

Roles of weathered bedrock and soil in seasonal water relations of *Pinus Jeffreyi* and *Arctostaphylos patula*

K.R. Hubbert, J.L. Beyers, and R.C. Graham

Abstract: In the southern Sierra Nevada, California, relatively thin soils overlie granitic bedrock that is weathered to depths of several metres. The weathered granitic bedrock is porous and has a plant-available water capacity of $0.124 \text{ m}^3\cdot\text{m}^{-3}$, compared with $0.196 \text{ m}^3\cdot\text{m}^{-3}$ for the overlying soil. Roots confined within bedrock joint fractures access this rock-held water, especially during late summer when overlying soils are dry. We sought to determine seasonal soil and bedrock water changes in a Jeffrey pine (*Pinus jeffreyi* Grev & Balf.) plantation and to examine concurrent effects on the water relations of Jeffrey pine and greenleaf manzanita (*Arctostaphylos patula* Greene). In 1996, plant-available water in the 75 cm thick soil was depleted by late June, with soil water potential (ψ_{soil}) < -2.2 MPa, but below 75 cm, bedrock water potential (ψ_{bedrock}) was still > -2.2 MPa. Thus, the bedrock, not the soil, supplied water to plants for the remainder of the dry season. Higher values of, and smaller fluctuations in, seasonal predawn pressure potential (ψ_{predawn}) for Jeffrey pine indicated that it is deeply rooted, whereas active roots of greenleaf manzanita were interpreted to be mostly within the upper 100 cm. The extra rooting volume supplied by weathered bedrock is especially important to pine relative to manzanita.

Résumé : Dans la partie méridionale de la Sierra Nevada en Californie, des sols relativement minces recouvrent une roche-mère granitique qui est altérée à des profondeurs de plusieurs mètres. La roche-mère altérée est poreuse et contient $0,124 \text{ m}^3\cdot\text{m}^{-3}$ d'eau disponible pour les plantes comparativement à $0,196 \text{ m}^3\cdot\text{m}^{-3}$ d'eau dans le sol qui la recouvre. Les racines confinées dans les fractures de la roche-mère ont accès à cette eau retenue dans la roche, particulièrement à la fin de l'été lorsque le sol qui la recouvre est sec. Nous avons cherché à déterminer les variations saisonnières dans l'eau du sol et de la roche-mère dans une plantation de pin de Jeffrey (*Pinus jeffreyi* Grev & Balf.) et à examiner les effets simultanés sur les relations hydriques du pin de Jeffrey et d'*Arctostaphylos patula* (Greene). En 1996, l'eau disponible pour les plantes dans le sol d'une épaisseur de 75 cm était épuisée à la fin du mois de juin, avec le potentiel hydrique du sol (ψ_{sol}) $< -2,2$ MPa alors que le potentiel hydrique de la roche-mère ($\psi_{\text{roche-mère}}$) au-dessous de 75 cm était encore $> -2,2$ MPa. Par conséquent, la roche-mère, non le sol, a fourni l'eau pour les plantes pendant le reste de la saison sèche. Des valeurs plus élevées et de moins grandes fluctuations du potentiel hydrique avant aube ($\psi_{\text{avant aube}}$) saisonnier chez le pin de Jeffrey indiquent qu'il est plus profondément enraciné alors que les racines actives d'*A. patula* ont été détectées dans les premiers 100 cm. Le volume d'enracinement supplémentaire fourni par la roche-mère altérée est surtout important pour le pin comparativement à *A. patula*.

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Introduction

In Mediterranean climate regions such as the Sierra Nevada of California, cool, wet winters are followed by a warm summer rainless period that varies in duration and intensity (Hanes et al. 1981). The growing season for mixed conifer

forests in the lower montane zone begins in early spring, and summer growth depends on water stored in the substrate (Chabot and Mooney 1985). Evapotranspirational drying through the spring and summer can exhaust plant-available water within the upper metre of soil by the end of summer (Anderson et al. 1995). Under these conditions, the vegetation must rely on water stored in deeper substrates to supplement forest growth and maintenance through late summer and fall (Arkley 1981).

Granitic bedrock makes up about one-fifth of California's land area, concentrated mainly in uplands, such as the Sierra Nevada and the southern California Peninsular Ranges (Norris and Webb 1990). Except at the highest elevations, where Pleistocene glaciation has exposed hard rock, weathering processes have generated substantial porosity, giving soil-like water-holding characteristics to the bedrock, although the fabric and structure of the rock is largely retained (Graham et al. 1994). The bedrock is further characterized by its fracturing and jointing patterns. Water infiltrates the

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Table 1. Selected properties of the soil and weathered granitic bedrock at the Sequoia National Forest study site.

Horizon	Depth (cm)	Texture	Gravel (%) [*]	Sand (%) [†]	Silt (%) [‡]	Clay (%) [‡]	Bulk density (g·cm ⁻³)	RLD (cm·cm ⁻³)	Organic C (%)
O	4–0								
A	0–9	Sandy loam	0	72	23	5	1.15 (0.02)	2.8 (1.46) [‡]	2.68
AB	9–15	Gravelly sandy loam	15	70	25	5	1.15 (0.02)	2.8 (1.46) [‡]	1.66
Bw1	15–29	Gravelly sandy loam	15	74	21	5	1.19 (0.10)	2.4 (0.91)	1.17
Bw2	29–40	Gravelly sandy loam	19	75	19	6	1.33 (0.04)	3.3 (1.34)	0.71
BC	40–53	Gravelly sandy loam	15	75	20	5	1.38 (0.03)	1.8 (1.05)	0.70
C	53–80	Gravelly sandy loam	29	76	18	6	1.38 (0.07)	nd	0.48
Cr1	80–160	Gravelly loamy sand	38	86	12	2	1.58 (0.25)	<0.08	0.09
Cr2	160–240	Gravelly loamy sand	45	85	13	2	1.80 (0.05)	<0.08	0.03
Fractures	80–240	nd	nd	nd	nd	nd	nd	4.3 (2.07)	3.72

Note: RDL, root length density; nd, not determined. Values for bulk density and root length density are means with SDs in parentheses.

^{*}Percent of whole soil.

[†]Percent of <2 mm fraction.

[‡]Sampling and analysis was for 0–15 cm depth as a whole.

joints, promoting weathering to depths approaching 30 m in some places (Wahrhaftig 1965), whereas the soils are often <1 m thick.

Granitic bedrock that is sufficiently weathered to crumble to grus in bare hands has been found to have plant-available water capacities of 0.096 m³·m⁻³ (Krammes 1969) and 0.124 m³·m⁻³ (Jones and Graham 1993) in southern California. Available water capacity for the weathered bedrock (Cr) horizon was even higher, 0.15 m³·m⁻³, in a giant sequoia (*Sequoiadendron giganteum* Buchh.) grove in the southern Sierra Nevada (Anderson et al. 1995). Because weathered bedrock is often thicker than the overlying soil, it can contribute as much or more plant-available water than the soil. In the southern Sierra Nevada, 90 cm thick soils can hold 17 cm of plant-available water, whereas the upper 180 cm of the underlying weathered bedrock can hold 27 cm of plant-available water (Anderson et al. 1995). Calculated water use by forest vegetation in the San Bernardino Mountains of southern California was found to be significantly underestimated when based on soil moisture measurements of limited depth (Arkley 1981), yet few studies have directly addressed plant utilization of water stored in weathered bedrock.

The Sierran mixed conifer forest on the west flank of the southern Sierra Nevada forms the largest area of commercial timberland on granitic terrain in California (FRRAP 1988). Within this forest zone, we sought to determine the extent to which rock-stored water affects the summer water status of a major timber species, Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), and one of its main shrub competitors, greenleaf manzanita (*Arctostaphylos patula* Greene). Jeffrey pine prospers under harsh environments throughout its range because of its cold hardiness, drought tolerance, and adaptation to short growing seasons and infertile sites (Jenkinson 1990). Roots of Jeffrey pine have been observed in bedrock fractures to depths >6 m (Hubbert et al. 2001). Greenleaf manzanita is a shade intolerant, broad-leaved, sclerophyllous evergreen species that prefers disturbed areas (Anderson and Helms 1994). Both species inhabit open areas having dry, coarse, well-drained soils (Jenkinson 1990). Differences in morphological and physiological characteristics between Jeffrey pine and greenleaf manzanita suggest that the two

species have evolved different adaptive traits in their patterns of water use and access of water (McDonald 1981; Jones 1992; Kramer and Boyer 1995). We expected their use of rock-held water to differ as well.

Materials and methods

Site description and regolith characteristics

This study was conducted in a Jeffrey pine plantation located in the southern Sierra Nevada at Parker Pass, immediately south of County Road M50 on the western slopes of the Greenhorn Mountains in the Sequoia National Forest (35.957°N, 118.630°W). The site occupied about 0.25 ha on the summit and upper back slopes (<10% slope gradient) of a subordinate ridge at an elevation of about 1950 m. The stand consisted of 25- to 30-year-old Jeffrey pine trees and some ponderosa pine (*Pinus ponderosa* Laws.), 8 to 10 m in height, with greenleaf manzanita (1 to 2 m in height) as the principal understory shrub. Mean annual precipitation was estimated from map isopleths to be about 760 mm (Rantz 1972). Precipitation falls primarily between November and April, when evapotranspiration is at a minimum, mostly in the form of snow. Summers are warm and dry. Heavy fogs in the San Joaquin Valley encroach up the western drainages and may contribute to soil and plant moisture through dew and canopy drip during the spring and fall (K.R. Hubbert, personal observation).

Tree species in the surrounding area were typical of the Sierran mixed conifer forest and included ponderosa pine, Jeffrey pine, white fir (*Abies concolor* (Gord. & Glend.) Lindl.), sugar pine (*Pinus lambertiana* Dougl.), and incense cedar (*Libocedrus decurrens* Torr.) The understory was dominated by greenleaf manzanita, but also included bearclover (*Chamaebatia foliolosa* Benth.), Sierra gooseberry (*Ribes roezlii* Regel.), squaw currant (*Ribes cereum* Dougl.), mountain whitethorn (*Ceanothus cordulatus* Kell.), and squirreltail grass (*Elymus elymoides* Swezey) (nomenclature follows Hickman 1993).

Throughout most of the site, chemical weathering has produced a relatively thick zone of weathered quartz monzonite bedrock (Cr material). Soils were mostly coarse-loamy, mixed, mesic Typic Dystraxerepts. Soil textures were all sandy loam to gravelly sandy loam, with sand content increasing from 71% in the A horizon to 84% in the Cr2 horizon (Table 1). The C horizon was massive, lacking both soil and rock structure. The Cr horizons retained rock fabric but could be easily crumbled to individual grains using bare hands, meeting the criteria for weathering class 6 of Clayton and

Arnold (1972). Bulk densities increased with depth, ranging from 1.15 to 1.38 g·cm⁻³ in the soil, and from 1.58 to 1.80 g·cm⁻³ in the weathered bedrock (Table 1). Organic carbon decreased steadily from 2.68% in the A horizon to 0.03% in the Cr2 horizon, but averaged 3.72% within the joint fractures. Within the bedrock, roots of Jeffrey pine were confined to fractures, and root distribution was closely defined by the pattern of joint fractures in the rock. Mean root length density (RLD) was 2.8 cm·cm⁻³ in the A horizon as compared with 4.3 cm·cm⁻³ in the joint fractures of the Cr horizon. The Cr horizon RLD expressed on a whole rock basis was <0.08 cm·cm⁻³ (Table 1). Auger borings revealed that average soil depth to weathered bedrock was 75 cm, and weathered bedrock extended, on average, another 275 cm to hard bedrock.

Laboratory analyses

Moisture retention curves were determined for the soil (Bw1) and the weathered bedrock (Cr1) (Hubbert et al. 2001). Intact core samples were taken in triplicate from the soil (Bw1) and weathered bedrock (Cr1) horizons. Soil and weathered bedrock water potentials > -0.01 MPa were determined using a hanging water balance, and a mid-range pressure plate system was used for water potentials of -0.01 to -0.1 MPa (Campbell and Gee 1986). Soil and bedrock water potentials < -0.1 MPa were determined using the filter paper method (Campbell and Gee 1986). Water content measurements were made gravimetrically after oven-drying (Gardner 1986). Gravimetric water contents were converted to volumetric values using measured mean bulk densities. We used limits of -0.01 MPa (field capacity) and -2.2 MPa (permanent wilting point) to calculate plant-available water content (AWC) as suggested for coarse-textured soils in a natural system (Cassel and Nielsen 1986; Savage et al. 1996). Mean calculated AWC was 0.196 m³·m⁻³ for soils and 0.124 m³·m⁻³ for weathered bedrock.

Root length densities were determined using the modified line-intersect method (Marsh 1971). Bulk density was determined using the paraffin-coated clod method (Blake and Hartge 1986). Particle size distribution was measured by the pipette method using samples that were air-dried and sieved to remove rock fragments >2 mm in diameter (Gee and Bauder 1986). Total C was measured by dry combustion using a Carlo Erba NA1500 C/N/S.³ Total C was assumed equivalent to organic C since carbonates were not present.

Meteorological and environmental measurements

Weather parameters measured at the site included air temperature, relative humidity, and wind speed. A thermistor was used to measure air temperature at 1 m above the ground in an open area between trees. Relative humidity was measured with a model HMD30YB humidity and temperature sensor (Vaisala Inc., Sunnyvale, Calif.), and wind speed was measured with an anemometer at 2 m height. Instruments were connected to a recording data logger (Campbell Scientific, Logan, Utah) programmed to measure every 60 s and average every 4 h. Vapor pressure deficit was calculated from air temperatures and relative humidity (Dingman 1994). Temperature probes were placed at 0.25, 0.50, 1, and 4 m depths at the site to measure substrate temperature year-long (reading once every hour and averaging every 6 h). An electronic recording rain gauge was used for the measurement of precipitation during the summer (May–October). A USDA Forest Service weather station located about 7 km southwest of the site and at approximately 1159 m elevation was used to obtain precipitation data during the remainder of the year (November–April), because road closures prevented winter access to the site. Weather conditions during field measurement days are summarized in Table 2.

Substrate water status

Instrumentation was installed in September of 1995. Substrate water status was monitored from April 1996 through September 1997. Cylindrical gypsum blocks (Soilmoisture Equipment Corp., Goleta, Calif.) were placed at 0.25, 1, 2, 3, and 4 m depths in nine separate locations to give a measure of substrate water potential (Ψ_{soil} and Ψ_{bedrock}), which was recorded four times daily. The gypsum blocks were calibrated following the methods of Campbell and Gee (1986) and were equilibrated in situ for 6 months before data collection began. The gypsum blocks were attached to solar powered data loggers (Campbell Scientific).

Ten holes were hand-augered at the site for the placement of neutron probe access tubes. Because of the variation in subsurface weathering patterns, the depth to which holes could be augered ranged from 2.7 to 4.3 m. The tubes were constructed of cellulose acetate butyrate pipe and sealed at the bottom. Hand-augering produced holes that minimized the free space between the tube and the hole wall. Neutron probe measurements (Troxler Electronics, Research Triangle Park, N.C.) of soil water content were conducted every 2 weeks during the summer dry season at 25-cm intervals to a maximum depth of 4 m. The neutron probe was calibrated at both the dry end and the wet end (0.04 to 0.24 cm³·cm⁻³) for both weathered bedrock and soil by gravimetric sampling of material removed while augering holes for the access tubes (Gardner 1986). Gravimetric water contents were converted to a volumetric basis using measured mean bulk densities of 1.25 g·cm⁻³ for soil and 1.60 g·cm⁻³ for weathered bedrock and correcting for coarse fragment volumetric contents in the soil. Bulk densities were determined using the clod method (Blake and Hartge 1986). Neutron probe measurements were used to monitor depletion of plant-available substrate moisture through the growing season.

A trench measuring 2.4 m deep, 1 m wide, and 5 m long was excavated by backhoe in late October 1996. Immediately after excavation, samples of weathered bedrock (150 cm depth) were collected at 10-cm intervals along a 120-cm horizontal transect to determine the water potential gradient between two vertical joint fractures. Water content was measured gravimetrically in the laboratory, and water potential of 20-g subsamples was analyzed using a chilled mirror water activity meter (AQUA LAB model CX2, Decagon Devices, Inc., Pullman, Wash.).

Plant water status

Plant predawn and midday xylem pressure potentials (Ψ_{predawn} and Ψ_{midday}) were measured using a Scholander-type pressure chamber (model 3005, plant water status console, Soilmoisture Equipment Corp.) (Scholander et al. 1965; Waring and Cleary 1967). Nine Jeffrey pines and nine greenleaf manzanitas were sampled at the site. Predawn sampling occurred from 4:00 to 5:30 AM Pacific daylight time (PDT), with midday measurements taken from 12:00 to 1:00 PM PDT. Three units of scaffolding were placed at the site such that the Jeffrey pine could be sampled near the crown at about 8 m height. Midday samples of both pine and manzanita were taken in the sunlit quarter of the canopy. Manzanita shoot tips (5–8 cm in length) containing three to five leaves were cleanly sliced with a razor blade from the upper portions of the shrub. For pine, mature fascicles from the third whorl were cut near the crown to ensure consistency in sampling. After cutting, samples from both manzanita and pine were quickly enclosed in a plastic bag. Elapsed time between sample collection and sealing in the pressure chamber was typically <1 min. The chamber was pressurized at 0.02 MPa·s⁻¹. End point was determined when xylem tissue changed color.

³Mention of a product is for information purposes only and does not imply endorsement by the USDA Forest Service or the University of California.

Table 2. Summary of weather and sky conditions during field measurement days.

Date	VPD _{max} (Pa)	T _{max} (°C)	T _{min} (°C)	PAR ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Sky conditions
1996					
5 Apr.	nd	nd	nd	546	Overcast
14 Apr.	nd	nd	nd	848	Partly cloudy
17 May	470	11.3	6.4	254	Fog
16 June	1120	19.8	10.8	1430	Clear
2 July	2620	27.0	10.2	1467	Clear
27 July	2080	30.0	14.2	1090	Partly cloudy
13 Aug.	2760	29.5	13.9	1577	Clear
20 Aug.	1430	30.0	7.6	938	Partly cloudy
4 Sept.	1920	26.2	11.0	926	Partly cloudy
20 Sept.	1960	24.7	2.9	1226	Clear
11 Oct.	840	17.5	3.9	1040	Clear
8 Nov.	1940	18.5	0.6	853	Clear
1997					
27 Mar.	960	13.54	3.78	660	Partly cloudy
18 Apr.	1320	19.27	2.2	1265	Clear
26 May	570	13.63	2.81	1447	Clear
11 June	650	18.82	4.25	1177	Clear
10 July	1840	27.07	12.98	1193	Clear
30 July	2130	26.14	8.45	1253	Clear
12 Sept.	400	18.14	7.73	984	Partly cloudy

Note: VPD, vapor pressure deficit; T_{max}, maximum daily air temperature; T_{min}, minimum daily air temperature; PAR, maximum daily photosynthetically active radiation; nd, no data.

Leaf conductance (g_l) was measured using a LI-COR 1600 null-balance steady state porometer (LI-COR, Inc., Lincoln, Nebr.) (Beardsell et al. 1972). Pine needle surface area for porometer calculations was determined from length and chord dimensions of the inner surfaces containing stomata, assuming that the cross-sectional shape of a needle is a one-third segment of a circle (Sands and Nambiar 1984). Greenleaf manzanita leaf area (single leaf) was measured using the dot grid method (Kvet and Marshall 1971), and the value was doubled for calculations because leaves of greenleaf manzanita were observed to be amphistomatous (stomates on both sides of the leaf). A cylindrical chamber was used for both pine and manzanita. Porometer measurements were taken from 9:00 to 11:00 AM PDT to obtain midmorning g_l rates at 2- to 3-week intervals from spring through mid-fall. For the nine Jeffrey pines, a single, south-facing fascicle of needles from the third whorl of the branch was sampled. A south-facing leaf was chosen for each of the nine greenleaf manzanita shrubs. To limit variability, the same fascicle or leaf was repeatedly sampled throughout the season.

Results

Precipitation and regolith temperature

In 1996, only 5 mm of precipitation fell at the study site from mid-May until October 25. From April to October of 1997, only 26 mm of rain fell (in July and September) (Fig. 1). Based on Forest Service data, total annual precipitation (July 1 to June 30) for hydrologic years 1995–1997 was above average, with 940 mm in 1995–1996 and 1070 mm in 1996–1997 (Fig. 1). Because of elevational differences between the Forest Service weather station and the location of the site, total precipitation may have been higher at the site. Snowmelt was complete at the study site by late-May in 1996 and by mid-April in 1997. Regolith temperatures never

dropped below freezing at either the 25 or 400 cm depths. Minimum regolith temperatures were about 5°C at 25 cm and 9°C at 400 cm during January of 1997.

Soil and weathered bedrock water status

Patterns of water depletion for soil and bedrock were similar in 1996 and 1997, with moisture loss clearly extending to depths of 400 cm (Fig. 2). Water loss was greatest and most rapid within the upper 75 cm, which is largely soil. From April to June, more than twice as much volumetric water was removed from the 25 cm depth than from the 100 cm depth (Fig. 2). At 75 to 100 cm, the transition from soil to weathered bedrock, water content showed an abrupt decrease in the spring and a steady decline through the summer of both years (Fig. 2).

Mean thickness of soil and weathered bedrock, together with appropriate AWC values, was used to calculate an average total plant-available water storage capacity of 48.8 cm within the 350 cm regolith, with 14.7 cm (30%) of this contributed by soil and 31 cm (70%) contributed by weathered bedrock (Hubbert et al. 2001). The earliest measurements in both 1996 and 1997 showed actual plant-available water in the soil (0–75 cm) to be 8 cm, indicating about one-half depletion early in the season. All plant-available water in the soil was depleted by about mid-June in both 1996 and 1997 (Fig. 3). During the monitored dry seasons, weathered bedrock supplied 15.8 cm of plant-available water through 8 November 1996, and 13.5 cm through 11 September 1997 (Fig. 3). Mean daily evapotranspiration rates between measurement periods were 0.11 cm·d⁻¹ for 14 April to 5 May, 0.38 cm·d⁻¹ for 5 May to 18 May, 0.10 cm·d⁻¹ for 18 May to 8 June, 0.17 cm·d⁻¹ for 8 June to 1 July, 0.10 cm·d⁻¹ for

Fig. 1. Monthly precipitation (snow and rain) was measured from June 1995 to September 1997. Winter precipitation data were provided by a USDA Forest Service weather station located about 7 km southwest of the site and at approximately 1159 m elevation. An onsite electronic recording rain gauge was used for the measurement of precipitation during the summer (May–October). Total precipitation measured for the 1996 season was 940 mm, and in 1997 it was 1070 mm (USDA Forest Service weather station + onsite electronic recording rain gauge).

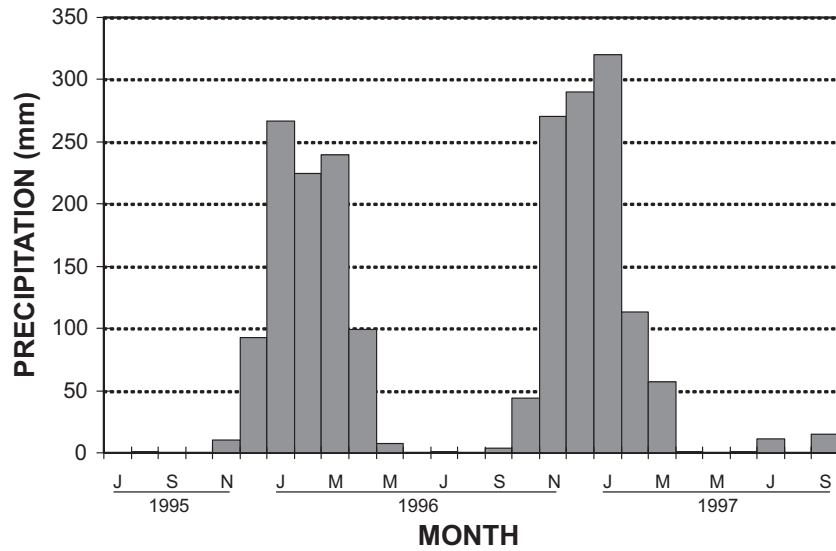
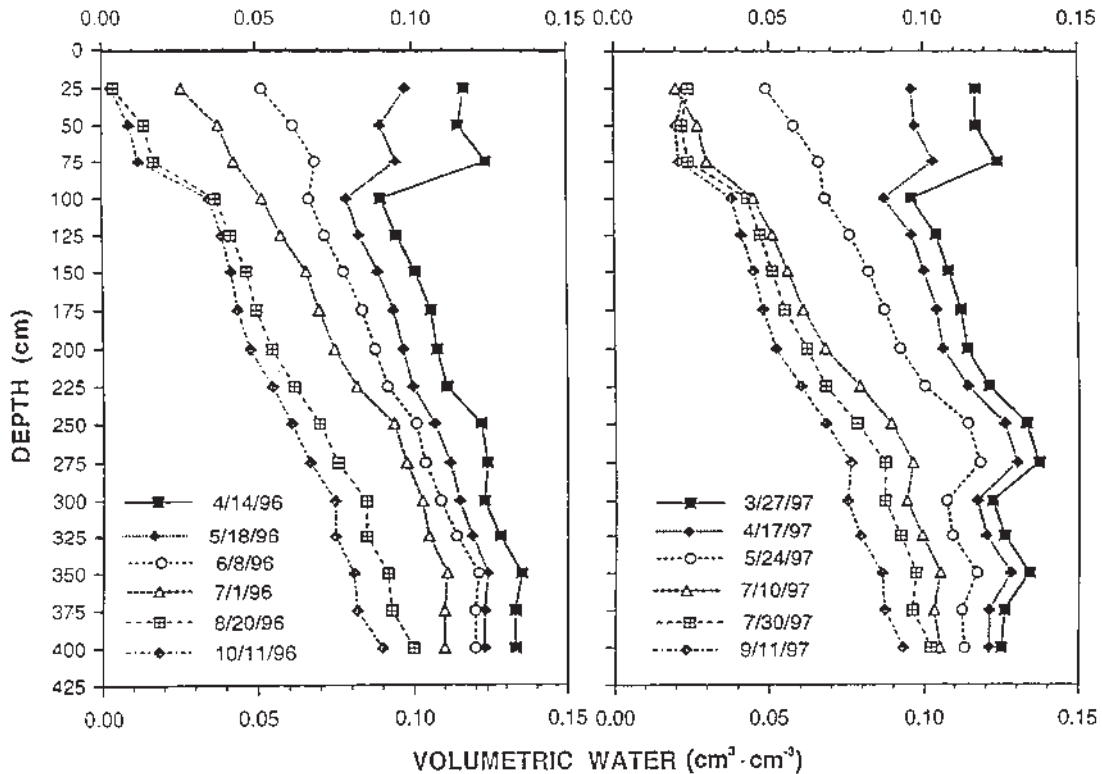


Fig. 2. Volumetric water content as a function of depth during the 1996 and 1997 growing seasons. Values at each depth are means calculated from neutron probe readings in 10 separate auger holes. SE is ± 0.23 or less.

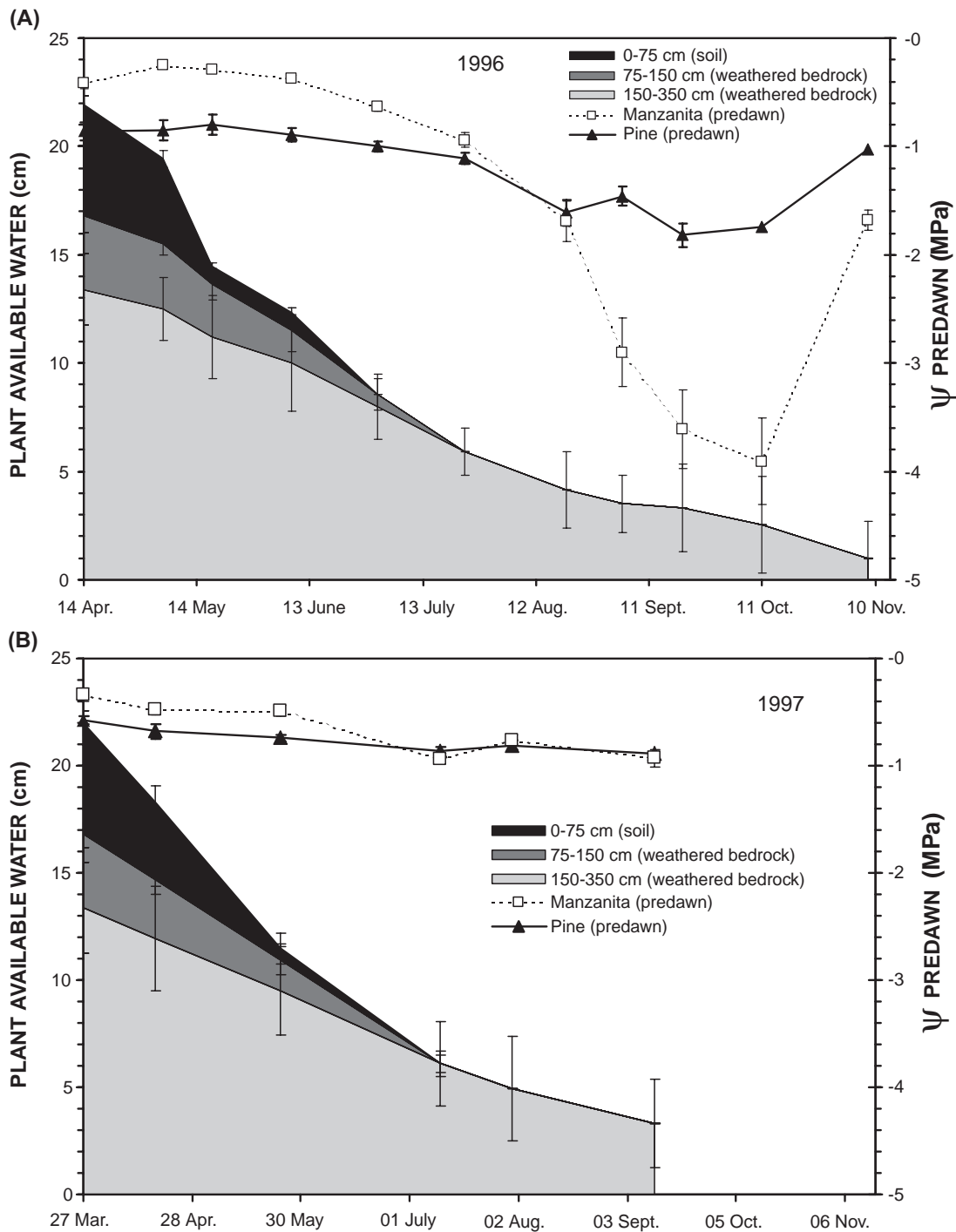


1 July to 24 July, and 0.065 cm^{-1} for 24 July to 20 August (Fig. 3a).

Soil water potentials were below -2.2 MPa (lower limit of plant-available water) by mid-June in both 1996 and 1997 (Fig. 4). In 1996, ψ_{soil} at the 25 cm depth dropped steeply from May (-1.5 MPa) to September (below -6 MPa), fol-

lowed closely in late June by a steep drop in ψ_{bedrock} at the 100 cm depth (Fig. 4). At the 100 cm depth (in weathered bedrock), -2.2 MPa was reached in early July in 1996 and in mid-June in 1997 (Fig. 4). By the end of August of 1996 and 1997, ψ_{bedrock} at both the 200 and 300 cm depths was below -2.2 MPa , and only water stored in bedrock at 400 cm was

Fig. 3. Plant-available water contents in soil and weathered bedrock compared with predawn leaf water potential (ψ_{predawn}) in Jeffrey pine and greenleaf manzanita during the 1996 (a) and 1997 (b) dry seasons. Error bars are 1 SE of the mean.



held at > -2.2 MPa (Fig. 4). Rain events in late July and early September of 1997 both resulted in increases of ψ_{soil} followed by a rapid drop (Fig. 4).

Along the 120-cm horizontal transect sampled between two joint fractures at 150 cm depth, water potentials became less negative (more moist) with distance from the joint fractures (Fig. 5). Water potential was > -1.5 MPa at distances of more than 30 or 40 cm from the two fractures, but mate-

rial near the fractures was drier with water potentials < -3.5 MPa (Fig. 5).

Seasonal variation in plant xylem pressure potentials

Predawn plant xylem pressure potentials (ψ_{predawn}) in pine were higher (less negative) than in greenleaf manzanita during late August, September, and October of 1996 (Fig. 3a). Through the summer of 1996 and up to the October rainfall,

mean ψ_{predawn} for greenleaf manzanita decreased from -0.4 to -3.9 MPa, whereas Jeffrey pine only decreased from -0.8 to -1.8 MPa (Fig. 3a). In contrast, in 1997 mean ψ_{predawn} for both pine and manzanita did not drop below -1.0 MPa and remained similar to each other throughout the season (Fig. 3b).

Seasonal leaf conductance

Seasonal patterns of mid-morning leaf conductance (g_1) were similar between greenleaf manzanita and Jeffrey pine in 1996, with peak conductance for both occurring in June, followed by a steep decrease in August (Fig. 6). Mean Jeffrey pine g_1 values ranged from 15 to 112 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in 1996 and from 65 to 113 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in 1997. Mean values of g_1 in manzanita ranged from 8 to 90 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in 1996 and from 36 to 110 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in 1997 (Fig. 6). From April to June 1996, g_1 of pine was 30 to 50 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ greater than that of manzanita, and from mid-August to October, g_1 of both species was below 35 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Fig. 6). In 1997, g_1 of pine was greater than that of manzanita both early in the season and late in the season, but from late May through mid-July there was no difference in g_1 between the two species. Mid-September g_1 values of pine and manzanita in 1997 were about 80 and 50 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ greater, respectively, than during the same period in 1996 (Fig. 6).

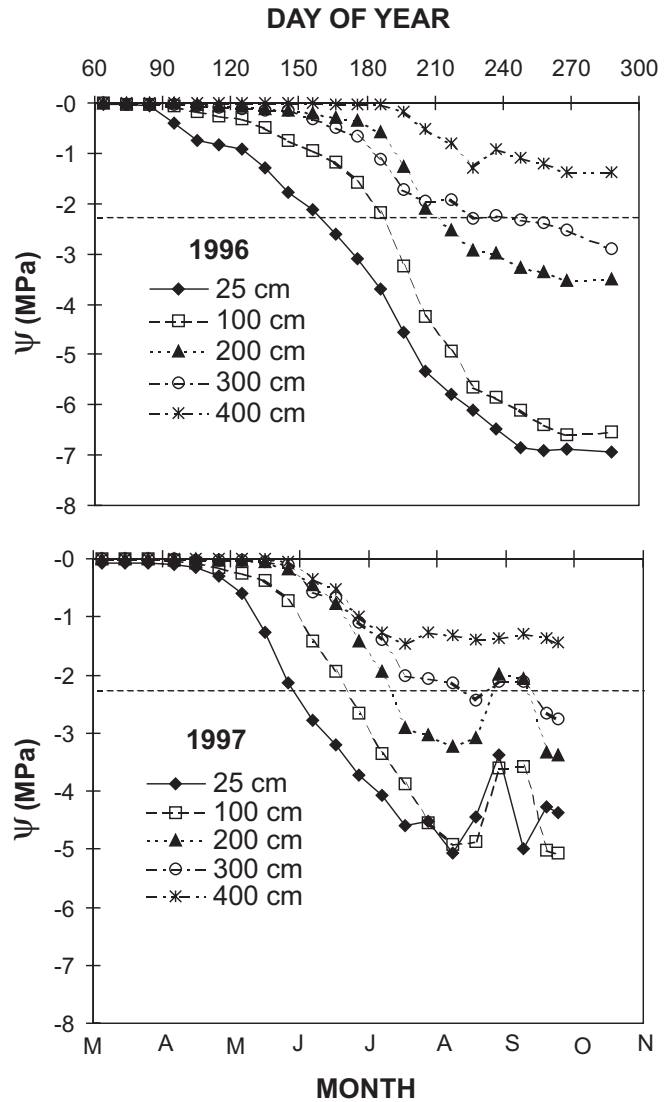
Discussion

Soil and weathered bedrock water depletion

Plant-available water was progressively depleted from shallower to deeper depths through the summer dry season. By mid-June in both years, soil water potentials were below -2.2 MPa (lower limit of plant-available water). We take this as evidence that plants were using water stored in the weathered bedrock as soil water was depleted. Similar regolith water depletion patterns were measured under a cover of whiteleaf manzanita (*Arctostaphylos viscida* Parry) in southwest Oregon, where Zwieniecki and Newton (1996) observed the manzanita roots penetrating fissures of weathered metasedimentary rock to >3 m depth. Roots occupied deep fractures in the weathered bedrock at our site as well.

As temperatures increased in spring and summer, water content decreased more rapidly in the soil (0–75 cm depth) than in the weathered bedrock (below 75 cm) (Fig. 2). While roots throughout the regolith allow for transpirational loss, the soil is also impacted by evaporative losses, a minimal process in the deeper zones. Disparate rates of water depletion between soil and bedrock were also observed under chaparral in southern California, with very little change in water content at the 300 cm depth (Sternberg et al. 1996). In the Jeffrey pine plantation, we observed water depletion of $\sim 0.05 \text{ cm}^3\cdot\text{cm}^{-3}$ in the weathered granitic bedrock at 300 cm depth (Fig. 2), despite a lower rooting density than in the surface soil (Hubbert et al. 2001). It appears that water was taken up concurrently by roots at both the shallow depths in the soil and at deeper depths in the bedrock throughout the season, although there was more rapid depletion of water at the shallow depths than at the deeper depths. Plants remove the deeper bedrock water as resistance to water uptake in the soil increases, even though the internal resistance to trans-

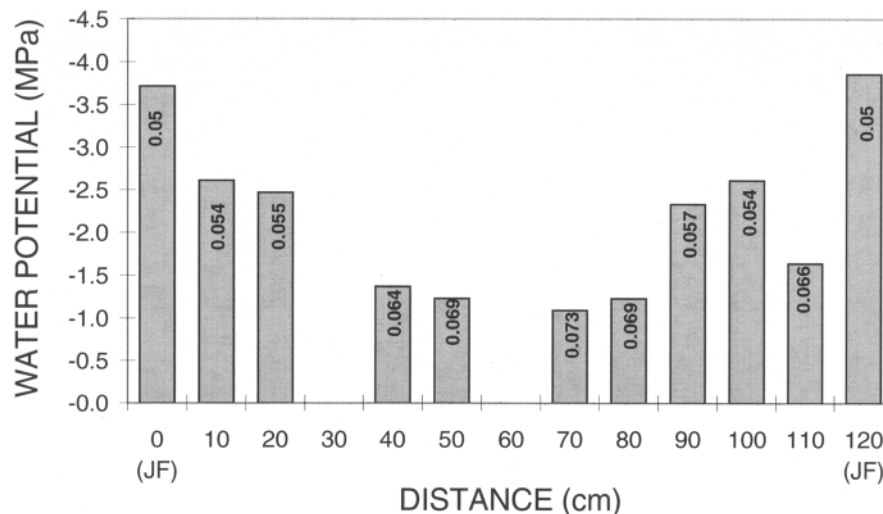
Fig. 4. Soil (25 cm depth) and bedrock (≥ 100 cm depths) water potentials as a function of depth during the dry seasons of 1996 and 1997. Each point represents the mean value from nine gypsum blocks. Horizontal broken line represents lower limit of plant-available water (-2.2 MPa). SE is ± 2.6 or less.



port increases as water is drawn from deeper depths. Continued depletion of water below $0.05 \text{ cm}^3\cdot\text{cm}^{-3}$ is likely a function of surface evaporation and uptake by manzanita at water potentials below -2.2 MPa (Fig. 2). This suggests that the permanent wilting point for manzanita needs to be redefined.

While snowmelt and above average winter precipitation probably recharged the soil to field capacity in the spring of both 1996 and 1997, this water was depleted by mid-June in both years (Fig. 3). For the remainder of the dry season, weathered bedrock provided the only water available to the plants except for rare and sparse rainfall (Fig. 1). Similarly, $\geq 90\%$ of the evapotranspirational demand of a southern California mixed conifer forest was found to be satisfied by water from weathered granitic bedrock at >120 cm depth

Fig. 5. Horizontal transect between two vertical joint fractures (JF) in weathered bedrock (Cr horizon) at the 150 cm depth from the soil surface (sampled 14 October 1996). Volumetric water content ($\text{cm}^3\cdot\text{cm}^{-3}$) values are shown in bar columns.



(Arkley 1981). The key role of weathered bedrock in supplying plant-available water depends upon sufficient winter precipitation to recharge the soil and bedrock. During a series of dry years, deeper bedrock is depleted by transpiration, and precipitation may be insufficient to effect recharge, so that very little stored water is available for plant use during the dry season. In any case, the soil and bedrock represent a substrate regolith continuum and must be considered together with regard to plant water supply.

Because roots in the bedrock are confined to joint fractures, where they are densely matted and flattened against fracture walls (Hubbert et al. 2001), the question arises as to how they extract water from the weathered rock matrix between the fractures. Distances between fractures ranged from 40 to 120 cm and were typically ~ 50 cm. Our data show that regolith water potentials between vertical fractures in the bedrock matrix became more negative adjacent to the fracture walls as compared with the center of the Cr matrix between the fractures (Fig. 5). This suggests that water moved along a strong negative pressure gradient toward the joint fractures. Root flattening probably enhanced water uptake by increasing the root surface contact with the fracture face, thus forming a bridge for water transport (Zwieniecki and Newton 1995). This may explain the more negative water potentials adjacent to the fracture walls, but it does not address the suggested transport of water from the center of the matrix. Unsaturated flow in similarly coarse-textured soils at water potentials < -0.1 MPa is typically on the order of $< 10^{-3} \text{ cm}\cdot\text{h}^{-1}$ (Jury et al. 1991). At this rate, it would take > 2000 days for water to travel the 60-cm distance from the center of the matrix block to the roots in the fracture that border it. This mechanism alone cannot explain water depletion between the fractures. While roots are apparently too large to penetrate microfractures that permeate the weathered rock matrix, ectomycorrhizae hyphae are sufficiently small ($< 20 \mu\text{m}$) and have been shown to function in water uptake by roots (Duddridge et al. 1980). Ectomycorrhizae hyphae can extend > 2 m from the infected root (Fogel 1983). Individual hypha and rhizomorphs (aggregated, coarse hyphal strands) may penetrate the Cr matrix and ab-

sorb the stored water and transport it to the roots. We did not assess this possibility directly, but we considered the pronounced heterorhizy of roots seen within joint fractures as evidence for ectomycorrhizal associations (Brundett et al. 1989; Hubbert et al. 2001).

Plant water status and rooting depth

Seasonal pattern of changes in ψ_{predawn} can provide evidence for differences in rooting depth among species (Davis and Mooney 1986). Shallow-rooted species generally show large annual fluctuations in plant water potentials and growth, whereas deep-rooted species display little or no annual fluctuation (Canadell and Zedler 1995). Greenleaf manzanita exhibited a large drop in ψ_{predawn} during the dry summer of 1996 (to -4.0 MPa). In 1997, ψ_{predawn} was maintained above -1.0 MPa, probably because late summer rainfall partially recharged the upper 25 cm of the soil (Figs. 1 and 3). Jeffrey pine showed little seasonal change in ψ_{predawn} during 1997 and only a slight change in 1996, suggesting that pine roots were deeper than those of manzanita and were able to access bedrock moisture for overnight recharge of plant tissue, even late in the season. Similar water potential patterns were found by DeLucia et al. (1988) on nutrient-poor soils derived from hydrothermally altered bedrock, with seasonal ψ_{predawn} decreasing slightly for ponderosa and Jeffrey pine (-0.4 to -0.9 MPa) and more dramatically for greenleaf manzanita (-1.0 to -3.0 MPa) as the dry season progressed.

It is recognized that ψ_{predawn} represents an integrated value of regolith water potential where roots are actively accessing water (Scholander et al. 1965; Percy et al. 1989). Predawn ψ can be used to estimate ψ_{soil} in the immediate proximity of active roots and as a baseline measure of plant water status (Pallardy et al. 1991). By comparing soil ψ and plant predawn ψ measurements of different species, an interpretation of depth at which roots are active can be made (Davis and Mooney 1986). By early September of 1996, ψ_{soil} at the 25, 100, and 200 cm depths was below -3.0 MPa, and ψ_{predawn} of manzanita was also below -3.0 MPa (Figs. 3a and 4). This suggests that active roots of greenleaf

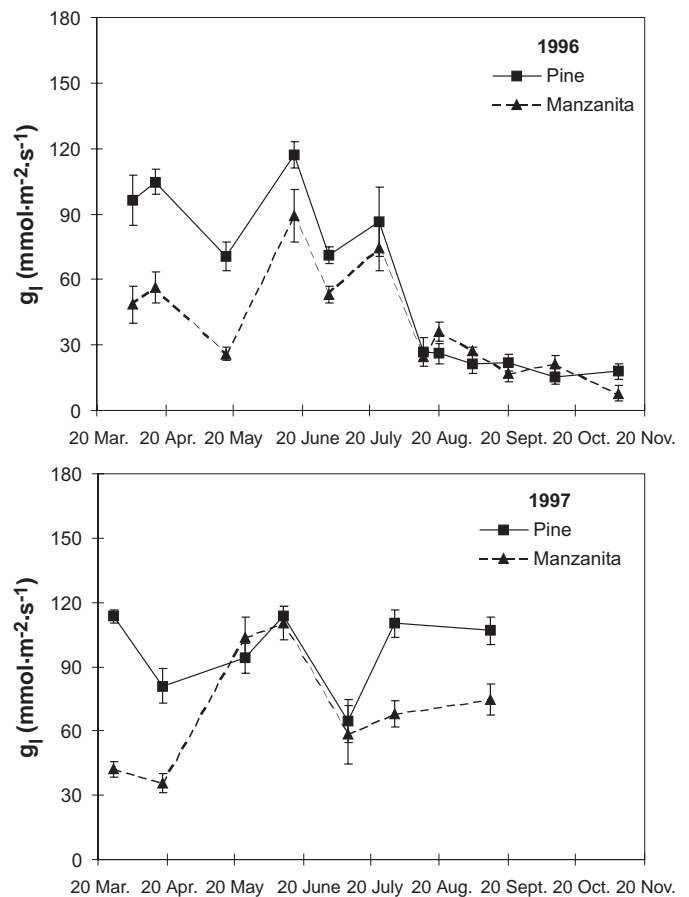
manzanita are within the upper 200 cm, a relatively shallow root system. On the other hand, the ψ_{predawn} of Jeffrey pine remained above -2.0 MPa through September of 1996, similar to substrate water potentials above -2.0 MPa at the 400 cm depth (Figs. 3a and 4).

Predawn water potentials indicated that pine always had access to plant-available water (water held above -2.2 MPa), but the high variability between ψ_{midday} and ψ_{predawn} suggests that other environmental factors controlled ψ_{midday} (Fig. 7). In contrast, the strong correlation between ψ_{midday} and ψ_{predawn} of manzanita (Fig. 7) suggests that the roots were tracking the plant-available water as the soil and bedrock matrix became progressively drier and less plant available, an indication that soil and weathered bedrock ψ contributed strongly to midday leaf water potential. Thus, there may be stratification in rooting depths between the two species, with manzanita roots active at shallow depths that reach low water potentials late in the season, and pine roots active at more considerable depth, in fractures of the bedrock, where water potential remained relatively high.

Stratification of Jeffrey pine and greenleaf manzanita roots may provide a mechanism by which the two species coexist on thin soils and compete for resources. Pine appears to rely on water stored in the bedrock during the summer dry season, whereas manzanita is able to access the remaining water in the soil, which is held at low (more negative) water potentials. Manzanita may even "steal" water from the pine. As the upper soil water potential becomes more negative than the internal water status of the pine, water drawn from the lower soil levels may leak into the drier soil for use by manzanita through hydraulic lift (Dawson 1993). A study by Zwieniecki and Newton (1996) showed that Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and ponderosa pine used water from the soil layer, but did not significantly deplete water from deeper parts of the profile, whereas Pacific madrone (*Arbutus menziesii* Pursh) and whiteleaf manzanita mostly used water stored in the rock layers to depths of 3 m. Possible explanations for the differences between the Zwieniecki and Newton (1996) study and ours include: (1) summer rainfall was more abundant and frequent during the summer at their site, allowing the Douglas-fir and ponderosa pine to fulfill water needs from the soil alone, and (2) differences in the available water capacity of the parent materials at the two sites ($0.124 \text{ m}^3 \cdot \text{m}^{-3}$ for weathered granitic bedrock at our site compared with $0.035 \text{ m}^3 \cdot \text{m}^{-3}$ for slightly to moderately weathered metasedimentary rock at their site). Rapid depletion of the small amount of water held in the metasedimentary rock would lead to more negative rock water potentials, yet the water could still be used by madrone and manzanita, which have both exhibited leaf water potentials as low as -5 MPa without changes in transpiration (Zwieniecki and Newton 1996).

When water is not available near the surface, shallow-rooted species will generally have lower g_1 than deeper-rooted species (Davis and Mooney 1986). By mid-June 1996, ψ_{soil} indicated that plant-available water in the upper 100 cm was depleted, so that both manzanita and pine had to extract water from the bedrock (Fig. 4). High g_1 in pine during the summer dry season suggests that pine had access to more water stored in the bedrock, satisfying atmospheric demand. Earlier seasonal decline of g_1 to lower values in

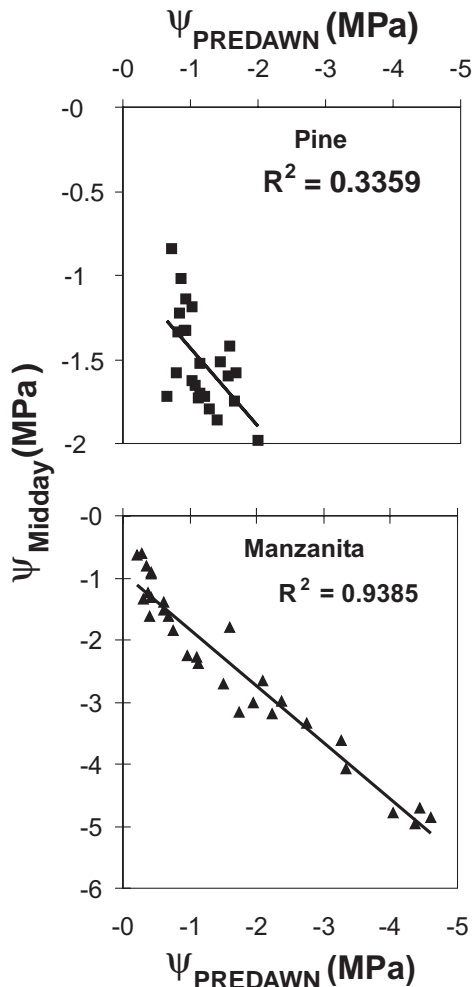
Fig. 6. Midday leaf conductance (g_1) in Jeffrey pine and green-leaf manzanita during the 1996 and 1997 growing seasons. Values are means of samples from nine greenleaf manzanita and nine Jeffrey pine. Error bars are 1 SE of the mean.



manzanita indicates limited access to bedrock water (Fig. 6). Davis and Mooney (1986) reported g_1 in intermediate rooted *Adenostoma fasciculatum* and shallow-rooted *Rhamnus californica* to be much lower than deeply rooted *Quercus durata* during August drought. Low values of g_1 for both pine and manzanita in mid-May of 1996 (Fig. 6) were likely the result of foggy (relative humidity = 98%), overcast conditions on the sampling day (Table 1).

Late summer rainfall was important to both species. Predawn water potential of both pine and manzanita increased sharply following 40 mm of rain in October 1996. This implies that there is rapid recovery and growth of surface roots in both species after 3 months of exposure to surface soil water potentials < -4.0 MPa (Ginter-Whitehouse et al. 1983; Smucker and Aiken 1992). In 1997, manzanita ψ_{predawn} did not show a sharp drop during late summer as it did in 1996, but instead remained near -1.0 MPa through September. Surface soil layers never reached the extremely dry levels in 1997 that they did in 1996 (Fig. 2). Rain events in July and September 1997 evidently supplied enough moisture to the soil so that ψ_{predawn} of the shallow-rooted manzanita was maintained at the higher level (Figs. 1 and 3). Similarly, a 24-mm rainfall penetrating to a soil depth of 20 cm resulted in an increase in ψ_{predawn} of shallow-rooted *Rhamnus californica*, but resulted in no response from deeper rooted

Fig. 7. Scatter diagram relating predawn leaf water potential (Ψ_{predawn}) to midday (solar noon) leaf water potential (Ψ_{midday}). Data represent all measured 1996 values. Predawn leaf water potential is interpreted to represent the water potential of the soil or bedrock where roots are accessing water.



Quercus durata (Davis and Mooney 1986). At our study site, both pine and manzanita responded to the July rain event with increased conductance (Fig. 6). This suggests that Jeffrey pine, while more deeply rooted than greenleaf manzanita, still depends on, and takes advantage of, surface soil moisture when it is available.

Conclusions

Roots of Jeffrey pine in a 30-year-old plantation can exploit bedrock joint fractures and use water that is stored within the weathered bedrock matrix. During the summer dry season, active roots of Jeffrey pine rely on water stored in the bedrock, whereas greenleaf manzanita accesses the remaining water in the soil, which is held at low (more negative) water potentials. Under drought conditions, plant-available water stored in the bedrock may be critical to tree survival, especially in areas where fire suppression has resulted in increased stand density and understory growth. Manzanita competition for water does not appear to be a ma-

nor negative influence on 30-year-old Jeffrey pines, especially in areas underlain by weathered granitic bedrock. From the results of our study, it is apparent that meaningful measurements of substrate water content must not stop at the soil-bedrock boundary, but should include the entire soil and weathered bedrock profile. Realizing that bedrock is a major water storage resource will allow for better forest management practices, including more accurate ecosystem and hydrologic models.

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