

Woody plants modulate the temporal dynamics of soil moisture in a semi-arid mesquite savanna[†]

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ABSTRACT

Climate variability and human activities interact to increase the abundance of woody plants in arid and semi-arid ecosystems worldwide. How woody plants interact with rainfall to influence patterns of soil moisture through time, at different depths in the soil profile and between neighboring landscape patches is poorly known. In a semi-arid mesquite savanna, we deployed a paired array of sensors beneath a mesquite canopy and in an adjacent open area to measure volumetric soil water content (θ) every 30 min at several depths between 2004 and 2007. In addition, to quantify temporally dynamic variation in soil moisture between the two microsites and across soil depths we analysed θ time-series using fast Fourier transforms (FFT). FFT analyses were consistent with the prediction that by reducing evaporative losses through shade and reducing rainfall inputs through canopy interception of small rainfall events, the mesquite canopy was associated with a decline in high-frequency (hour-to-hour and day-to-day) variation in shallow θ . Finally, we found that, in both microsites, high-frequency θ variation declined with increasing soil depth as the influence of evaporative losses and inputs associated with smaller rainfall events declined. In this case, we argue that the buffering of shallow soil moisture against high-frequency variations can enhance nutrient cycling and alter the carbon cycle in dryland ecosystems. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS *Prosopis velutina*; soil moisture; fast Fourier transform; Santa Rita Experimental Range; time domain reflectometry

Received 30 January 2009; Accepted 26 August 2009

INTRODUCTION

Temporal variation in resource availability has long been recognized as an important factor shaping the function of individual organisms, the composition of biological communities and ecosystem function (Odum, 1969; Colwell, 1974; Stearns, 1981; Halley, 1996; Katul *et al.*, 2007). Environments in which resource availability fluctuates widely and rapidly may favour organisms with a particular suite of life-history strategies, while environments in which resource availability is relatively constant may favour other life-history strategies (Grime, 1974). Similarly, the duration and magnitude of variation in resource availability is biologically relevant (Noy-Meir, 1973). For example, in otherwise water-limited ecosystems, small rainfall events, whose effect on soil moisture may persist just a few hours, trigger a metabolic response among soil microbes (Cable and Huxman, 2004). In contrast, in the same ecosystem, a larger rainfall event whose influence on soil moisture extends deeper into the soil and persists for several days is required to trigger a metabolic response among plants (Schwinning and Sala, 2004).

Soil moisture responds to and shapes patterns of atmospheric circulation on a global scale (Delworth and Manabe, 1988). At the same time, soil moisture is an

important resource that modulates biological responses to anthropogenic global warming, atmospheric CO₂ enrichment and changing land-use patterns on local and regional scales (Weltzin *et al.*, 2003). Predicting future patterns of soil moisture in the environment is complicated by these multiple and interacting biological and physical processes (Western *et al.*, 2002; Li *et al.*, 2007). In water-limited ecosystems (drylands), soil moisture strongly constrains and is influenced by biological activity (Noy-Meir, 1973; Breshears and Barnes, 1999; Weltzin *et al.*, 2003; Grayson *et al.*, 2006). For example, in a southern Arizona semi-arid grassland, antecedent soil water content controls the physiological and growth responses of bunchgrasses to subsequent rainfall (Ignace *et al.*, 2007) in turn shaping patterns of evapotranspiration and soil moisture (Huxman *et al.*, 2004; Potts *et al.*, 2006).

Many drylands worldwide have recently experienced or are currently experiencing an increase in the density and cover of woody plants. The cause of this phenomenon, termed 'woody-encroachment' (Goodale and Davidson, 2002), may involve interactions between human-mediated factors such as domestic livestock grazing and fire suppression and natural variability in temperature and rainfall (McPherson, 1997). Whatever the cause, woody encroachment influences the spatial and temporal distributions of soil moisture with potentially important effects on local and regional hydrologic cycling (Huxman *et al.*, 2005; D'Odorico *et al.*, 2007).

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[†] The contribution of Russell L. Scott was prepared as part of his duties as a United States Federal Government Employee.

The spatial and temporal dynamics of soil moisture above- and belowground are altered by woody plants. Aboveground, woody plant canopies interact with characteristics of rainfall, such as rainfall intensity, to influence patterns of soil water content through rainfall interception and shading the soil surface (Dunkerley, 2000; Schade and Hobbie, 2005). Woody plant litter that accumulates on the soil surface may increase soil water infiltration (Bhark and Small, 2003; Ludwig *et al.*, 2005) and reduce soil temperatures (Breshears *et al.*, 1998) thereby prolonging periods of increased soil water. Belowground, the greater functional rooting depth of woody plants may decrease deep soil moisture drainage (Seyfried and Wilcox, 2006; Scanlon *et al.*, 2005), while uptake and hydraulic redistribution by roots may further alter temporal variation of soil water content beneath woody plants (Caldwell and Richards, 1989; Miller *et al.*, 2007; Scott *et al.*, 2008). Although individually these mechanisms are well described, the ways in which they interact to influence patterns of soil moisture through time, at different depths in the soil profile and between neighboring landscape patches, is poorly understood.

Our objective was to better understand the influence of woody plant canopies on the spatial and temporal dynamics of soil moisture in a semi-arid mesquite savanna. Utilizing arrays of sensors measuring soil water content every 30 min at several depths in distinct microsites (beneath a mesquite canopy and in an open area), we made several predictions. First, we predicted that the shading influence of the mesquite canopy would reduce the duration and magnitude of extremely dry conditions in shallow soils, while enhanced root uptake of soil moisture in deeper soil layers beneath the canopy would reduce soil moisture in comparison with similar soil layers in an open microsite. Second, we predicted that the mesquite canopy would be associated with a decline in higher frequency (hour-to-hour and day-to-day) variation in soil moisture because of the role canopies have in shading the soil surface to reduce soil water evaporation and in potentially reducing rainfall inputs through canopy interception while not influencing the magnitude of lower frequency (month-annual) variation in soil moisture. Finally, we predicted that high-frequency variation in soil moisture would decline with increasing depth in the soil profile as the immediate influence of evaporative losses and moisture inputs associated with small rainfall events declined.

METHODS

Site description

We conducted this research at the University of Arizona's Santa Rita Experimental Range (SRER) approximately 45 km south of Tucson, Arizona (31.82°N, 110.86°W, elev. 1116 m). The plant community there consisted of the woody leguminous tree, velvet mesquite (*Prosopis velutina* Woot.) growing in a matrix of the non-native, perennial bunchgrass Lehman lovegrass (*Eragrostis lehmanniana* Nees), scattered native,

warm-season perennial bunchgrasses (e.g. *Digitaria californica* Benth., *Muhlenbergia porteri*, *Bouteloua eriopoda*, *Aristida* spp.), the sub-shrub burroweed (*Isocoma tenuisecta* Greene) and succulents (*Opuntia* spp.). The total growing season canopy cover of perennial grasses, sub-shrubs and succulents was ~22% and the canopy cover of mesquite was ~35%. Similar to the observations of McClaran and Angell (2007) made in a similar setting on another portion of the SRER, bunchgrass cover does not contrast distinctly between open areas and areas beneath the canopy of larger mesquite. At this site, mesquite ranged in height from 0.25–6 m with an average height of 2.5 m ($SD = 1.6$, $n = 95$) and form deep taproots and extensive lateral root systems that can extend more than 15 m beyond the canopy (Cable, 1977). Leaf flush occurs in early April for mesquite and their leaves are shed after autumn frosts in mid-November.

The site was subjected to year-round cattle grazing between 1957 and 2005 with about 0.028 animals $ha^{-1} year^{-1}$, the equivalent of ~50% forage utilization (Martin and Severson, 1988; Ruyle, 2003). In 2006, the pasture in which our experimental site was located received only minimal grazing of 25 cattle for 9 days and was not grazed by cattle in 2007.

Soils at the site are a course-textured loamy sandy derived from Holocene-aged alluvium eroded from the nearby Santa Rita Mountains. The mean annual precipitation at a nearby long-term monitoring station is 377 mm (rain gage #45, 1937–2007). In southern Arizona, the winter months (December–March) are cool with occasional nighttime frosts. During the winter, about 30% of the annual rainfall is associated with frontal storms. Spring (April–June) is characterized by increasing temperatures and usually very dry conditions. The arrival of the North American monsoon in July signals a slight decline in daytime maximum temperatures and an increase in relative humidity. Approximately 50% of annual rainfall arrives as high-intensity, convective storms associated with monsoon circulation during the months of July–September (Adams and Comrie, 1997). The autumn months of October and November are characterized by declining temperatures and low rainfall.

Soil water measurement and analysis

In conjunction with an ongoing program to monitor ecosystem CO_2 and H_2O vapour exchange (Potts *et al.*, 2008; Scott *et al.*, 2008), we measured volumetric soil water content using commercial soil water content probes (CS616, Campbell Scientific, Logan, Utah). Probes were positioned at 2.5–5, 5–10, 15–20, 20–30, 40–50 and 60–70 cm with the probes increasingly angled from horizontal with increasing depth at two adjacent microsites. For the sake of clarity, these probes are referred to by their maximum depth (5, 10, 20, 30, 50 and 70 cm). The first array was situated in an open area where the sparse plant canopy consisted of bunchgrasses and sub-shrubs approximately 3 m from the nearest mesquite canopy.

Hereafter, this microsite is referred to as the open location to reflect its mainly bare-soil composition. The second array was located 7 m from the first array, beneath the canopy of a large mesquite tree positioned approximately halfway between the trunk and the drip-edge of the canopy. Hereafter, this microsite is referred to as the canopy location. Between January 2004 and December 2007, measurements were recorded every 30 min and stored on a data logger (CR-10X, Campbell Scientific, Logan, UT).

Output values from the soil water probes were temperature corrected using factory-supplied correction terms. Temperature-corrected values were then used to compute θ using a laboratory calibration curve produced with soil collected from the site. Soils were uniform loamy sands with no visually obvious changes in soil texture between the two microsites. During the 4-year period of record, there was a single, 5-day gap in the collection of soil water content data that occurred from January 1 to January 4, 2006. In addition to monitoring soil moisture, we monitored daily rainfall totals using a tipping-bucket rain gage located at the site.

We calculated daily mean θ from 30-min values for each depth at each microsite to compare patterns of soil moisture abundance with depth and microsite. To address our first prediction that the presence of the mesquite canopy would ameliorate dry conditions in shallow soils while causing a decline in moisture at greater depths, we compared patterns of soil moisture between depths and microsites using both frequency plots and cumulative frequency distributions of 30-min θ for the period 2004–2007. Given the limitations inherent in the unreplicated design of our experiment, we focused on qualitatively documenting trends that emerged from microsite comparisons with depth in the shape of θ frequency distributions.

We used FFT (Cooley and Tukey, 1965) to address our predictions regarding shifts in the magnitude of hour-to-hour and day-to-day fluctuations in θ associated with microsite and depth. We used the θ time series for the period 2004–2007 to derive Fourier amplitudes and compare the spectral properties of θ between depths and across microsites normalized by the variance of the original time series (Katul *et al.*, 2007). FFT divides a signal (in this case, a θ time series) into a series of sine and cosine functions of different frequencies and can be thought of as describing the amount of variability in the original time series, which can be explained by those functions (Stearns, 1981). A property of the FFT is that the original signal variance is recovered when all squared amplitudes are summed (Platt and Denman, 1975). This analysis allowed us to contrast the relative importance of fluctuations in soil moisture between microsites and soil depths across a range of fluctuation frequencies. Specifically, we compared the power spectrum associated with variance in soil moisture by comparing summed squared amplitudes across three frequency ranges: 3–12-month period (4–1 cycles year⁻¹),

3–7-day fluctuations (121–52 cycles year⁻¹), and 2–24-h fluctuations (365–4380 cycles year⁻¹) in soil moisture. To be clear, our objective was not to use FFT to determine the frequency at which soil moisture fluctuations were the most pronounced (e.g. signal strength at 1 cycle year⁻¹). Rather, we used FFT to quantify changes in soil moisture associated with both periodic and non-periodic fluctuations (noise), in particular frequency bands, in order to assess the temporally dynamic modulating influence of a woody plant canopy on soil moisture. In other words, this approach allowed us to explore the idea that a woody plant canopy may act as a low-pass filter on soil moisture variation: dampening high frequency soil moisture fluctuations (those associated with hours and days) while having little influence on low frequency fluctuations (those associated with months). FFT analyses were conducted using the built-in function in GNU Octave (www.octave.org).

RESULTS

Annual rainfall totals during the period of observation varied between 285 mm in 2004 and 332 mm in 2005. Annual rainfall totals were below the historic average but well within the range of historic variability for this site (mean = 377 mm; *SD* = 92; 1936–2006). Seasonal patterns of rainfall reflected the contribution of both cool-season frontal storms and high-intensity convective storms during July, August and September (Figure 1A). We observed that there was considerable inter-annual variation in the seasonal distribution of rainfall. For example, above-normal monsoon rainfall during the summer of 2005 was followed by an extremely dry winter where only 35 mm of rain fell between December 2005 and March 2006.

Patterns of monthly precipitation are reflected in the depth distribution of daily average soil moisture (θ) at both the open and canopy microsites (Figure 1B and C respectively). In both microsites, summer rainfall consistently wetted the soil profile to a depth of more than 50 cm, while the infiltration of less abundant, cool-season rainfall was generally limited to depths less than 30 cm. The effect of cool-season precipitation on θ in the open location appeared to be greater and longer lasting than in the canopy location at shallower depths in the soil profile (<20 cm; Figure 1B). A comparison of daily mean θ microsite differences revealed a dynamic pattern of soil moisture with depth and time (Figure 1D). In the open microsite, shallow soils were occasionally drier than those in the canopy microsite. In contrast, at intermediate depths and during the summer rainy season, the canopy microsite was frequently drier than the open microsite.

A comparison of the frequency distributions of 30-min θ for the period 2004–2007 revealed microsite and depth-mediated differences (Figure 2A–F). In the shallowest soil layers, the microsites shared similar mode θ values (~2.5%). Near the soil surface, the microsites differed primarily in the distribution of driest soil moisture values

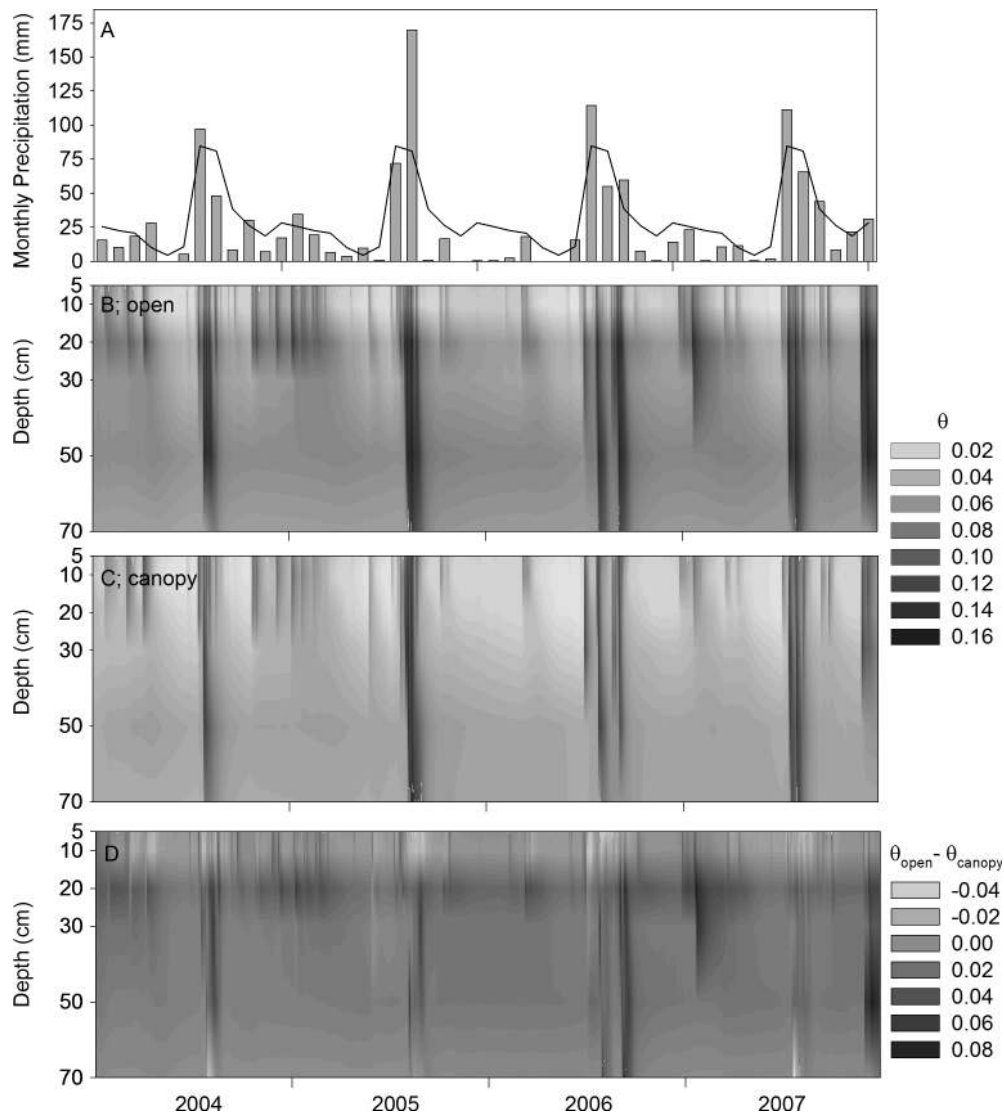


Figure 1. (A) Bars indicate monthly precipitation totals (mm) for the period 2004–2007 in a semi-arid mesquite savanna. The solid line indicates historic patterns of mean monthly precipitation (1937–2007) at a nearby weather station. (B–C) Daily mean volumetric soil moisture (θ) interpolated from measurements at six depths in the soil profile in a (B) open location and (C) nearby beneath the canopy of a mature mesquite. (D) Depth- and time-specific microsite differences in θ expressed as $\theta_{open} - \theta_{canopy}$. Darker shades indicate depths and times where and when the open microsite is wetter than the canopy microsite.

at the open location, although these differences were small ($\sim 1\%$ volumetric soil moisture). During wetter periods, microsite-mediated differences in θ became less apparent (Figure 2A and B insets).

Between 20 and 50 cm depth, microsite differences in θ reversed, indicating a trend towards greater mode θ values in the open microsite than those in the canopy microsite (Figure 2C–E). At 70 cm depth in the soil profile, microsite differences in mode θ values were small (Figure 2F). Across microsities, cumulative frequency distributions were increasingly ‘I’ shaped with increasing depth, reflecting increasingly persistent conditions of intermediately abundant θ punctuated by brief periods of wetting associated with monsoonal rainfall (Figure 2A–F insets).

Spectral density plots of θ illustrate qualitative similarities in spectral properties of soil moisture across depths and between microsities. Plotted on a log–log

scale, the spectral density plots of $\theta_{10\text{ cm}}$ in the open and canopy microsities were representative of the spectral density plots from other depths (Figure 3A and B respectively). The negative relationship between frequency and amplitude is consistent with a ‘reddened’ spectrum where low-frequency fluctuations in soil moisture contribute to the signal in excess (Halley, 1996). In this case, low-frequency fluctuations in θ peaked with a frequency of approximately 1 cycle year⁻¹, a pattern that was repeated across depths and between microsities.

To quantify microsite- and depth-specific differences in the amplitude of θ fluctuations, we compared summed squared amplitudes of the spectral density plots across three frequency ranges: 3–12-month period (4–1 cycles year⁻¹), 3–7-day fluctuations (121–52 cycles year⁻¹) and 2–24-h fluctuations (365–4380 cycles year⁻¹). At the shallowest soil depths, θ in the canopy microsite had reduced high-frequency variance (365–4380 cycles

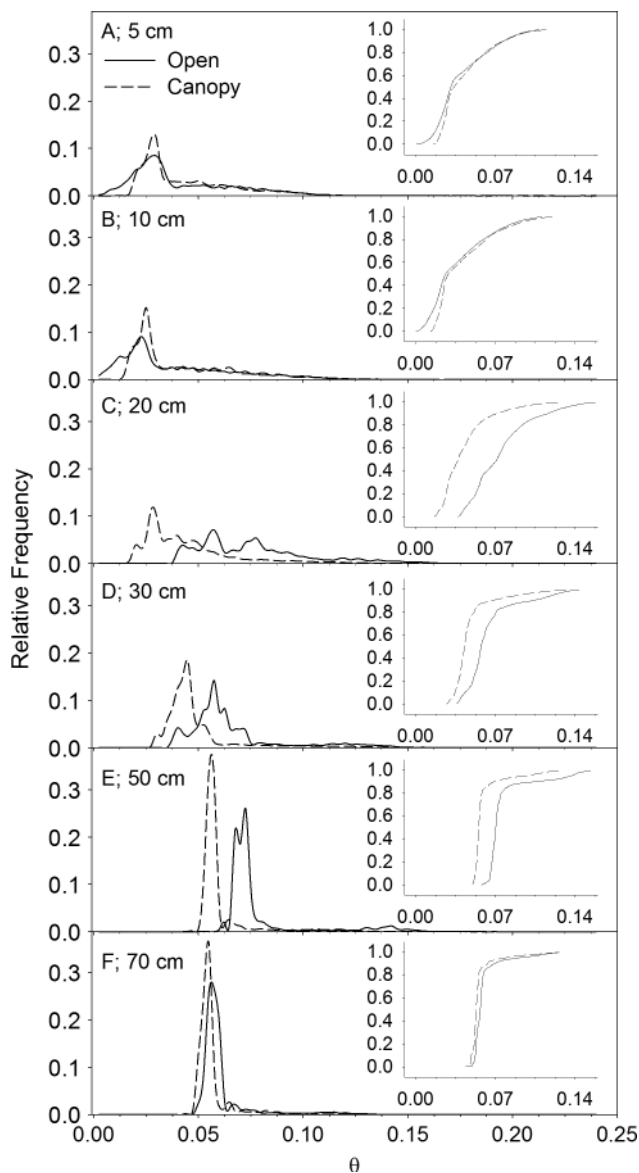


Figure 2. (A–F) Probability density functions (*main figures*) and cumulative frequency distribution (*inset figures*) of volumetric soil moisture measured at 30-min intervals for the period 2004–2007 at (A) 5, (B) 10, (C) 20, (D) 30, (E) 50 and (F) 70 cm depth in the soil profile. Solid lines indicate the open microsite; dashed lines indicate the canopy microsite.

year⁻¹ corresponding to fluctuations with a 2–24-h period and 52–121 cycles year⁻¹ corresponding to fluctuations with a 3–7-day period) compared to the open microsite (Figure 4A and B respectively). In contrast, microsite differences in low-frequency variance (1–4 cycles year⁻¹ corresponding to fluctuations with a 3–12-month period) were depth specific (Figure 4C). Consistent with our prediction, microsite-mediated differences in the magnitude of variance across a range of frequencies generally declined with increasing soil depth (Figure 4A–C).

DISCUSSION

Our objective was to better understand the spatial and temporal influence of a woody plant canopy on soil

moisture in a semi-arid mesquite savanna near Tucson, Arizona. Consistent with our first prediction, the mesquite canopy was associated with an amelioration of extremely dry conditions in the shallow soil and a reduction in soil moisture at intermediate depths (Figure 2A–F). Analysis of FFT θ time series support our predictions that the mesquite canopy reduces high-frequency θ fluctuations in shallow soils and that, in general, fluctuations in θ decline with increasing depth (Figure 4A–C).

The influence of the mesquite canopy can be seen clearly in differences in the minimum relative θ observed in shallow soils (Figure 2A and B). At intermediate depths, we observed increased microsite differences in the temporal distribution of soil moisture over the 4-year period of observation that were consistent with the prediction that abundant roots associated with woody plants were acting to deplete soil moisture quickly at the canopy microsite compared to the open microsite. In both microsites, minimum θ at 70 cm depth was greater than that in shallower soils and was stable over long periods of time (Figure 2F). At this depth, long periods of stable minimum values of soil moisture suggest that minimum values of soil moisture were dictated by the permanent wilting point of plants rather than the influence of surface evaporation (Grayson *et al.*, 2006).

In comparison with bare or sparsely vegetated patches, the shallow soils beneath mesquite canopies have greater macronutrients including inorganic nitrogen (Virginia and Jerrell, 1983; Wilson and Thompson, 2005; Throop and Archer, 2008), increased soil organic carbon (Thompson *et al.*, 2006; Throop and Archer, 2008), increased abundance of heterotrophic bacteria (Herman *et al.*, 1995) and correspondingly greater rates of soil respiration (McCulley *et al.*, 2004; McLain *et al.*, 2008; Potts *et al.*, 2008). The damping effect of the mesquite canopy on high-frequency fluctuations in θ (Figure 4A and B) and the associated reduction in the duration and severity of dry conditions in shallow soils (Figure 3A and B) are consistent with the biogeochemical effects of mesquite canopies in an environment where nutrients are concentrated in shallow soil horizons and nutrient mineralization is water limited. Furthermore, canopy effects on shallow soil θ dynamics compliment other mechanisms, such as the quantity and quality of litter produced by woody plant canopies (Wilson and Thompson, 2005), that have been proposed to explain these biogeochemical contrasts.

It is possible that the reduced high-frequency θ fluctuations beneath the mesquite canopy might be related to microsite differences in soil temperature fluctuations despite our efforts to correct the output of the soil moisture probes for temperature variations. If high-frequency soil temperature fluctuations were responsible for corresponding fluctuations in soil moisture probe output, we would expect both microsite depth profiles to show similar, if offset, declines in high-frequency θ fluctuation with increasing depth. However, high-frequency θ fluctuations in the open microsite declined rapidly with increasing depth, while the magnitude of high-frequency

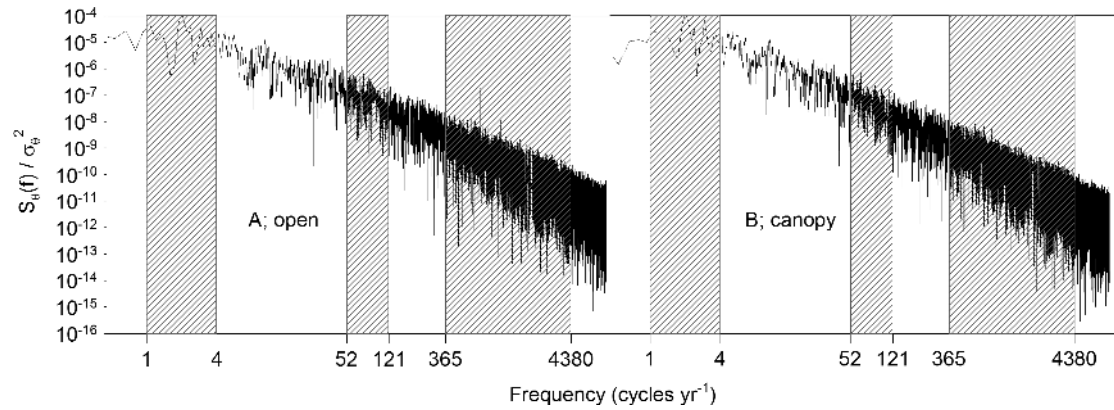


Figure 3. (A–B) Spectra of soil moisture (S_θ) normalized by the variance (σ_θ^2) of their respective time series as a function of frequency at 10 cm depth in the soil profile from (A) the open microsite and (B) the canopy microsite. Cross-hatching indicates frequency ranges of particular interest. The spectra illustrated here are representative of spectra from other depths.

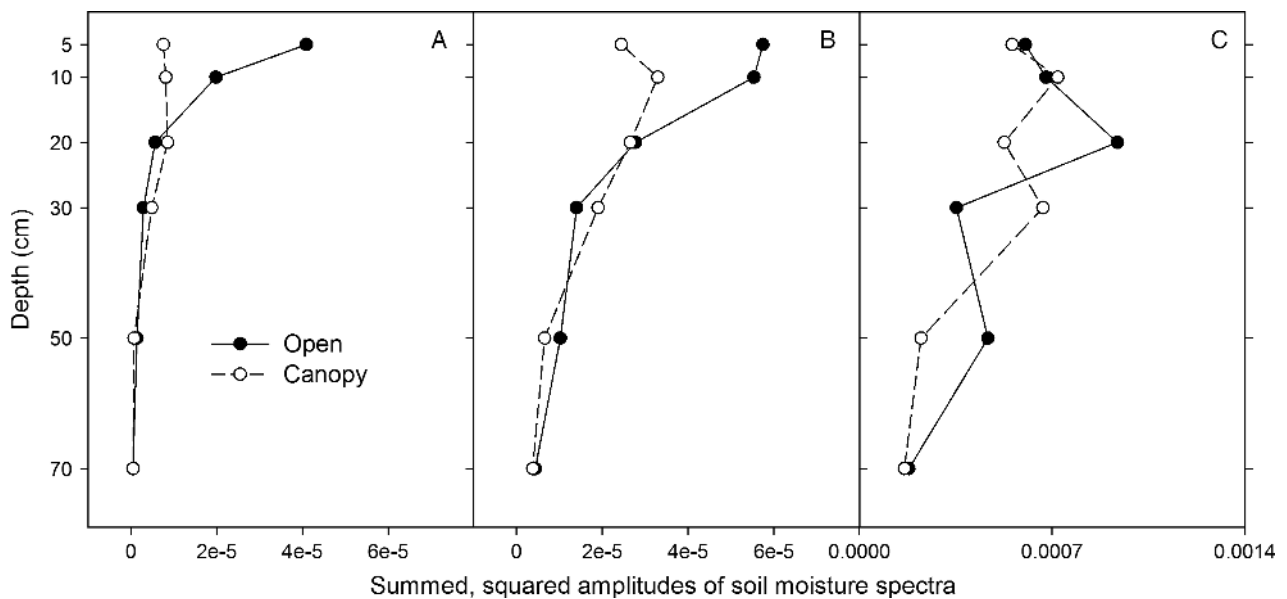


Figure 4. (A–C) Summed squared amplitudes of normalized soil moisture spectra at six depths in the soil profile across a range of soil moisture fluctuation frequencies. Larger integrated power values correspond to larger amplitude fluctuations in soil moisture within a given range of frequencies: (A) 4380–365 cycles year⁻¹ = 2–24-h fluctuations; (B) 121–52 cycles year⁻¹ = 3–7-day fluctuations; (C) 4–1 cycles year⁻¹ = 3–12-month fluctuations. Solid lines indicate the open microsite; dashed lines indicate the canopy microsite.

θ fluctuations remained constant with increasing depth in the soil beneath the mesquite canopy (Figure 4A). We believe our data accurately represent soil moisture at all depths and not variations in soil temperature.

At intermediate depths, cool-season θ was persistently greater in the open microsite than that in the canopy microsite (Figure 1D). Hydraulic redistribution, a passive process in which roots conduct water according to soil water potential gradients (Caldwell and Richards, 1989), has been observed among mesquite growing at our research site (Scott *et al.*, 2008) and could explain cool-season θ at intermediate depths. Moreover, Scott *et al.* (2008) found that hydraulic redistribution by mesquite occurs throughout the year including during the winter dormant season when soil moisture is redistributed downwards to deeper, drier soil layers. Likewise, the amelioration of extremely low θ beneath the mesquite canopy in shallow soils during the early summer (Figure 1D) could

be explained by the upward redistribution of water by mesquite roots.

The effects of woody plant canopies on soil moisture may directly influence understory plant community composition and productivity and alter the spatial patterns of soil nutrients. McClaran and Angell (2007) examined contrasting patterns of bunchgrass community composition in open grassland patches and beneath the canopies of mature mesquite across a range of nearby sites on the SRER. They attributed observed differences in bunchgrass community composition to increased soil N concentrations and reduced stomatal conductance and water stress under lower light intensity for the grasses growing beneath mesquite canopies. These findings, coupled with the observation that the physiological response of bunchgrasses in southern Arizona may lag several days following rainfall (Ignace *et al.*, 2007), suggests that the amplitude damping of θ over periods of 3–7 days are

biologically relevant to shallow-rooted understory plants (Figure 4B).

Several previous studies have examined the influence of vegetation and soil depth on the temporal fluctuations in soil moisture. In an analysis of 16 years of grassland soil moisture data collected at 17 stations across the state of Illinois, Wu *et al.* (2002) demonstrated the effect of soil depth on damping the amplitude of soil moisture fluctuations and increasing soil moisture persistence. Katul *et al.* (2007) examined a long-term record of soil moisture and micrometeorological data collected in a loblolly pine stand to better understand the effects of precipitation and evapotranspiration and the spectrum of θ from hours to years. Similarly, Parent *et al.* (2006) used wavelet analysis to characterize temporal variability of soil moisture in a southern Quebec crop field in response to precipitation over time scales of hours to weeks. While these studies have clarified the relationship between soil moisture variability and hydrologic processes, much remains to be learned regarding the biogeochemical and ecological implications of such dynamics.

The present study, though limited in its scope of inference by a lack of microsite replication, supports the idea that woody plant canopies exert a modulating influence on hydrological processes to influence the dynamics of soil moisture. Future investigations should use a replicated design to assess the degree to which these modulating effects vary across soil types and between mesquite of differing size classes. Finally, future studies may be able to establish whether or not these modulating effects extend to other woody plants species and investigate the degree to which canopy effects on soil moisture are influenced by the precipitation regime.

ACKNOWLEDGEMENTS

This work was supported in part by the USDA-ARS, Sustainability of semi-Arid Hydrology and Riparian Areas (SAHRA) under the STC Program of the National Science Foundation, Agreement No. EAR-9876800 and Buffalo State College. Rainfall data were provided by the Santa Rita Experimental Range Digital Database which is supported by the University of Arizona. K. Delp, J. Manning and D. Ettestad provided important insight in the analysis of soil moisture data and the interpretation of Fast Fourier Transforms. We gratefully acknowledge the support and contributions of W. Cable, N. English, E. Hamerlynck, M. Heitlinger, T. Huxman, M. McClaran and the thoughtful comments of two anonymous reviewers.

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