New Phytologist

Research

Hydraulic redistribution of soil water in two old-growth coniferous forests: quantifying patterns and controls

Jeffrey M. Warren[1], Frederick C. Meinzer[1], J. Renée Brooks[2], Jean-Christophe Domec[3] and Rob Coulombe[4]

[1]USDA Forest Service, PNW Research Station, Corvallis, OR 97331; [2]Western Ecology Division, US EPA/NHEERL, Corvallis, OR 97333; [3]Department of Wood Science and Engineering, Oregon State University, Corvallis, OR 97331; [4]Dynamac Corporation, 200 SW 35th St, Corvallis, OR 97333, USA

Author for correspondence:
Jeffrey M. Warren
Tel: +1 (541) 758 8766
Fax: +1 (541) 750 7329
Email: jeffwarren@fs.fed.us

Received: *10 September 2006*
Accepted: *7 November 2006*

Summary

- Although hydraulic redistribution of soil water (HR) by roots is a widespread phenomenon, the processes governing spatial and temporal patterns of HR are not well understood. We incorporated soil/plant biophysical properties into a simple model based on Darcy's law to predict seasonal trajectories of HR.
- We investigated the spatial and temporal variability of HR across multiple years in two old-growth coniferous forest ecosystems with contrasting species and moisture regimes by measurement of soil water content (θ) and water potential (Ψ) throughout the upper soil profile, root distribution and conductivity, and relevant climate variables.
- Large HR variability within sites (0–0.5 mm d^{-1}) was attributed to spatial patterns of roots, soil moisture and depletion. HR accounted for 3–9% of estimated total site water depletion seasonally, peaking at 0.16 mm d^{-1} (ponderosa pine; *Pinus ponderosa*) or 0.30 mm d^{-1} (Douglas-fir; *Pseudotsuga menziesii*), then declining as modeled pathway conductance dropped with increasing root cavitation.
- While HR can vary tremendously within a site, among years and among ecosystems, this variability can be explained by natural variability in Ψ gradients and seasonal courses of root conductivity.

Key words: Douglas-fir (*Pseudotsuga menziesii*), hydraulic lift, hydraulic redistribution, ponderosa pine (*Pinus ponderosa*), root conductivity, soil water content, water potential.

New Phytologist (2007) **173**: 753–765

doi: 10.1111/j.1469-8137.2006.01963.x

Introduction

Hydraulic redistribution of soil water (HR), in which root systems passively transfer water from moist to drier soil along a water potential (Ψ) gradient, is a widespread phenomenon (e.g. Caldwell *et al.*, 1998; Espeleta *et al.*, 2004; Meinzer *et al.*, 2004), but factors controlling HR and its spatial and temporal variability have not been well quantified. Hydraulic redistribution frequently occurs in ecosystems containing woody species with large, often dimorphic root systems that transport water upward from deep roots located in moist soil to shallow roots located in drier soil (e.g. Richards & Caldwell, 1987; Caldwell & Richards, 1989; Dawson, 1993; Caldwell *et al.*, 1998; Burgess *et al.*, 2000; Meinzer *et al.*, 2004). Roots may also redistribute water downward in the soil following a Ψ gradient; this redistribution occurs, for example, in plants that have their upper roots in moist soil (e.g. following rainfall) and deeper roots in drier soil (Schulze *et al.*, 1998; Burgess & Adams, 2001; Scholz *et al.*, 2002; Hultine *et al.*, 2003; Ryel *et al.*, 2003). In addition, lateral HR along a Ψ gradient generated by localized irrigation has been demonstrated for several species (Smart *et al.*, 2005; Brooks *et al.*, 2002, 2006). The hyphae and/or rhizomorphs of symbiotic mycorrhizal fungi associated with fine roots can also transport hydraulically redistributed water in the soil (Querejeta *et al.*, 2003), and directly between trees through a common mycorrhizal network (J. Warren, unpublished).

Although HR involves relatively small amounts of water (< 0.5 mm d^{-1}), its impact on plant and ecosystem function is significant. Enough water is moved by HR to maintain root xylem conductivity in the nutrient-rich upper soil throughout the dry season by maintaining root and soil Ψ above the critical thresholds that would provoke embolism, leading to catastrophic xylem dysfunction and eventual death of roots (Brooks *et al.*, 2002; Domec *et al.*, 2004, 2006; Meinzer *et al.*, 2004). The Ψ of roots involved in HR is higher (less negative) than that of the soil, thereby tempering the generation of the hydraulic and chemical signals in roots that reduce stomatal conductance and thus limit plant water use and carbon uptake (Domec *et al.*, 2004, 2006; Meinzer *et al.*, 2004; Warren *et al.*, 2005). The seemingly small diel changes in soil moisture attributable to HR can have significant impacts on seasonal patterns of evapotranspiration, as modeled for desert shrubland and temperate and tropical forests (Dawson, 1996; Emerman & Dawson, 1996; Jackson *et al.*, 2000; Ryel *et al.*, 2002; Lee *et al.*, 2005). One model for Amazonian trees predicts the daily replacement of transpired water by HR may increase total dry season evapotranspiration by 40%, which would impact regional climate dynamics (Lee *et al.*, 2005). In addition, higher rates of evapotranspiration across biomes have been linked to increased ecosystem production and potential carbon sequestration in terrestrial ecosystems (Law *et al.*, 2002). Water released into the upper soil may also be available for use by shallowly rooted plant species and other soil biota that do not have direct access to deep water sources (Caldwell & Richards, 1989; Dawson, 1993; Brooks *et al.*, 2006), which has implications for seedling establishment, competition, carbon and nutrient cycling and ultimately patterns of plant distribution and species richness.

Although the existence of HR has been documented for many species in both moist and dry ecosystems, its seasonal initiation, timing and magnitude, and the below- and aboveground plant and environmental factors controlling it are poorly characterized. For example, previous estimates of the magnitude of HR vary widely in the ways in which they are reported, and include estimates of the rates of reverse sap flow in single roots (Burgess *et al.*, 2000; Scholz *et al.*, 2002), rapid increases in soil water content (θ) at depth following a rainfall event (Burgess & Adams, 2001; Leffler *et al.*, 2002; Oliveira *et al.*, 2005), whole-tree HR (Emerman & Dawson, 1996) and the percentage of daily evapotranspiration attributed to HR (Caldwell & Richards, 1989; Brooks *et al.*, 2002; Ryel *et al.*, 2002), and estimates on a soil surface area basis (Meinzer *et al.*, 2004; Brooks *et al.*, 2002, 2006). Some studies have estimated water transport and HR using mechanistic models that necessitate assumptions regarding soil moisture parameters, root conductivity and physiological processes (e.g. Mendel *et al.*, 2002; Ryel *et al.*, 2002). While these models provide insight into broad patterns of HR, the simulations are limited to general conditions and cannot account for fine-scale temporal or spatial variation in HR, or resolve the factors controlling HR. Some HR studies have compared contrasting ecosystems (Brooks *et al.*, 2002; Meinzer *et al.*, 2004), and other studies have tracked HR from year to year (Millikin-Ishikawa & Bledsoe, 2000; Leffler *et al.*, 2002; Espeleta *et al.*, 2004; Oliveira *et al.*, 2005), but none has focused on high-resolution temporal or spatial variability within ecosystems, or the climatic and physiological factors controlling patterns of HR.

This study focused on HR variability across multiple years in two old-growth coniferous forest ecosystems with contrasting species and moisture regimes. We assessed spatial and temporal variability of HR in relation to soil, root and climatic parameters. In addition, we incorporated soil/plant biophysical properties into a simple model that would adequately predict seasonal trajectories of HR. We present estimates of total HR on a soil surface area basis in units of mm d^{-1}, these being readily scaleable units that can be incorporated into broader hydrologic models of water transport. To this end, we quantified HR by fine-scale measurement of soil θ throughout the soil profile, related HR variability to soil water dynamics and relevant climate parameters, and independently modeled HR using vertical patterns of soil Ψ gradients, seasonal courses of root conductivity, and previous estimates of vertical distribution of root surface area.

Materials and Methods

Site descriptions

Data were collected in Oregon and Washington, USA during the seasonal dry periods of 2000–2005 in an old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)/mixed-conifer stand (OG-DF, 2002–2005), and an old-growth/mixed-age ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) stand (OG-PP, 2000–2003).

The OG-DF stand is located at the Wind River Canopy Crane Research Facility (WRCCRF) within the Gifford Pinchot National Forest south-east of Mount Saint Helens in south central Washington, USA (45°49′N, 121°57′W, elevation 370 m), and is approx. 450 yr old, having been established after a stand-replacing fire. Douglas-fir and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) are the dominant canopy species, with some western red cedar (*Thuja plicata* Donn ex D. Don) and true firs (*Abies* spp.) sharing the canopy. The mid-canopy consists of Pacific silver fir (*Abies amabilis* Dougl. ex Forbes) and Pacific yew (*Taxus brevifolia* Nutt.) and the understory is dominated by vine maple (*Acer circinatum* Pursh.), salal (*Gaultheria shallon* Pursh.) and Oregon-grape (*Berberis nervosa* Pursh.) (Shaw *et al.*, 2004). Soils at the OG-DF site are deep, well-drained andisols that transition from sandy loam in the upper soil to loamy sand in the subsoil (Klopatek, 2002; Shaw *et al.*, 2004; Warren *et al.*, 2005). The water table varies seasonally, and is often less than 2 m below the surface during the wet season at the OG-DF site (Shaw *et al.*, 2004). Douglas-fir roots have been observed at this site at depths of at least 2 m (J. Licata and T. Hinckley, pers. comm.).

Table 1 Stand characteristics for the old-growth Douglas-fir (*Pseudotsuga menziesii*) (OG-DF) and ponderosa pine (*Pinus ponderosa*) (OG-PP) sites

	OG-DF	OG-PP
Precipitation[a,b]		
Annual (mm)	2200	550
Dry season* (mm)	8–48 (2002–2005)	13–50 (2000–2004)
Dry season length (d)	50–110	130–190
Soil water storage at 15–65 cm (cm^3 cm^{-3})		
Start of dry season	0.24–0.28 (2002–2005)	0.22–0.23 (2002–2005)
Dry season minimum	0.13–0.16	0.08–0.09
Soil water potential[c] at 20 cm (MPa)		
Dry season minimum (± SE) in 2002	−0.73 (± 0.28)	−2.19 (± 0.23)
Root surface area[c] (< 0.5 cm diameter) (m^2 m^{-2})		
0–20 cm	2.3	1.4
20–40 cm	0.9	0.9
40–60 cm	0.7	0.5
Leaf area index[d,e,f] (m^2 m^{-2})	9	2.1
Stand density[d,e] (trees ha^{-1})	427	555/72 (50/250 yr old)

*The onset of the dry season was defined as the initiation of sustained soil drying following last significant seasonal rainfall event (> 25 mm).

[a] Wind River Canopy Crane Research Facility (WRCCRF) microclimate data archive: http://departments.washington.edu/wrccrf/metdata/microclimate.html

[b] National Oceanic & Atmospheric Administration (NOAA) climate station, Sisters, OR, USA.

[c] Warren *et al*. (2005); [d] Phillips *et al*. (2002); [e] Law *et al*. (2001); [6] Shaw *et al*. (2004).

The OG-PP stand is located within the Metolius Research Natural Area within the Deschutes National Forest in the rain-shadow east of the Cascade Mountains in central Oregon, USA (44°30′N, 121°37′W, elevation 915 m). The canopy contains 250–300-yr-old dominant trees, groups of suppressed trees ranging from 50 to 100 yr old, and a sparse herbaceous understory dominated by bracken fern (*Pteridium aquilimum* (L.) Kuhn), bitterbrush (*Purshia tridentata* (Pursh) (DC), wild strawberry (*Fragaria vesca* L.) and pine regeneration (Ryan *et al.*, 2000; Law *et al.*, 2001). Soil at the OG-PP site has been classified as an alfic vitrixerand (Law *et al.*, 2001) that transitions from a loamy sand in the upper soil to a sandy loam in the subsoil (Warren *et al.*, 2005). The water table was below 2.5 m at the OG-PP site during the study period based on observations collected during equipment installation. Rooting depth has been estimated to be > 3 m based on measurements of wind-thrown trees (Ryan *et al.*, 2000).

Both sites experience a prolonged seasonal drought between late spring and early to late fall, when < 10% of annual precipitation occurs. Past and concurrent work has documented the existence of HR (Brooks *et al.*, 2002; Domec *et al.*, 2004; Meinzer *et al.*, 2004; Warren *et al.*, 2005), although spatial, seasonal and interannual variability and the variables driving HR have not been characterized. Specific climate and stand characteristics are described in Table 1 and by Warren *et al.* (2005).

Soil and plant water potential

Soil Ψ was measured at both sites during the 2002 season only, using thermocouple psychrometers (PST-55; Wescor, Logan, UT, USA) installed at depths of 20, 30, 40, 50, 60 and 100 cm. Before installation, the psychrometers were individually calibrated in the laboratory against salt solutions of known osmolality (Brown & Bartos, 1982). A soil auger was used to excavate 1-m-deep holes, psychrometers were placed into the intact soil profile in the side of the hole at each depth, and then holes were repacked with the excavated soil by layer. Four replicate arrays were spaced out across a representative 25-m^2 area at each site in the vicinity of old-growth trees. From June to November 2002, water potentials were measured every 30 min, with a 30-s cooling time to accommodate the Peltier effect, and data were recorded using a datalogger (CR-7; Campbell Scientific, Logan, UT, USA). Psychrometer cables and dataloggers were insulated to minimize temperature gradients that could influence water potential calculations.

To assess plant Ψ, leaf samples were collected from the canopy trees before dawn approximately monthly during the 2002 drought season using an access tower (in the fully exposed mid-canopy at *c.* 25 m; OG-PP) or a canopy crane (in the upper canopy at *c.* 55 m; OG-DF). Trees were selected based on proximity to location of soil measurements. Leaf Ψ values were determined for pine fascicles or Douglas-fir shoots ($n = 5$) using a Scholander-type pressure chamber (PMS, Corvallis, OR, USA).

Soil volumetric water content

The soil volumetric water content (θ) was quantified using multisensor, frequency domain capacitance probes (Paltineanu & Starr, 1997; Brooks *et al.*, 2002; Warren *et al.*, 2005). These probes contained eight annular capacitance sensors (EnviroSCAN; Sentek Pty Ltd, Adelaide, Australia) capable of quantifying minute changes in θ (± 0.003%). The probes have been reported to be relatively insensitive to fluctuations in soil temperature (3.5×10^{-4} change in θ °C^{-1} between 10 and 30°C; Paltineanu & Starr, 1997). Each probe was installed into a *c.* 6-cm-diameter PVC access tube, to a depth of 2 m, with sensors spaced at depths of 20, 30, 40, 50, 60, 100, 150 and 200 cm. Each capacitance sensor was frequency-normalized by calibration against air and water in the laboratory to ensure the precision of measurements. Field-based calibration to the specific sandy loam soils of the Pacific North-West (PNW) was necessary to ensure the accuracy of measurements (Morgan *et al.*, 1999), as described by Warren *et al.* (2005). Volumetric water contents were measured during the 2000–2005 drought seasons every 10–30 min and recorded using a datalogger (model RT6; Sentek Pty Ltd). In 2002 at both sites, four replicate capacitance probes were randomly located in a 100-m^2 area near the psychrometer arrays to provide concurrent measurements at similar locations. At OG-DF, equal numbers of probes were installed near the two major canopy species, Douglas-fir and western hemlock, and four additional probes were installed in 2003 *c.* 100 m from the first set of probes.

Hydraulic redistribution and soil water depletion

The HR of soil water was calculated based on diel fluctuations in θ within each soil layer centered at 20, 30, 40, 50 and 60 cm for years with complete data sets: 2001–2003 (OG-PP) and 2002–2005 (OG-DF). Previous work at the sites showed that HR was not occurring in deeper soils (Brooks *et al.*, 2002). Both θ and Ψ declined during the day as roots extracted water to meet vegetation transpirational demands. At night, or during other periods when lower atmospheric vapor pressure deficit (VPD) and stomatal closure reduced foliar water loss, both θ and Ψ increased in the upper soil, which we attributed to HR. The magnitude of HR was expressed independently for each sensor at each depth as the overnight recovery of θ from the minimum values of the previous day. HR values were averaged by depth, and then integrated across the profile to provide total daily HR within the 15–65-cm soil layer. As the timing of HR varied for each soil layer, a portion of reported mean daily HR across the upper soil profile *may* represent interlayer transfers of water (e.g. θ declining in the 45–55-cm layer while simultaneously θ increasing in the 15–25-cm layer), rather than exclusive influx of water from depths > 65 cm. HR was not calculated during periods following precipitation events when measurements were confounded by water infiltration and changes in Ψ driving forces.

Daily water depletion rates from each soil layer were calculated as the difference between maximum and minimum daily θ for each sensor at each depth. Mean daily water depletion from the entire 15–65-cm layer was calculated by summing the mean daily depletion in θ for each 10-cm depth. Depletion values were also calculated for the deeper 65–200-cm layer, and the entire 15–200-cm profile by linear interpolation between sensors. Water depletion and HR were not calculated for the upper 0–15-cm layer, where our previous measurements of θ using the capacitance probes were sometimes erratic.

Micrometeorological data were collected onsite each year at OG-DF by staff at the Wind River Canopy Crane Research Facility, and included photosynthetically active radiation (PAR), air temperature (T) and relative humidity (RH) at different vertical and horizontal locations. Daytime (10:00–18:00 h) and nighttime (22:00–06:00 h) T and RH were used to calculate VPD and VPD night:day ratios (VPDn/d) in the upper canopy (60 m), which ultimately provide the driving force for water movement in the soil–plant–atmosphere continuum. The 8-h periods used to calculate VPD were chosen on the basis of the timing of minimum and maximum HR, thereby avoiding much of the transition periods. We also calculated various soil water characteristics on a daily basis, including average upper soil θ (SWC), total depletion (TD) and the ratio of upper to lower soil depletion (DR). SWC reflects the spatial variation in microsites and development of Ψ gradients necessary to drive HR. TD reflects the root area and strength of water extraction and DR reflects root distribution in the context of root extraction strength and development of Ψ gradients.

These micrometeorological data were used to explain the spatial, seasonal and annual variability exhibited in HR at OG-DF by standard analysis of variance (ANOVA), correlation and regression analyses techniques using SAS statistical software (version 9.1; SAS Institute Inc., Cary, NC, USA). In stepwise regression analyses, additional parameters were only considered for inclusion if there was an improvement of $R^2 >$ 5%, and if parameter estimates were significant. In addition, concurrent evaluation of colinearity between the independent variables was tested by establishing a threshold value of 0.9 for tolerance. The tolerance for each independent variable ranged from 0 to 1, with low values indicative of an increased linear relationship with other independent variables, which corresponds to variance inflation that can impact regression results. The regression analysis was limited to the OG-DF site as micrometeorological data were not collected at the OG-PP site.

Root conductivity and relative water efflux

To assess potential controls driving release of hydraulically redistributed water by roots, we modeled relative root water efflux independently of HR during the 2002 seasonal dry period for both sites. We calculated the potential for seasonal root efflux based on a modification of Darcy's law:

$$Q_p = \frac{KA\Delta\Psi}{L} \approx \frac{(100\text{–PLC})A\Delta\Psi}{L}$$

where potential water flux (Q_p) through a cross-sectional area (A) is a function of root hydraulic conductivity (K) and the driving force, $\Delta\Psi/L$, where $\Delta\Psi$ is the difference in soil Ψ between two points separated by distance L. For our model, we used estimates of fine-root surface area to represent A, root xylem vulnerability to embolism and rhizosphere Ψ to estimate K, soil Ψ differences between upper sink soil where HR occurs and deeper source soil (100 cm) to represent $\Delta\Psi$, and the depth difference between source and sink to represent L. In 2002, we previously quantified fine-root (< 2 mm diameter) surface area in these stands (Warren *et al.*, 2005), and established root (2–4-mm-diameter) xylem vulnerability to embolism curves that relate the per cent loss of root conductivity (PLC) to measured soil Ψ (Domec *et al.*, 2004). Relative root conductivity was estimated based on 100-PLC, which progressively declined from 100 under moist conditions towards zero as the soils dried out. The modeled result represents a relative potential for root water efflux, as only the axial and not the radial resistance to root water efflux was estimated. The data were therefore normalized so that maximum calculated $Q_p = 1$.

Results

Hydraulic redistribution was detected at both sites in all years based on diel fluctuations in θ and Ψ (2002 only). Early in the season, the capacitance sensors could readily distinguish HR; in contrast, the psychrometers were less sensitive at high Ψ, and often needed several additional weeks of soil drying before they detected HR. Even so, in 2002 there was a strong positive linear relationship ($R^2 > 0.7$) between overnight recovery of soil θ and Ψ at both sites (data not shown), indicating that the two types of index were measuring the same process. The relationship between soil θ and Ψ showed a distinct diel hysteresis during the drought; that is, for a given value of soil θ, soil Ψ was 0.01–0.05 MPa greater (less negative) during the nocturnal recovery period associated with HR than during the daytime, when water was being taken up by shallow roots (Fig. 1). Recovery of θ and Ψ was greater under cloudy conditions with relatively low VPD and low net radiation, resulting in > 100% overnight recovery of daily water depletion by HR on some days.

Large spatial and temporal variability in total HR in the upper soil was found across the landscape, ranging from 0 to 0.29 mm d^{-1} at the OG-PP site to 0–0.50 mm d^{-1} at the OG-DF site for individual probes in specific years. When averaged across multiple years, some probes measured consistently higher values of HR than other probes within both sites (Fig. 2a,b). At the Douglas-fir site, probes P1–P4 (installed in 2002) had lower HR than three of the four other probes (P5–P8, installed in 2003) (Fig. 2b), such that 2002 HR values may not reflect total site HR variability. Spatial variation in HR across the site was partially attributable to differences in climate-driven upper soil θ and patterns of water extraction; probes in locations with relatively dry upper soil (SWC) and with active daily root water depletion from deep soil (DR) displayed higher HR (Table 2a). These factors accounted for up to 54% of spatial variation at OG-DF. In contrast, at the pine site there was less absolute variation among the four main probes (Fig. 2a), and when data from other probes installed in 2000 and probes installed near younger trees for a separate study (2003–2005; data not shown) were considered, spatial variability of total HR in late August remained relatively small at OG-PP (0.06–0.16 mm d^{-1}) in comparison with OG-DF (0–0.41 mm d^{-1}; Fig. 2a,b).

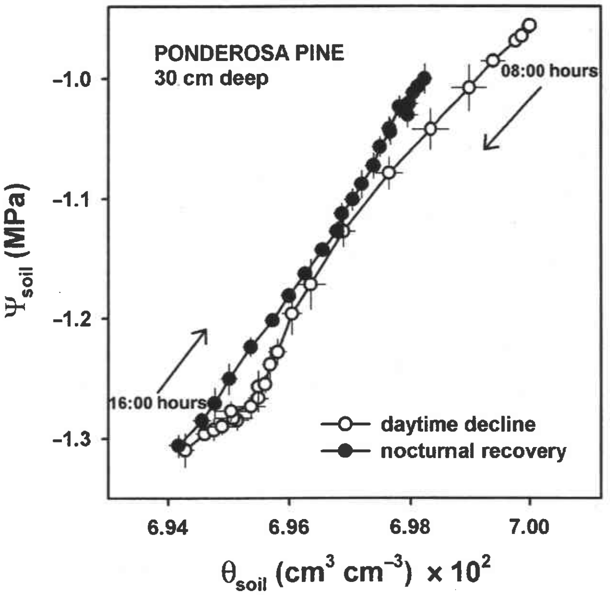

Fig. 1 Typical pattern of diel hysteresis of soil water content (θ) and water potential (Ψ_{soil}) during mid-August in an old-growth ponderosa pine (*Pinus ponderosa*) stand. The nocturnal recovery of both θ and Ψ_{soil} is evidence of hydraulic redistribution of soil water (HR). Values represent means ±1 standard deviation for Day of Year 225–230 in 2002.

Large vertical variations in HR also existed within the soil profile, ranging from 0 to 0.12 and from 0 to 0.18 mm d^{-1} per 10-cm layer at the OG-PP and OG-DF sites, respectively. At the Douglas-fir site, seasonal mean HR was highest in the upper 40 cm of soil and then declined at 50 and 60 cm, in contrast to the pine site, where no vertical trends in HR in the upper 60 cm were detected (Fig. 3). Vertical variation in HR at the OG-DF site was associated with root distribution (Fig. 4). Maximum daily rates of HR initially increased sharply then saturated with increasing root areas between 0.0075 and 0.014 cm^2 cm^{-3}. No apparent relationship was found between maximum HR and root area at the OG-PP site.

HR was initiated on average during the first 5 wk after significant precipitation ceased, increased to a peak during the second 5 wk (mid-drought), and then began to decline (Fig. 5). The earliest evidence of HR based on nocturnal increases in θ was found several weeks after the soil had begun to dry, when Ψ ranged from −0.05 to −0.25 MPa in the upper soil. A rapid increase in HR from background levels occurred

Table 2 Statistical summary relating measured patterns of hydraulic redistribution (HR; dependent variable) to environmental and climate parameters at the old-growth Douglas-fir (*Pseudotsuga menziesii*)/mixed-conifer stand.* (a) Spatial variation within years by probe; (b) seasonal variation within years across probes; (c) seasonal variation across years and across probes

(a)

		Correlation analysis					
		Parameters with significant correlation to HR			Regression analysis		
Year	*n*	SWC	TD	DR	Model parameters	*F*	R^2_{adj}
2002	176	-0.74^{a}	0.15^{d}	-0.73^{a}	SWC^{a}	207	0.54
2003	289	-0.14^{d}	0.46^{a}	-0.52^{a}	DR^{a}	106	0.27
2004	164	-0.26^{b}	0.21^{c}	ns	SWC^{b}, TD^{c}	10	0.09
2005	575	-0.28^{a}	0.37^{a}	-0.37^{a}	DR^{a}, TD^{a}	195	0.40
All	1204	-0.19^{a}	0.28^{a}	-0.29^{a}	DR^{a}, TD^{a}	118	0.19

(b)

		Correlation analysis							
		Parameters with significant correlation to HR					Regression analysis		
Year	*n*	SWC	TD	DR	PAR	VPDn	Model parameters	*F*	R^2_{adj}
2002	49	-0.76^{a}	-0.33^{d}	-0.86^{a}	ns	ns	DR^{a}, $VPDd^{d}$	77	0.76
2003	55	-0.69^{a}	ns	-0.71^{a}	-0.38^{c}	ns	DR^{a}, TD^{c}, $VPDn^{c}$	26	0.58
2004	24	-0.52^{c}	-0.59^{c}	0.54^{c}	ns	ns	DR^{c}, TD^{c}	12	0.48
2005	80	-0.79^{a}	-0.41^{b}	-0.49^{a}	-0.40^{b}	-0.26^{d}	SWC^{a}, $VPDn/d^{b}$	81	0.67
All	208	-0.33^{a}	-0.16^{d}	-0.26^{a}	-0.46^{a}	-0.15^{a}	PAR^{a}, SWC^{b}	37	0.26

(c)

		Correlation analysis								
		Parameters with significant correlation to HR						Regression analysis		
Weeks	*n*	SWC	TD	DR	PAR	VPDn	VPDn/d	Model parameters	*F*	R^2_{adj}
1–3	71	0.41^{b}	ns	-0.26^{d}	-0.38^{b}	0.37^{b}	0.56^{a}	SWC^{a}, $VPDn^{a}$	20	0.35
4–6	67	ns	ns	-0.22^{d}	ns	ns	ns	DR^{d}	3	0.03
7–9	55	0.24^{d}	0.44^{b}	ns	ns	ns	ns	TD^{b}, PAR^{d}	8	0.22
10–12	18	ns	ns	-0.39^{d}	ns	ns	ns	SWC^{d}, $VPDn^{d}$	3	0.20
13–15	17	ns	0.65^{c}	0.66^{c}	0.57^{d}	ns	-0.48^{d}	DR^{c}, $VPDd^{d}$	10	0.52

*Model parameters included canopy vapor pressure deficit (VPD) during the day (VPDd) or night (VPDn) or the night:day VPD ratio (VPDn/d), photosynthetically active radiation (PAR), upper soil water content (SWC; 15–65 cm), total daily depletion (TD; 15–200 cm), and the ratio of upper soil depletion to total depletion (DR). Significant Pearson correlation coefficients, and multiple linear regression model parameters, *F* and adjusted R^2 values are given for different spatial and temporal analyses including time (wk) since HR initiation, which varied annually by up to 39 d. Note that HR developed into weeks 10–15 only for year 2005. Results were considered significant at $P < 0.0001$, $P < 0.001$, $P < 0.01$ and $P < 0.1$, denoted by superscript letters a, b, c and d, respectively.

just before total soil water depletion in the upper 200 cm peaked at both sites. Within 2 wk after initiation of HR, the contribution of the upper soil to TD began to decline (Fig. 5a,b), reflecting both declining water availability in the upper soil and the ensuing development of Ψ gradients necessary for driving HR. During this period, HR increased to levels that accounted for 5% of total daily depletion from the entire 2-m profile at both sites. HR clearly peaked in August at the OG-PP site and then declined into the fall (Fig. 5c). Maximum rates of HR for a particular layer were reached *c.* 3–6 wk after the onset of HR when soil Ψ declined to values close to, or below, predawn leaf Ψ, which allowed the upper soil to compete with the above-ground portion of the tree for water taken up by deep roots at night. In 2002, maximum HR for the entire 15–65-cm layer at OG-PP was reached when soil Ψ at a depth of 60 cm approached predawn

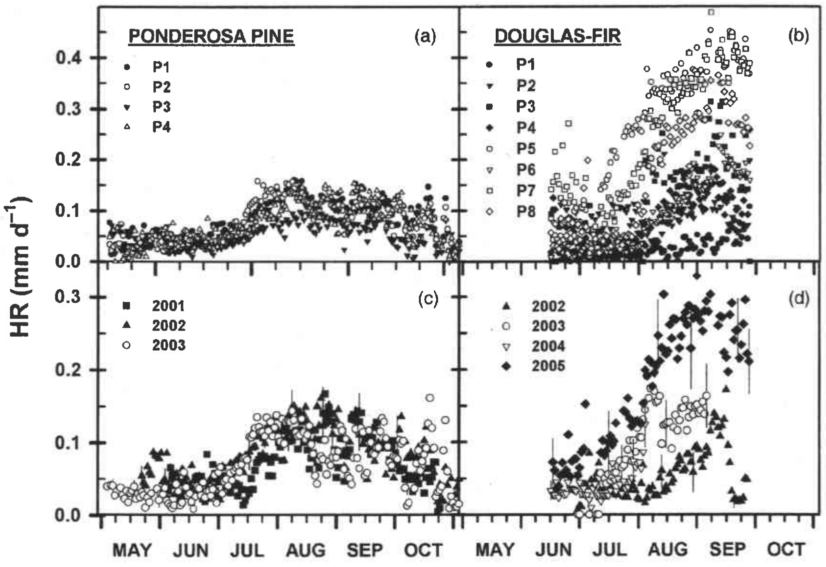

Fig. 2 Seasonal trends in hydraulic redistribution of soil water (HR) for old-growth ponderosa pine (*Pinus ponderosa*) (a, c) or old-growth Douglas-fir (*Pseudotsuga menziesii*)/mixed-conifer forests (b, d) illustrating spatial variability among probe locations averaged across years (a, b), and temporal variability among years averaged across probes (c, d) (mean ± 1 standard error). HR was quantified from diel (generally nocturnal) increases in soil water content in the upper 15–65 cm of the soil profile (see the Materials and Methods section for more details).

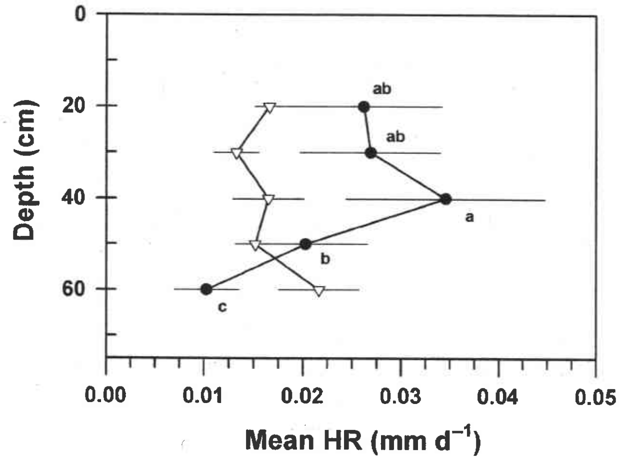

Fig. 3 Seasonal mean daily hydraulic redistribution of soil water (HR) measured across multiple years in relation to vertical depth in the upper soil profile for old-growth ponderosa pine (*Pinus ponderosa*) (triangles) and old-growth Douglas-fir (*Pseudotsuga menziesii*) (circles)/mixed-conifer forests. Values represent average HR during the seasonal dry period following the last significant rainfall event (> 25 mm) for four (pine) or eight (Douglas-fir) sensors per depth, ±1 standard error. Significant depth effects on HR were found for the Douglas-fir site ($P < 0.001$) as indicated by different letters using Duncan's multiple range test (alpha = 0.05; $n = 27$ per depth). No depth effects on HR were found for the pine site ($P = 0.2$).

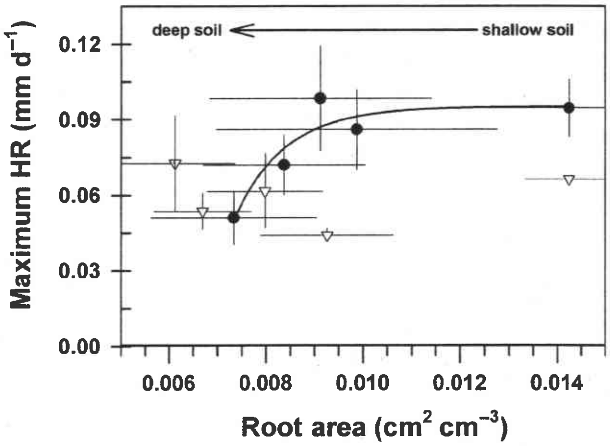

Fig. 4 Maximum daily hydraulic redistribution of soil water (HR) measured across multiple years in relation to total root surface area at 10-cm increments from 20 to 60 cm depth for old-growth ponderosa pine (*Pinus ponderosa*) (triangles) and old-growth Douglas-fir (*Pseudotsuga menziesii*) (circles)/mixed-conifer forests. Values represent the average of the 10 highest days of HR each year for four (pine) or eight (Douglas-fir) probes, ±1 standard error. A regression curve ($R^2 = 0.88$) was fit to the Douglas-fir data.

leaf Ψ (−0.65 MPa). Early rains in some years effectively shut off increasing HR at the OG-DF site as moisture penetrated the upper soil and the Ψ differences between soil layers diminished. Nonetheless, averaging across years, HR at OG-DF appeared to reach a maximum by early September (Fig. 5d). Peak HR replaced *c*. 10% of total daily depletion for both sites, and at OG-PP, where HR was not interrupted by fall precipitation, the contribution of HR to total daily depletion continued to increase up to 15%, even as absolute HR declined.

Hydraulic redistribution had an even greater influence on the upper soil (15–65 cm) water budget and that influence changed seasonally. Early in the drought periods, nocturnal HR replaced < 10% of daily water depletion from the upper soil layer at both sites. By mid-drought, nocturnal HR replaced 30–50% of daily water depletion from the upper soil. At the OG-PP site, HR replaced > 60% of daily water depletion from the upper soil late in the drought period. For some

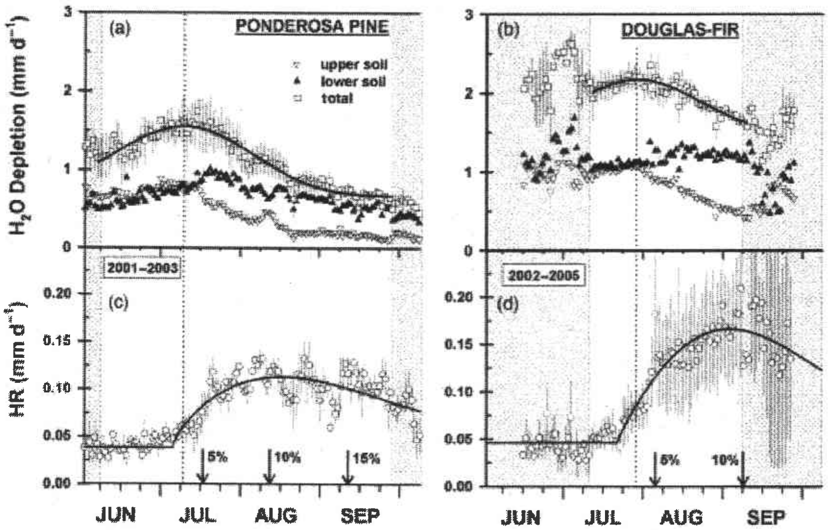

Fig. 5 Seasonal patterns of mean daily water depletion from the upper (15–65 cm), lower (65–200 cm) and entire (15–200 cm) soil profiles for (a) old-growth ponderosa pine (*Pinus ponderosa*) and (b) old-growth Douglas-fir (*Pseudotsuga menziesii*)/mixed-conifer stands across multiple years. Seasonal patterns of hydraulic redistribution of soil water (HR) averaged across multiple years are illustrated in (c) and (d) (±1 standard error), including Weibull curve fits ($R^2 = 0.71$ (c) or $R^2 = 0.90$ (d)). Dotted vertical lines represent the maximum daily water depletion from the entire profile based on fitted curves ($R^2 = 0.94$ (a) or 0.84 (b)). Modeled per cent daily replacement by HR (HR/total depletion) is indicated by arrows with 5, 10 or 15%. Shaded areas represent significant rain in one or more years, which increases variability. HR still occurred during this period as precipitation did not occur on all days in every year over which the data were averaged.

days during mid (OG-DF) and late (OG-PP) drought periods when evaporative demand was low, nocturnal HR replaced a much larger fraction of the water use of the previous day, exceeding 60% (OG-DF) or 100% (OG-PP) of water depletion from the upper soil. Cumulative seasonal HR varied annually, ranging from 7.5 to 9.5 mm (average = 0.094 mm d^{-1}) for 1 July to 1 October at OG-PP, and from 1.4 to 15.2 mm seasonally at OG-DF for dry periods between 23 d (2004) and 93 d (2005). Average HR at OG-DF during a seasonal 2-month dry period (9 July 8 to 7 September) was 0.111 mm d^{-1} (range 0.048–0.189 mm d^{-1}) for years 2002, 2003 and 2005.

Significant interannual variability existed at both sites in the seasonal initiation and magnitude of total HR (Fig. 2c,d). The statistical analysis at OG-DF demonstrated that climate and spatial patterns of soil water depletion accounted for at least 26% of HR variation among years (Table 2b), driven specifically by PAR, VPD and precipitation, as reflected in the upper soil water content (SWC). At OG-DF, variation in seasonal initiation of HR across years was partially attributable to prevailing PAR, VPDn/d and SWC early in the season (weeks 1–3; Table 2c). In 2005, low daytime PAR and VPD combined with high nighttime VPD reduced tree canopy sink strength for soil water, which allowed relatively high HR (Fig. 2d). In contrast, seasonal PAR levels in 2002 were 20% higher than in 2005, which increased the tree sink for water and thereby reduced HR (Fig. 2d). The ability to maintain TD rates as water extraction shifted to deeper layers (reducing DR) was related to continuing HR in the middle of the season. By the end of the season, the magnitude of HR was correlated with periods of high PAR and low VPDn/d, a pattern opposite to that exhibited earlier in the season before significant soil drying (Table 2c).

Modeled root water efflux (Q_p) based on measured soil Ψ gradients and estimated root axial conductivity in 2002 was highly correlated ($r = 0.86$–0.88; $P < 0.0001$) with actual HR (3-d averages) based on independently measured diel fluctuation in soil θ at both sites (Fig. 6a,b). The drier OG-PP site developed larger Ψ gradients between the upper and lower soil layers than the wetter OG-DF site, but concurrent losses to root conductivity at OG-PP led to a seasonal decline in modeled root water efflux (Fig. 6c,d). In contrast, at OG-DF in 2002 the increasing rates of modeled efflux and measured HR were abruptly halted by rain events before losses in root conductivity could outweigh increases in Ψ gradients.

Discussion

In this study, climate and patterns of soil water depletion during the extended annual dry season induced the vertical soil Ψ gradients that acted as the driving force for HR. Maximum rates of HR for each layer occurred when the upper soil became a strong competitor with the tree canopy for deep soil water, and then HR declined as root conductivity was lost and water extraction shifted to deeper soil layers. Large variability in HR was driven by spatial patterns of soil water depletion by roots, vertical patterns of root distribution, and seasonal patterns of root conductivity as influenced by both

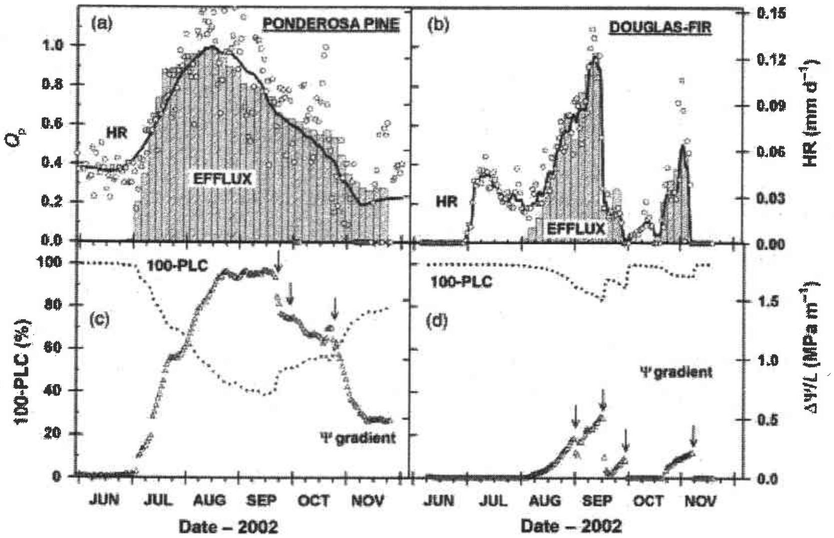

Fig. 6 (a, b) Estimated seasonal patterns of potential relative fine-root (< 2 mm) water efflux (Q_p; bars) in the upper soil profiles in relation to measured hydraulic redistribution of soil water (HR) (daily, open circles; mean, smoothed solid line) for old-growth ponderosa pine (*Pinus ponderosa*) or Douglas-fir (*Pseudotsuga menziesii*)/ mixed-conifer forests in 2002. Normalized efflux was calculated based on root area and (c, d) seasonal patterns of per cent loss of root conductivity as a result of embolism (100-PLC) and soil water potential gradients ($\Delta\Psi/L$). Arrows represent rainfall events.

climatic and edaphic conditions. Knowledge of the balance between the development of Ψ gradients necessary for HR and the seasonal loss of root conductivity that hinders HR can be used to accurately model root water efflux as HR.

Evidence of HR

Our results agree with those of other studies indicating that drying soils must reach a certain threshold Ψ that causes water to flow in the reverse direction from roots to soil. In a previous investigation of a blue oak (*Quercus douglasii* Hook and Arn.) ecosystem, HR was initiated at soil $\Psi < -0.4$ MPa (Millikin-Ishikawa & Bledsoe, 2000), while research in a longleaf pine (*Pinus palustris* Mill.) ecosystem detected HR initiation at soil $\Psi < -0.2$ MPa (Espeleta *et al.*, 2004). Meinzer *et al.* (2004) reported a similar threshold for HR initiation across a variety of sites including coniferous forests and Brazilian savannas. Although we found that HR initiation could occur at soil Ψ close to zero, maximum HR for specific soil layers generally occurred when $-0.8 < \Psi < -0.4$ MPa. While HR by roots may be active early in the season, its importance is likely outweighed by concurrent water flux directly through the soil as saturated and unsaturated flow.

Under certain conditions, liquid or vapor transport of water through the soil independent of roots can significantly contribute to the diurnal patterns of water flux assumed to be HR (Jackson, 1973). However, models predict that water fluxes associated with root HR are much greater than those associated with direct soil transport (Richards & Caldwell, 1987; Ryel *et al.*, 2002). In this study, liquid transport between layers independent of HR occurred early in the season when unsaturated soil hydraulic conductivity (K) was high. The daily recovery in soil θ attributable to liquid flow was evidenced as steady values of 'apparent' HR < 0.05 mm d^{-1} early in the season (e.g. June in Fig. 5c,d). As unsaturated hydraulic conductivity declines exponentially as upper soils dry (Philip & de Vries, 1957), the continual increase in 'apparent' HR above background levels was an indicator that roots, rather than soils, were increasingly responsible for the movement of water between soil layers. At the relatively dry OG-PP site, estimates of K for the upper soil were $< 10^{-7}$ mm h^{-1} (< 5% of HR) by early September based on the equations of Brooks & Corey (1964) using soil hydraulic parameters derived from soil water release curves (Warren *et al.*, 2005) and estimates of saturated soil hydraulic conductivity ($K_s = 5.2$ cm h^{-1}) based on soil texture using equations from Campbell (1985). Under moister conditions earlier in the season at OG-PP, or throughout the season at OG-DF, the lack of accurate fine-scale spatial variability of Ψ driving forces between 10-cm layers limits our assessment of soil water flux via unsaturated liquid flow, which may be a significant confounding component of HR in moist systems. Nonetheless, while unsaturated flow does increase in moister soils, at OG-DF there was a strong overall negative correlation between soil moisture and HR, which provides further evidence for root HR. Other efforts to separate root HR from liquid or vapor water transport are limited; however, they do suggest a small (< 5%) yet distinct contribution of nonroot water transport co-occurring with HR late in the season (e.g. Ryel *et al.*, 2002; Brooks *et al.*, 2006).

Root water transport, recharge and efflux

Up to three times as much water was leaving the 65–200-cm layer during the night as was entering the upper 15–65-cm layer as HR water, which illustrates the abundance of water available for HR and stem recharge from depth, and the strength of the competing sinks of the trees. Even with readily available water at depth, root capacity for uptake may be limited by the relative scarcity of deep roots to transport water, and internal pathway resistances. Theoretically, the magnitude of nocturnal HR would only be limited by the resistance of available pathways if competition with the tree canopy was removed, provided that a sufficient Ψ gradient and sink for transported water existed within the system. In a tree-cutting study at a young Douglas-fir site, Brooks *et al.* (2006) found that root sapflow away from the tree base (HR) at night could be equal in magnitude to sapflow toward the tree during the daytime if a sufficiently strong sink exists. In that study, HR also increased by an order of magnitude immediately after cutting, and then subsided as the Ψ gradient diminished (Brooks *et al.*, 2006). Thus the magnitude of HR within a single root does not seem to be limited by directional resistance (Schulte, 2006), only by transport capacity and the relative sink strengths in the soil–plant system. However, the fate of HR water in the entire root system is directed by xylem resistance, including differential resistances at root junctions (Schulte, 2006), and patterns of root conductivity.

Spatial patterns of HR

Sensor detection of HR at a specific location within the landscape was very patchy, ranging from 0 to 0.18 mm d^{-1} for individual sensors. Spatial variability was partially dependent on sensor proximity to roots, soil pores, organic matter, rocks, small animal burrows, etc., but also on localized soil water content (Table 2a). High values of measured HR were associated with areas of lower soil water content, where root water extraction patterns had shifted to deeper soils where water contents were still high. Capacitance probes that measured relatively high daytime depletion rates from the upper 2 m also measured high nocturnal HR, further suggesting that relative root distribution was an important underlying condition impacting the spatial variability of HR. In a concurrent study, Meinzer *et al.* (2007) found that species-specific patterns of water extraction may also impact HR, with sensors near Douglas-fir trees displaying accelerated rates of water extraction and subsequent soil drying which led to higher maximum HR than detected by sensors near western hemlock trees.

Across species, the OG-DF site had *c.* 25% more fine-root surface area in the upper 100 cm than the OG-PP site (Warren *et al.*, 2005), which should enable higher rates of water efflux under similar Ψ gradients. In fact, across multiple years, peak HR was 32% higher at OG-DF, which also had 29% higher total daily depletion from the upper 2 m than the drier OG-PP site. Maximum HR declined with depth at OG-DF, where both fine-root area for water efflux and Ψ gradients were reduced. In contrast, at OG-PP there was no difference in HR at different depths, although there was a distinct reduction in fine-root area with depth. The two sites had similar patterns of root distribution weighted toward the upper soil; however, more severe soil drying at OG-PP disproportionately impacted the conductivity of upper roots and thus limited HR. While root area at 60 cm was less than half that at shallower soil layers at OG-PP, this depth displayed the highest rates of mean and maximal HR. At OG-PP, the impacts of reduced root area on HR at depth were offset by higher seasonal deep root conductivity, which was attributable to higher Ψ and higher deep root resistance to cavitation (J. Warren, unpublished observations).

Temporal patterns of HR

Seasonal timing of HR initiation did not always progress from shallower soils to deeper soils as was expected; rather, there was wide variability in the initiation and development of HR within the vertical profile. Daily initiation of HR generally occurred first in the upper soil, progressing to deeper layers over a period of several hours. Daily depletion of soil water by trees usually began between 05:00 and 09:00 h, and then tapered off between 14:00 and 18:00 h, at which point HR was initiated. HR sometimes peaked by 23:00 h or earlier, but often continued increasing through the night until stomatal opening induced the driving force necessary for water movement towards the tree.

Interannual variation of HR initiation was dependent primarily on climate patterns. Early in the season under conditions of low PAR, but high nighttime:daytime VPD, tree and atmospheric sink strength was limited by stomatal closure (and thus reduced depletion), and the abundance of source water in the system permitted HR even under high upper soil moisture conditions. In contrast, later in the season strong Ψ gradients could drive HR as cooler nighttime temperatures reduced nighttime:daytime VPD, thereby reducing any potential nocturnal transpiration.

Seasonal initiation of HR was observed first at the pine site, where soil dried more quickly than at the Douglas-fir site. After increasing from background levels, HR at OG-DF increased for *c.* 4–6 wk during the drought until it was interrupted by late summer rains. In contrast, HR at the PP site clearly peaked in August, *c.* 6 wk after HR initiation, and then declined into autumn in the absence of precipitation. The decline in HR was a result of increased resistance to root water efflux as a result of loss of root xylem conductance. Even as soil Ψ dropped below −2 MPa at the OG-PP site or below −0.5 MPa at the OG-DF site, medium-sized roots (2–4 mm) appeared to maintain hydraulic conductivity throughout the summer drought. However, fine roots (< 2 mm diameter) arising from the medium roots became largely embolized based on estimates of seasonal fine-root relative water deficit in relation to conductivity (Domec *et al.*, 2004). The loss of fine-root conductivity may be particularly acute at the OG-PP site, where roots are exposed to much higher water stress earlier in the season, thereby leading to increased pathway resistances which could partially account for lower absolute HR at the OG-PP site. Fine roots along with attached mycorrhizas provide most of the surface area available for release of water via HR, and thus their loss of conductivity probably contributed significantly to the reductions in HR exhibited as the soils dried.

HR impacts on evapotranspiration

In both the moist OG-DF and dry OG-PP forests studied, the fraction of daily depletion from the upper 2 m replaced by HR increased from 4% (at maximum daily depletion), at both sites, to a maximum of 10% at OG-DF or 15% at OG-PP later in the season. Estimates of water depletion from deeper layers (> 2 m) at OG-PP based on previous eddy covariance studies (Law *et al.*, 2000; Anthoni *et al.*, 2002; Warren *et al.*, 2005) suggest additional site water depletion of *c.* 0.5 mm d^{-1}, which reduces the contribution of HR to a seasonal range of 3–9% of total site water use. In contrast, at OG-DF, most water extraction was likely limited to the upper 2 m, as it is unlikely that significant numbers of functional roots existed below the water table, which seasonally fluctuates from 0.3–1.9 m in January to 2.1–2.6 m in October. At OG-DF, eddy covariance measurements during late summer show high interannual variability in water flux (e.g. Chen *et al.*, 2004), but a value of 2.3 mm d^{-1} has been reported for late July 1999 (Unsworth *et al.*, 2004), which is only slightly higher (< 10%) than average soil water depletion from the 15–200-cm layer during late July in this study. Assuming that 10% of OG-DF water use is extracted from below 2 m, the contribution of HR to total site water use is 3–9%, similar to that calculated for the much drier pine site, and similar to the seasonal average of 3.5% calculated for an *Artemisia tridentata* shrubland (Ryel *et al.*, 2002). In these ecosystems, HR replacement of daily water use likely prolonged root functionality (Domec *et al.*, 2004), thereby enabling higher seasonal rates of evapotranspiration (Jackson *et al.*, 2000; Ryel *et al.*, 2002; Lee *et al.*, 2005) which could increase gross ecosystem productivity (e.g. Law *et al.*, 2002).

Modeling HR

Maximum HR is a trade-off between root area, root conductivity and the Ψ driving forces underlying the competing sinks of the soil, tree and atmosphere. Early in the season, when soil Ψ was close to zero, root conductivity (100-PLC) remained high. Later, as the soil dried, root conductivity declined as the Ψ driving force necessary for HR developed. As HR reached a maximum, further increases in the Ψ driving force were more than offset by the loss of root conductivity, resulting in reduced total HR (e.g. Fig. 6a,c). Our simple model of root efflux correctly predicted HR for two very different ecosystems, which have a three- or fourfold difference in annual precipitation, minimum seasonal soil Ψ, woody plant diversity, leaf area index, and maximum HR. The model highlights the two key mechanisms that define HR: a Ψ gradient in the system, and existence of a conductive root pathway for water transport. The minimum necessary input parameters for this model include measuring or estimating soil Ψ gradients, root distribution and root vulnerability to embolism curves. The model can be used to accurately estimate seasonal patterns of relative root water efflux. To estimate the actual magnitude of HR, relative efflux would need to be adjusted by a constant representing integrated radial root conductivity, which is not readily measured but could be parametrized using several point measurements of HR calculated based on diel variation in θ or Ψ. More complex mechanistic models of water flux to and from roots incorporate estimates of soil water retention curves, saturated and unsaturated soil conductivity, root density distributions and radial root conductivity (Mendel *et al.*, 2002; Ryel *et al.*, 2002). These models can produce robust estimates of HR when adequately parametrized; however, the process of parametrization requires significant effort and iteration which may confound the relative importance of factors controlling HR. In contrast, the simple model presented in this study uses empirical data which strongly fit the independent and concurrently measured values of HR.

The model and regression analysis provide insight into mechanisms driving the variability and magnitude of HR across sites, across seasons, and across years, which is relevant for modeling and understanding regional patterns of water use under changing environmental conditions. The similarities between these sites in seasonal patterns of HR and relative HR replacement of evapotranspiration underscore the common mechanisms controlling HR in PNW conifers, which may be applicable to addressing HR in other ecosystems with different species.

Acknowledgements

This research was supported by the USDA Forest Service Ecosystem Processes Program, the US Environmental Protection Agency, and the Wind River Canopy Crane Research Facility located within the Wind River Experimental Forest, T. T. Munger Research Natural Area in Washington State, USA. The facility is a cooperative scientific venture among the University of Washington, the USDA Forest Service Pacific North-west Research Station and Gifford Pinchot National Forest. This manuscript has been subjected to the Environmental Protection Agency's peer and administrative review, and it has been approved for publication as an EPA document. Mention of trade names or commercial products does not constitute endorsement or recommendation for use. We thank Kevin Hultine and three anonymous reviewers for commenting on an earlier version of the manuscript, Ken Bible and Bev Law for providing site data, and David Woodruff and Hollie Oakes-Miller for fieldwork and data analysis.

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