uplands and that at any point on our landscapes the net difference between runoff and runoff is zero. Although there is evidence that this is not always the case for either ecosystem type, the available evidence suggests that runoff in these arid and semiarid systems is infrequent (Pierson and others 2001; Wilcox and others 1989). For instance, Wilcox and others (1989) evaluated long-term data from four sagebrush dominated watersheds at the Reynolds Creek Experimental Watershed in southwestern Idaho and found that runoff accounted for less than 2 % of the water budget for all of the watersheds.

AET accounted for an average of 88 and 96 % of precipitation inputs for our IM and GP sites, respectively (Table 2, Tables A3, A4 in Supplementary material). The remainder of precipitation input was accounted for by deep drainage; it represented an average of 12 % of MAP for the IM and 4 % for the GP. Deep drainage in the IM is closely related to the amount of water received as precipitation during the time when PET is low and plants are not active (Figure 7). Paruelo and Sala (1995) found an average of 10 % loss to deep drainage over a 19-year simulation in the Patagonian Steppe. Scanlon and others (2006) synthesized groundwater recharge for global arid and semiarid regions and reported a range of 0.1–5 % of MAP. Our sites were slightly biased toward semiarid climates, rather than arid, which likely accounts for our relatively high values.

Climate Change Implications

Climate change predictions for both the IM and GP are dominated by increases in temperature and net

drying (Karl and others 2009; MacDonald 2010; Overpeck and Udall 2010; Seager and Vecchi 2010). Predictions about precipitation change tend to be less certain, but for the GP include no change or decreases in the spring, summer, and fall and small increases in the winter (Karl and others 2009). Predictions for the IM are similar, but with larger, 10–20%, increases in the winter. The other important prediction for the IM is reduced snowpack and earlier snowmelt (Karl and others 2009). An interesting question with respect to our analysis is: Are climate change predictions likely to increase or decrease the similarity between the ecohydrology of the IM and GP?

Assuming that warming, net drying, and decreased snowpack are the key effects of climate change, soil water availability patterns in the IM are more likely to be influenced by near-term climate change than the GP and those influences may change IM soil water dynamics in the direction of becoming more pulse dominated and less storage dominated. The key water balance processes in the GP currently operate in a high temperature and high evaporative demand environment and water storage from the cool season for use by vegetation in the warm season, either in the form of wet soil or snow, is of limited importance. The IM is almost exactly opposite; the important IM water balance processes occur in a relatively low temperature and low evaporative demand environment with water storage in snow and deep soil playing a key role in spring and early summer soil water availability. The importance of pulse dynamics in the IM may be enhanced by increased temperature, higher evaporative demand, and decreased snowfall, because these changes will result in higher temporal variability in soil water content and longer dry periods during the historical wet soil season (Figure 3). Predicted increases in fall and winter precipitation and predicted decreases in May and June precipitation for the IM would strengthen the cool season precipitation pattern and maintain differences between the IM and GP.

Predicted temperature increases over the next century may make key water balance features of the IM more similar to the GP, promoting a trend toward pulsed soil water patterns and away from seasonal water storage. However, increases in winter precipitation in the IM could have the opposite effect by providing additional water during the cool season. The overall consequences of these potentially offsetting forces for depth and seasonal patterns of plant-available soil water remain unclear and may be non-linear across gradients representing the relative importance of snow

to total precipitation as demonstrated in sagebrush systems (Schlaepfer and others 2012c). Our results suggest that the climatic conditions and resulting seasonal soil water dynamics of these regions are demonstrably divergent and climatic changes would need to be very dramatic, and in the correct direction, to have a high probability of changing the dominant plant type in either the IM or GP. In both cases, the predicted changes seem most likely to remain favorable for the continued success of shrubs in the IM and grasses in the GP.

ACKNOWLEDGMENTS

We thank Kyle Taylor for assistance with the maximum likelihood analysis. The work was made possible by funding from the University of Wyoming, the USDA Forest Service, and the US Department of Interior Geologic Survey. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

REFERENCES

- Bailey HP. 1979. Semi-arid climates: Their definition and distribution. In: Hall AE, Cannell GH, Lawton HW, Eds. *Agriculture in semi-arid environments*. Berlin: Springer-Verlag. p 73–97.
- Bailey HP. 1981. Climatic features of deserts. In: Evans DD, Thames JL, Eds. *Water in desert ecosystems*. Dowden, Hutchinson & Ross: Stroudsburg.
- Bradford JB, Schlaepfer DR, Lauenroth WK. 2014a. Ecohydrology of adjacent sagebrush and lodgepole pine ecosystems: the consequences of climate change and disturbance. *Ecosystems* 17:590–605.
- Bradford JB, Schlaepfer DR, Lauenroth WK, Burke IC. 2014b. Shifts in plant functional types have time-dependent and regionally variable impacts on dryland ecosystem water balance. *J Ecol*. doi:10.1111/1365-2745.12289.
- Coffin DP, Lauenroth WK. 1993. Successional dynamics of a semiarid grassland: effects of texture and disturbance size. *Vegetatio* 110:67–82.
- Debele B, Srinivasan R, Gosain A. 2010. Comparison of process-based and temperature-index snowmelt modeling in SWAT. *Water Resour Manag* 24:1065–88.
- Dodd MB, Lauenroth WK. 1997. The influence of soil texture on the soil water dynamics and vegetation characteristics of a shortgrass steppe ecosystem. *Plant Ecol* 133:13–28.
- Epstein HE, Lauenroth WK, Burke IC, Coffin DP. 1997. Regional productivity patterns of C₃ and C₄ functional types in the Great Plains of the United States. *Ecology* 78:722–31.
- Karl TR, Melillo JM, Peterson TC, Eds. 2009. *Global Climate Change Impacts in the United States*. Cambridge: Cambridge University Press.
- Kolb KJ, Sperry JS. 1999. Transport constraints on water use by the Great Basin shrub, *Artemisia tridentata*. *Plant Cell and Environment* 22:925–35.

- Lauenroth WK, Burke IC. 1995. Great Plains, climate variability. In: Nierenberg WA, Ed. Encyclopedia of environmental biology, Vol. 2. San Diego: Academic Press Inc. p 237–49.
- Lauenroth WK, Urban DL, Coffin DP, Parton WJ, Shugart HH, Kirchner TB, Smith TM. 1993. Modeling vegetation structure–ecosystem process interactions across sites and ecosystems. *Ecological Modelling* 67:49–80.
- Lauenroth WK, Sala OE, Coffin DP, Kirchner TB. 1994. Recruitment of *Bouteloua gracilis* in the shortgrass steppe: a simulation analysis of the role of soil water. *Ecological Applications* 4:741–9.
- Lauenroth WK, Bradford JB. 2006. Ecohydrology and the partitioning AET between transpiration and evaporation in a semiarid steppe. *Ecosystems* 9:756–67.
- Lauenroth WK, Bradford JB. 2009. Ecohydrology of dry regions of the United States- precipitation pulses and intraseasonal drought. *Ecohydrology* 2:173–81.
- Lauenroth WK, Bradford JB. 2011. Ecohydrology of dry regions of the United States- Water balance consequences of small precipitation events. *Ecohydrology* . doi:10.1002/eco.195.
- MacDonald GM. 2010. Water, climate change, and sustainability in the southwest. *Proc Natl Acad Sci* 107:21256–62.
- Nagler PL, Glenn EP, Kim H, Emmerich W, Scott RL, Huxman TE, Huete AR. 2007. Relationship between evapotranspiration and precipitation pulses in a semiarid rangeland estimated by moisture flux towers and MODIS vegetation indices. *J Arid Environ* 70:443–62.
- Neitsch S, Arnold J, Kiniry J, Williams J. 2005. Soil and water assessment tool (SWAT) theoretical documentation, version 2005. Blackland Research Center, Texas Agricultural Experiment Station: Temple, TX.
- Noy-Meir I. 1973. Desert ecosystems: environment and producers. *Annu Rev Ecol Syst* 4:25–41.
- Overpeck J, Udall B. 2010. Dry times ahead. *Science* 328:1642–3.
- Parton WJ. 1978. Abiotic section of ELM. In: Innis GS, Ed. Grassland simulation model. *Ecological Studies* 26, Springer-Verlag: New York.
- Paruelo JM, Sala OE. 1995. Water losses in the Patagonian steppe: a modeling approach. *Ecology* 76:510–20.
- Paruelo JM, Lauenroth WK, Epstein HE, Burke IC, Aguiar MR, Sala OE. 1995. Regional climatic similarities in the temperate zones of North and South America. *J Biogeogr* 22:2689–99.
- Paruelo JM, Lauenroth WK. 1996. Relative abundance of plant functional types in grasslands and shrublands of North America. *Ecol Appl* 6:1212–24.
- Pierson FB, Carlson DH, Spaeth KE. 2001. A process-based hydrology submodel dynamically linked to the plant component of the simulation of production and utilization on rangelands SPUR model. *Ecol Model* 141:241–60.
- Reynolds JF, Kemp PR, Tenhunen JD. 2000. Effects of long-term rainfall variability on evapotranspiration and soil water distribution in the Chihuahuan Desert: a modeling analysis. *Plant Ecol* 150:145–59.
- Ryel R, Caldwell M, Yoder C, Or D, Leffler A. 2002. Hydraulic redistribution in a stand of *Artemisia tridentata*: evaluation of benefits to transpiration assessed with a simulation model. *Oecologia* 130:173–84.
- Sala OE, Lauenroth WK, Gollucio RA. 1997. Semiarid plant functional types in temperate semiarid regions. In: Smith TM, Shugart HH, Woodward FI, Eds. Plant functional types. Cambridge: Cambridge University Press.
- Sala OE, Lauenroth WK. 1982. Small rainfall events: an ecological role in semiarid regions. *Oecologia* 53:301–4.
- Sala OE, Lauenroth WK, Parton WJ, Trlica MJ. 1981. Water status of soil and vegetation in a shortgrass steppe. *Oecologia* 48:327–31.
- Sala OE, Lauenroth WK, Parton WJ. 1992. Long term soil water dynamics in the shortgrass steppe. *Ecology* 73:1175–81.
- Scanlon BR, Keese KE, Flint AL, Flint LE, Gaye CB, Edmunds WM, Simmers I. 2006. Global synthesis of groundwater recharge in semiarid and arid regions. *Hydrol Process* 20:3335–70.
- Schenk HJ, Jackson RB. 2003. Global distribution of root profiles in terrestrial ecosystems. Data set. doi:10.3334/ORNLDAAC/660. <http://www.daac.ornl.gov>. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA.
- Schlaepfer D, Lauenroth WK, Bradford JB. 2012a. Ecohydrological niche of sagebrush ecosystems. *Ecohydrology* 5:453–66.
- Schlaepfer DR, Lauenroth WK, Bradford JB. 2012b. Effects of ecohydrological variables on current and future ranges, local suitability patterns, and model accuracy in big sagebrush. *Ecography* 35:374–84.
- Schlaepfer DR, Lauenroth WK, Bradford JB. 2012c. Consequences of declining snow accumulation for water balance of mid-latitude dry regions. *Glob Change Biol* 18:1988–97.
- Schlaepfer DR, Ewers BE, Shuman BN, Williams DG, Frank JM, Massman WJ, Lauenroth WK. 2014. Terrestrial water fluxes dominated by transpiration: Comment Arising from S. Jasechko and others. *Nature* 496, 347–51 (2013). *Ecosphere* 5:Article 61.
- Seager , Vecchi . 2010. Greenhouse warming and the 21st century hydroclimate of southwestern North America. *Proc Natl Acad Sci* 107:21277–82.
- Sridhar , Nayak . 2010. Implications of climate-driven variability and trends for the hydrologic assessment of the Reynolds Creek Experimental Watershed, Idaho. *J Hydrol* 385:183–202.
- Teeri JA, Stowe LG. 1976. Climatic patterns and the distribution of C₄ grasses in North America. *Oecologia* 23:1–12.
- Walter H. 1973. Vegetation of the Earth. Berlin: Springer-Verlag. 274 pp
- West NE, Young JA. 2000. Intermountain valleys and lower mountain slopes. Chapter 7 In: Barbour MG, Billings WD. North American terrestrial vegetation. Cambridge: Cambridge University Press.
- Wight JR, Hanson CL, Cooley KR. 1986. Modeling evapotranspiration from sagebrush grass rangeland. *J Range Manag* 39:81–5.
- Wilcox BP, Hanson CL, Wight JR, Blackburn WH. 1989. Sagebrush rangeland hydrology and evaluation of the spur hydrology model. *Water Resour Bull* 25:653–66.
- Williams CA, Hanan N, Scholes RJ, Kutsch W. 2009. Complexity in water and carbon dioxide fluxes following rain pulses in an African savanna. *Oecologia* 161:469–80.