

MEDITERRANEAN CLIMATE EFFECTS. I. CONIFER WATER USE ACROSS A SIERRA NEVADA ECOTONE¹

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Xylem water potential of the midelevation conifers *Pinus jeffreyi*, *Pinus lambertiana*, *Abies concolor*, and *Calocedrus decurrens*, the higher elevation *Pinus monticola* and *Abies magnifica*, and co-occurring evergreen angiosperm shrubs, together with soil moisture under these plants, were monitored at three sites on the Kern Plateau in the southernmost Sierra Nevada Range of California. Site locations spanned the ecotone between the mid- and upper montane forests at elevations of 2230–2820 m. Measurements were made through a low-snowfall year and a heavy-snowfall year.

In the Mediterranean climate of the Sierra Nevada, the heavy winter snowpack persists into late spring, after precipitation has effectively stopped. We found the subsequent depletion of soil moisture due to plant water uptake to result in predawn xylem water potentials for conifers more negative by 0.6–1.4 MPa than those for shrubs or inferred soil potentials. Shrubs generally depleted soil moisture more rapidly and ultimately extracted a greater fraction of the available soil moisture than did the conifers. This depletion of soil moisture by shrubs, particularly *Arctostaphylos patula*, may limit conifer growth and regeneration by prematurely terminating growth on the shallow soils studied. The conifers all generally showed similar patterns of soil moisture use, except that *A. magnifica* extracted moisture more rapidly early in the season.

Key words: *Abies*; *Arctostaphylos*; competition; conifer; drought; *Pinus*; shrub; snowpack.

The montane Mediterranean climate of the Sierra Nevada mountain range of California is characterized by heavy winter precipitation and an extended summer drought (Major, 1990). An ecotone between the midmontane forest and upper montane forest of the Sierra is marked by a major discontinuity in the distribution of tree, shrub, and forb species (Mellmann-Brown and Barbour, 1995; Barbour and Minnich, 2000). The overall objective of the work reported in this and in a companion paper in this issue (Royce and Barbour, 2001) was increased understanding of environmental factors and their interactions affecting conifer species distribution across this ecotone.

The midmontane–upper montane ecotone is typically a 250 m wide zone of elevations. In the southernmost Sierra Nevada (south of Sequoia National Park) and in the Transverse Range (adjoining the Sierra to the southwest) it occurs at elevations where winter precipitation changes from predominantly rain to predominantly snow with increased elevation (Kunz, 1988; Barbour et al., 1991; cf. Minnich, 1986), between 2200 and 2800 m. Snowpack in the upper montane forest is deep (>2 m), but temperatures are mild, compared to continental mountain ranges (Baker, 1944).

During summer months, a scarcity of precipitation leads to a moisture deficit, particularly in the southern Sierra (Kruse, 1990; Parker, 1994)—even at cool, high elevations (Major, 1990). This drought is a normal event, though its intensity varies with exposure, elevation, and year. It occurs even though total annual precipitation, falling mostly in winter, is

well in excess of potential annual evapotranspiration (Major, 1990). This montane Mediterranean climate occurs in the mountains of Morocco, Spain, and Turkey (Walter, 1984). It also occurs in the mountains of northwest California and southwest Oregon, but not in other North American mountain ranges (Baker, 1944).

The midmontane (mixed conifer) forest is a somewhat open four-layer community (Barbour and Minnich, 2000). On slopes of the southernmost Sierra Nevada both the overstory and understory are dominated by yellow pine (*Pinus ponderosa* Laws or *Pinus jeffreyi* Grev. & Balf.), Sierra white fir (*Abies concolor* Gordon & Glend. var. *lowiana* (Gordon) Murray), sugar pine (*Pinus lambertiana* Douglas), incense cedar (*Calocedrus decurrens* (Torry) Florin), and black oak (*Quercus kelloggii* Newb.). A patchy shrub canopy includes species of *Arctostaphylos*, *Ceanothus*, and *Quercus*, and numerous understory forbs are seasonally common in open areas. (Nomenclature follows the Jepson Manual [Hickman, 1993].)

The upper montane (red fir) forest is a simpler, two-layer community (Barbour and Woodward, 1985). In the southernmost Sierra it is dominated by Shasta red fir (*Abies magnifica* Murray var. *shastensis* Lemmon) and western white pine (*Pinus monticola* Douglas) and includes a minor forb understory. Although commonly a more closed community than the midmontane forest, the upper montane forest canopy opens near the ecotone, and shrubs such as *Chrysolepis sempervirens* (Kellogg) Hjelmq. may be locally dense.

Sites near and within the ecotone, such as those in this study, are of a woodland character, with 20–30% overstory cover and sometimes with extensive shrub or forb cover where trees are absent. The ecotone forest is marked by the co-occurrence of the dominants *P. jeffreyi*, *A. concolor*, *A. magnifica*, and sometimes *P. monticola*, together with shrubs from both the mid- and upper montane communities.

The objective of this study was to identify and quantify species-specific differences in patterns of water use in response to the seasonal climate of the Sierra Nevada and to identify how these differences might influence conifer species distri-

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bution. We report measurements of the seasonal progression of soil and plant water status in the relatively unstudied southernmost Sierra, where the summer drought is most severe (Parker, 1994). A Mediterranean climate is unusual for coniferous forests, and most understanding of the ecophysiology of conifers is for climates with wetter summers and/or colder temperatures.

SITE CHARACTERISTICS AND METHODS

Research sites—All measurements were made at field sites on the Kern Plateau in the southernmost Sierra Nevada. The 100-km² study area was located around 36°00' N and 118°18' W, in Sequoia National Forest ~70 km south of Sequoia National Park. Measurements were made through the 1994 and 1995 seasons every 2–3 wk, from the date of local snow melt, typically in May, to the first fall storm, typically in October or November. Fortunately, these two seasons offered near extreme conditions (based on a subjective review of snow sensor records extending over 20–25 yr, California Data Exchange Center, <http://cdec.water.ca.gov>). The winter of 1994 began a drought year in California, with a seasonal precipitation 75% of normal and a snowpack on 1 April 55% of normal in the southern Sierra, leading to an early onset of an extended summer drought. The winter of 1995 saw seasonal precipitation 160% of normal and a snowpack on 1 April 185% of normal, leading to an unusually late onset of the summer drought (California Department of Water Resources, 1994–1995; normals based on records extending back up to 50 yr).

Approximate boundaries of the ecotone were determined by a vegetation survey of 167 sites, in preparation for the selection of three permanent research sites for the present study. One of these permanent sites was located below (elevation 2230 m) and another above (elevation 2820 m) the ecotone. Site vegetation was typical for their elevation and general location, and sites were selected with as many tree species as possible present. These sites generally showed little sign of human disturbance. However, the frequent heavy shrub cover was, in part, probably the result of many years of fire suppression, and forb and grass coverage was probably reduced from continued cattle grazing. The third permanent site was located at an elevation of 2700 m, within the ecotone. This site had been logged selectively and lightly a number of years earlier, but large trees were still present, and extensive patches of several shrub species were present.

All permanent sites were on level ridge-tops and were typically 100–200 m across. Sites were rocky, with poorly developed soils (sandy to loamy entisols or inceptisols) and with soil parent rock the common southern Sierra granodiorite. The depth to parent rock varied over 50–170 cm at differing locations at each site, based on our experience drilling neutron probe holes. Except immediately near the surface, the soils were quite compact, being formed from in-place decomposition of the parent rock. Some roots probably penetrated fractures in the parent rock (cf. Zwieniecki and Newton, 1994, 1996), but we could not verify the extent of such fracturing or penetration. (The first two sites are the sites designated “A” and “B,” respectively, on Fig. 1 of the companion paper [Royce and Barbour, 2001], while the third site is located on the ridge separating the two sites designated “Y” on that figure.)

At each site one or two mature trees of each species present were selected, generally the largest visibly healthy specimens at the site, with reachable foliage to permit cutting specimens for water potential measurements. These trees were selected with immediate neighbors of the same species, so that neutron probe soil moisture measurements under them could be associated with that species.

Environmental conditions—On-site temperatures were measured using maximum–minimum thermometers, and a funnel-type bulk rain gage was mounted in an open location near the thermometer enclosure at each site (Royce and Barbour, 2001). Data from a continuous recording weather station (Pascoe) located ~2 km from the highest site and at a comparable elevation were used to fix the timing of storms occurring between site visits. The timing of snow melt on each site was fixed with more frequent site visits at critical

times in the late spring. Environmental measurements were continued through the 1996 season, a near normal water year.

Soil moisture—Soil water content was monitored with a neutron-scattering probe (CPN Company, Martinez, California, USA, model 503 Hydroprobe; Kramer and Boyer, 1995; Brady and Weil, 1996). Access holes were between 50 and 170 cm deep, 5 cm in diameter, and lined with thin-walled aluminum irrigation pipe. Standard probe depths used in the measurements were 20, 40, 70, 100, and 150 cm, where permitted.

Single neutron probe holes were drilled at the drip line under mature trees: *A. concolor*, *P. jeffreyi*, *P. lambertiana*, *C. decurrens*, and *Q. kelloggii* at the low site; *A. magnifica* and *P. monticola* at the high site; and *A. concolor*, *A. magnifica*, and *P. jeffreyi* at the ecotone site. Holes were drilled beneath a patch of the shrub *Arctostaphylos patula* Greene (greenleaf manzanita) at the low site, beneath a patch of the shrub *C. sempervirens* (bush chinquapin) at the high site, and beneath patches of the shrubs *A. patula*, *C. sempervirens*, *Ceanothus cordulatus* Kellogg (mountain whitethorn), and *Cercocarpus ledifolius* Nutt. (curl-leaf mountain-mahogany) at the ecotone site.

The presence of numerous rocks and stones in the immediate vicinity of each access hole resulted in neutron counts varying by as much as 50% at different depths in the same hole or between holes, under what should have been water saturation conditions. This variation required that the probe be calibrated in situ at each depth station in each hole. This was accomplished by assuming that the soil was saturated with water as the snow melted and that rapid draining of gravitational water at the end of snowmelt led to a field capacity some 3 d after that date. All moisture measurements were then reported in terms of this field capacity, as a soil moisture fraction (SMF), rather than in absolute terms. This calibration was estimated to have an uncertainty ~5%.

Xylem water potential—Predawn xylem water potential was monitored for all trees studied in 1994 and 1995 and for all shrub species studied in 1995. In addition to the trees and shrub species for which soil moisture was measured, water potentials were measured on the shrubs *Ceanothus pinetorum* Cov. (Kern ceanothus) and *C. cordulatus* at the low site and *C. pinetorum* and *Ribes cerium* Douglas (squaw or wax current) at the ecotone site. Midday xylem water potential was also monitored on trees in 1994.

Measurements in the field used a Scholander pressure chamber and were made on needle- or leaf-covered twigs for the firs, incense cedar, and shrubs, and on single fascicles for the pines. Change in measured water potential resulting from transpiration from these small specimens was prevented by sealing the specimen in the pressure chamber within 30 sec after cutting. Additionally, mid-day cuttings were bagged in plastic covered with aluminum foil at least an hour before cutting, to induce stomatal closure. Bleeding from resin canals was distinguished from the emergence of xylem water by its location on the stem cross section. Otherwise, the recommendations of Ritchie and Hinckley (1975) were generally followed. The accuracy of these measurements was estimated as ± 0.1 MPa (cf. Waring and Cleary, 1967).

Water potential measurements were also made on trees and shrubs at four additional permanent sites within the ecotone, in conjunction with growth measurements reported in the companion paper (Royce and Barbour, 2001). Summary statistics on water potentials reported here include data from these sites and data from saplings and pole-sized trees at all permanent sites, in order to improve the strength of the statistical analyses. Analyses were carried out using JMP (SAS Institute, 1995). Method details are given elsewhere (Royce, 1997).

RESULTS

Environmental conditions—Month-long temperature differences of up to 10°C between the years 1994 and 1995 were seen in maximum–minimum temperature records across the study area at times during the measurement periods. The heavy snowfall in the winter of 1995 shifted snow melt later by ~30 d, compared to 1994. Spring temperatures in 1995, particularly minima, were depressed compared to 1994, and the entire pro-

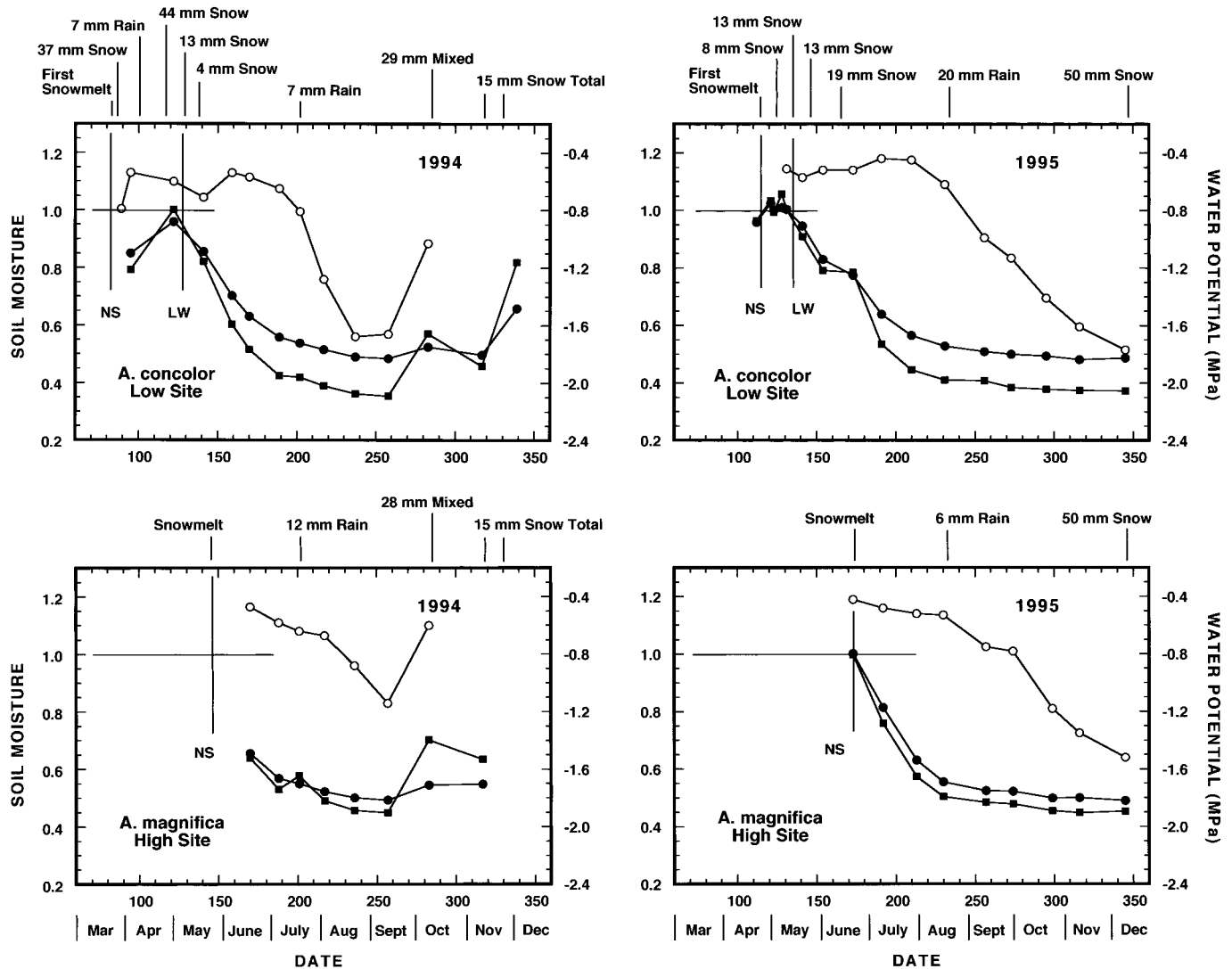


Fig. 1. Contrasting patterns of soil moisture depletion under the low-elevation conifer *Abies concolor* and the high-elevation conifer *A. magnifica* in the light snow year 1994 and the heavy snow year 1995. Data for the other conifers studied are similar (Royce, 1997). “Soil moisture” is the soil moisture fraction (SMF), soil moisture content as a fraction of field capacity. Near-surface measurements at a depth of 20 cm (filled squares) and average of measurements at depths of ≥ 40 cm (filled circles) are shown. Also shown is the average predawn xylem water potential (open circles) for these trees. In the precipitation chronology shown at the top of each graph, snowfall amounts are measured as water content. The no-snow (NS) and last-water (LW) dates are marked by vertical lines.

gression of temperatures was shifted later by ~ 30 d (Fig. 3 and discussion in the companion paper [Royce and Barbour, 2001]).

We defined a no-snow date as the earliest spring date on which two-thirds of the ground at a site was free of snow, drifts typically remaining in shaded spots. If late spring snow or rain storms brought substantial additional water to a site, we defined a last-water date as the last date when the soil column was saturated with water. This was the date when uninterrupted soil drying began due to evaporation and transpiration. Uncertainty in the estimation of the no-snow and last-water dates was probably ± 3 d.

A less sharply defined low-moisture date, typically 60 d after the last-water date, marked the transition from a spring growth period to the summer drought period. Appreciable precipitation between the no-snow and low-moisture dates, the growth period, fell at the low-elevation site with its early no-

snow date. For the higher elevation sites, with later snow melt, most of this precipitation fell before their no-snow dates and did not contribute to a growth-period total. As a result, the total growth-period precipitation was strongly correlated with no-snow date ($r = -0.69$). This growth-period precipitation extended the growth period by delaying the onset of the summer drought. Total drought period precipitation, falling between the low-moisture date and the first major fall storm, was only 23 mm averaged over all sites (precipitation data for 1994–1996, six sites, $N = 18$).

Soil moisture—Soil moisture (SMF) approximately followed an exponential depletion curve (Fig. 1). Soil at shallow depth (20 cm) was more rapidly and completely depleted of water than were deeper layers. Early in the season there was sometimes a more rapid depletion of water at the 40- and 70-

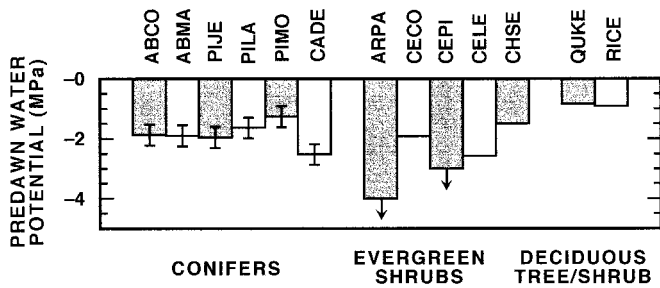


Fig. 2. Most negative predawn xylem water potentials observed at the end of the summer drought. Tree species: ABCO = *Abies concolor*; ABMA = *A. magnifica*; PIJE = *Pinus jeffreyi*; PIMO = *P. monticola*; CADE = *Calocedrus decurrens*; QUKE = *Quercus kelloggii*. Shrub species: ARPA = *Arctostaphylos patula*; CECO = *Ceanothus cordulatus*; CEPI = *Ceanothus pinnatus*; CELE = *Cercocarpus ledifolius*; CHSE = *Chrysolepis sempervirens*; RICE = *Ribes cereum*. Values indicated for *A. patula* and *C. pinnatus* correspond to the maximum pressure that could be reliably achieved in the pressure chamber. Actual xylem water potentials were probably more negative than indicated by these values.

cm levels, as compared to water from 100 cm and below. (Cf. Ziemer, 1978; Running, 1980; or Arkley, 1981.)

Water potential—When water was plentiful shortly after snow melt, predawn xylem water potentials were roughly independent of soil moisture. Predawn potentials declined more rapidly than soil moisture after there had been depletion of soil moisture, typically to SMF ≤ 0.6 . By this time, moisture depletion had slowed markedly. In late summer, when soil moisture depletion had nearly stopped, predawn water potentials continued to become more negative, minimum values (Fig. 2) occurring just before the first fall storm.

The diurnal fall of water potentials from predawn to more negative values at midday under drought conditions was not as great as the corresponding fall under nondrought conditions, the regression of midday potentials against predawn potentials yielding regression line slopes < 1.00 (Fig. 3). Differences in these slopes between species were not significant. Mean differences between midday and predawn values were also comparable for all species, except that the two five-needle haploxylon pines, *P. lambertiana* and *P. monticola*, showed only about half the value for the other conifers. These two conifers also did not reach midday potentials as negative in late summer as did other conifers, while *C. decurrens* reached substantially more negative potentials than the other conifers (Fig. 2).

ANALYSIS

Soil moisture—Soil desiccation at 20 cm (Fig. 1) was excessive as compared to desiccation at greater depth probably caused, at least in part, by evaporation. (The density of roots encountered in drilling the probe access holes and in other excavations did not appear to be greater at 20 cm as compared to deeper.) At greater depths plant water use should have been the main mechanism of soil moisture depletion. Under a deciduous *Q. kelloggii*, soil moisture depletion was substantially less than that under the conifers until the oak developed a new canopy of leaves, consistent with the model that soil moisture depletion at 40 cm and below was due mainly to transpiration. Ziemer (1963, 1964, 1978) has also shown data that are most consistent with soil moisture depletion at depth being due al-

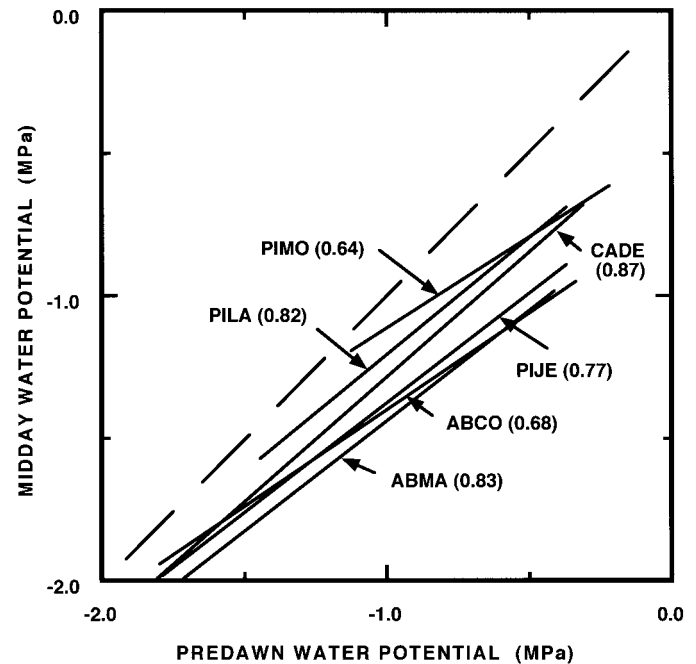


Fig. 3. Regressions of midday water potential on predawn water potential for all conifers studied. The dashed line indicates midday potential equal to predawn potential. Numbers in parentheses are regression line slopes. Species abbreviations are as in Fig. 2.

most entirely to forest plant water uptake. (Cf. Oren and Sheriff, 1995.)

In order to compare soil-moisture depletion rates between individuals and species, the depletion rate was modeled by the quadratic expression

$$-dx/dt = s(x - c) [1 - (x + c) / (2q)] \quad (1)$$

where x is the SMF averaged over all depths ≥ 40 cm. The change in the depletion rate with soil moisture is then

$$d(-dx/dt) / dx = s(1 - x/q). \quad (2)$$

Integration of Eq. 1 over time yields the following expression for the depletion of soil moisture as a function of the Julian date ($= t$, time)

$$x = q - (q - c) \tanh [s(q - c)(t - t_1) / (2q)] \quad (3)$$

where the constant t_1 is given by the expression

$$t_1 = t_0 - \{2q / [s(q - c)]\} \operatorname{arctanh} [(q - 1) / (q - c)]. \quad (4)$$

In this model, SMF is initially unity on the date $t = t_0$ and declines to a limiting value given by the parameter c . If the shape-controlling parameter q is large, the model reduces to one of simple exponential decay, where the depletion rate is proportional to the available moisture remaining ($x - c$), constantly declining as moisture is depleted. The quantity $s(1 - c)$ is then the initial rate of depletion, and s is the coefficient appearing in the exponent of the exponential. For $q = 1$, on the other hand, the depletion rate is initially constant, then declining more slowly than in the exponential case as moisture depletion takes place. A constant depletion rate might correspond to evaporation or transpiration from a free water surface of constant area, as would be the case in the absence of stomatal control.

The model assumes that there is no substantial input of

moisture due to precipitation during the depletion cycle. Since daily evapotranspiration in the absence of drought stress was probably ~2 mm/d with transpiration reduced by stomatal closure during the summer (Royce, 1997), at most the observed average drought-period total precipitation of 23 mm could have made only a minor contribution to replenishing deep soil moisture. Furthermore, during the period of our observations, summer storms each yielded only a few millimeters of precipitation, this precipitation only wetted the surface of leaves or soil, and most appeared to have been lost to direct evaporation by the next day. Localized heavier summer rainfall does occur, but only rarely on any particular site. Its importance may be diminished, because subsequent evaporation during warm days should be enhanced, as the radiatively cooled night time surface attracts moisture from warmer deep soil.

Soil moisture fraction (SMF) data for dates after the last spring rain and before the first fall rain were fitted to Eq. 3 with the use of a nonlinear least-square routine. The resulting parameters, s , c , and q , were then used in Eq. 1 to calculate the depletion rate. This procedure allowed the determination of the depletion rate without the data scatter that would have resulted from the numerical differentiation of the original data. Parameter values (except t_0) for individual trees or shrub patches typically showed insignificant differences when determined from the 1994 or 1995 data. In most cases, the best fits were obtained with $q = 1$, consistent with plant limitation of water use only after some soil moisture depletion had taken place. However, in a few cases best fits were found for larger values of q (≥ 2), reflecting more immediate plant regulation or other restriction of water use. These differences were sometimes seen between trees of the same species and, so, cannot be attributed to interspecies differences.

Values of c showed small differences (~5%) between individual trees or shrub patches of the same species. These differences may have been due to errors in the neutron probe calibration between holes or to minor differences in soils. The data for each tree or shrub patch were normalized, so that c values were the same for all individuals of each species. The resulting SMF depletion-rate values for different individuals of a species then differed typically by 20%, whether individuals were on the same site or one at the ecotone site and one at a nonecotone site. These depletion rates were averaged over all individuals at each SMF value (Fig. 4).

The SMF depletion rates for the low-elevation conifers were consistently lower than depletion rates for the shrubs. Initially (SMF > 0.75), this difference was only ~15%, but at later times (SMF < 0.7), the shrub moisture depletion rates averaged ~35% more than rates for the low-elevation conifers. Residual (asymptotic) values of SMF when depletion had stopped, the parameter c , show no significant ($P < 0.05$) differences for different species within the conifer or shrub groups. However, means for each of these groups were significantly different from each other, and the mean surface depletion value was significantly different from the mean conifer value. (Mean values of final SMF: Conifers = 0.48 [depth \geq 40 cm, SD = 0.02]; Shrubs = 0.42 [depth \geq 40 cm, SD = 0.03]; Surface = 0.39 [depth = 20 cm, conifers or shrubs, SD = 0.03]. $P < 0.001$.)

Water potential—With plentiful soil moisture (SMF > 0.65), predawn water potentials showed considerable variation, between -0.4 and -0.7 MPa for conifers and between -0.2

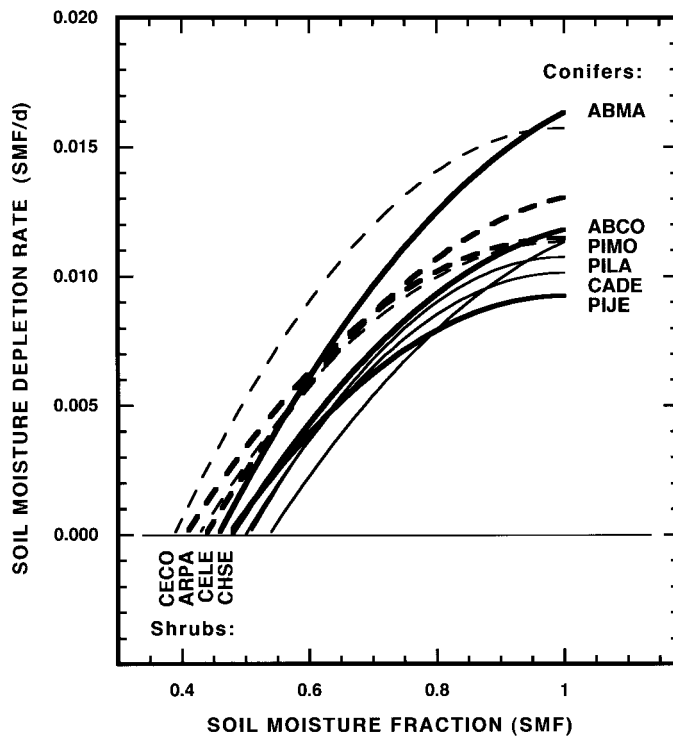


Fig. 4. Soil moisture fraction (SMF) depletion rates for conifers (solid lines) and shrubs (dashed lines). Heavy lines are average data from two or more trees or shrub patches and have standard errors of ~10%. Light lines are data from only one tree or shrub patch. The SMF values are averages for depths \geq 40 cm. Species abbreviations are as in Fig. 2.

and -0.3 MPa for the shrubs, but appeared roughly independent of SMF (cross-hatched areas on Fig. 5).

The steady fall of water potentials as soil moisture became depleted (cf. Hallgren and Helms, 1988) was fitted to a function exponential in the SMF. Such an exponential relationship was suggested by data on soil water potentials (Kozłowski, Kramer, and Pallardy, 1991; Kramer and Boyer, 1995; Brady and Weil, 1996). Conifers entered this regime at higher SMF values than did the shrubs. (At -1 MPa, mean values of SMF were conifers = 0.50 [SD = 0.04] and shrubs = 0.43 [SD = 0.04]. $P < 0.001$.) However, with further increased soil moisture depletion, the distinction between conifers and shrubs was no longer significant. (At -2 MPa, mean values of SMF were conifers = 0.46 [SD = 0.04] and shrubs = 0.41 [SD = 0.04]. $P > 0.13$.) Toward the end of summer, some shrubs reached more negative predawn water potentials than did any of the conifers (Fig. 2).

While differences in performance among shrub species were not significant at a high confidence level, the data do suggest important differences between *A. patula* and *C. sempervirens*, the most common shrubs found on the study sites. For *A. patula*, soil moisture depletion led to an average residual SMF value of 0.41, next to the lowest value found under any tree or shrub. For *C. sempervirens*, on the other hand, the residual soil moisture was 0.44, the highest value for any shrub. Late-summer predawn xylem water potentials were more negative than -4 MPa for *A. patula* but no more negative than -1.5 MPa for *C. sempervirens*. *Arctostaphylos patula* often forms monospecific stands, suggesting a strong capability of excluding other species, but *C. sempervirens* does not. (The less com-

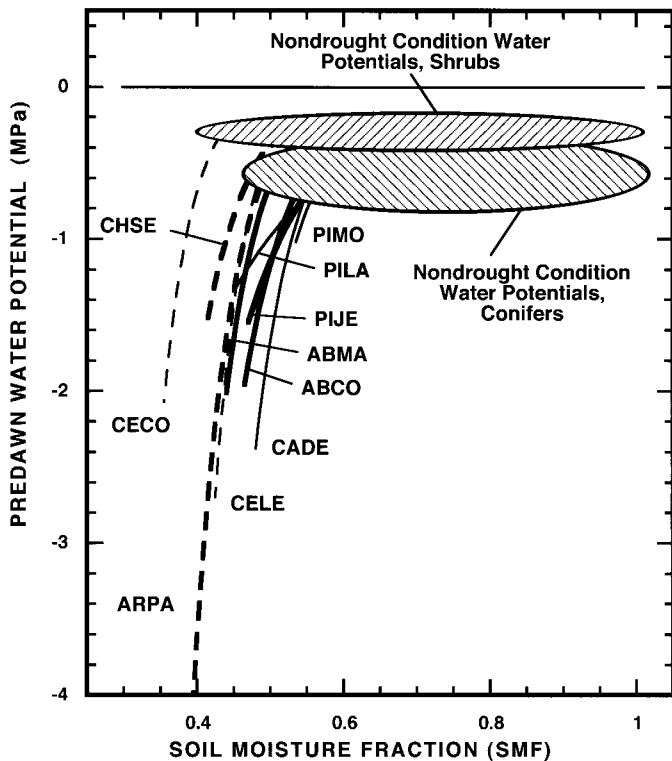


Fig. 5. Predawn xylem water potentials for conifers (solid lines) and shrubs (dashed lines). Heavy lines are average data from two or more trees or shrub patches, while light lines are data from only one tree or shrub patch. The SMF values are averages for depths ≥ 40 cm. The hatched areas indicate the range of water potentials found under nondrought conditions. Species abbreviations are as in Fig. 2.

mon *C. cordulatus*, with the lowest residual SMF observed [0.39] also forms similar monospecific stands.)

DISCUSSION

Conifers of the mountains of the arid southwestern United States are reported to follow a conservative life strategy of avoiding desiccation by minimizing transpiration during drought, whereas angiosperm shrubs growing with them are more profligate in their use of water, maintaining transpiration (Conard and Radosevich, 1981; DeLucia and Heckathorn, 1989; DeLucia and Schlesinger, 1991; Jaindl, Doescher, and Eddleman, 1993), making more extensive osmotic adjustments (Bowman and Roberts, 1985) and developing a more extensive root system to support this continued transpiration (Hellmers et al., 1955). Shrub and forb competition for water has been widely cited as a major negative influence on young conifers (e.g., Tappeiner and Radosevich, 1982; Lanini and Radosevich, 1986; Drivas and Everett, 1988; Parker and Yoder-Williams, 1989; Callaway et al., 1996) and appears to be particularly strong for shrubs of the Ericaceae (Conard and Radosevich, 1982; Radosevich, 1984; White, 1985; Shainsky and Radosevich, 1986; Anderson and Helms, 1994) such as *A. patula*. However, Rejmánek and co-workers found that water is not the dominant factor in this competition on deep soils in the Sierra Nevada (Rejmánek and Messina, 1989; Randall and Rejmánek, 1993).

In our study, on relatively shallow soils (50–170 cm deep), we found that the low-elevation conifers reduced their water

uptake more than did the shrubs at moderate drought conditions (Fig. 4, SMF ~ 0.5 – 0.55), and that predawn xylem water potentials in conifers, but not in shrubs, became increasingly negative at these SMF values (Fig. 5). *Abies magnifica* showed an initial water uptake rate larger than the other conifers and most shrubs, but this rate declined rapidly, to values similar to those for the other conifers. The high initial depletion rate for *A. magnifica* is consistent with the observation that *A. magnifica* seedlings in a growth chamber developed a more extensive root system than did *A. concolor* seedlings (Barbour, Pavlik, and Antos, 1990). We presume that changes in water uptake, as inferred from soil moisture depletion, reflect primarily changes in transpiration. (Cf. Whitehead and Jarvis, 1981; Kramer and Boyer, 1995; or Oren and Sheriff, 1995.) This is consistent with Kunz' (1988) central-Sierra measurement of higher June leaf conductances in *A. magnifica* than in *A. concolor*, but similar conductances for the two species at later dates.

Conifer predawn water potentials under drought conditions were substantially more negative than shrub predawn water potentials. But soil water potentials cannot be more negative than shrub predawn water potentials, or shrubs could not extract soil moisture. Hence, conifer water potentials must have been substantially more negative than soil water potentials, demonstrating an apparent inability of the conifers to recharge depleted water storage over a single night. This inability could have been due to an inadequate root system and/or the limited conduction capability of conifer tracheids, compared to shrub xylem vessels. (Cf. Oren and Sheriff, 1995; or Pallardy et al., 1995.)

As soil moisture was further depleted, conifers apparently exercised more decisive control of their transpiration. Conifer water uptake was cut off at soil moisture levels (SMF ~ 0.45) where the shrubs were still depleting soil moisture, and the diurnal fall in water potential was not as great as under early-season conditions. When all water use was cut off, conifer water potentials were less negative than shrub water potentials (-1.8 MPa vs. < -4 MPa), further demonstrating the ability of the conifers to control their transpiration and water status. (In general drought-resistant conifers such as *P. ponderosa* or *A. magnifica*, and probably others in this study, show only 2–3% residual stomatal conductance under drought conditions, while other conifers show up to 20% residual conductance [Larcher, 1975; Running, 1976; Hinckley, Lassoie, and Running, 1978].)

The shrubs more completely extracted soil moisture than did the conifers (average residual soil moisture, SMF = 0.42 vs. 0.48), consistent with their continued transpiration under low soil moisture conditions. The observations that *A. patula* final water potentials were extremely negative, that residual soil moisture under *A. patula* was lower than under most plants, and that *A. patula* is distributed in monospecific stands are all consistent with identifying it as a particularly strong competitor for water. *Arctostaphylos patula* was present on only 20% of the higher elevation survey sites dominated by *A. magnifica*, but was present on 64% of survey sites where *A. magnifica* was absent. This mutual avoidance between *A. patula* and *A. magnifica* may be associated, at least in part, with competition for water between them.

We observed surprisingly little difference in water management between the two years of observation, except that the phenology of water use was uniformly shifted to earlier dates in the drought year.

In conclusion, differences in seasonal water use patterns between conifer species were observed. However, these differences by themselves do not suggest a direct elevation-dependent competitive advantage of one species over another that might explain species distribution across the midmontane upper montane forest ecotone. These water use patterns must be combined with differences in growth phenology between conifer species, as discussed in the companion paper (Royce and Barbour, 2001), in order to understand species distribution. As compared to the conifers, we found that angiosperm shrubs show water use patterns that may make them particularly effective competitors for moisture from shallow soils, and this is especially true for *A. patula*. These differences between conifers and shrubs may be important in explaining forest-shrubland ecotones and forest structure changes during post-fire or post-logging succession.

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