

Density-Dependent Ecohydrological Effects of Piñon–Juniper Woody Canopy Cover on Soil Microclimate and Potential Soil Evaporation

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Abstract

Many rangeland processes are driven by microclimate and associated ecohydrological dynamics. Most rangelands occur in drylands where evapotranspiration normally dominates the water budget. In these water-limited environments plants can influence abiotic and biotic processes by modifying microclimate factors such as soil temperature and potential soil evaporation. Previous studies have assessed spatial variation in microclimate and associated ecohydrological attributes within an ecosystem (e.g., under vs. between woody canopies) or across ecosystems (e.g., with differing amounts of woody canopy cover), but generally lacking are assessments accounting systematically for both, particularly for evergreen woody plants. Building on recently quantified trends in near-ground solar radiation associated with a piñon–juniper gradient spanning 5% to 65% woody canopy cover, we evaluated trends in soil temperature and associated estimates of potential soil evaporation as a function of amount of woody canopy cover for sites overall and for associated canopy vs. intercanopy locations. Quantified soil temperature trends decreased linearly with increasing woody canopy cover for intercanopy as well as canopy patches, indicating the coalescing influence of individual canopies on their neighboring areas. Notably, intercanopy locations within high-density (65%) woody canopy cover could be as much as ~10°C cooler than intercanopy locations within low-density (5%) cover. Corresponding potential soil evaporation rates in intercanopies within high-density woody canopy cover was less than half that for intercanopies within low density. Our results highlight ecohydrological consequences of density-dependent shading by evergreen woody plants on soil temperature and potential soil evaporation and enable managers to rapidly estimate and compare approximate site microclimates after assessing amounts of woody canopy cover. Such predictions of microclimate have general utility for improving management of rangelands because they are a fundamental driver of many key processes, whether related to understory forage and herbaceous species or to wildlife habitat quality for game or nongame species.

Resumen

Muchos procesos en los pastizales están definidos por microclimas y sus dinámicas ecohidrológicas asociadas. Muchos pastizales se localizan en zonas áridas donde la evapotranspiración normalmente es el flujo dominante del balance hídrico. En estos ambientes donde el agua es escasa, las plantas pueden influenciar procesos ecológicos, bióticos y abióticos, mediante la modificación de factores micro-climáticos, como temperatura del suelo el potencial de evaporación desde la superficie. Estudios previos han definido que la variación en microclimas y los atributos asociados con la eco-hidrología dentro de los ecosistemas (por ejemplo debajo del dosel vs. en espacios entre el dosel aéreo de dos árboles) o a través de los ecosistemas (por ejemplo con diferentes cantidades de cobertura de dosel). Sin embargo, se carece generalmente de la determinación sistemática de ambos, particularmente para las plantas arbustivas siempre verdes. Basándose en tendencias cuantificadas recientemente para la radiación solar cerca de suelo en un gradiente de pino–junípero abarcando una cubierta de 5% a 65% de cobertura de dosel, se evaluaron las tendencias en la temperatura del suelo y se desarrollaron estimaciones asociadas con el potencial de evaporación de suelo en función de la cantidad de cubierta arbórea tanto para sitios en general (en función de la cobertura), como para aquellos asociados con la cubierta contra sitios ubicados entre los árboles (no directamente debajo de las copas). Las temperaturas del suelo cuantificadas tendieron a decrecer linealmente con el incremento en la cobertura arbórea en los espacios entre árboles, así como los espacios cubiertos por los árboles, indicando la relación entre la influencia de las copas individuales sobre sus áreas vecinas. Notablemente, los espacios entre árboles dentro de lugares con altas densidades (65%) de cubierta arbórea pueden ser hasta 10°C más fríos que los espacios entre árboles dentro de una densidad baja de cobertura aérea (5%). Con respecto al potencial de las tasas de evaporación en los espacios

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entre árboles en las áreas con niveles altos de cubierta de dosel, resultó siendo menos de la mitad de la que ocurriría en espacios iguales abiertos, pero localizados en zonas con baja cobertura de dosel arbóreo. Nuestros resultados resaltan los efectos ecohidrológicos de la sombra producida por los árboles sobre la temperatura del suelo y el potencial de evaporación del suelo, y que dependen de la cantidad y densidad de árboles en el paisaje. Estos resultados permiten a los manejadores una rápida estimación y comparación del microclima en diversos sitios, después de determinar la cantidad de cubierta arbórea. Tales predicciones de microclimas tienen una utilidad general para mejorar el manejo de pastizales porque son fundamentales para muchos procesos esenciales, si se relacionan con pastos que se encuentran debajo de la cobertura arbórea, así como con las especies herbáceas o para la calidad del hábitat de la vida silvestre de especies cinegéticas y no cinegéticas.

Key Words: intercanopy, near-ground radiation, piñon pine, soil temperature

INTRODUCTION

Key environmental processes in water-limited rangelands are strongly affected by ecohydrological relationships between vegetation and hydrology (Rodríguez-Iturbe and Porporato 2004; Wilcox and Newman 2005). Improved estimates of microclimate and soil evaporation are needed for more effective rangeland management. Semiarid ecosystems in particular are inherently water-limited because annual potential evapotranspiration exceeds precipitation, and consequently evapotranspiration can dominate the water budget and have important ecological and hydrological effects (Wilcox et al. 2003). A predominant component of overall evapotranspiration is soil evaporation, which can significantly reduce water availability for plants (Huxman et al. 2005). Therefore, improved estimates of microclimate and potential soil evaporation are needed for more effective land management (Huxman et al. 2005; Wilcox and Newman 2005; Newman et al. 2006). Furthermore, information about soil evaporation also is important for understanding how the soil surface beneath woody plants (i.e., canopy patches) and the grass-dominated areas between crowns of woody plants (i.e., intercanopy patches) contribute to evapotranspiration (Newman et al. 2010).

Nonoverlapping canopy cover of woody plants (hereafter referred to as “woody canopy cover”) is an important architectural attribute that strongly influences ecohydrological microclimate and ecohydrological processes in rangeland ecosystems. Woody canopy cover affects vertical water fluxes, such as interception (Owens et al. 2006), evaporation and transpiration (Breshears et al. 1998; Kurc and Small 2004; Huxman et al. 2005), sublimation (Veatch et al. 2009), infiltration and soil moisture (Bhark and Small 2003; Lebron et al. 2007; Madsen et al. 2008; Zou et al. 2008), recharge (Loik et al. 2004; Seyfried et al. 2005), and horizontal water fluxes, such as baseflow, overland flow, run off, and lateral redistribution (Brooks et al. 2002; Ludwig et al. 2005; Newman et al. 2010). Importantly, woody canopy cover relates directly to the partitioning of total evapotranspiration into its constituent components; evaporation from land surface (E), and transpiration from plants (T; Huxman et al. 2005; Breshears 2006; Moore and Heilman 2011). Previous studies have revealed correlations and systematic relationships between the total amount of woody plant density and variation in microclimate factors; near-ground solar radiation, soil temperature, and potential soil evaporation (Martens et al. 2000; Veatch et al. 2009; Breshears and Ludwig 2010; Villegas et al. 2010b; Yasseef et al. 2010; Zou et al. 2010). Previous research also has highlighted how variation in microclimate differs between canopy and intercanopy patch types (Breshears et al.

1998; Kurc and Small 2004; Lebron et al. 2007; Newman et al. 2010). Importantly, these studies have not accounted for the role of woody canopy cover in determining trends within a given ecosystem. The magnitude of microclimate differences between canopy and intercanopy patches differs at low vs. high amounts of woody canopy cover (Breshears et al. 1998; Loik et al. 2004; Ludwig et al. 2005; Lebron et al. 2007; Villegas et al. 2010b). Understanding the role of woody canopy cover is necessary because the proportion of woody plant cover can span a broad range: from sparse, as in grasslands with few woody plants, to approaching total canopy closure, as is the case for high-density shrublands, woodlands, or forests (Breshears 2006). Large-scale changes in woody plant cover can result in large-scale microclimate shifts (e.g., as triggered by drought-induced plant die-off [Royer et al. 2011] and are also relevant for large-scale management by thinning). Further, the effects of woody plants on herbaceous plants and site hydrology are topics of debate in rangeland management (Huxman et al. 2005; Breshears 2006; Wilcox and Thurow 2006; Moore and Heilman 2011). Soil temperature and potential soil evaporation are influenced by many factors besides just the presence or absence of and amount of woody canopy cover, including microtopography, aspect, soil texture, species composition, and depth to groundwater (Geiger et al. 2003). In addition, the presence and distribution of species that comprise the woody canopy cover can be influenced by many factors as well (House et al. 2003). Nevertheless, the presence or absence of woody canopy cover within gradients of varying amounts of woody canopy cover is a key characteristic of drylands which alone can affect trends in many ecosystem properties and consequently warrants particular focus (Breshears 2006).

In this study, our overall objective was to address the effect of amount of woody canopy cover on potential soil evaporation in piñon–juniper woodlands. We assessed how canopy and intercanopy patches influenced soil temperature through their effects on near-ground solar radiation, and consequently potential soil evaporation. We also evaluated ecohydrological implications with respect to potential soil evaporation, including density-dependent differences in potential soil evaporation at the patch scale. We focused on a piñon–juniper gradient ranging from 5% to 65% woody plant canopy cover. More specifically, we assessed 1) spatiotemporal variation in near-ground solar radiation, soil temperature, and potential soil evaporation (PE) across the gradient; 2) near-ground solar radiation and soil temperature trends specific to canopy and intercanopy patches within and across the gradient; and 3) implications for potential soil evaporation based on field-derived temperature data. We discuss observed systematic

relationships between total cover and the absence or presence of canopy within the entire cover gradient and their more general ecohydrological implications.

MATERIAL AND METHODS

Study Site

Our study site was located in semiarid woodland dominated by piñon (*Pinus edulis* Engelm.) and juniper (*Juniperus monosperma* [Engelm.] Sarg.) at a previously established research site in northern Arizona (approximately 60 km north of Flagstaff, Arizona: lat 35.535°N, long 111.853°W) with a series of seven separate east-to-west-bearing, 50-m transects (Royer et al. 2010). Average monthly maximum temperature is 24°C, average monthly minimum temperature is 0.4°C, and average annual rainfall is 280 mm. Evapotranspiration rates are high, at about 410 mm year⁻¹, with average precipitation exceeding evapotranspiration only from December to February. Soils are generally clay-loam, with a small but notable sandy-loam component directly under canopy and along canopy edges. The transects spanned a gradient of increasing cover by woody plants at levels of 5%, 15%, 25%, 35%, 45%, 55%, and 65% canopy cover. Intercanopy areas had herbaceous to suffrutescent plants and grasses ranging from 5–100% cover (for a more complete account of species see Royer et al. 2010).

Near-Ground Solar Radiation

Hemispherical photographs were taken 1 m above the land surface at 1-m intervals along each transect. Images were processed using Hemiview Canopy Analysis (version 2.1; Delta-T devices, 1999, Cambridge, United Kingdom), which is a software utility used to estimate the amount of potential incoming near-ground solar radiation based on the percent of attenuated radiation (gap fraction) estimated by photographs and land position (e.g., Royer et al. 2010; Villegas et al. 2010b). Near-ground potential solar radiation (hereafter referred to as “near-ground solar radiation”) was expressed as Direct Site Factor (DSF)—ranging from 0 for a completely covered location to 1 for a completely open one—and as energy input (i.e., W·m⁻²). The estimates correspond to clear-sky conditions and do not vary with weather conditions. They represent maximum possible direct radiation governed by attenuation from overhead canopy cover and usually have greater values than field measurements, which account for actual cloud cover. Based on instrumentation constraints, we used a separate 18-m contiguous subset for each of the seven transects, where each subset had approximately the same woody canopy cover as the corresponding previously studied 50-m transect. The 18-m subset transects were selected iteratively within the original 50-m transect by attempting to obtain approximately the same target woody canopy cover as for the original transects. The average woody canopy cover of the subset transects we obtained was, on average, within 3% of that for the whole 50-m transect. We reevaluated the trend in near-ground solar radiation for each 18-m subset of locations within each transect to verify that relationships were similar to those found for the full 50-m transects, thereby enabling us to link the results of this study to the previous one.

Soil Temperature and Potential Soil Evaporation

We measured soil temperature at 1-m intervals along each of the 18-m transects, using Thermochron temperature sensors (Maxim Integrated Products, Inc.; Sunnyvale, CA). Soil temperature measurements were recorded every 2 h for a total time period of 1 yr. We buried the temperature sensors at 5 cm, a depth intermediate between soil surface and a depth of 10 cm, which in this ecosystem and climate, is generally the maximum depth in the soil profile for soil water evaporation (Breshears et al. 1998; Newman et al. 2006; Lebron et al. 2007). Sensors in canopy patches were placed at 5 cm below the approximate litter–soil surface interface, based on visual observation and as similar to a related study (Breshears et al. 1998). All sensors were installed in August 2007 and collected September 2008. To assess stand-level potential soil evaporation across the transects, we used the Hargreaves (1975) equation, which uses average monthly minimum, maximum, and average soil temperature data to estimate monthly potential soil evaporation (PE).

In addition to estimating PE with the Hargreaves equation, we measured soil evaporation from canopy and intercanopy patches under discrete temperatures in a controlled experiment. This secondary analysis contributed greater detail to patch-scale PE, and allowed us to account for additional differences between canopy and intercanopy due to litter and soil type. Soil cores were taken from random intercanopy and canopy locations ($n = 5$ each) along a transect with intermediate woody canopy cover (35%). The soil samples were collected in polyvinyl chloride (PVC) tubes (10-cm depth by 10-cm diameter) by driving PVC tubes with serrated edges into the soil profile, digging around the core sample, and capping the bottom before removal. We made an effort to keep soil profiles, including litter if present, and soil composition intact and relatively undisturbed. Soils were subsequently stored in the laboratory at ~ 23°C prior to the potential soil evaporation measurements.

Soil evaporation measurements were conducted in a controlled growth chamber (E7/2; Conviron, Pembina, ND). All soil cores were dried, weighed, wetted to saturation, allowed to drain overnight, reweighed, and then dried using a 48-hr temperature regime corresponding to peak daily August temperatures for a cover × canopy scenario. Soil water loss was calculated gravimetrically at 2 h, 4 h, 7 h, 12 h, 25 h, 36 h, and 48 h. This process was done for four cover × canopy scenarios: under canopy in an area with 35% canopy cover, intercanopy in an area with 35% canopy cover, intercanopy in an area with 5% canopy cover, and intercanopy in an area with 65% canopy cover. These scenarios were selected to compare rates of potential soil evaporation in canopy vs. intercanopy patches in an area with intermediate cover (first vs. second), and to compare intercanopy situations between areas with low vs. high cover (third vs. fourth). The temperature regime for a given cover × canopy scenario was determined by soil temperature data from the field measurements described above. We used peak August temperatures to focus on maximum differences in potential soil evaporation, which are expected to accompany peak air temperatures (Breshears et al. 1998), and to aid in comparing our results to related studies of evapotranspiration (e.g., Maseyk et al. 2008; Yaseef et al. 2010).

Data Analysis

We calculated average daily maximum, daily average, and average daily minimum temperature for each of the seven levels of canopy cover (5–65%) for each of 4 mo (February, April, August, and November). We used these values to assess the relationship between solar radiation and soil temperature using simple linear regressions in which the independent variable was near-ground solar radiation and the dependent variable was one of the above temperature variables. Separate regressions were done for each of the 4 mo. We also calculated mean values for incoming energy and temperature by patch type (canopy and intercanopy) at each canopy cover level (5–65%). We analyzed trends for the effect of total canopy cover and patch type on response variables (incoming energy and temperature) using multiple regression analysis. For soil evaporation values derived from the soil cores, we compared soil evaporation values between soil types (canopy vs. intercanopy) within each of the four cover \times canopy scenarios using paired *t*-tests. We also compared soil evaporation values for 35% cover canopy soils and temperature vs. 25% cover intercanopy soils and temperature, and for 5% intercanopy soils and temperature vs. 65% cover intercanopy soils and temperature using paired *t*-tests. All statistical analyses used JMP 5.1 statistical software (SAS Institute, Cary, NC). Results were considered significant using an alpha level of 0.05.

RESULTS

Overall Trends with Woody Canopy Cover in Microclimate and Potential Soil Evaporation

The 18-m transects used in this study, which were selected to have similar amounts of woody canopy cover to that of the previously studied 50-m transects within which they were embedded, exhibited trends in near-ground solar radiation similar to the full 50-m transects (Fig. 1). As expected, near-ground solar radiation estimated for cloudless conditions decreased with increasing woody canopy cover. The decrease between 5% and 65% woody cover was by a factor of two or more for most months, with the reduction being greatest in summer months (Fig. 2A). Annual soil temperature exhibited trends similar to those of near-ground solar radiation, with the greatest difference between 5% and 65% woody cover occurring in summer months. Observed deviations from a smooth spline interpolation curve in annual soil temperature data were expected, because temperature readings reflect true temporal variations in ambient temperature and cloud cover (Fig. 2B). This is in contrast to perfect interpolation of near-ground radiation between months, which does not reflect any field-based ambient data, and assumes zero cloud cover (Fig. 2A). Soil temperature differed between low and high amounts of woody plant canopy cover by as much as a factor of two. Potential soil evaporation estimated from soil temperature data similarly decreased with canopy cover, again by as much as a factor of two (Fig. 2C).

Seasonal Correlations Between Near-Ground Radiation and Soil Temperature

Overall, monthly soil temperatures (minimum, average, and maximum) were positively correlated with near-ground solar

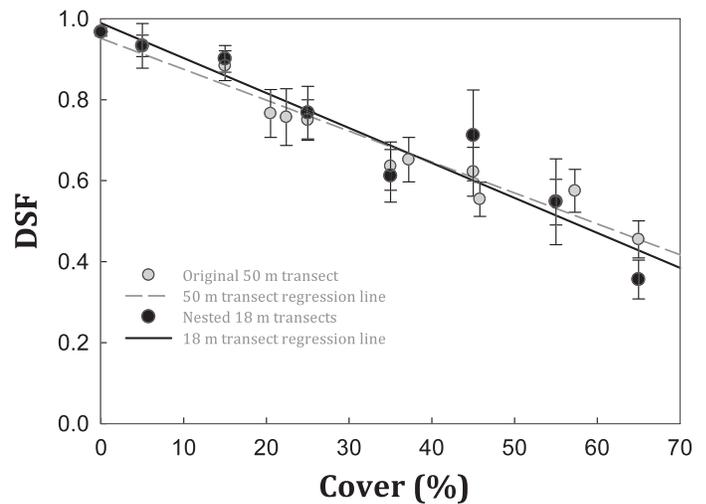


Figure 1. Comparison of incoming near-ground solar radiation trends, estimated as the direct site factor (DSF) for values along a discrete canopy cover interval series. Original 50-m (grey circles and dashed line) transects from Royer et al. (2010), and 18-m transects used in the current study (black circles and solid line) that were nested within the previous transects. Direct Site Factor is a dimensionless value between 0.0 and 1.0, indicating the amount of direct solar radiation throughout the year, correcting for surface orientation and global location. Circles represent mean and error bars represent standard error.

radiation, with the exception of February, the coldest of the 4 mo, for which minimum temperature decreased in response to increasing near-ground solar radiation (Fig. 3). Correlations were stronger with warmer seasonal temperatures—maximum and average temperatures in April ($R^2 = 0.80$ and 0.88 , respectively), and August ($R^2 = 0.87$ and $R^2 = 0.90$, respectively)—and even with minimum temperature in the warmest month (August: $R^2 = 0.82$, $P < 0.01$). Correlations were not as strong for intermediate temperatures (for November, maximum temperature with $R^2 = 0.71$, $P = 0.02$, and average temperature with $R^2 = 0.67$, $P = 0.02$). Soil temperature was not correlated with near-ground solar radiation at cooler times, except for under the coldest conditions, when the correlation had a negative slope (minimum February temperatures, $R^2 = 0.80$, $P < 0.01$).

Seasonal Heterogeneity in Canopy and Intercanopy Microclimate and Potential Soil Evaporation

Near-ground solar radiation decreased significantly with woody canopy cover within intercanopy as well as canopy patches in every month assessed ($P < 0.01$) except for February ($P = 0.06$; Fig. 4, top panels). However, the difference in near-ground solar radiation between canopy and intercanopy was only significant for the month of April ($P < 0.01$). Differences in soil temperature–woody canopy cover relationships were significant between canopy and intercanopy patches under warmer conditions (April, $P = 0.01$; August, $P = 0.02$; Fig. 4, bottom panels). Under cooler temperatures, we noted an interaction between patch type and cover (November and February, both $P < 0.03$; test for interaction-nonzero slope); temperature decreased under canopy, but remained steady in intercanopy patches as woody canopy cover increased, (Fig. 4, bottom panels). Notably, the amount of woody canopy cover measured over the

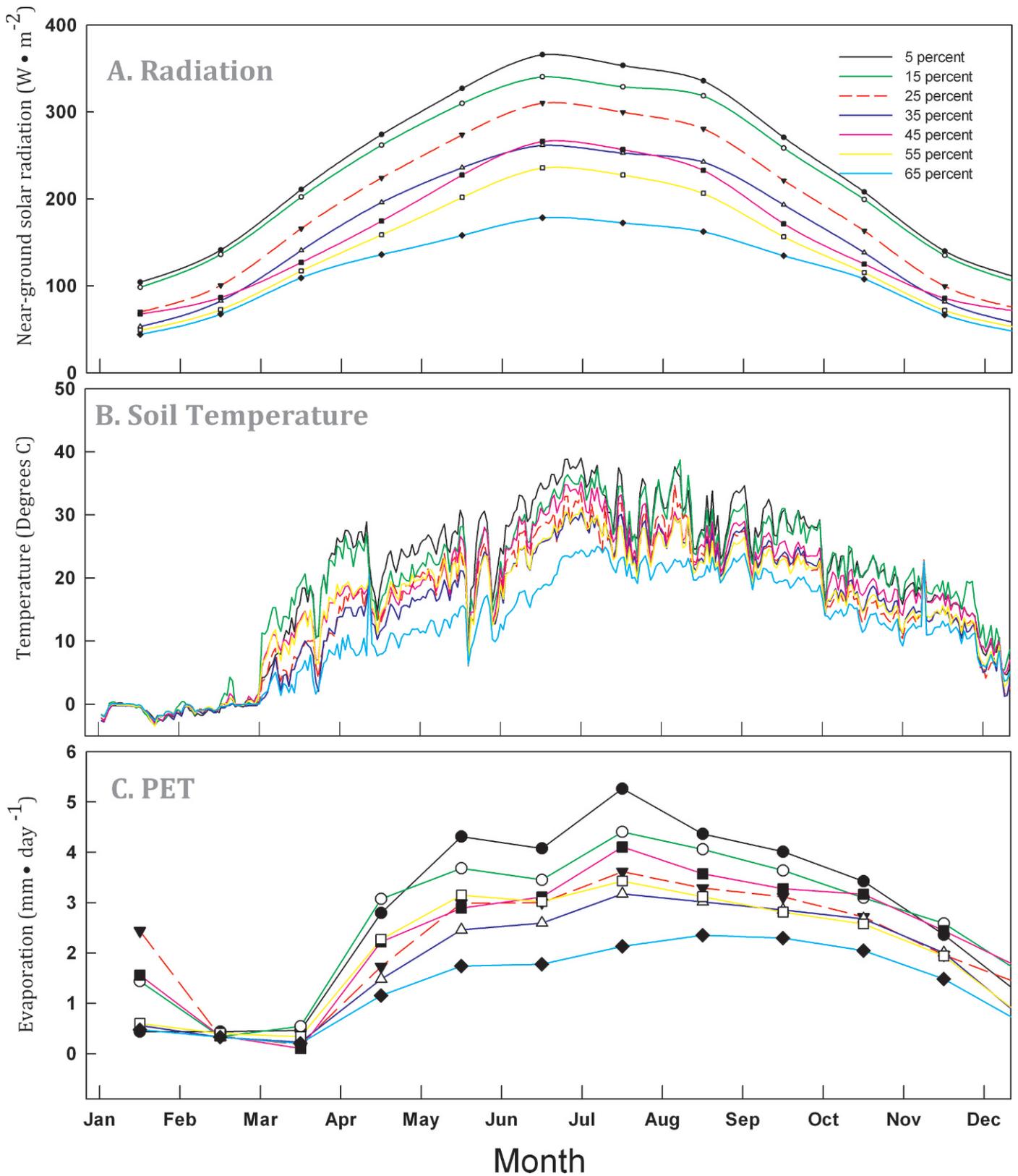


Figure 2. A, Near-ground radiation ($W \cdot m^{-2}$); B, daily maximum soil temperature ($^{\circ}C$); and C, potential evapotranspiration ($mm \cdot day^{-1}$), for 18-m transects in seven levels of woody canopy cover.

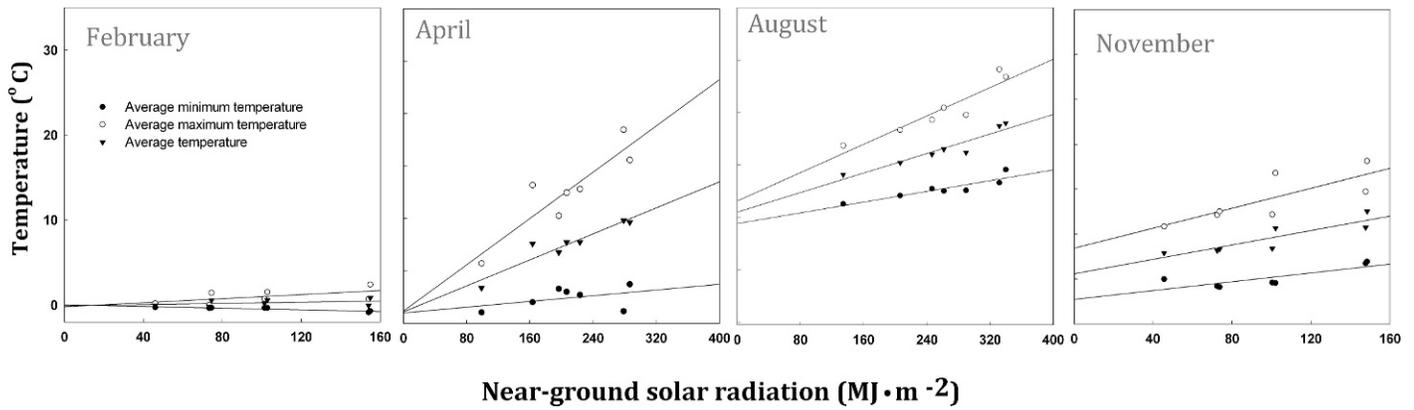


Figure 3. Trend-derived functions correlating average minimum, average maximum, and average soil temperature ($^{\circ}\text{C}$) with near-ground radiation ($\text{W} \cdot \text{m}^{-2}$) for February, April, August, and November.

entire transect affected diurnal patterns of near-ground solar radiation and soil temperature, and this effect was particularly pronounced during warmer months (Fig. 5).

There were greater rates of potential soil evaporation from intercanopy soils compared to canopy soils at all temperatures (based on soil cores from the intermediate site with 35% woody canopy cover; Fig. 6; all P values < 0.01). Potential soil evaporation was more than three times greater for intercanopy than canopy soils when we matched each patch type to its respective maximum August temperature over 48 h (Fig. 6D, derived from Fig. 6A and B). Notably, the difference in potential soil evaporation rate for intercanopy samples (at intercanopy temperatures) from the low (5%) vs. high (65%) canopy cover sites (Fig. 6E, derived from Fig. 6A and 6C) was of the same magnitude as the difference in soil evaporation from the canopy–intercanopy comparison at 35% cover (Fig. 6D). This finding highlights spatial variation in soil evaporation within an ecosystem (e.g., under vs. between woody canopies) and across ecosystems (e.g., with differing amounts of woody canopy cover). To our knowledge, such spatial variations have not been simultaneously considered.

DISCUSSION

Spatiotemporal Trends in Microclimate Across the Continuum

Our study simultaneously assessed relationships between woody canopy cover and soil temperature both within and across sites along a grassland–evergreen forest continuum. Our results document clear trends in microclimate in response to woody canopy cover, consistent with findings for similar semiarid woody plant architectures such as low-elevation mesquite bosque (Villegas et al. 2010b), and mixed conifer woodlands (Yaseef et al. 2010). The decrease in near-ground solar radiation with increasing woody canopy cover in piñon–juniper woodland documented previously (Royer et al. 2010; Villegas et al. 2010b) and focused on here (Fig. 1) forms the basis for assessing other trends in microclimate, beginning with average site temperature and potential soil evaporation as a function of woody canopy cover (Fig. 2). Notably, the effects of woody canopy cover on near-ground solar radiation translated into soil temperature patterns during warmer months (Fig. 3), similar to other findings for similar plant

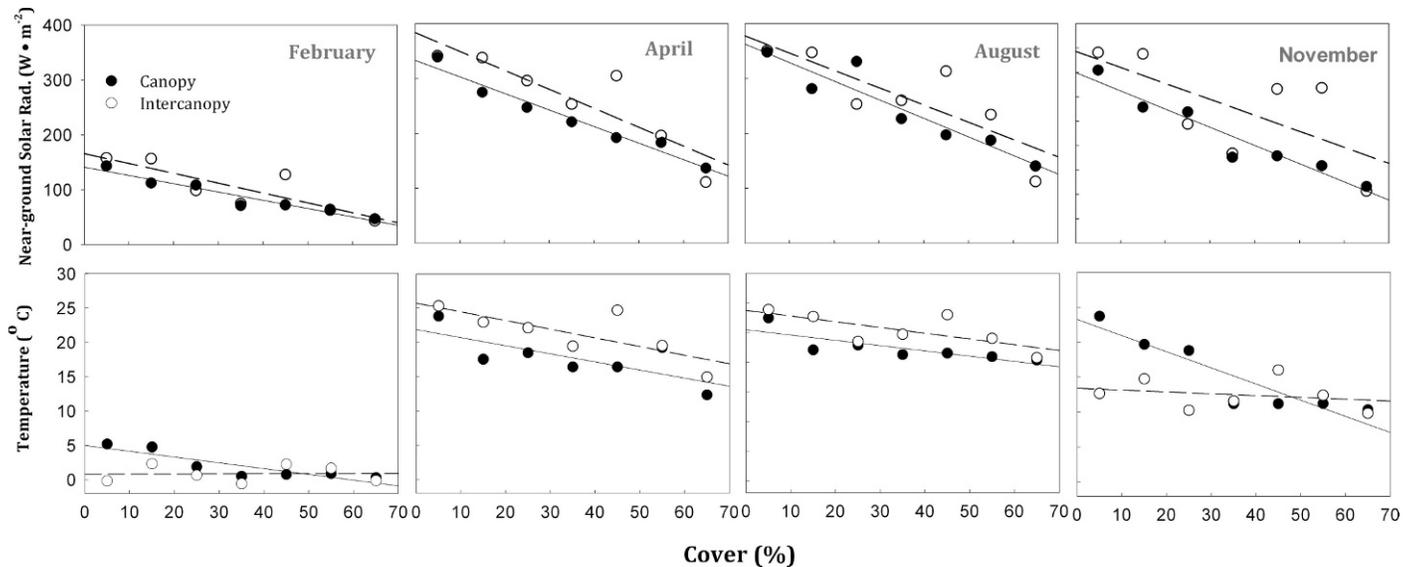


Figure 4. Trends in soil temperature (**bottom**, $^{\circ}\text{C}$) and near-ground solar radiation (**top**, $\text{W} \cdot \text{m}^{-2}$) for canopy (solid circles and solid lines) and intercanopy (empty circles and dashed lines) patches along gradients.

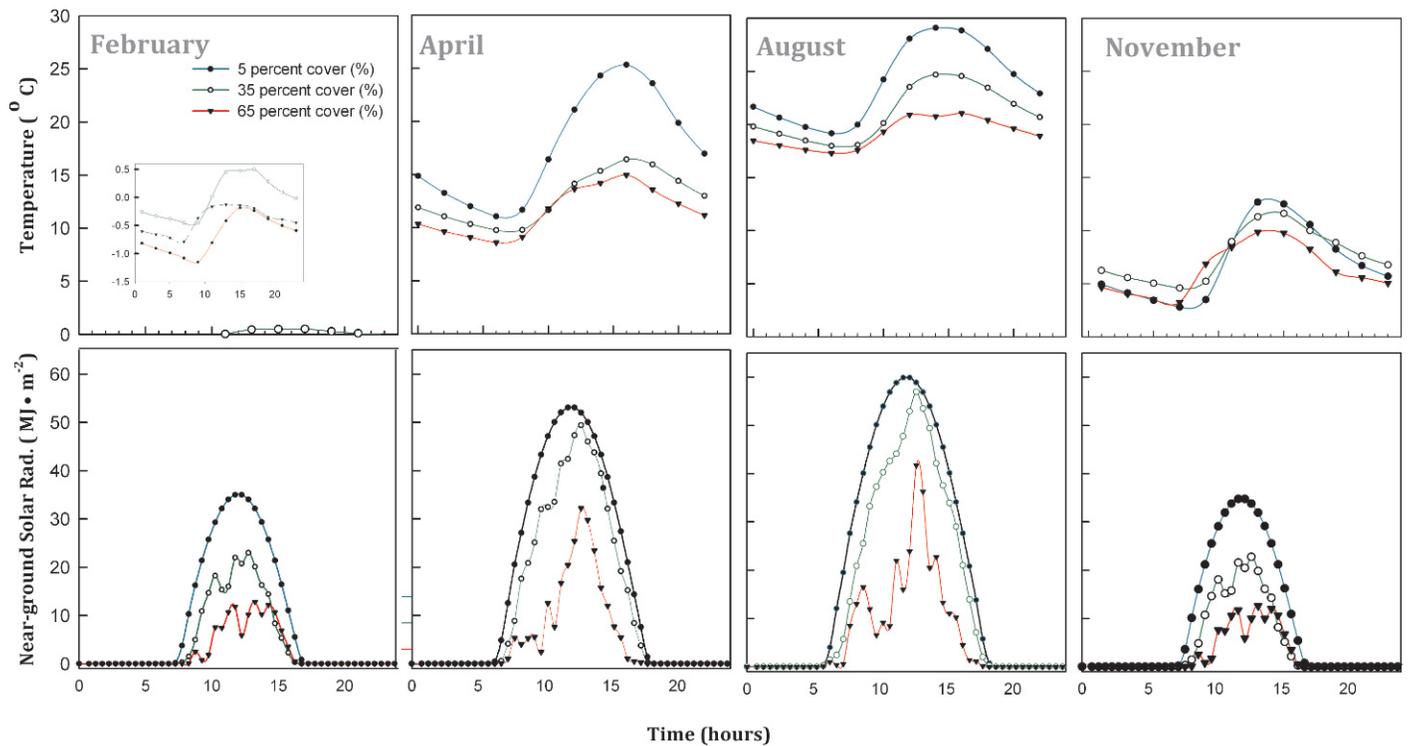


Figure 5. Diurnal values for near-ground solar radiation (**bottom**, $\text{W} \cdot \text{m}^{-2}$) and soil temperature (**top**, $^{\circ}\text{C}$) in intercanopy patches for 5%, 35%, and 65% woody canopy cover transects.

architecture (Yaseef et al. 2010) and more pronounced than for systems with woody plants with lower foliar density, such as mesquite (Villegas et al. 2010a).

The effect of woody canopy cover on microclimate at the patch scale was most evident in the diurnal responses of temperature and near-ground solar radiation in intercanopy patches: maximum differences and peak values within a day were both substantially lower in transects with 5% cover relative to those with 65% cover (Fig. 5). This finding is similar to those of others evaluating effects of neighboring trees (Breshears et al. 1988; Naumburg and DeWald 1999; Forseth et al. 2001; Drezner 2006, 2007; Lebron et al. 2007) but extends those findings to a broad gradient of woody canopy cover.

The effects of woody canopy cover influence both site conditions across the gradient and patch heterogeneity within it (Fig. 7). Several trends occur concurrently along the grassland-forest continuum from low to high woody canopy cover: overall site soil temperature decreases, canopy patches are cooler than intercanopy patches, and the relative influence of intercanopy patches decreases while that of canopy patches increases. Interestingly, the difference between intercanopy soil temperatures at low vs. high density is comparable to the difference between intercanopy and canopy patches at low stand density (Fig. 7). These results build on other studies of trends in near-ground solar radiation along the continuum (Martens et al. 2000; Roberts 2000; Fu and Rich 2002; Zou et al. 2007; Royer et al. 2010; Villegas et al. 2010a, 2010b) and extend them to soil temperature. Importantly, they indicate overall woody canopy cover needs to be accounted for in addition to site-specific differences in microclimate associated with canopy/intercanopy patch type (Breshears et al. 1998; Lebron et al. 2007; Newman et al. 2010).

Ecohydrological Relevance of Density-Dependent Microclimate Trends

The differences in microclimate along the gradient and with respect to patch type have important ecohydrological implications. Our simplified potential soil evaporation estimates indicate large differences in rates at multiple scales: for canopy vs. intercanopy patches within a site, for intercanopy patches at low vs. high density, and in overall soil evaporation along the gradient. These results not only contrast potential soil evaporation regimes between patch types at a site or between two sites but also aid in the development of a more comprehensive understanding of the partitioning of evapotranspiration along the continuum (Breshears et al. 1998; Kurc and Small 2004; Wang et al. 2010). In addition to the connections through shading that we quantify here, we note that use of intercanopy water by woody plants is another important process that connects canopy and intercanopy patches (Newman et al. 2010). The differences in potential soil evaporation that we have assessed here have important implications for soil water content and other components of the water budget in addition to evapotranspiration (Lebron et al. 2007; Madsen et al. 2008; Newman et al. 2010). More direct measures of actual soil evaporation, such as those from small field lysimeters (e.g., Villegas et al. 2010b) are needed to more fully evaluate the density-dependent ecohydrological effects of woody plants.

IMPLICATIONS

Rangelands are inherently gradients with varying amounts of woody plant cover. Much management of rangelands focuses

Increasing Temperature

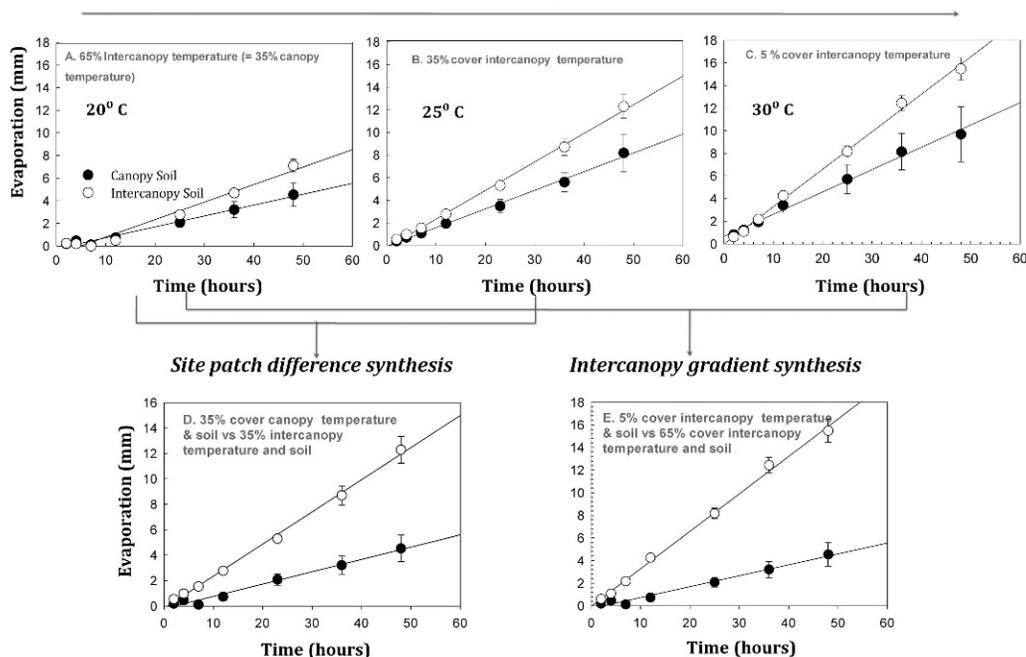


Figure 6. Potential soil evaporation as a function of time for soils from canopy (solid circles) and intercanopy (empty circles) soil types from drying experiments based on maximum temperatures during August for selected amounts of canopy cover. Results correspond to increasing soil temperatures (along top row) of **A**, 65% woody canopy cover and maximum intercanopy temperature of $\sim 20^{\circ}\text{C}$; **B**, 35% woody canopy cover and maximum intercanopy temperature of $\sim 25^{\circ}\text{C}$; and **C**, 5% woody canopy cover and maximum intercanopy temperature of $\sim 30^{\circ}\text{C}$. The $\sim 20^{\circ}\text{C}$ simulation also corresponds to 35% woody canopy cover and maximum canopy temperature. These three simulations allowed for synthetic comparisons (bottom row) focused on patch type (**D**, at 35% woody canopy cover, intercanopy soil and temperature vs. canopy soil and temperature) and intercanopy contrasts along the gradient (**E**, intercanopy soil and temperature for 5% and 65% woody canopy cover). Circles are means and error bars are standard errors.

on predicting and managing the effects of overstory woody plants on understory herbaceous plants, not only through competitive interactions, but also indirectly through the effects of woody plants on microclimate. Notably, while many studies of rangeland microclimate compare two or three rangeland sites with different amounts of woody plant cover, few studies have evaluated such effects as a continuous gradient from low to high amounts of woody plant canopy cover. Our results highlight how mean conditions for a site and the conditions separately associated with canopy patches and with intercanopy patches vary continuously along such a gradient,

quantifying important changes in patch-scale heterogeneity. We documented expected decreases in near-ground solar radiation, soil temperature, and potential soil evaporation of as much as a factor of two or more with increasing canopy cover. Similar to the response for near-ground solar radiation, soil temperature at the patch scale generally decreased with woody canopy cover for intercanopy as well as canopy patches, indicating coalescing influence of individual canopies on neighboring areas. Intercanopy patches were as much as 10°C cooler at high- compared to low-density sites, yielding a potential soil evaporation difference that rivaled that between

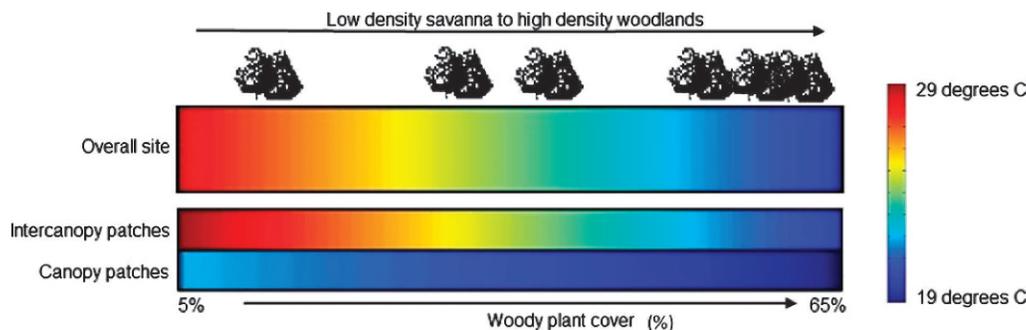


Figure 7. Synthesis of trends in soil temperature during August for overall site, and canopy and intercanopy patch type, all as a function of woody canopy cover. The temperature gradient ($\sim 19^{\circ}\text{C}$ to 29°C) reflects the actual field derived values for the range of soil temperatures. Note that soil temperature for intercanopy patches at high amounts of woody canopy cover approximates that of canopy patches. Differences in soil evaporation between patch types would be further exaggerated due to soil texture and litter effects.

canopy and intercanopy patches at a lower density sites. Collectively, our results highlight the ecohydrological consequences of density-dependent shading by evergreen woody plants through their amelioration of intercanopy temperature, which in turn can affect potential soil evaporation. Accounting more explicitly for how continuous gradients of woody plant cover affect microclimate and associated ecohydrological processes is directly relevant for predicting and managing numerous rangeland attributes related directly and indirectly to ecohydrological processes, such as understory biomass and productivity, and soil respiration and associated carbon dynamics. Specifically, our results enable rangeland managers to rapidly estimate approximate site microclimate after assessing amount of woody canopy cover. In addition, they enable rough assessments of the microclimate impacts of increases in woody canopy cover, such as associated with “encroachment” of woody plants, or decreases in woody canopy cover such as due to thinning or drought-induced die-off.

LITERATURE CITED

- BHARK, E. W., AND E. E. SMALL. 2003. Association between plant canopies and the spatial patterns of infiltration in shrubland and grassland of the Chihuahuan Desert, New Mexico. *Ecosystems* 6:185–196.
- BRESHEARS, D. D. 2006. The grassland–forest continuum: trends in ecosystem properties for woody plant mosaics? *Frontiers in Ecology and the Environment* 4:96–104.
- BRESHEARS, D. D., AND J. A. LUDWIG. 2010. Near-ground solar radiation along the grassland–forest continuum: tall-tree canopy architecture imposes only muted trends and heterogeneity. *Austral Ecology* 35:31–40.
- BRESHEARS, D. D., J. W. NYHAN, C. E. HEIL, AND B. P. WILCOX. 1998. Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and intercanopy patches. *International Journal of Plant Sciences* 159:1010–1017.
- BROOKS, J. R., F. C. MEINZER, R. COULOMBE, AND J. GREGG. 2002. The hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests. *Tree Physiology* 22:1107–1117.
- DREZNER, T. D. 2006. Plant facilitation in extreme environments: the non-random distribution of saguaro cacti (*Carnegiea gigantea*) under their nurse associates and the relationship to nurse architecture. *Journal of Arid Environments* 65:46–61.
- DREZNER, T. D. 2007. An analysis of winter temperature and dew point under the canopy of a common Sonoran Desert nurse and the implications for positive plant interactions. *Journal of Arid Environments* 69:554–568.
- FORSETH, I. N., D. A. WAI, AND B. B. CASPER. 2001. Shading by shrubs in a desert system reduces the physiological and demographic performance of an associated herbaceous perennial. *Journal of Ecology* 89:670–680.
- FU, P. D., AND P. M. RICH. 2002. A geometric solar radiation model with applications in agriculture and forestry. *Computers and Electronics in Agriculture* 37:25–35.
- GEIGER, R., R. H. ARON, AND P. TODHUNTER. 2003. The climate near the ground. 6th ed. Lanham, MD, USA: Rowman and Littlefield. 584 p.
- HARGREAVES, G. H. 1975. Moisture availability and crop production. *Transactions of the ASAE* 18:980–984.
- HOUSE, J., S. ARCHER, D. D. BRESHEARS, R. J. SCHOLLES, AND TREE–GRASS INTERACTIONS WORKING GROUP. 2003. Conundrums in mixed woody–herbaceous plant systems. *Journal of Biogeography* 30:1763–1777.
- HUXMAN, T. E., B. P. WILCOX, D. D. BRESHEARS, R. L. SCOTT, K. A. SNYDER, E. E. SMALL, K. HULTINE, W. T. POCKMAN, AND R. B. JACKSON. 2005. Ecohydrological implications of woody plant encroachment. *Ecology* 86:308–319.
- KURC, S. A., AND E. E. SMALL. 2004. Dynamics of evapotranspiration in semiarid grassland and shrubland ecosystems during the summer monsoon season, central New Mexico. *Water Resources Research* 40:W09305. doi:10.1029/2004WR003068
- LEBRON, I., M. D. MADSEN, D. G. CHANDLER, D. A. ROBINSON, O. WENDROTH, AND J. BELNAP. 2007. Ecohydrological controls on soil moisture and hydraulic conductivity within a pinyon–juniper woodland. *Water Resources Research* 43:W08422. doi:10.1029/2006WR005398
- LOIK, M. E., D. D. BRESHEARS, W. K. LAUENROTH, AND J. BELNAP. 2004. A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. *Oecologia* 141:269–281.
- LUDWIG, J. A., B. P. WILCOX, D. D. BRESHEARS, D. J. TONGWAY, AND A. C. IMESON. 2005. Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes. *Ecology* 86:288–297.
- MADSEN, M. D., D. G. CHANDLER, AND J. BELNAP. 2008. Spatial gradients in ecohydrologic properties within a pinyon–juniper ecosystem. *Ecohydrology* 1:349–360.
- MARTENS, S. N., D. D. BRESHEARS, AND C. W. MEYER. 2000. Spatial distributions of understory light along the grassland/forest continuum: effects of cover, height, and spatial pattern of tree canopy. *Ecological Modelling* 126:79–93.
- MASEYK, K. S., T. LIN, E. ROTENBERG, J. M. GRÜNZWEIG, A. SCHWARTZ, AND D. YAKIR. 2008. Physiology-phenology interactions in a productive semi-arid pine forest. *New Phytologist* 178:603–616.
- MOORE, G. W., AND J. L. HEILMAN. 2011. Proposed principles governing how vegetation changes affect transpiration. *Ecohydrology* 4:351–358.
- NAUMBURG, E., AND L. E. DEWALD. 1999. Relationships between *Pinus ponderosa* forest structure, light characteristics, and understory graminoid species presence and abundance. *Forest Ecology and Management* 124:205–215.
- NEWMAN, B. D., B. P. WILCOX, S. A. ARCHER, D. D. BRESHEARS, C. N. DAHM, C. J. DUFFY, N. G. McDOWELL, F. M. PHILLIPS, B. R. SCANLON, AND E. R. VIVONI. 2006. Ecohydrology of water-limited environments: a scientific vision. *Water Resources Research* 42:W06302. doi:10.1029/2005WR004141
- NEWMAN, B. D., D. D. BRESHEARS, AND M. O. GARD. 2010. Evapotranspiration partitioning in a semiarid woodland: ecohydrological heterogeneity and connectivity of vegetation patches continuum. *Vadose Zone Journal* 9:561–572.
- OWENS, M. K., R. K. LYONS, AND C. L. ALEJANDRO. 2006. Rainfall partitioning within semiarid juniper communities: effects of event size and canopy cover. *Hydrological Processes* 20:3179–3189.
- ROBERTS, J. 2000. The influence of physical and physiological characteristics of vegetation on their hydrological response. *Hydrological Processes* 14:2885–2901.
- RODRÍGUEZ-ITURBE, I., AND A. PORPORATO. 2004. Ecohydrology of water-controlled ecosystems: soil moisture and plant dynamics. Cambridge, UK: Cambridge University Press. 464 p.
- ROYER, P. D., D. D. BRESHEARS, C. B. ZOU, N. S. COBB, AND S. A. KURC. 2010. Ecohydrological energy inputs in semiarid coniferous gradients: response to management- and drought-induced tree reductions. *Forest Ecology and Management* 260:1646–1655.
- ROYER, P. D., N. S. COBB, M. J. CLIFFORD, C. Y. HUANG, D. D. BRESHEARS, H. D. ADAMS, AND J. C. VILLEGAS. 2011. Extreme climatic event-triggered overstorey loss increases understory solar input regionally: primary and secondary ecological implications. *Journal of Ecology* 99:714–723.
- SEYFRIED, M. S., S. SCHWINNING, M. A. WALVOORD, W. T. POCKMAN, B. D. NEWMAN, R. B. JACKSON, AND E. M. PHILLIPS. 2005. Ecohydrological control of deep drainage in arid and semiarid regions. *Ecology* 86:277–287.
- VEATCH, W., P. D. BROOKS, J. R. GUSTAFSON, AND N. P. MOLOTOCH. 2009. Quantifying the effects of forest canopy cover on net snow accumulation at a continental, mid-latitude site. *Ecohydrology* 2:115–128.
- VILLEGAS, J. C., D. D. BRESHEARS, C. B. ZOU, AND D. J. LAW. 2010a. Ecohydrological controls of soil evaporation in deciduous drylands: how the hierarchical effects of litter, patch and vegetation mosaic cover interact with phenology and season. *Journal of Arid Environments* 74:595–602.
- VILLEGAS, J. C., D. D. BRESHEARS, C. B. ZOU, AND P. D. ROYER. 2010b. Seasonally pulsed heterogeneity in microclimate: phenology and cover effects along deciduous grassland–forest continuum. *Vadose Zone Journal* 9:537–547. doi:10.2136/vzj2009.0032
- WANG, L. X., K. K. CAYLOR, J. C. VILLEGAS, G. A. BARRON-GAFFORD, D. D. BRESHEARS, AND T. E. HUXMAN. 2010. Partitioning evapotranspiration across gradients of woody plant cover: assessment of a stable isotope technique. *Geophysical Research Letters* 37:L09401. doi:10.1029/2010GL043228

- WILCOX, B. P., D. D. BRESHEARS, AND M. S. SEYFRIED. 2003. Water balance on rangelands. *In*: B. A. Stewart and T. A. Howell [EDS.]. *Encyclopedia of Water Science*. New York, NY, USA: Marcel Dekker. p. 791–794.
- WILCOX, B. P., AND B. D. NEWMAN. 2005. Ecohydrology of semiarid landscapes. *Ecology* 86:275–276.
- WILCOX, B. P., AND T. L. THUROW. 2006. Emerging issues in rangeland ecohydrology. *Hydrological Processes* 20:3155–3157.
- YASEEF, N., E. ROTENBERG, AND D. YAKIR. 2010. Effects of spatial variations in soil evaporation caused by tree shading on water flux partitioning in semi-arid pine forest. *Agricultural and Forest Meteorology* 3:454–462.
- ZOU, C. B., G. A. BARRON-GAFFORD, AND D. D. BRESHEARS. 2007. Effects of topography and woody plant canopy cover on near-ground solar radiation: relevant energy inputs for ecohydrology and hydrogeology. *Geophysical Research Letters* 34:L24S21. doi:10.1029/2007GL031484
- ZOU, C. B., D. D. BRESHEARS, B. D. NEWMAN, B. P. WILCOX, M. O. GARD, AND P. M. RICH. 2008. Soil water dynamics under low- versus high-ponderosa pine tree density: ecohydrological functioning and restoration implications. *Ecohydrology* 1:308–315.
- ZOU, C. B., P. D. ROYER, AND D. D. BRESHEARS. 2010. Density-dependent shading patterns by Sonoran saguaros. *Journal of Arid Environments* 74:156–158.