

Converging patterns of uptake and hydraulic redistribution of soil water in contrasting woody vegetation types

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Summary We used concurrent measurements of soil water content and soil water potential (Ψ_{soil}) to assess the effects of Ψ_{soil} on uptake and hydraulic redistribution (HR) of soil water by roots during seasonal drought cycles at six sites characterized by differences in the types and amounts of woody vegetation and in climate. The six sites included a semi-arid old-growth ponderosa pine (*Pinus ponderosa* Dougl. ex P. Laws & C. Laws) forest, a moist old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forest, a 24-year-old Douglas-fir forest and three Brazilian savanna sites differing in tree density. At all of the sites, HR was confined largely to the upper 60 cm of soil. There was a common threshold relationship between the relative magnitude of HR and Ψ_{soil} among the six study sites. Below a threshold Ψ_{soil} of about -0.4 MPa, overnight recharge of soil water storage increased sharply, and reached a maximum value of 80–90% over a range of Ψ_{soil} from ~ -1.2 to -1.5 MPa. Although amounts of water hydraulically redistributed to the upper 60 cm of soil were relatively small (0 to 0.4 mm day^{-1}), they greatly reduced the rates of seasonal decline in Ψ_{soil} . The effectiveness of HR in delaying soil drying diminished with increasing sapwood area per ground area. The relationship between soil water utilization and Ψ_{soil} in the 20–60-cm layer was nearly identical for all six sites. Soil water utilization varied with a surrogate measure of rhizosphere conductance in a similar manner at all six sites. The similarities in relationships between Ψ_{soil} and HR, soil water utilization and relative rhizosphere conductance among the six sites, suggests that, despite probable differences in maximum rooting depth and density, there was a convergence in biophysical controls on soil water utilization and redistribution in the upper soil layers where the density of finer roots is greatest.

Keywords: coniferous forest, *Pinus ponderosa*, *Pseudotsuga menziesii*, rhizosphere, roots, soil water potential, tropical savanna.

Introduction

Plant root systems not only extract water from the soil to supply the shoot, but also passively redistribute water within the soil profile according to gradients of soil water potential (Caldwell et al. 1998). The passive movement of water upward from moist to drier portions of the soil profile was originally termed “hydraulic lift” (Richards and Caldwell 1987, Caldwell and Richards 1989), but is now more commonly referred to as hydraulic redistribution (HR) because it has been shown that roots can also redistribute water downward (Burgess et al. 1998, 2001, Sakuratani et al. 1999, Smith et al. 1999) and laterally (Brooks et al. 2002). Hydraulically redistributed water may be available for reabsorption by the same plant or by neighboring plants of the same or other species that have active roots in the layer to which water is distributed (Corak et al. 1987, Richards and Caldwell 1987, Brooks et al. 2002, Moreira et al. 2003). The magnitude and consequences of HR are governed by multiple factors including water potential gradients between various points within the soil–plant system, relative resistances to water flow within the plant, resistances to water flow in the soil and the spatial distribution of plant root systems. In a recent modeling effort, the effects of some of these variables were quantified for an *Artemisia tridentata* Nutt. stand (Ryel et al. 2002). Although more than 50 cases of HR comprising both woody and herbaceous species have been reported (Jackson et al. 2000), there is relatively little information available on key controlling variables that may reveal common features of HR among sites with different vegetation and soils. Global surveys of rooting depth indicate that woody plants growing in a wide range of chronically and transiently water-limited ecosystems have root distributions that should allow HR to occur under appropriate conditions (Schenk and Jackson 2002a, 2002b).

The ability of plants to continue extracting water from the soil as soil water potential (Ψ_{soil}) declines is known to vary widely among different growth forms and species adapted to

different climatic regimes. The effects of Ψ_{soil} on water uptake and transpiration have been studied in a number of field- and greenhouse-grown cultivated species (e.g., Muchow et al. 1986), but relatively little information exists on water uptake and transpiration in relation to Ψ_{soil} for plants growing in natural environments where Ψ_{soil} may fall substantially below values normally experienced by cultivated plants. Moreover, responses observed when soil drying is imposed on plants in containers in a greenhouse may not reflect the ability of a species to continue taking up water in the field, when its surface roots are found in extremely dry soil and its deeper roots are found in relatively wet soil (Nilsen et al. 1983). Although Ψ_{soil} is often measured directly in studies of cultivated plants, in field studies conducted in natural environments, predawn plant water potential is more commonly used as a surrogate for Ψ_{soil} (Richter 1997, Ameglio et al. 1999). However, recent work demonstrating that predawn disequilibrium between plant and soil water potential can be substantial (Donovan et al. 1999, 2001, Bucci et al. 2004) suggests the need for caution in drawing inferences about Ψ_{soil} from plant Ψ , and in comparing surrogate measures of Ψ_{soil} based on Ψ of different species growing under different environmental conditions.

In this study, we compared soil water uptake and HR in relation to soil water status among sites dominated by different types and amounts of woody vegetation and subjected to different climatic regimes. The three temperate coniferous forests and three tropical savanna sites studied presented the requisite conditions for HR, namely prolonged seasonal drought and deep, well-drained soils that allow penetration of roots to depths of 2 m or more. Previous studies utilizing independent techniques demonstrated the existence of HR in the tropical savanna system (Scholz et al. 2002, Moreira et al. 2003) and in two of the three temperate coniferous forest sites studied (Brooks et al. 2002). We employed nearly identical measurement techniques and protocols at all sites, allowing detection of a number of similarities among sites in responses of HR and soil water uptake to Ψ_{soil} .

Materials and methods

Site descriptions and environmental conditions

Measurements were carried out in three temperate coniferous forest sites and three tropical savanna sites (Table 1). Although trees were a conspicuous component of the vegetation at all sites, the sites differed markedly with respect to the number of trees per ha and tree size, and therefore, the total basal sapwood area per ha. The two Douglas-fir (*Pseudotsuga menziesii*) stands were located in the Gifford Pinchot National Forest in southern Washington within and adjacent to the Wind River Canopy Crane Research Facility, about 25 km north of the Columbia River and 80 km east of Vancouver, Washington. The younger *P. menziesii* stand was logged about 24 years earlier. The soils at the *P. menziesii* sites were deep, well-drained, medium-textured sandy loams classified as medial, mesic Entic Vitrandis (Klopatek 2002). The ponderosa pine (*Pinus ponderosa*) stand was located in the Metolius Research Natural Area near the base of Black Butte (1950 m) in the Metolius River region of Oregon. The soil was a sandy loam with 73% sand, 21% silt and 6% clay (Law et al. 1999). The tropical savanna sites were located in the Instituto Brasileiro de Geografia e Estatística (IBGE) Ecological Reserve, an experimental field station located 33 km south of Brasília, Brazil. This type of savanna is known as Cerrado in Brazil, where it covers more than 1.5 million km² of land area. Cerrado vegetation is classified into various subtypes differing mainly in abundance of trees (Scholz et al. 2002). The soils are deep oxisols consisting of about 72% clay. Despite their high percentage of clay, they behave as coarser-textured soils and are extremely well drained.

Although three of the sites are located in the temperate zone and three in the tropics, their environmental regimes exhibit some important similarities (Table 2). The environmental similarities most relevant to the present study include a 3- to 6-month dry season with little rainfall, and the prevalence of high temperatures and atmospheric evaporative demand during the dry season. This combination of features leads to pro-

Table 1. Location and tree characteristics at the six study sites:

Site	Location	Coordinates	Elevation (m)	Trees ha ⁻¹	Age (years)	Sapwood basal area (m ² ha ⁻¹)
<i>Pseudotsuga menziesii</i> old-growth	Washington, USA	45°49' N, 121°57' W	355	437	450	20
<i>Pseudotsuga menziesii</i> 24-year-old	Washington, USA	45°49' N, 121°57' W	370	1529	24	18
<i>Pinus ponderosa</i> old-growth	Oregon, USA	44°30' N, 121°37' W	940	73	250	11
<i>Campo cerrado</i> savanna	Brasília, Brazil	15°56' S, 47°53' W	1100	1733	Unknown	4
<i>Cerrado sensu stricto</i> savanna	Brasília, Brazil	15°56' S, 47°53' W	1100	2690	Unknown	11
<i>Cerrado denso</i> savanna	Brasília, Brazil	15°56' S, 47°53' W	1100	2828	Unknown	18

Table 2. Selected climatic characteristics of the six study sites.

Site	Precipitation (mm)		Length of dry season (months)	Dry season temperature (°C)	
	Annual	Dry season		Maximum	Daily mean
<i>P. menziesii</i> old-growth	2500	~ 125	3–4	25	17
<i>P. menziesii</i> 24-year-old	2500	~ 125	3–4	25	17
<i>P. ponderosa</i> old-growth	550	< 100	5–6	24	14
<i>Campo cerrado</i> savanna	1500	~ 110	4–5	27	22
<i>Cerrado sensu stricto</i> savanna	1500	~ 110	4–5	27	22
<i>Cerrado denso</i> savanna	1500	~ 110	4–5	27	22

longed seasonal soil drying cycles at all sites. The dry season typically extends from late spring through early fall at the temperate coniferous forest sites, and from May into September (winter) at the Brazilian savanna sites. The results reported here were obtained between May and September 2001 at the *P. ponderosa* and Brazilian savanna sites, and between July and September 2002 at the two *P. menziesii* sites.

Soil water potential

Soil water potential at 20, 30, 40, 50, 60 and 100 cm in the coniferous forest sites and at 20, 30, 60 and 100 cm in the Brazilian savanna sites was continuously monitored with soil psychrometers (PST-55, Wescor, Logan, UT). Before placement in the field, the psychrometers were individually calibrated against salt solutions of known osmolality following the procedures of Brown and Bartos (1982). A set of psychrometers was installed in the vicinity of each of the four PVC access tubes used for measurement of soil water content (see Soil volumetric water content). Soil water potential was measured every 30 min with a 30-s cooling time for the Peltier effect and data were recorded with a data logger (CR-7, Campbell Scientific, Logan, UT). An integrated Ψ_{soil} for the 20–60-cm layer was estimated by averaging the values for all psychrometers between and including these depths. A Ψ_{soil} -based index of the relative magnitude of HR when Ψ_{soil} in the 20–60-cm layer was less than -0.4 MPa, was derived by dividing the overnight partial recovery of Ψ_{soil} by the absolute value of the difference between maximum and minimum values observed during the previous day (Ψ_{soil} recovery/ Ψ_{soil} decline). To predict the time course of Ψ_{soil} in the 20–60-cm layer in the absence of HR, absolute values of the differences between successive daily maximum and minimum values were subtracted from the initial value near the beginning of the soil drying cycle, when HR was negligible.

Soil volumetric water content

Soil volumetric water content was continuously monitored with multi-sensor frequency domain capacitance probes (Paltineanu and Starr 1997, Starr and Paltineanu 1998) at seven to eight depths concurrently at four locations per site. The highly sensitive probes, containing annular capacitance sensors (Sentek PTY LTD, Adelaide, Australia) mounted on a single plastic shaft, were placed in weatherproof PVC access tubes installed, with a minimum of 10 cm between successive sensors, to a depth of 2 m in the coniferous forest sites and 2.5 m in

the tropical savanna sites. Each sensor was monitored every 10 min and the measurements stored by a data logger (Model RT6, Sentek). The vertical arrangement of sensors in the upper 2 m of soil was similar, but not identical among all six sites. Sensors were located at 20, 30, 40, 50, 60, 100, 150 and 200 cm in the old-growth and 24-year-old *P. menziesii* sites, at 20, 30, 40, 60, 100, 150 and 200 cm in the old-growth *P. ponderosa* site, and at 20, 30, 60, 100, 150, 190 and 250 cm in the three Brazilian savanna sites. The results presented here include data recorded from sensors located in the upper 2 m of soil only. Each sensor was calibrated in the field for the air and water frequency reading endpoints for determination of the normalized frequency. The factory default calibration equation was used because an earlier study reported little variation in calibration over a broad range of soil types from different locations (Paltineanu and Starr 1997). The main advantages of this system are that: (1) the access tubes are minimally intrusive; (2) the sensors integrate over a 10 cm radial distance from the access tube; (3) the minimum sensor spacing of 10 cm allows detailed characterization of changes in water storage throughout the soil; and (4) the probes are relatively insensitive to fluctuations in soil temperature (3.5×10^{-4} change in volumetric water content $^{\circ}\text{C}^{-1}$ between 10 and 30 $^{\circ}\text{C}$; Paltineanu and Starr 1997). Soil water storage (measured in mm) was calculated by summing the water content for each 10-cm sensor. When there was a gap between sensors (e.g. 60 or 100 cm), water storage in the intervening layer was interpolated as an average of the sensors above and below the layer summed over the number of 10-cm intervals in the layer. Total daily water use was calculated as the difference between the maximum and minimum soil water storage measured within a daily time period. Net daily water use was calculated as the difference between one diel maximum and the next diel maximum in soil water storage. Daily partial recovery of soil water storage associated with HR for the 20–60-cm layer was estimated by subtracting diel minimum water storage values from the subsequent diel maximum values.

Because our objective was to assess the effects of soil water status on HR and soil water depletion across a range of sites, we attempted to standardize measurement conditions and minimize variability by reporting data from the probe where HR, and therefore root activity, was strongest at each site. However, we have also reported the mean values and ranges of HR activity recorded by the four probes at each site for the measure-

Table 3. Hydraulic redistribution and corresponding mean soil water potential (Ψ_{soil}) in the 20–60-cm soil layer at the six study sites. Mean ($\pm$ SE), maximum and minimum values of hydraulic redistribution represent mm of water per day added to the 20–60-cm soil layer as determined from four multi-sensor frequency domain capacitance probes installed at each site. Individual site means were calculated from 5 to 7 days of measurements when hydraulic redistribution was maximal.

Site	Ψ_{soil} (MPa)	Hydraulic redistribution (mm day ⁻¹)		
		Maximum	Minimum	Mean
<i>P. menziesii</i> old-growth	-0.62	0.18	0.01	0.08 $\pm$ 0.04
<i>P. menziesii</i> 24-year-old	-0.85	0.14	0.02	0.10 $\pm$ 0.04
<i>P. ponderosa</i> old-growth	-1.07	0.16	0.05	0.08 $\pm$ 0.02
<i>Campo cerrado</i> savanna	-1.38	0.22	0.15	0.18 $\pm$ 0.01
<i>Cerrado sensu stricto</i> savanna	-1.44	0.41	0.10	0.25 $\pm$ 0.07
<i>Cerrado denso</i> savanna	-1.45	0.18	0.12	0.15 $\pm$ 0.01

ment periods included in the present study (Table 3). In subsequent reports, additional data collected from all four probes at each site will be integrated to quantify ecosystem level HR and its spatial variability.

Soil zones

For subsequent analyses, the upper 2 m of soil was divided into two zones, 20–60 cm and 60–200 cm, based on observations of vertical stratification of soil water utilization and HR (Brooks et al. 2002) and the expectation that most of the finer roots are located in the upper 60 cm of soil (Schenk and Jackson 2002a and 2002b). Although previous observations indicated that root penetration below 2 m was likely at all sites (Jackson et al. 1999, Brooks et al. 2002), technical constraints prevented installation of soil psychrometers deeper than 1 m at all sites and frequency domain capacitance sensors deeper than 2.5 m in the savanna sites and 2 m in the temperate forest sites.

Results

Hydraulic redistribution

Representative time courses of soil water storage and Ψ_{soil} for three study sites during the peak of the dry season are shown in Figure 1. At all three sites, overnight partial recovery of soil water storage and Ψ_{soil} consistent with HR was confined largely to the upper 60 cm of soil. The magnitude of overnight partial recovery of soil water storage and Ψ_{soil} varied markedly among sites. In the *campo cerrado* savanna site, HR was sometimes sufficient to prevent net declines in soil water storage and Ψ_{soil} over periods of several days. At depths greater than 60 cm, soil water storage declined steadily in a “descending staircase” pattern in old-growth *P. ponderosa* and declined nearly linearly in 24-year-old *P. menziesii*.

The time courses of soil water storage and Ψ_{soil} suggested that significant HR did not occur until mean Ψ_{soil} in the 20–60-cm layer had fallen below -0.2 to -0.4 MPa. To examine

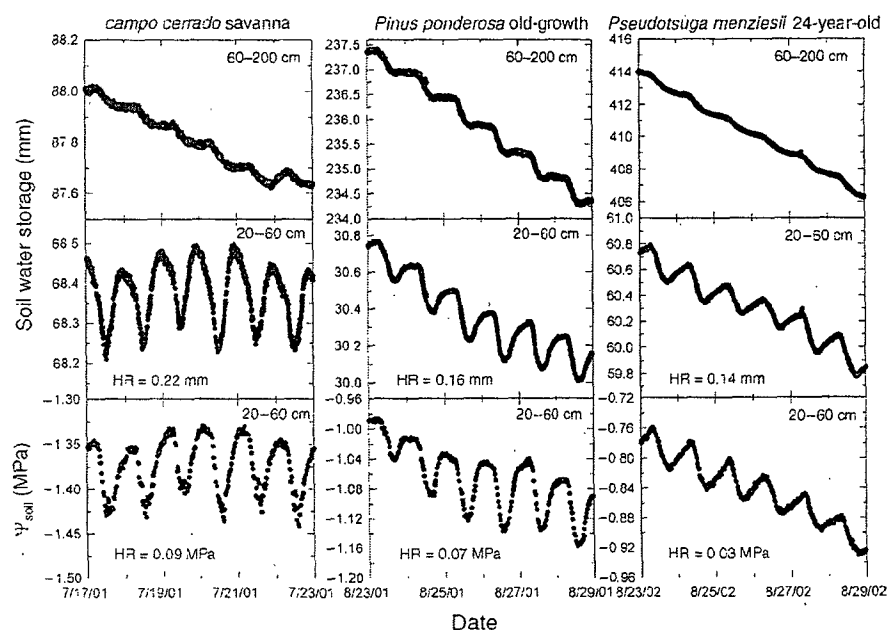


Figure 1. Partial seasonal time courses of soil water storage and soil water potential (Ψ_{soil}) in three of the study sites listed in Table 1. Mean daily hydraulic redistribution (HR) was estimated by subtracting diel minimum water storage values from the subsequent diel maximum values, and by taking the absolute value of the overnight partial recovery of Ψ_{soil} .

this relationship, daily amounts of water redistributed in the 20–60-cm layer were normalized by the total daily water utilization in that layer and plotted against the mean Ψ_{soil} in the 20–60-cm layer (Figure 2). The resulting relationship between normalized HR and Ψ_{soil} appeared to be similar among all study sites. No significant overnight replenishment of soil water storage was observed above a threshold range of Ψ_{soil} of -0.2 to -0.4 MPa. When Ψ_{soil} was below -0.4 MPa, overnight recharge of soil water storage increased sharply and appeared to reach a maximum value of 80–90% of the previous day's utilization over a range of Ψ_{soil} from -1.2 to -1.5 MPa.

Nearly continuous records of seasonal decline in Ψ_{soil} were available only for the three coniferous forest sites (Figure 3). The seasonal decline in Ψ_{soil} was slowest in the old-growth *P. menziesii* stand and most rapid in the 24-year-old *P. menziesii* stand. The predicted seasonal decline in Ψ_{soil} in the absence of HR (see Materials and methods) was substantially more rapid than the observed decline. Consistent with the pattern in Figure 2, notable deviation between observed and predicted time courses of Ψ_{soil} did not occur until Ψ_{soil} had fallen below about -0.2 to -0.4 MPa. Below this threshold, the deviation between observed values of Ψ_{soil} and predicted values in the absence of HR was greatest in the old-growth *P. ponderosa* site and smallest in the old-growth *P. menziesii* site, suggesting that HR was more effective in delaying the seasonal decline in Ψ_{soil} in the *P. ponderosa* site. Because there was nearly a two-fold difference in basal sapwood area between the two sites, these results suggest that variation in the effectiveness of HR in delaying seasonal declines in Ψ_{soil} may have been associated with variation in basal sapwood area. This possibility was evaluated by calculating the mean ratio of the overnight recovery of Ψ_{soil} to the total decline during the previous day as an alternative index of HR (see Materials and methods) and plotting it against basal sapwood area (Figure 4). Sufficient data to calculate this index were available only for the three coniferous forest sites plus the *campo cerrado* savanna site. Nevertheless, the strong negative correlation between basal sapwood area and the ratio of daily recovery to decline in Ψ_{soil} was con-

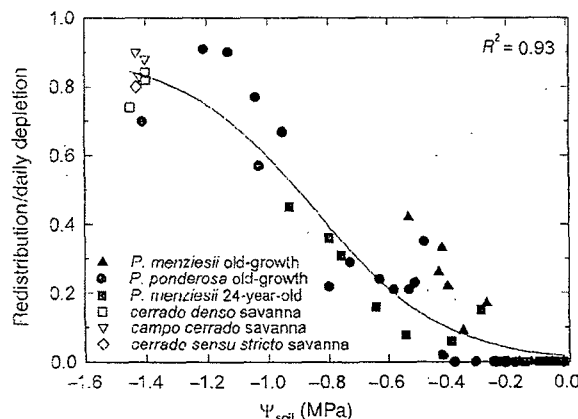


Figure 2. Influence of soil water potential (Ψ_{soil}) on hydraulic redistribution normalized by total daily water utilization in the 20–60-cm soil layer.

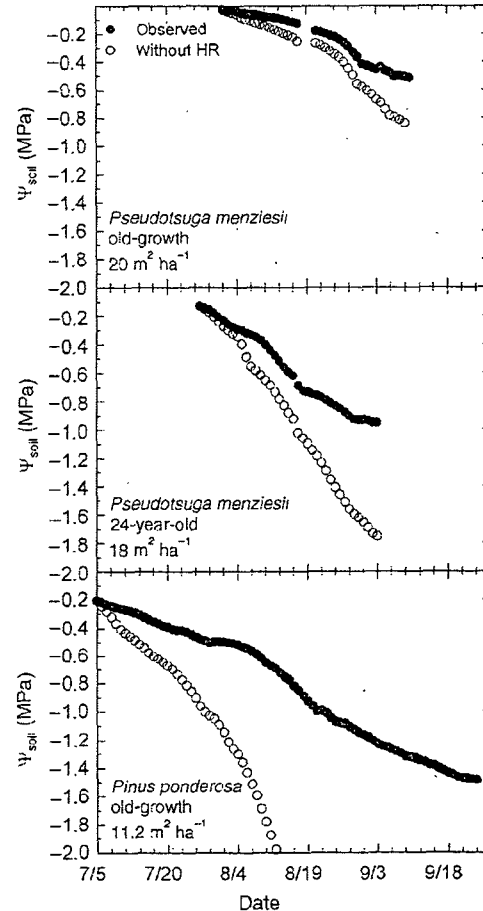


Figure 3. Seasonal courses of mean soil water potential (Ψ_{soil}) between depths of 20 and 60 cm. Seasonal courses of Ψ_{soil} in the absence of hydraulic redistribution were estimated as described in the text. Values of basal sapwood area per ha are shown.

sistent with the negative impact of stand sapwood area on the effectiveness of HR in delaying soil drying in the upper 60 cm of soil.

Soil water utilization

Because HR appeared to be largely confined to the upper 60 cm of soil, soil water utilization was characterized either in two zones, 20–60 cm and 60–200 cm, or the entire measured layer (20–200 cm). Total daily water utilization in the 20–60-cm soil layer declined exponentially with decreasing mean Ψ_{soil} of that layer (Figure 5). The relationship between soil water utilization and Ψ_{soil} appeared to be nearly identical for all six sites. Soil water utilization dropped steeply from 2 to 0.35 mm day^{-1} over the Ψ_{soil} range from zero to approximately -0.4 MPa, and then decreased asymptotically over the remaining range of Ψ_{soil} values observed. In contrast with the common relationship between Ψ_{soil} and soil water utilization in the 20–60-cm layer, each of the coniferous forest sites exhibited a unique relationship between Ψ_{soil} (20–60 cm) and water utilization in the 20–200-cm layer (Figure 6a). Data for the three

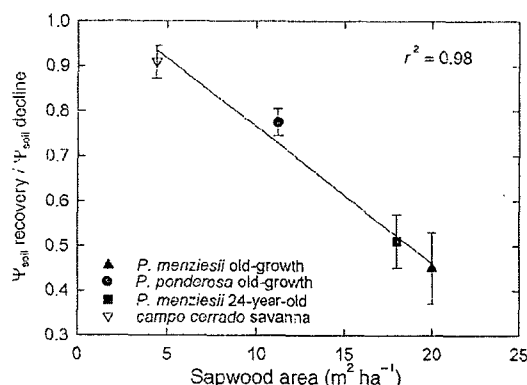


Figure 4. Relative hydraulic redistribution (expressed as the ratio of partial overnight recovery of soil water potential (Ψ_{soil}) to the previous day's decline) in relation to basal sapwood area for four study sites.

Brazilian savanna sites were pooled in order to obtain a more reliable curve fit. Over most of the observed Ψ_{soil} range, water utilization in the 20–200-cm soil layer was lower in the savanna sites than in any of the coniferous forest sites. Relative differences in the reliance on water extracted from progressively deeper soil layers with intensifying drought in the upper soil layers were assessed by expressing soil water utilization from the 60–200-cm layer as a percentage of total utilization from the 20–200-cm layer and plotting it against Ψ_{soil} in the 20–60-cm layer (Figure 6b). In the three coniferous forest sites, relative reliance on water extracted from deeper soil layers increased sharply with declining Ψ_{soil} to between about –0.2 and –0.4 MPa, then remained relatively constant at about 80 to 95% of total utilization from the 60–200-cm layer. In the Brazilian savanna sites, reliance on water extracted from the 60–200-cm layer was variable as Ψ_{soil} declined.

Discussion

There were notable similarities in relationships between Ψ_{soil}

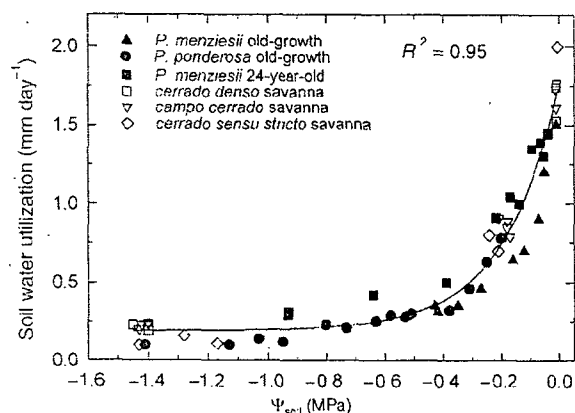


Figure 5. Total daily water utilization in the 20–60-cm soil layer in relation to mean soil water potential (Ψ_{soil}) in the same layer for the six study sites.

and HR and soil water utilization among the six sites differing in the abundance and size of woody plants, soil type and climate. The results suggest that despite probable differences in maximum rooting depth and density among the sites studied, there was a convergence in the biophysical controls on soil water utilization and redistribution in the upper soil layers where the density of finer roots is greatest.

Hydraulic redistribution

The apparent restriction of significant HR to the upper 60 cm of soil at all sites was probably a consequence of both the vertical distribution of roots and the vertical profile of Ψ_{soil} . In these and other sites dominated by woody vegetation, finer roots, from which release of hydraulically redistributed water is likely to occur, are largely confined to the upper 50 cm of soil (Schenk and Jackson 2002a, 2002b). The higher relative density of roots in the upper 60 cm, along with surface evaporation and water uptake by shallow-rooted species, accelerated soil drying relative to greater depths resulting in a steep vertical Ψ_{soil} gradient capable of driving water movement from deeper to shallower soil layers via roots. Although the mean minimum Ψ_{soil} in the 20–60-cm layer was about –1.5 MPa under the conditions of the present study, minimum values of –2.0 to –2.5 MPa at 20 cm were not uncommon. At 100 cm, the greatest depth at which soil psychrometers were installed, minimum Ψ_{soil} ranged from –0.1 to –0.4 MPa. Because soil water content continued to increase with depth below 100 cm, Ψ_{soil} was likely to have remained near zero below 100 cm. Maximum Ψ_{soil} gradients were thus as steep as 2.5 MPa m^{-1} between 100 cm and the layers above 60 cm. Previous observations indicated that roots penetrated to greater than 200 cm at all study sites (Jackson et al. 1999, Brooks et al. 2002).

Features of the soil–plant system responsible for the threshold response of HR to Ψ_{soil} (Figure 2) were not identified. The threshold range of Ψ_{soil} for induction of significant HR appeared to coincide with the range of Ψ_{soil} at which water utilization from the 60–200-cm layer relative to total utilization from the 20–200-cm layer approached its maximum (Figure 6b). Certainly, a Ψ_{soil} difference less than the 0.2 to 0.4 MPa required to induce significant HR would have been more than adequate to drive water movement through the soil external to the roots. However, soil hydraulic conductivity, and therefore unsaturated flow, begin to drop precipitously at values of Ψ_{soil} well above those required to induce HR (Sperry et al. 2002). Hydraulic redistribution is not expected to occur unless roots in drier soil layers effectively compete with the shoot as a sink for water taken up by deeper roots. The relative sink strength of the shoot versus roots in drier soil is determined both by their absolute values of Ψ and by relative resistances to water movement from deeper roots to shallow roots versus the shoot. The common relationship between HR and Ψ_{soil} among the six study sites probably reflects convergence in partitioning of relative hydraulic resistances between shoots and roots and convergence in nighttime values of shoot Ψ relative to that of shallow roots.

The maximum amount of water hydraulically redistributed to the 20–60-cm soil layer was approximately 0.4 mm day^{-1} with an overall mean of 0.14 mm day^{-1} among the six sites

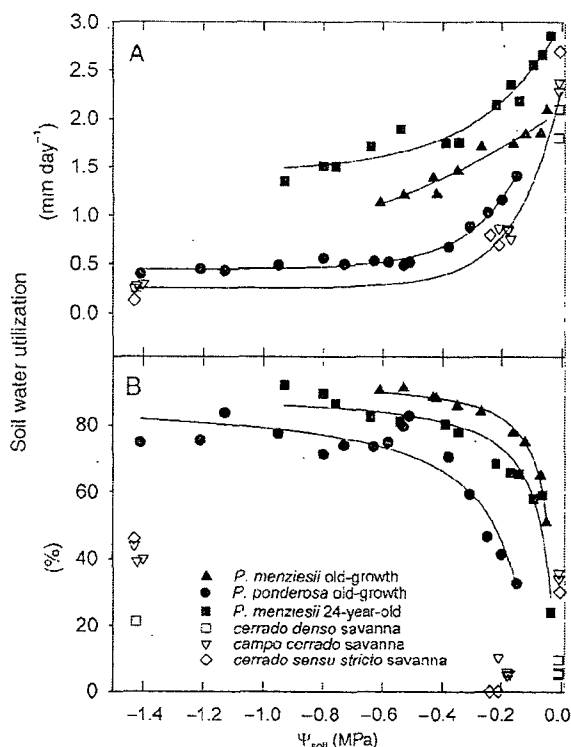


Figure 6. (a) Water utilization in the 20–200-cm soil layer, and (b) water utilization between 60 and 200 cm as a percentage of total utilization between 20 and 200 cm in relation to mean soil water potential (Ψ_{soil}) between 20 and 60 cm.

(Table 3). Although this was a relatively small amount of water, it was sufficient to replace 80–90% of the water used in the 20–60-cm layer under the driest conditions observed (Figure 2). Over the range of Ψ_{soil} in which HR was observed in the present study, the water potential of most soils change rapidly with small changes in water content. In the absence of HR, the rate of seasonal decline in Ψ_{soil} was predicted to be substantially greater (Figure 3), especially at sites with lower sapwood area per ground area (Figure 4). However, it should be noted that the procedure used to predict time courses of Ψ_{soil} in the absence of HR may have overestimated the rate of decline in Ψ_{soil} as Ψ_{soil} became increasingly negative. When Ψ_{soil} is extremely low, root water transport capacity may be impaired or lost because of the loss of hydraulic conductivity associated with xylem embolism (Sperry et al. 1998, Jackson et al. 2000, Domec et al. 2004). Thus, one of the primary consequences of HR in our study sites may have been maintenance of physiological activity in shallow roots rather than enhanced exploitation of soil water for transpiration. By delaying the onset of physiologically damaging Ψ in roots, HR may also be beneficial for mycorrhizae (Querejeta et al. 2003) and other soil organisms associated with roots.

Both the relative magnitude of HR and its effectiveness in retarding soil drying diminished with increasing dominance of woody plants expressed as sapwood area per hectare (Fig-

ures 3 and 4). At first sight, this observation may seem counterintuitive because greater dominance of woody plants implies a greater density of both deep and shallow roots to facilitate HR. However, a number of processes antagonistic to HR may be more important in dense stands of woody vegetation. For example, as long as the air temperature remains above dew point, nocturnal transpiration would prolong the period during which the shoot competes with shallow roots in dry surface soil as a sink for water absorbed by deeper roots. Significant nocturnal stomatal opening and transpiration are relatively common among woody species (Meinzer et al. 1988, Becker 1998, Benyon 1999, Donovan et al. 2003, Bucci et al. 2004). Even cuticular transpiration could sustain the transpiration-induced disequilibrium between the water potential of the shoot and that of the wettest portions of the soil profile that the roots are able to access. Rehydration is another process that would lead to competition between shoots and shallow roots for water uptake by deeper roots. Utilization of water stored in stems and other organs transiently uncouples canopy transpiration from water absorption by roots (Phillips et al. 1997, Goldstein et al. 1998). Internal water storage compartments are recharged at night and during other periods of low transpirational demand, and total storage capacity increases sharply with tree size (Goldstein et al. 1998, Phillips et al. 2003). Both nocturnal transpiration and rehydration may be responsible for the low but steady rates of sap flow that often persist throughout much of the night in stems of large trees (Phillips et al. 2003). Consistent with shoots behaving as persistent sinks for water absorbed by deep roots, severing a large descending root in the 24-year-old *P. menziesii* stand resulted in a 4.5 mm increase in soil water storage in the 20- to 60-cm layer in the vicinity of the root over a period of several days (unpublished observations).

Soil water utilization and rhizosphere conductance

Similarity among the six study sites in the dependence of soil water utilization on Ψ_{soil} in the 20–60-cm layer (Figure 5) was unexpected. These results suggest that, despite differences among sites in soil physical properties, woody plant density and probably shallow root density, exploitation of water resources in the upper portion of the soil profile was maximal, and that the ability of the different species to extract water from the soil as its Ψ declined was similar. Consistent with this, daily minimum leaf water potentials were similar among sites, ranging from -2.0 to -2.5 MPa under the driest conditions observed (data not shown). However, it is important to note that the behavior depicted in Figure 5 does not necessarily reflect that of total transpiration on a ground area basis because water uptake from only the upper portion of the rooting zone was considered. As more and more of the rooting zone is included in estimates of soil water utilization, the response of soil water utilization to Ψ_{soil} in the upper 60 cm should increasingly resemble that of transpiration on a ground area basis. Thus, when total water utilization in the 20–200-cm layer was determined, its response to Ψ_{soil} in the upper 60 cm differed among sites, with sites having the greatest amount of sapwood area tending to show higher rates of soil water utilization over

the entire range of Ψ_{soil} observed (Figure 6). Despite uncertainties concerning the relationship between soil water utilization and transpiration, convergence in the dependence of soil water utilization on Ψ_{soil} observed in the present study was in qualitative agreement with the response of transpiration to Ψ_{soil} in seedlings of several conifer species (Lopushinsky and Klock 1974) and with predictions from a model describing the dependence of transpiration on Ψ_{soil} when the root area:leaf area ratio was set at one (Sperry et al. 1998). Similar relationships between soil water utilization and Ψ_{soil} among the six study sites further suggests that soil porosity, or at least soil water release curves, did not differ markedly among them (Hacke et al. 2000).

Convergence in the relationship between soil water utilization and soil water potential (Figure 5) among sites suggests that water extraction from the upper portion of the soil profile was limited by rhizosphere conductance, and that during soil drying, rhizosphere conductance declined with Ψ_{soil} in a similar fashion at all sites. If the vapor pressure deficit remains high and relatively constant during soil drying, and if plant leaf area and hydraulic conductance remain relatively stable, then soil water utilization should be directly related to rhizosphere conductance. A linearized index of changes in rhizosphere conductance in the 20–60-cm layer during soil drying was obtained by plotting soil water utilization against $\ln(-\Psi_{\text{soil}}^{-1})$ (Figure 7a). However, the linearized relationship in Figure 7a cannot be extrapolated beyond the range of Ψ_{soil} observed because it does not account for the upper limit of water utilization as Ψ_{soil} approaches zero. Unlike the common relationship between rhizosphere conductance (as indicated by soil water utilization) and $\ln(-\Psi_{\text{soil}}^{-1})$ obtained for the 20- to 60-cm layer at all sites (Figure 7a), each of the coniferous forest sites exhibited a unique relationship, and the savanna sites a common relationship, between apparent rhizosphere conductance in the 20–200-cm layer and $\ln(-\Psi_{\text{soil}}^{-1})$ (Figure 7b). Nevertheless, the slopes of the four lines shown in Figure 7b were nearly identical, indicating that changes in the water status of the upper 60 cm of soil consistently predicted rates of change in water utilization and apparent rhizosphere conductance over a larger portion of the profile. Based on the model developed by Sperry et al. (1998), the results in Figures 5 and 7 further imply that xylem embolism did not limit soil water extraction over the range of conditions observed and that either xylem vulnerability curves were similar among dominant species at the study sites, or plant water potentials never crossed thresholds, causing significant embolism-induced loss of conductivity (Sperry et al. 1998).

Earlier empirical and theoretical studies differed in their conclusions concerning the relative magnitudes of rhizosphere and soil resistance during soil drying. In a study of sunflower, root plus interfacial (rhizosphere) resistance increased sharply and soil resistance was negligible as soil matric potential declined below threshold values of about -0.1 to -0.3 MPa (Bristow et al. 1984). In an *Artemisia tridentata* stand, rhizosphere conductance began to drop sharply when Ψ_{soil} reached about -0.5 MPa (Ryel et al. 2002). In the present study, when rhizosphere resistance was estimated as the ratio of the absolute value of Ψ_{soil} to daily soil water utilization, resistance be-

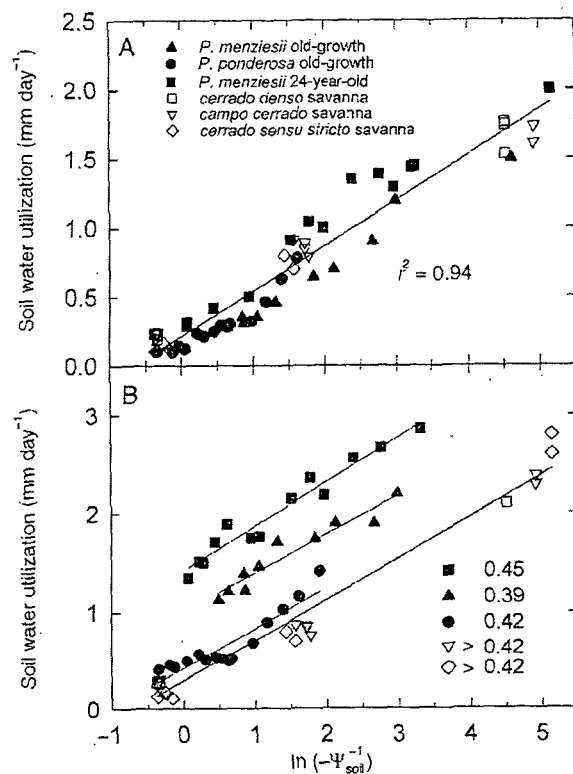


Figure 7. Linearized relationship between soil water potential (Ψ_{soil}) in the 20–60-cm layer and soil water utilization in the (A) 20–60-cm layer and (B) 20–200-cm layer. Soil water utilization is an index of apparent rhizosphere conductance. Numbers adjacent to the symbols in (B) represent slopes of the linear relationships.

gan to increase sharply when Ψ_{soil} fell below about -0.25 MPa (data not shown). However, a theoretical assessment of the relative importance of rhizosphere and soil resistances in drying soils indicated that rhizosphere resistance should not be limiting at moderate values of Ψ_{soil} unless the root length per unit ground area is low (Newman 1969).

In conclusion, our results have potential implications for modeling belowground processes involving movement and utilization of water in ecosystems dominated by woody plants. Given sufficiently similar soil physical properties and sufficient rooting depth to access freely available water, relationships such as those reported here may be sufficiently robust to allow useful predictions of soil water utilization and redistribution across a broad range of woody vegetation types.

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