INTRA- AND INTERSPECIFIC VARIATION FOR SUMMER PRECIPITATION USE IN PINYON–JUNIPER WOODLANDS

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Abstract. In the arid southwest of North America, winter precipitation penetrates to deep soil layers, whereas summer ''monsoon'' precipitation generally wets only surface layers. Use of these spatially separated water sources was determined for three dominant tree species of the pinyon–juniper ecosystem at six sites along a gradient of increasing summer precipitation in Utah and Arizona. Mean summer precipitation ranged from 79 to 286 mm, or from 18% to 60% of the annual total across the gradient. We predicted that, along this summer rainfall gradient, populations of dominant tree species would exhibit a clinal off–on response for use of water from upper soil layers, responding at particular threshold levels of summer precipitation input. This prediction was largely supported by our observations of tree water source use over a two-year period and from irrigation experiments.

Hydrogen and oxygen stable isotope ratios (δD and $\delta^{18}O$) of tree xylem water were compared to that of precipitation, groundwater, and deep and shallow soil water to distinguish among possible tree water sources. δD–$\delta^{18}O$ relationships and seasonal xylem water potential changes revealed that trees of this ecosystem used a mixture of soil water and recent precipitation, but not groundwater. During the monsoon period, a large proportion of xylem water in *Pinus edulis* and *Juniperus osteosperma* was from monsoon precipitation, but use of this precipitation declined sharply with decreasing summer rain input at sites near the regional monsoon boundary in Utah. *Quercus gambelii* at most sites along the gradient used only deep soil water even following substantial inputs of summer rain. Populations of *Quercus* at sites with the highest average summer precipitation input, however, predominantly used water in upper soil layers from recent summer rain events. Soil temperature correlated with patterns of summer precipitation use across the gradient; high soil temperatures north of the monsoon boundary may have inhibited surface root activity for some or all of the three tree species.

Irrigation experiments with deuterium-labeled water revealed that *Quercus gambelii* in northern Arizona and southern Utah did not use water from surface layers. In contrast, *Juniperus osteosperma* at these sites responded significantly to the irrigations: between 37% and 41% of xylem water originated from irrigations that wetted only the top 30 cm of soil. Responses by *Pinus edulis* to these irrigations were variable; uptake of labeled water by this species was greater in September at the end of the summer than during the hot midsummer period. Inactivity of *Pinus* roots in midsummer supports the hypothesis that root activity in this species is sensitive to soil temperature.

Seasonal patterns of leaf gas exchange and plant water potential corresponded to the seasonality of rainfall at different sites. However, no correlation between a species' ability to use summer rainfall and its tolerance to water deficits at the leaf level was found. Midday stomatal conductance (g_s) for *Pinus* needles approached zero at predawn water potentials near -2 MPa, whereas g_s in *Quercus* and *Juniperus* declined to zero at -2.8 and -3.7 MPa, respectively. The relationship between photosynthesis (A) and g_s was similar among the three species, although *Quercus* maintained higher overall rates of gas exchange and tended to operate higher on the A/g_s curve than the two conifers. At sites in eastern Arizona where *Quercus* fully used moisture from summer rains, leaf gas exchange characteristics were similar to those of *Pinus* and *Juniperus*.

Key words: D/H ratios; Juniperus osteosperma; Pinus edulis; pinyon–juniper ecosystem; plant water sources; precipitation use; Quercus gambelii; roots.

INTRODUCTION

Precipitation in southwestern North America is extremely variable in space and time, both seasonally and interannually. Rainfall patterns in this dry region are dominated by two major air circulations. Winter precipitation from slow-moving Pacific frontal systems falls over extended periods and penetrates to deep soil layers in part accentuated by low evaporative conditions. Alternatively, moisture originating from subtropical parts of the eastern

Pacific and the Gulf of Mexico during the late summer "monsoon" provides some areas in New Mexico and eastern Arizona with as much as 60% of total annual precipitation input (Bryson and Lowery 1955, Mitchell 1976). High rates of evaporation and short, intense convective rainfall events tend to restrict moisture to upper soil layers during this period.

Many perennial plants in the arid and semiarid zones of the southwest have a dimorphic root system; a network of branched surface roots potentially takes up water from growing season rains, but at the same time, deeper roots extract water stored deep in the soil that has recharged from winter and spring precipitation. These species extract water from a wide range of soil depths, but considerable variation exists at the intra- and interspecific levels (Ehleringer et al. 1991, Flanagan et al. 1992, Evans and Ehleringer 1994, Dawson 1996, Dawson and Pate 1996, Lin et al. 1996, Snyder et al. 1998). The availability of surface moisture during hot summer periods and the ability of dominant plants to use this moisture for photosynthetic gas exchange and growth has important ramifications at the community and ecosystem levels. For instance, differentiation among species for water source use can affect ecosystem water balance (Canadell et al. 1996, Jackson et al. 1996, Schulze et al. 1996), vegetation response to climate changes (Neilson 1986, 1995, Schlesinger et al. 1990, Ehleringer et al. 1998), and local patterns of species coexistence (Caldwell and Richards 1986, Fowler 1986, Franco and Nobel 1990).

Variation in the depth of water extraction by perennial plants implies a trade-off between the activity of, or allocation to, surface and deep roots. This trade-off should be manifested physiologically at the intraspecific level across environments that differ in the reliability of precipitation falling in the winter/summer seasons, but this topic has received limited attention to date. Ehleringer and Dawson (1992) hypothesized that in many arid and semiarid ecosystems, it may not be advantageous for perennial plants to maintain active roots in upper soil layers during the summer if summer precipitation is unreliable. However, as the amount or predictability of summer precipitation increases, as it does along summer precipitation gradients or that may occur over time as climate changes, populations of perennial plant species will alter their functional rooting depth and utilize greater amounts of soil moisture in the upper soil layers (Fig. 1). This response may arise from plasticity or from genetic changes within populations and would be especially important for species in regions where, during the growing season, stored water from winter precipitation is available together with summer precipitation (Dawson and Pate 1996). More importantly, patterns of surface moisture use across geographic gradients or through time may not be linearly related to surface moisture availability. As summer precipitation becomes sufficiently predictable, a threshold may be reached where long-lived perennial
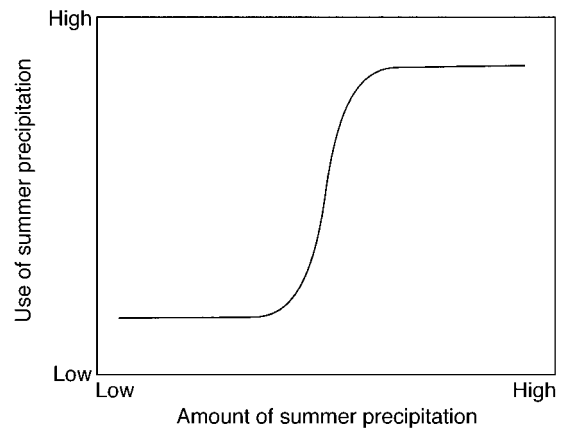

FIG. 1. Theoretical relationship between the use of summer precipitation among populations for perennial woody plant species and the mean amount of summer precipitation input across a broad gradient in semiarid and arid regions.

plants will develop and maintain roots necessary for uptake of moisture from upper soil layers (10–30 cm) during the summer growing period.

Gregg (1991) provided evidence that populations of Utah juniper (*Juniperus osteosperma*) growing near the Arizona–Utah border region differed in their use of summer rains in a manner consistent with that predicted by the above hypothesis. Populations of this drought-tolerant tree took up monsoon precipitation in northern Arizona where summer rains are reliable, but not in southern Utah where summer monsoon rains are less reliable and of lower magnitude. Flanagan et al. (1992) and Evans and Ehleringer (1994), however, observed that Utah juniper exhibited interannual variation in its use of summer rain near the Utah–Arizona border region that did not appear to be related to variation in summer rain amount.

Some general circulation models predict changes in the seasonal distribution of precipitation in the arid west of North America which likely will have impacts on vegetation distribution and ecosystem water balance (Neilson 1986, 1995, Stephenson 1990). Packrat midden evidence indicates that the distribution of summer precipitation has changed substantially since the last glacial period (Betancourt et al. 1990). Evidence from middens throughout western North America indicate that in response to the general migration southward of the monsoon, species once abundant have disappeared from northern plant communities. From ecophysiological studies, it is clear that some species may be enhanced while others are negatively affected by shifts in the seasonality of precipitation in this region (Lin et al. 1996, Weltzin and McPherson 1997).

Patterns of water uptake are key to our understanding of vegetation responses to these spatial and temporal changes in precipitation seasonality. Belowground

functions of plants, however, are very difficult to assess. Analysis of the stable isotopes of hydrogen (^1H, ^2H or deuterium, D) and oxygen (^{16}O, ^{18}O) in water at natural abundance levels has proved to be very useful for surveying water sources used by plants (Ehleringer and Dawson 1992, Brunel et al. 1995, Dawson and Ehleringer 1998) in such environments. Summer and winter precipitation have distinct isotopic signatures in inland areas of southwestern North America (Milne et al. 1987, Friedmann et al. 1992). Water penetrating to deep soil layers from winter precipitation is more depleted in the heavier isotopes than is summer precipitation. These variations provide the basis for quantitative determinations of plant use of summer rains and active rooting depth across different populations (White et al. 1985, Ehleringer et al. 1991, Brunel et al. 1995).

In this study we evaluated monsoon rain usage by several dominant tree species of the pinyon–juniper ecosystem along a broad monsoon precipitation gradient in southwestern North America. We tested the hypothesis that a sharp cline for summer precipitation use would be observed along a continuous monsoon precipitation gradient, reflecting threshold precipitation requirements for the activity of surface roots by these trees. We concurrently measured plant water potential and leaf gas exchange responses to gain supporting evidence for geographic differences in seasonal water use and to evaluate associations between functional rooting depth, drought tolerance, and water-use efficiency in the widespread pinyon–juniper ecosystem.

METHODS

Study species and sites

The pinyon–juniper ecosystem of the southwestern United States occupies an intermediate position between more xeric steppe vegetation at lower elevation and higher elevation mesic coniferous forests. These short-statured woodland communities have an open canopy with a diverse composition of herb, shrub, and dominant tree species (West 1988). Our investigation was conducted within this ecosystem at six sites found from northern Utah to southeastern Arizona (Fig. 2). The sites were selected within a narrow elevational range (1860–2120 m) and had similar average annual precipitation and growing season air temperature, but were systematically different in precipitation seasonality (Fig. 2, Table 1). Mean amounts of precipitation falling during the monsoon period (July–September) varied more than threefold among these sites. We assessed summer precipitation use by three dominant tree species: two gymnosperms, *Pinus edulis* Engelm. and *Juniperus osteosperma* (Torr.) Little; and a winter-deciduous angiosperm, *Quercus gambelii* Nutt. These trees are commonly found together in pinyon–juniper communities throughout Utah and Arizona, but their relative dominance and the presence of other tree spe-

cies varied among our field sites (Fig. 3). In eastern Arizona, species comprising the southern Rocky Mountain pinyon–juniper ecosystems co-occur with those more typical of pinyon–juniper ecosystems of the Colorado Plateau (Little 1971, West 1988). Percent canopy cover of trees was estimated within one large plot (0.25–0.5 ha) at each site using line transects (8–10 transects, from 35 to 50 m long). Canopy cover of *Pinus edulis* was greatest at sites in eastern Arizona. Canopy cover of *Quercus gambelii* tended to decrease as monsoon precipitation increased along the gradient (Fig. 3, Table 1).

Use of natural precipitation along the monsoon gradient

Tree water sources were determined for adult trees that were randomly selected from within the large plot at each site. Trees were selected within the intermediate size class (10- to 20-cm basal diameter) to avoid the possibility that juvenile or senility effects would influence our results. Between four and six trees from each species at each of the six sites were sampled repeatedly from May through September of 1993 and 1994 to determine tree water sources. Three to four suberized twigs ($\sim 8 \times 40$ mm) were cut at midday from different locations on a tree canopy and immediately enclosed in screw-cap glass vials and sealed using Parafilm. Soil samples were collected from 20- and 50-cm depths at each study site in 1993 and from 2-, 10-, 30-, and 50-cm depths in 1994. It was impractical to obtain soil samples from deeper than 50 cm because of the underlying rock at most sites. Soil samples were separated into two parts; one part was sealed in glass vials for isotopic analysis of water, the other was sealed in a soil tin and analyzed for gravimetric water content (percentage water, measured as g water/g soil $\times$ 100). All samples were kept in a dry cooler in the field until transfer to the lab.

Precipitation falling during the growing season (April–October) was collected at each site in 1993 and 1994 in standard rain gauges. Rain was allowed to accumulate in the collectors between visits to the sites. A 5-mm layer of clear white mineral oil was added to the rain collector to prevent evaporation and potential isotopic enrichment between sample collection periods. Contact with mineral oil does not alter the δD value of water; in a 122-d experiment of continually mixing water and mineral oil we could not detect any changes in the hydrogen isotope ratio of the water.

Groundwater was obtained from springs and wells close to each site. Rain and groundwater samples were stored in a refrigerator in tightly sealed glass vials. Soil and stem samples collected for isotopic analysis were kept frozen in the lab until water was extracted using cryogenic vacuum distillation (Ehleringer and Osmond 1989).

Water samples were prepared for isotopic analysis by reacting 3 μL of the water sample with 100 mg of
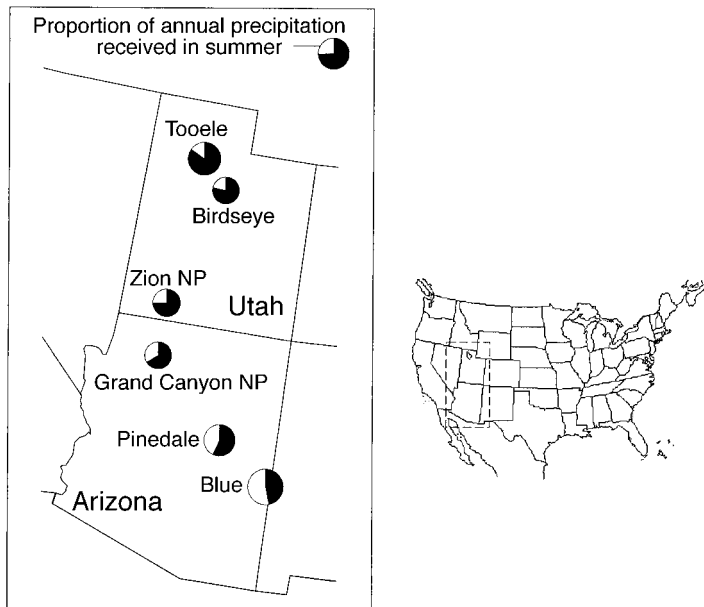
FIG. 2. Locations of study sites along the summer precipitation gradient in the southwestern United States. Pie charts show the proportion of mean annual precipitation received during the monsoon season, July–September (white part of pie). The sizes of pie charts are scaled proportionately to total amount of annual precipitation among the sites.

zinc at 500°C for 1 h in sealed Pyrex tubes (modified after Coleman et al. 1982). The zinc was obtained from J. M. Hayes, Departments of Chemistry and Geology, Indiana University, Bloomington, Indiana. The hydrogen gas liberated by the reaction was analyzed for isotopic composition on a dual inlet Finnigan Delta-S isotope ratio mass spectrometer (Finnigan, San Jose, California, USA) at the University of Utah Stable Isotope Facility for Environmental Research (SIRFER). The stable isotope ratio of hydrogen in water is expressed using standard delta notation (δ) in parts per thousand (‰) as

$$\delta D = (R_{sample}/R_{standard} - 1) \times 1000 \qquad (1)$$

where R_{sample} and $R_{standard}$ are the molar ratios of D/H of the sample and standard water (V-SMOW), respectively. Standard lab waters were calibrated against the international standards GISP and V-SMOW (International Atomic Energy Agency [IAEA] 1995) and were

used in linear corrections of raw values obtained from the mass spectrometer.

A two-component mixing equation was used to estimate the proportion of a tree's total water supply derived from recent summer rain. The form of the equation is

$$\delta D_{tree} = f(\delta D_{precip}) + (1 - f)(\delta D_{deep\ soil}) \qquad (2)$$

where $\delta D_{deep\ soil}$ represents the most negative deuterium isotope values measured over the growing season. $\delta D_{deep\ soil}$ values closely matched δD values of soil water at 50-cm depth in those instances when all these data were available together. δD_{tree} represents tree xylem sap values and δD_{precip} represents isotopic values from precipitation samples integrated over the few weeks prior to sampling tree xylem water.

$\delta^{18}O$ was measured on the same samples used for δD analysis collected from the Blue, Arizona site during the 1993 growing season. Water samples were equili-

TABLE 1. Habitat information for study sites used to investigate responses of pinyon–juniper species to summer precipitation. Climate data are long-term averages from stations near the study sites (NOAA climatological data annual summaries for Utah and Arizona).

Site	Latitude (°N)	Elevation (m)	Mean annual precipitation (mm)	Mean July–September precipitation (mm)	Clay content (%)	Sand content (%)	Soil textural class†
Blue, AZ	33.6	1980	490	286	43	21	clay
Pinedale, AZ	34.3	1970	427	183	43	34	clay
Grand Canyon, AZ	34.7	2120	367	123	39	24	clay loam
Zion, UT	37.2	2000	374	95	57	31	clay
Birdseye, UT	39.9	1860	368	80	37	22	clay loam
Tooele, UT	40.5	1980	448	79	26	22	silt loam

Note: Soil texture at 10-cm depth was evaluated on one composite sample from four intercanopy locations at each site.
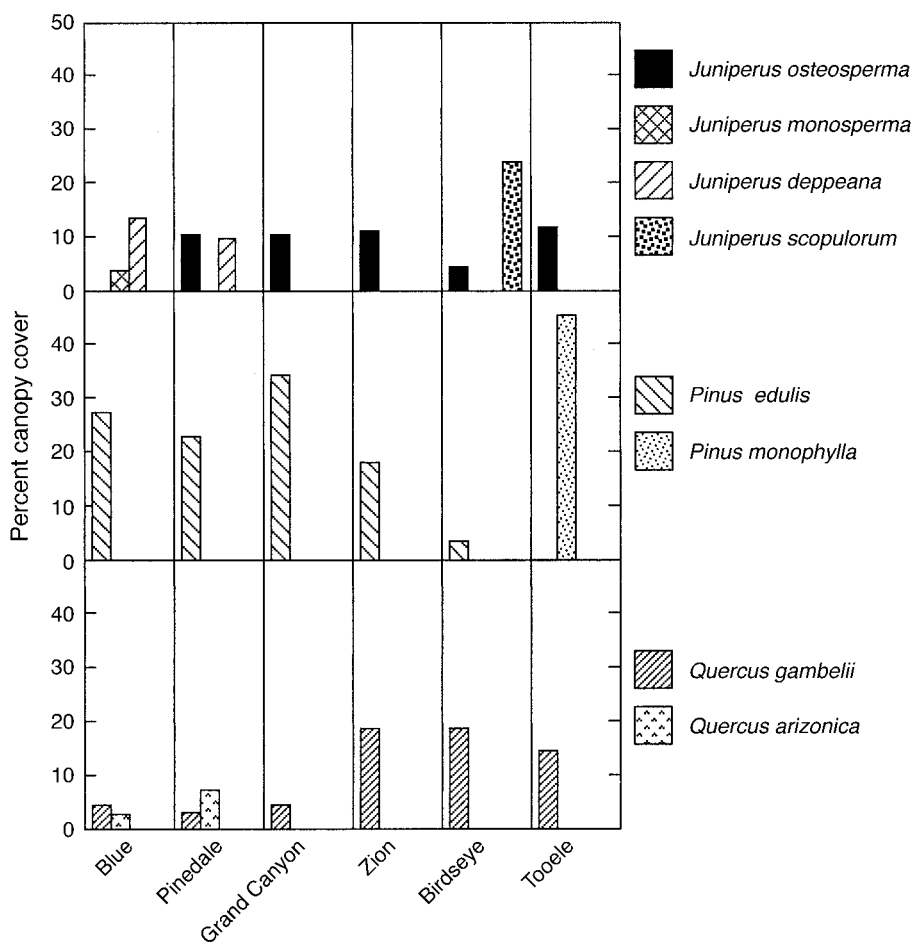† SCS texture classification system.

Fig. 3. Percent canopy cover for tree species recorded in line transects at the six study sites along the summer precipitation gradient. From eight to ten line transects between 35- and 50-m length were sampled at each site.

brated with CO_2 gas of known $\delta^{18}O$ composition in pre-evacuated sealed vials (Socki et al. 1992). The equilibrated CO_2 was extracted from the vials then cryogenically trapped and sealed in Pyrex tubes. The $\delta^{18}O$ of the CO_2 gas was analyzed on the mass spectrometer as described for δD. Lab standards were equilibrated, extracted, and analyzed with the unknowns and were used to correct raw $\delta^{18}O$ values. $\delta^{18}O$ values are reported relative to V-SMOW.

Water source data were analyzed using the JMP statistical software for the Macintosh (Version 3.1, SAS Institute 1995). Seasonal patterns of plant δD and percentage rain use were investigated with an analysis of variance for repeated measures (ANOVAR), where multiple measurements on a given plant through time represent the repeated variables (Potvin et al. 1990). Seasonal variation and species × season interactions were tested as within subjects effects. The assumption of compound symmetry in the covariance matrix was frequently violated with these data. In the absence of compound symmetry, we performed an Huynh-Feldt

corrected analysis of variance for repeated measures (Potvin et al. 1990). Our analyses of within-subjects effects are based on these corrected F and P values. Pairs of means were compared using Student's t tests and protected LSD tests.

Photosynthetic gas exchange and water potential

Leaf gas exchange was monitored over the growing season in 1993 and predawn water potential (Ψ_{pd}) was measured in 1993 and 1994 on three or four trees from each species at each site. Measurements were made on the same days that stems were collected for isotopic analysis. Instantaneous measures of net photosynthetic carbon assimilation (A) and stomatal conductance (g_s) were determined on fully sunlit leaves near the top of the canopy of three or four trees per site using a portable photosynthesis system (model LI-6200, LI-COR, Lincoln, Nebraska, USA). Typically, only one measurement was made per tree. One-sided leaf area was determined using a leaf area meter (model LI-3100, LI-COR, Lincoln, Nebraska, USA). The terminal 2–3 cm

of photosynthetic twig in *Juniperus,* the 1992 cohort of needles in *Pinus* and young, fully expanded leaves in *Quercus* were measured. Ψ_{pd} was measured using a pressure chamber (PMS Instruments, Corvallis, Oregon, USA) between 0300 and 0530 local time within 2 min after twigs were cut from the plants to minimize changes in Ψ due to water loss. We did not measure δD, Ψ_{pd} or gas exchange for *Quercus gambelii* in May because leaves were not fully expanded at this time. Phillips and Ehleringer (1994) have previously shown that determination of water sources for *Quercus* is unreliable until after spring leaf flush when leaves become mature (late May or early June at our field sites).

We arbitrarily subsampled plants from among target trees at a site for the gas exchange and water relations measurements and did not ensure that the same plants were sampled repeatedly through the course of the study. Thus, we performed standard least squares analysis of variance (ANOVA) on the gas exchange and water relations data instead of ANOVAR.

Soil temperature

Soil temperature was measured continuously using thermocouples at the Blue, Grand Canyon, Zion, and Tooele sites from early May through September, 1994. Copper-constantan thermocouples (Omega Engineering, Stamford, Connecticut, USA) were placed at 10-cm depth in intercanopy locations at each site and were monitored with data loggers (CR21X, Campbell Scientific, Logan, Utah, USA).

Irrigation experiments

Responses of *Juniperus osteosperma, Pinus edulis,* and *Quercus gambelii* to surface irrigation was evaluated at the Grand Canyon and Zion sites. We chose these sites for these experiments because they lie close to the northwestern boundary of the region influenced by the Arizona monsoon (Adang and Gall 1989) and it was near these sites where previous studies have shown interannual and site-to-site differences for summer rain use in two of the three species included in our investigation (Gregg 1991, Flanagan et al. 1992, Evans and Ehleringer 1994).

Deuterium-enriched irrigation water was applied to the soil around target plants to simulate a summer rainfall event that could be traced through the soil–plant pathway. In a large water tank, 21–28 mL of D_2O were mixed with ~2200 L of natural groundwater collected from nearby wells. δD values of irrigation water labeled with D_2O ranged from 10–51‰ for different watering episodes and were distinguishable from natural plant water source values which were always negative (δD of deep soil and precipitation at these sites ranged from -110 to -25‰). Irrigation water was applied as evenly as possible over a circular area (2.5-m radius) around target plants. The area watered extended about one meter beyond the perimeter of the target tree canopy into

the interspaces between plants. Target plants were spaced by at least 15 m and care was taken not to contaminate interspaces around control plants with labeled water. The amount of water applied to each plant was monitored closely to achieve irrigations that were similar to 10- or 25-mm rainfall events. Stems were collected for isotopic analysis (see *Methods: Use of natural precipitation along the monsoon gradient* for description) from irrigated plants and nonirrigated control plants just prior to irrigation on the same day, and again at two and five days following irrigation. Predawn water potential was measured on plants over the same period. We concluded that plants did not take up the irrigation water if, after five days, the δD of watered plants did not increase significantly compared to nonirrigated control plants. We used a two-member mixing model (Eq. 2) to estimate the fraction of plant xylem water that was derived from the artificial rain events. In this case, the two compartments for the mixing equation included the artificial rain and the isotopic composition of xylem water measured just prior to irrigation.

Ten randomly chosen adult plants from *Quercus, Juniperus,* and *Pinus* at the Zion site were given 25-mm irrigation during the monsoon season of 1994. Half were watered during the hottest period of the summer on 24 July and the remainder was watered near the end of the monsoon season on 12 September when air and soil temperatures were much cooler. Five additional plants served as controls for comparison to the irrigated plants. A similar experiment was conducted at the Grand Canyon site except that irrigation was applied on one date only (10 August 1995). For the Grand Canyon experiment, both 10- and 25-mm rain events were simulated by the irrigations. Tree responses to the artificial summer rains were evaluated statistically by comparing mean percentage use of irrigation water to zero after correcting for slight shifts in the δD of control plants over the 5-d measurement periods.

RESULTS

Use of natural precipitation along the monsoon gradient

Over the two years of our study, precipitation amounts followed the expected seasonal pattern across the region. July-to-September precipitation amounts were greatest at the southern locations of the monsoon gradient (Table 2). Precipitation amounts at all sites, however, deviated from normal during this period. The El Niño of 1992–1993 resulted in higher winter and spring precipitation prior to the 1993 growing season than in the same period prior to the 1994 growing season, especially at our southern sites. Winter and spring precipitation tended to be closer to normal in 1994. Overall, monsoon-season precipitation amounts were either similar to or less than normal across the gradient for the two years of this study.

TABLE 2. Winter and spring precipitation (November–May) and monsoon season precipitation (July–September) recorded near six study sites in Utah and Arizona.

Site	November–May precipitation (mm)		July–September precipitation (mm)	
	1992–1993	1993–1994	1993	1994
Blue, AZ	368 (189)	172 (−8)	148 (−138)	292 (6)
Pinedale, AZ	368 (178)	244 (54)	167 (−16)	151 (−32)
Grand Canyon, AZ	351 (146)	167 (−38)	124 (1)	107 (−16)
Zion NP, UT	436 (198)	223 (−15)	71 (−24)	60 (−35)
Birdseye, UT	495 (259)	305 (69)	67 (−13)	74 (−6)
Tooele, UT	448 (147)	288 (−13)	53 (−26)	39 (−40)

Note: Absolute difference from normal precipitation over the same time period is shown in parentheses.

δD values from local groundwater (springs and wells) were more positive on the southern end of our gradient than to the north and values changed little through repeated samplings over the two years of observation (Fig. 4). δD of groundwaters likely reflects the contribution of summer monsoon and winter precipitation to the recharge of local aquifers in this region (Ingraham et al. 1991). The amount and frequency of rainfall at most of the study sites tended to increase from May to September in 1993 and 1994 (Fig. 4). The number of events and total amounts, however, declined from May to mid-September at the two northern sites (Birdseye and Tooele, Utah) in 1993 and 1994. These sites are farther north than where the monsoon air typically advances during the summer. δD of rainfall collected and integrated over 3- to 4-wk periods between visits to field sites ranged from −60 to −20‰ during the peak summer period and early monsoon season (Fig. 4). Rainfall in September at the Blue and Pinedale sites, however, were depleted isotopically compared to rains earlier in the summer at these sites. δD of soil water at 50-cm depth was generally more negative than that of summer rains at all sites (Fig. 4); values ranged between −130 and −75‰ among all sites and fluctuated slightly through the season in both years. These fluctuations likely resulted from displacement by summer rainfall and evaporation since values tended to rise during the growing season.

Pinus edulis and *Juniperus osteosperma* exhibited greater seasonal variations in xylem water δD values than did *Quercus gambelii* (Fig. 4). δD values of xylem water for *Pinus* and *Juniperus* during the monsoon months of July through September were as much as 72‰ greater than that during the premonsoon period from May to late June (Fig. 4). δD values of xylem water during the peak monsoon period in these conifers was generally more positive than that in *Quercus gambelii*. Significant sampling date × species interactions were found at Pinedale, Grand Canyon, and Birdseye in 1993 and at all sites except Blue and Tooele in 1994 (Table 3). These significant interactions indicate that, within those sites, seasonal patterns of plant isotope ratios differed among species. At all but the two southern-most sites (Blue and Pinedale, Arizona), δD values of *Quercus gambelii* over the growing season changed little and were comparable to that of deep soil water and early spring precipitation (Fig. 4). δD values of *Quercus* increased by 10‰ and 20‰ from the premonsoon drought period to the monsoon period at Blue and Pinedale, but increased only slightly or not at all over the same period at the other sites. The magnitude of upward shift in δD from premonsoon to the monsoon period was not different between *Quercus* and *Pinus* at Blue for 1993 and 1994.

Quercus and *Pinus* at the Blue, Arizona site in 1993 appeared to be using a mixture of deep soil water and recent precipitation. There was no evidence from δD–δ^{18}O plots that these species used groundwater at this site (Fig. 5). Groundwater and rain plotted very close to the global meteoric water line (GMWL, δD = 8·(δ^{18}O) + 10; Craig 1961). Soil and plant samples plotted to the right of the GMWL indicating that water in these samples had undergone isotopic enrichment due to evaporation. Soil from 20-cm depth showed greater ^{18}O enrichment than soil water from 50-cm depth. Plant δD–δ^{18}O values for *Quercus* and *Pinus* at this site were similar and plotted between soil water and precipitation that fell between June and mid-August prior to sampling.

Using the linear mixing equation (Eq. 2), we converted the absolute hydrogen isotope ratios in tree xylem water into the fractions derived from upper soil versus deep soil water sources (Fig. 6). In the analysis, we assumed that groundwater was not a water source available to plants at these sites. In these upland habitats, stable groundwater sources are very deep, and are well beyond the presumed rooting depth of these trees. For instance, at two Arizona sites (Blue and Pinedale), depth to groundwater is 60 m or greater (T. Subirege, U.S. Forest Service, *personal communication*). That plants are not using groundwater at these sites was verified isotopically at the Blue, Arizona site (Fig. 5). We were confident in using early season δD values of plants as an indication of the δD value of deep soil. This allowed
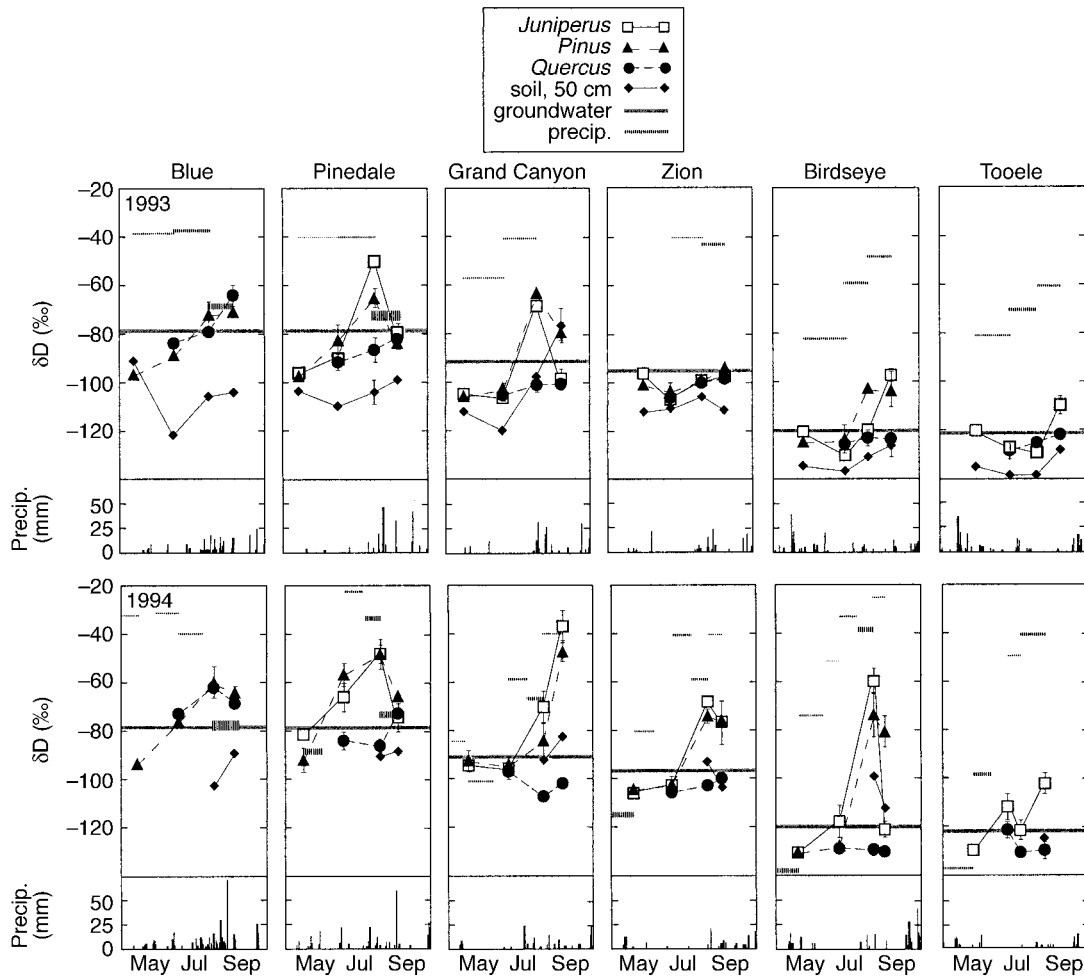
FIG. 4. Deuterium isotopic composition (δD) of stem xylem water for *Juniperus osteosperma, Pinus edulis,* and *Quercus gambelii* measured in 1993 and 1994 from six sites along the summer precipitation gradient. Vertical bars on symbols represent ± 1 SE of mean values. Horizontal bars show integrated δD values of precipitation falling at each site. Bar thickness is scaled proportionally to show the relative amount of precipitation over the indicated time period. Periods without horizontal bars indicate missing data or no precipitation.

TABLE 3. *F* values and significance levels for repeated-measures analysis of variance (ANOVAR) of xylem water isotopic composition (δD).

Sources of variation	Blue, AZ	Pinedale, AZ	Grand Canyon, AZ	Zion, UT	Birdseye, UT	Tooele, UT
1993						
Between subjects						
Species	0.6 NS		49.2***	1.6 NS	7.5*	1.2 NS
Within subjects		4.5 NS				
Sampling date	14.5***	24.8***	94.6***	14.1***	30.5***	13.6***
Date × species	2.6 NS	6.8**	23.8***	0.5 NS	8.3***	3.7 NS
1994						
Between subjects						
Species	0.1 NS	14.8***	11.2**	60.0***	35.3***	15.5**
Within subjects						
Sampling date	7.2**	6.1**	44.1***	148.8***	36.8***	0.1 NS
Date × species	0.6 NS	8.9***	13.7***	27.0***	17.5***	2.6 NS

Note: Data are for *Quercus gambelii, Pinus edulis,* and *Juniperus osteosperma* from several sampling dates during the growing seasons of 1993 and 1994.

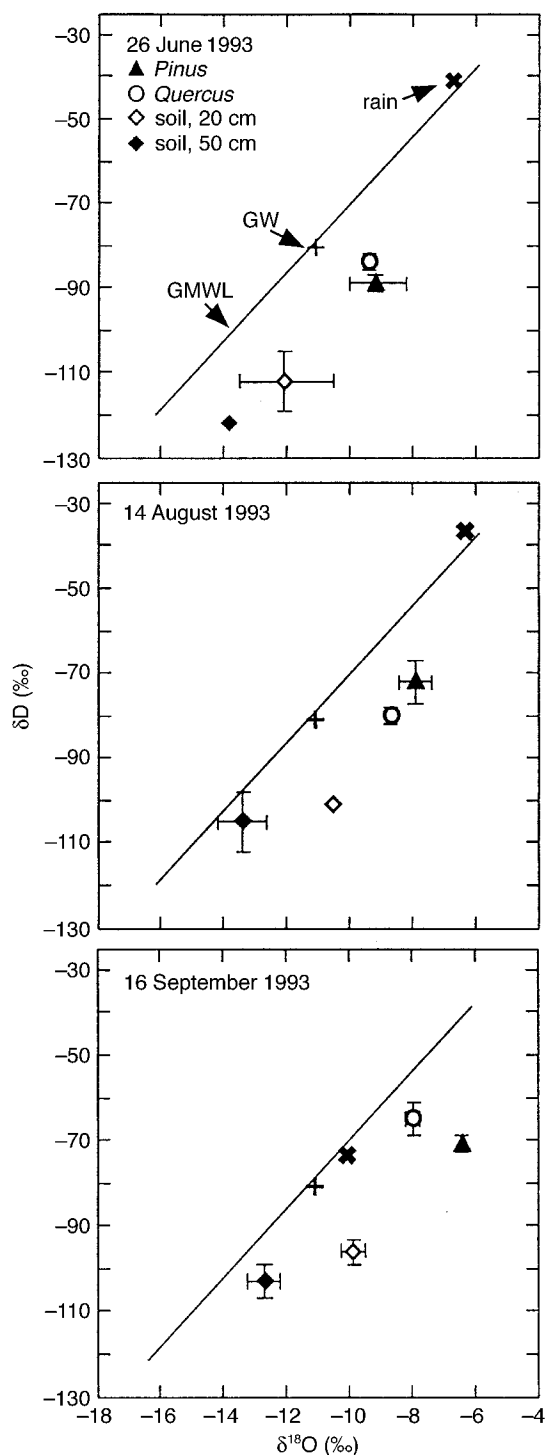* $P \leq 0.05$; ** $P \leq 0.01$; *** $P < 0.001$; NS, not significant.

FIG. 5. Relationship between δD and δ¹⁸O of xylem water in *Pinus edulis* and *Quercus gambelii*, precipitation, soil water, and groundwater during the growing season at Blue, Arizona, in 1993. Also shown is the global meteoric water line (GMWL) where δD = 8(δ¹⁸O) + 10 (Craig 1961). Error bars are ± 1 SE.

us to analyze the data in terms of a simple two-ended mixing model (Eq. 2). Assuming our end members for the mixing model were accurate, it appeared that *Juniperus* and *Pinus* consistently used very shallow soil water compared to *Quercus.* With limited exceptions, the percentage use of summer rainfall by the two conifers increased as the season progressed into the monsoon period. At sites south of the average monsoon boundary in southern Utah, from 40 to 100% of xylem water in *Pinus* and *Juniperus* in 1994 was derived from surface moisture. At sites north of the average monsoon boundary, only 0–40% of the plant's xylem water came from these surface moisture pulses. In contrast, during 1993 surface moisture use tended to be lower than that in 1994. *Quercus* had negligible fractions (typically 10% or less) of xylem water derived from the surface. At the southern-most Arizona sites (Blue and Pinedale), however, *Quercus* appeared to rely significantly on surface soil water that became available during the monsoon period.

Maximum surface moisture use by these trees during the monsoon periods is plotted as a function of average monsoon precipitation of the sites in Fig. 7. From this plot it appears that use of monsoon-derived moisture increased sharply from a minimum at sites where monsoon rain input is minimal, to almost 100% use where monsoon rain input is high. We used the maximum value of surface moisture use observed during the monsoon period rather than the August or September values only since plant water source sampling did not occur continuously, and it is possible that individual observations during the summer may have reflected a diminished use of moisture in the upper layers as those layers periodically dried out. Transition from low to high use of this upper-soil-layer moisture occurred at different positions along the geographic gradient dependent on the three tree species.

The same threshold curve from Fig. 1 is plotted over the data in Fig. 7, but is shifted for each species to best characterize the observed patterns. The sensitivity of *Juniperus* and *Pinus* was such that populations were capable of using surface moisture during the late summer even at sites receiving less than 100 mm summer rain. Summer rain use by these conifers, however, appeared to decline abruptly at these northern Utah sites. These transitional sites are found just north of the monsoon boundary position (Mitchell 1976, Adang and Gall 1989) where surface soil temperature is comparatively high along the gradient (Fig. 8). In contrast, the threshold amount of summer rain for *Quercus* was higher; this species seems to require at least 125–175 mm monsoon rain input and lower surface soil temperatures to have active surface roots (Figs. 7 and 8).

The δD value of soil water near the surface (10-cm depth) during the peak monsoon period in August, 1994

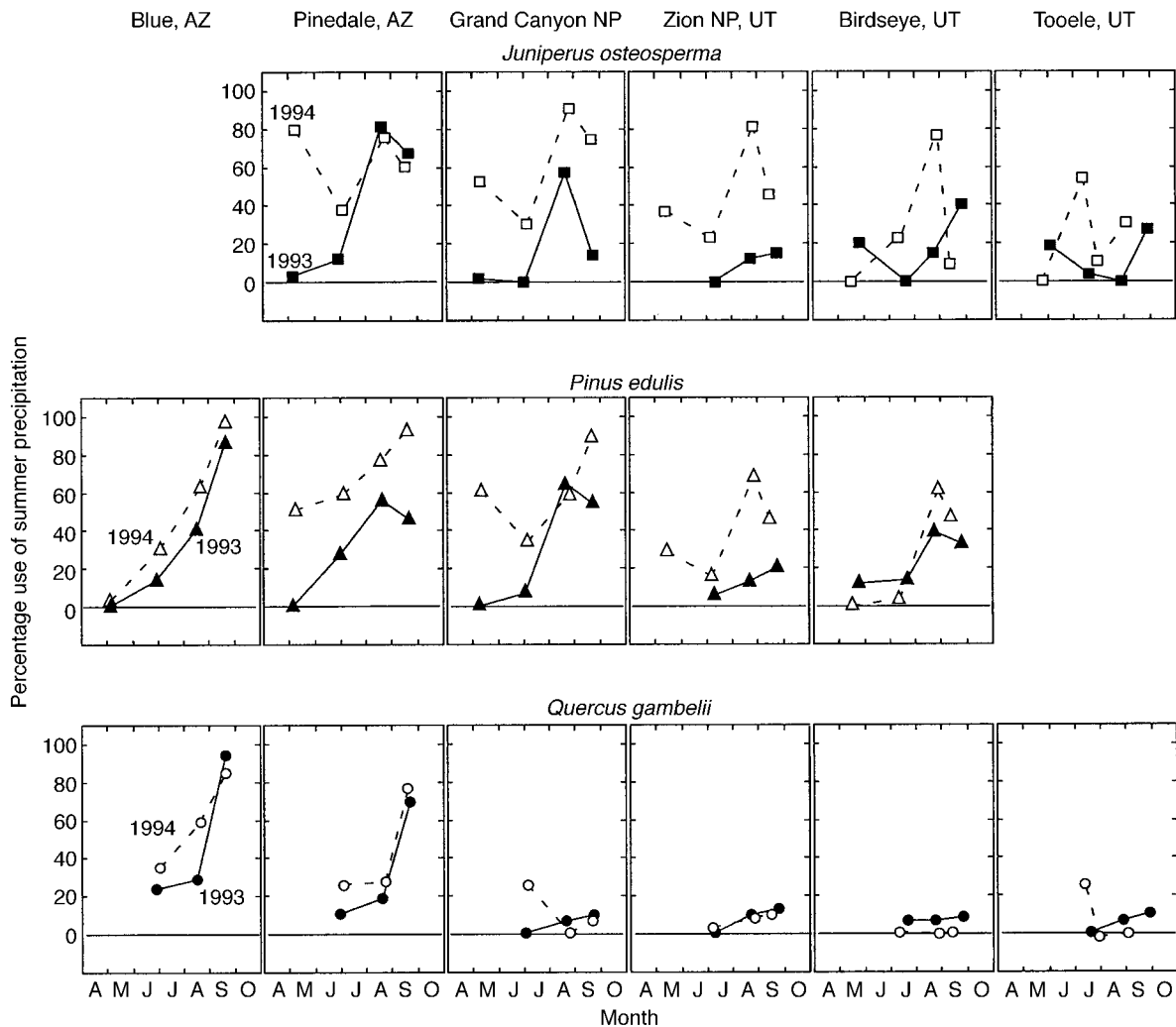FIG. 6. Seasonal course of percentage surface moisture use by *Juniperus osteosperma, Pinus edulis,* and *Quercus gambelii* in 1993 (closed symbols) and 1994 (open symbols) at six sites along the summer precipitation gradient. Values were determined from a two-member mixing equation using recent precipitation and deep soil water δD values as end members (see *Methods: Use of natural precipitation along the monsoon gradient* for details).

was enriched relative to water deeper in the soil (Fig. 9). The relatively positive δD values at the surface in 1994 likely resulted from both recent inputs of isotopically heavy monsoon precipitation (Fig. 4) and evaporative enrichment (Fig. 5; Allison et al. 1983). We collected soil δD and moisture values only from two depths (20 and 50 cm) in August, 1993 (Figs. 9 and 10). Interannual differences in soil water δD were minimal at the 50-cm depth but were greater at shallower depths in the profile. At all sites, δD values for soil water at 20-cm depth in 1993 were more negative than those at 30-cm depth in 1994. Likewise, soil moisture content was greater at the 20-cm depth in August 1993 than at the 30-cm depth in 1994 (Fig. 10).

Comparison of plant xylem water δD to that of soil water at different depths in August of 1993 and 1994 suggests that *Pinus edulis* and *Juniperus osteosperma*

were withdrawing water from the upper soil layers at all sites (Fig. 9). Extrapolation of plant xylem water δD values over the range of soil δD values indicated that these evergreen conifers took up soil water from between 10- and 30-cm depth during this period. It was difficult to assess the depth of water uptake for the trees in 1993 because of the limited soil isotope data. However, at the Arizona sites in 1993, δD values of the xylem water in these trees tended to be more positive than that of soil water at 20- and 50-cm depths (Figs. 4 and 9). If one assumes that δD values of shallow soil water in 1993 were similar to that in 1994, then it appears that some moisture used by these conifers in Arizona in August, 1993 came from above 20-cm depth. This is supported by δD–δ¹⁸O plots from Blue that show that water being taken up by plants had undergone evaporative enrichment. *Pinus* and *Juni-*
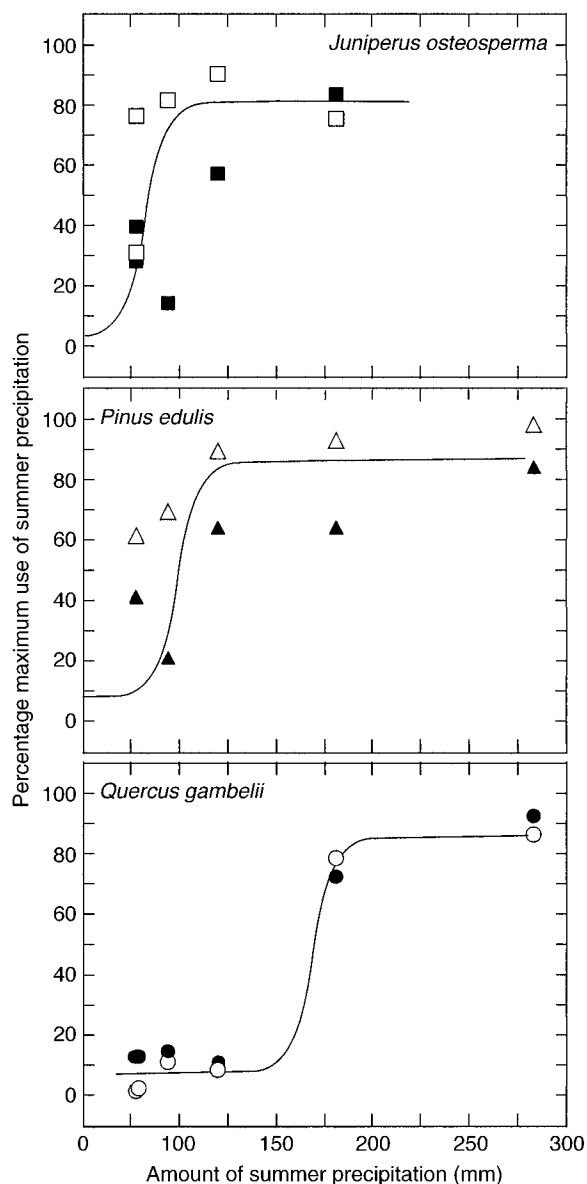
FIG. 7. Maximum percentage of summer precipitation use by *Juniperus osteosperma, Pinus edulis,* and *Quercus gambelii* during the summer in 1993 (closed symbols) and 1994 (open symbols) plotted as a function of site mean summer precipitation amount. The most positive value observed within a particular year's monsoon season was used for this figure. The threshold curve from Fig. 1 is plotted over the data and shifted accordingly for each species to visually fit the data.

perus used moisture from the upper soil layers during August 1994 even at the more northern sites where soil moisture content was relatively low during this period (Fig. 10). Moisture content at 10-cm depth at the Arizona sites in August 1994 was relatively high (7–13% H_2O). *Quercus gambelii* took up shallow soil moisture during August at the Blue site and to a lesser degree

at the Pinedale site (Fig. 9). At all other locations, *Quercus* extracted water predominantly from deep in the soil profile (>50 cm).

Tree responses to irrigation

Irrigation water penetrated no deeper than 30 cm (D. Williams, *personal observation*), but had significant impact on the water relations of *Pinus* and *Juniperus* plants in northern Arizona and southern Utah. *Juniperus osteosperma* took up labeled irrigation water at both Zion and Grand Canyon sites. Irrigation that was applied to simulate a 25-mm rain event during the hottest part of the summer (late July and early August) caused xylem water δD of *Juniperus* to increase significantly compared to that of nonirrigated control plants at both the Grand Canyon and Zion sites (Fig. 11). Approximately 40% of the xylem water in *Juniperus* five days after irrigation was from the 25-mm simulated rains. *Juniperus* also took up water from a 10-mm irrigation in August at Grand Canyon (Fig. 11). Predawn water potential (Ψ_{pd}) increased significantly compared to controls for *Juniperus* plants irrigated with 25-mm water at the Zion site (Table 4). Ψ_{pd}, however, did not increase significantly for plants supplemented with 10 or 25 mm of irrigation water compared to that of control plants at Grand Canyon. *Quercus gambelii* did not take up the labeled water during midsummer at either Grand Canyon or Zion; the δD values of xylem water in irrigated plants did not increase significantly compared to that of control plants following the irrigations (Fig. 11). Ψ_{pd} of irrigated *Quercus* plants like-
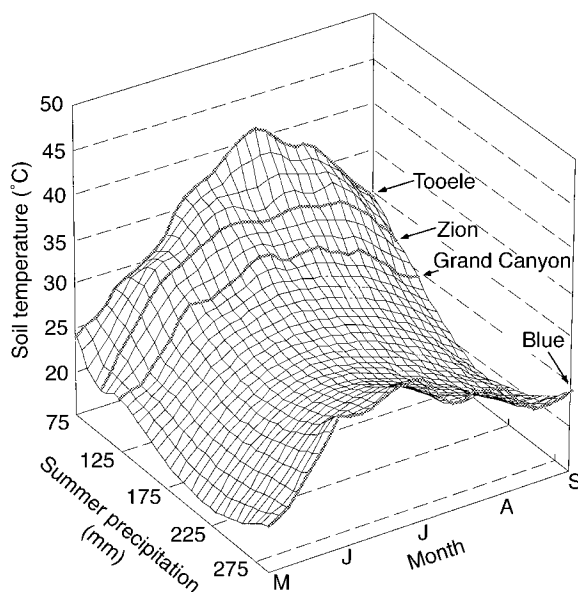

FIG. 8. Soil temperature at 10-cm depth over the growing season in 1994 for four sites along the monsoon gradient in Utah and Arizona. The surface response plot was generated from 3-d running means of daily maximum temperatures. Thickened lines show locations of actual data collected at the four sites.
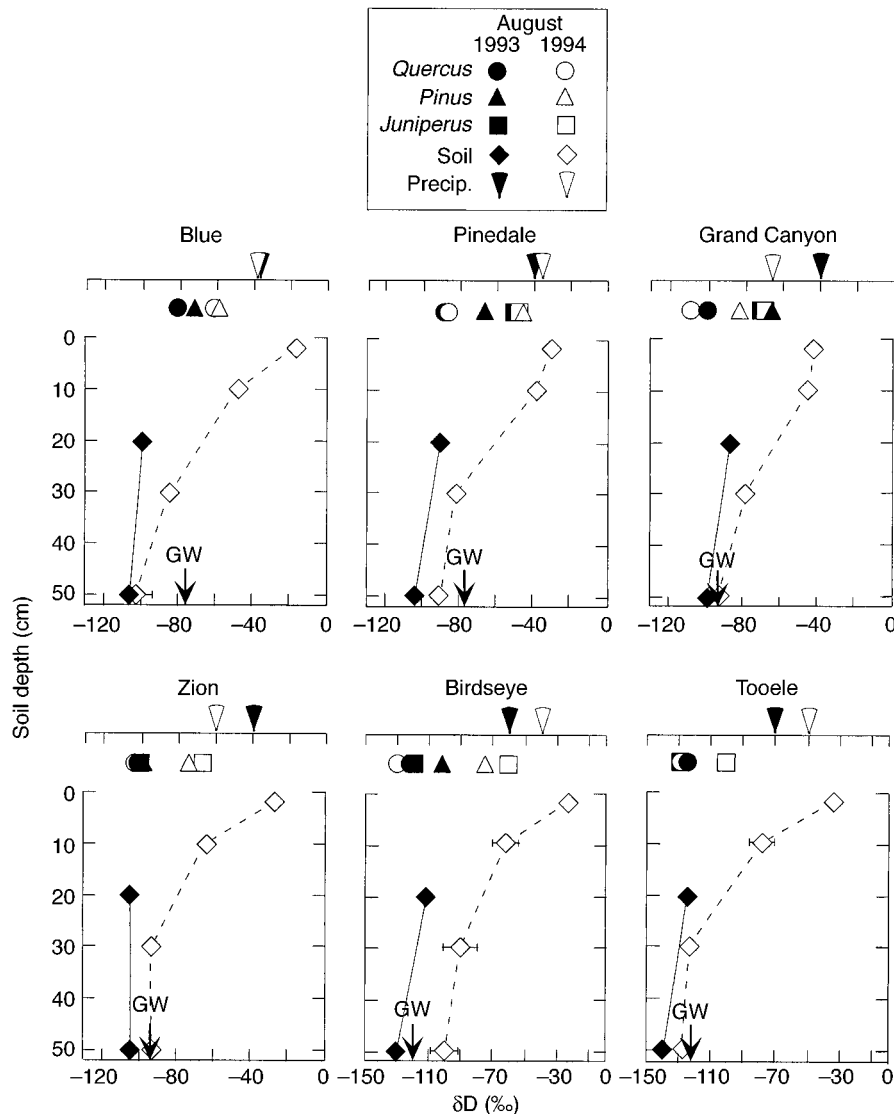
FIG. 9. Hydrogen isotope ratios (δD) of water through the soil profile ($n = 3-4$) determined in August 1994 at six sites along the summer precipitation gradient. Shown also are corresponding measurements of tree xylem water δD values for *Juniperus osteosperma, Pinus edulis,* and *Quercus gambelii* during this period. Horizontal bars on symbols represent $\pm$ 1 SE of mean values.

wise did not increase significantly compared to that of control plants at either Grand Canyon or Zion (Table 4).

Pinus at the Grand Canyon site took up irrigation water during midsummer when water was supplied as either a 10- or 25-mm irrigation (Fig. 11), but did not take up irrigation water at the Zion site during midsummer. Ψ_{pd} of *Pinus* plants did not increase significantly compared to that of nonirrigated control plants following irrigation during the midsummer period at the Grand Canyon or Zion sites (Table 4). *Pinus* used a greater fraction of irrigation water for transpiration in September at the Zion site than during the hot, mid-

summer period. Ψ_{pd} of *Pinus* responded to the irrigation in September, but not in July at this site (Table 4). Use of surface irrigation water changed little from midsummer to early fall for *Juniperus* and *Quercus* at this site.

Photosynthetic gas exchange and water potential

Stomatal conductance (g_s) and predawn water potential (Ψ_{pd}) were greater for *Quercus gambelii* than for *Pinus edulis* and *Juniperus osteosperma* (Fig. 12, Table 5) at most sites along the monsoon gradient in 1993 and 1994. The exceptions were at the southernmost sites (Blue and Pinedale, Arizona), where Ψ_{pd} in at least one of the two years was not significantly dif-
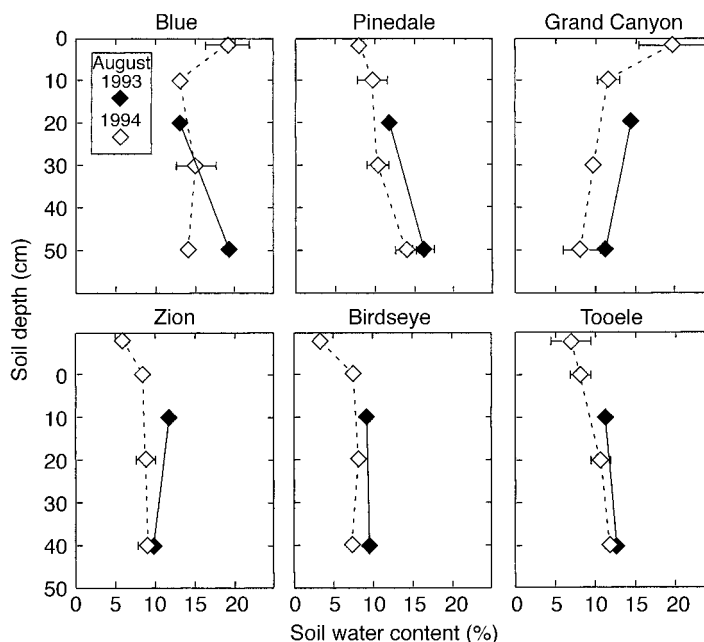
FIG. 10. Percentage gravimetric water (measured as [g water/g soil] $\times$ 100) through the soil profile ($n = 3$–4) determined in August 1994 at six sites along the monsoon gradient. Horizontal bars on symbols represent $\pm$ 1 SE of mean values.

ferent among these tree species (Table 5). Maximum stomatal conductance observed over the growing season tended to increase as summer rains decreased along the gradient from south to north for *Quercus,* but did not change over the same gradient for *Juniperus* and *Pinus* (Fig. 12). For the most part, g_s and Ψ_{pd} changed through the course of the growing season coincident with seasonal precipitation. For instance, g_s and Ψ_{pd} increased significantly for *Pinus* and *Quercus* at the Blue, Arizona site from late June to the monsoon months of August and September in 1993, but tended to decline over the same period in the north where rains were less effective. Curiously, g_s and Ψ_{pd} in 1993 did not change significantly for any of the species over the period spanning the premonsoon drought and monsoon season at Pinedale, Arizona. At Pinedale in 1994, however, Ψ_{pd} increased significantly for all of the species over the same period. Although *Pinus* and *Juniperus* took up summer rains at Grand Canyon in 1993, Ψ_{pd} declined through the growing season. Although *Quercus* did not take up summer rains at sites north of Pinedale, Ψ_{pd} did not change significantly through the growing season at Grand Canyon or Birdseye.

Leaf photosynthetic characteristics and apparent tolerance to water deficits were not correlated to plant water source usage for the three tree species. The dependence of net CO_2 assimilation (*A*) on g_s and the relationship between g_s and Ψ_{pd} in 1993 for the three species are shown in Fig. 13. The initial slope of the A/g_s relationship, an indication of intrinsic water-use efficiency, was similar among the three species, although *Quercus* tended to operate at higher photosynthetic rates with higher g_s. Stomatal conductance in *Pinus* declined to zero at a predawn water potential of

only -2 MPa, whereas g_s in *Quercus* and *Juniperus* declined to zero at -2.8 and -3.7 MPa, respectively (Fig. 13).

DISCUSSION

Shifts in the intensities of the Arizona monsoon and Pacific storm systems that have occurred over the Holocene (Van Devender and Spalding 1979, Neilson 1986, Spaulding and Graumlich 1986, Stine 1994), that currently occur as decadal cyclic patterns, and that are predicted to occur in the future (Schlesinger and Mitchell 1987, Mitchell et al. 1990, Houghton et al. 1996) have important ramifications for the structure and function of ecosystems in the arid southwest of North America. Our results, along with those reported by Lin et al. (1996) and Weltzin and McPherson (1997), suggest that changes in the intensity of the summer monsoon system in this region could alter water-use and productivity patterns among coexisting perennial plant species. When combined with the expected increases in water-use efficiency and potentially extended growing season length because of reduced transpiration under elevated CO_2 (Field et al. 1997), the dynamics of these arid ecosystems may be altered significantly in the near future. Together these factors suggest the potential for compositional and/or functional changes in these water-limited ecosystems.

In the present study, we found systematic variation for summer precipitation use among populations of dominant woody species across a broad geographic range. Patterns of summer precipitation use by *Quercus gambelii, Juniperus osteosperma,* and *Pinus edulis* across the summer precipitation gradient in this study illustrates the existence of threshold responses to this
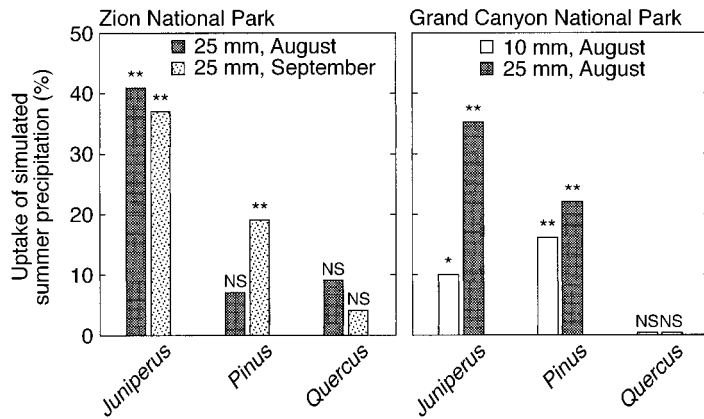
FIG. 11. Percentage use of 10- and 25-mm simulated summer rain events by *Juniperus osteosperma, Pinus edulis,* and *Quercus gambelii* at Zion National Park, Utah, and Grand Canyon National Park, Arizona. δD of trees was assessed 5 d after receiving water labeled with deuterium (see *Methods: Use of natural precipitation along the monsoon gradient* for details). Each bar represents the mean value from four or five plants after compensating for changes in δD of control plants over the 5-d experiments. Statistical significance from *t*-test comparisons between irrigated plants and nonirrigated control plants is indicated as follows: $*P < 0.05$; $**P < 0.01$.

limiting resource; a critical level of summer rain input apparently is required to stimulate root activity in surface layers in these woody species. However, response of these woodland ecosystems to potential future shifts in the seasonality of precipitation at any single site will depend on the rate and extent of root physiological or morphological adjustment at the individual and population levels. Here we could not distinguish between potential sources of interpopulation phenotypic variation for soil moisture use. Some combination of environmental, plastic, and genotypic variation contributed to the threshold patterns of surface root activity that we observed in *Pinus, Juniperus,* and *Quercus.* The relative contributions of these sources of variation will determine the rate of ecosystem response to climate changes (Schimel 1993).

Interpretation of monsoon precipitation use from isotopic signals in this study hinges on the assumption that *Quercus, Pinus,* and *Juniperus* have little or no access to groundwater at our study sites. The δD value of groundwater, especially at the Blue and Pinedale, Arizona sites, was often intermediate to that of deep

soil and rain values used in the linear mixing calculations. Normally, this would confound a simple two-ended analysis of water sources (see Brunel et al. 1995). However, trees at our study sites apparently had no access to groundwater sampled from wells and springs in adjacent areas. Although $\delta^{18}O$ data were collected only at the Blue, Arizona site, the δD–$\delta^{18}O$ relationships clearly show that plants at this site were using a mixture of soil water that had undergone evaporative enrichment and rain water from recent precipitation, but not groundwater. Results from this site are critical to our interpretation of threshold responses to summer precipitation in this system because it was here that *Quercus,* normally assumed not to use moisture from upper soil layers (Phillips and Ehleringer 1994, Ehleringer and Phillips 1996), in fact, was behaving physiologically and isotopically like a shallow-rooted species. Second, predawn water potentials for all three species tended to track seasonal precipitation. Predawn Ψ values for the three species dropped below -1 MPa at all of the study sites during periods of limited rainfall. Plants with access to groundwater in these semi-

TABLE 4. Predawn water potential (Ψ_{pd}) for three tree species at two sites used to evaluate uptake of artificial summer rains.

	Juniperus osteosperma		*Pinus edulis*		*Quercus gambelii*	
Treatment	Initial	Difference	Initial	Difference	Initial	Difference
Zion NP, 24 July 1994						
Control	-1.60 ± 0.14^a	-0.06 ± 0.04^a	-1.51 ± 0.07^a	0.09 ± 0.06^a	-1.34 ± 0.15^a	-0.03 ± 0.11^a
25 mm	-2.16 ± 0.08^b	0.68 ± 0.09^b	-1.39 ± 0.05^a	0.23 ± 0.06^a	-1.61 ± 0.09^a	0.14 ± 0.04^a
Zion NP, 12 September 1994						
Control	-2.33 ± 0.23^a	-0.28 ± 0.13^a	-1.68 ± 0.03^a	-0.20 ± 0.04^a	-2.10 ± 0.13^a	0.06 ± 0.10^a
25 mm	-2.68 ± 0.07^b	1.16 ± 0.04^b	-1.56 ± 0.03^b	0.31 ± 0.05^b	-2.01 ± 0.07^a	0.06 ± 0.23^a
Grand Canyon NP, 10 August 1995						
Control	-1.48 ± 0.11^a	0.05 ± 0.03^{ab}	-1.33 ± 0.03^a	0.00 ± 0.06^a	-1.14 ± 0.08^{ab}	-0.01 ± 0.02^a
10 mm	-1.24 ± 0.01^a	0.01 ± 0.01^b	-1.46 ± 0.09^a	0.06 ± 0.06^a	-0.89 ± 0.07^a	-0.05 ± 0.05^a
25 mm	-1.41 ± 0.06^a	0.21 ± 0.09^a	-1.40 ± 0.06^a	0.11 ± 0.04^a	-1.24 ± 0.09^b	0.05 ± 0.11^a

Note: Data shown are means $\pm$ 1 SE for plants the morning before irrigation and the difference in Ψ_{pd} measured three days following irrigation from initial values. Ψ_{pd} values among treatments within a site and species followed by the same letter are not significantly different (*t* test, $P > 0.05$). Tests were performed independently for comparisons among initial and difference values.
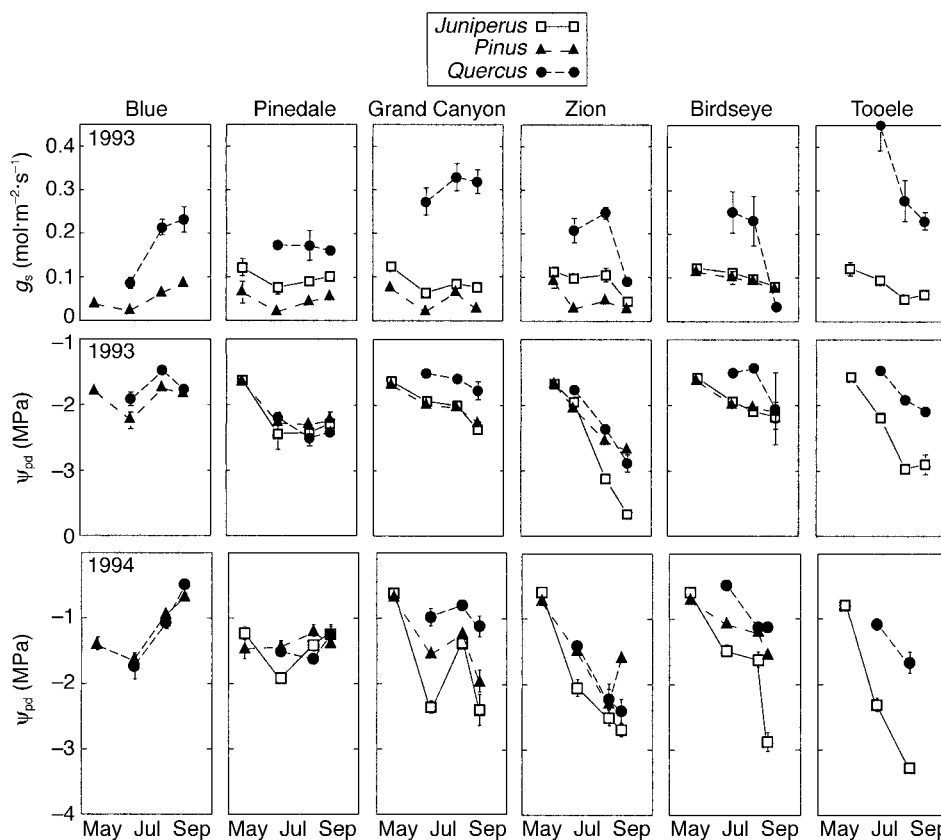
Fig. 12. Seasonal course of midday stomatal conductance (g_s) in 1993 and predawn water potential (Ψ_{pd}) in 1993 and 1994 for *Juniperus osteosperma, Pinus edulis,* and *Quercus gambelii* at six sites along the monsoon gradient. Vertical bars on symbols represent ± 1 SE of mean values. Statistical analyses for these data are shown in Table 6.

TABLE 5. *F* values and significance levels for standard least squares analysis of variance (ANOVA) of predawn water potential (Ψ_{pd}) and stomatal conductance (g_s).

Sources of variation	Blue, AZ	Pinedale, AZ	Grand Canyon, AZ	Zion, UT	Birdseye, UT	Tooele, UT
1993						
g_s						
Species	73.6***	49.3***	168.2***	81.5***	6.7**	115.7***
Sampling date	19.0***	0.7 NS	3.1 NS	22.3***	7.7**	12.1***
Date × species	3.6 NS	0.5 NS	0.5 NS	6.6**	3.9*	5.7*
Ψ_{pd}						
Species	11.5**	0.9 NS	51.4***	56.0***	8.7**	257.6***
Sampling date	15.7***	0.4 NS	20.8***	234.0***	4.0*	66.1***
Date × species	1.4 NS	0.9 NS	0.8 NS	17.6***	1.3 NS	3.9*
1994						
Ψ_{pd}						
Species	0.1 NS	6.2**	64.8***	18.8***	145.2***	219.3***
Sampling date	75.2***	16.9***	28.3***	24.6***	86.8***	65.1***
Date × species	1.7 NS	9.5***	4.2**	4.9**	19.3***	3.7 NS

Notes: Data are for *Quercus gambelii*, *Pinus edulis*, and *Juniperus osteosperma* from several sampling dates during the growing seasons of 1993 and 1994. Repeated-measures analysis was not performed on these data because different sets of replicate plants were measured through the course of the season at a given site.

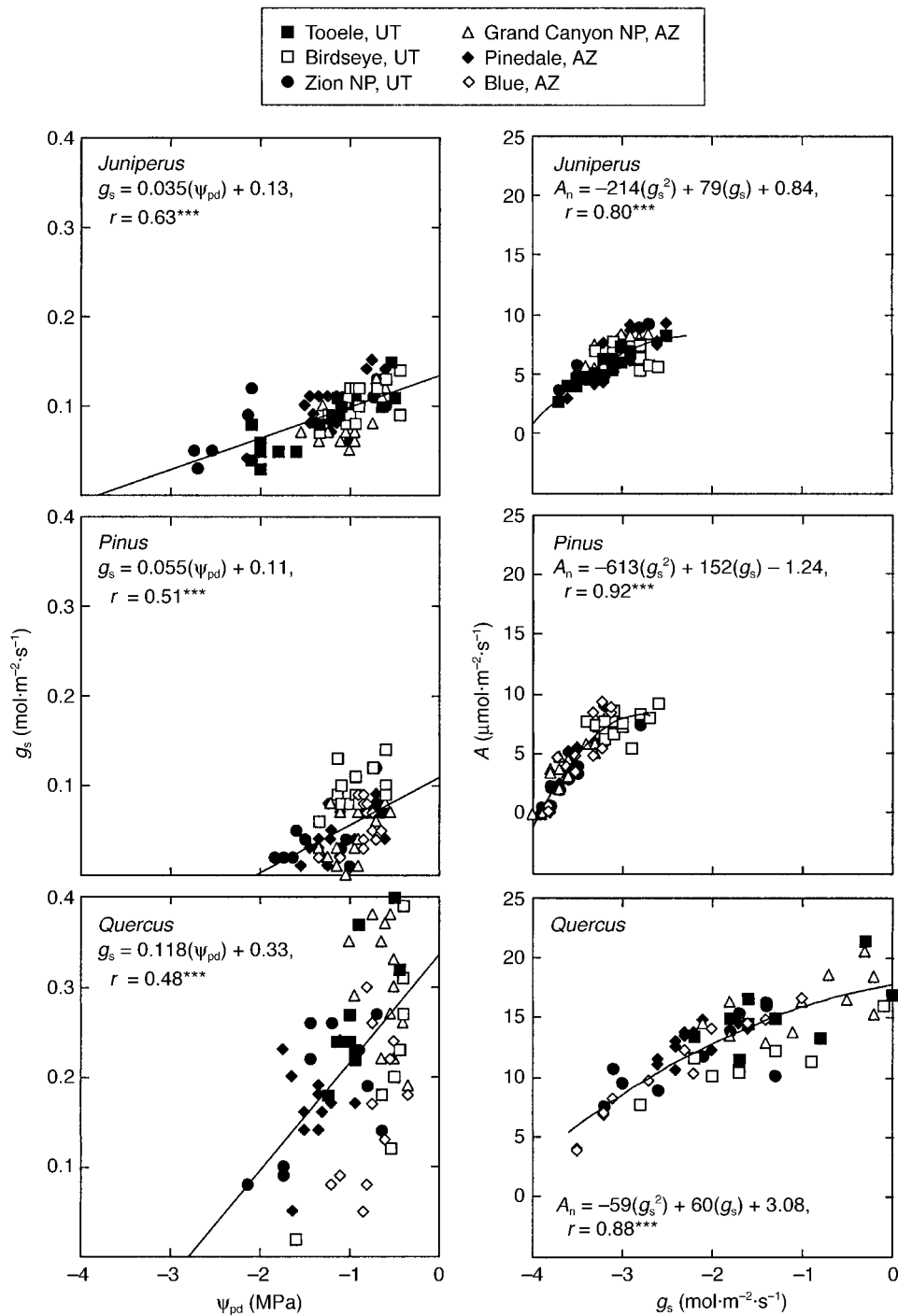* $P \leq 0.05$; ** $P \leq 0.01$; *** $P < 0.001$; NS, not significant.

Fig. 13. Relationships between stomatal conductance (g_s) and predawn water potential (Ψ_{pd}) (in left panels) and net assimilation (A) and g_s (in right panels) for *Juniperus osteosperma, Pinus edulis,* and *Quercus gambelii.* Data in each panel are from all sites and sampling periods during the 1993 growing season. Correlation coefficients (r) for the polynomial and linear regressions shown in each panel are significant: ***$P < 0.001$.

arid environments predictably would have high and seasonally unchanging predawn water potential values. Even predawn water potential values in *Quercus* dropped below -2 MPa at one of our sites indicating that roots are deployed only in the portion of the soil profile that undergoes seasonal drying. Third, groundwater depths at two Arizona sites (Blue and Pinedale, where groundwater δD values are problematic) are greater than 60 m (T. Subirege, U.S. Forest Service, *personal communication*). Mesquite (*Prosopis juliflora*) roots in the Sonoran Desert grow to a maximum depth of 53 m (Phillips 1963), and in the Kalahari Desert roots of woody perennials have been observed to 68 m (Jennings 1974). It is unlikely that species examined in our study produce roots to that depth. Furthermore, if *Pinus, Juniperus,* or *Quercus* did grow roots beyond 60 m, the contribution of groundwater from this depth to plant water balance presumably would be negligible, since no stem water δ values were consistent with groundwater values.

Overall, the evergreen conifers, *Pinus* and *Juniperus,* had greater capacity to use monsoon rains than did *Quercus,* the winter-deciduous angiosperm. Interspecific partitioning of water sources appears to be common among woody perennial species in arid and semiarid ecosystems and may reduce competition for soil water and promote species coexistence. Valentini et al. (1992) observed similar partitioning between *Juniperus* and *Quercus* for summer rain use in a European Mediterranean ecosystem. Differential capacities for summer rain use and soil moisture partitioning likewise have been observed among cold desert shrub species in Utah (Ehleringer et al. 1991, Donovan and Ehleringer 1994, Lin et al. 1996, Phillips and Ehleringer 1996) and between adult oak trees (*Quercus emoryi*) and C_4 perennial grasses in a savanna ecosystem in southern Arizona (Weltzin and McPherson 1997).

Pinus edulis is currently at the northwestern limits of its distribution at our Birdseye and Zion, Utah sites. In Great Basin pinyon–juniper communities to the west and northwest, this species is replaced by another pinyon pine, *Pinus monophylla,* which occurs at similar elevations and is associated with *Juniperus osteosperma.* The presence of interspecific hybrid populations between *Pinus monophylla* and *P. edulis* beyond the current northern limit of *P. edulis* (Lanner 1974) suggests that *P. edulis* has retreated southward within the last several hundred years. Ehleringer and Phillips (1996) argue that the distribution of relict oak hybrids between *Quercus turbinella* and *Q. gambelii* in northern Utah, together with ecophysiological responses of the parent species and hybrids, is evidence for recent (last 2000 yr) reductions in the intensity of monsoon rain inputs in northern Utah. The distribution of *Juniperus osteosperma* is not limited by the presence or absence of monsoon rainfall and can be found throughout the Great Basin where summer rains are infrequent or of low magnitude. Unfortunately, we have no information on the capacity for *J. osteosperma* to use moisture from infrequent summer storms in the Great Basin beyond our study sites in northern Utah. However, *Juniperus* populations at sites near the northwestern monsoon boundary in southern Utah and northern Arizona responded to our irrigations. The sharp decline in surface moisture use for this species near the monsoon boundary from our analysis of natural δD variation in northern Utah may have related more to patterns of surface moisture availability than to differences in the potential activity of surface roots, although summer precipitation occurred in both years of our study. Soil moisture at 10-cm depth declined abruptly north of the Grand Canyon site and mirrored patterns of natural summer rain use by *Juniperus.*

Pinus edulis is capable of using moisture from small rain events, but this species does not extend into the Great Basin region where use of summer rains is potentially critical for its survival through the extended summer dry period. Flanagan et al. (1992) noted that *Pinus edulis* was more sensitive to monsoon rains than was *Juniperus osteosperma* at a site near the Utah–Arizona border. Results from our irrigation experiment at Grand Canyon support this observation. Only 10% of xylem water in *Juniperus* compared to 15% in *Pinus* was derived from the small 10-mm irrigation at the Grand Canyon site in August, 1995. Surface roots of *Pinus* (but not of *Juniperus*), however, were inactive during August at the hotter Zion site. High soil temperature has been shown to promote root mortality (Hendrick and Pregitzer 1993), inhibit root elongation (Kramer and Kozlowski 1979, Drennan and Nobel 1998), and promotes high and costly rates of root respiration (Palta and Nobel 1989, Nobel et al. 1991, 1992). At the hotter Zion site *Pinus* used proportionally less moisture from the 25-mm irrigation in July than in September. Surface roots of *Pinus* either die and fail to regrow during the hot midsummer period or persist but remain inactive even after pulses of moisture move into the soil. The restricted geographic distribution of *Pinus edulis* may be controlled, at least partially, by high surface temperatures and reduced surface root activity in the Great Basin–Colorado Plateau transition area. Recent observations from a comparable irrigation study in a cold desert ecosystem in southern Utah also suggest that soil temperature is an important regulator of summer rain use. The shrubs *Artemisia filifolia, Atriplex canescens, Coleogyne ramosissima,* and *Vanclevea stylosa* took up more irrigation water in September than in July (Lin et al. 1996).

Another mechanism that may contribute to clinal variation in summer rain use involves the susceptibility of roots to xylem cavitation. Episodes of drought may limit surface water extraction by causing cavitation in primary surface roots. Vulnerability to drought cavitation in roots is known to vary among woody plants (Sperry and Saliendra 1994, Alder et al. 1996), and

recently has been shown to differ between *Juniperus osteosperma* and *Pinus edulis* (Linton et al. 1998).

Annual winter recharge of water to deeper soil layers partially accounts for interannual differences in monsoon season precipitation use by *Pinus* and *Juniperus*. Surface moisture use during summer was dampened in these conifers during a summer following a wet winter (1993) compared to that in the following year after a drier winter. Predawn water potential (Ψ_{pd}) was 0.5–1 MPa lower in *Pinus* and *Juniperus* during the driest part of 1994 than during the same period in 1993, reflecting differences between the two years in the magnitude of winter and spring recharge of the soil profile. Consequently, the amount of winter-derived water taken up by deep roots during the monsoon season potentially was greater in 1993 than in 1994, and may have contributed to interannual differences in δD for these two species at most or all of our study sites. Roots compete for limited plant carbon and respond to source–sink relationships (Eissenstat and Yanai 1997). Consequently, roots exploiting patches of deep moisture might grow at the expense of roots developing in shallow soil layers. Flanagan et al. (1992) similarly observed interannual differences for summer rain use by *Juniperus osteosperma* and *Pinus edulis* growing near our Zion site, but it was not clear if availability and isotopic composition of water deep in the soil profile varied between the two years in that study.

Comparisons between the δD of tree xylem sap and that of precipitation and soil water revealed that *Quercus* was capable of taking up water from shallow soil layers only at the two southern sites in eastern Arizona. The lack of response to monsoon precipitation by *Quercus* at the majority of our field sites suggests that this species is functionally deep rooted and its growth and productivity over the summer is dependent on moisture supplied by winter and spring precipitation penetrating to deep soil layers. Results from our irrigation experiments confirm this for two sites and support findings from other studies (Phillips and Ehleringer 1994, Ehleringer and Phillips 1996, Williams and Ehleringer 2000). Lin et al. (1996), likewise, found that *Chrysothamnus* in cold desert shrub communities were insensitive to summer rains. Our study revealed that *Quercus* significantly uses monsoon season precipitation from shallow soil layers at sites in eastern Arizona where this precipitation comprises a large fraction of mean annual precipitation. δD of xylem water and predawn water potential for *Quercus* increased following the onset of the summer rainy period at our Blue and Pinedale, Arizona sites. Furthermore, δD–δ¹⁸O relationships from 1993 confirmed that *Quercus* along with *Pinus edulis* were using predominantly water from upper soil layers at the Blue site. Interestingly, *Quercus gambelii* produces surface lateral roots even in northern Utah where uptake of summer rains do not occur (Clary and Tiedemann 1986, Phillips and Ehleringer 1994). Surface roots in *Q. gambelii* at sites in northern Arizona

and in Utah may function primarily for nutrient acquisition or for water uptake during the cool spring months, but have limited ability to take up water during the summer growing period.

Patterns of plant photosynthetic gas exchange, growth, and resource-use efficiency tend to reflect resource supply, and are linked to the amount and seasonal distribution of moisture available to plants of water-limited ecosystems (Smith and Nobel 1986, Chapin 1991, Comstock and Ehleringer 1992a). Plants with deep roots that have access to a relatively stable supply of soil moisture often experience lower levels of drought stress and maintain higher rates of gas exchange and higher c_i/c_a (ratio of leaf internal to ambient CO_2 concentration) than do plants with the majority of their roots deployed in periodically dry surface soil layers (Knapp and Fahenstock 1990, Flanagan et al. 1992, Donovan and Ehleringer 1994). Furthermore, Comstock and Ehleringer (1992b) demonstrated that populations of perennial plants growing during periods of high evaporative demand (summer monsoon season) develop leaves with high intrinsic water-use efficiency (low c_i/c_a) compared to populations growing at cooler periods of the year. Relationships between net photosynthetic rate (*A*) and stomatal conductance (g_s) differed among the woody perennial species in this study and correlated to use of summer rains. The initial portion of the curve relating *A* to g_s, however, was not greatly different between *Q. gambelii* and the two coniferous species in this study. What was different was the operational range of g_s for the three species; photosynthesis tended to be limited largely by low stomatal conductances in *Pinus* and *Juniperus* compared to that in *Quercus*.

Interspecies differences in this study for gas exchange traits correlate with patterns of leaf δ¹³C reported by Williams and Ehleringer (1996). Carbon isotope discrimination (Δ; Farquhar et al. 1989) measured at the same sites was greater (lower c_i/c_a) for *Q. gambelii* (20‰) than for *P. edulis* (14‰) and *J. osteosperma* (15‰). Correlations between leaf gas exchange traits, plant water potential, and plant water sources have been observed for species in other ecosystems (Flanagan et al. 1992, Valentini et al. 1992, Lin et al. 1996). One mechanism that potentially links water sources and gas exchange characteristics involves the role of stomata in preventing drought-induced xylem dysfunction in periodically water-limited environments (Tyree and Sperry 1989). Species or populations that rely on moisture in surface soil layers may be more susceptible to drought and will predictably have lower stomatal conductances such that cavitation is avoided. This appeared to be true for the different populations of *Q. gambelii* in our study and generally holds for the three species growing at any one site. Curiously, *Pinus edulis* is the most drought intolerant species of the three that we studied. *Pinus* is most vulnerable to drought-induced xylem cavitation (Sperry and Sullivan 1992,

Linton et al. 1998) and had the highest stomatal sensitivity to tissue water potential (Linton et al. 1998, Fig. 13).

In short, there appear to be no general "syndromes" of ecophysiological response to summer rains in the pinyon–juniper woodland ecosystems. Long-lived shallow-rooted species that use summer rains for photosynthetic gas exchange and growth (e.g., *Pinus edulis* and *Juniperus osteosperma*) are not necessarily more tolerant to tissue water deficits than are deeply rooted species that do not use summer rains (e.g., *Quercus gambelii*). Thus, the link between ecosystem water balance and seasonal patterns of photosynthetic gas exchange depends on the unique assemblage of dominant plants in these woodlands. Threshold patterns of intraspecific variation for use of soil moisture from summer "monsoon" rains, furthermore, should be considered in models of community change in the expansive pinyon–juniper ecosystem.

LITERATURE CITATIONS

Adang, T. C., and R. L. Gall. 1989. Structure and dynamics of the Arizona monsoon boundary. Monthly Weather Review **117**:1423–1438.

Alder, N. N., J. S. Sperry, and W. T. Pockman. 1996. Root and stem xylem embolism, stomatal conductance, and leaf turgor in *Acer grandidentatum* populations along a soil moisture gradient. Oecologia **105**:293–301.

Allison, G. B., C. J. Barnes, and M. W. Hughes. 1983. The distribution of deuterium and ^{18}O in dry soils 2. Experimental. Journal of Hydrology **64**:377–379.

Betancourt, J. L., T. R. Van Devender, and P. S. Martin. 1990. Packrat middens: the last 40,000 years of biotic change. Chihuahuan Desert: vegetation and climate. University of Arizona Press, Tucson, Arizona, USA.

Brunel, J.-P., G. R. Walker, and A. K. Kennett-Smith. 1995. Field validation of isotopic procedures for determining sources of water used by plants in a semi-arid environment. Journal of Hydrology **167**:351–368.

Bryson, R. A., and R. P. Lowry. 1955. Synoptic climatology of the Arizona summer precipitation singularity. Bulletin of the American Meteorological Society **36**:329–339.

Caldwell, M. M., and J. H. Richards. 1986. Competing root systems: morphology and models of absorption. Pages 251–273 *in* T. J. Givnish, editor. On the economy of plant form and function. Cambridge University Press, Cambridge, UK.

Canadell, J., R. B. Jackson, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E.-D. Schulze. 1996. A global review of rooting patterns. II. Maximum rooting depth. Oecologia **108**:583–595.

Chapin, S. F., III. 1991. Integrated responses of plants to stress: a centralized system of physiological responses. BioScience **41**:29–36.

Clary, W. P., and A. R. Tiedemann. 1986. Distribution of

biomass in small tree and shrub form *Quercus gambelii* stands. Forest Science **32**:234–242.

Coleman, M. L., T. J. Shepard, J. J. Durham, J. E. Rouse, and G. R. Moore. 1982. Reduction of water with zinc for hydrogen isotope analysis. Analytical Chemistry **54**:993–995.

Comstock, J. P., and J. R. Ehleringer. 1992*a*. Plant adaptation in the Great Basin and Colorado Plateau. The Great Basin Naturalist **52**:195–215.

Comstock, J. P., and J. R. Ehleringer. 1992*b*. Correlating genetic variation in carbon isotopic composition with complex climatic gradients. Proceedings of the National Academy of Sciences **89**:7747–7751.

Craig, H. 1961. Isotopic variations in meteoric waters. Science **133**:1702–1703.

Dawson, T. E. 1996. Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: the roles of tree size and hydraulic lift. Tree Physiology **16**:263–272.

Dawson, T. E., and J. R. Ehleringer. 1998. Plants, isotopes, and water use: A catchment-scale perspective. Pages 165–202 *in* C. Kendall and J. J. McDonnell, editors. Isotope tracers in catchment hydrology. Elsevier Science B.V., Oxford, UK.

Dawson, T. E., and J. S. Pate. 1996. Seasonal water uptake and movement in root systems of Australian phreatophytic plants of dimorphic root morphology: a stable isotope investigation. Oecologia **107**:13–20.

Donovan, L. A., and J. R. Ehleringer. 1994. Water stress and use of summer precipitation in a Great Basin shrub community. Functional Ecology **8**:289–297.

Drennan, P. M., and P. S. Nobel. 1998. Root growth dependence on soil temperature for *Opuntia ficus-indica*: influences of air temperature and a doubled CO_2 concentration. Functional Ecology **12**:959–964.

Ehleringer, J. R., and T. E. Dawson. 1992. Water uptake by plants: perspectives from stable isotope composition. Plant Cell and Environment **15**:1073–1082.

Ehleringer, J. R., R. D. Evans, and D. Williams. 1998. Assessing sensitivity to change in desert ecosystems—a stable isotope approach. Pages 223–237 *in* H. Griffiths, editor. Stable isotopes integration of biological, ecological, and geochemical processes. BIOS Scientific Publishers, Oxford, UK.

Ehleringer, J. R., and C. B. Osmond. 1989. Stable isotopes. Pages 281–300 *in* R. W. Pearcy, J. Ehleringer, H. A. Mooney, and P. W. Rundel, editors. Plant physiological ecology. Field methods and instrumentation. Chapman & Hall, London, UK.

Ehleringer, J. R., and S. L. Phillips. 1996. Ecophysiological factors contributing to the distributions of several *Quercus* species in the intermountain west. Annals of Forest Science **53**:291–302.

Ehleringer, J. R., S. L. Phillips, W. S. F. Schuster, and D. R. Sandquist. 1991. Differential utilization of summer rains by desert plants. Oecologia **88**:430–434.

Eissenstat, D. M., and R. D. Yanai. 1997. The ecology of root lifespan. Advances in Ecological Research **27**:1–60.

Evans, R. D., and J. R. Ehleringer. 1994. Water and nitrogen dynamics in an arid woodland. Oecologia **99**:233–242.

Farquhar, G. D., J. R. Ehleringer, and K. T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. Annual Revue of Plant Physiology and Plant Molecular Biology **40**:503–537.

Field, C. B., C. P. Lund, N. R. Chiariello, and B. E. Mortimer. 1997. CO_2 effects on the water budget of grassland microcosm communities. Global Change Biology **3**:197–206.

Flanagan, L. B., J. R. Ehleringer, and J. D. Marshall. 1992. Differential uptake of summer precipitation among co-oc-

curring trees and shrubs in a pinyon–juniper woodland. Plant, Cell and Environment **15**:831–836.

Fowler, N. 1986. The role of competition in plant communities in arid and semi-arid regions. Annual Review of Ecology and Systematics **17**:89–110.

Franco, A. C., and P. S. Nobel. 1990. Influences of root distribution and growth on predicted water uptake and interspecific competition. Oecologia **82**:151–157.

Friedman, I., G. I. Smith, J. D. Gleason, A. Warden, and J. M. Harris. 1992. Stable isotope composition of waters in southeastern California. I. Modern precipitation. Journal of Geophysical Research **97**:5795–5812.

Gregg, J. 1991. The differential occurrence of the mistletoe, *Phoradendron juniperinum,* on its host, *Juniperus osteosperma,* in the Western United States. Thesis. University of Utah, Salt Lake City, Utah, USA.

Hendrick, R. L., and K. S. Pregitzer. 1993. Patterns of fine root mortality in two sugar maple forests. Nature **361**:59–61.

Houghton, J. T., L. G. Miera Filho, B. A. Callander, N. Harris, A. Kattenberg, and K. Maskell. 1996. Climate change 1995: the science of climate change. Published for the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Ingraham, N. L., B. F. Lyles, R. L. Jacobson, and J. W. Hess. 1991. Stable isotopic study of precipitation and spring discharge in southern Nevada. Journal of Hydrology **125**:243–258.

International Atomic Energy Agency (IAEA). 1995. Reference and intercomparison materials for stable isotopes of light elements. Proceedings of a Consultants Meeting held in Vienna, 1–3 December 1993. IAEA-TECDOC-825, IAEA, Vienna, Austria.

Jackson, R. B., J. Canadell, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E.-D. Schulze. 1996. A global review of rooting patterns. I. Root distribution by depth for terrestrial biomes. Oecologia **108**:389–411.

Jennings, C. M. H. 1974. The hydrology of Botswana. Dissertation. University of Natal, Pietermartizburg, South Africa.

Knapp, A. K., and J. T. Fahnestock. 1990. Influence of plant size on the carbon and water relations of *Cucurbita foetidissima* HBK. Functional Ecology **4**:789–797.

Kramer, P. J., and T. T. Kozlowski. 1979. Physiology of woody plants. Academic Press, New York, New York, USA.

Lanner, R. M. 1974. Natural hybridization between *Pinus edulis* and *Pinus monophylla* in the American Southwest. Silvae Genetica **23**:108–116.

Lin, G., S. Phillips, and J. R. Ehleringer. 1996. Monsoonal precipitation responses of shrubs in a cold desert community of the Colorado Plateau. Oecologia **106**:8–17.

Linton, M. J., J. S. Sperry, and D. G. Williams. 1998. Limits to water transport in *Juniperus osteosperma* and *Pinus edulis*: implications for drought tolerance and regulation of transpiration. Functional Ecology **12**:906–911.

Little, E. L. 1971. Atlas of United States trees. Miscellaneous Publication Number 1146, U.S. Department of Agriculture, Washington, D.C., USA.

Milne, W. K., L. V. Benson, and P. W. McKinley. 1987. Isotope content and temperature of precipitation in southern Nevada, August 1983–August 1986. U.S. Geological Survey Open-File Report **87–463**.

Mitchell, J. M. 1990. Climatic variability—past, present, and future. Climate Change **16**:231–246.

Mitchell, V. L. 1976. The regionalization of climate in the western United States. Journal of Applied Meteorology **15**:920–977.

Neilson, R. P. 1986. High-resolution climatic analysis and southwest biogeography. Science **232**:27–34.

Neilson, R. P. 1995. A model for predicting continental-scale vegetation distribution and water balance. Ecological Applications **5**:362–385.

Nobel, P. S., D. M. Alm, and J. Cavelier. 1992. Growth respiration, maintenance respiration and structural carbon costs for roots of three desert succulents. Functional Ecology **6**:79–85.

Nobel, P. S., F. B. Lopez, and D. M. Alm. 1991. Water uptake and respiration of root systems of two cacti: observations and predictions based on individual roots. Journal of Experimental Botany **42**:1215–1223.

Palta, J. A., and P. S. Nobel. 1989. Root respiration for *Agave deserti*: influence of temperature, water status and root age on daily patterns. Journal of Experimental Botany **40**:181–186.

Phillips, S. L., and J. R. Ehleringer. 1994. Limited uptake of summer precipitation by bigtooth maple (*Acer grandidentatum* Nutt) and Gambel's oak (*Quercus gambelii* Nutt). Trees **9**:214–219.

Phillips, W. S. 1963. Depth of roots in soil. Ecology **44**:424.

Potvin, C., M. J. Lechowicz, and S. Tardif. 1990. The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. Ecology **71**:1389–1400.

SAS Institute. 1995. JMP user's guide, version 3.1 JMP. SAS Institute, Cary, North Carolina, USA.

Schimel, D. S. 1993. Population and community processes in the response of terrestrial ecosystems to global change. Pages 45–54 *in* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic interactions and global change. Sinauer Associates, Sunderland, Massachusetts, USA.

Schlesinger, M. E., and J. F. B. Mitchell. 1987. Climate model simulations of the equilibrium climatic response to increased carbon dioxide. Reviews of Geophysics **25**:760–798.

Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Heunneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford. 1990. Biological feedbacks in global desertification. Science **247**:1043–1048.

Schulze, E.-D., H. A. Mooney, O. E. Sala, E. Jobaggy, N. Buchmann, G. Bauer, J. Canadell, R. B. Jackson, J. Loreti, M. Osterheld, and J. R. Ehleringer. 1996. Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. Oecologia **108**:389–411.

Smith, S., and P. Nobel. 1986. Deserts. Pages 13–62 *in* N. R. Baker and S. P. Long, editors. Photosynthesis in contrasting environments. Elsevier Science Publishers B.V., Amsterdam, The Netherlands.

Snyder, K. A., D. G. Williams, and V. L. Gempko. 1998. Water source determination for cottonwood, willow and mesquite in riparian forest stands. Pages 185–188 *in* E. F. Wood, A. G. Chebouni, D. C. Goodrich, D. J. Seo, and J. R. Zimmerman, technical coordinators. Proceedings from the special symposium on hydrology. American Meteorological Society, Boston, Massachusetts, USA.

Socki, R. A., H. R. Karlsson, and E. K. J. Gibson. 1992. Extraction technique for the determination of Oxygen-18 in water using preevacuated glass vials. Analytical Chemistry **64**:829–831.

Spaulding, W. G., and L. J. Graumlich. 1986. The last pluvial climatic episodes in the deserts of southwestern North America. Nature **320**:441–444.

Sperry, J. S., and N. Z. Saliendra. 1994. Intra- and inter-plant variation in xylem cavitation in *Betula occidentalis*. Plant, Cell and Environment **17**:1233–1241.

Sperry, J. S., and E. M. Sullivan. 1992. Xylem embolism in response to freeze–thaw cycles and water stress in ring-porous, diffuse porous, and conifer species. Plant Physiology **100**:605–613.

Stephenson, N. L. 1990. Climatic control of vegetation dis-

tribution: the role of the water balance. The American Naturalist **135**:649–670.

Stine, S. 1994. Extreme and persistent drought in California and Patagonia during medieval time. Nature **369**:546–549.

Tyree, M. T., and J. S. Sperry. 1989. Vulnerability of xylem to cavitation and embolism. Annual Review of Plant Physiology and Plant Molecular Biology **40**:19–38.

Valentini, R., G. E. S. Mugnozza, and J. R. Ehleringer. 1992. Hydrogen and carbon isotope ratios of selected species of a mediterranean macchia ecosystem. Functional Ecology **6**:627–631.

Van Devender, T. R., and W. G. Spaulding. 1979. Development of vegetation and climate in the southwestern United States. Science **204**:701–710.

Weltzin, J. F., and G. R. McPherson. 1997. Spatial and temporal soil moisture resource partitioning by trees and grasses in a temperate savanna, Arizona, USA. Oecologia **112**: 156–164.

West, N. E. 1988. Intermountain deserts, shrub steppes, and woodlands. Pages 209–230 *in* M. G. Barbour and W. D. Billings, editors. North American terrestrial vegetation. Cambridge University Press, Cambridge, UK.

White, J. W. C., E. R. Cook, J. R. Lawrence, and W. S. Broecker. 1985. The D/H ratios of sap in trees: implications for water sources and tree ring D/H ratios. Geochimica et Cosmochimica Acta **49**:237–246.

Williams, D. G., and J. R. Ehleringer. 1996. Carbon isotope discrimination in three semi-arid woodland species along a monsoon gradient. Oecologia **106**:455–460.

Williams, D. G., and J. R. Ehleringer. 2000. Carbon isotope discrimination and water relations in oak hybrid populations in southwestern Utah. Western North American Naturalist **60**:121–129.