

Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests

J. RENÉE BROOKS,¹ FREDERICK C. MEINZER,^{2,3} ROB COULOMBE⁴ and JILLIAN GREGG¹

¹ US EPA/NHEERL, Western Ecology Division, Corvallis, OR 97333, USA

² USDA Forest Service, Forestry Sciences Laboratory, 3200 SW Jefferson Way, Corvallis, OR 97331-4401, USA

³ Author to whom correspondence should be addressed (fmeinzer@fs.fed.us)

⁴ Dynamac Corporation, 200 SW 35th Street, Corvallis, OR 97333, USA

Received December 3, 2001; accepted April 6, 2002; published online October 1, 2002

Summary The magnitude of hydraulic redistribution of soil water by roots and its impact on soil water balance were estimated by monitoring time courses of soil water status at multiple depths and root sap flow under drought conditions in a dry ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) ecosystem and in a moist Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) ecosystem. The fate of deuterated water applied to small plots to create a strong horizontal soil water potential gradient was also monitored to assess the potential for horizontal redistribution of water and utilization of redistributed water by co-occurring shallow-rooted plants. In a 20-year-old Douglas-fir stand, approximately 28% of the water removed daily from the upper 2 m of soil was replaced by nocturnal hydraulic redistribution during late August. In an old-growth ponderosa pine stand, approximately 35% of the total daily water utilization from the upper 2 m of soil appeared to be replaced by hydraulic redistribution during July and August. By late September, hydraulic redistribution in the ponderosa pine stand was no longer apparent, even though total water use from the upper 2 m of soil was nearly identical to that observed earlier. Based on these results, hydraulic redistribution would allow 21 and 16 additional days of stored water to remain in the upper soil horizons in the ponderosa pine and Douglas-fir stands, respectively, after a 60-day drought. At both sites, localized applications of deuterated water induced strong reversal of root sap flow and caused soil water content to cease declining or even temporarily increase at locations too distant from the site of water application to have been influenced by movement of water through the soil without facilitation by roots. Xylem water deuterium values of ponderosa pine seedlings suggested utilization of redistributed water. Therefore, hydraulic redistribution may enhance seedling survival and maintain overstory transpiration during summer drought. These first approximations of the extent of hydraulic redistribution in these ecosystems suggest that it is likely to be an important process in both wet and dry forests of the Pacific Northwest.

Keywords: Douglas-fir, hydrogen isotope ratio, ponderosa pine, root sap flow, soil volumetric water content, soil water potential.

Introduction

One aspect of the structural complexity of forest canopies is the belowground root system architecture, which influences patterns of soil water utilization by trees and ultimately canopy transpiration. Deeply rooted trees and other plants can lift water hydraulically from moist soil horizons several meters below ground to drier portions of the soil profile where it is released into the soil. This redistributed water may be available for reabsorption by the same plant and by neighboring plants of the same or other species that have active roots in the same layer (Corak et al. 1987, Richards and Caldwell 1987). The process is thought to be largely passive, requiring only a water potential gradient from moist soil layers through the root xylem to dry soil layers, and a relatively low resistance to reverse flow from the roots. Although the direction of water movement is typically upward, towards drier, shallow soil layers, recent measurements of sap flow in taproots and lateral roots of trees have demonstrated that roots can also redistribute water either downward or laterally from moist surface soils to drier regions of soil (Burgess et al. 1998, 2001, Schulze et al. 1998, Sakuratani et al. 1999, Smith et al. 1999). Because it can be bidirectional and is apparently passive, “hydraulic redistribution” has been proposed as a more comprehensive term than “hydraulic lift” to describe the phenomenon (Burgess et al. 1998).

Hydraulic redistribution usually occurs at night when transpiration has diminished sufficiently to allow the water potential of the roots to exceed that of the drier portions of the soil profile. Evidence for hydraulic redistribution consists largely of time courses of soil water potential showing increasing water potential in drier soil layers during the night or other periods when transpiration is reduced (Richards and Caldwell 1987, Dawson 1993a, Yoder and Nowak 1999, Millikin Ishikawa and Bledsoe 2000). Deuterated water supplied to deep roots of shrubs has also been used to trace the movement of water to shallow roots of grasses (Caldwell and Richards 1989). Based on this and other evidence, it is believed that hydraulic redistribution can contribute significantly to the water balance, not only of the plant responsible for it, but also of

neighboring plants of other species (Dawson 1996). In addition to its potential positive influence on plant water balance during dry periods, hydraulic redistribution may also enhance availability of nutrients in shallow soil layers and facilitate the uptake of nutrients by shallow fine roots (Caldwell et al. 1998). Now that more than 60 cases of hydraulic redistribution have been reported (Jackson et al. 2000), there is reason to expect that its existence is widespread wherever conditions are conducive to its occurrence. However, the significance of hydraulic redistribution for the individual tree and ecosystem-level water fluxes remains to be evaluated.

The magnitude of hydraulic redistribution has been debated. Some studies have concluded that the quantities of water redistributed by this mechanism are minute (Song et al. 2000), whereas others have concluded that hydraulically redistributed water has a significant impact on plant drought tolerance and total water utilization (Wan et al. 2000). Ideally, the significance of hydraulic redistribution should be evaluated in ecosystems spanning a broad range of annual precipitation, such as the coniferous forests in the Pacific Northwest (Waring and Franklin 1979, Gholz 1982). In the drier sites of the Pacific Northwest, frequently dominated by ponderosa pine (*Pinus ponderosa* Dougl. ex Laws), annual precipitation may be as low as 300 mm, an amount too low to support forest vegetation in many areas. However, even forests growing at the wetter end of the precipitation gradient typically experience a prolonged summer drought leading to severe drying in the upper portion of the soil profile. These are conditions under which hydraulic redistribution, if present, is likely to have a significant impact on individual tree and ecosystem water budgets.

We monitored detailed time courses of changes in soil volumetric water content at multiple depths and root sap flow during portions of the summer drought season in two contrasting Pacific Northwest forest types: a ponderosa pine ecosystem receiving an average of 500 mm of precipitation annually, and a Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) ecosystem receiving 2500 mm of precipitation. In addition, the fate of deuterated water applied to small plots to create strong horizontal soil water potential gradients was monitored. Our objectives were to determine whether hydraulic redistribution of soil water by roots plays a role in the water economy of key Pacific Northwest forest types, and to obtain initial estimates of its magnitude and impact on soil water balance over the course of the summer dry season in forests experiencing contrasting climatic regimes.

Materials and methods

Site descriptions and environmental conditions

The measurements were carried out in the mid- to late summer of 2000 at two sites: one dominated by old-growth ponderosa pine and the other dominated by 20-year-old Douglas-fir. The ponderosa pine site was located at an elevation of 940 m near the base of Black Butte (1950 m), a volcanic cinder cone in the Metolius River region of Oregon (44°30' N, 121°37' W), and

contained 250-year-old trees with a mean diameter at breast height (DBH) of 65 cm. The sparse understory was dominated by bitterbrush, (*Purshia tridentata* (Pursh) DC), bracken fern (*Pteridium aquilinum* (L.) Kuhn) and other herbaceous species. The soil was a sandy loam with 73% sand, 21% silt and 6% clay (Law et al. 1999). Most of the site's mean annual precipitation of 550 mm falls during the autumn, winter and early spring. Measurements were carried out at this site from July 27 to August 15 and again from September 15 to 29. No measurable precipitation fell during the measurement periods and only 2.9 mm fell between the two periods. Total precipitation from June 1 through July 26 was 20 mm.

The Douglas-fir site was located at about 370 m elevation in the Gifford Pinchot National Forest in southern Washington 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 site was logged approximately 20 years earlier and contained a closely spaced stand of Douglas-fir trees about 16 m tall and 11 cm DBH forming a dense canopy with some overlapping of crowns. The soil was a medium-textured sandy loam classified as a medial mesic, Entic Vitrand (Klopatek 2002). Although mean annual precipitation at the site is about 2500 mm, summer droughts characterized by 3 or more months with no significant precipitation are common. Only 101 mm of precipitation was recorded at this site during the period between June 1 and August 18, with most of it falling in June. The only precipitation during the August 18 to 31 measurement period was 2 mm recorded on August 31. Besides site differences in precipitation regimes, summer temperatures and air vapor pressure deficits are lower at the Douglas-fir site. Although winter minimum temperatures are lower at the ponderosa pine site, snow accumulations are greater at the Douglas-fir site.

Soil water status

A multi-sensor, frequency domain capacitance technique (Paltineanu and Starr 1997, Starr and Paltineanu 1998) was used to monitor soil volumetric water content continuously at seven depths concurrently. These highly sensitive probes, containing seven annular capacitance sensors (Sentek PTY, Adelaide, Australia) mounted on a single plastic shaft, were placed in weatherproof PVC access tubes installed to varying depths at three to four locations at each site (see Figure 1). Measurements were recorded every 10 min and stored by a data logger (Model RT6, Sentek PTY). The minimum allowable spacing between successive sensors using this system was 10 cm. The initial goal was to monitor changes in soil water content between 0.2 and 2 m at all probe locations. However, obstructions in the soil, such as rocks and roots, prevented the installation of access tubes to a depth of 2 m in most locations. Nevertheless, measurement depths between 0.2 and 1 m were comparable for all probe locations at both sites, with Probes 1 to 4 having sensors at 20, 30, 40, 60 and 100 cm. In addition, Probe 1 had sensors at 80 and 130 cm, Probe 2 at 80 and 110 cm, Probe 3 at 150 and 190 cm and Probe 4 at 150 and 180 cm. 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 (Paltineau and Starr 1997). The main advantages of this system are: (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 $^{\circ}\text{C}$ (Paltineau and Starr 1997)). Soil water storage (in mm of water) was calculated by summing the water content for each 10-cm sensor. When there was a gap between sensors, such as between 80 and 100 cm, water content in the intervening layer was interpolated as an average of the sensors above and below the layer. Total daily water use was calculated as the difference between the maximum and minimum soil water content measured within a daily time period. Net daily water use was calculated as the difference between one diel maximum to the next diel maximum in soil water content. To estimate the additional days of stored water provided by hydraulic redistribution before a given soil water content was reached, we calculated the number of days required to reach that water content in the absence of hydraulic redistribution using the mean total daily water use (without nightly partial recovery), which was then subtracted from the estimated number of days required to reach the same water content in the presence of the measured net daily decline in water content (with nightly partial recovery).

In addition, soil water potential was measured at the ponderosa pine site during the summer of 2001 with soil psychrometers (PST-55, Wescor, Logan, UT) placed at 20, 30, 40, 50, 60 and 100 cm depth to permit comparison with concurrent measurements of soil water content. Before placement in the field, the psychrometers were individually calibrated against salt solutions of known osmolality following the procedures of Brown and Bartos (1982). The psychrometers were installed in June within 1 m of a 2-m-long soil water content probe access tube and the measurements reported here were made during August. Because the psychrometric measurements were part of a separate field effort initiated the following year at a location approximately 100 m from the original site, the sensor locations are not depicted in Figure 1. Psychrometric data are included here to allow a comparison between soil moisture and soil water potential measurements at the same depths and similar locations, but were not used in other calculations presented here. Soil water potential was measured every 30 min with a 30-s cooling time for the Peltier effect and data were recorded by a data logger (CR-7, Campbell Scientific, Logan, UT).

Deuterated water experiments

To measure the response to a strong lateral water potential gradient in the soil, 1-m² watering plots were established at the edges of the crown areas of three target trees at each site (see

Figure 1). A circular plastic barrier was placed around the plots to prevent runoff and ensure that all the water infiltrated into the soil within the plot. Seven hundred liters of water enriched with deuterated water to +1300‰ were applied with a watering wand at a slow trickle to the plots over 3 days: September 19–21 in the old-growth ponderosa pine stand and August 28–30 in the Douglas-fir stand. Samples for hydrogen isotope analysis in plant and soil water were collected in glass vials sealed to prevent evaporation. Samples were collected on four occasions: before the application of deuterated water and again 3, 5 and 8 days after irrigation began at the Douglas-fir site, and 3, 5 and 11 days after irrigation at the ponderosa pine site. Tissue samples for water extraction were collected from trees with a 12 mm diameter increment borer (Haglöf, Långsele, Sweden), and suberized branch or stem tissue was clipped from other plants. Plant samples were collected at midday when transpiration was near its maximum. Soil samples were collected at 10 cm depth before dawn when the proportion of redistributed water in the soil was expected to have been at its maximum.

Water was extracted from the plant and soil samples by cryogenic vacuum distillation (Ehleringer and Osmond 1989, Dawson 1993b). Water samples were analyzed for hydrogen isotope ratios on an isotope ratio mass spectrometer (Delta plus, ThermoQuest Finnigan, Bremen Germany) interfaced with a high temperature conversion/elemental analyzer (TC/EA, ThermoQuest Finnigan) located at the Integrated Stable Isotope Research Facility at the Western Ecology Division of the EPA, Corvallis, OR. All hydrogen isotope ratios are expressed as δD values relative to Vienna-standard mean ocean water (V-SMOW) in ‰:

$$\delta\text{D} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) 1000, \quad (1)$$

where R is the ratio of deuterium to hydrogen atoms of the sample and the standard V-SMOW. Measurement precision was 2‰.

Root sap flow

Root sap flow was measured using the thermal dissipation technique (Granier 1987) modified to permit the direction of flow to be detected (J.R. Brooks and R. Coulombe, unpublished data). In its original form, this technique relies on a probe that indicates the magnitude of flux by measuring the difference between a heated temperature sensor and a single unheated reference temperature sensor and is therefore insensitive to the direction of flow and unsuitable for monitoring reversal of flow in roots associated with hydraulic redistribution (Burgess et al. 2000a). When an additional reference sensor and a directional probe were added, the thermal dissipation method became highly sensitive for detecting reversal of flow (J.R. Brooks and R. Coulombe, unpublished data).

Root sap flow was monitored in two roots on one of the target trees for the deuterated watering experiment (described above) in each ecosystem: one root on the side where water

was applied, and one root on the opposite side (see Figure 1 for locations at each site). In the old-growth ponderosa pine stand, sap flow sensors were installed on 80- (R1) and 70-mm (R2) diameter roots, and in the Douglas-fir stand on 35- (R1) and 45-mm (R2) diameter roots. These large lateral roots were traced by probing the soil from the base of the tree a distance of about 1–2 m, and then about 30 cm of soil was excavated for installation of the probes. For the flux magnitude probe, a cylindrical heated temperature sensor 10 mm in length was inserted into the xylem in the center of the exposed root. Two unheated reference temperature sensors (10 mm in length) were placed axially 100 mm upstream and downstream from the heater sensor and wired to measure the temperature differences between the heated and unheated sensors. For the directional probe, two thermocouples were inserted 8 mm axially to a depth of 7.5 mm upstream and downstream from the heater probe. The movement of the heated water raised the temperature of the downstream thermocouple relative to that of the upstream thermocouple, providing a highly accurate and sensitive gauge to the direction of flow (J.R. Brooks and R. Coulombe, unpublished data). The temperature of the reference probe that was determined to be upstream of the direction of flow was used to calculate sap flux density ($\text{g m}^{-2} \text{s}^{-1}$; Granier 1987). Sap flow moving acropetally (toward the tree) was indicated as positive, whereas sap flow moving basipetally (away from the tree) was indicated as negative.

Results

Time courses of soil water content at both sites were consistent with nocturnal redistribution of soil water by roots. At the ponderosa pine site, soil volumetric water content at both 20 to 60 cm and 60 to 100 cm exhibited transient nightly increases during July and August rather than the steady “descending

staircase” diel pattern of soil water depletion expected in the absence of hydraulic redistribution (Figure 2). In the upper soil layer (20–60 cm), total daily water use ranged between 0.20 and 0.22 mm day^{-1} for the three different probes. However, the net water use, which included the nightly increase due to redistribution, was lower, ranging between 0.13 and 0.19 mm day^{-1} . A similar pattern was observed in the deeper soil layer (60–100 cm). The amount of water redistributed to these soil layers at night relative to total daily soil water utilization ranged from 14 to 35% (mean = 21%) between 20 and 60 cm depth and from 22 to 39% (mean = 29%) between 60 and 100 cm depth for the three probe locations. For the probe extending the deepest into the soil (190 cm), about 35% of total daily water use of 0.77 mm from the upper 2 m of soil appeared to be due to hydraulic redistribution during July and August (Figure 3a). Comparable results were obtained for another probe (Probe 4), which had its deepest sensor at 180 cm (data not shown). If hydraulic redistribution had not occurred, the soil water content observed at the end of the 19-day monitoring period shown in Figure 3a would have been attained about 6 days sooner (Figure 3a, dashed line). By mid- to late September, the transient nighttime increase in soil water content characteristic of hydraulic redistribution was no longer apparent, even though total daily water use from the upper 2 m of soil was nearly identical to that observed during July and August (Figure 3b).

Diel oscillations in soil water content between 20 and 60 cm at the ponderosa pine site in August 2001 were also reflected in psychrometric measurements of soil water potential at the same depths (Figure 4a and 4b). Diel fluctuations in soil water potential and water content were essentially synchronous and therefore highly correlated ($r^2 = 0.95$). The fluctuations in soil water potential and water content were not significantly correlated with fluctuations in soil temperature ($r^2 = 0.05$ and 0.12,

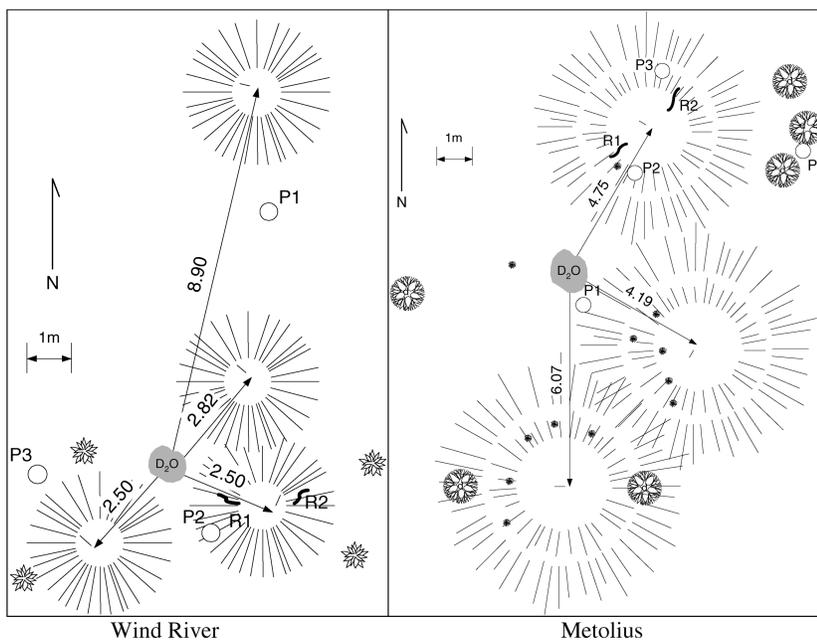


Figure 1. Stem maps of the two study sites. Area marked D_2O (deuterated water) is where water with a δD signal of +1300‰ was applied to the soil. Distances from the water to each target tree are given in meters. Circles indicate the location of soil water content probes and probes are labeled P1–P4. Roots where root sap flow was measured are labeled R1–R2. The symbols indicate other plants sampled for D_2O . In the Wind River Douglas-fir stand, the other species sampled was *Berberis nervosa* Pursh (Oregon grape). In the Metolius ponderosa pine stand, the small symbols represent ponderosa pine seedlings and the larger symbols represent *Purshia tridentata* (bitterbrush) plants.

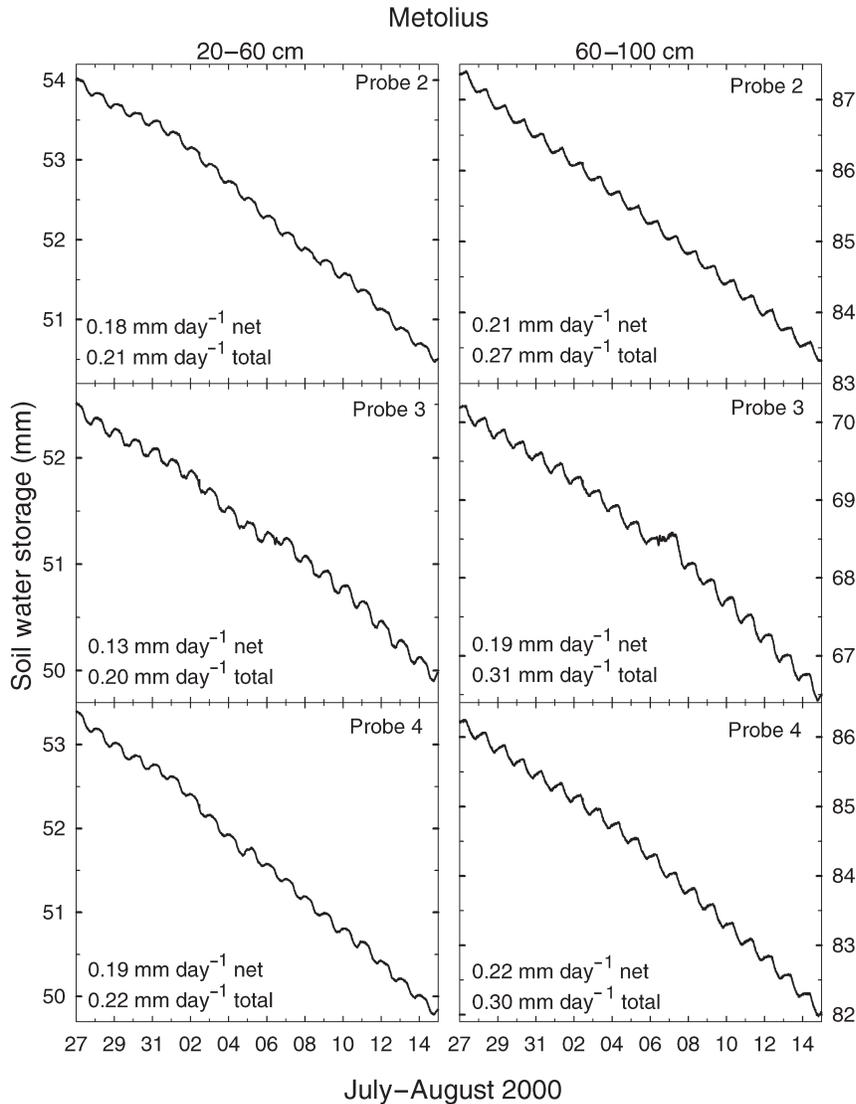


Figure 2. Time courses of soil volumetric water content over two depth ranges at three probe locations in an old-growth ponderosa pine stand (Metolius). Values represent total water content over the entire depth ranges shown. Data were obtained from sensors at 20, 30, 40 and 60 cm for the 20–60 cm depth range, and from sensors at 60 and 100 cm for the 60–100 cm depth range. Probe locations are given in Figure 1. Total daily water use (mm day^{-1}) was calculated as the difference between the daily maximum and minimum soil water content, and net daily water use was calculated as the difference between the maximum soil water content from one day to the next.

respectively), which were relatively small and ranged from about $2.5\text{ }^{\circ}\text{C}$ at 20 cm to $<1.5\text{ }^{\circ}\text{C}$ at 60 cm. Mean soil water potential for the period shown ranged from about -0.77 MPa at 20–60 cm depth to -0.15 MPa at 1 m depth, indicating a po-

tential driving force of at least 0.6 MPa for hydraulic redistribution. Total soil water content between 20 and 60 cm was somewhat lower during August 2001 than during August 2000 (cf. Figures 2 and 4b), but the extent to which this difference

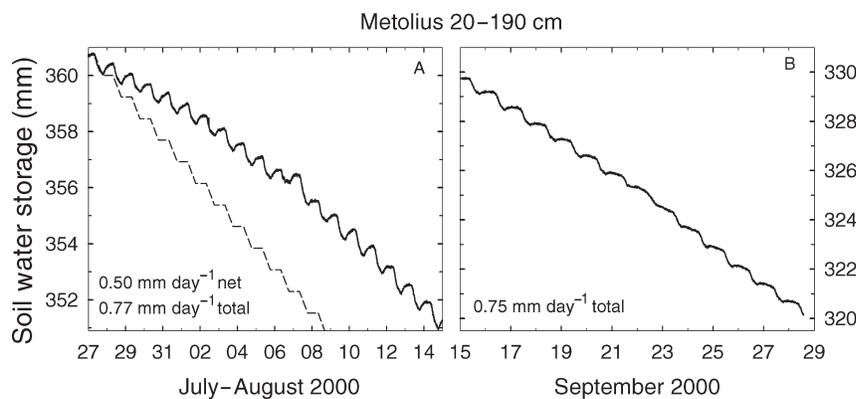


Figure 3. Time courses of total soil volumetric water content between 20 and 190 cm depth (solid lines) measured by Probe 3 at the ponderosa pine site (Metolius). Data were obtained from sensors at 20, 30, 40, 60, 100, 150 and 190 cm. The dashed line represents the predicted time course of soil water content in the absence of nightly partial recharge.

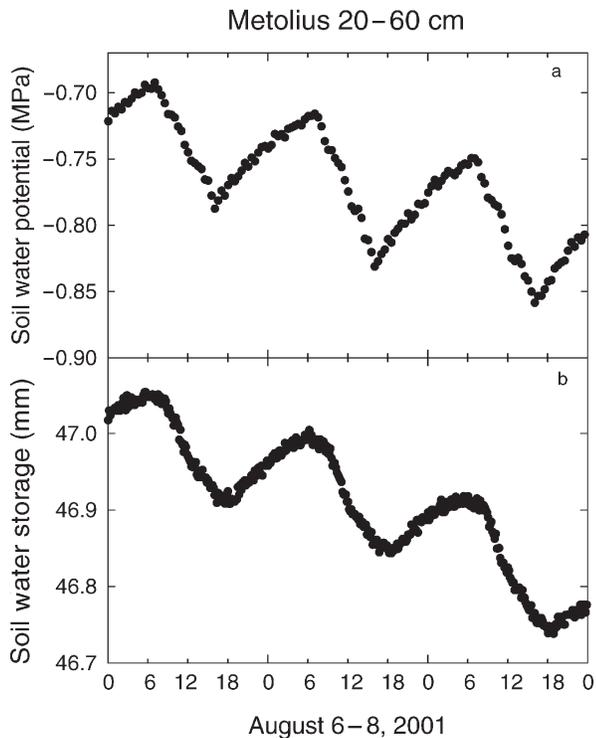


Figure 4. Time courses of mean soil water potential and total soil volumetric water content between 20 and 60 cm at the ponderosa pine site (Metolius) from August 6 to 8, 2001. Soil psychrometers were located at 20, 30, 40, 50 and 60 cm and frequency domain capacitance sensors at 20, 30, 40 and 60 cm.

was associated with year-to-year variation versus the difference in soil probe locations is unknown.

At the Douglas-fir site (Wind River), time courses of soil water content between 20 and 60 cm depth during the latter part of August (Figure 5) were similar in appearance to those observed at the ponderosa pine site between late July and mid-August. At Wind River, the apparent contribution of hydraulic redistribution to total daily soil water use between 20 and 60 cm depth ranged from 40 to 41% for the three probes. However, in contrast with the ponderosa pine site, no transient nighttime increase in soil water content was observed over the 60 to 100 cm depth range (Figure 5). About 28% of the total daily water use of 1.23 mm from the upper 2 m of soil appeared to be derived from hydraulic redistribution during late August (Figure 6). In the absence of hydraulic redistribution, the soil water content observed at the end of the 10-day monitoring period shown in Figure 6 would have been attained about 2 days sooner (Figure 6, dashed line).

Applications of 700 l of deuterated water to 1-m² plots to create strong horizontal soil water potential gradients (Figure 1) provided further evidence for hydraulic redistribution at both sites. At the ponderosa pine site, gradual application of water over a 3-day period induced reverse nocturnal sap flow in a root located approximately 4 m away from the point where the water was applied (Root 1, Figure 7a). Before application of water, the root exhibited positive flow during the day and

essentially zero flow at night. Water content in the upper 60 cm of the soil at a probe located 0.5 m away from the watering site began to increase on the final day of application and continued for about 5 days (Figure 7b, Probe 1). During this period, the magnitude of nocturnal reverse flow in Root 1 also increased (Figure 7a), indicating that the fine roots associated with Root 1 were in relatively dry soil and another root, not measured, supplied water from the irrigation site. Total water content in the upper 60 cm of soil near the root that exhibited nocturnal reverse flow (Probe 2) did not change significantly during the same time period (Figure 7b). However, at 20 cm depth, soil water content stopped declining and began to increase slightly after reverse flow had reached its maximum (Probe 2, Figure 7c). Daily courses of sap flow in a second root on the opposite side of the north tree (Figure 1) were unaffected by the irrigation and reverse flow was not significant in this root (Root 2, Figure 7a), indicating that the resistance to flow across the stem base must have been relatively large. In the soil surrounding the probe farthest from the point of water application, water content at 20 cm depth ceased declining after reverse flow in Root 1 peaked (Probe 4, Figure 7b) indicating that, despite the lack of measured reverse flow in Root 2, some hydraulic redistribution occurred on this side of the tree. To determine whether cessation of soil water depletion at 20 cm may have been associated with a period of reduced evaporative demand or other constraint on soil water depletion by the vegetation, time courses of soil water content at 100 cm depth were also examined. Unlike the pattern observed at 20 cm depth, water content at 100 cm declined steadily during the entire monitoring period for the irrigation experiment (Figure 7d, Probes 2 and 4).

A similar irrigation experiment conducted at Wind River yielded comparable results, indicating that Douglas-fir root systems also hydraulically redistributed soil water. Prior to irrigation with deuterated water, sap flow in both the stem and root of the same tree were positive during the day and zero at night (Figure 8a). During the night, immediately following the initiation of irrigation, the direction of sap flow in the root reversed, indicating that water was moving from the root out toward the soil. The magnitude of reverse flow in the root increased during the second night following the onset of irrigation. Consistent with the onset of reverse flow in the root, soil water content 2 m from the watering site, beside the tree where root sap flow was measured (Figure 1), continued to exhibit daily cycles, but temporarily ceased declining (Figure 8b). However, soil water content at another probe located 6 m from the site of water application continued to exhibit an uninterrupted net decline superimposed on daily cycles of partial nighttime recovery (Figure 8c). A partial excavation of root systems of comparable trees located approximately 100 m away using an air spade revealed an extensive network of woody lateral roots and numerous woody sinker roots extending to depths greater than the 1.5 m of soil that was excavated (T. Hinckley, University of Washington, personal communication).

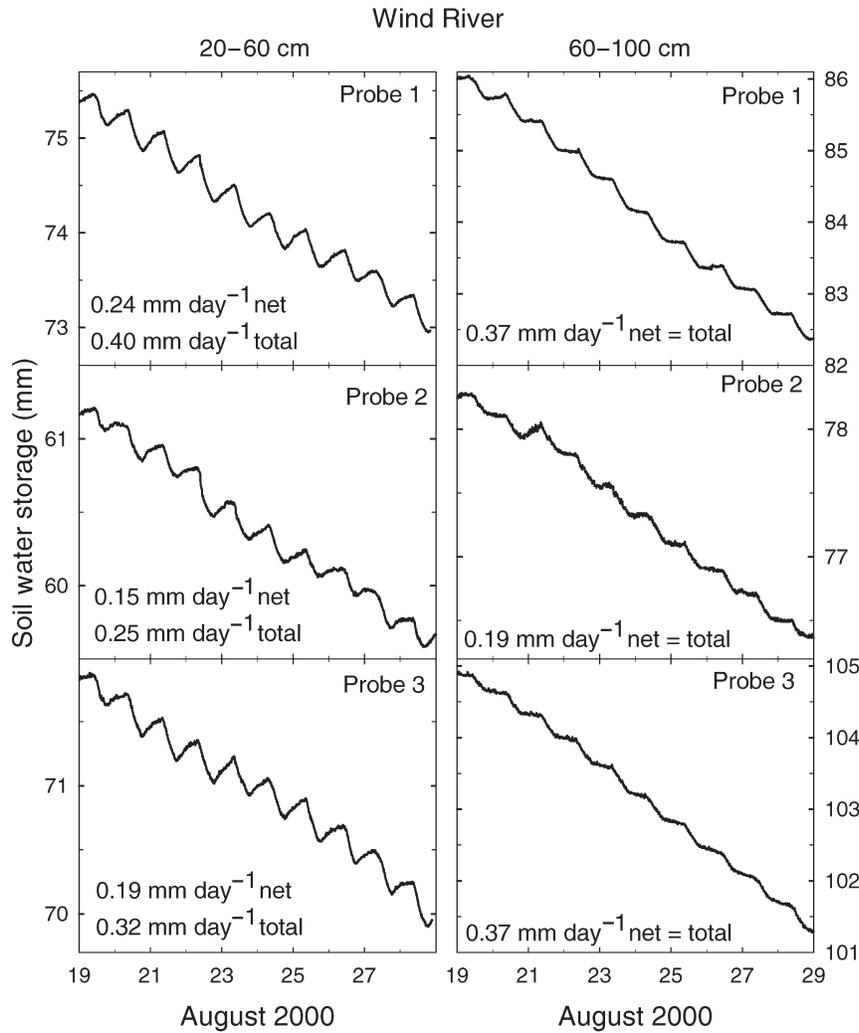


Figure 5. Time courses of total soil volumetric water content over two depth ranges at three probe locations in a Douglas-fir stand in the Wind River region in southwestern Washington. Sensor configurations were as described in Figure 2. Probe locations are given in Figure 1.

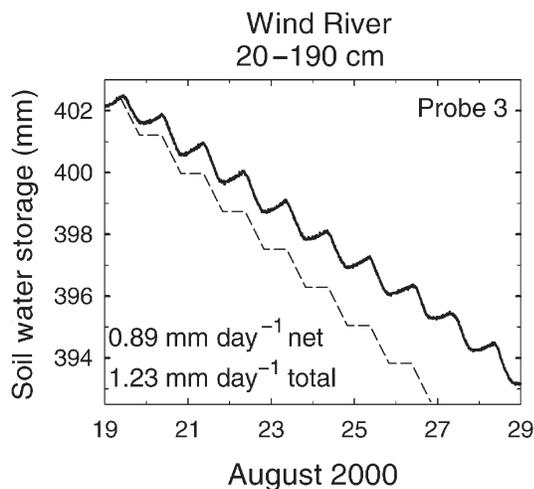


Figure 6. Time course of total soil volumetric water content between 20 and 190 cm depth (solid line) measured by Probe 3 at the Wind River site. Data were obtained from sensors at 20, 30, 40, 60, 100, 150 and 190 cm. The dashed line represents the predicted time course of soil water content in the absence of nightly partial recharge.

There was some redistribution of deuterated water at each site. At the ponderosa pine site, deuterated water was not detected in the target trees on either the third or fifth day after watering. However, 11 days after watering, 11% of the water collected from one target tree ($\delta D = +64\text{‰}$, Figure 9) originated from the deuterated irrigation water. Deuterated water was not found in samples collected from the north target tree where reverse sap flow was found in the root ($\delta D = -109\text{‰}$). Water extracted on the same day from 12 ponderosa pine seedlings located around the target trees had δD values ranging from about -53 to -111‰ (Figure 9). Six of the seedlings clustered near the base of the tree in which labeled water was detected yielded xylem δD values greater than -90‰ , suggesting a modest enrichment associated with uptake of labeled water. There was only one seedling found near the north tree and it contained no labeled water (-95‰). The *Purshia tridentata* shrubs and the other target trees sampled yielded xylem δD values between -120 and -110‰ .

At the Douglas-fir site, deuterated water was detected in one target tree 3 days after water was applied. At 5 days, between 4 and 17% of the water extracted from all three target trees

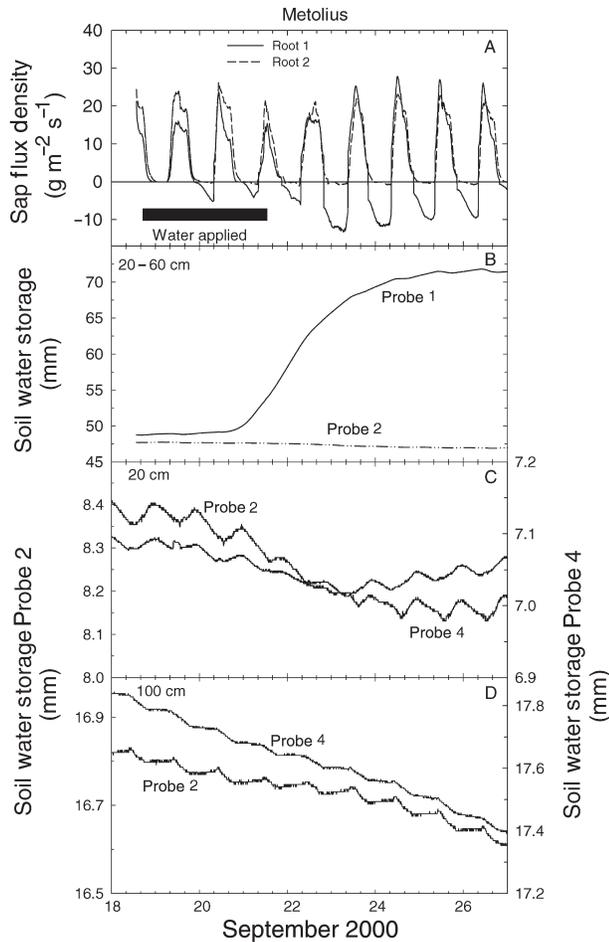


Figure 7. Time courses of root sap flow and soil volumetric water content during an irrigation experiment at the ponderosa pine (Metolius) site. In (A), sap flow was monitored in two roots of an old-growth ponderosa pine tree. In (B–D), time courses of soil volumetric water content at various probe locations and sensor depths are shown. See Figure 1 for locations of irrigation, trees, roots and soil monitoring probes.

originated from the deuterated irrigation water, and after 8 days, the proportion was between 5 and 18%. In addition, one *Berberis nervosa* Pursh plant located 2.5 m from the watering source had a slightly enriched signal compared to control samples (–55 versus –69‰), but the other three *B. nervosa* plants sampled around the target trees were not different from the controls. The high variability of both control and treatment plot samples prevented detection of significant changes in the soil water isotopic signal at 10 cm.

Discussion

Our results indicate that hydraulic redistribution of soil water occurred at both study sites, suggesting that it could be an important process in both wet and dry forests of the Pacific Northwest. Time courses of soil water content at multiple locations and depths were consistent with nocturnal release of

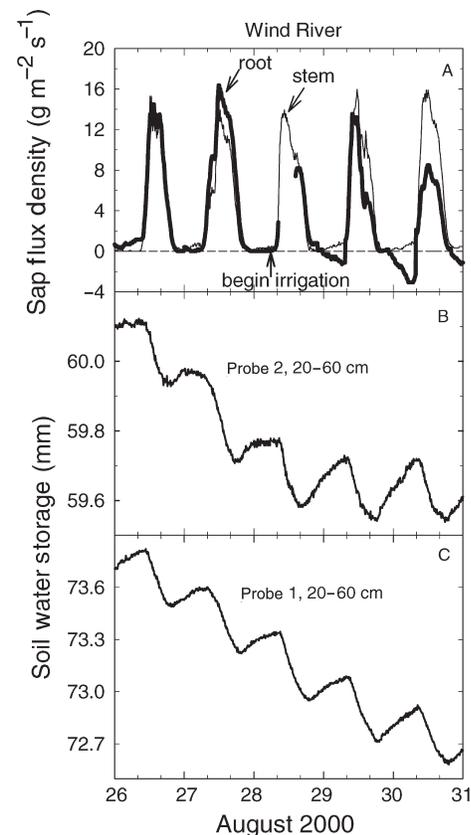


Figure 8. Time courses of root and stem sap flow and soil volumetric water content during an irrigation experiment at the Douglas-fir (Wind River) site. In (A) sap flow was monitored at the stem and a root of the same Douglas-fir tree. In (B) and (C), time courses of total soil volumetric water content between 20 and 60 cm at two probe locations are shown. See Figure 1 for locations of irrigation, soil monitoring probes and tree in which root and stem sap flow were monitored.

water from roots to the soil. Typically, psychrometric measurements of soil water potential have been used to provide evidence for hydraulic redistribution of soil water by roots (Richards and Caldwell 1987, Dawson 1993a), and our own psychrometric data support hydraulic redistribution (Figure 4a). However, measurements of soil water potential do not furnish information concerning the quantities of water redistributed unless the moisture release properties of the soil at each psychrometer depth and location are known. We used measurements of soil volumetric water content to estimate quantitatively the contribution of hydraulically redistributed water to total daily soil water utilization in the upper 2 m of the soil profile. It could be argued that measurements of soil water potential provide direct evidence for release of water from roots to the soil, whereas techniques for measuring soil water content may be confounded by changes in water content of nearby roots rather than the soil. However, given the number of locations and depths at which patterns consistent with hydraulic redistribution were observed in our study, it is highly unlikely that fluctuations in root rather than soil water content

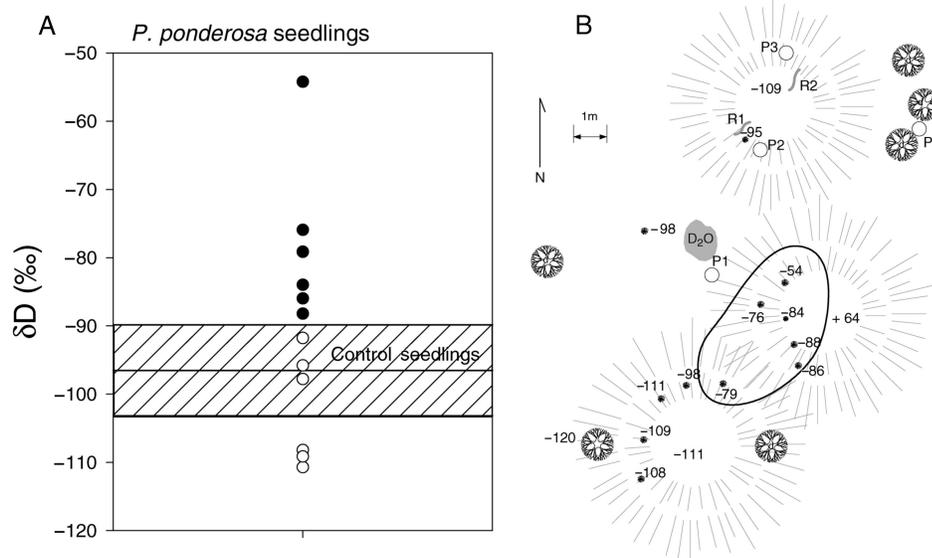


Figure 9. (A) Xylem δD values and (B) locations of the target ponderosa pine trees and 12 ponderosa pine seedlings collected around the target trees 11 days after irrigation with deuterated water started. In (A), the hatched band across the center of the graph is the mean ± 1 SD of six control seedlings (points not included in figure) collected in an open area 50 m from the watering site. In (B), the circled area indicates the location of all seedlings that are enriched above one standard deviation of the mean for control seedlings (hatched area in (A)).

dominated. Furthermore, fluctuations in soil water potential and water content were highly correlated at the ponderosa pine site (Figure 4). In addition, time courses of soil water depletion at the Douglas-fir site pointed to the presence of roots at both the 20–60 and 60–100 cm depth ranges, but partial nighttime recovery of soil water content was observed only between 20 and 60 cm (Figure 5). Between 60 and 100 cm, soil water depletion was more rapid during the daylight hours followed by little or no depletion at night. The possibility that the small diel fluctuations in soil temperature observed at the ponderosa pine site significantly influenced the response of the frequency domain capacitance sensors is unlikely in view of a recent technical evaluation of this system, which demonstrated that temperature effects on calibration were negligible over a range of 20 °C (Paltineau and Starr 1997). In addition, at the ponderosa pine site, we observed partial nighttime recovery of soil water content at depths experiencing little or no diel temperature fluctuations (60–100 cm, Figure 2). We suggest that concurrent measurements of soil water potential and water content are desirable to characterize the magnitude and direction of the driving forces for water movement in the soil–plant system as well as the absolute amounts of water moved.

During August, hydraulic redistribution appeared to contribute about 28% to the total daily water use from the upper 2 m of the soil profile in the Douglas-fir stand and approximately 35% in the ponderosa pine stand. These percentages are consistent with those reported for *Artemisia tridentata* Nutt. stands (Caldwell and Richards 1989, Ryel et al. 2002). Based on our results, the presence of hydraulic redistribution would allow the equivalent of 21 additional days of stored water to remain in the upper 2 m of soil at Metolius and an additional 16 days at Wind River after a 60-day drought period. After a longer, but not uncommon 90-day drought, an additional 31 days of stored water would remain at Metolius and 25 days at Wind River. In contrast, hydraulic redistribution was predicted to increase canopy transpiration by only 3.5%

over a 100-day drying cycle in an *A. tridentata* stand (Ryel et al. 2002). However, maximum rooting depth of *A. tridentata* was only 160 cm and 90% of the roots were distributed above 120 cm. Nevertheless, results obtained at the ponderosa pine site suggest that pronounced changes in the magnitude of hydraulic redistribution occurred as the soil dried. Eddy covariance data from the ponderosa pine site suggest that total evaporative water loss was approximately 2 mm day⁻¹ in July and 1 mm day⁻¹ in September (Anthoni et al. 2002). However, the soil water use in the upper 2 m remained constant at ~0.76 mm day⁻¹ (Figure 3) even though the soil water content in these 2 m was substantially lower near the end of September than in July and August. Based on the eddy covariance data and Figure 3, it appears that the major source of soil water shifted between July and September. In July, roots penetrating to depths greater than 2 m appeared to contribute over 60% to daily evaporative flux, but dropped to 25% in September, and the layer between 60 cm and 2 m became the main source. Also, once the deeper soil layers (below 2 m) were no longer the main source, evidence of hydraulic redistribution in the upper 2 m disappeared. The apparent absence of hydraulic redistribution in September suggests that the water potential gradient between the deep soil and that above 2 m was no longer steep enough to drive hydraulic redistribution, probably because of sharply reduced soil–root conductance associated with soil drying (Ryel et al. 2002).

Eddy covariance data from the Douglas-fir site in 1999 suggest that the evaporative loss from the 20-year-old stand was between 1.4 and 1.0 mm day⁻¹ for July to September (Chen et al. 2002). In August 2000, we measured soil water loss in the top 2 m as about 1.2 mm day⁻¹ (Figure 6), which suggests that most water use at this site occurs within the upper 2 m.

In the absence of knowledge about the specific root system architecture of individual trees, it was not possible to determine the precise pathway followed by water taken up and redistributed during our irrigation experiments. Some results

were unexpected, but can probably be explained by pathway resistance to water transport. For example, horizontal distribution of water was much greater on the side where the watering took place compared to the other side of the tree. The north root (R2) of the north tree did not demonstrate reverse flow, as expected. Instead, the root on the same side as the watering (R1) did, which was also unexpected. This counterintuitive result implies that the transport pathway for water from one side of the tree to the other had a high resistance relative to that between the roots on the same side of the tree. In addition, the north root must not have been in direct contact with the applied water, but must have been attached to another root that was in contact. Another example of a counterintuitive result is that the deuterated label was not found in samples collected from the north tree where reverse flow in the roots was observed. The root data suggest that this tree was taking up the applied water. However, xylem in *P. ponderosa* can spiral around the trunk, so the likely explanation is that the 12 mm increment core did not intersect the pathway of the deuterated water. These results suggest that pathway resistance and xylem interconnectedness play an important role in hydraulic redistribution. Nevertheless, patterns observed at the ponderosa pine site suggest that water moved via lateral roots from the site of irrigation toward the base of the tree, then out through other nearby lateral roots surrounded by drier soil. Previous studies have shown that depending on vertical gradients in soil water potential, water can be hydraulically redistributed either upward or downward via transfer between largely horizontal lateral roots and largely vertical taproots or sinker roots (Schulze et al. 1998, Smith et al. 1999, Burgess et al. 2000b, 2001). Both the results of our irrigation experiments and consideration of the mechanism of hydraulic redistribution suggest that substantial horizontal redistribution of water via relatively superficial lateral roots is equally possible. The magnitude of horizontal redistribution will depend on rooting density, the magnitude of the driving forces involved and the magnitudes of the hydraulic resistances traversed by the water being redistributed as well as the relative strengths of the competing sinks represented by dry soil and transpiring foliage.

Previous work in a range of Pacific Northwest forest types has shown that about 90% of the total fine root biomass may be restricted to the upper 0.5 m of the soil profile (Santantonio et al. 1977, Vogt et al. 1981, Fogel 1983). However, patterns of soil water depletion observed in the present study and previous and ongoing stand-level measurements of total evaporative flux for the ponderosa pine and Douglas-fir sites suggest that fine roots contributed little to total soil water utilization during the summer drought period. For example, at the ponderosa pine site, about 25–30% of the total daily water depletion in the upper 2 m of the soil profile occurred in the upper 60 cm during July and August, falling to only 18% in September. Similarly, at the Douglas-fir site, about 26% of the total daily soil water depletion in the upper 2 m occurred in the upper 60 cm during August. Thus, based on these estimates and those of the eddy covariance data, which show total evaporative water loss for the site, water obtained from the upper

60 cm of soil would comprise only about 12–14% of daily canopy evaporative flux throughout the summer months. The estimated contribution of water stored in the upper 60 cm of soil to daily canopy evaporative flux during the summer diminishes even further when it is considered that some or all of nightly partial recharge observed in this layer probably originated from water taken up at greater depths. Regardless of the contribution of fine roots to bulk water utilization, nightly partial recharge in the upper portion of the soil profile and the resulting delay in soil drying are consistent with a role of hydraulic redistribution in maintaining nutrient uptake by, and microbial activity around, fine roots.

Understory species and small seedlings are likely to use and benefit from redistributed water as well (Dawson 1993a). Ponderosa pine seedlings were approximately 10 to 15 cm tall and the roots appeared to be confined to the upper 20–30 cm. Hence, any mechanism that would slow soil drying by adding water to the upper portion of the soil profile is likely to increase survival of these seedlings. Evidence from the deuterated watering experiment suggests that these seedlings use redistributed water, but the labeling of +1300‰ was insufficient to cause strong labeling of surrounding plants by redistributed irrigation water. At the ponderosa pine site, for example, the nightly increase in soil water at 20 cm amounted to only 0.5% of the total water in the soil at that depth (Figure 7c). If the signature of that redistributed water were +1300‰, the δD value of the soil would have been raised from -96 to -10‰ over an 11-day period. However, the labeled water in the roots was likely diluted by existing water, and by water taken up from other sources, thus reducing the signal strength even more. Thus, the modest enrichment we observed in some seedlings was within the enrichment range expected given the redistribution of the deuterated water. Furthermore, the clustering of the seedlings with an enriched signal near the labeled tree along with other evidence of redistribution suggest that these ponderosa pine seedlings were using redistributed water (Figure 9). Dawson (1993a) showed that a wide variety of understory plants use water redistributed from a groundwater source by a large maple tree. Some species obtained as much as 60% of their water from the redistributed source. In drier ecosystems, such as the ponderosa pine system, utilization of redistributed water could be even greater.

Taken together, our results indicate that, in Pacific Northwest forests, hydraulically redistributed water can constitute a significant fraction of the total daily evapotranspiration during the dry summer months and can retard the rate of water depletion in the upper portion of the soil profile. Furthermore, redistributed water may increase survival of understory seedlings during periods of severe drought. Further work will focus on species-specific, tree size-specific, seasonal and substrate-related differences in the magnitude of hydraulic redistribution of soil water across climatic gradients. The role of pathway resistance to flow, such as the apparent large resistance across the stem base–root junction, also warrants further investigation.

Acknowledgments

This work was supported by the US Environmental Protection Agency and the USDA Forest Service. This manuscript has been subjected to the US Environmental Protection Agency's peer and administrative review, and it has been approved for publication as a US EPA document. Mention of trade names or commercial products does not constitute endorsement or recommendation for use. We thank B. Law, K. Bible and J. Irvine for access to field sites and supporting climate data, T. Hinckley and P. Schulte for stimulating discussions, and D. Hatfield, D. Woodruff and H. Keirstead for field help. We also thank S. Burgess, N. McDowell, D. Sprugel and C. McFarlane for reviewing earlier versions of this manuscript.

References

- Anthoni, P.M., M.H. Unsworth, B.E. Law, J. Irvine, D. Baldocchi and D.J. Moore. 2002. Seasonal differences in carbon and water vapor exchange in young and old-growth ponderosa pine ecosystems. *Agric. For. Meteorol.* 111:203–222.
- Brown, R.W. and D.L. Bartos. 1982. A calibration model for screen-caged Peltier thermocouple psychrometers. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, 155 p.
- Burgess, S.S.O., M.A. Adams and T.M. Bleby. 2000a. Measurement of sap flow in roots of woody plants: a commentary. *Tree Physiol.* 20:909–913.
- Burgess, S.S.O., M.A. Adams, N.C. Turner, C.R. Beverly, C.K. Ong, A.A.H. Khan and T.M. Bleby. 2001. An improved heat pulse method to measure low and reverse rates of sap flow in woody plants. *Tree Physiol.* 21:589–598.
- Burgess, S.S.O., M.A. Adams, N.C. Turner and C.K. Ong. 1998. The redistribution of soil water by tree root systems. *Oecologia* 115:306–311.
- Burgess, S.S.O., J.S. Pate, M.A. Adams and T.E. Dawson. 2000b. Seasonal water acquisition and redistribution in the Australian woody phreatophyte, *Banksia prionotes*. *Ann. Bot.* 85:215–224.
- Caldwell, M.M. and J.H. Richards. 1989. Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by roots. *Oecologia* 79:1–5.
- Caldwell, M.M., T.E. Dawson and J.H. Richards. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia* 113:151–161.
- Chen, J., K.T. Paw U, T. Suchanek et al. 2002. Energy budget and fluxes of CO₂ and H₂O of a 20, 40, and 500 year-old Douglas-fir forest. *Ecosystems*. In press.
- Corak, S.J., D.G. Blevins and S.G. Pallardy. 1987. Water transfer in an alfalfa/maize association. *Plant Physiol.* 84:582–586.
- Dawson, T.E. 1993a. Hydraulic lift and water use by plants: implications for water balance, performance and plant–plant interactions. *Oecologia* 95:565–574.
- Dawson, T.E. 1993b. Water sources of plants as determined from xylem-water isotopic composition: perspectives on plant competition, distribution, and water relations. *In Stable Isotopes and Plant Carbon–Water Relations*. Eds. J.R. Ehleringer, A.E. Hall and G.D. Farquhar. Academic Press, San Diego, pp 465–496.
- Dawson, T.E. 1996. Determining water use by trees and forests from isotopic, energy balance, and transpiration analysis: the roles of tree size and hydraulic lift. *Tree Physiol.* 16:263–272.
- Ehleringer, J.R. and C.B. Osmond. 1989. Stable isotopes. *In Plant Physiological Ecology: Field Methods and Instrumentation*. Eds. R.W. Pearcy, J.R. Ehleringer, H.A. Mooney and P.W. Rundel. Chapman and Hall, London, pp 281–300.
- Fogel, R. 1983. Root turnover and productivity of coniferous forests. *Plant Soil* 71:75–85.
- Gholz, H.L. 1982. Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. *Ecology* 63:469–481.
- Granier, A. 1987. Evaluation of transpiration in a Douglas-fir stand by means of sapflow measurements. *Tree Physiol.* 3:309–320.
- Jackson, R.B., J.S. Sperry and T.E. Dawson. 2000. Root water uptake and transport: using physiological processes in global predictions. *Trends Plant Sci.* 5:482–488.
- Klopatek, J.M. 2002. Belowground carbon pools and processes in different age stands of Douglas-fir. *Tree Physiol.* 22:197–204.
- Law, B.E., M.G. Ryan and P.M. Anthoni. 1999. Seasonal and annual respiration of a ponderosa pine ecosystem. *Global Change Biol.* 5:169–182.
- Millikin Ishikawa, C. and C.S. Bledsoe. 2000. Seasonal and diurnal patterns of soil water potential in the rhizosphere of blue oaks: evidence for hydraulic lift. *Oecologia* 125:459–465.
- Paltineanu, I.C. and J.L. Starr. 1997. Real-time soil water dynamics using multisensor capacitance probes: laboratory calibration. *Soil Sci. Soc. Am. J.* 61:1576–1585.
- Richards, J.H. and M.M. Caldwell. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* 73:486–489.
- Ryel, R.J., M.M. Caldwell, C.K. Yoder, D. Or and A.J. Leffler. 2002. Hydraulic redistribution in a stand of *Artemisia tridentata*: evaluation of benefits to transpiration assessed with a simulation model. *Oecologia* 130:173–184.
- Sakuratani, T., T. Aoe and H. Higuchi. 1999. Reverse flow in roots of *Sebania rostrata* measured using the constant power heat balance method. *Plant Cell Environ.* 22:1153–1160.
- Santantonio, D., R.K. Hermann and W.S. Overton. 1977. Root biomass studies in forest ecosystems. *Pedobiologia* 17:1–31.
- Schulze, E.-D., M.M. Caldwell, J. Canadell, H.A. Mooney, R.B. Jackson, D. Parson, R. Scholes, O.E. Sala and P. Trimbom. 1998. Downward flux of water through roots (i.e., inverse hydraulic lift) in dry Kalahari sands. *Oecologia* 115:460–462.
- Smith, D.M., N.A. Jackson, J.M. Roberts and C.K. Ong. 1999. Reverse flow of sap in tree roots and downward siphoning of water by *Grevillae robusta*. *Funct. Ecol.* 13:256–264.
- Song, Y., M.B. Kirkham, J.M. Ham and G.J. Kluitenberg. 2000. Root-zone hydraulic lift evaluated with the dual-probe heat-pulse technique. *Aust. J. Soil Res.* 38:927–935.
- Starr, J.L. and I.C. Paltineanu. 1998. Soil water dynamics using multisensor capacitance probes in nontraffic interrows of corn. *Soil Sci. Soc. Am. J.* 62:114–122.
- Vogt, K.A., R.L. Edmonds and C.C. Grier. 1981. Season changes in biomass and vertical distribution of mycorrhizal and fibrous-textured conifer fine roots in 23- and 180-year-old subalpine *Abies amabilis* stands. *Can. J. For. Res.* 11:223–229.
- Wan, C., W. Xu, R.E. Sosebee, S. Machado and T. Archer. 2000. Hydraulic lift in drought-tolerant and -susceptible maize hybrids. *Plant Soil* 219:117–126.
- Waring, R.H. and J.F. Franklin. 1979. Evergreen coniferous forest of the Pacific Northwest. *Science*. 204:1380–1386.
- Yoder, C.K. and R.S. Nowak. 1999. Hydraulic lift among native plant species in the Mojave Desert. *Plant Soil* 215:93–102.

