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EFFECTS OF WOODY PLANTS ON MICROCLIMATE IN A SEMIARID WOODLAND: SOIL TEMPERATURE AND EVAPORATION IN CANOPY AND INTERCANOPY PATCHES

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The canopies of woody plants in semiarid ecosystems modify the microclimate beneath and around them, with canopy patches usually having lower soil temperatures than intercanopy patches. However, lacking are studies that have evaluated how heterogeneity in soil temperature, induced by woody plant canopies, influences soil evaporation rates and the consequent effects on plant-available water. Soil temperatures were measured and soil evaporation rates were estimated for canopy and intercanopy patches in a semiarid piñon-juniper woodland (Pinus edulis and Juniperus monosperma) in northern New Mexico. Soil temperature was measured at 2-cm depths in four canopy and four intercanopy locations during 1994. Maximum soil temperature in intercanopy patches was greater than in canopy patches between May and September, by as much as 10°C, while soil temperatures in intercanopy patches were lower than in canopy patches during colder parts of the day in the fall and winter months. Equations for soil drying rates for sandy loam soil samples were determined in laboratory experiments over a range of temperatures and soil water contents. Drying rates were disproportionately greater at high soil moisture and high soil temperature. Intercanopy patches were predicted to dry more than canopy patches for days in April through September by as much as 2% volumetric soil water content per day. The difference between patches was amplified at lower soil water contents when expressed as soil water potential, which more directly determines plant-available water. Our results quantify the effects of woody plants on the microclimate with respect to soil temperature and evaporation, which in turn affect herbaceous and woody plants by modifying factors such as germination, the potential for facilitation, and the amount of plant-available water.

Introduction

Both herbaceous and woody plants in semiarid ecosystems depend on pulses of soil moisture resulting from precipitation events (Noy-Meir 1973). The canopies of woody plants modify the microclimate beneath and around them through interception of precipitation and by shading, both of which influence the amount of soil moisture available to plants. Relative to intercanopy patches, canopy patches receive reduced precipitation inputs because of foliar interception of precipitation (Johnsen 1962; Skau 1964; Collings 1966; Young and Evans 1987; Belsky et al. 1989; Breshears et al. 1997b). Canopy patches also usually have lower soil temperatures than intercanopy patches (Everett and Sharrow 1985; Belsky et al. 1989; Pierson and Wight 1991) as a result of effects of shading and litter accumulation. Near-surface soil temperatures, which reflect integrated energy relationships, affect soil evaporation rates (Hillel 1980), and hence, woody canopies can modify soil moisture not only directly via interception but also indirectly via influences on soil evaporation rates. Loss of soil

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moisture by soil evaporation in turn reduces the amount of water available to plants. However, lacking are studies that have evaluated how heterogeneity in soil temperature induced by woody plant canopies influences soil evaporation rates and the consequent effects on plant-available water (see Scholes and Archer 1997 for a review of related studies).

Our objectives were (1) to quantify the diurnal differences in soil temperature between canopy and intercanopy patches in a semiarid woodland throughout the year, (2) to determine soil evaporation rates as a function of soil temperature and soil moisture, and (3) to estimate the differences in soil evaporation rates between the two patch types as a function of time of year in terms of soil moisture and soil water potential, the latter of which more directly determines plant-available water. We used field measurements of soil temperature from a semiarid piñon-juniper (Pinus edulis Engelm. and Juniperus monosperma [Engelm.] Sarg.) woodland and laboratory experiments to address these objectives. We focused on soil temperature and moisture in the top 2 cm because a large proportion of precipitation events in semiarid climates are small, only wetting surface soils and evaporating rapidly (Emerson 1932; Sala and Lauenroth 1982; Bowen 1990; Roundy et al. 1997). Our results, which quantify large soil temperature differences between canopy and intercanopy patches and the synergistic effects between soil moisture and soil temperature on

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soil evaporation rates, have implications for the germination of and plant water use by herbaceous and woody species.

Material and Methods

Study Site

Soil temperatures were measured at the Mesita del Buey site—an upper-elevation (2140 m) piñon-juniper woodland (Pinus edulis Engelm. and Juniperus monosperma [Engelm.] Sarg.) in northern New Mexico, within Technical Area 51 of the Los Alamos National Laboratory (latitude 34.30°N, longitude 106.27°W). The dominant herbaceous species is Bouteloua gracilis [H.B.K.] Lag., located primarily in intercanopy patches. The site has a temperate mountain climate and receives ca. 40 cm of precipitation annually, mainly in the form of winter snowfall and late summer precipitation; mean ambient air temperature is ca. 9° C, ranging from -2° C in January to 21°C in June (estimated as means of Los Alamos and White Rock sites from data in Bowen 1990). The upper soil layer at Mesita del Buey is classified as Hackroy sandy loam (Nyhan et al. 1978); soil profile depths vary from 30 to 130 cm, and the canopy and intercanopy locations do not differ significantly in most soil morphological properties, except for the litter layer (O horizon) present in canopy patches (Davenport et al. 1996).

Soil Temperature Measurements

Soil temperature was measured at eight locations that were selected to be representative of patch-scale variability within the woodland: four beneath canopy patches (including P. edulis and *I. monosperma* canopies) and four in intercanopy patches (including both bare soil and B. gracilis locations). A shallow pit was dug at each location and a temperature probe (107B, Campbell Scientific, Logan, Utah) was inserted vertically into the pit-face such that temperature readings were obtained in the undisturbed portion of soil profile at a depth of 2 cm from the soil surface for intercanopy patches and at 2 cm beneath the litter in canopy patches (mean litter depth for the four canopy locations was 2.4 cm). Most of the soil evaporation should occur at these shallow depths, consistent with results of stable isotope studies (Newman et al. 1997). The probes were attached to an automated data acquisition system, and the pits were then backfilled.

Measurements were obtained during the 1994 calendar year at 2-h intervals, except for the months of January and February, when measurements were for 6-h intervals. The temperatures for each patch type—canopy and intercanopy—were summarized by calculating monthly mean temperature and mean diurnal curves for each month. Differences between canopy and intercanopy patches were tested using analysis of variance for repeated measures (ANOVAR). Hourly values for the mean diurnal curve for each patch type were estimated by linear interpolation between sampling times. The mean ambient air temperature for each month in 1994 was within 2°C of the long-term average for the site (Bowen 1990), except for June 1994, which was 3.5°C lower than the long-term average.

Soil Drying Experiments

Soil drying experiments were conducted using soil samples that were removed intact. These samples were Ascalon sandy loam, collected from the Pawnee Experimental Site (41°N, 108°W; Nyhan 1975), and were similar in texture and herbaceous vegetation (B. gracilis) to the Hackroy sandy loam at the Mesita del Buey site. One hundred soil samples were removed in tact and placed in soil incubation containers (plastic boxes 16 cm high and 12.5×12.5 cm with a 12×12 -cm square cut out of the top and covered with Dacron curtain material [1 × 1-mm openings]). Each container received a 12.5-mm simulated rain within a 30-min period, which was applied using a Plexiglas tank and 26-gauge hypodermic needles, yielding initial volumetric soil water contents of 20%. The containers were placed in laboratory incubators set at 5°, 20°, 30°, 40°, 50°, and 60°C (n = 10 each). All of the air in each incubator was replaced 14 times daily, using a MMX-110 Mini-Mixer (Little Giant Pump Co., Oklahoma City, Okla.). Soil water content was determined gravimetrically from the top 2.5 cm for five containers at each time interval (n = 2 samples per container); the duration of the measurements ranged from 46 h at 60°C to 115 h at 5°C.

The influence of soil water content on soil drying rates was evaluated in an additional set of experiments. The top 3 cm of soil was removed from 30 samples taken from the field. In each of 24 plastic boxes ($12.2 \times 2.2 \times 3$ cm) we placed 200 g (oven-dry weight basis) of soil. Water was slowly pipetted onto the soil to bring the water contents to 2%, 7%, 12%, 17%, 22%, 27%, 32%, and 36% (oven-dry weight basis) for each of three replicate samples. The samples were sealed and the soil was equilibrated for 24 h at room temperature. The samples were then placed in an incubator at 20° C with the incubator air exchanged with laboratory air 14 times a day using the Mini-Mixer pump. Soil water content was estimated gravimetrically at 4.5, 10.0, 23.0, 31.0, 58.0, 105.5, and 123.5 h

The data from these two laboratory experiments were used to determine soil drying rates as functions of soil temperature and volumetric soil water content (Nyhan 1974). A function for soil water drying rate was fitted for each soil temperature treatment using an exponential model: volumetric soil water content (%) = $a + e^{-bt}$, where a is the intercept, b is the soil drying rate (change in percentage of volumetric soil water content per hour), and t represents the hours of drying time. A correction factor to include the influence of volumetric soil water content on the soil drying rate was determined by least squares regression. This correction factor takes into account that the soil drying rate at higher water contents (>8% for Hackroy sandy loam) is a function of the ability of the soil profile to deliver water to the soil evaporation zone (the falling rate stage of Hillel 1980), while at lower water contents, evaporation rates remain constant (constant rate stage of Hillel 1980). The correction factor was calculated by dividing the drying rate predicted at a given soil water content by that at 8%. The correction factor was then multiplied by the initial estimate of soil drying rate at a specific soil temperature to yield an improved estimate of soil drying rate.

Canopy and Intercanopy Soil Drying Differences

The mean diurnal temperature curves for each month and each patch type were used in conjunction with the soil drying relationships developed in the laboratory to estimate differences in soil drying rates between canopy and intercanopy patches over a range of initial soil moisture conditions (15%, 25%, and 35%) at hourly intervals over the mean 24-h period for each month of the year. The soil water content curves were converted to soil water potential using a previously determined empirical conversion for Hackroy sandy loam (Breshears et al. 1997a). The difference in the predicted soil water potential between canopy and intercanopy patches was integrated over the mean 24-h interval for each month.

Results

Soil Temperature Differences

Mean monthly soil temperature ranged from -1.6°C to 25.9°C for intercanopy patches and 0.4°C to 22.5°C for canopy patches (fig. 1). Mean monthly soil temperature in intercanopy patches exceeded that in canopy patches by at least 1°C from April through August, while the converse was true from October through February; the transition between these two intervals occurred near the spring and fall equinoxes. These differences were statistically significant (ANOVAR interaction for patch type × time; P < 0.001).

The magnitude and direction of the differences in soil temperature between the two patch types varied diurnally by month (fig. 2). During late spring (e.g., May; fig. 2c) and sum-

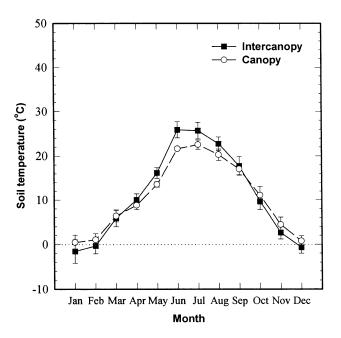


Fig. 1 Average monthly soil temperature (°C) in canopy and intercanopy patches at a depth of 2 cm in a semiarid woodland. Data are from 1994; n = 4 for each patch type. Error bars = 1 standard deviation.

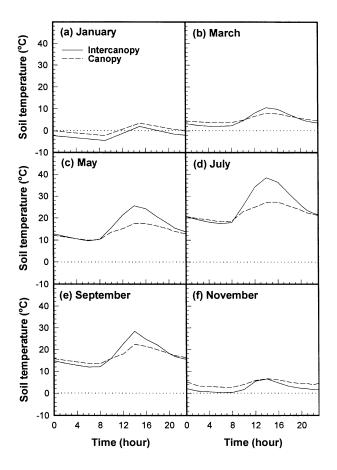


Fig. 2 Average diurnal soil temperatures (°C) in canopy and intercanopy patches for 4 mo during 1994.

mer (e.g., July; fig. 2*d*), soil temperature was greater in intercanopy than canopy patches during late afternoon (ANOVAR interaction for patch type × time; P < 0.001), with the maximum diurnal temperature from intercanopy soils exceeding that from canopy soils by as much as 10° C (e.g., 38.5° C in intercanopy vs. 27.2° C in canopy in July; fig. 2*d*). In contrast, during colder months minimum soil temperature was lower in intercanopy than canopy patches (e.g., November; fig. 2*f*; ANOVAR contrast for patch type × time; P < 0.05). Transitions between the two periods—intercanopy warmer than canopy midday versus intercanopy colder than canopy most of the day—occurred near the equinoxes (e.g., March and September; fig. 2*b*, *e*).

Effects of Soil Temperature and Water Content on Soil Drying Rates

Soil drying rate increased with increasing soil temperature (fig. 3a). Relative to the soil drying rate at 5°C, the drying rates for other soils increased by factors of 1.5 at 20°, 1.9 at 30°, 3.2 at 40°, 8.8 at 50°, and 11 at 60°C. Soil drying rates were also affected by the initial volumetric soil water content (fig. 3b). A correction factor (unitless) that was determined by dividing the drying rate predicted at a given volumetric soil

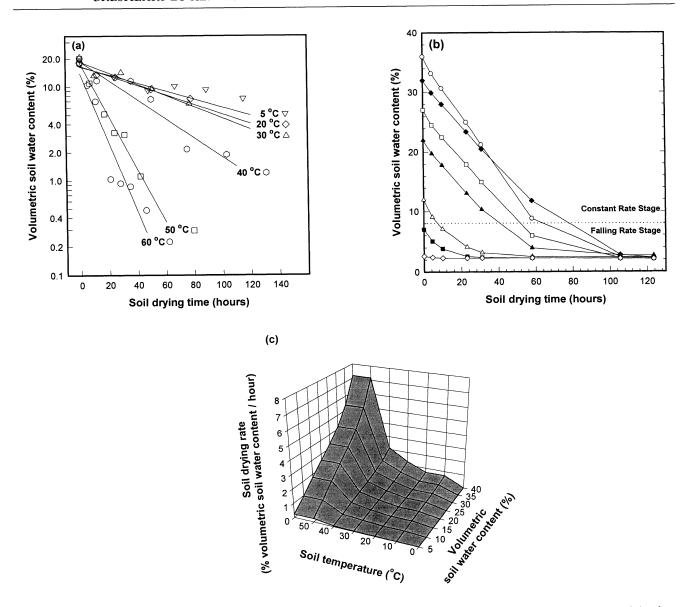


Fig. 3 a, Volumetric soil water content (%) as a function of soil drying time at constant soil temperatures; regressions are of this form: volumetric soil water content (%) = $a + e^{-bt}$, where t is the soil drying time in hours and a and b are temperature-dependent parameters (5°C: a = 16.4, $b = 1.0E^{-2}$; 20°C: a = 16.7, $b = 1.2E^{-2}$; 30°C: a = 18.6, $b = 1.4E^{-2}$; 40°C: a = 18.7, $b = 2.3E^{-2}$; 50°C: a = 17.9, $b = 6.5E^{-2}$; 60°C: a = 13.9, $b = 8.5E^{-1}$; P < 0.05 for all regressions). b, Effect of initial volumetric soil water content on rate of soil drying rate. c, Combined effects of soil temperature and volumetric soil water content (%) on soil drying rate (change in percentage of volumetric soil water content per hour).

water content (M) by that at 8% yielded the following relationship ($r^2 = 0.93$):

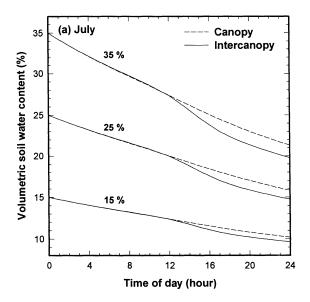
Correction =
$$\{-1.6 + 3.8 \cdot \log[\log(M \cdot 100)] + 0.56/M + [2.0E - 5 \cdot (|M - 18|)^3] - 1.5E - 4 \cdot M^2\}/0.23.$$

This correction factor produced estimates of ~ 1.0 at M = 8%, 1.4 at M = 15%, and 1.8 at M = 35%. The combined effects of soil temperature and initial soil moisture on soil drying rates (change in percentage of volumetric water content per hour) were synergistic such that soil drying rates were

much greater under conditions of high soil moisture and high soil temperature (fig. 3c).

Soil Evaporation Rates for Canopy and Intercanopy Patches

Soil drying rates were estimated for canopy and intercanopy patches using the field measurements (fig. 2) and the soil drying relationships that were based on soil temperature and soil water content (fig. 3c). One of the largest differences between the two patch types occurred during July (fig. 4a). The major dif-



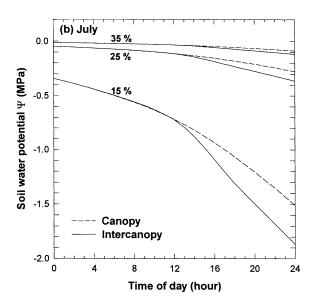


Fig. 4 *a*, Change in volumetric water content for canopy versus intercanopy patches for an average 24-h period in July at initial volumetric soil water contents of 15%, 25%, and 35%. *b*, Corresponding changes in soil water potential for July.

ference in the soil drying rates occurred between 1200 and 1800 hours (fig. 4a), when soil temperature differences were large (fig. 2). The differences between the two patch types were amplified at low soil water content when expressed as soil water potential (fig. 4b).

The integrated areas between the curves of soil water potential for the two patch types were summarized by month for initial volumetric soil water contents of 15%, 25%, and 35% (fig. 5). During late spring and summer (May-August), the integrated difference in soil water potential between the two patch types over a day was positive, indicating that soil evaporation was greater in intercanopy than canopy patches. In

July, the integrated difference in soil water potential between the two patch types ranged from 0.2 MPa h⁻¹ for an initial volumetric soil water content of 35% to 2.2 MPa h⁻¹ for an initial volumetric soil water content of 15%. In contrast, during fall and winter months, the difference between intercanopy and canopy soil water potential was negative (fig. 5), indicating that soil evaporation was less in intercanopy than in canopy patches. Spatial differences in soil temperature produce differences in soil evaporation only when the temperature is above freezing; hence, the difference between intercanopy and canopy soil water potential (fig. 5) is less negative during months when soil temperatures are mostly below freezing (January, February, and December) than during other months in the fall and winter (March, October, and November).

Discussion

Effects of Woody Plants on Microclimate

Our results showing higher temperatures in intercanopy than canopy patches during warmer months are similar to the differences between the two patch types reported in other semiarid shrublands and woodlands (Everett and Sharrow 1985; Belsky et al. 1989; Pierson and Wight 1991). In addition, our results show that between the fall and spring equinoxes (October–March), this relationship changes direction such that canopy patches have warmer average temperatures. This reversal results from the combined effects of lower sun angle and insulation by litter. The lower solar angle diminishes the difference in near-ground solar radiation between canopy and

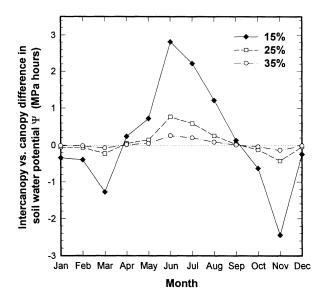


Fig. 5 Summary of integrated differences in soil water potential between intercanopy and canopy patches for each month of the year at initial volumetric soil water contents of 15%, 25%, and 35%. Positive values are associated with evaporation rates that are higher in intercanopy than canopy patches, while negative values are associated with the converse.

intercanopy patches (Breshears et al. 1997b) and the litter layer dampens diurnal variance in temperature.

The soil evaporation relationships that we quantified can be applied to other soils with similar texture. These relationships can also be used to evaluate the relative amount of evapotranspiration that results from soil evaporation through the year. The amount of evapotranspiration from soil evaporation relative to that from transpiration should increase with soil temperature as a result of the synergystic effect of soil temperature on evaporation, as we quantified, and the reduction in stomatal conductance (and hence transpiration) associated with increasing leaf temperature. Model estimates of evapotranspiration from a location near our site quantify this effect seasonally: soil evaporation represents a larger fraction of total evapotranspiration during June and July than during other months (Lane and Barnes 1987). Our results also highlight the importance of distinguishing between canopy and intercanopy soil evaporation rates. The horizontal heterogeneity in soil evaporation between canopy and intercanopy patch types is particularly large under conditions of high temperature when water flux rates are also greatest. At lower temperatures, e.g., in fall and winter, soil evaporation rates tend to be greater in canopy than intercanopy patches, but the magnitude of this difference is greatly reduced when soil temperatures drop below freezing for much of the day.

The horizontal heterogeneity in soil temperature and evaporation rates is particularly important when relating soil hydrological processes to stand-level fluxes of water for stands in which woody patches comprise an intermediate proportion of cover. Variance in near-ground solar radiation for a stand is greatest when woody plants comprise an intermediate proportion of cover as opposed to very low or very high proportions (S. N. Martens, D. D. Breshears, and C. W. Meyer, unpublished manuscript).

Soil evaporation is one of several processes—including foliar interception, runoff generation and redistribution, and plant water use-that can contribute to spatial differences in soil moisture between canopy and intercanopy patches. Soil moisture heterogeneity between the two patch types varies temporally in magnitude and direction (Ryel et al. 1996; Breshears 1997b). Soil moisture input to canopy patches is reduced relative to intercanopy patches as a result of foliar interception and could be lost at a greater rate because of increased plant uptake, as suggested by root distributions (Young and Evans 1987; McDaniel and Graham 1992; Davenport et al. 1996). In contrast, soil moisture loss from canopy patches can be reduced relative to that from intercanopy patches during warmer months because of lower soil evaporation rates and reduced runoff. The relative importance of these processes differs among sites (Joffre and Rambal 1993; Breshears 1997b). Hence, the soil evaporation rates that we quantified can dampen or amplify the soil moisture heterogeneity between canopy and intercanopy patches that results from other factors. Our results can be used to assess the relative roles of these processes under a variety of conditions. More generally, our results show how the woody canopies modify microclimate in terms of soil temperature and soil evaporation, and these modifications, in turn, have implications for both herbaceous and woody plants.

Effects of Microclimate on Herbaceous and Woody Plants

The effects of soil temperature and evaporation rates are important for both herbaceous and woody plants. The differences in soil temperature between the patch types directly affect biological processes such as germination for both woody and herbaceous species (Jordan and Haferkamp 1989; Fulbright et al. 1995; Roundy and Biedenbender 1996). For example, germination rates for *Pinus edulis* at a soil temperature of 30°C are more than four times less than at 20°C (Floyd 1983). The soil temperature differences between the two patch types correspond to differences in the distributions of herbaceous species: C₃ species are more abundant in the cooler canopy patches, and C4 species are more abundant in the warmer intercanopy patches (Arnold 1964; Armentrout and Pieper 1988), similar to the differences observed at landscape scales (Epstein et al. 1997). Woody canpoy effects on microclimate, then, may provide facilitation for germinating plants (Martens et al. 1997).

Soil evaporation rates modify the amount of soil moisture that is available to plants. The differences in soil evaporation rates between the two patch types become increasingly important biologically, as indicated by soil water potential at lower soil moistures. The amount of plant-available water, in turn, affects germination percentages and rates of herbaceous (Briske and Wilson 1976; Everett and Sharrow 1985; Aguilera and Lauenroth 1995) and woody (Daubenmire 1943; Meagher 1943) species. Small differences in soil moisture may have disproportionately greater effects on germination (Lauenroth et al. 1987). Herbaceous and woody plants are differentially affected by patch-scale heterogeneity in soil moisture. Herbaceous species in semiarid shrublands and woodlands primarily use resources from one patch type or the other, while woody plants obtain resources from surrounding shallow regions of intercanopy areas (Peláez et al. 1994; Montaño et al. 1995; Breshears et al. 1997a; Martens et al. 1997) as well as in the canopy patches beneath them (Young and Evans 1987).

Increasingly, models of water balance and vegetation dynamics in semiarid shrublands and woodlands are focusing on the horizontal heterogeneity created by woody plants (Sharpe et al. 1986; Mauchamp et al. 1994; Reynolds et al. 1997). Our results demonstrate the importance of accounting for this type of horizontal heterogeneity and can be used to improve predictive hydrological and ecological models of semiarid systems. In summary, our study quantifies how woody plants modify the microclimate at the canopy/intercanopy patch scale, with respect to soil temperature, soil moisture, and soil evaporation, all of which in turn affect the germination and plant-available water of herbaceous and woody plants.

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Literature Cited

- Aguilera MO, WK Lauenroth 1995 Influence of gap disturbances and type of microsites on seedling establishment in *Bouteloua gracilis*. | Ecol 83:87–97.
- Armentrout SM, RD Pieper 1988 Plant distribution surrounding Rocky Mountain pinyon pine and oneseed juniper in south-central New Mexico. J Range Manage 41:139–143.
- Arnold JF 1964 Zonation of understory vegetation around a juniper tree. J Range Manage 17:41–42.
- Belsky AJ, RG Amundson, JM Duxbury, SJ Riha, AR Ali, SM Mwonga 1989 The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. J Appl Ecol 26:1005–1024.
- Bowen BM 1990 Los Alamos climatology. LA-11735-MS; UC-902. National Technical Information Service, Springfield, Va.
- Breshears DD, OB Myers, SR Johnson, CW Meyer, SN Martens 1997a Differential use of spatially heterogeneous soil moisture by two semiarid woody species: *Pinus edulis* and *Juniperus monosperma*. J Ecol 85:289–299.
- Breshears DD, PM Rich, FJ Barnes, K Campbell 1997b Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. Ecol Appl 7:1201–1215.
- Briske DD, AM Wilson 1976 Temperature effects on adventitious root development in blue grama seedlings. J Range Manage 30: 276–280.
- Collings MR 1966 Throughfall for summer thunderstorms in a juniper and pinyon woodland, Cibecue Ridge, Arizona. Geological Survey Professional Paper 485-B. U.S. Government Printing Office, Washington, D.C.
- Daubenmire RF 1943 Soil temperature versus drought as a factor determining lower altitudinal limits of trees in the Rocky Mountains. Bot Gaz 105:1–13.
- Davenport DW, BP Wilcox, DD Breshears 1996 Soil morphology of canopy and intercanopy sites in a piñon-juniper woodland. Soil Sci Soc Am J 60:1881–1887.
- Emerson FW 1932 The tension zone between grama grass and pinon-juniper associations in northeastern New Mexico. Ecology 13: 347–358.
- Epstein HE, WK Lauenroth, IC Burke, DP Coffin 1997 Productivity patterns of C₃ and C₄ functional types in the U.S. Great Plains. Ecology 78:722–731.
- Everett RL, SH Sharrow 1985 Soil water and temperature in harvested and nonharvested pinyon-juniper stands. U.S. Forest Service Research Paper INT-342. Ogden Utah.
- Floyd ME 1983 Dioecy in five *Pinus edulis* populations in the Southwestern United States. Am Midl Nat 110:405–411.
- Fulbright TE, JO Juti, AR Tipton 1995 Effects of nurse-plant canopy temperatures on shrub seed germination and seedling growth. Acta Oecol–Int J Ecol 16:621–632.
- Hillel D 1980 Applications of soil physics. Academic Press, New York.
- Joffre R, S Rambal 1993 How tree cover influences the water balance of Mediterranean rangelands. Ecology 74:570–582.
- Johnsen TN Jr 1962 One-seed juniper invasion of northern Arizona grasslands. Ecol Monogr 32:187–207.
- Jordan GL, MR Haferkamp 1989 Temperature responses and calculated heat units for germination of several range grasses and shrubs. J Range Manage 42:41–45.
- Lane LJ, FJ Barnes 1987 Water balance calculations in Southwestern woodlands. Pages 480–488 in Proceedings, Pinyon-Juniper Con-

- ference. USDA Forest Service Intermountain Research Station General Technical Report INT-215. USDA Forest Service, Fort Collins, Colo.
- Lauenroth WK, OE Sala, DG Michunas, RW Lathrop 1987 Root dynamics of *Bouteloua gracilis* during short-term recovery from drought. Funct Ecol 1:117–124.
- Martens SN, DD Breshears, CW Meyer, FJ Barnes 1997 Scales of above- and below-ground competition differ in a semiarid woodland as detected from spatial pattern. J Veg Sci 8:655–664.
- Mauchamp A, S Rambal, J Lepart 1994 Simulating the dynamics of a vegetation mosaic: a spatialized functional model. Ecol Model 71: 107–130.
- McDaniel PA, RC Graham 1992 Organic carbon distribution in shallow soils of pinyon-juniper woodlands. Soil Sci Soc Am J 56: 499–504.
- Meagher GS 1943 Reaction of piñon and juniper seedlings to artificial shade and supplemental watering. J For 41:480–482.
- Montaño C, B Cavagnaro, O Briones 1995 Soil water use by coexisting shrubs and grasses in the Southern Chihuahuan Desert, Mexico. J Arid Environ 31:1–13.
- Newman BD, AR Campbell, BP Wilcox 1997 Tracer-based studies of soil water movement in semi-arid forests of New Mexico. J Hydrol 196:251–270.
- Noy-Meir I 1973 Desert ecosystems: environment and producers. Annu Rev Ecol Syst 4:25–41.
- Nyhan JW 1974 Decomposition of Bouteloua gracilis plant materials in a grassland ecosystem. Ph.D. diss. Colorado State University, Fort Collins.
- 1975 Decomposition of carbon-14 labeled plant materials in a grassland soil under field conditions. Soil Sci Soc Am Proc 39: 643–648.
- Nyhan JW, LW Hacker, TE Calhoun, DL Young 1978 Soil survey of Los Alamos County, New Mexico. LA-6779-MS; UC-11. National Technical Information Service, Springfield, Va.
- Peláez, DV, RA Distel, RM Bóo, OR Elia, MD Mayor 1994 Water relations between shrubs and grasses in semi-arid Argentina. J Arid Environ 27:71–78.
- Pierson FB, JR Wight 1991 Variability of near-surface soil temperature on sagebrush rangeland. J Range Manage 44:491–497.
- Reynolds JF, RA Virginia, WH Schlesinger 1997 Defining functional types for models of desertification. Pages 195–216 in TM Smith, HH Shugart, FI Woodward, eds. Plant functional types: their relevance to ecosystem properties and global change. Cambridge University Press, Cambridge.
- Roundy BA, LB Abbott, M Livingston 1997 Surface soil-water loss after summer rainfall in a semidesert grassland. Arid Soil Res Rehab 11:49–62.
- Roundy BA, SH Biedenbender 1996 Germination of warm-season grasses under constant and dynamic temperatures. J Range Manage 49:425–431.
- Ryel RJ, MM Caldwell, JH Manwaring 1996 Temporal dynamics of soil spatial heterogeneity in sagebrush-wheatgrass steppe during a growing season. Plant Soil 184:299–309.
- Sala OE, WK Lauenroth 1982 Small rainfall events: an ecological role in semiarid regions. Oecologia (Berl) 53:310–304.
- Scholes RJ, SR Archer 1997 Tree-grass interactions in savannas. Annu Rev Ecol Syst 28:517–544.
- Sharpe PJH, J Walker, LK Penridge, HI Wu, EJ Rykiel Jr 1986 Spatial

considerations in physiological models of tree growth. Tree Physiol 2:403-421.

Skau CM 1964 Interception, throughfall, and stemflow in Utah and alligator juniper cover types in northern Arizona. For Sci 10: 283–287.

Young JA, RA Evans 1987 Stem flow on western juniper (*Juniperus occidentalis*) trees. Pages 373–381 *in* Proceedings, Pinyon-Juniper Conference. USDA Forest Service Intermountain Research Station General Technical Report INT-215. USDA Forest Service, Fort Collins, Colo.