# The Influence of Spatial Patterns of Soil Moisture on the Grass and Shrub Responses to a Summer Rainstorm in a Chihuahuan Desert Ecotone

## William T. Pockman[1]* and Eric E. Small[2]

[1]Department of Biology, MSC03 2020, University of New Mexico, Albuquerque, New Mexico 87131-0001, USA; [2]Department of Geological Sciences, University of Colorado—Boulder, Boulder, Colorado 80309-0399, USA

## ABSTRACT

The cycling of surface water, energy, nutrients, and carbon is different between semiarid grassland and shrubland ecosystems. Although differences are evident when grasslands are compared to shrublands, the processes that contribute to this transition are more challenging to document. We evaluate how surface redistribution of precipitation and plant responses to the resulting infiltration patterns could contribute to the changes that occur during the transition from grassland to shrubland. We measured soil water potential under grasses (*Bouteloua eriopoda*), shrubs (*Larrea tridentata*) and bare soil and changes in plant water relations and gas exchange following a 15 mm summer storm in the grassland–shrubland ecotone at the Sevilleta National Wildlife Refuge in central New Mexico USA. Following the storm, soil water potential ($\Psi_s$) increased to 30 cm depth beneath both grass and shrub canopies, with the greatest change observed in the top 15 cm of the soil. The increase in $\Psi_s$ was greater beneath grass canopies than beneath shrub canopies. $\Psi_s$ under bare soil increased only to 5 cm depth. The substantial redistribution of rainfall and different root-

ing depths of the vegetation resulted in high $\Psi_s$ throughout most of the rooting volume of the grasses whereas soil moisture was unchanged throughout a large portion of the shrub rooting volume. Consistent with this pattern, predawn water potential ($\Psi_{PD}$) of grasses increased more than 5 MPa to greater than $-1$ MPa whereas $\Psi_{PD}$ of shrubs increased to $-2.5$ MPa, a change of less than 2 MPa. Transpiration increased roughly linearly with $\Psi_{PD}$ in both grasses and shrubs. In grasses, assimilation was strongly correlated with $\Psi_{PD}$ whereas there was no relationship in shrubs where assimilation showed no significant response to the pulse of soil moisture following the storm. These data show that preferential redistribution of water to grass canopies enhances transpiration and assimilation by grasses following large summer storms. This process may inhibit shrubland expansion at the ecotone during periods without extreme drought.

**Key words:** precipitation pulses; surface hydrology; plant gas exchange; soil moisture; grass–shrub interactions; spatial pattern of soil moisture.

## INTRODUCTION

In the Southwestern U.S., and semiarid environments worldwide, extensive areas of grassland have been replaced by shrubland over the past century (van Vegten 1983; Pelaez and others 1994; Archer

1994; Gill and Burke 1999). This process has been variously attributed to climatic variability and change, grazing, fire management practices, and rising atmospheric $CO_2$ concentration (Neilson 1986; Bahre and Shelton 1993; Archer and others 1995; Huxman and others 2005). Identifying the relative importance of these individual factors is challenging because interactions among them may be strong (Archer 1994). Furthermore, historical records of vegetation change are limited (Buffington and Herbel 1965; Gibbens and others 2005), making it difficult to determine whether woody encroachment has occurred in a continuous but gradual manner or rapidly during intermittent events such as severe drought.

The many structural and functional differences between grasses and shrubs, and the related differences between grassland and shrubland ecosystems, lead to dramatic environmental changes when shrubs replace grasses as the dominant vegetation (Schlesinger and others 1990). In particular, these changes may include modified cycling of surface water, energy, nutrients, and carbon (Abrahams and others 1995; Wilcox 2002; Houghton and others 1999; Pacala and others 2001; Jackson and others 2002; Kurc and Small 2004; Kurc and Small 2007). Although these differences are evident when grasslands are compared with shrublands, the development of these changes during the transition from grassland to shrubland is more difficult to evaluate. In this paper, we document how plants at a grassland–shrubland ecotone use soil water that infiltrated during a typical summer rainfall event. We focus on the ecotone because this portion of the landscape is expected to be the most sensitive to a variety of forcing mechanisms (Peters 2002; Peters and others 2006a). Our goal is to quantify the spatial pattern of infiltration and soil water availability associated with this event and to identify how this pattern controls transpiration and assimilation by grasses and shrubs.

At the Sevilleta National Wildlife Refuge in central New Mexico, USA, large areas of black grama (*Bouteloua eriopoda*) grassland and creosote bush (*Larrea tridentata*) shrubland are separated by a narrow ecotone where the dominant grass and shrub species co-occur. In addition to contrasts in cover, there are several differences between shrub and grass species, such as those at the Sevilleta, that influence water use and carbon fixation in this system in response to precipitation (Huxman and others 2004). First, creosote bush has deeper roots (Kurc and Small 2004), as is typical for woody species (Schenk and Jackson 2002). Second, the evergreen creosote bush can potentially exhibit

photosynthesis and transpiration whenever conditions are favorable whereas the activity of black grama is restricted to the summer months. Third, creosote bush maintains gas exchange at lower soil water potentials ($\Psi_s$; Odening and others 1974; Ogle and Reynolds 2002) than is typical for black grama (for example, Morgan and others 2001). Finally, as is typical of $C_4$ grasses and $C_3$ shrubs, the $C_4$ black grama, exhibits higher maximum photosynthetic rates ($A_{max}$), lower maximum transpiration rates ($E_{max}$) and increased water use efficiency (WUE) compared to the $C_3$ creosote bush (for example, Hamerlynck and others 2000).

The differences between grassland and shrubland, such as those at Sevilleta, are not limited to the specific functional differences between black grama and creosote bush. Organic carbon and nutrients in both grassland and shrubland are concentrated beneath plant canopies relative to the surrounding bare soil (for example, Schlesinger and others 1990). These ''islands of fertility'' are more strongly developed in the shrubland than in the grassland (Schlesinger and others 1996; Kieft and others 1998). There are also important differences in water cycling between these two ecosystems. At the hillslope scale, there is more overland flow in shrublands, leading to soil redistribution and erosion (Abrahams and others 1995; Schlesinger and others 2000). This soil erosion, in conjunction with rain-splash, exposes finer textured soils with lower infiltration capacity in the large interspaces that exist in shrubland. The resulting spatial pattern of infiltration capacity, high under canopies and low in interspaces, leads to focused, deep infiltration beneath shrub canopies (Bhark and Small 2003). Due to the combination of these factors, the spatial distribution of soil and water resources is more heterogeneous in shrubland (for example, Schlesinger and others 1990). In addition, there is greater horizontal redistribution of mineral and organic matter in the shrubland. Whether the transported material is simply redistributed locally or removed entirely is believed to vary with environmental conditions (for example, Ludwig and others 2002; Schlesinger and others 1990).

The well documented biotic and abiotic differences between grassland and shrubland have long been used as a starting point for conceptual models of how herbaceous and woody species interact at the ecotone between the two ecosystems. Walter's two-layer model (1971, 1973) is based on a soil column split into two layers corresponding to the rooting depth of woody and herbaceous plants: (1) an upper-layer from which herbaceous plants can more efficiently extract soil water; and (2) a

lower-layer in which only woody plants have roots, and thus the ability to extract water. Although originally conceived for savanna environments, this model has been applied to mixed assemblages of shrubs and grass (for example, Soriano and Sala 1984). Likewise, the pulse-reserve model (Westoby and Bridges unpublished, cited in Noy-Meir 1973), which relates precipitation pulses to the resulting reserves of carbon, has also been widely applied. In contrast, the Schlesinger and others (1990) model of desertification is focused on horizontal heterogeneities in the distribution of resources: as shrub encroachment proceeds, water and soil nutrients are increasingly concentrated beneath shrub canopies while the intervening areas become more barren. Subsequent models have incorporated additional complexity to better reflect field conditions and to broaden the applicability to diverse systems. The 'threshold-delay' model (Ogle and Reynolds 2004) modifies the two-layer and pulse-reserve models, incorporating threshold-specific responses, delays associated with plant responses and differences among plant functional types (Reynolds and others 2004). To assess the interaction of herbaceous and woody vegetation in a piñon-juniper savanna, Breshears and Barnes' (1999) 'four-compartment' model considered both vertical and horizontal heterogeneity in soil water availability and acquisition by different species.

Data from environments where herbaceous and woody species coexist have been used to assess how accurately these disparate conceptual models describe the actual plant–water interactions that occur. Although many studies have supported the two-layer model, others have noted species and sites that were exceptions (Ogle and Reynolds 2004). For example, at a Chihuahuan desert site, Montaña and others (1995) found that the shrub *Flourensia cernua* and the grass *Hilaria mutica* both responded strongly to an artificial rainfall event that only wetted the top 40 cm of soil, whereas the shrub *L. tridentata* showed little response and presumably was more hydraulically connected to deeper soil. Fewer studies have focused on horizontal heterogeneities of soil moisture, particularly in environments where woody and herbaceous species are mixed. Reid and others (1999) showed that horizontal redistribution of surface water, and the resulting horizontal and vertical variability of soil moisture, is critical to understand plant–water interactions in these areas.

In this study, we document the horizontal and vertical variations of soil water, with respect to the spatial arrangement of grasses and shrubs, before and after a rainfall event. Then, we compare how shrubs and grasses respond to this event, and link the differences in their response to the observed pattern of soil water. Our goal is to answer the following questions. First, is soil water distributed uniformly across the landscape, or does the horizontal redistribution of surface water provide grasses or shrubs access to more soil water? If the latter is true, then conceptual models that explicitly address horizontal heterogeneities (for example, Schlesinger and others 1990; Breshears and Barnes 1999) may be superior to the Walter two-layer model, at least in environments where woody and herbaceous species are not completely intermixed (that is, where bare soil is a significant component of total cover). Second, how does the depth of the wetting front resulting from a summer storm compare to the rooting depths of grasses and shrubs? It is expected that the wetting front is shallow and therefore does not propagate below the root zone of grasses (for example, Sala and others 1992). If this is the case, then shrubs do not have exclusive access to any portion of the soil moisture resulting from summer rainfall. And third, do shrubs utilize the soil moisture associated with a summer storm as rapidly and as efficiently as grasses, or is their response less dramatic? Shrubs might be less responsive because (1) their roots are deep relative to summertime wetting fronts (for example, Ehleringer and others 1991; Montaña and others 1995) or (2) their physiological responses sometimes lag behind increases in water availability (Yan and others 2000). Finally, we sought to evaluate the utility of the various existing conceptual models in light of the patterns of infiltration and plant responses that we observed.

## STUDY AREA AND THE GRASS–SHRUB ECOTONE

### Site Description

This study was conducted at the McKenzie Flats area of the Sevilleta National Wildlife Refuge in central New Mexico USA (34°20′N 106°45′W). The grassland–shrubland ecotone is narrow at McKenzie Flats: end-member grassland and shrubland ecosystems exist within 2 km of each other in this area. The end-member grassland is dominated by black grama (*B. eriopoda*) and has 50–60% canopy cover (Figure 1), with individual plants and the bare soil interspaces of equal size. The microtopography associated with each grass clump isolates adjacent interspaces. In contrast, the end-member shrubland is dominated by creosote bush (*L. tridentata*) with approximately 25% plant cover

(Figure 1) and interspaces are topographically interconnected, allowing for lateral redistribution of surface water and the materials it transports (Abrahams and others 1995; Schlesinger and others 2000; Bedford and Small 2008). Rooting distributions measured for each species at the site showed that 90% of the grass roots were above 20 cm depth whereas the peak root density for the shrubs was at 30 cm with roots extending to at least 60 cm (Kurc and Small 2004). In this study, we collected data from the middle of the ecotone where the dominant species from the end-member ecosystems co-occur, roughly 1 km from either of the end-member ecosystems. The spatial arrangement of the grasses and shrubs is described in more detail below. Secondary species include *Bouteloua gracilis* (blue grama), *Hilaria* sp., *Sporobolus* sp., and *Guttierezia sarothrae*, which together cover less than 5% of area. The area has not been grazed by livestock since the 1970s.

The study area is located in the northeast portion of the Sevilleta, where the elevation is approximately 1500 m. In this area, the active stream channel network has not incised McKenzie Flats and the surface slope is 1–2%. The soil is a sandy loam with a K-horizon that starts at a depth of 40 cm below the surface. A water retention curve for soil from the site, based on both field and laboratory measurements (Bhark 2002), is shown in Figure 2. As expected for a sandy loam soil, volumetric water content ($\theta$) changes by only 10% when $\Psi_s$ varies between $-0.1$ and $-10$ MPa. In contrast, nearly the entire range of $\theta$ exists when $\Psi_s$ varies from $-0.1$ MPa to saturation.
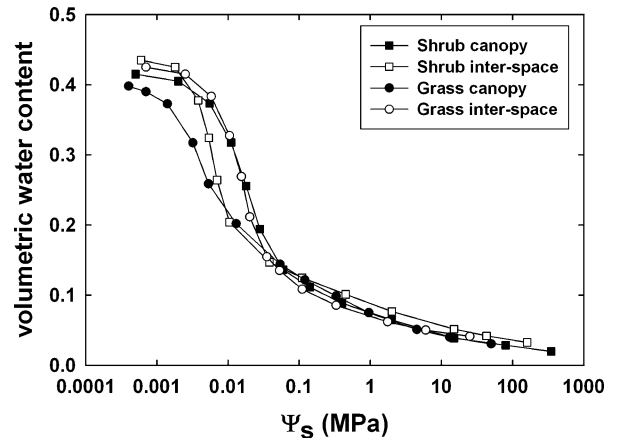
**Figure 2.** Soil moisture release curves for soil under canopy and bare soil inter-space in the grassland and shrubland end members within 1 km of the study site.

## Climate and Storm Details

Annual precipitation at the study site is 230 mm, with roughly half of the annual precipitation occurring during the summer monsoon (July–September). Data were collected before and after a 15 mm rain storm on 16 September 2001 (day 259). From June through mid-September of 2001, there was 115 mm of precipitation at the site, roughly 10% above the average for this period. There was a large, multi-day event around day 225 (35 mm), followed by a 12 mm event on day 240. Then, there was no rainfall for 20 days before or for 15 days after this event. So, although the soil had been largely drying over the days prior to the event, the monsoon of 2001 was not a drought
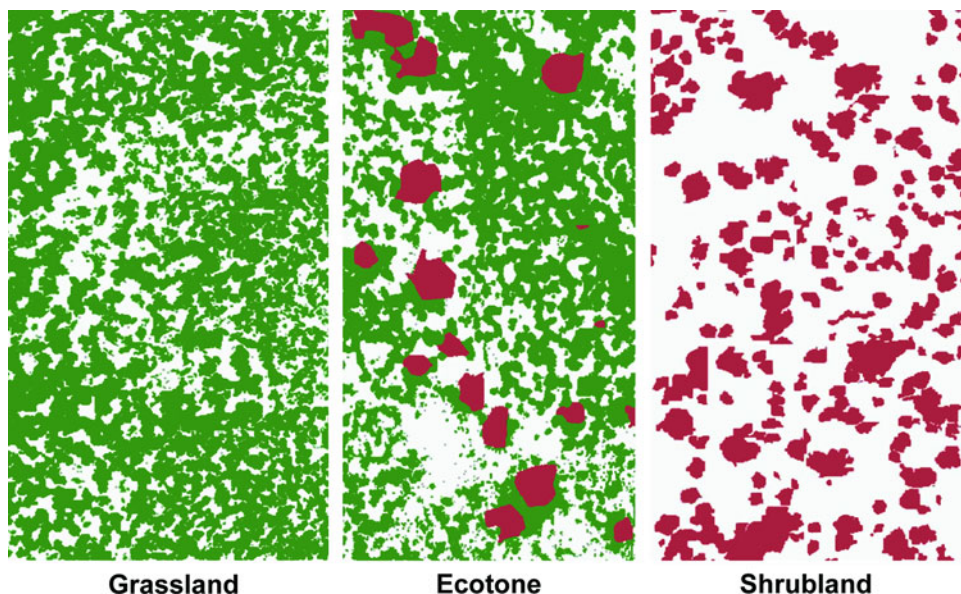
**Figure 1.** Digitized photographs, taken from 6 m above the soil surface, of grassland, ecotone and shrubland vegetation communities in the Five Points area of the Sevilleta National Wildlife Refuge. *Light* (or *green*) and *dark* (or *red*) shaded areas denote grass and shrub canopy, respectively, whereas *white* space denotes bare soil interspace. Each image is 15 × 25 m (Color figure online).

Grassland          Ecotone          Shrubland

year. Although cooling temperatures in the fall can initiate grass senescence during September and October in some years, in 2001 temperatures remained high throughout the study period before cooling in mid-October.

The rainstorm on DoY 259 was large compared to most storms at the site and in other semiarid environments (Sala and others 1992). The daily rainfall total on DoY 259 (15 mm) was greater than that observed on 90% of the rainy days during the monsoon season at the Sevilleta site (Figure 3). Although large storms do not occur frequently, a disproportionately large fraction of the total rainfall accumulates during these storms: 40% of the total rainfall accumulates on days when rainfall is 15 mm or greater. The DoY 259 rainfall event lasted roughly 20 min, with an average intensity of about 40 mm/h. More than 75% of the rainfall recorded throughout the Sevilleta occurs at intensities lower than 40 mm/h. Although the DoY 259 storm was both large and intense, there was no runoff in the first-order channels below McKenzie Flats during or after the event. However, we did observe substantial ponding and surface redistribution at a length scale of approximately 10 m.

## Ecotone Geometry

We now describe the spatial distribution of shrubs and grasses at and around the ecotone (compare Peters and others 2006a–c for additional description). The ecotone is composed of a matrix of grassland with interspersed shrub patches. The area and number of individuals in each shrub patch vary

with distance from the grassland and shrubland end members. On the grassland side of the ecotone, individual shrubs, the smallest patch possible, exist within the grass matrix (Peters and others 2006a, b). The size of shrub patches and the number of shrubs that they contain increase from the grassland to shrubland. On the shrubland side of the ecotone, only discontinuous bands of grasses exist amidst the nearly continuous shrub cover and large bare soil interspaces (Peters and others 2006c).

We collected data from the geographic middle of the ecotone. In this area, the shrub patches typically include between 3 and 10 individuals and cover an area of 10–50 m$^2$. The spacing between adjacent shrub patches is about 10 m or greater. The interspaces within the shrub patches are large ($\sim$1 m), as in the shrubland (Figure 1), consisting primarily of bare soil. The interspaces in the grassland matrix are much smaller ($\sim$20 cm) and more disconnected. Few of the grass clumps at the ecotone are found beneath or directly adjacent to shrub canopies, and we estimate that less than 5% of the total grass biomass is found in these locations. Instead, adjacent shrubs and grass clumps are typically separated by large interspaces ($>$1 m), similar to those found within the shrub patches or end-member ecosystem (Figure 1). Even where some grasses do occur under the shrub canopy, it is rare for these grasses to surround the shrub base leaving the sub-canopy soil connected to the bare soil interspaces that appear around shrubs in the ecotone. These large interspaces define a boundary between the grasses and shrubs at the ecotone (Peters and others 2006a). Given this spatial arrangement, it is difficult to apply the Walter two-layer model at the grass–shrub ecotone. Nearly all of the grasses at the ecotone are spatially isolated from the shrubs, given that the lateral spread of plants like the shrubs and grasses studied here is typically 2 m or less (Schenk and Jackson 2002). However, horizontal redistribution of surface water may still yield strong interactions between these spatially disparate woody and herbaceous plants (for example, Breshears and Barnes 1999; Schlesinger and others 1990).

## METHODS

### Plot Selection, Design, and Installation

We collected plant and soil data from six 10 × 15 m plots established for a manipulative study of the effects of drought on the ecotone between grassland and shrubland. The data for the present study were collected after plot installation was complete but before any treatment had
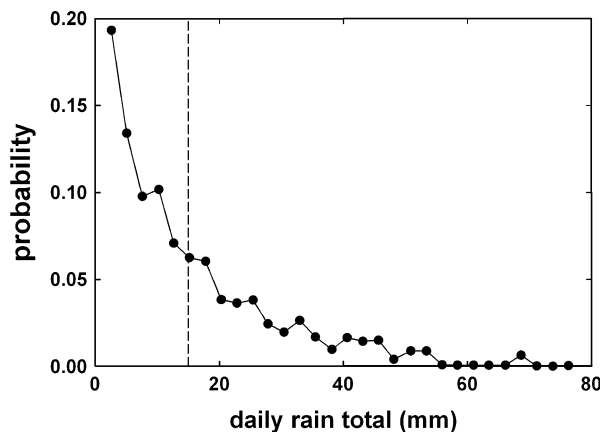


**Figure 3.** Probability density function for daily rainfall total on days with rain, based on the Socorro, NM (32 km from the study site) rainfall record from 1950 to 1990. The *dashed line* marks the rainfall total delivered in the storm on day 259.

commenced. The location of each plot was randomly selected, with the constraint that the plot must contain three or more shrubs. Without this constraint, the plots would have contained few or no shrubs, given that the grassland matrix covers 80–90% of the vegetated area at the geographic center of the ecotone. Therefore, our plots do not represent the average ecotone, but instead are centered on the boundary where shrub patches meet the grass matrix. An additional constraint was that the distance between plots could not result in prohibitive cable lengths to dataloggers.

After plot selection, plot edges were trenched to a depth of 1 m using a trencher (Ditch Witch Model 3700, Charles Machine Works, Perry OK, USA), the trench was lined with a double layer of heavy plastic sheeting and backfilled to prevent lateral movement of sub-surface water into or out of the plots. During trenching, plywood boards were used to distribute the weight of the trencher and prevent damage to the surface of the plot. Since the inception of the study, all work on the plots has been completed from transportable scaffold planks suspended above the plots, to prevent alteration of the soil surface and vegetation. After trenching, galvanized sheet metal was inserted along the plot boundary to prevent water from moving onto the plots from the areas impacted by foot traffic around the plots.

## Soil Water Potential

To assess variations in soil water content and potential with depth under the different cover types present (grass canopy, shrub canopy, and bare soil interspace), we made automated measurements of soil water potential ($\Psi_s$) using ceramic Heat Dissipation Sensors (HDS; model 229-L, Campbell Scientific, Logan Utah USA) and stainless steel screen caged thermocouple psychrometers (TCP; model PST-55-30, Wescor, Logan Utah USA). The HDS sensors were measured every hour by a datalogger (model CR10X, Campbell Scientific Logan UT USA). The HDS sensors were individually calibrated under saturated and air dry conditions (Bristow and others 1993; Reece 1996). These sensors have limited sensitivity under very dry conditions. We assigned a value of −7 MPa to all HDS readings equal to or lower than that value. The TCP sensors were individually calibrated in salt solutions at 25°C (Brown and Bartos 1982) before installation and, once installed, were measured every 6 h using a datalogger (model CR7X or CR7XL, Campbell Scientific). For this study, we used TCP data collected daily at 0600 h, when the

near surface temperature gradients that can influence the interpretation of psychrometer data are minimized.

Soil moisture sensors (HDS and TCP) were installed in vertical profiles under each cover type (see below). For each vertical profile, a hand auger was used to dig a hole 15 cm in diameter to a depth of roughly 70 cm. Sensors were then installed in holes parallel to the soil surface on the uphill side of the augered hole. The HDS sensors, which are more responsive at water potentials near zero, were installed at depths of 5 and 15 cm. Contact with surrounding soil was established by using damp soil, excavated from the same depth and cover type of the plot, to completely fill the installation hole. The TCP sensors were installed at depths of 15, 30, 45, and 60 cm, with the minimum depth determined by the sensitivity of these sensors to temperature gradients in shallower soils. The sensor head was installed in a horizontal passage, 5–10 cm in length, drilled parallel to the soil surface into the wall of the hole. At least 1 m of the sensor cable was buried several cm below the sensor depth to minimize thermal gradients caused by heat transfer along the cable from the surface, and to eliminate water traveling along the sensor cable from the surface to the sensor head. HDS and TCP data from 15 cm depth were linearly related (HDS = 1.4411*TCP −0.6478, $r^2 = 0.86$) for values greater than −7 MPa. Under the wettest conditions, HDS sensors were more sensitive to changes in soil water potential whereas TCP sensors could differentiate between low water potentials after HDS output had reached a minimum.

In each plot, the vertical profiles of $\Psi_s$ sensors were installed at three locations: beneath a shrub, beneath a grass canopy, and beneath an interspace. In total, $\Psi_s$ was measured at 90 locations across the six plots. These locations were selected randomly, with three constraints. First, all points had to be within the range of $\Psi_s$ probe cable leads and datalogger locations. Second, locations within 1.5 m of the bottom and sides of the plots and within 3 m of the top of the plots were excluded to minimize the effects of trenching and eliminate the effects of no surface water redistribution from above the plots. Third, only particular locations, relative to the boundary of shrub patches, were determined to be acceptable. Only shrubs within patches of 3 or more individuals were selected. Only grasses within 2–5 m of the selected shrub patch were selected for grass soil probes. Interspace $\Psi_s$ probes were located beneath the bare soil that exists between shrub patches and the grass matrix.

As described below, plant water potential and gas exchange data were collected from three grasses and three shrubs in each plot, located less than 2 m from the profiles measured for soil water potential. Some shrub roots may exist beneath grass canopies that are 2–5 m from shrubs (for example, Breshears and Barnes 1999). However, it is unlikely that shrub roots exist within the top 30 cm of the soil at these locations, given that the grass root density is high to this depth. In the discussion, we address the potential role of shrub roots at depths greater than 30 cm below grasses. Given this sampling design, our data collection provides no information about the grass matrix far removed from shrub patches or the limited grass cover that exists beneath shrubs. Instead, we have focused on the plants and soil at the boundaries of shrub patches and the surrounding grass matrix. Quantifying the plant–water interactions at these locations is critical to understand how the shrub and grass patches within the ecotone expand or contract.

## Estimating Soil Water Content

Our sensors measure $\Psi_s$ but not volumetric water content ($\theta$) at the study site. However, changes in $\theta$ are important for the goals of our study. Calculating $\theta$ from $\Psi_s$ for wet soils ($\Psi_s > 1$ MPa) is not possible: the uncertainty of $\Psi_s$ is large ($\sim$0.2 MPa) relative to changes in $\theta$. Therefore, we do not calculate $\theta$, but simply refer to the water retention curve (Figure 2) to assess when the observed changes in $\Psi_s$ indicate a large change in water content.

## Plant Water Potential

To assess changes in plant water status before and after the storm, we measured plant water potential using a Scholander pressure chamber (Turner 1987) at predawn ($\Psi_{PD}$; 1 h preceding sunrise) and midday ($\Psi_{MD}$; solar noon $\pm$1 h). At each sampling time, we collected small terminal twigs (shrubs) or stems (grasses) from three individuals in each of the six plots. Samples were immediately placed in small plastic bags with a damp paper towel to minimize subsequent evaporation from leaf tissues and were measured within 30 min of collection at predawn and within 10 min of collection at midday.

## Plant Gas Exchange

Leaf level assimilation and transpiration were measured at midday with a LI-6400 open path gas exchange system (Li-Cor Inc, Lincoln, Nebraska, USA), using the $CO_2$ mixer to maintain a reference cell $CO_2$ concentration of 400 ppm (yielding sample concentrations near ambient), standard leaf chamber oriented toward the sun, and chamber temperature and relative humidity tracking ambient conditions. We measured three leaves on each of three individuals of grass and shrub in each of the six study plots. Leaves were harvested when the measurement was complete and actual leaf areas were determined after drying in the laboratory using a regression between leaf area and leaf dry weight constructed using samples from the site for shrub ($y = 90.449x - 0.4036$, $R^2 = 0.998$) and for grass ($y = 110.16x + 1.0285$, $R^2 = 0.847$). Transpiration and assimilation were recalculated using the actual leaf area in the cuvette during the measurement.

## Statistical Analyses

Longitudinal analyses of the response of soil water content under different cover types and the responses of gas exchange and water potential of grasses and shrubs following the rainfall event were performed using mixed general linear models with repeated measures (Proc Mixed, SAS 8e, SAS Institute, Cary NC). Specifically, we tested predawn and midday plant water potential of *B. eriopoda* and *L. tridentata* from 2 days before the storm through day 15. Similarly, transpiration and assimilation measurements from the same individuals were compared between vegetation types throughout the same period. Soil water potential data from each sensor type and depth were analyzed separately to assess the presence of differences among cover types at each depth.

## RESULTS

### Soil Water Potential and Water Content

Prior to the storm on day 259, $\Psi_s$ was decreasing as the soil dried following 12.5 mm of rain on day 240 (Figure 4). As expected, $\Psi_s$ increased following the rain on day 259, with the magnitude and timing of the wetting and subsequent varying by soil depth and cover type. We calculated the change in $\Psi_s$, $\overline{\Delta\Psi}$, averaged over the 15 days following the storm, relative to the value measured on the day before the storm. This was calculated separately for each soil depth, cover type and sensor type using the equation:c

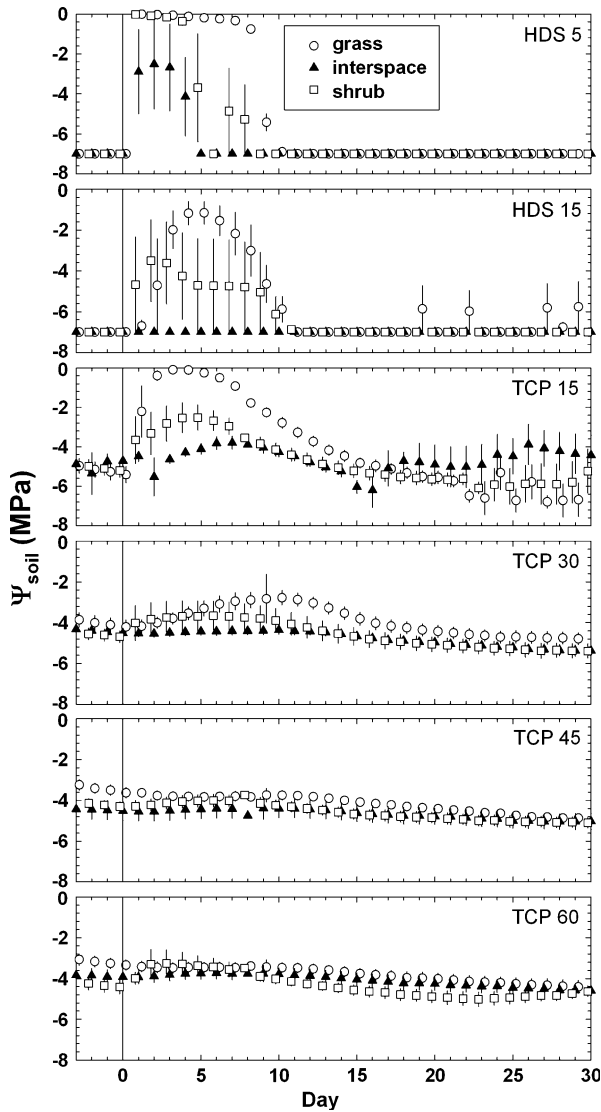$$\overline{\Delta\Psi} = \frac{1}{15} \sum_{d=1,15} \Psi_s^d - \Psi^{d=0}.$$

**Figure 4.** The response of soil water potential ($\Psi_s$) to rainfall (day 0 = day 259, *vertical line*). Each panel shows $\Psi_s$ under grass (*open circle*), shrub (*open square*), and bare soil interspace (*filled triangle*), using either heat dissipation sensors (HDS) or thermocouple psychrometers (TCP) at depths of 5, 15, 30, 45 or 60 cm below the soil surface. *Shrub symbols* are plotted slightly before and *grass symbols* slightly after the actual day value to separate error bars (±1 SE). Each data point and error bar represent the mean of six measurements, one from each plot, made in early morning when soil temperature gradients were small.

We also calculated the maximum increase in $\Psi_s$ over the 15 day interval relative to the pre-storm $\Psi_s$.

As expected for a wetting front propagating downward through the soil, $\Psi_s$ response was larger

and occurred more quickly in surface soil than deeper in the root zone. The maximum change in $\Psi_s$ and the average $\Psi_s$ following the storm were greatest at the 5 cm depth (Figures 4, 5). Both of these changes decreased in magnitude at greater soil depths. This pattern arose because $\Psi_s$ was lowest at the surface prior to the storm and the surface soil became wettest after the storm, with $\Psi_s$ indistinguishable from 0 MPa under shrub and grass canopy. Observed changes in $\Psi_s$ indicated that nearly all of the increase in water content occurred in the upper 15 cm of soil underneath the shrub and, especially, the grass canopies. Smaller increases in $\Psi_s$ were also observed in the upper 5 cm under the bare soil interspaces (Figure 4A, values greater than −2 MPa). No significant response was observed under any cover type at depths greater than 30 cm, with the exception of soil at 60 cm under the shrub canopy (Figure 4F). In this location, $\Psi_s$ increased over the 2 days following the storm and remained significantly
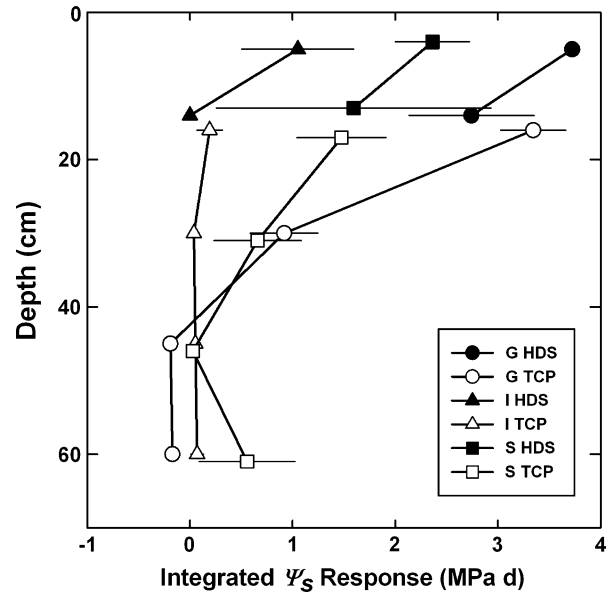


**Figure 5.** Average change in water potential over the 15 day response period relative to the value on the day before the storm as a measure of the integrated soil water potential response to the day 259 storm. Data were calculated as the mean of the integrated deviation of soil water potential at each depth and under each cover type (*G* grass; *S* shrub; *I* interspace) in six plots measured with heat dissipation sensors (HDS) or thermocouple psychrometers (TCP). At 15 cm, HDS and TCP data are plotted at slightly different depths to separate error bars (±1 SE). Similarly, for each depth × sensor type combination, grass data are plotted slightly above the actual depth while shrub data are plotted slightly below the actual depth.

greater than the initial $\Psi_s$ until day 266. The absence of a significant change in $\Psi_s$ at 45 cm (Figure 4E) and the slower response at 30 cm (Figure 4D) under the shrub canopy raises the possibility that the increase in $\Psi_s$ at 60 cm was mediated by redistribution of water via the roots.

The changes in soil water potential following the storm on day 259 also exhibited a clear spatial pattern related to cover type. Overall, increases were greater beneath grass canopy than shrub canopy, whereas shrub canopy changes were greater than beneath interspace (Figures 4, 5). The greatest differences between cover types were observed at 15 cm, in both the TCP and HDS data (Figure 4). At this depth, the maximum change and the average change in $\Psi_s$ were greatest under grass and smallest under interspaces with shrub canopies intermediate in their response. For example, the maximum $\Psi_s$ observed was close to zero for grass, but did not exceed $-2$ MPa for shrub or $-4$ MPa for bare soil (Figure 4). At 30 cm, the maximum $\Psi_s$ was observed beneath grass canopies, although the differences were less than higher in the soil column. At 5 cm, the maximum change in $\Psi_s$ and the maximum $\Psi_s$ observed are similar for grass and shrub canopy. However, the high $\Psi_s$ values near the surface were relatively short lived for the shrub canopies (Figure 4) so the average changes were smaller, perhaps due to more rapid direct evaporation from soil. Below 30 cm, all changes were relatively small so cover type contrasts were negligible.

## Plant Water Potential

Consistent with $\Psi_s$ under the two canopy types, predawn plant water potential ($\Psi_{PD}$) was lower in grasses than in shrubs before the storm on day 259 (Figure 6A). At the same time, midday plant water potential ($\Psi_{MD}$) was similar for shrub and grass, both about $-5.5$ MPa (Figure 6A). This value was the same as $\Psi_{PD}$ in grass and lower than $\Psi_{PD}$ in shrubs, suggesting that transpiration was only occurring in the shrubs. Following the storm, the magnitude of the change in $\Psi_{PD}$ and the absolute values of $\Psi_{PD}$ were greater in grasses than in shrubs. Grass $\Psi_{PD}$ increased to a maximum value of $-1$ MPa, a change of greater than 5 MPa relative to the initial value. In contrast, shrub $\Psi_{PD}$ only increased to $-2.5$ MPa, a change of less than 2 MPa. This contrast in response is consistent with the observed changes in $\Psi_s$ and the different rooting depths of grass and shrub.

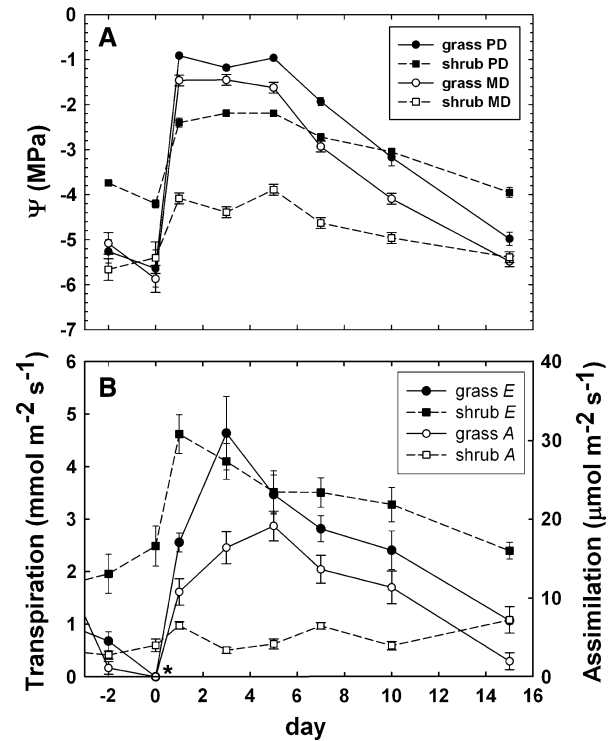The temporal pattern of the $\Psi_{PD}$ response was the same for grass and shrub (Figure 6A). Both



**Figure 6.** Response of **A** grass and shrub water potential at predawn ($\Psi_{PD}$) and midday ($\Psi_{MD}$) and **B** grass and shrub transpiration and assimilation, to rainfall (day 0 = day 259). Gas exchange measurements were made on day 0 before a convective storm developed in late afternoon but were not possible in grasses because of limited availability of suitable leaves (see text). The reduced number of leaves measured exhibited very low rates of transpiration and assimilation (*).

achieved maximum observed $\Psi_{PD}$ values on the first day after the storm. Values remained elevated above pre-storm values at least through day 10, only returning to pre-storm values on day 15. After the storm, $\Psi_{PD}$ for grass was higher than that for shrubs, again consistent with the observed $\Psi_s$ time series for different cover types. The $\Psi_{MD}$ response was greater for grass than shrub but the duration of the increase is similar for the two plant types. Values of $\Psi_{MD}$ remained elevated through day 7, returning to the pre-storm values by day 10.

## Plant Gas Exchange

Prior to the storm, shrubs were transpiring at approximately 2 mmol m$^{-2}$ s$^{-1}$ whereas grass transpiration was less than 1 mmol m$^{-2}$ s$^{-1}$ (Figure 6B). On the day of the storm, many grass leaves were curled and somewhat yellowed, making it difficult to locate leaves for gas exchange measurement; measurements of even the greenest leaves showed very little activity. Among grasses,

the rapid increase in transpiration one and three days after the storm was primarily the result of the recovery of these curled leaves, indicating that their condition reflected the low water potentials of the plants rather than senescence. During the 10 day interval when $\Psi_s$ and $\Psi_{PD}$ were elevated relative to pre-storm values, the transpiration rates from grasses and shrubs were very similar, both 3–5 mmol m$^{-2}$ s$^{-1}$. On the first day following the storm, transpiration from grass was slightly less than the maximum values observed subsequently. Elevated transpiration, relative to the pre-storm period, lasted through and including the sampling on day 10, similar to that for both $\Psi_s$ and $\Psi_{PD}$. By day 15, transpiration from both plant types was back to the initial pre-storm values. Overall, the shrub transpiration response to the storm was

smaller than for the grasses, increasing by a factor of 2 while grass transpiration increased fivefold.

Overall, the grass assimilation response to the rainfall event far exceeded that of the shrubs (Figure 6B). Prior to the storm, assimilation was greater for shrubs than grass, almost 3 and about 1 μmol m$^{-2}$ s$^{-1}$. Over the 5 days following the storm, grass assimilation increased day-by-day to nearly 20 μmol m$^{-2}$ s$^{-1}$. Then, grass assimilation decreased over the next 10 days to the pre-storm value. In contrast, shrub assimilation reached its maximum value on day 1, but the value was only 6.5 μmol m$^{-2}$ s$^{-1}$. Over the following 15 days, shrub assimilation varied between this value and that observed pre-storm. After the period with elevated $\Psi_s$ and $\Psi_{PD}$, the shrub assimilation values were again higher than for grass, as was the case before the storm.

Transpiration increased roughly linearly with $\Psi_{PD}$ for both grasses and shrubs (Figure 7A). The scatter around the best fit line is similar ($R^2$ is 0.82 and 0.76 for grass and shrub, respectively, $P < 0.01$ for both). The slope of the relationship is somewhat greater for shrub than grass, 0.96 and 0.68, respectively. Assuming that we can extrapolate this relationship beyond the data, then we can make two observations. First, if infiltration patterns resulted in similar water potential in shrubs and grasses, we would expect that peak transpiration rates following the storm would be greater in the shrubs than in the grasses. Second, we would expect both grasses and shrubs to cease transpiring at $\Psi_{PD}$ of roughly −6.5 MPa. Assimilation increased linearly with $\Psi_{PD}$ for grasses (Figure 7B, $R^2 = 0.87$ and $P < 0.001$) whereas there was no significant relationship between assimilation and $\Psi_{PD}$ for shrubs ($P = 0.99$).
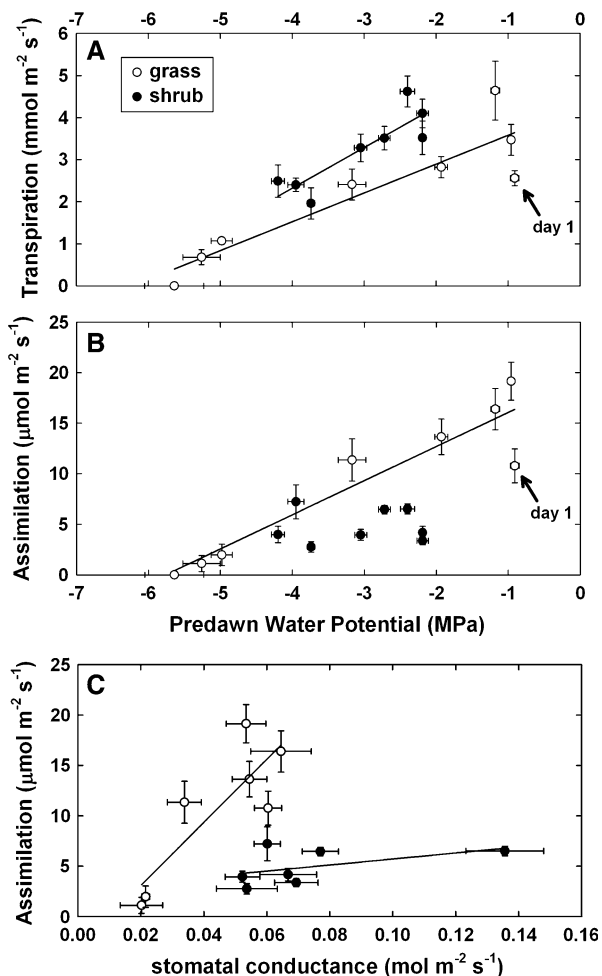
## DISCUSSION

### Soil Moisture Dynamics Following Precipitation Pulse

One of the primary goals of our study was to determine whether the distribution of soil water after a relatively large summer storm was uniform or if horizontal redistribution via overland flow yielded wetter soil beneath plant canopies. Although, the data collected do not directly show the importance of this process during the smaller storms that occur more frequently in this system, our results clearly show that horizontal redistribution from this large storm led to enhanced soil water potential under plant canopies, with the greatest increases observed beneath grass clumps



Figure 7. Grass and shrub transpiration (**A**) and assimilation (**B**) expressed as a function of predawn water potential ($\Psi_{PD}$) during the response to a single summer storm. **C** shows assimilation of grasses and shrubs as a function of stomatal conductance ($g_s$) during the same response period.

(Figures 4, 5). Infiltration increased $\Psi_s$ consistently and substantially in the top 15 cm of the soil column. Even at 30 cm depth, notable changes in $\Psi_s$ were only observed at some locations. The increases in $\Psi_s$ at greater depths were less than 1 MPa, which represents a very small change in water content given the low starting $\Psi_s$ and the very low slope of the WRC at these potentials (Figure 2). In the top 20 cm of the soil, the increase in $\Psi_s$ differed dramatically between cover types. The increase in $\Psi_s$ beneath grass canopies was much greater in magnitude and duration than beneath shrub canopies, particularly at a depth of approximately 15 cm. Beneath bare soil, the increase in $\Psi_s$ was extremely limited relative to that observed beneath either grass or shrub canopy. This is expected given the differences in micro-topography, soil texture, and soil structure that exist between plant canopies and interspaces at this field site (Bhark and Small 2003; Bedford and Small 2008) and in similar semiarid environments (for example, Dunkerley 2002).

The observed patch-type differences in $\Psi_s$, and therefore in the amount of water that infiltrated, are the result of horizontal redistribution of surface water during and soon after the storm. Our observations during the storm suggest that runoff was generated within shrub patches and then transferred to adjacent grass covered areas, where the soil micro-topography and grass clumps trapped the water and it eventually infiltrated. We refer to this process as preferential redistribution, which has been observed in other semiarid environments (for example, Reid and others 1999). We have observed this same process in other storms. The water is redistributed across the soil surface over distances of meters and is directed primarily by the local micro-topography. Therefore, the surface redistribution is not simply unidirectional, down the relatively uniform slope that exists across the study site.

Our second goal was to compare the depth of infiltration under grass and shrub canopies with the rooting profiles of these functional types. The water potential response of both grasses and shrubs demonstrates that the lateral redistribution of surface water and associated horizontal variability of $\Psi_s$ affects how much water these two types of plants were able to access following the storm. The $\Psi_{PD}$ of grasses increased to −1 MPa after the storm, similar to the $\Psi_s$ measured beneath grass canopies over the depth interval in which grass roots are most dense. The same was observed for shrubs: the $\Psi_{PD}$ of shrubs increased to −2.5 MPa, which is equivalent to the highest $\Psi_s$ observed beneath

shrubs (at 15 cm), excluding the 5 cm surface layer where shrub roots are largely absent. A large fraction of the shrub roots were below the wetting front observed during the storm. However, shrub plant water potentials did not reflect the more negative $\Psi_s$ observed in the lower portion of the shrub's root zone during the 15 day post-storm period. This result suggests that the water potentials of both grasses and shrubs are tightly tied to the water potential of the soil beneath each cover type, given the spatial distribution of plants at the ecotone. We expect that this result would not be as straightforward if the two plant types were intermingled or congregated in patches that are small relative to the length scale of lateral root spreading. Our results do not show that shrubs never extract soil water from beneath grass canopies, or vice versa, but that the plants are responding most strongly to $\Psi_s$ beneath their own canopy type.

Our finding that soil wetting from a large rainfall event was restricted to the top 30 cm of soil is consistent with the results of previous studies in adjacent grassland and shrubland ecosystem at Sevilleta (Kurc and Small 2004, 2007). Across the transition from shrubland to grassland, soil depth increases somewhat, however, we are not able to assess the effect of this change based on our data from a single storm at one point along the transition. Under extremely wet conditions, for example a series of large storms, we might expect soil wetting at our study site to extend to greater depth but without additional data any estimate of the increase in shrub response associated with this rare phenomena would be purely speculative.

Our third goal was to link the observed patterns of infiltration and plant water status to the transpiration and assimilation following the summer storm. The transpiration data show that the lateral redistribution of surface water and the resulting horizontal variability of $\Psi_s$ played a fundamental role in controlling how the shrubs and grasses were able to use water following the storm. Consistent with the patterns observed in previous studies (Davis and Mooney 1985; Bassirirad and others 1999), the shrubs were transpiring before the rainfall event, and continued to transpire once $\Psi_{PD}$ and $\Psi_s$ values returned to pre-storm values on day 15. In contrast, measurable grass transpiration only occurred during the period with elevated $\Psi_{PD}$ and $\Psi_s$. During the period when $\Psi_{PD}$ and $\Psi_s$ were higher than the pre and post-storm values, grass and shrub transpiration were equal on a per leaf area basis. The transpiration rates were equal because of the preferential redistribution of surface water to grass canopies, which yielded higher $\Psi_s$

beneath grass canopies and higher grass water potential. If the $\Psi_s$ and $\Psi_{PD}$ of grasses only increased to the values observed in the shrub patches, it is likely that grass transpiration would have been lower than shrub transpiration (Figure 7). This is demonstrated by the conditions observed on day 10: $\Psi_s$ and $\Psi_{PD}$ of grasses and shrubs were very similar and grass transpiration was significantly less.

The grass assimilation response to the rainfall event was more rapid and dramatic than the shrub response. Integrated throughout the post-storm period, the grasses fixed 2.5 times as much carbon as the shrubs, on a per leaf area basis. The grass–shrub difference was greatest 5 days after the storm, when grass assimilation was higher by a factor of five, a response similar to that observed under similar conditions in *Hilaria jamesii* in the Great Basin (Schwinning and others 2002). The assimilation by grasses was higher than that by shrubs for two reasons. First, as expected for $C_4$ grasses, assimilation was faster at a given $\Psi_{PD}$, at least for $\Psi_{PD}$ greater than $-3$ MPa (Figure 7). Second, the preferential surface water redistribution to grass patches was critical. The extra water that infiltrated beneath grass canopies lead to higher values of $\Psi_s$ and $\Psi_{PD}$, which in turn allowed for more rapid assimilation by grasses. If grass $\Psi_s$ and $\Psi_{PD}$ had only increased to the values observed in shrub patches ($-2.5$ MPa), then the total assimilation by grasses during the post-storm interval would have been roughly half of that measured, based on the observed relationship between grass assimilation and $\Psi_{PD}$. Therefore, in the absence of surface water redistribution, the assimilation by grasses would have been equal to or only slightly higher than the assimilation by shrubs.

The assimilation response of the shrubs was surprising in that it increased slightly in the first few days after rainfall but showed no clear pattern even though such a pattern was evident in measurements of both water potential and transpiration (Figure 7). This pattern suggests that the assimilation response was not limited simply by stomatal responses but by other factors that are most likely related to the state of the photosynthetic biochemistry in leaves. This phenomenon has been observed previously for *L. tridentata* in southern New Mexico where it appeared to be a function of the rainfall history preceding the actual rainfall event after which gas exchange was measured (Yan and others 2000).

Overall, surface water redistribution and the resulting horizontal heterogeneities in $\Psi_s$ played a critical role in controlling the differences in how grasses and shrubs used water and fixed carbon following the storm studied here. Our results do not prove that this process is important at other locations and for all storm sizes. However, our findings suggest that manipulative experiments intended to understand ecosystem responses to precipitation regime that utilize designs that do not allow for horizontal redistribution may not yield meaningful conclusions (Weltzin and others 2003). Next, we consider how our results relate to the different conceptual models used to describe the interactions between woody and herbaceous plants. We also discuss how the importance of surface water redistribution on grass–shrub interactions may vary across climate and locations.

## Models of Herbaceous–Woody Plant Interactions

The Walter two-layer model does not describe the key processes and herbaceous–woody plant interactions that were observed following the summer rain event at the Sevilleta grass–shrub ecotone. Although shrub roots were deeper than grass roots, this did not give the shrubs sole access to any portion of the rainfall that infiltrated during the storm because the wetting front did not propagate below the root zone of grasses. The rain event studied here was larger than 90% of the storms that occur at the study site during the monsoon season (Figure 3). Therefore, our results demonstrate that the infiltration associated with nearly all summer storms will not wet the soil below the grass root zone. The wetting front may only propagate below the deepest grass roots following the largest storms, or after a series of storms in rapid succession. Shrubs are therefore even less likely to experience high water potential throughout their rooting profile as the result of summer storms, probably the reason that they have been shown to be more responsive to winter precipitation (Reynolds and others 1999). The spatial arrangement of woody and herbaceous plants at the ecotone also makes it difficult to consider the observed plant–water interactions within the framework of the Walter model. The shrubs are restricted to distinct patches. Many of the grasses are located far enough from these patches that it is unlikely that shrub roots exist beneath the grass canopies. Although Brisson and Reynolds (1994) found roots of *L. tridentata* occupied soil under bare soil patches, their measurements, in a monodominant shrubland in southern New Mexico USA, showed gaps and lower root density where separation between shrubs was greatest. On the shrubland side of the ecotone within 1 km of the study site at Sevilleta,

root density is around 10 times lower between shrub canopies than beneath them (Kurc and Small 2004, Figure 3). Therefore, it is unlikely that shrub roots extend farther from the shrubs in the ecotone.

A conceptual model that explicitly represents the horizontal arrangement of different plant types (Breshears and Barnes 1999; Loik and others 2004) and the lateral redistribution of surface water is necessary to describe how the grasses and shrubs responded differently to the rain event studied here. The magnitude of surface water redistribution and the impact of water redistribution on different plant types should depend on four key factors. First, the spatial distribution of grasses and shrubs is critical. If two species are completely intermixed, then redistribution of surface water would not yield an advantage to either plant type. If woody and herbaceous plants are segregated, details of the spatial pattern will control the impact of surface water redistribution. At the Sevilleta ecotone, we expect that shrub patches equal in size or smaller than those studied here lose water to adjacent grasses, with grasses on the periphery of patches potentially benefiting more than those in the patch interior. In contrast, in larger shrub patches, the surface water redistribution and infiltration processes will more closely match those observed in the end-member shrubland ecosystem: overland flow from interspaces to canopies yields relatively deep infiltration beneath shrubs (Bhark and Small 2003). As the size of a shrub patch grows, a greater fraction of shrubs occupy positions in the landscape where they can receive run-on from upslope interspaces. In environments where vegetation is arranged in bands, surface water redistribution from bare soil to the bands will favor grasses when these species preferentially grow on the uphill side of the band (for example, Montaña and others 1995).

Second, the characteristics of a rainfall event will control the amount of surface water redistribution, and therefore the effects of this process on shrub–grass interactions. In the Sevilleta grassland and shrubland, surface water redistribution and focused infiltration beneath plant canopies grows in intensity as rainfall event size increases (Bhark and Small, 2003). We expect the same would be true at the ecotone. Because the storm studied here was large, the contrasts in grass and shrub $\Psi_s$ and plant responses described here may be greater than typically occurs at this site. High storm intensity also increases runoff, and should therefore have a similar effect on redistribution as storm size. Given these hypothesized controls of storm size and

intensity, the climate at a site should impact the importance of surface water redistribution on shrub–grass interactions. Likewise, shifts in climate that alter size distribution of rainfall events have the potential to significantly alter the amount of water available to grasses and shrubs. A seasonal bias in these shifts may also favor one functional type over the other.

Third, other physical attributes of a site that influence surface water redistribution and infiltration patterns will also be critical. For example, the relationship between microtopography, soil properties, and hillslope geometry controls surface water redistribution in semiarid environments (Dunne and others 1991; Dunkerley 2002). For example, surface water redistribution will be less important where coarse soils yield high infiltration rates.

Fourth, the season during which a rainfall event occurs should control how important surface water redistribution and heterogeneous infiltration is for the differential response of woody and herbaceous plants. In many semiarid environments, rainfall intensities are lower during the winter months, which would tend to limit overland flow. The extreme of this scenario would occur at sites, such as the Great Basin, where a large portion of annual precipitation is in the form of snow that melts slowly and infiltrates more evenly. However, such systems are often characterized by $C_3$ grasses that utilize soil water during the spring and reproduce before the stored water is exhausted. In systems where winter precipitation is less, we expect that this effect is negligible when compared to the overriding controls of plant phenology. The dominant grass at the Sevilleta ecotone (*B. eriopoda*) is only active during the warmest months of the year. Therefore, the grasses would not be able to capitalize on any preferential redistribution and infiltration that occurs during the winter months (Schwinning and Ehleringer 2001). Although some water may remain deep in the soil profile until the grasses become active in July, we expect a large fraction to be lost through evaporation during the hot and dry spring.

The results described here have the following implications for shrub invasion, for environments similar to the grass–shrub ecotone at the Sevilleta. Preferential surface water redistribution to grass canopies and the resulting enhanced grass $\Psi_s$, $\Psi_{PD}$ and assimilation should slow the rate at which shrub patches expand at the ecotone. The extra water available to grasses at the margins of shrub patches should help maintain grass biomass. Given the horizontal redistribution of resources to grasses, the shrub patches may only expand under extreme

conditions such as multi-year drought, when the drought tolerance of shrubs and their potential to use water at any time during the year is critical. Above, we proposed that the importance of preferential transfer of water to grasses may diminish as the size of shrub patches increase and therefore this process may only slow expansion of shrub patches when they are small. The soil textural changes that accompany the development of large inter-spaces would only serve to reinforce the redistribution of water to shrub canopies.

## ACKNOWLEDGMENTS

## REFERENCES

Abrahams AD, Parsons AJ, Wainwright J. 1995. Effects of vegetation change on interrill runoff and erosion, walnut gulch, southern Arizona. Geomorphology 13:37–48.

Archer S. 1994. Woody plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes. In: Vavra M, Laycock WA, Pieper RD, Eds. Ecological implications of livestock herbivory in the west. Denver, CO: Society For Range Management. p 13–68.

Archer S, Schimel DS, Holland EA. 1995. Mechanisms of shrubland expansion: land use, climate or $CO_2$? Clim Change 29:91–9.

Bahre CJ, Shelton MJ. 1993. Historic vegetation change, mesquite increases, and climate in southeastern Arizona. J Biogeogr 20:489–504.

Bassirirad H, Tremmel DC, Virginia RA, Reynolds JF, DeSoyza AG, Brunell MH. 1999. Short-term patterns in water and nitrogen acquisition by two desert shrubs following a simulated summer rain. Plant Ecol 145:27–36.

Bedford DR, Small EE. 2008. Spatial patterns of ecohydrologic properties on a hillslope-alluvial fan transect, vol. 73, no. 1, central New Mexico: Catena. pp 34–48.

Bhark EW. 2002. Water availability to vegetation across a semiarid shrubland and grassland ecotone, Sevilleta Wildlife Refuge, Neew Mexico. Master's Thesis. New Mexico Tech, Socorro, NM.

Bhark EW, Small EE. 2003. Association between plant canopies and the spatial patterns of infiltration in shrubland and grassland of the Chihuahuan Desert, New Mexico. Ecosystems 6:185–96.

Breshears D, Barnes F. 1999. Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. Landsc Ecol 14:465–78.

Brisson J, Reynolds JF. 1994. The effect of neighbors on root distribution in a creosotebush (*Larrea tridentata*) population. Ecology 75:1693–702.

Bristow KL, Campbell GS, Calissendorff K. 1993. A test of a heat-pulse probe for measuring changes in soil water content. Soil Sci Soc Am J 57:930–8.

Brown R, Bartos D. 1982. A calibration model for screen-caged peltier thermocouple psychrometers. Usda Forest Service, Ogden, Ut, Int-293.

Buffington LC, Herbel CH. 1965. Vegetational changes on a semidesert grassland range from 1858–1963. Ecol Monogr 35:135–64.

Davis SD, Mooney HA. 1985. Comparative water relations of adjacent California shrub and grassland communities. Oecologia 66:522–9.

Dunkerley D. 2002. Infiltration rates and soil moisture in a groved mulga community near Alice Springs, arid central Australia: evidence for complex internal rainwater redistribution in a runoff-runon landscape. J Arid Environ 51:199–219.

Dunne J, Dennis A, Bartolome JW, Barrett RH. 1991. Chaparral response to a prescribed fire in the Mount Hamilton Range, Santa Clara County, California. Madroño 38:21–9.

Ehleringer JR, Phillips SL, Schuster WSF, Sandquist DR. 1991. Differential utilization of summer rains by desert plants. Oecologia 88:430–4.

Gibbens RP, McNeely RP, Havstad KM, Beck RF, Nolen B. 2005. Vegetation changes in the Jornada Basin from 1858 to 1998. J Arid Environ 61:651–68.

Gill RA, Burke IC. 1999. Ecosystem consequences of plant life form changes at three sites in the semiarid United States. Oecologia 121:551–63.

Hamerlynck EP, Huxman TE, Loik ME, Smith SD. 2000. Effects of extreme high temperature, drought and elevated $CO_2$ on photosynthesis of the Mojave Desert evergreen shrub, *Larrea tridentata*. Plant Ecol 148:183–93.

Houghton R, Hackler J, Lawrence K. 1999. The US carbon budget: contributions from land-use change. Science 285:574–8.

Huxman TE, Tissue D, Snyder K, Leffler J, Ogle K, Pockman WT, Sandquist DR, Williams DG. 2004. Precipitation pulses and carbon dynamics in semi-arid and arid ecosystems. Oecologia 141:254–68.

Huxman TE, Wilcox BP, Scott R, Snyder K, Breshears D, Small EE, Hultine KH, Pockman WT, Jackson RB. 2005. Woody plant encroachment and the water cycle: an ecohydrological framework. Ecology 86:308–19.

Jackson RB, Banner JL, Jobbagy EG, Pockman WT, Wall DH. 2002. Ecosystem carbon loss with woody plant invasion of grasslands. Nature 418:623–6.

Kieft TL, White CS, Loftin SR, Aguilar R, Craig JA, Skaar DA. 1998. Temporal dynamics in soil carbon and nitrogen resources at a grassland–shrubland ecotone. Ecology 79:671–83.

Kurc SA, Small EE. 2004. Dynamics of evapotranspiration in semiarid grassland and shrubland ecosystems during the summer monsoon season, central New Mexico. Water Resour Res 40:W09305.

Kurc SA, Small EE. 2007. Soil moisture variations and ecosystem-scale fluxes of water and carbon in semiarid grassland and shrubland. Water Resour Res 43:W06416. doi:10.1029/2006WR005011.

Loik ME, Breshears DD, Lauenroth WK, Belnap J. 2004. A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. Oecologia 141:269–81.

Ludwig J, Eager R, Bastin G, Chewings V, Liedloff A. 2002. A leakiness index for assessing landscape function using remote sensing. Landsc Ecol 17:157–71.

Montaña C, Cavagnaro B, Briones O. 1995. Soil-water use by coexisting shrubs and grasses in the southern Chihuahuan Desert; Mexico. J Arid Environ 31:1–13.

Morgan JA, LeCain DR, Mosier AR, Milchunas DG. 2001. Elevated CO2 enhances water relations and productivity and affects gas exchange in C-3 and C-4 grasses of the Colorado shortgrass steppe. Glob Chang Biol 7:451–66.

Neilson RP. 1986. High-resolution climatic analysis and southwest biogeography. Science 232:27–34.

Odening WR, Strain BR, Oechel WC. 1974. The effect of decreasing water potential on net $CO_2$ exchange of intact desert shrubs. Ecology 55:1086–95.

Ogle K, Reynolds JF. 2002. Desert dogma revisited: coupling of stomatal conductance and photosynthesis in the desert shrub, *Larrea tridentata*. Plant Cell Environ 25:909–21.

Ogle K, Reynolds JF. 2004. Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds and delays. Oecologia 141:282–94.

Pacala SW, Hurtt GC, Baker D, Peylin P, Houghton RA, Birdsey RA, Heath L, Sundquist ET, Stallard RF, Ciais P, Moorcroft P, Caspersen JP, Shevliakova E, Moore B, Kohlmaier G, Holland E, Gloor M, Harmon ME, Fan SM, Sarmiento JL, Goodale CL, Schimel D, Field CB. 2001. Consistent land- and atmosphere-based us carbon sink estimates. Science 292:2316–20.

Pelaez DV, Distel RA, Boo RM, Elia OR, Mayor MD. 1994. Water relations between shrubs and grasses in semiarid Argentina. J Arid Environ 27:71–8.

Peters DPC. 2002. Plant species dominance at a grassland–shrubland ecotone: an individual-based gap dynamics model of herbaceous and woody species. Ecol Modell 152:5–32.

Peters DPC, Small EE, Gosz J, Parmenter RR, Collins SL, Pockman WT. 2006a. Biotic transitions at multiple scales: merging patch dynamics with ecotones. Landsc Ecol 21:19–33.

Peters DPC, Yao J, Gosz JR. 2006b. Woody plant invasion at a semin-arid/arid transition zone: importance of ecosystem type to colonization and patch expansion. J Veg Sci 17(3):389–96.

Peters DPC, Mariotto I, Havstad KM, Murray LW. 2006c. Spatial variation in remnant grasses after a grassland-to-shrubland state change: implications for restoration. Rangel Ecol Manage 59(4):343–50.

Reece CF. 1996. Evaluation of line heat dissipation sensor for measuring soil matric potential. Soil Sci Soc Am 60:1022–8.

Reid K, Wilcox B, Breshears D, Macdonald L. 1999. Runoff and erosion in a pinon-juniper woodland: influence of vegetation patches. Soil Sci Soc Am J 63:1869–79.

Reynolds JF, Virginia RA, Kemp PR, de Soyza AG, Tremmel DC. 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. Ecol Monogr 69:69–106.

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

Sala OE, Lauenroth WK, Parton WJ. 1992. Long-term soil–water dynamics in the shortgrass steppe. Ecology 73:1175–81.

Schenk HJ, Jackson RB. 2002. The global biogeography of roots. Ecol Monogr 72:311–28.

Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG. 1990. Biological feedbacks in global desertification. Science 247:1043–8.

Schlesinger WH, Raikes JA, Hartley AE, Cross AE. 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77:364–74.

Schlesinger WH, Ward TJ, Anderson J. 2000. Nutrient losses in runoff from grassland and shrubland habitats in Southern New Mexico: I. Field plots. Biogeochemistry 49:69–86.

Schwinning S, Ehleringer JR. 2001. Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. J Ecol 89:464–80.

Schwinning S, Davis K, Richardson L, Ehleringer JR. 2002. Deuterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado plateau. Oecologia 130:345–55.

Soriano A, Sala O. 1984. Ecological strategies in a Patagonian arid steppe. Vegetatio 56:9–15.

Turner NC. 1987. The use of the pressure chamber in studies of plant water status. International conference on measurement of soil and plant water status, Logan, Utah, vol. 2, pp 13–24.

Van Vegten JA. 1983. Thornbush invasion in a savanna ecosystem in eastern Botswana. Vegetatio 56:3–7.

Walter H. 1971. Ecology of tropical and subtropical vegetation. Edinburgh: Oliver & Boyd.

Walter H. 1973. Vegetation of Earth. Heidelberg: Springer-Verlag.

Weltzin JF, Loik ME, Schwinning W, Williams DG, Fay PA, Haddad BM, Harte J, Huxman TE, Knapp AK, Lin G, Pockman WT, Shaw MR, Small EE, Smith MD, Smith SD, Tissue DT, Zak JC. 2003. Assessing the response of terrestrial systems to potential changes in precipitation. Bioscience 53:941–52.

Wilcox B. 2002. Shrub control and streamflow on rangelands: a process based viewpoint. J Range Manage 55:318–26.

Yan SG, Wan CG, Sosebee RE, Wester DB, Fish EB, Zartman RE. 2000. Responses of photosynthesis and water relations to rainfall in the desert shrub creosote bush (*Larrea tridentata*) as influenced by municipal biosolids. J Arid Environ 46:397–412.