

Spatial and temporal patterns of water availability in a grass–shrub ecotone and implications for grassland recovery in arid environments[†]

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ABSTRACT

Encroachment of woody shrubs into historic desert grasslands is a major problem throughout the world. Conversion of grasslands to shrub-dominated systems may result in significant alteration of biogeochemical processes and reduced resource availability in shrub interspaces, making grassland recovery difficult. Soil petrocalcic horizons, which are common in arid and semi-arid regions globally, have been shown to dramatically alter plant water availability. To assess how soil water dynamics are affected by woody encroachment in petrocalcic soils under contrasting precipitation patterns, we conducted a 3-year replicated study in a mixed shrub–grass system measuring soil water in unvegetated interspaces and under mesquite canopies. Plots were instrumented with time-domain reflectometry (TDR) moisture probes, both above and within the soil petrocalcic horizon. Soils under both cover types maintained large increases in available water content for several months during a wetter than normal winter and summer (increases of 0.08–0.16 m³ m⁻³). Interspace soils absorbed significantly greater quantities of water during the winter and retained more water into the spring than soils under shrubs. In contrast, soils under shrubs initially absorbed greater volumes of water during and following summer rains. Differing seasonal dynamics were attributed to interactions between the unique properties of soils with petrocalcic horizons and canopy-induced variability in evapotranspiration. Observed patterns of plant-available water do not support the hypothesis of greater resource availability under shrubs. Similar or greater water availability in shrub interspaces indicates that concentration of soil water under shrubs may not be a process limiting grass recovery on these soils. Published in 2010 by John Wiley & Sons, Ltd.

KEY WORDS desertification; petrocalcic; soil water; available water; *Prosopis*; *Bouteloua*; Chihuahuan desert

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INTRODUCTION

Invasion of grasslands by woody perennials is a persistent problem for arid and semi-arid land managers in many areas of the world, including the southwestern United States (van Auken, 2000; Briggs *et al.*, 2005; Gibbens *et al.*, 2005). Local scale consequences of shrub encroachment in native grasslands include loss of economically important herbaceous forage, increased soil erosion, habitat loss (Grover and Musick, 1990) and other ecosystem services (Havstad *et al.*, 2007). The transition from grasslands to shrublands may be difficult to reverse due to changes in water and nutrient cycling resulting from increased resource heterogeneity (Schlesinger *et al.*, 1996). The composition of plant communities in grasslands, mixed grass–shrub, and shrub communities has been attributed in large part to the spatio-temporal patterns of soil moisture (Walter, 1971; Breshears and Barnes, 1999; Schwinning and Ehleringer, 2001). It is not clear, however, to what

extent the concentration of resources, or ‘resource island’ (Reynolds *et al.*, 1999) phenomenon, applies to soil water availability and whether these processes are important in grass–shrub ecotone communities not yet dominated by shrubs.

Canopy structure and soil–vegetation feedbacks can alter spatial patterns of hydrologically important soil properties following the conversion of grasslands to shrublands. Soil structure under some shrubs is improved when compared to bare interspaces due to higher soil organic matter inputs (Bird *et al.*, 2002), thus increasing infiltration capacity (Pierson *et al.*, 1994). Shrub canopies may also increase infiltration rates by protecting the soil surface from erosion and physical crust formation associated with raindrop impacts. Shrub canopy interception of small rain events, however, can reduce soil water inputs (Abrahams *et al.*, 2003; Loik *et al.*, 2004). Plant litter on the soil surface under shrubs can slow overland flow and decrease losses due to runoff (Abrahams *et al.*, 2006). Additionally, greater canopy shading of the soil surface and increased plant litter under shrubs may reduce soil temperatures, which can decrease soil evaporation rates (Breshears *et al.*, 1998). Increased macrofauna activity and woody root decomposition under shrubs can result

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in a greater density of macropores, which are an important mechanism for infiltration (Devitt and Smith, 2002; Weiler and Naef, 2003).

Results from the literature documenting the effect of woody vegetation on temporal soil water dynamics in arid and semi-arid ecosystems are mixed. Several studies in arid and semi-arid mixed woody–grass ecosystems found consistently drier conditions under shrubs despite lower evaporation rates (Hennessy *et al.*, 1985; Breshears *et al.*, 1997, 1998), while others observed greater soil water contents under shrubs immediately following summer rains (Bhark and Small, 2003). Soil water contents measured on the Jornada long-term ecological research (LTER) site were not consistently affected by the size of the shrub coppice dunes (Reynolds *et al.*, 1999). Long-term, landscape-level soil water data from the Jornada LTER found little evidence that soils under shrubs have greater soil water (Snyder *et al.*, 2006), even though other studies have shown increased infiltration rates under shrubs. Furthermore, soil profiles under mesquite appeared to have lower water contents when compared to interspaces. These contradictory results can be partially explained by differing temporal resolution of the studies and variable storm characteristics. Most of the studies monitored soil water contents on a bi-weekly to monthly basis (Breshears *et al.*, 1997, 1998; Reynolds *et al.*, 1999; Snyder *et al.*, 2006), potentially missing important, but short periods following summer precipitation events like those observed by Bhark and Small (2003) within a few hours of rain events.

While canopy structure and vegetation–soil feedbacks can alter upper soil profile hydrologic properties, deeper soil profile horizon characteristics can also influence vegetation community composition through their effects on spatio-temporal patterns of plant-available water (PAW) (McAuliffe, 1994; Hamerlynck *et al.*, 2000, 2002). For example, shallow rooted species that are drought-deciduous appear to dominate soils with high near-surface water holding capacity and little deep soil water (McAuliffe, 1994). One of the more striking and common subsurface horizons in older soils of arid and semi-arid regions are petrocalcic horizons. Petrocalcic horizons can be over 1 m thick and occur extensively in arid and semi-arid soils globally (Reeves, 1976; Machette, 1985; Monger *et al.*, 2005). Petrocalcic horizons (commonly referred to as ‘caliche’) occur in older soils when a horizon is continuously indurated with carbonates (Soil Survey Staff, 1999), and have been shown to dramatically alter patterns of soil water availability by reducing deep percolation and keeping more water shallow (Duniway, 2006; Duniway *et al.*, 2007) with potential implications for vegetation dynamics (Herbel *et al.*, 1972). Little is known, however, about how soil–vegetation feedbacks associated with woody shrub encroachment function within the context of soils shallow to petrocalcic horizons or potential limitations to grass recovery in these shrub-invaded grasslands.

The goal of this study was to improve our understanding of soil–water dynamics associated with shrub

canopies and associated interspaces in soils shallow to petrocalcic horizons. We addressed this general goal by testing specific soil water hypotheses in a mixed shrub–grass community located on a sandy soil shallow to a petrocalcic horizon. This community, like much of the southwestern United States, was covered by a grassland as recently as 100 years ago (Gibbens *et al.*, 2005). Our approach was to continuously measure soil water contents above and within the petrocalcic horizon both under shrubs and in interspaces lacking perennial vegetation. We hypothesized that soils under shrubs differ when compared to interspace positions in the (1) amount of soil water and (2) amount of plant-available soil water above and within a shallow petrocalcic horizon. Additionally, we hypothesized that (3) wetting and drying dynamics differ between shrubs and interspaces. We explored potential soil–vegetation feedbacks with correlation analyses.

MATERIAL AND METHODS

Study location

The study was located on the USDA-ARS Jornada Experimental Range in the northern Chihuahuan Desert of southern New Mexico, USA (Figure 1). The climate is arid to semi-arid, with a long term (1915–1995) average annual rainfall of 245 mm, of which more than half usually falls from July through October (Wainwright, 2006). Rainfall amount, timing, and intensity are highly variable within and between years. Summer rainfall totals are generally less variable between years but are dominated by intense, localized thunderstorms. Rainfall during the remainder of the year is generally of lower intensity and highly variable between years. The annual rainfall coefficient of variation is 36% (1915–1995). Annual pan evaporation rates far exceeds rainfall, with a measured annual average of 2204.1 mm (1953–1979) (Wainwright, 2006).

Unusually high variability in seasonal and annual precipitation during the study allowed us to evaluate soil water dynamics in interspaces between shrubs and beneath shrub canopies under a wide variety of conditions. Seasonal precipitation totals during winter 2004–2005 and spring 2005 were well above average. These unusually wet seasons were followed by a dry summer in 2005, very dry winter in 2005–2006 and a very dry spring in 2006. This was the second driest November through April since records began in 1914. This extremely dry winter and spring was followed by the wettest August through October recorded on the Jornada.

The study was carried out on a sandy soil shallow to a petrocalcic horizon (50–60 cm) of the Hueco series (coarse-loamy, mixed, superactive, thermic Argic Petrocalcids) located on the broad alluvial plain of the ancestral Rio Grande River (106°51'14"W 32°35'31"N) (Figure 1). The petrocalcic horizon has a stage V morphology with a laminar layer and pisoliths evident (Birkland, 1999). Additionally, there is a 1–10-cm-thick horizon of coarse

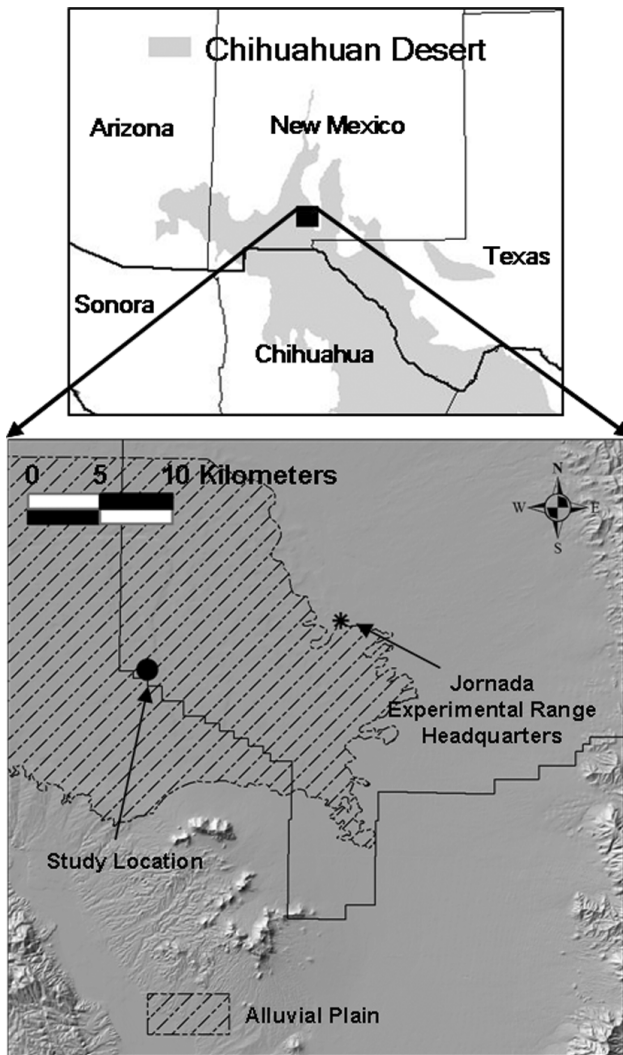


Figure 1. The study, which was located on the broad alluvial plain of the ancient Rio Grande River within the USDA-ARS Jornada Experimental Range (black lines) in the northern Chihuahuan Desert in southern New Mexico, USA. Chihuahuan Desert boundary after Schmidt (1979); alluvial plain after Monger *et al.* (2006).

petrocalcic rubble above the laminar horizon. This is common in many shallow petrocalcic horizons (Hirmas and Allen, 2007). The study site has a mixed shrub–grass vegetation community dominated by mesquite (*Prosopis glandulosa*) and black grama (*Bouteloua eriopoda*). The study site represents a transitional location in the

grassland to shrubland continuum, with no coppice dune formation under shrubs or significant soil loss in the shrub interspaces (Figure 2).

Soil water content

We instrumented the site with time-domain reflectometry (TDR) soil moisture sensors in a split plot design with two whole plot treatment levels of vegetation cover type (Shrub and Interspace) and five subplot treatment levels of soil depth (Shallow, Intermediate, Upper Petrocalcic, Mid Petrocalcic, and Deep Petrocalcic) (Figure 3). Six instrumented soil pits were located in shrub interspaces, approximately 60 cm from the base of *B. eriopoda* (grass) plants; and six pits under the canopies of *P. glandulosa* (shrubs), approximately one-third of the canopy radius in from the shrub drip line. We located the soil pits such that the petrocalcic horizon depth was similarly shallow (50–60 cm). The lateral extent of the site was limited to approximately 25 m due to allowable sensor cable lengths.

Soil moisture probes were placed relative to depth and horizon in small individual mini-pits (approximately 50 cm × 75 cm × 85 cm deep) (Figure 3). Two soil moisture probes were installed at depths above the petrocalcic: one at 30 cm (Shallow) and the other just above the laminar horizon or petrocalcic rubble that occurred on top of the laminar horizon (Intermediate). The petrocalcic horizon was instrumented with three soil moisture sensors installed at 5 cm (Upper Petrocalcic), 10 cm (Mid Petrocalcic), and 20 cm (Deep Petrocalcic) into the horizon, relative to the upper horizon boundary (Figure 3). We concentrated petrocalcic horizon measurements in the upper sections because these locations were more likely to interact with the rhizosphere. To allow insertion of TDR rods into the petrocalcic horizon, we drilled undersized pilot holes (2.778 mm) using a cordless hammer drill guided by a metal jig. However, in some excessively hard material it was not possible to insert TDR rods into undersized holes, and holes matching the TDR rod diameter (3.175 mm) were used. With the jig in place as a guide, probes were inserted partially by hand and finished using a wood block and hammer. The jig also served as a guide during probe installation for Shallow and Intermediate depths. We replaced and repacked soil by depth, compacting to approximate field bulk density

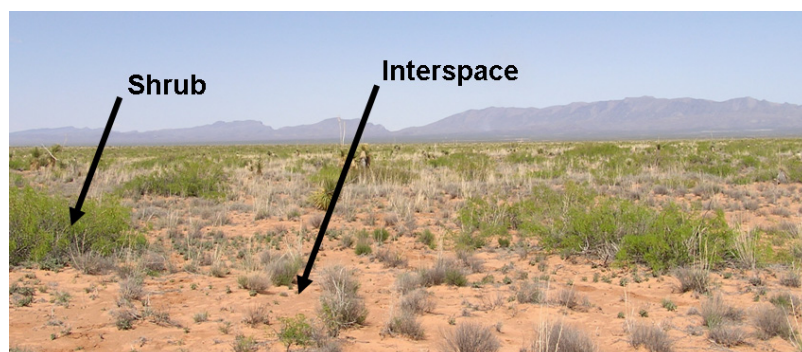


Figure 2. Study site location photo with vegetation cover type examples labeled.

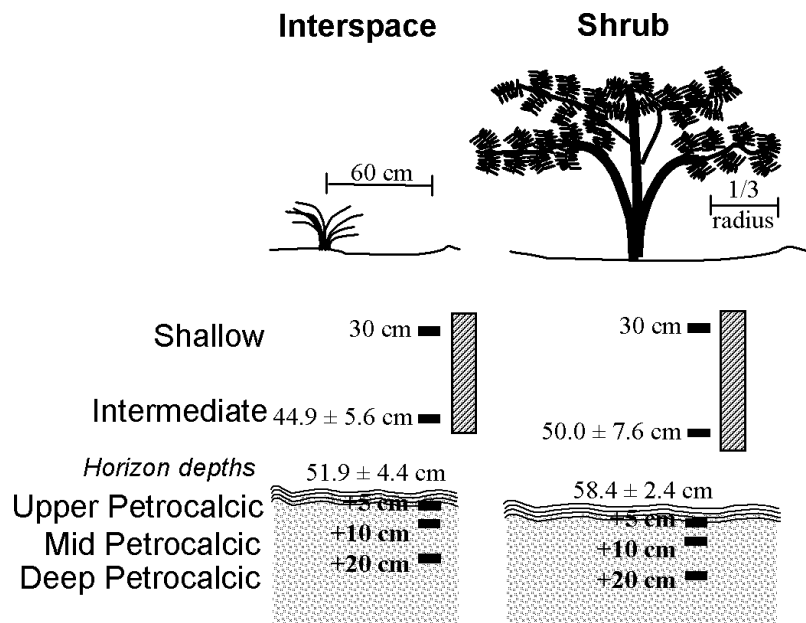


Figure 3. Site soil moisture monitoring instrumentation schematic. Trifilar TDR soil moisture probes (black rectangles) were inserted horizontally. Shallow probe depth was kept constant (30 cm) at all locations. Intermediate and Petrocalcic probes were located at standard vertical distances above and below the top of the petrocalcic horizon. The Intermediate and horizon boundary depths are site averages with standard deviations. Cross-hatched bars represent Upper Profile depths used for analysis.

using a steel plate and heavy iron pipe. In repacking the petrocalcic horizon, extra care was taken to tightly repack the removed material to original horizon density and depth. Completed pits were flush with the soil surface.

TDR sensors were connected to multiplexers and a wave propagator to generate probe wave forms (SDMX50, TDR100, Campbell Scientific, Logan, UT). Two measurements from each probe were taken every 8 h, and wave forms saved by the data logger (CR10X, Campbell Scientific, Logan, UT) were later analysed for sensor travel time using the TACQ program (Evelt, 2000). The measured apparent dielectric constant was converted to volumetric water content using Topp's equation (Topp *et al.*, 1980) for Shallow and Intermediate depths and a soil specific calibration equation was used for the Petrocalcic depths (see Duniway, 2006 for detailed TDR methods).

To facilitate comparing soil water content among horizons with strongly contrasting pore size distributions, the amount of PAW was estimated by subtracting the permanent wilting point volumetric water content (θ_{PWP}) specific for each probe from measured volumetric water contents. We used the conventional plant permanent wilting point of -1.5 MPa to make the results broadly applicable (Romano and Santini, 2002). Although most species on the study site likely can persist (and not 'permanently wilt') at xylem or leaf water potentials drier than -1.5 MPa (Senock *et al.*, 1994), plant water utilization from a soil layer with a bulk soil water potential of less than -1.5 MPa likely is small. Thus, the PAW concept is still useful for comparing soil water content measurements among contrasting soil types and horizons. Estimates of θ_{PWP} were determined for Shallow and

Intermediate depths using a predictive relationship (pedotransfer function) based on measured soil texture and bulk density (Schaap *et al.*, 2001). Due to their unique physical and chemical characteristics, pedotransfer functions were not used to determine θ_{PWP} in the petrocalcic horizon. Instead, we measured the characteristic soil water release curve (SWRC) for the soil material at each probe from approximately -0.5 MPa to <-5.0 MPa using a chilled mirror psychrometer (WP4 Potentiometer, Decagon Devices, Pullman, WA; Scanlon *et al.*, 2002). Water retained at -1.5 MPa was obtained by extrapolating measured SWRCs using the van Genuchten (1980) equation modified for gravimetric water content. Gravimetric water contents were converted to volumetric water contents using estimated bulk densities based on a multiple regression relationships (Duniway, 2006) and validated with petrocalcic horizon bulk density values from nearby soil pits (Soil Survey Staff, 2006).

Vegetation characterization

To better understand how vegetation responded to the wet winter of 2004–2005 and wet summer of 2006, site vegetation was characterized using the point intercept method (Herrick *et al.*, 2005) in July 2005 and October 2006. Square 1-m grids were centred on each of the 12 soil moisture arrays and cover measured with 100 points per grid.

Statistical analyses

Diurnal variability of TDR soil water contents was generally less than $0.01 \text{ m}^3 \text{ m}^{-3}$, so daily average water contents for each TDR probe were used. Upper Profile PAW was calculated by averaging Shallow and Intermediate

depth PAW. Petrocalcic PAW was calculated by weighting PAW measurements within the petrocalcic horizon by their representative depth to generate a horizon average. For petrocalcic replicates with a missing measurement depth, we used the average of the two remaining probes within each replicate (Duniway, 2006).

Average Intermediate measurement depths were not significantly different between vegetation cover types ($p = 0.213$) but within cover type variability did exist, so depth was included as a covariate in Upper Profile analyses. Petrocalcic horizon depth was significantly different between vegetation cover types ($p = 0.009$) (Figure 3). Therefore, we did not include probe depth as a covariate in reported petrocalcic water dynamic statistical analyses. On average, Shrub Petrocalcic probe depth was 6.6 cm deeper than in the Interspace. We tested the assumption that the 6.6 cm difference in average petrocalcic depth did not have any significant effect on the results by adding a depth covariate and re-running all statistical tests. Including a petrocalcic depth covariate did increase our power to detect differences in a few instances; however, it had no effect on the significance of any results reported here.

To test hypotheses addressing amount of PAW through time, analysis of variance (PROC GLM, SAS Institute, 2001) was done for each day of measurement. We tested for significant differences in Upper Profile and Petrocalcic PAW between vegetation cover types ($\alpha = 0.05$). While this approach can cause a high experiment-wise type I error rate, for this exploratory study we were more concerned with minimizing the type II error rate and increasing power to detect when significant differences were most likely to exist.

To evaluate differences in petrocalcic horizon wetting and drying rates, a linear model was fit to Petrocalcic PAW through time for specific wetting and drying events. We used a repeated measures analysis with a heterogeneous autoregressive covariance structure and Satterthwaite degrees of freedom (PROC MIXED, SAS Institute, 2001). To test for differences in rate of wetting or drying between vegetation cover types, a full model was fit with cover type, time and cover type by time effects. To estimate rate of drying in each cover type, analyses were re-run using a reduced model without the time (common slope) term. Five-day means were used to facilitate analysis of long time periods (>60 days). The calendar year was divided into three seasons that captured much of the

important annual variability in climate and plant phenology at the study site: summer (July through October), winter (November through February) and spring (March through June).

Analysis of variance was used to test for significant differences ($\alpha = 0.05$) in average cover by functional group for each year of vegetation measurements in each vegetation cover type (PROC GLM, SAS Institute, 2001). To allow for parametric analysis, we arcsine-transformed the data for significance tests and calculating variances (Snedecor and Cochran, 1980). Reported data were back-calculated to percent.

Correlation analyses were performed to test for possible relationships between relative plant cover and amount of PAW (PROC CORR, SAS Institute, 2001). Variables used were average season Shallow and Petrocalcic PAW for the spring 2005 and summer 2006 and cover of vegetation functional groups for the measurement period.

RESULTS

Vegetation and soils

Significant differences were detected in the hydrologically important attributes of total cover and bare ground between vegetation cover types in 2005 but not after the wet summer of 2006 (Table I). Litter cover was consistently significantly greater under the shrubs in both years. The Interspace did not have greater cover of perennial grasses than the Shrubs but did have significantly higher cover of *B. eriopoda* when data from both years were combined. The lack of differences detected in the perennial grass functional group was due to the relatively high cover of *Sporobolus* species in a few Shrub plots. The increase in perennial grass cover between years was driven by increases in *B. eriopoda* in the Interspace and *Sporobolus* species under the shrubs. *P. glandulosa* was the only shrub present at the soil moisture sensor locations. Although no significant differences were detected in annual cover or cover of any annual species following the wet winter of 2004–2005, Shrub locations did have higher total average cover of the late-winter, early-spring-active annuals panamint cryptantha (*Cryptantha angustifolia*) and pinnate tansymustard (*Descurainia pinnata*). Following the wet summer of 2006, Interspace plots had significantly greater cover of annual species, primarily due to the presence of the annual grass *Bouteloua barbata* in most interspaces.

Table I. Average July 2005 and October 2006 canopy cover by functional group. Standard deviations in parentheses.

Year	Cover type	N	Total canopy (%)	Bare ground (%)	Litter (%)	Perennial grasses (%)	Shrubs (%)	Perennial forbs/sub-shrubs (%)	Annuals (%)
2005	Interspace	6	46.9b* (14.6)	42.9a (16.6)	26.3c (11.3)	13.9b (8.8)	0.0b (0.0)	7.2a (8.9)	34.5b (11.4)
	Shrub	6	86.2a (12.6)	9.4b (7.9)	58.9b (22.3)	11.5b (8.3)	62.4a (9.3)	5.0a (4.3)	43.7b (10.7)
2006	Interspace	6	85.9a (9.8)	6.4a (8.3)	71.0b (25.7)	33.1ab (30.8)	0.0b (0.0)	2.5a (3.6)	80.3a (30.8)
	Shrub	6	87.3a (8.7)	3.3a (4.7)	87.5a (21.8)	41.4a (25.4)	55.0a (17.4)	4.5a (3.3)	47.1b (17.4)

* Values within columns with the same letter do not differ as determined by Fisher's protected LSD ($p < 0.05$).

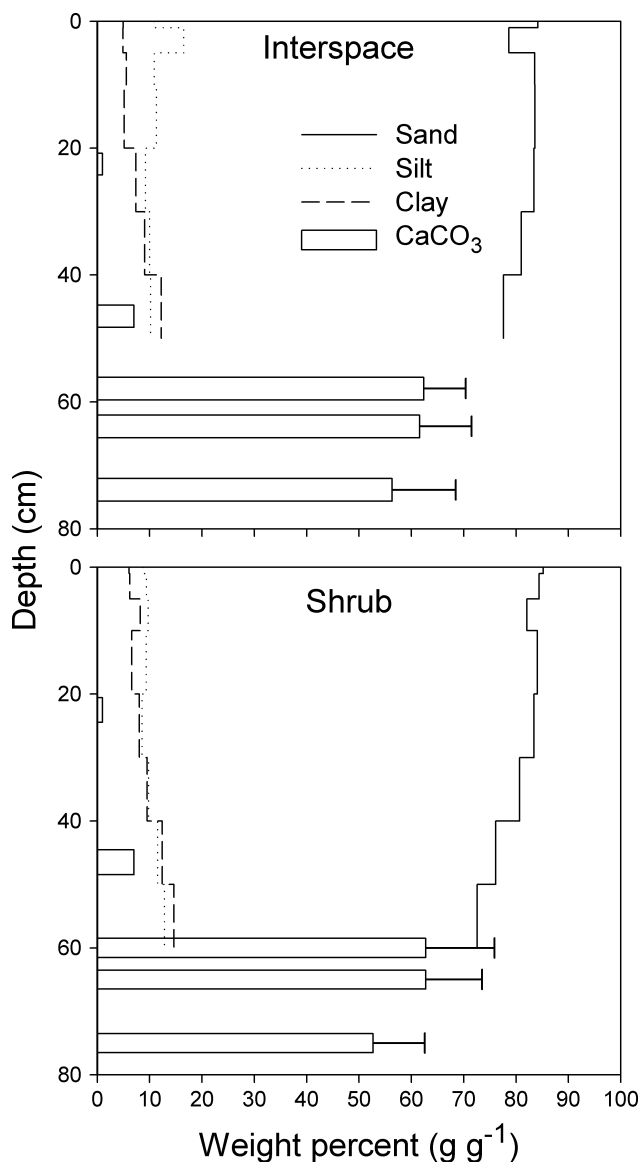


Figure 4. Soil profile texture and carbonate content. Sand, silt and clay values are site means from non-carbonate depths. CaCO_3 values are average measurements from petrocalcic carbonate horizon soil moisture sensor positions. Other CaCO_3 values represent horizon values from similar soils in the same series located near the study sites (Soil Survey Staff, 2006). Particle size was measured by the hydrometer method (Gee and Or, 2002) and CaCO_3 content by the manometer method (Nelson, 1982).

Soil profile characteristics were very similar in the Shrub and Interspace cover types. Soil textures ranged from loamy sands to sandy loams in both profile locations (Figure 4). Soil bulk density θ_{PWP} and Petrocalcic percent CaCO_3 were all similar between cover types (Table II, Figure 4). Percent CaCO_3 within the petrocalcic horizons was 9–10 times higher than maximum upper profile carbonate contents for a similar Hueco series soil.

Soil water

Shallow and Intermediate depth water contents closely mirrored precipitation in both vegetation cover types (Figure 5). Large increases occurred at both depths in response to the winter 2004–2005 rains, reaching peak

water contents of $0.14\text{--}0.17\text{ m}^3\text{ m}^{-3}$ by mid-February. Most winter precipitation stored in the Shallow and Intermediate depths was depleted by April 2005. Shallow and Intermediate water contents continued to decrease slightly during the spring and early summer, reaching minimums of $0.04\text{--}0.05\text{ m}^3\text{ m}^{-3}$ for the 2005 calendar year in early August. After rising slightly in response to the few precipitation events during the summer 2005, Shallow water contents declined steadily during the very dry winter 2005–2006 and spring 2006, with both cover types reaching a minimum water content of $0.03\text{ m}^3\text{ m}^{-3}$ for the study in early July 2006. Shallow and Intermediate water contents in both cover types increased abruptly in response to the intense rains in August 2006, quickly exceeding peak winter 2004–2005 water contents. The Shallow and Intermediate depths reached maximum water contents of $0.22\text{--}0.26\text{ m}^3\text{ m}^{-3}$ on September 4 and then slowly decreased through the relatively dry month of September. Muted versions of this cycle of wetting and drying repeated again from October to December 2006 and January to April 2007.

Throughout the study period, the petrocalcic horizons had consistently higher soil water contents than the Shallow and Intermediate depths in both cover types (Figure 5). All Petrocalcic measurement depth water contents increased rapidly during the wet winter 2004–2005. Under shrubs and in the shrub interspaces, Petrocalcic water contents reached very high maxima at the end of the winter season of $0.25\text{--}0.29\text{ m}^3\text{ m}^{-3}$. All Petrocalcic depths lost much of the retained winter moisture during the first 2 months of spring 2005, similar to the Shallow and Intermediate depths. In contrast to the Shallow and Intermediate depths, however, the petrocalcic horizons continued to slowly dry during May and June, not reaching pre-winter levels until mid-July 2005. During summer 2005, the downward trend in average petrocalcic horizon water contents ceased, with a slight upward trend evident under the shrubs canopies. Petrocalcic horizon drying resumed during the following dry period, reaching minimum values in the late winter of $0.14\text{--}0.16\text{ m}^3\text{ m}^{-3}$. All petrocalcic horizon water contents increased sharply following the intense summer rains in August 2006, reaching soil water contents $0.37\text{--}0.40\text{ m}^3\text{ m}^{-3}$, which is at or near saturation (Duniway *et al.*, 2007). Similar to the upper profile, soil water contents in the petrocalcic declined during the relatively dry month of September 2006. Rains that fell in late September and early October 2006 recharged the petrocalcic horizon in both cover types back to water contents of $0.31\text{--}0.34\text{ m}^3\text{ m}^{-3}$, similar to maximum levels observed during the winter of 2004–2005. These high water contents were maintained until March 2007. Similar to the dry-down after the wet winter of 2004–2005, petrocalcic horizons slowly dried throughout the spring of 2007.

PAW

The Upper Profile interspace PAW was higher during cool wet periods but there were few differences in PAW

Table II. Average soil properties at soil moisture sensor locations. Standard deviations in parentheses.

Depth	θ_{PWP}		Bulk density	
	Interspace ($\text{m}^3 \text{m}^{-3}$)	Shrub ($\text{m}^3 \text{m}^{-3}$)	Interspace (g cm^{-3})	Shrub (g cm^{-3})
Shallow	0.051 (0.003)	0.050 (0.005)	1.46 (0.05)	1.44 (0.05)
Intermediate	0.055 (0.005)	0.060 (0.011)	1.35 (0.07)	1.36 (0.04)
Petrocalcic				
Upper	0.135 (0.025)	0.149 (0.016)	1.76 (0.03)	1.70 (0.16)
Mid	0.135 (0.020)	0.142 (0.007)	1.78 (0.11)	1.69 (0.19)
Deep	0.136 (0.012)	0.148 (0.019)	1.68 (0.08)	1.64 (0.13)

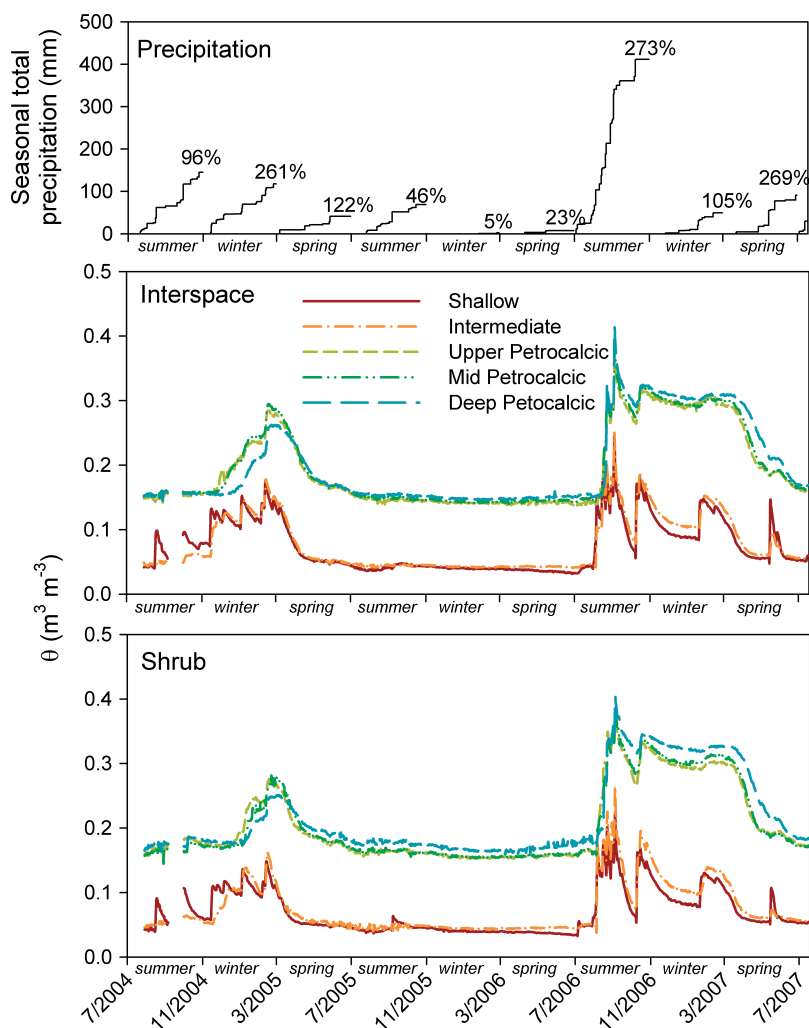


Figure 5. Seasonal accumulated daily precipitation as a percent of 1915–1995 average (upper panel) and average water contents (θ) by depth under Interspace and Shrub cover types (lower two panels). Precipitation was recorded daily by a weighing bucket rain gauge located approximately 50 m from the site.

between cover types during warm wet periods (Figure 6). For a period from the last week of October through the end of November 2004, Interspace Upper Profile depths had significantly more PAW than the Shrub. During the drying that occurred in the Upper Profile beginning in late winter, Shrub positions dried sooner, resulting in significantly less PAW than the Interspace for the month of March 2005. After mid-spring 2005, there was no PAW in the Upper Profile in either vegetation cover type until the summer rains began in August 2006. In contrast to the cool season rains during the winter of 2004–2005,

however, Upper Profile wetting during the summer of 2006 was not different in the two cover types. Similar to the winter 2004–2005 wetting and drying events, however, the Interspace had periods with significantly greater PAW in March and May 2007.

In contrast to the Upper Profile, there were almost no significant cover type differences detected in Petrocalcic PAW (Figure 6). Although not statistically significant, Interspace Petrocalcic PAW was higher on average than the Shrub during the winter 2004–2005 and early spring 2005. In early March 2005, the Interspace and Shrub

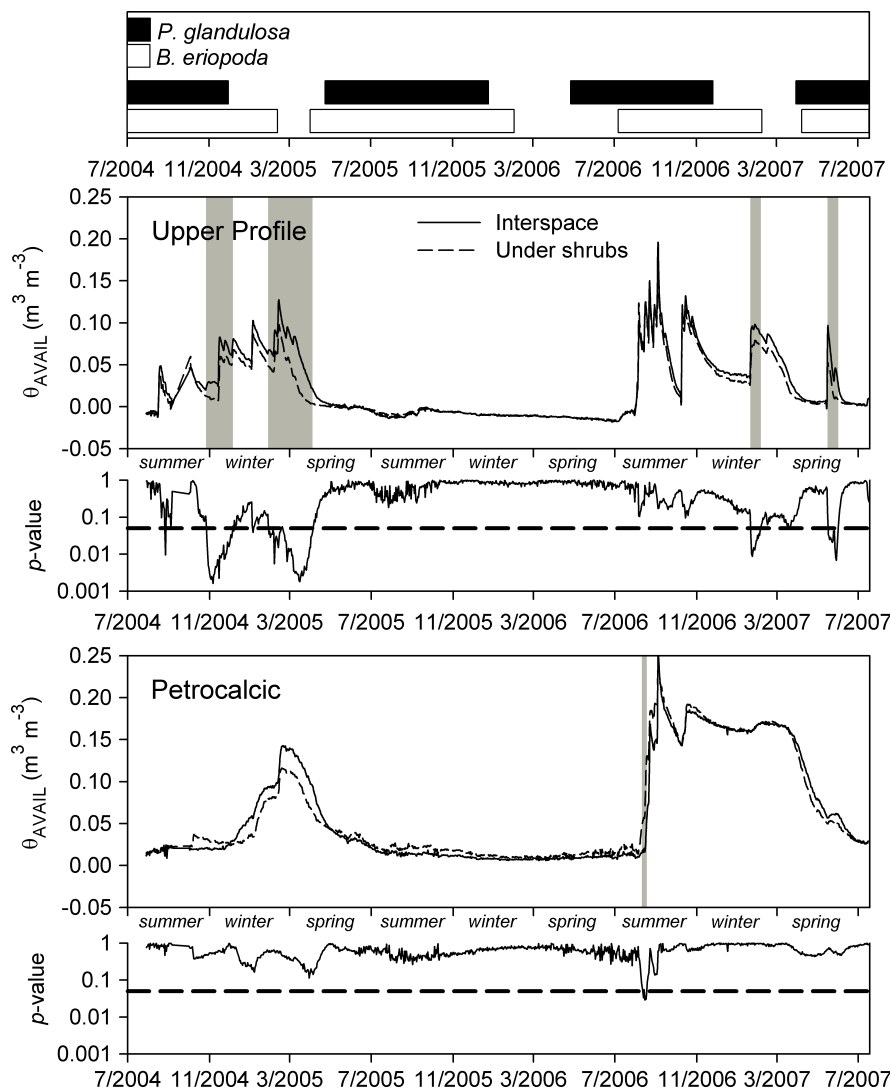


Figure 6. Dominant species phenology (upper panel), plant-available water (PAW) (θ_{AVAIL}) for the Upper Profile ($\sim 25\text{--}48$ cm) and Petrocalcic ($\sim 55\text{--}75$ cm) and contrast p -values testing for significant differences in cover type available water through time. The 0.05 probability level is delineated with a dashed line in the p -value panels. Grey shading on PAW panels indicate periods where contrast p -values are < 0.05 . Bars in the phenology panel indicate periods when $< 50\%$ of individuals of each species were dormant at nearby (< 2 km away) Jornada LTER research sites with the same soil type and vegetation community as the study site (Jornada Basin LTER, 2006).

Petrocalcic reached maximum average PAW of 0.14 and $0.11 \text{ m}^3 \text{m}^{-3}$, respectively. Petrocalcic PAW converged during April 2005 and the Shrub Petrocalcic retained slightly more PAW during the following dry seasons. Minimum Petrocalcic PAW occurred during early March 2006 with average water contents only slightly larger than θ_{WP} , 0.006 and $0.011 \text{ m}^3 \text{m}^{-3}$ of PAW in the Interspace and Shrub, respectively. The Shrub Petrocalcic positions increased sooner than the Interspace in response to the intense summer 2006 rains, reaching significantly higher PAW for a period of 1 week in August. After the initial difference in wetting rates, the petrocalcic horizons in the two cover types had nearly identical wetting and drying dynamics with neither drying to pre-summer levels before the end of the study, 18 July 2007.

Petrocalcic wetting and drying dynamics

Wetting and drying dynamics in the Upper Profile were reflected in the petrocalcic horizons (Figures 5, 7;

Table III, IV). After an initially faster Petrocalcic Interspace wetting (Period A), the two vegetation cover types wet and dried in a fairly parallel pattern in the central periods of maximum PAW during winter 2004–2005 (periods B, C and D Figure 7; Table III). Convergence of the Petrocalcic PAW occurred during April 2005 (period E), causing the significant cover type by time interaction. The Shrub Petrocalcic wet significantly faster than the Interspace following the initial intense summer rains in August 2006 (period J and K, Figure 7; Table III) but the Shrub and Interspace petrocalcic horizons wet and dried at the same rates after the initial wetting. This was similar to the dynamics in the winter of 2004–2005.

Decreasing trends in Petrocalcic PAW were detected during periods with minimal precipitation inputs (periods F and H, Figure 7; Table IV). During the long dry period from October 2005 through March 2006 (period H), there was a significant cover type by time interaction effect,

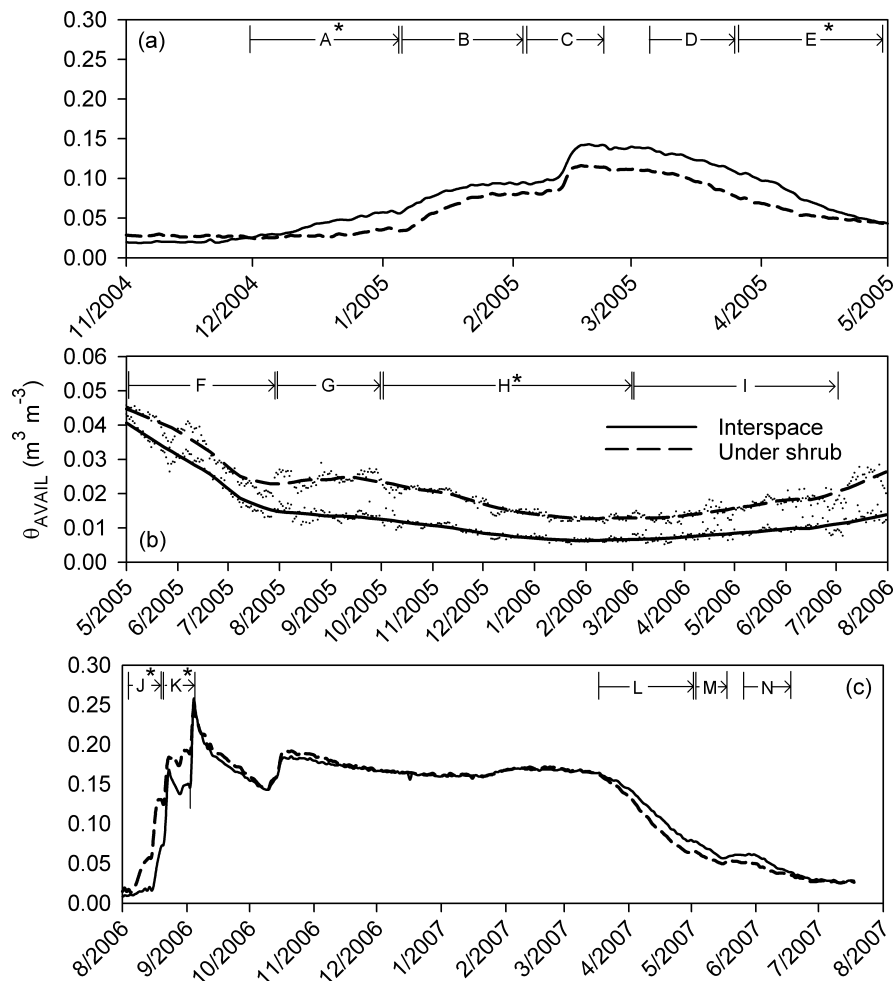


Figure 7. Petrocalcic wetting and drying events analysed with repeated measures: Winter, 2004–2005 through spring 2005 (wet period) (a); May 2005 through August 2006 (dry period) (b); and summer 2006 through spring 2007 (wet period) (c). For the dry period (b), data were smoothed for analysis: small dots are the observed data. Periods analysed are noted by letters, and asterisk following letters indicates rate of change in the two cover types that were significantly different ($p < 0.05$).

indicating the higher Shrub drying rate was significantly faster than the Interspace rate. There was no detectable drying, however, of either cover type Petrocalcic during the summer of 2005 (period G), even though seasonal precipitation was less than half of long-term average (Figure 5).

DISCUSSION

In general, there were few differences in amount of soil water between the two vegetation cover types. Significantly different PAW was observed during only 4 of the nearly 36 months monitored. When differences did occur, however, it was contrary to previous studies and expectations based on hydrologic processes. For example, greater amounts of Upper Profile PAW in the Interspace vegetation cover type during the early winter of 2004–2005, a time frame when *P. glandulosa* was still leafed out (Figure 6), contradict expected results based on presumed greater infiltration capacity and reduced soil surface evaporation under shrub canopies, indicating other hydrological processes were more important during the cool season rains. During this period, storm events

were generally small, the average daily total for days with precipitation during this period was only 5.2 mm and winter rain events on the Jornada are typically of low intensity (Wainwright, 2006). The importance of possible differences in infiltration capacity between the two cover types would be less during small low-intensity rain events. The higher Shrub canopy cover (Table I) may have led to greater water loss through canopy interception of rain and subsequent evaporation, thereby reducing the Shrub winter soil water inputs relative to the Interspace (Loik *et al.*, 2004). Drier Shrub antecedent soil water content would also delay percolation of later winter moisture to the depths of the first probes. Although canopy cover measurements are not a good predictor of soil water extraction by the extensive root system of *P. glandulosa* (Gile *et al.*, 1997), it is likely that the Shrub soils had greater rooting densities and thus more soil water lost to transpiration than the Interspace prior to senescence of *P. glandulosa* in December (Figure 6). A similar combination of greater transpirational loss and water lost through canopy interception could explain the 2-week period in spring 2007 with significantly less PAW under the shrubs.

Table III. Rate of change in petrocalcic horizon available soil water content during wet periods. Repeated measures analysis results for select wetting and drying events. Period lettering corresponds to Figure 7.

Cover type	Period A	Period B	Period C	Period D	Period E	Period J	Period K	Period L	Period M	Period N
	26 November 2004 to 6 January 2005 ($\text{m}^3 \text{m}^{-3} \text{d}^{-1} \times 10^{-3a}$)	7 January to 29 January 2005 ($\text{m}^3 \text{m}^{-3} \text{d}^{-1} \times 10^{-3a}$)	8 February to 18 February 2005 ($\text{m}^3 \text{m}^{-3} \text{d}^{-1} \times 10^{-3a}$)	06 March to 25 March 2005 ($\text{m}^3 \text{m}^{-3} \text{d}^{-1} \times 10^{-3a}$)	25 March to 29 April 2005 ($\text{m}^3 \text{m}^{-3} \text{d}^{-1} \times 10^{-3a}$)	5 August to 22 August 2006 ($\text{m}^3 \text{m}^{-3} \text{d}^{-1} \times 10^{-3a}$)	22 August to 2 September 2006 ($\text{m}^3 \text{m}^{-3} \text{d}^{-1} \times 10^{-3a}$)	19 March to 29 April 2007 ($\text{m}^3 \text{m}^{-3} \text{d}^{-1} \times 10^{-3a}$)	29 April to 15 May 2007 ($\text{m}^3 \text{m}^{-3} \text{d}^{-1} \times 10^{-3a}$)	1 June to 18 June 2007 ($\text{m}^3 \text{m}^{-3} \text{d}^{-1} \times 10^{-3a}$)
Interspace	1.06*** 0.25* b	1.19*** 1.55*** a	2.31*** 1.43*** a	-0.99** -1.01** a	-2.34*** -1.51*** a	0.55b 4.28*** a	-3.66** -0.19a	-2.19*** -2.40*** a	-1.05*** -0.52* a	0.20a 0.00a

* Rate of change significantly different than zero at the 0.05 probability level.

** Rate of change significantly different than zero at the 0.01 probability level.

*** Rate of change significantly different than zero at the 0.001 probability level.

a Reported values are the actual values multiplied by 1000.

b Values within columns with the same letter do not differ as determined by the time \times cover type interaction test ($p > 0.05$).

This pattern of significantly greater PAW in the Interspace during cooler periods was repeated in the spring of 2005 and winter of 2006–2007, time periods when *P. glandulosa* was leafless (Figure 6). In addition to drier antecedent conditions, transpiration losses from annual plant species appear to have contributed to the observed variability in PAW during spring 2005. Both the Shrub and Interspace cover types had high amounts and variability in cover of annual species (Table I). Cover of annual species was strongly and significantly negatively correlated with spring 2005 average Shallow soil water contents across all plots (Table V). Cover of litter in July, much of which was likely dead annual species from the previous winter, was strongly and significantly negatively correlated with Shallow spring 2005 soil water content across cover types as well as both Shallow and Petrocalcic spring 2005 PAW within the Shrub cover type. These trends indicate that the drier Upper Profile spring 2005 water contents were strongly influenced by annual plant uptake, uptake that possibly reduced the amount of winter moisture that reached the petrocalcic horizon. Additionally, downward hydraulic redistribution by *P. glandulosa* roots to soil layers below the petrocalcic horizon could have contributed to the drier conditions in the Upper Profile under the shrubs during these periods. A *P. glandulosa* tap root excavated by Gibbens and Lenz (2001) near the study site extended through cracks in the petrocalcic horizon to much deeper soil layers, and another species of *Prosopis* (*P. velutina*) has been shown to move significant amount of soil water from wetter upper soil layers to dry deeper layers when dormant (Hultine *et al.*, 2004).

The more rapid Shrub Petrocalcic wetting and greater water availability during August 2006 is attributed to greater water infiltration and bypass flow occurring under the shrub canopies during intense summer rains (Abrahams *et al.*, 2003). In contrast to the gentle winter rains, storms during August 2006 had nearly three times the average winter rainy day totals (14.9 mm). During this period, the Shrub Petrocalcic increased by $0.12 \text{ m}^3 \text{m}^{-3}$ compared to only a $0.04 \text{ m}^3 \text{m}^{-3}$ increase in the Interspace Petrocalcic (Figure 6). The wetting of the Shrub Petrocalcic lagged behind Upper Profile wetting by less than the 8-h measurement interval, indicating rapid deep penetration of the summer rains, potentially due to macropores and preferential flow along woody roots (Devitt and Smith, 2002). The importance of flow through macropores and along woody roots is further supported by the lack of differences in Upper Profile PAW between cover types, indicating that the additional water that reached the Shrub petrocalcic bypassed the Upper Profile along preferential routes.

None of the measured cover attributes explained any of the variability in summer 2006 PAW across the whole site or within the Shrub cover type. Interspace perennial grass cover, however, was significantly and very strongly positively correlated with summer 2006 Interspace Petrocalcic PAW, indicating the potential importance of perennial grass root systems for enhancing infiltration capacity

Table IV. Rate of change in petrocalcic horizon available soil water content during dry periods. Petrocalcic repeated measures linear modeling of dry periods. Period lettering corresponds with those on Figure 7.

Cover type	Period F	Period G	Period H	Period I
	1 May to 1 August 2005 ($\text{m}^3 \text{m}^{-3} \text{d}^{-1} \times 10^{-3a}$)	1 August to 1 October 2005 ($\text{m}^3 \text{m}^{-3} \text{d}^{-1} \times 10^{-3a}$)	1 October 2005 to 1 March 2006 ($\text{m}^3 \text{m}^{-3} \text{d}^{-1} \times 10^{-3a}$)	1 March to 1 July 06 ($\text{m}^3 \text{m}^{-3} \text{d}^{-1} \times 10^{-3a}$)
Interspace	-0.250*** <i>a</i> ^b	0.023 <i>a</i>	-0.130*** <i>a</i>	0.023 <i>a</i>
Shrub	-0.190*** <i>a</i>	0.045 <i>a</i>	-0.190*** <i>b</i>	0.032 <i>a</i>

*** Rate of change significantly different than zero at the 0.001 probability level.

^a Reported values are the actual values multiplied by 1000.

^b Values within columns with the same letter do not differ as determined by the time \times cover type interaction test ($p > 0.05$).

Table V. Relationship between relative plant cover and amount of plant available water. Pearson's correlation coefficient (r) of average spring 2005 and summer 2006 available soil water contents and July 2005 and October 2006 vegetation cover, respectively. Correlations were done across the whole plot and by cover type for both Shallow and Petrocalcic depths.

Cover type	Depth	<i>N</i>	Total canopy	Bare ground	Litter	Perennial grasses	Shrubs	Annuals
<i>Spring, 2005</i>								
Whole site	Shallow	12	-0.71**	0.79**	-0.86***	-0.14	N/A [†]	-0.63*
	Petrocalcic	12	-0.23	0.21	-0.42	0.48	N/A	-0.30
Interspace	Shallow	6	-0.83*	0.87*	-0.78	-0.32	N/A	-0.48
	Petrocalcic	6	0.13	-0.11	0.11	0.59	N/A	-0.04
Shrub	Shallow	6	-0.23	0.37	-0.91*	-0.24	0.65	-0.56
	Petrocalcic	6	-0.63	0.73	-0.88*	0.29	0.25	-0.53
<i>Summer, 2006</i>								
Whole site	Shallow	12	-0.05	0.01	-0.09	-0.25	N/A	-0.02
	Petrocalcic	12	-0.15	-0.15	0.25	0.53	N/A	-0.51
Interspace	Shallow	6	0.18	-0.21	0.03	-0.26	N/A	0.07
	Petrocalcic	6	-0.46	0.06	-0.23	0.91*	N/A	-0.56
Shrub	Shallow	6	-0.18	0.29	-0.21	-0.24	0.34	-0.23
	Petrocalcic	6	0.10	-0.36	0.49	-0.13	0.55	0.10

[†] Only done for Shrub cover type because no shrubs in Interspace cover type.

* Correlation coefficient significantly different than zero at the 0.05 probability level.

** Correlation coefficient significantly different than zero at the 0.01 probability level.

*** Correlation coefficient significantly different than zero at the 0.001 probability level.

and soil structure, thereby facilitating deep penetration of the intense summer rains. The lack of significant correlations between summer 2006 perennial grass cover and PAW in the Upper Profile is probably due to the opposing processes of greater infiltration and higher transpirational losses in plots with greater grass cover.

It is possible that systematic differences in small-scale microtopography (<5 cm vertical differences occurring over ~1 m) contributed to observed differences in soil water contents between vegetation cover types. Interspaces were generally very slightly concave, and Shrubs were generally linear or very slightly convex. Overland flow of water off convex positions and onto concave positions should be greater following high-intensity storms. The results presented here, i.e. greater Interspace PAW in the winter (low-intensity rain) and greater Shrubs PAW in the summer (high-intensity rain) (Figure 6), do not follow this pattern and suggest that lateral redistribution was not an important mechanism at the study site.

Estimates of Petrocalcic wetting and drying rates indicate that petrocalcic horizons have a very low hydraulic

conductivity when dry (Table IV) but can have fairly high rates when nearly saturated (Table III). These dynamics can be observed in the slowing of Petrocalcic water dynamics at fairly high water contents (~0.18 $\text{m}^3 \text{m}^{-3}$) (periods E and M, Figure 3; Table III). The initial rates of wetting under the shrubs during the intense summer storms were nearly double the fastest wetting rates observed during the winter 2004–2005 rains (Table III). These high rates of wetting indicate that petrocalcic horizons can have relatively high hydraulic conductivity when nearly saturated.

Decreasing trends in petrocalcic horizon PAW during periods with minimal precipitation inputs suggest that the Petrocalcic was slowly releasing stored water (periods F and H, Table IV; Figure 7). Although it appears that petrocalcic horizons readily release stored water into the rhizosphere when fairly wet (Figure 7), the very slow dynamics during the very dry late-spring, early-summer 2006 growing season (period I) indicates water extraction was primarily limited by the very slow hydrological conductivity of the fairly dry soil horizon. TDR sensors

used in medium to coarse textured soils have been shown to be very insensitive to temperature effects, even in high-carbonate soils (Evelt *et al.*, 2005), indicating that the gradual drying observed was not an equipment effect. Furthermore, it is unlikely that water loss at these depths (50–60 cm) can be attributed to soil surface evaporation in these sandy soils (Yamanaka and Yonetani, 1999). During a very dry period in the summer of 2003 (1 year prior to the beginning of this study), the deuterium isotopic value of water in the petrocalcic horizon ($-55 \delta D\%$) at the study site was within the range of the deuterium isotopic value of *P. glandulosa* xylem water (range 63–53 $\delta D\%$) at the site (Snyder and Duniway, unpublished data), indicating potential use by *P. glandulosa* of water stored within the petrocalcic. Given this evidence of possible utilization of petrocalcic water by *P. glandulosa*, a species known to sustain very low xylem water potentials (e.g. Reynolds *et al.*, 1999), the lack of petrocalcic horizon drying in either vegetation cover type below -1.5 MPa (with $0.14\text{--}0.16 \text{ m}^3 \text{ m}^{-3}$ of soil water remaining) during drought indicates that water utilization is likely limited to bulk flow to roots in contact with the top of the horizon or sparse root or associated mycorrhizal networks within the petrocalcic horizons (Monger *et al.*, 1991) that are not of sufficient density or capacity to fully exploit soil water stored within the horizon.

CONCLUSION

The pattern of PAW observed in this study does not support the hypothesis of greater resource availability under shrub canopies. Although improved water infiltration capabilities under the *P. glandulosa* canopy were important for intense summer rains, the impacts of the quicker summer recharge were quickly negated, likely by shrub transpirational demands. For most of the 3-year study, the amount of available water under shrub canopies was either equal or less than that in the interspaces, indicating that in ecotone communities there is generally greater depletion and less recharge of soil water under shrub canopies than in shrub interspaces. In soil systems where there is available deep water, species with extensive and deep rooting systems such as *P. glandulosa* are believed to have greater resilience to drought due to their ability to rely on deeper soil water reserves during dry periods (Gile *et al.*, 1997; Snyder and Williams, 2003; Gibbens *et al.*, 2005). Retention of excess precipitation by the petrocalcic horizon and apparent slow release of the stored soil water within the rooting zone of grasses and forbs observed in this study, however, indicates that *P. glandulosa* may not have access to any more soil water resources than species with less extensive root systems. Furthermore, the greater frequency of near-surface available water in the interspaces could be beneficial to establishment and persistence *B. eriopoda*. Similar or greater water availability in shrub interspaces indicates that concentration of soil water under shrubs may not be

a process limiting grass recovery on these soils. Further work is needed to quantify the importance of petrocalcic horizons for resistance of grasslands to woody-shrub invasions at the landscape scale.

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