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Association between Plant Canopies and the Spatial Patterns of Infiltration in Shrubland and Grassland of the Chihuahuan Desert, New Mexico

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ABSTRACT

Shrubs have invaded extensive areas of grassland in the southwestern United States. The zones of nutrient-rich soil found beneath plant canopies, referred to as "islands of fertility," are more intense and spaced farther apart in shrubland than in grassland. This difference in the spatial pattern of soil nutrients may reinforce shrub invasion. Changes in water availability in the soil could also influence shrub invasion. Here we compare the spatial patterns of infiltration, defined as the total equivalent water depth entering the soil following individual rainfall events or summed over many events, at adjacent grass- and shrub-dominated sites in the Sevilleta National Wildlife Refuge. We use two infiltration data sets. First, following four rainfall events, we measured soil moisture and wetting front depth at 10-cm intervals along 24-m transects. We estimate infiltration from these data. Second, we use vertical arrays of soil moisture probes to compare infiltration between adjacent canopies and interspaces following 31 storms. In both the grassland and shrubland, infiltration is typically greater beneath plant canopies than beneath interspaces. Canopies are oases where soil moisture is higher than in the surrounding areas. However, infiltration is not greater beneath canopies when surface runoff is limited. In the shrubland, the canopy–interspace infiltration ratio increases as storm size, and therefore runoff, increases. This relationship also exists in the grassland, but it is not as strong or clear. The magnitude of spatial variability of infiltration is similar in shrubland and grassland. In addition, the distance over which infiltration is correlated is approximately 50 cm in both environments. Most of the spatial variability exists between the stem and canopy margin in the shrubland and straddling the canopy margin in the grassland. The most notable difference is that subcanopy oases are spread farther apart in the shrubland because canopies are separated by larger interspaces in this environment.

Key words: plant canopies; infiltration; shrubland; grassland; desertification; semiarid ecosystems; rainfall interception; water availability; soil moisture dynamics; Chihuahan Desert.

INTRODUCTION

In the early 19th century, large areas of grassland were present in the southwestern United States. However, over the past 200 years, the density of shrubs such as mesquite (*Prosopis glandulosa*) and creosotebush (*Larrea tridentata*) has increased dramatically, converting these ecosystems from herbaceous to woody-dominated areas (Buffington and Herbel 1965; Grover and Musick 1990; Bahre and Shelton 1993; Archer 1994; Van

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Auken 2000). Similar invasions of grasslands by shrubs have been observed worldwide (Graetz 1994). The following factors have been proposed to explain shrub invasion in the American Southwest: livestock grazing, altered fire regime, drought, climatic change, and increased atmospheric carbon dioxide (CO_2) concentration (Archer 1994). However, it is not possible to establish a clear cause–effect relationship between these factors and observed vegetation changes. There are only limited data to constrain the history of shrub invasion (see, for example, Buffington and Herbel 1965), and interactions between or among these different factors could lead to complex ecosystem changes (Archer 1994).

Previous research has focused on the changes in processes that accompany the transition from grassland to shrubland ecosystems, with the goal of understanding how different factors, such as grazing or droughts, may influence shrub invasion. One key difference is that the spatial patterns of soil fertility are different in grassland and shrubland. First, the zones of nutrient-rich soil found beneath plant canopies, which have been termed “islands of fertility” (see, for example, Schlesinger and others 1990), are more intense in shrubland than grassland. The intensity of islands was gauged by measuring the canopy-to-interspace ratio of various plant nutrients and carbon, which is typically higher in shrubland than grassland (Schlesinger and others 1996; Kieft and others 1998). Second, geostatistical analyses were used to measure the scale of spatial variability in grass and shrub ecosystems. In grasslands, most of the variability in soil fertility exists at distances of less than 20 cm, interpreted to represent accumulations of nutrients beneath grass clumps (Schlesinger and others 1996). In contrast, spatial variability of soil fertility increases up to distances of 1–3 m in shrublands, believed to represent cycling beneath individual shrub canopies. These changes in the spatial patterns of soil fertility associated with the transition from grassland to shrubland may act as a positive feedback that reinforces shrub invasion.

The most critical factor controlling plant productivity and reproduction in arid to semiarid environments is water availability in the soil (Noy-Meir 1973; Rodriguez-Iturbe 2000). The influence of soil fertility—for example, available nitrogen—is considered to be of secondary importance, as the effects of enhanced soil fertility are typically only observed once the limitations from water availability are eliminated (see, for example, Sharifi and others 1988). Schlesinger and others (1990) proposed that, as observed for soil fertility, soil moisture is more heterogeneous in shrublands than grasslands. This soil moisture change could be a feedback that reinforces shrub invasion if the soil water available to grasses is reduced, either due to changes in spatial distribution or temporal variability.

Several differences in water cycling between these two ecosystems have been observed. First, intensified rainsplash in large shrubland interspaces reduces infiltration capacity in these areas (Lyford and Qashu 1969; Abrahams and others 1995). Second, more overland flow is observed in shrublands (Abrahams and others 1995; Schlesinger and others 2000). This increases soil erosion, exposing finer-textured, and therefore less permeable, soils at the surface (for example, Kieft and others 1998). Third, differences in soil moisture have been observed (Schlesinger and others 1990; Kieft and others 1998). The soil moisture field exhibits substantial temporal variability in arid and semiarid environments—the soil is typically dry except for brief periods following rainfall events. Therefore, single surveys or repeat sampling at intervals unrelated to wetting and drying cycles provide limited information about soil moisture dynamics (see, for example, Schlesinger and others 1990; Kieft and others 1998).

In this study, we compared infiltration and soil moisture between grassland and shrubland ecosystems. We defined “infiltration” as the total equivalent depth of water that enters the soil (units of length), resulting either from a single rainfall event or a series of events. This is equivalent to a volume of water passing through a unit area of the soil surface. Our goal was to understand how the transition from grassland to shrubland affects the amount of soil water that is available to plants. Here we focus on the spatial and temporal variability of infiltration that occurs during individual rainfall events. This enabled us to characterize the soil moisture state immediately following rainfall events in grassland and shrubland, so that we could assess how shrub invasion influences the spatial distribution of soil water availability. We did not examine processes that influence soil moisture distribution on longer time scales, such as lateral redistribution within the soil, evaporation, and transpiration. We divided the landscape into subcanopy and interspace patches for much of our analyses. Previous work has demonstrated that the influence of desert shrubs on soil hydraulic properties extends beyond their canopy margins (see, for example, Dunkerley 2000), so this canopy–interspace binary division is a simplification. Therefore, we also employed geostatistical techniques to gauge the variability throughout the landscape.

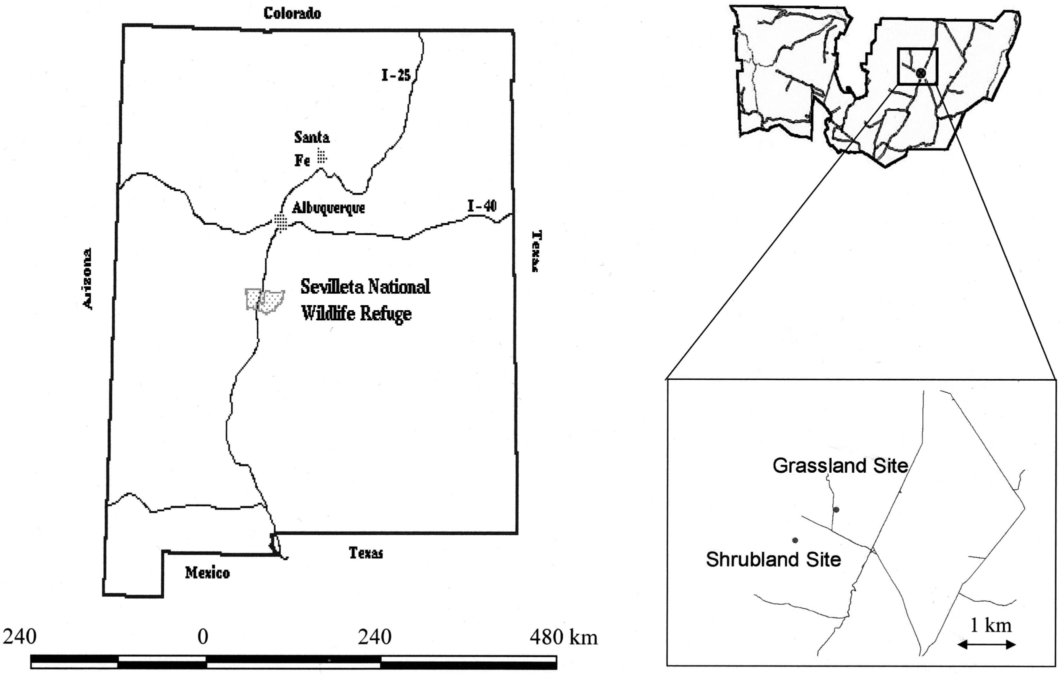

Figure 1. Location of the grassland and shrubland sites within the Sevilleta National Wildlife Refuge, central New Mexico.

We tested four hypotheses regarding infiltration in semiarid grassland and shrubland ecosystems. First, there is more infiltration beneath plant canopies than at interspaces in both grassland and shrubland, either following a single rainfall event or summed over many events. If this hypothesis is correct, then the fertile islands found beneath plant canopies are also locations where infiltration is highest and soil moisture is concentrated. Second, the difference in infiltration between canopy and interspace is greater in shrublands than grasslands—that is, the "oases" beneath canopies are more intense in shrubland, as observed for soil fertility. Third, infiltration is more spatially variable in shrubland than in grassland. And fourth, the correlation length of infiltration variability is greater in shrubland because canopies are spread farther apart and infiltration is controlled by the presence or absence of vegetation. If the latter two hypotheses are correct, then the transition from grassland to shrubland is accompanied by increased heterogeneity of soil water, as is the case for soil nutrients.

METHODS

Study Area

We measured infiltration in grassland and shrubland ecosystems at the McKenzie Flats research area in the Sevilleta National Wildlife Refuge, central New Mexico, USA (Figure 1). Our measurements are from the same sites sampled in previous studies (see, for example, Schlesinger and others 1996; Kieft and others 1998). Annual precipitation is approximately 250 mm, and more than half of the precipitation falls between July and September. The grass–shrub ecotone is narrow at McKenzie Flats; the shrub and grass sites sampled were within 2 km of each other. The grassland is dominated by black grama (*Bouteloua eriopoda*) and has approximately 50% canopy cover. The shrubland is dominated by creosotebush (*Larrea Tridentata*), with approximately 25% plant cover. According to historical information and repeat photography, the shrubland was dominated by herbaceous species in the early 20th century. Therefore, we are comparing grassland infiltration with infiltration in an area that was recently transformed from grassland to shrubland. The slope at all sites is less than 2°, and the surface soil is a sandy loam that has developed on fan deposits from the Los Pinos Mountains to the west. Kieft and others (1998) documented soil texture differences between the grassland and shrubland, and they attributed these differences to the shrub invasion process. The entire area has not been grazed by livestock since the 1970s.

Table 1. Precipitation and Infiltration Statistics for the Four Rainfall Events Followed by Infiltration Transects

	Date	Precipitation (mm)	Mean Infiltration (mm)	Infiltration Variance (mm^2)	Infiltration Coefficient of Varation
Grassland					
Transect 1	10-8-00	15.8	11.9	29.9	0.46
Transect 2	6-26-01	10.1	6.1	12.9	0.59
Shrubland					
Transect 1	8-18-00	12.8	10.8	21.5	0.43
Transect 2	8-31-00	7.4	4.6	25.9	1.10

Spatial Variability of Infiltration and Soil Moisture

Data Collection. We measured infiltration along transects following four rainfall events, two each in the grassland and shrubland ecosystems (Table 1). Each event had a rainfall total above 5 mm, and infiltration was measured within a few hours of rainfall. Given personnel, equipment, and time constraints, it was not possible to complete infiltration surveys following the same event in both environments. This would have required 2 days of sampling, so the effects of evapotranspiration and subsurface redistribution would be much more important at the site sampled on the 2nd day following rainfall. Each transect was selected haphazardly, was between 12 and 24 m long, and had sampling intervals of 10 cm. Measurement locations were designated as either canopy or interspace, depending on the presence or absence of standing vegetation above the sample location.

We estimated infiltration by combining water content and wetting front measurements. Volumetric water content was measured using the time domain reflectometry (TDR) method (Topp and others 1980; Schmugge and others 1980). TDR probes were inserted at an angle, so that the top end of the rods were located approximately 1 cm below the soil surface and extended to a depth of 5 cm (Figure 2), providing an estimate of the average water content over the top 5 cm of the soil. We used three-pronged probes with 15-cm rods that were spaced 2.0 cm apart. A probe with this geometry samples an elliptical region around the rods: 90% of the signal is derived from the medium between 0.75 cm above and below the rods (Ferre and others 1998). Given this geometry, the volume sampled by the probe did not extend above the soil surface. All data were collected following rain events sufficient to provide a wetting front of at least 5 cm. Therefore, the probes did not extend into dry soil. TDR provides an indirect measure of volumetric soil moisture. We have checked the accuracy of this method for Sevilleta soils in the laboratory. Soil moisture values from TDR were within several percent of values determined gravimetrically. Within 1 h of the TDR measurements along any portion of each transect, we trenched the soil to expose the wetting front. The wetting depth was measured at the same locations as water content. The wetting front was identified by the strong color contrast between wet and dry soil (Figure 3).

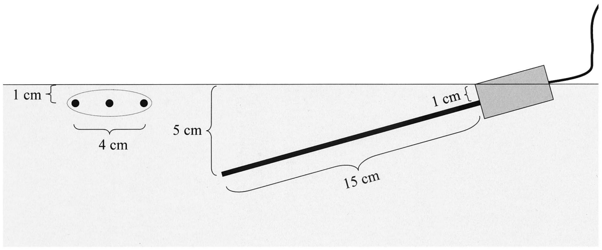

Figure 2. **A** Sketch of TDR probe inserted into soil (gray area), showing 15-cm rod extending from 1 cm below soil surface to 5 cm below surface. **B**: Cross section of TDR probe at upper end of rods. The ellipse shows area around the rods from which 90% of the signal is derived (Ferre and others 1998).

At a point, the infiltration, *I*, or the total equivalent water depth that enters the soil following a rainfall event (units = cm), can be written as:

$$I = \int_{z=0}^{Sf} (\theta_t(z) - \theta_i(z))dz \qquad (1)$$

where θ_t is volumetric water content at some time after the rainfall event, θ_i is volumetric water content preceding the rainfall event, S_f is the wetting front depth (cm), and z is distance below the surface. In this study, we calculate infiltration based upon the Green

Figure 3. A wetting front in the Sevilleta shrubland is exposed in a trench face. The wet soil above the front is dark; the dry soil below the front is light. The trench was completed and the photograph was taken approximately 1 h after a rainfall event of several millimeter. The wetting front is deeper beneath the canopy than in the interspace. The absence of fingering indicates wetting front stability. Wetting fronts in the adjacent grassland are also sharp and distinct.

and Ampt (1911) model: Infiltration proceeds as a plug, with uniform water content above the wetting front. Using the water content and wetting front measurements at each location, we approximate infiltration as:

$$I = \int_{z=0}^{Sf} (\theta_t (z) - \theta_i (z))dz \approx (\theta_t - \theta_i) \cdot S_f \quad (2)$$

This approximation of infiltration is based on two assumptions. First, water content is uniform above the wetting front. We used the average volumetric water content measured in the top 5 cm of soil via TDR for this value. Second, the water content prior to the passage of the wetting front (that is, the initial water content, θ_i) is also uniform. We used soil moisture values typical of air-dry conditions for the initial value: All four of the rainstorms we studied occurred after rain-free intervals longer than 15 days in duration. Previously, we measured volumetric water content of field-dry soil, by reweighing a known volume of soil following 24 h of oven-drying at 100°C. In the grasslands, field-dry soil had an average water content of 2.1 ± 0.6 % and 2.3 ± 0.5% across canopy and interspace patches, respectively. In the shrubland, the canopy and interspace water contents were 2.7 ± 0.6 % and 2.6 ± 0.5%, respectively. We use values of 2.2% for grass and 2.6% for shrub in our infiltration calculations.

We have not directly tested these two assumptions. However, several lines of evidence indicate that our approximation of infiltration is reasonable. First, we have observed that wetting fronts are sharp; the water content distribution with depth is a step function (Figure 3) (Philip 1975). In addition, we did not observe unstable wetting fronts (Raats 1973), which would indicate that the Green–Ampt model is inappropriate. Second, infiltration calculated using Eq. (2) is similar to independent estimates based on cored samples and subsequent volumetric water content measurements; the values from the two different methods are within approximately 10%. And third, the mean infiltration value from each transect is 2–4 mm less than the measured precipitation (Table 1). This difference is expected, given that interception loss in these semiarid environments is on the order of several mm (Navar and Bryan 1990; Dunkerley and Booth 1999; Tromble 1988).

Statistical Analyses. Mean and variance were calculated across entire transects and separately for canopy and interspace infiltration. We used *t*-tests and *F*-tests to compare mean and variance values, respectively.

We used geostatistics to examine the spatial structure of infiltration variability, as done in previous studies of soil fertility at the Sevilleta and other locations (see, for example, Schlesinger and others 1996). We constructed raw variograms for each transect, which show the variance of infiltration, γ^*, as a function of measurement separation or lag distance, h (Kitanidis 1997). The variogram data, $\gamma^*(h)$, was then used to construct a model variogram for each transect, using an exponential model of the form:

$$\gamma(h) = c^*\left[1 - \exp\left(\frac{-3h}{a}\right)\right] + c_o \qquad (3)$$

where c is the variance component of the model (cm^2), a is the variogram range (cm), and c_0 is the nugget (cm^2) (Isaaks and others 1989). The nugget represents both TDR probe error and spatial variability that exists at scales smaller than the sampling interval of 10 cm.

We used two features of the modeled variogram, $\gamma(h)$, to compare the spatial variability of infiltration between grassland and shrubland. First, the range provides an estimate of the correlation length, or the distance at which measurements become independent (Kitanidis 1997). We used the range to test the hypothesis that spatial correlation of infiltration exists at greater distances in the shrubland because canopies are spread further apart. Second, at distances beyond the range, the modeled variogram approaches the sill. This sill is equivalent to the sample variance, σ^2, across each transect, equal to $c + c_0$. We used the sill to identify patterns beyond the range that appear as hole effects, or periodic deviations from the sill. We did not force the modeled variogram to fit the hole effect present in the raw variogram data, $\gamma^*(h)$. Instead, we assessed the observed hole effect in terms of the wavelength at which the (raw) variogram data deviates from the modeled sill. Both the range and the sill, and therefore the hole effects, are useful statistical measures if infiltration is spatially stationary across each transect—that is, if soil moisture values vary spatially at a relatively small scale about a constant mean value that is maintained through the entire sampling domain. A sill exists only if the distribution is stationary.

Temporal Variability of Infiltration

We used continuous monitoring of soil moisture to complement the spatially intensive surveys. In both grassland and shrubland, we measured soil moisture beneath a single plant canopy and the adjacent, upslope interspace. The canopy and interspace patches we monitored were selected based on two criteria. First, their dimensions were typical of that observed in each environment. Second, they were close enough to existing data acquisition systems to minimize cable length requirements.

At each of the four locations, we inserted Campbell Scientific water content reflectometers (WCR) at three depths: 2.5, 12.5, and 22.5 cm. WCRs provide an estimate of soil moisture based on the TDR method. The WCRs have two 30-cm rods spaced 3.2 cm apart. A probe with this geometry samples a semicyclindrical region around the rods; 90% of the signal is derived from soil between 2.5 cm above and below the rods (Ferre and others 1998). Probes were inserted horizontally in the upslope direction from a shallow pit that was subsequently filled. We used the three probes at each location to estimate the average soil moisture throughout the top 27.5 cm of the soil. The value from each probe was weighted assuming it represents soil moisture over depth intervals of, 0–7.5, 7.5–17.5, and 17.5–27.5 cm, a reasonable assumption if soil wetting is uniform. These depth intervals were chosen according to the midpoints between each probe and to place equal weighting at each depth.

Soil moisture was measured every 15 min between 1 June, 2000 and 1 January, 2002. There were 31 precipitation events that exceeded 2 mm during this interval. We calculated infiltration, I, for each of these events as:

$$I = (\theta_{\max} - \theta_i) \cdot D \tag{4}$$

where $\theta_{\max}$ is the maximum volumetric water content after the event, θ_i is the volumetric water content before the event, and D is the depth over which the measurements were made (27.5 cm). Soil moisture rises to a maximum typically within about 1 h of each rainfall event, followed by a slow decline due to evapotranspiration and vertical redistribution below 27.5 cm for larger storms. The maximum value following each event was used for our infiltration calculations. We compared infiltration beneath canopy and interspace in both the shrub and grass environments.

RESULTS

First, we describe the relationship among volumetric water content, wetting depth, and infiltration, demonstrating how the method applied here yields estimates of infiltration. Then we test the hypotheses presented above by analyzing the spatial and temporal variability of infiltration. In each transect, the spatial patterns of water content and wetting depth (θ, S_f) were similar; the magnitudes of θ and S_f were typically higher beneath canopies and lower within interspaces (Table 2). A positive correlation exists between variations in θ and S_f, with values of 0.21 to 0.66 for all four transects. Because infiltration is the product of θ and S_f, it is also higher beneath canopies and lower in interspaces.

In the shrubland, most of the observed variability in θ and S_f exists beneath plant canopies (Table 2). Because θ and S_f positively covary, most of the variability in infiltration also exists beneath canopies (Figure 4). The variance of θ, S_f, and I are all significantly higher beneath shrub canopies than in the interspaces. In contrast, the variance of grassland θ, S_f, and I beneath canopies and interspaces are equal. The greatest variations are found near the junction of adjacent canopies and interspaces. In both environments, the spatial patterns of θ, S_f, and I are similar. Therefore, we focus the remainder of our analysis on infiltration, which reflects the combined variation in θ and S_f.

Canopy versus Interspace Infiltration

We compared the magnitude of infiltration beneath canopy and interspace patches to test the first two hypotheses: (a) There is more infiltration beneath canopies, and (b) the canopy–interspace infiltration contrast is greater in shrubland.

Infiltration was higher beneath plant canopies than beneath interspaces in both grassland transects and in one of the shrubland transects (Figure 4 and

Table 2. Comparison of the Mean and the Variance of Water Content (θ), Wetting Front Depth (S_f), and Infiltration (I) beneath Canopy and Interspace

	Variable	Grassland Transect 1	Grassland Transect 2	Shrubland Transect 1	Shrubland Transect 2
	θ	$<10^{-5}$[a]	$<10^{-5}$[a]	$<10^{-5}$[a]	0.05
	S_f	$3.06 \cdot 10^{-4}$[a]	$<10^{-5}$[a]	0.85	$<10^{-5}$[a]
Mean	I	$<10^{-5}$[a]	$<10^{-5}$[a]	0.95	$<10^{-5}$[a]
P Value (one-tailed *t*-test)	Canopy-to-Interspace Infiltration Ratio	1.64	2.18	0.91	1.54
Variance	θ	0.28	0.22	$1.80 \cdot 10^{-3}$[a]	$<10^{-5}$[a]
P Value (one-tailed *F*-test)	S_f	0.31	0.02	$4.81 \cdot 10^{-3}$[a]	$1.32 \cdot 10^{-4}$[a]
	I	0.34	0.03	$<10^{-5}$[a]	$<10^{-5}$[a]

P values show results of one-tailed tests for H_a: $\mu_{canopy} > \mu_{interspace}$ *or* $\sigma^2_{canopy} > \sigma^2_{interspace}$.
[a] *Significant difference at* $\alpha = 0.01$

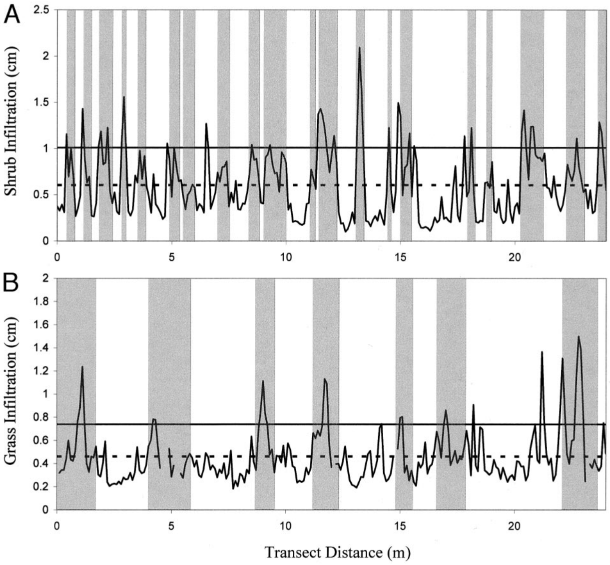

Figure 4. Profiles of infiltration from shrubland (**A**) and grassland (**B**) transects. Shaded areas indicate the presence of plant canopies. The upper horizontal line indicates the measured rainfall; the lower dashed line indicates the average infiltration.

Table 2). In these cases, infiltration beneath canopies was greater than the rainfall that accumulates during an event, whereas interspace infiltration was less than the accumulated rainfall. The first shrub transect is an exception, as the canopy and interspace values were not significantly different. These results demonstrate that the first hypothesis is sometimes correct: There is more infiltration beneath plant canopies than under interspaces. However, the results from the first shrub profile demonstrate that this hypothesis is not always valid.

The results from our spatial analysis do not support the second hypothesis: that the canopy–interspace infiltration contrast is more intense in shrubland than in grassland. The ratios of canopy-to-interspace infiltration in both shrubland transects (0.91 and 1.54) were lower than the ratios measured in the two grass transects (1.64 and 2.18) (Table 2). These tests of the first two hypotheses were based on measurements of infiltration following different storms in the grassland and shrubland. The partitioning of infiltration between canopies and interspaces may depend on the magnitude and intensity of rainfall events. Therefore, we examined the time series of soil moisture in both grassland and shrubland to test these hypotheses over a broader range of conditions.

In contrast to the spatial surveys, our continuous measurements of soil moisture show that there was more intense canopy infiltration in shrubland than in grassland. In the shrubland, there were 31 events totaling 290 mm of precipitation. Measurements of infiltration beneath a canopy and adjacent interspace show that 405 mm of water infiltrated beneath the shrub canopy and only 198 mm infiltrated in the adjacent interspace, or approximately 140% and 68% of measured precipitation, respectively (Table 3). Therefore, when infiltration is summed over many events, the canopy-to-interspace infiltration ratio is nearly 2.0 in the shrubland. In contrast, the total infiltration measured beneath grassland canopy and interspace was more similar. There was 248 mm and 202 mm of infiltration beneath canopy and interspace, equal to 77% and 64% of the measured precipitation, respectively. Over 31 events, the canopy–interspace ratio was 1.2 in the grassland. Therefore, both the first

Table 3. Comparison of Canopy and Interspace Infiltration from Time Series Data

	Precipitation (mm)	Infiltration (mm)		Canopy-to-Interspace Infiltration Ratio		
		Canopy	Interspace	Total	Maximum	Minimum
Shrubland	290	405	198	1.9	4.6	0.1
Grassland	318	248	202	1.0	3.1	0.2

Precipitation and infiltration are summed over 31 rainfall events.
The total canopy-to-interspace infiltration ratio is calculated over 31 events.
Maxima and minima ratios are based on calculations from individual events.

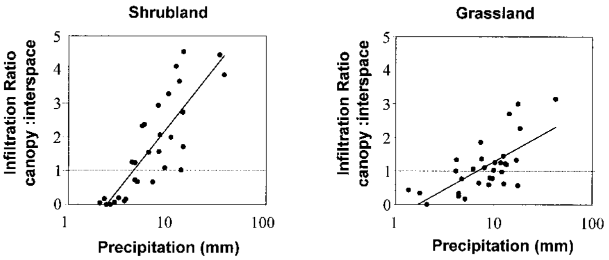

Figure 5. The ratio of canopy to interspace infiltration plotted against the rainfall total during each of 31 precipitation events in the grassland and shrubland. If the difference is greater than 1.0 (*dashed line*), then canopy infiltration is greater than interspace infiltration. Lines are least-squares linear fits to the data with the form $y = a\ln + b$. $r^2 = 0.71$ in shrubland and 0.45 in grassland.

and second hypotheses are supported when infiltration is considered over many events.

The contrast in results between our spatial and temporal analyses suggests that differences between canopy and interspace infiltration vary dramatically from event to event in both shrubland and grassland. In the shrubland, the maximum canopy-to-interspace infiltration ratio observed during a single event is 4.6 and the minimum is 0.1 (Table 3). The ratio of canopy-to-interspace infiltration is higher during events with greater total precipitation (Figure 5). When rainfall is less than approximately 5 mm, there is more infiltration beneath the shrubland interspace than under the canopy. The opposite is true during larger events. In general, the canopy–interspace difference increases logarithmically with precipitation amount ($r^2 = 0.71$). In the grassland, there is also substantial variability from event to event; the maximum canopy-to-interspace ratio is 3.1 and the minimum is 0.2. However, the relationship between the ratio of canopy-to-interspace infiltration and precipitation falling during each event is not as strong or clear ($r^2 = 0.45$) (Figure 5). These results need to be tested with data from multiple plant canopies and interspaces.

Spatial Variability

The third hypothesis, that the spatial variability of infiltration is greater in shrubland than grassland, was not supported by our infiltration transect data. The profile variance was highest in the first grassland transect and lowest in the second grassland transect, whereas the two shrubland transects exhibited intermediate values (Table 1). This comparison does not account for differences in mean infiltration between the four transects. When variability was normalized by the mean infiltration in each transect, variations in the two shrubland transects were the highest and lowest, and the grassland values were intermediate (Table 1). Therefore, spatial variability of infiltration was not consistently higher in the shrubland than the grassland, regardless of how variability is calculated.

We analyzed variograms to test the fourth hypothesis: that the correlation length of infiltration variability is greater in the shrubland because of the larger separation distance between adjacent canopies in this environment. Our results suggest that the radius of plant canopies strongly influences the spatial patterns of infiltration in the shrubland. There was more variability beneath shrub canopies than beneath interspaces (Table 4). Infiltration maxima existed near the center of canopies, and infiltration decreased rapidly toward the canopy margins (Figures 4 and 6). In contrast, infiltration was relatively constant within each interspace, except for minor variations that had the appearance of noise rather than of a spatially correlated series. The distance between the canopy infiltration maxima and the lower values found near the canopy–interspace margins controlled the shrubland variogram ranges, 70 cm and 37 cm (Figure 6 and Table 5). Therefore, the correlation length of infiltration appeared to be controlled by the length of shrub canopies in the measured transects. The average lengths were 59 cm and 30 cm in the two profiles (Table 5). The average spacing between shrub can-

Table 4. Comparison of Infiltration Variance beneath Canopy and Interspace

	Variance (cm^2)		
	Canopy	Interspace	P Value
Grassland			
Transect 1	0.27	0.24	0.34
Transect 2	0.09	0.06	0.03
Shrubland			
Transect 1	0.25	0.16	$<10^{-5^a}$
Transect 2	0.08	0.03	$<10^{-5^a}$

P values are calculated using a one-tailed F-test for H_a: $\sigma^2_{canopy} > \sigma^2_{interspace}$.
[a] *Significant result at* $\alpha = 0.01$

opies was much greater, equal to 270 cm and 380 cm, and does not appear to influence the range. The average length of shrub canopies along the transects is less than the average radii of shrub canopies throughout the landscape, because the transects do not necessarily cross all shrubs through their midpoint. However, the canopy length measured along the transect is the relevant measure for comparison to the spatial patterns of infiltration.

In the grassland, the relationship between infiltration variability and the geometry of canopies and interspaces was not as straightforward. Contrary to the pattern seen in the shrubland, the decrease in infiltration away from grass canopies extends into the adjacent interspace (Figures 4 and 6). Although mean infiltration was greater beneath grass canopies than within interspaces, canopy and interspace patches exhibit similar variability (Table 4). Therefore, infiltration variability in both canopies and interspaces contributes to the total variance and affects the range. The range was 41 cm and 44 cm in the first and second transects, respectively (Table 5 and Figure 6). The range reflects the distance over which the canopy-to-interspace decrease in infiltration occurs, which was not directly controlled by either canopy size or spacing. The range was greater than the average grass canopy radii, which were 22 cm and 26 cm in the two transects (Table 5). This was consistent with the observed infiltration profiles: The decrease in infiltration from subcanopy maxima extended into adjacent interspaces.

Based on the four surveys described here, we reject the fourth hypothesis. The correlation length of infiltration was not greater in Sevilleta shrubland than grassland, even though shrub canopies were spaced further apart. However, canopy spacing did influence the spatial variability of infiltration. In both grassland and shrubland, periodic variations about the sill show how canopy spacing influenced infiltration variability at distances greater than the range (Figure 6). In the shrubland variograms, local minima in variance occurred at approximately 3-m intervals. Enhanced infiltration beneath the center of shrub canopies, which were spaced at roughly 3-m intervals (Table 5), is the source of the periodic minima. In the grassland variograms, the periodic variance minima occur approximately every 1 m. Again, this length is similar to the distance between adjacent canopy centers, where infiltration is typically highest (Figures 4 and 6). Therefore, canopy spacing was the primary control of infiltration variability at scales beyond the range in both the grassland and the shrubland.

DISCUSSION

We will now discuss (a) why canopy infiltration is greater than interspace infiltration; (b) why the canopy–interspace infiltration contrast varies between storms and location, and (c) why the canopy–interspace infiltration ratio is typically higher in shrubland than grassland. We assumed that precipitation above the canopy was uniform over an area of approximately 100 m^2, equivalent to the scale at which measurements were collected. There are three processes that could have produced the variability of infiltration and soil moisture on the time scales studied here: interception of rainfall and subsequent evaporation, stemflow of intercepted rainfall, and lateral redistribution of water via surface runoff.

Vegetation intercepts rainfall, and a substantial fraction of this intercepted rainfall may evaporate directly from the surface of plant leaves and stems (see, for example, Tromble 1988). In the absence of wind, evaporation of intercepted rainfall would result in less water reaching the soil surface beneath plant canopies than in interspaces. The net effect would be greater infiltration within interspaces than beneath canopies, if all water infiltrates where it hits the ground. In the presence of wind, the effects of interception loss on infiltration and soil moisture occur downwind of individual plants, with the downwind distance depending on wind speed and plant dimensions and spacing.

The magnitude of soil moisture variability resulting from evaporation of intercepted rainfall depends on the amount of interception loss, which is controlled by canopy interception storage capacity and rainfall amount and intensity. Compared to forest ecosystems, there are few measurements of interception loss in semiarid shrub and grass systems (see, for example, Dunkerley and Booth

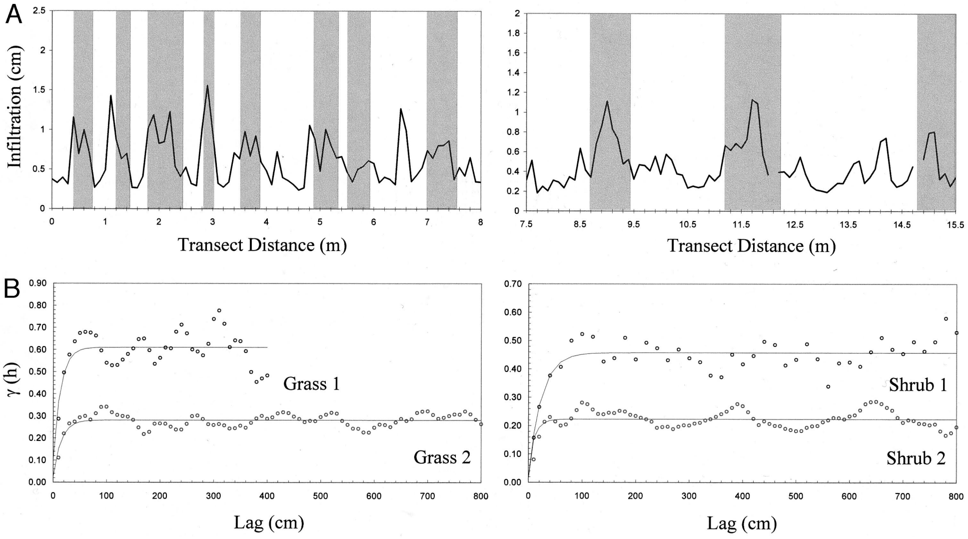

Figure 6. Grassland and shrubland variograms (**A**) and transect segments of grassland and shrubland infiltration (**B**), included as conceptual aides. Shaded areas in the infiltration plots represent plant canopies. Table 5 contains corresponding geostatistical parameters for variogram models γ(h).

Table 5. Range Estimates from Exponential Infiltration Variograms

	Range (cm)	Average Canopy Radius (cm)	Distance between Canopy Centers (cm)
Grassland			
Transect 1	41	22	101
Transect 2	44	26	80
Shrubland			
Transect 1	70	59	268
Transect 2	37	30	384

1999). Desert shrubs typically have a canopy storage capacity of several millimeter (Navar and Bryan 1990; Dunkerley and Booth 1999). For example, creosotebush in southern New Mexico has a canopy capacity of approximately 3 mm (Tromble 1988). Fewer measurements of interception loss in semiarid grasslands have been made, but estimates are higher per unit dry weight of plant matter than for shrubland (Thurow and others 1987).

In the shrubland, the effects of interception loss were apparent in our time series data. The infiltration measured beneath the shrub canopy was lower than that in the interspace (a canopy–interspace ratio of less than 1) during events when the rainfall total was less than approximately 5 mm (Figure 5). This suggests that several millimeter of water were stored and subsequently evaporated from the shrub canopy, consistent with previous observations of creosotebush interception (Tromble 1988). The effects of interception loss were not as obvious in the grassland, but higher infiltration beneath interspaces was observed during the smallest events. Our spatial sampling shows that canopies are typically wetter than interspaces (Table 2), the reverse of what is expected due to interception loss. The temporal data provide the same result, except in small storms. Based on this information, we believe that the evaporation of intercepted rainfall has a small impact on the spatial variability of infiltration.

Stemflow of intercepted rainfall preferentially transports water toward shrub stems. Whitford and others (1997) reported that 16% of rainfall was converted to stemflow in creosotebush. Martinez-Meza and Whitford (1996) found that creosotebush typically has a canopy storage capacity of 3 mm, beyond which significant stemflow occurs. They reported that the stem–root system of creosotebush channels water to depths significantly greater than the wetting front in the surrounding soil (Martinez-Meza and Whitford 1996), similar to the results of Devitt and Smith (2002). For example, Martinez-Meza and Whitford found that following natural rainfall, a maximum root channel flow of 35 cm was observed when the ambient wetting front was only 10 cm. Lyford and Qashu (1969) found that the infiltration capacity at the stem of creosotebush is nearly three times greater than that in the areas between plants. In grassland, stemflow is probably less important due to the lack of a single woody stem to focus the flow.

Stemflow should influence both the spatial and temporal measurements discussed above, since canopy storage was exceeded in all four spatial surveys and most of the 17 events sampled by our automated system. We expect that stemflow is the source of the infiltration maxima located near the center of shrub canopies (Figures 4 and 6). The higher variance beneath shrub canopies than at interspaces is the result of these peaks. Stemflow may redirect the water intercepted by canopies. However, it cannot yield canopy-to-interspace infiltration ratios much greater than 1.0, unless canopy shading robs interspaces of precipitation in the presence of wind.

Our infiltration data and observations during rainfall events suggest that lateral redistribution of water via surface runoff is the key process underlying the higher canopy infiltration in both the grassland and shrubland. Surface ponding and overland flow originate when the precipitation rate exceeds the infiltration capacity. Infiltration capacity is typically higher in canopy soils than interspaces in a variety of environments (Lyford and Qashu 1969; Reid and others 1999; Dunkerley 2000). Therefore, ponding and overland flow will occur sooner and during more rainfall events in interspaces than in canopy patches. The runoff from interspace areas then runs onto canopy patches and may infiltrate there (Reid and others 1999). We have observed this transfer of surface water from interspace to canopies in the Sevilleta shrubland. In the grassland, we noted that rainfall that does not immediately infiltrate in the interspaces ponds on the uphill side of grass canopies. This was the result of the raised topography associated with grass clumps.

If surface redistribution leads to differences between canopy and interspace infiltration, then the canopy-to-interspace infiltration ratio should be higher in situations with greater runoff. Surface runoff is enhanced when storm intensity or magnitude is high and when areas with low infiltration capacity are pervasive (Cordova and Rodriguez-Iturbe 1985). The canopy-to-interspace infiltration ratio we measured was typically higher under these conditions. First, canopy infiltration did not exceed interspace infiltration along the second shrub profile only. This was the only profile measured on nearly flat ground, where runoff should be negligible. The other three transects were measured on slopes of approximately 1.5°. Second, the canopy-to-interspace infiltration ratio clearly increases with storm size and therefore runoff (Figure 5). This relationship was not as strong in the grassland, perhaps due to the lack of connectivity between adjacent interspaces. And third, the canopy–interspace ratio was higher in the shrubland when summed over the range of storms sizes and intensities included in the 31 sampled events. The area covered by interspace is roughly twice as high in the shrubland than in the grassland. Therefore, in the shrubland, there are more low-infiltration areas that provide runon to canopies.

The four transects described here do not show that the magnitude of the spatial infiltration variability was different in shrubland and grassland. Data documenting the spatial variability of infiltration over a range of storms were necessary to fully test our third hypothesis. However, our data did show that there were similarities and differences between the spatial structure of infiltration in grassland and shrubland. There were three key similarities between infiltration variability in the two environments. First, most of the spatial variability is found in the vicinity of plant canopies: between the stem and canopy margin in the shrubland and straddling the canopy margin in the grassland. Second, the distance over which most of this variability exists was approximately 50 cm. And third, there was often more infiltration beneath canopies than in interspaces; following rainfall events, canopies were oases where water availability was greater than in the surrounding areas. The notable difference between the two environments was that oases are more intense and spread farther apart in the shrubland because canopies are separated by larger interspaces in this environment.

We examined the spatial patterns of infiltration in grassland and shrubland. Further research is needed to investigate how the observed differences between canopy and interspace infiltration impact plants. We expect that the observed canopy–interspace infiltration contrast will influence plant productivity in two ways. First, water that infiltrates beneath the canopy will more likely be absorbed by plant roots. Root density is greater beneath canopies than beneath bare soil in the Sevilleta grassland and shrubland. In addition, direct evaporation from subcanopy soil is much less than from interspace soil because the canopy reduces midday surface temperatures by approximately 10°C or more. Second, a synergistic interaction between soil moisture and nutrient cycling should exist beneath plant canopies. Enhanced infiltration beneath canopies will promote more intense and longer pulses of nitrogen mineralization following rainfall (see, for example, Cui and Caldwell 1997).

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