Differential use of spatially heterogeneous soil moisture by two semiarid woody species: *Pinus edulis* and *Juniperus monosperma*

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Summary

1 Soil moisture in semiarid woodlands varies both vertically with depth and horizontally between canopy patches beneath woody plants and the intercanopy patches that separate them, such that shallow soil layers in intercanopy locations are wettest, yet few studies have considered both dimensions of spatial variability in testing for acquisition of resources by plants.

2 Three hypotheses were tested relative to the use of shallow water in intercanopy locations by two coexisting semiarid-woodland tree species, *Pinus edulis* (a piñon) and *Juniperus monosperma* (a juniper): (i) both *P. edulis* and *J. monosperma* can use shallow water from intercanopy locations;. (ii) *J. monosperma* is able to obtain more shallow water from intercanopy locations than *P. edulis*, and (iii) the spatial arrangement of the trees influences the amount of water they obtain. Soil moisture and plant water potential (i.e. plant water stress) were measured before and after the addition of water to shallow depths (0–30 cm) of intercanopy locations for trees of both species in two spatial arrangements: isolated and paired with a contiguous tree of the other species.

3 Both species responded to the addition of shallow water in intercanopy locations, as measured by plant water potential. The response of *J. monosperma* was significantly greater than that of *P. edulis*, as measured by depletion of shallow soil moisture in intercanopy locations and by change in plant water potential per unit change in soil water potential (the difference was not detectable on the basis of plant water potential alone); in addition, the amount of depletion was correlated with basal area of *J. monosperma* but not of *P. edulis*. The responses were not influenced by spatial arrangement (isolated vs. paired with a contiguous tree of the other species).

4 The results of this study are consistent with differences in the relative abundances of the two species across locations, suggesting that species differences in ability to use shallow water in intercanopy locations is important in structuring semiarid woodlands. Further, the results suggest that current theoretical concepts for semiarid ecosystems, which ignore either vertical or horizontal variability in soil moisture, may be inadequate for predicting changes in the ratio of woody to herbaceous plant biomass, particularly for plant communities with co-dominant woody species that differ in ability to acquire spatially heterogeneous resources.

Keywords: competition, juniper, piñon, plant water potential, woodland

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Introduction

Most current theories of vegetation dynamics in semiarid ecosystems assume that differences among species in the use of below-ground resources – particularly water – are explained by vertical differences in root distributions between shallow and deeper soil layers. A theoretical concept proposed by Walter (1971) has been used to explain the relative proportions of woody and herbaceous plant biomass at semiarid sites on the basis of vertical heterogeneity in soil moisture. This concept (Walter 1971) assumes that woody plants use soil moisture primarily from the deeper soil layers but

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it does not differentiate among woody plant species with respect to the depth from which they obtain soil moisture; herbaceous plants are assumed to have predominant access to shallow soil moisture. Models based on this concept predict differences in the proportions of woody and herbaceous plants in semiarid savannas (Walker & Noy-Meir 1982; Eagleson 1982, 1986) and steppe (Coffin & Lauenroth 1990). Vertical heterogeneity in soil moisture has been documented at several sites (Lauenroth *et al.* 1993). Soil moisture is most variable at shallow depths (Joffre & Rambal 1988, 1993; Breshears 1993) because of the greater exposure of shallow soils to both precipitation and solar radiation (which increases evaporation). Vertical differences in use of soil moisture have been shown between woody and herbaceous species (Sala *et al.* 1989; Peláez *et al.* 1994), and have been related to the composition of plant communities (Knoop & Walker 1985; Liang *et al.* 1989).

Vegetation dynamics can also be influenced by horizontal differences among species in the use of below-ground resources. A concept proposed by Schlesinger *et al.* (1990) for explaining the relative proportions of woody and herbaceous plant biomass at semiarid sites focuses on the horizontal component of soil moisture heterogeneity and ignores vertical heterogeneity. In this approach, land use impacts are assumed to increase runoff from intercanopy areas and redistribute it to beneath the canopies of woody plants, resulting in an increase in the ratio of plant biomass for woody to herbaceous species. Schlesinger *et al.*'s (1990) concept does not distinguish between woody plant species with respect to their abilities to obtain soil moisture. Recent work has confirmed that horizontal variations in soil moisture are governed largely by the presence or absence of canopies of woody plants. This horizontal heterogeneity in soil moisture between canopy vs. intercanopy patches can be substantial in semiarid woodlands. (Joffre & Rambal 1988, 1993; Breshears 1993; Dawson 1993; Belsky & Canham 1994; Breshears *et al.* 1997). Intercanopy areas receive larger precipitation inputs because woody canopies intercept a portion of the precipitation before it reaches the soil below (Johnsen 1962; Collings 1966) and consequently intercanopy areas usually contain more soil moisture (Breshears 1993; Breshears *et al.* 1997); exceptions occur when runoff from intercanopy patches is redistributed to canopy patches (Joffre & Rambal 1988, 1993). Similar horizontal differences between canopy and intercanopy patches are expected in semiarid shrublands.

Despite the fact that soil moisture – a primary limiting resource in semiarid shrublands and woodlands – varies both horizontally and vertically, field studies in these ecosystems have generally assumed homogeneity in either the horizontal or the vertical dimensions, or in both. The few studies that have investigated use of intercanopy resources by semiarid woody plants were designed around other objectives:

they assumed vertical homogeneity in soil moisture (Emerson 1932; Ansley *et al.* 1991), did not directly measure water use (Sturges 1977), measured resources other than water (Caldwell *et al.* 1985; Jackson & Caldwell 1996), were done under disturbed conditions (Emerson 1932; Sturges 1977; Ansley *et al.* 1991; Caldwell *et al.* 1985), and generally were limited to a single woody species. No studies simultaneously considered both the vertical and horizontal components of variability in soil moisture by directly testing (1) for use of shallow soil moisture in intercanopy locations by woody plants in undisturbed conditions, and (2) for species-specific differences among woody plants in ability to use shallow rather than deeper soil moisture in intercanopy locations.

We designed a study to test directly for use by woody plants of shallow water from intercanopy locations. It focuses on two semiarid woodland tree species, *Pinus edulis* Englem. (a piñon) and *Juniperus monosperma* (Englem.) Sarg. (a juniper), in a natural plant community. The three hypotheses tested in our study are (1) both *P. edulis* and *J. monosperma* can use shallow water from intercanopy locations; (2) *J. monosperma* is able to obtain more shallow intercanopy water than *P. edulis;* and (3) the spatial arrangement of the trees influences the amount of water they obtain. Our hypotheses were derived from previous findings in piñon–juniper woodlands. First, studies showing an increase in herbaceous cover following tree thinning suggest that both piñon and juniper (*P. edulis* and *J. monosperma*, as well as closely related species) compete with intercanopy grasses for shallow water in intercanopy locations (Clary 1971, 1974, 1987; Clary & Jameson 1981; Clary & Jensen 1981; Everett & Sharrow 1985; Bledsoe & Fowler 1992). However, these studies have not directly demonstrated uptake of shallow water – the herbaceous response could be due to other factors such as changes in the microclimate associated with thinning of the overstorey, rather than plant–plant interactions for below-ground resources.

Secondly, studies measuring plant water potential (which reflects the level of water stress) showed that plant water potential of *J. monosperma* varies more through time than does that of *P. edulis* (as observed at eight sites: Barnes 1986; Schott & Pieper 1987; Breshears 1993); and that plant water potential of *J. monosperma* correlates with variations in soil moisture at shallow depths, whereas that of *P. edulis* does not correlate strongly with soil moisture variations at any depth (Breshears 1993). These results suggest but do not demonstrate that *P. edulis* and *J. monosperma* differ with respect to the depths from which they obtain soil moisture (Barnes 1986; Breshears 1993). Further, they do not provide a basis for distinguishing between uptake from intercanopy as opposed to canopy locations.

Thirdly, studies of the spatial arrangement of *P. edulis* and *J. monosperma* trees along a climatic

gradient found that as elevation increases (and with it precipitation and, presumably, soil moisture), the spacing of the trees changes from regular to clumped, and tree coverage becomes more dense (Padien & Lajtha 1992). These observations suggest that the spatial arrangement of trees influences the amount of shallow water they obtain from intercanopy locations.

Our three hypotheses directly test the spatially explicit characteristics of water use – considering both a vertical and a horizontal dimension of heterogeneity – by *P. edulis* and *J. monosperma*. Further, these tests allow evaluation of some of the simplifying assumptions of theoretical concepts for plant community dynamics in semiarid environments, particularly in environments where there are two or more co-dominant woody species.

Materials and methods

STUDY SITE

Our field experiment was conducted at an upper-elevation (2140 m a.s.l.) piñon–juniper woodland in northern New Mexico, within Technical Area 51 of the Los Alamos National Laboratory; this site has been the subject of several previous studies (Barnes 1986; Lajtha & Barnes 1991; Lin *et al.* 1992; Padien & Lajtha 1992; Lajtha & Getz 1993; Breshears 1993; Wilcox 1994; Wilcox & Breshears 1995). Trees at this site are clumped (Padien & Lajtha 1992; Martens et al. 1997). The landscape of this area and the disturbances that have affected it (such as land use, fire, drought, and insect outbreaks) were described by Allen (1989). The soils (Hackroy clay loam) were described by Nyhan *et al.* (1978) and Davenport (1993); soil depths vary from 30 to 130 cm (Davenport *et al.* 1996). The site has a temperate mountain climate and receives ≈ 40 cm of annual precipitation, mainly in the form of winter snowfall and late-summer precipitation (Bowen 1990).

EXPERIMENTAL DESIGN

We designed our experiment around two kinds of measurements. The first, predawn plant water potential, was structured as a $2 \times 2 \times 2$ factorial analysis of variance of repeated measures (Potvin *et al.* 1990), to test the relative effects on plant water stress of (1) tree species; (2) spatial arrangement of trees, and (3) amounts of shallow intercanopy soil moisture. We therefore measured plant water potential for eight experimental configurations: two species (*P. edulis* and *J. monosperma*) in two spatial arrangements (isolated and paired with a contiguous tree of the other species) under two soil moisture regimes (treated and untreated [control]) created by adding water to intercanopy soils surrounding half of the trees and not to those surrounding the other half.

The second kind of measurement, soil water potential, was designed to test for differences in the rates of soil moisture depletion among three types of study plots: isolated *J. monosperma*, isolated *P. edulis*, and *P. edulis* – *J. monosperma* pairs (the last were considered a single plot type because the components of the measurement corresponding to individual trees could not be isolated).

To determine an appropriate sample size (number of trees) for our experiment, we took preliminary measurements of plant water potential, using one *P. edulis* and one *J. monosperma*. Water was added to intercanopy patches adjacent to both trees, and plant water potential was measured from two twigs per tree because variance within an individual tree was less than variance among trees (Breshears 1993). These measurements were used with previously reported data on variances within a species (Breshears 1993) to calculate statistical power for various sample sizes. We estimated that the probability of detecting species-level differences in plant water potential following the addition of water was greater than 90% for a sample size of 4 trees for each of the 8 experimental configurations – a total of 32 trees. Because eight of the trees – four *J. monosperma* and four *P. edulis* – were paired and shared a plot, the total number of study plots was 24.

STUDY PLOTS

The 24 study plots were selected such that there were 8 plots of each of the three plot types: isolated *P. edulis* (no contiguous canopy), isolated *J. monosperma* (no contiguous canopy), and those containing a pair of trees (one of each species) having a contiguous canopy with one another but not with any other trees (the bases of the paired trees were no more than 1 m apart, except for one pair in which they were 1.8 m apart). Several criteria guided selection of the study plots: (1) tree heights should not vary beyond a certain range (*P. edulis* we selected range from 2.9 to 6.9 m in height, *J. monosperma* from 1.5 to 3.8 m); (2) any seedlings or other woody vegetation under a tree canopy should not exceed 50 cm in height; (3) for plots containing *P. edulis*-*J. monosperma* pairs, the trees should not differ greatly in height – a ratio of less than 3.0, *P. edulis* to *J. monosperma* (the ratio of our tree pairs ranged from 0.7 to 2.7; (4) intercanopy areas surrounding a subject tree or tree pair should be large enough to accommodate four 1-m × 2-m metal frames (to contain ice) placed at 90° angles, with the edge of the frame 1 m from the edge of the canopy (Fig. 1); and (5) subject trees should be separated from any ice frame belonging to a different study plot by at least 8 m. After 24 study plots meeting these criteria had been selected, 12 (4 each of isolated *J. monosperma*, isolated *P. edulis*, and *P. edulis*-*J. monosperma* pairs) were randomly chosen to receive
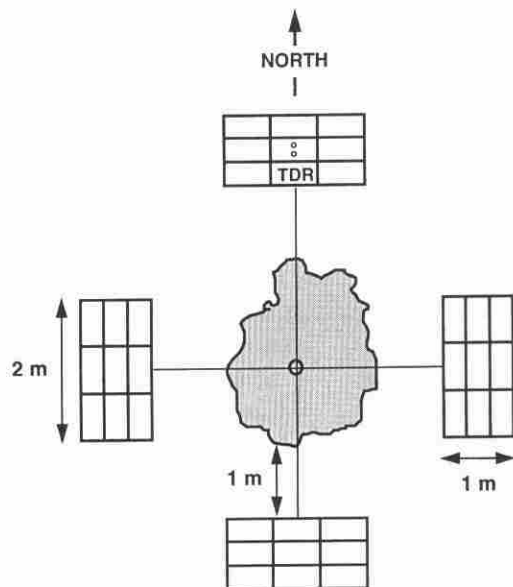
Fig. 1. Study plot layout. Each plot was centred on a subject tree or pair of neighbouring trees. In the area surrounding the trees(s), four 1-m × 2-m intercanopy sectors were delineated, each 1 m from the edge of the tree or tree pair and orientated at a 90° angle with respect to the trunk(s) of the tree(s). For each plot, soil moisture was measured by time-domain reflectometry (TDR) in the northernmost of the four sectors. For treated plots, each of the four sectors contained a 1-m × 2-m metal frame that were used to add water (ice) to the soil.

additional moisture. The remaining 12 were used as controls.

For each study plot, we selected the northernmost 1-m × 2-m intercanopy patch for the soil-moisture measurements (Fig. 1). These measurements were made by means of time-domain reflectometry (TDR – Topp *et al.* 1980), using a system similar to that described by Baker & Allmaras (1990). A small pit (≈ 20 cm × 30 cm at the surface, 15 cm × 10 cm at the bottom, and 30 cm deep) was dug 1.5 m from the edge of the tree canopy. Three pairs of 30-cm-long TDR probes were inserted into undisturbed soils of the vertical face of the pit at a 33° downward angle: one pair in the 0–15-cm depth interval, one in the 15–30-cm depth interval, and one in the 30–45-cm depth interval. To each pair of probes was attached a measurement cable. The pits were back-filled, leaving the ends of the cables exposed, and the soil was compacted such that it was level with the surrounding soil. Because of their small size, these pits should not have had any significant effect on root distributions. Similarly, any effect of the pits on infiltration of water at the TDR measurement locations should have been minimal, because the probes were inserted into undisturbed soil in the vertical face of the pit. Finally, because all TDR probes were installed in the same way, any effects would be consistent from plot to plot, making the results valid for comparison purposes. For each study plot selected to receive water treatment, we installed additional probes under the canopy to

confirm that soil moisture added in the intercanopy had not spread laterally through the soil into the canopy zone. These probes were inserted into the top 15 cm of the soil at a 33° downward angle, halfway between the tree trunk(s) and the canopy edge.

We began by calculating the amount of water necessary to raise volumetric water content from 5% to 30% (the corresponding change in soil water potential being from −23.7 to −0.02 MPa) over a 1-m × 2-m area of soil 15 cm deep. To ensure that the water would be spread uniformly over the intercanopy areas to be treated, we used ice, distributed evenly within 9-compartment metal frames having outer dimensions of 1 m × 2 m. Each compartment contained two 3.6-kg bags of ice, translating to 3.24 cm of water per frame. Four such frames were used for each treated plot (Fig. 1). On 27 June, between 07.50 and 08.30 Mountain Daylight Time, the ice was dumped from the bags into the nine compartments and spread evenly. The frame was covered with black plastic and sealed with tape to reduce evaporation and water use by herbaceous plants. The outside edges of the frames had been previously packed with soil and, where necessary, covered with plastic strips to minimize leakage.

MEASUREMENTS

Precipitation at the site – which occurred only once during the experiment – was measured by seven True-check gauges. Each gauge was installed in the centre of an intercanopy patch with its top 1 m above ground.

Soil moisture was measured twice before addition of the ice: 3 days before and 1 day before. For both the treated and the control plots, TDR readings were taken on 27 June, ≈ 2 h following addition of the ice (most of the ice had melted by that time). Additional readings were taken from the treated plots only, 5 h and 7 h after the ice had been added. On 28 June, one day after the ice was added, soil moisture was measured for both the treated and the control plots in the morning and in the afternoon. Finally, on the 2nd, 3rd, 4th and 8th days, we took measurements during the morning only for all plots. On the second day we also took soil moisture readings from the TDR probes in the top 15 cm under the canopies of trees in the the treated-plots. A small amount of rain (0.2 mm) fell on the afternoon of the second day, and we remeasured soil moisture in five of the control plots to verify that changes in soil moisture were small. Soil water potential in the top 15 cm increased from −8.2 to −6.6 MPa (corresponding to a change of < 1% volumetric water content).

We converted the soil moisture measurements (volumetric water content) to soil water potential values (MPa) using equations from site-specific data (Daniel B. Stephens and Associates, Inc., unpublished report LAB-94(1)·4800·LANL-RPT.494; for volumetric water content [%] < 45.4: soil water potential

$$[\text{MPa}] = -10^{[7.06 - 3.85\log(\text{volumetric water content})]}/1000;$$

for volumetric water content [%] > 45.4: soil water potential

$$[\text{MPa}] = -10^{[78.3 - 46.9\log(\text{volumetric water content})]}/1000;$$

$n = 5$; $r^2 = 0.79$. [See Nyhan *et al.* (1997) for comparable Van Genuchten (1980) parameters.]

We collected and analysed twig samples 3 days before the ice was added (24 June 1994) and just before it was added (the morning of 27 June) to obtain background measurements for comparison. Three twigs were collected from each subject tree from different branches for *P. edulis* and from different boles for *J. monosperma*. These were sealed in locking plastic bags and kept cool and in the dark until analysed. The time between sample collection and analysis was kept to a minimum (usually less than 1 hour). To confirm that plant water potential had not changed during the sample collection period, we collected another sample from the first tree as the final one. Predawn plant water potential was measured to the nearest 0.05 MPa (using a PMS Model 1000 pressure chamber, Corvallis, OR) on two of the twigs (the third twig was used in the event of damage of one of the original two during insertion into the pressure chamber).

Using the same procedure, we then collected and analysed twig samples on the 1st, 2nd, 3rd, 4th, and 8th days (28 June – 5 July) following addition of the ice. This 8-day period was long enough for the mean plant water potential of three of the four species/spatial arrangement combinations (isolated *P. edulis*, paired *P. edulis*, and isolated *J. monosperma*) to return to within less than 0.1 MPa of that of the controls.

ANALYSIS

Our analytical approach was to analyse repeatedly samples from individual trees for plant water potential and soil water potential in the corresponding intercanopy patches through time (TIME). Both data sets (plant water potential and soil water potential) were evaluated using a repeated measures analysis of variance (ANOVAR). The response variable was $\log_{10}$ (–MPa). For plant water potential, we tested for the effects of (1) differences between species (SPP); (2) differences between spatial arrangements (isolated trees vs. paired trees: PAIR), and (3) differences between treated and control trees (TRT). For soil water potential, we tested for the effects of (1) differences among the three plot types (isolated *J. monosperma*, isolated *P. edulis*, and *P. edulis* – *J. monosperma*): PTYPE, and (2) differences between treated and control plots (TRT). We used Huynh–Feldt epsilon-adjusted *F*-values (SAS 1989) to test for differences within experimental configurations and within plot types.

Tree size may have influenced soil moisture

depletion. Our selection criteria limited differences in tree size to a specified range but variaiton in tree size was not eliminated. To test if the residual variation in the ANOVAR was related to tree size, we checked for correlations between the residuals from each analysis and two indices of tree size: basal area (totalled across boles for each *J. monosperma*) and canopy volume (estimated as an elliptical volume from measurements of canopy height and radii).

In addition to the repeated measures analyses, we used analyses of covariance (ANCOVAR) to test for differences between species and between spatial arrangements on the relationship between plant water potential ($\log_{10}(-\text{MPa})$) and soil water potential ($\log_{10}(-\text{MPa})$) for treated plots. (Because predawn plant water potential reflects soil moisture conditions of the previous night, we paired each plant water potential value with the corresponding soil water potential value obtained the previous day.) As part of this analysis, we fitted a line for each of the four species/spatial arrangement combinations and then tested for differences among the slopes (SAS 1989).

Results

PREDAWN PLANT WATER POTENTIAL

When the first measurements were taken (before water was added), the plant water potentials of trees in both treated and control plots were declining, which reflects increasing stress (Fig. 2). Following the addition of water, the plant water potentials of trees in treated plots increased significantly over those of trees in control plots, which continued to decrease ($P < 0.001$; ANOVAR within-tree TIME × TRT effect). This result shows that both *P. edulis* and *J. monosperma* trees can use shallow water from intercanopy locations. The plant water potential data do not, on their own, show any differences attributable either to species of tree (the increase in water potential of treated *J. monosperma* did not differ significantly from that of treated *P. edulis*: $P > 0.5$; ANOVAR TRT × SPP contrast) or to the spatial arrangement of trees (changes in plant water potential for isolated trees did not differ from those for paired trees: $P > 0.7$; ANOVAR TIME × TRT × PAIR effect). The residuals from this analysis showed no correlation with tree size (basal area or canopy volume) for either species.

SOIL MOISTURE

Changes in soil moisture were apparent in all the treated plots after water was added (Fig. 3): mean soil water potential increased from −2.40 to −0.04 MPa (9% to 26% volumetric water content) in the top 15 cm and from −0.21 to −0.11 MPa (17% to 20% volumetric water content) at the 15–30-cm depth after addition of water, but remained relatively constant at the 30–45-cm depth. In contrast, the control plots
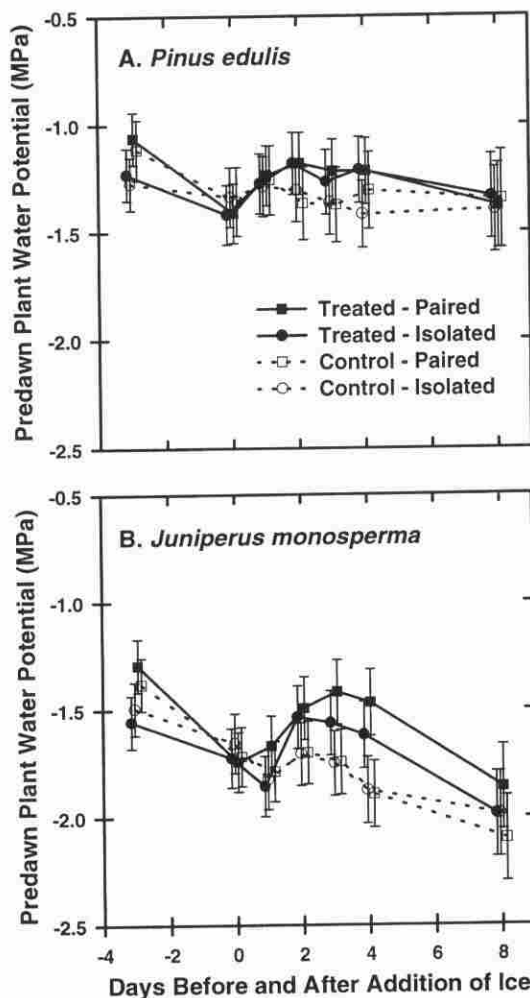
Fig. 2. Time series: Predawn plant water potential (MPa) for control trees and treated trees. Values shown are least-squares means and the corresponding standard error for each (SAS 1989).

showed relatively constant soil water potential for the duration of the experiment at all three depths. The moisture that was added to the intercanopy areas of the treated plots did not spread laterally to canopy areas, as shown by the fact that soil water potential in the top 15 cm beneath treated-plot canopies remained similar to that in the top 15 cm of intercanopy soils in control plots (Fig. 3A).

Soil water potential in the top 15 cm of the treated intercanopy areas was greatest one day after the addition of water on 28 June. Over the next several days, soil water potential declined at significantly different rates for at least one of the three plot types ($P = 0.028$; ANOVAR within-plot TIME × TRT × PTYPE effect). Moisture depletion was greater for inter-canopy patches around isolated *J. monosperma* (mean decrease = -0.61 MPa; 14% volumetric water content) than for those around isolated *P. edulis* (mean decrease = -0.15 MPa; 9% volumetric water content) as early as the 2nd day following the water additions ($P = 0.006$; ANOVAR TRT × PTYPE contrast for plots with isolated *P. edulis* vs. isolated *J. mono-sperma*).
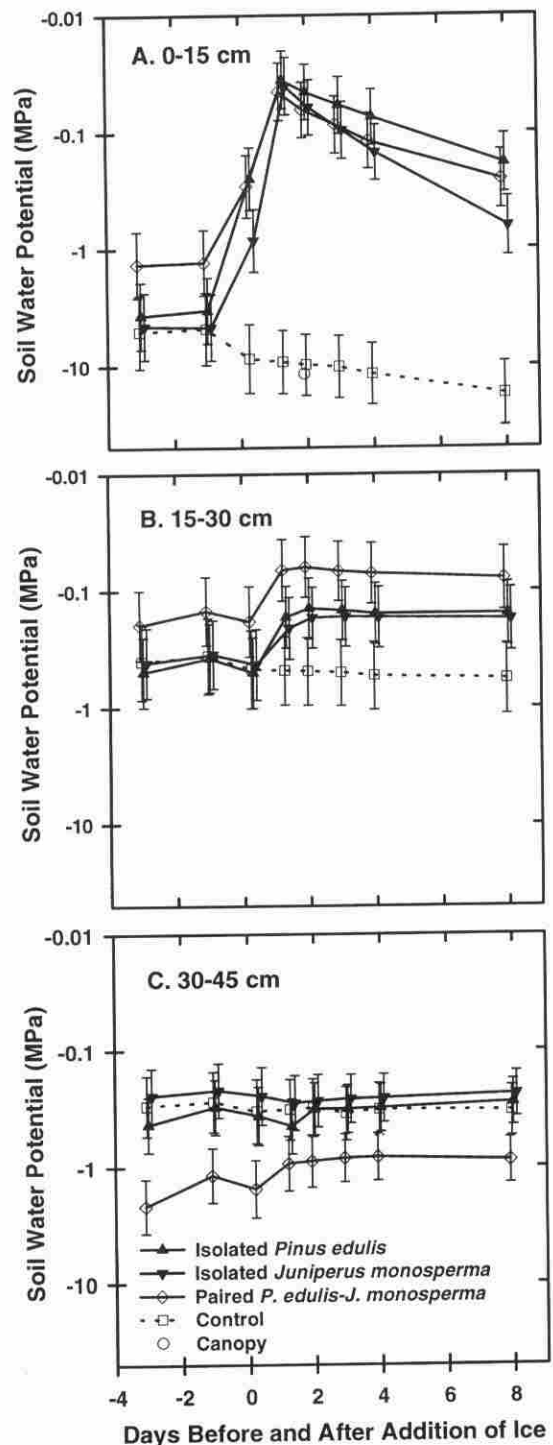

Fig. 3. Soil water potential (MPa) in intercanopy soil vs. time for control and treated study plots, at three depths: (A) 0–15 cm; (B) 15–30 cm, and (C) 30–45 cm. Values shown are least-squares means and the corresponding standard error for each (SAS 1989); the data for control plots are an average of least-squares means and the corresponding standard errors for the three plot types (isolated *J. monosperma*, isolated *P. edulis*, and *P. edulis – J. monosperma* pairs). (A) also shows soil water potential under the canopies of treated plots two days after water was added.

The remaining unexplained variance from the ANO-VAR (the residuals) for soil moisture did show a relationship with tree size for one of the four spe-

cies/spatial arrangement combinations: residuals were positively correlated with basal area of isolated *J. monosperma* (i.e. isolated larger trees of this species depleted more water than isolated small trees). The residuals did not show a correlation with basal area for any of the other combinations (paired *J. monosperma*, isolated *P. edulis*, or paired *P. edulis*), nor was there a significant relationship between the residuals and canopy volume for any of the four combinations.

COVARIANCE BETWEEN SOIL MOISTURE AND PLANT WATER POTENTIAL

We detected significant effects attributable to differences between spatial arrangements only by examining the covariance between plant water potential and soil moisture. For the treated plots, the slope relating plant water potential to soil water potential was significantly greater for isolated *J. monosperma* ($P < 0.001$; ANCOVAR test for non-zero slope) than for the three other combinations (paired *J. monosperma*, isolated *P. edulis*, or paired *P. edulis*, which did not differ from 0 ($P > 0.2$; ANCOVAR test for non-zero slope).

Discussion

USE OF SHALLOW INTERCANOPY WATER BY TREES

Our first hypothesis – that both *P. edulis* and *J. monosperma* can use shallow water in intercanopy locations – was confirmed by our experimental results. Plant water potential consistently increased (reflecting reduced water stress) in the treated trees (Fig. 2).

These trees are therefore able to extract soil moisture from the top 30 cm of intercanopy locations: this is the region in which root density is greatest for dominant understorey herbaceous species, such as *Bouteloua gracilis* (Coffin & Lauenroth 1991) – the dominant grass species at our site and in many other piñon–juniper woodlands. Although other studies have noted an increase in herbaceous cover following a reduction in piñon and/or juniper tree cover, and attributed the increase to competition between the two plant types (Clary 1971, 1974, 1987; Clary & Jameson 1981; Clary & Jensen 1981; Everett & Sharrow 1985; Bledsoe & Fowler 1992), the ability of woody species to extract shallow moisture from these intercanopy locations had not previously been demonstrated. In addition, although two other studies have addressed water use by *P. edulis* (Flanagan *et al.* 1992; Evans & Ehleringer 1994), neither determined if this species can obtain shallow water from intercanopy locations. The responses that we measured resulted from water addition to only a small fraction of the surrounding intercanopy area (e.g. only 25% of the 2-m-wide intercanopy ring surrounding a 1.5-m radius canopy, and an even smaller fraction if roots

extend beyond the frames, as indicated by other tracer studies – Breshears 1993). Therefore, responses to actual wetting events should be much greater than those we observed.

Our results also support our second hypothesis – that use of intercanopy water varies between species (*J. monosperma* responds more to the addition of water than does *P. edulis*). On the basis of the simplest of the three types of analyses (plant water potential alone), the increase shown by *J. monosperma* was not significantly greater than that shown by *P. edulis*. However, the statistical power of this analysis was less than expected – our preliminary measurements of a single *P. edulis* and a single *J. monosperma* had indicated that we would be able to detect absolute differences between species (*J. monosperma* responded to the added water, whereas *P. edulis* did not) but in the actual experiment, the treated *P. edulis* also responded. This difference between the preliminary and the experimental measurements may have been caused by differences in conditions at the time of water addition: a lower predawn plant water potential (indicating greater stress) at the start of the experiment than during the preliminary measurements, and related changes in the potential in the soil-to-root air gap, which can be particularly important during dry conditions (Nobel 1994). In addition, plant water potentials varied more than we expected over the course of the experiment, further reducing our statistical power. Species differences might have been detectable from plant water potential alone if the sample size had been larger.

Using the second type of analysis (soil water potential), we found evidence for species differences: soil moisture was significantly more depleted from under the covered frames surrounding isolated *J. monosperma* than from those surrounding isolated *P. edulis* (Fig. 3A). The differences in depletion can be attributed to differences in woody species due to the experimental design; uptake by herbaceous plants was minimized since the frames were covered with black plastic. Although some of the moisture depletion was probably due to evaporation from the soil (even though the frames were covered), the evaporation rates should have been relatively equal among treatments – shading of the frames by trees should not have differed substantially among plots, even though *J. monosperma* were generally shorter than *P. edulis*, because neighbouring trees of both species also shaded the frames. Further, the amount of moisture depletion was related to basal area for *J. monosperma* but not for *P. edulis*, also suggesting that *J. monosperma* uses more shallow intercanopy water than does *P. edulis*.

The third type of analysis (covariance, i.e. plant water potential in relation to soil water potential) also supported species differences: isolated *J. monosperma* were more responsive per unit change in soil water potential than isolated *P. edulis*. Under dry conditions

when water stress is high, rates of transpiration and photosynthesis by *J. monosperma* exceed those of *P. edulis* (Lajtha & Barnes 1991; Breshears 1993); hence the differences between the two species are probably amplified in terms of actual water use, even though *J. monosperma* trees are generally smaller than *P. edulis* trees. The greater response of *J. monosperma* to additional soil moisture in shallow intercanopy locations is consistent with observations of dense root networks in those locations (Johnsen 1962) and of differences between the two species in plant water potential – that of *J. monosperma* varies more through time than does that of *P. edulis* (Barnes 1986; Schott & Pieper 1987; Breshears 1993). However, our study differentiated between horizontal and vertical heterogeneity in soil moisture and hence provides direct evidence of differences among woody species in ability to use shallow soil moisture in intercanopy locations.

Our third hypothesis, that the spatial arrangement of trees influences the amount of water they obtain, was not supported by our study results. Only the analysis of covariance yielded data indicating a difference attributable to spatial arrangement, and this was only for one species, *J. monosperma*.

The ability of trees to use shallow intercanopy moisture appears to influence strongly both the composition of piñon–juniper woodland communities and the spacing of trees in those communities. Spatial patterns of piñon and juniper trees within sites (neighbourhood relationships – Weldon *et al.* 1990; Martens *et al.* 1997) and across sites along climatic gradients (regular vs. clumped – Padien & Lajtha 1992) indicate that the use of resources in intercanopy areas determines woodland community structure.

The distributions of semiarid piñon–juniper woodlands (dominated by the species we studied, as well as other closely related species) have shifted extensively and rapidly in past centuries and millenia in relation to climate and land use (Miller & Wigand 1994; Keeley & Mooney 1993; Tausch *et al.* 1993; Betancourt *et al.* 1993). In both past and present distributions, junipers are more abundant than piñons at more xeric sites (at the more xeric sites, piñons are not present at all). Further shifts in the numbers and distribution of these species have been predicted in conjunction with future climate changes (Gosz 1992). The differences in the relative abundances between piñon and juniper are usually attributed to physiological differences: junipers are more drought-resistant than piñons – *J. monosperma* has a higher water-use efficiency under dry conditions, and its rates of transpiration and photosynthesis are less affected by temperature, plant water potential, and nitrogen than those of *P. edulis* (Barnes 1986; Lajtha & Barnes 1991; Lajtha & Getz 1993; Breshears 1993); similar differences have been documented between *Juniperus oesteosperma* and *Pinus monophylla* (DeLucia *et al.* 1988, 1989; DeLucia & Schlesinger 1991). Our results suggest that the differences in the relative abundances of piñons and

junipers are also related to the ability of junipers to extract more shallow soil moisture than piñons, i.e. the relative abundances of piñons and junipers are consistent not only with differences in how they *use* water (physiological differences), but also with differences in where they *obtain* water (related to differences in root morphology).

IMPLICATIONS FOR RATIOS OF WOODY TO HERBACEOUS PLANTS

In semiarid regions, the ratio of woody-to-herbaceous plant biomass is an important ecosystem property because it reflects the relative proportions of forage and fuelwood, and modifies other ecosystem attributes (e.g. water balance, potential for erosion, use of habitat by vertebrates). Walter's (1971) concept for predicting the ratio of herbaceous to woody biomass at a site focused on differences with respect to the depths from which each obtains moisture (herbaceous species were assumed to have an advantage at shallow depths, woody plants to have sole access to deeper soil layers). However, a shift in the ratio, especially one produced by a reduction of herbaceous cover, can to lead to a new ratio that appears relatively stable (Schlesinger *et al.* 1990). Such a new ratio is possible because, contrary to the assumption of Walter (1971), not all woody plants obtain their water primarily from deeper layers; some obtain water from shallow layers (Peláez *et al.* 1994; Montaña *et al.* 1995) – particularly from shallow layers of intercanopy areas (e.g. *J. monosperma* in our study). Schlesinger *et al.* (1990) hypothesized that if herbaceous vegetation is temporarily removed (e.g. by heavy grazing or off-road vehicle use), shallow-extracting woody plants can exploit the newly available intercanopy water source, to the point of impeding the reestablishment of herbaceous plants. This process can give rise to a relatively long-term shift in the ratio of woody to herbaceous biomass at a site. (Similar conceptual models have been proposed – Loehle 1985; Jameson 1987; Lockwood & Lockwood 1993; Tausch *et al.* 1993; Davenport *et al.* 1998). Hence, while in some cases the ratio of herbaceous to woody biomass can be predicted by distinguishing between plant types on the basis of the depths from which they obtain soil moisture (particularly for locations that differ substantially in the proportions of moisture at the various depths), in other cases consideration of the ability of woody plants to obtain water from shallow intercanopy locations is required. Our results suggest that theoretical concepts for semiarid plant communities that ignore either horizontal or vertical variability may be inadequate for predicting changes in the ratio of woody to herbaceous plants, particularly for plant communities with co-dominant woody plant species that differ in ability to acquire spatially heterogeneous resources. The two types of models (i.e. Walter 1971; Schlesinger *et al.* 1990) can be unified by dis-

tinguishing between canopy and intercanopy soil locations, as well as upper and lower soil layers, and between shallow- and deeper-extracting woody plants (Breshears 1993). Studies that address both the vertical and the horizontal components of resource acquisition, such as this one, should improve our ability to predict changes in the composition of semi-arid woodlands and shrublands – and the corresponding changes in ecosystem properties such as water balance, erosion, net primary productivity, and vertebrate habitat quality.

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