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## Native root xylem embolism and stomatal closure in stands of Douglas-fir and ponderosa pine: mitigation by hydraulic redistribution

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**Abstract** Hydraulic redistribution (HR), the passive movement of water via roots from moist to drier portions of the soil, occurs in many ecosystems, influencing both plant and ecosystem-water use. We examined the effects of HR on root hydraulic functioning during drought in young and old-growth Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] and ponderosa pine (*Pinus ponderosa* Dougl. Ex Laws) trees growing in four sites. During the 2002 growing season, in situ xylem embolism, water deficit and xylem vulnerability to embolism were measured on medium roots (2–4-mm diameter) collected at 20–30 cm depth. Soil water content and water potentials were monitored concurrently to determine the extent of HR. Additionally, the water potential and stomatal conductance ( $g_s$ ) of upper canopy leaves were measured throughout the growing season. In the site with young Douglas-fir trees, root embolism increased from 20 to 55 percent loss of conductivity (PLC) as the dry season progressed. In young ponderosa pine, root embolism increased from 45 to 75 PLC. In contrast, roots of old-growth Douglas-fir and ponderosa pine trees never experienced more than 30 and 40 PLC, respectively. HR

kept soil water potential at 20–30 cm depth above  $-0.5$  MPa in the old-growth Douglas-fir site and  $-1.8$  MPa in the old-growth ponderosa pine site, which significantly reduced loss of shallow root function. In the young ponderosa pine stand, where little HR occurred, the water potential in the upper soil layers fell to about  $-2.8$  MPa, which severely impaired root functioning and limited recovery when the fall rains returned. In both species, daily maximum  $g_s$  decreased linearly with increasing root PLC, suggesting that root xylem embolism acted in concert with stomata to limit water loss, thereby maintaining minimum leaf water potential above critical values. HR appears to be an important mechanism for maintaining shallow root function during drought and preventing total stomatal closure.

**Keywords** Cavitation · Hydraulic conductivity · Hydraulic lift · Stomatal regulation · Water stress

### Introduction

Hydraulic redistribution (HR) involves transfer of water from wetter to drier portions of the soil profile via roots (Richards and Caldwell 1987; Caldwell and Richards 1989). Although HR has been reported in a wide variety of ecosystems (Burgess et al. 1998; Jackson et al. 2000), our understanding of its significance for plant functioning is still incomplete. Estimates of ecosystem-level fluxes of hydraulically redistributed water are few, but some reports point to values of the order of only  $0.1$ – $0.2$  mm day<sup>-1</sup>, raising questions concerning the role of HR in enhancing evapotranspiration of some vegetation types (Meinzer et al. 2004; Moreira et al. 2003). Nevertheless, recent studies suggest that as soil water deficits increase, the relatively small nocturnal fluxes of water associated with HR are sufficient to significantly delay further drying of the upper portion of the soil profile by replacing most of the water utilized during the day (Brooks et al. 2002; Meinzer et al. 2004). This nearly complete overnight replenishment by HR of soil water surrounding shallow roots could have a

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significant impact on their continued functioning during drought, and therefore on rhizosphere processes associated with the uptake and transport of water and nutrients and maintenance of mycorrhizal symbioses (Caldwell et al. 1998; Querejeta et al. 2003). However, no studies have specifically assessed relationships between vulnerability of roots to water stress-induced embolism and seasonal patterns of HR and root xylem dysfunction in situ.

Water flow along the soil-to-leaf continuum is governed by a combination of the driving forces and the hydraulic properties of the pathway (Mencuccini 2003). Typically, 50% or more of the total resistance to water flow occurs belowground (Tyree and Ewers 1991). During drought periods, HR could influence two potential hydraulic weak points along the belowground portion of the continuum: the root-soil interface where steep soil water potential ( $\Psi_{\text{soil}}$ ) gradients create dry non-conductive zones (Oertli 1996), and the root xylem where tension can reach critical values ( $\Psi_{\text{crit}}$ ), leading to embolism and interruption of the continuum (Sperry et al. 1998). Previous investigations have demonstrated that roots are not only more vulnerable to embolism than stems, but also operate closer to  $\Psi_{\text{crit}}$  than stems (Hacke and Sauter 1995), so small reductions in  $\Psi_{\text{soil}}$  can significantly enhance root embolism rates. Further, fine (<2 mm diameter) and medium (2–3 mm diameter) roots are more vulnerable to embolism than coarse (>3 mm diameter) roots (Sperry and Ikeda 1997). Loss of functional xylem due to embolism prevents root water uptake and reduces whole-plant hydraulic conductance. Field studies have shown significant embolism in root xylem of woody plants during drought with recovery occurring only following rain (Jaquish and Ewers 2001; Davis et al. 2002). Therefore, root embolism may be irreversible during the dry season (Borghetti et al. 1991), which coincides with the growing season in many temperate ecosystems.

Because the roots and rhizosphere are likely to contain the most vulnerable components of the soil-to-leaf hydraulic pathway (Jackson et al. 2000), avoidance of hydraulic failure through passive leakage of water from shallow roots into drying soil may play a major role in the success of species growing under a wide range of precipitation regimes, especially those characterized by summer drought (Gholz 1982). Partial loss of root

hydraulic conductivity through embolism could lower root water potential resulting in the generation of a hydraulic signal that reduces stomatal conductance ( $g_s$ ), and therefore transpiration, to maintain shoot water potential at a nearly constant minimum value above  $\Psi_{\text{crit}}$  (Cochard et al. 1996). It is likely that isohydric behavior, the maintenance of a nearly constant minimum leaf water potential independent of soil or root water status, is linked to an interaction between both chemical and hydraulic information (Tardieu and Davis 1993). A number of tree species exhibit at least partial isohydric behavior during gradual soil drying cycles (Gollan et al. 1985), but the extent to which stomatal regulation of leaf water status is determined by shoot versus root and rhizosphere water status and hydraulic properties is largely unexplored.

We monitored seasonal changes in root embolism, HR, plant and soil water status and  $g_s$  during and after the summer drought period in young and old trees growing in two contrasting Pacific Northwest forest ecosystems: a ponderosa pine (*Pinus ponderosa* Doug. ex Laws.) ecosystem receiving an average of 500 mm of precipitation annually, and a Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] ecosystem receiving 2,500 mm of precipitation. We hypothesized that HR plays a critical role in maintaining the water transport capacity of shallow roots during summer drought and that embolism-induced loss of root conductivity influences stomatal regulation of upper canopy leaf water status. Our specific objectives included (1) examining relationships between root embolism, HR and plant and soil water status, (2) assessing age- and species-specific variation in the vulnerability of roots to water-stress-induced embolism and whether differences in vulnerability are reflected in seasonal patterns of embolism in situ, and (3) identifying potential linkages between stomatal behavior and the degree of embolism in shallow roots.

## Materials and methods

### Plant material and field sites

The study was carried out from June to December 2002 in four stands: one dominated by old-growth (280-year-old) and intermediate age (52-year-old) ponderosa pine, one dominated by young

**Table 1** Characteristics of the ponderosa pine and Douglas-fir sites

	Ponderosa pine		Douglas-fir	
	Old-growth	Young	Old-growth	Young
Mean annual precipitation (mm)	525	550	2,500	2,500
Mean summer precipitation (mm)	35	33	250	250
Mean annual temperature (°C)	7.7	7.5	8.7	8.6
Mean summer temperature (°C)	18	19	16	15.5
Age (years)	280 (o), 52 (I)	16	450	24
Mean height (m)	36 (o), 16 (I)	3.3	60	17
Soil classification <sup>a, b</sup>	Alfic Vitrixerands	Ultic Haploxeralf	Entic Vitrands	Entic Vitrands
Soil texture <sup>a, b</sup>	Sandy loam	Sandy loam	Sandy loam	Sandy loam
sand/silt/clay	73/21/6	65/25/10	65/18/17	65/18/17
Stand Leaf area <sup>c, d</sup> index	2.1	1.0	9.0	6.0

At the old-growth ponderosa pine site, both old (o) and intermediate (I) age trees were studied

<sup>a</sup>Law et al. (1999)

<sup>b</sup><http://depts.washington.edu/wrcrf/>

<sup>c</sup>Irvine et al. (2002)

<sup>d</sup>Phillips et al. (2002)

(15-year-old) ponderosa pine, one dominated by old-growth (450-year-old) Douglas-fir and one dominated by young (24-year-old) Douglas-fir (Table 1). The old-growth and young ponderosa pine stands are located in the Metolius River region of Oregon (44°30' N, 121°37' W) at an elevation of 915 and 1,200 m, respectively. The young ponderosa pine stand was previously an old-growth stand that had been harvested in 1978. The old-growth and young Douglas-fir stands are located within the Wind River Experimental Forest near the Wind River Canopy Crane Research Facility in southern Washington (45°49' N, 121°57' W) at an elevation of 370 and 560 m, respectively. The young stand was planted after a clear-cut, whereas the old-growth stand regenerated naturally after a stand-replacing fire. Although mean annual precipitation is about 2,500 mm, this region has a Pacific maritime climate with dry summers (<120 mm precipitation between June and September).

### Native root hydraulic conductivity and embolism

Specific hydraulic conductivity ( $k_s$ ,  $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ ) and embolism were measured in roots collected four to six times at each site between June and December 2002. Summer sampling was approximately monthly, with a final sampling after the fall rains had rewet the soils. Because of the distance between sites, it was not possible to sample at all sites on the same day. In the early morning of each sampling date, lateral medium roots 2–4 mm in diameter and greater than 25 cm in length were excised near the base of five different trees at about 20-cm depth in the soil. Before excision, roots were checked to insure they were attached to the target tree. Roots were wrapped in aluminum foil and placed in a sealed plastic bag with a moist towel and immediately transported to the laboratory in a cooler, to be processed within 3 h of sampling.

In the laboratory, a 10–15 cm long section of each root was cut, and the bark and cambium were removed from the entire sample. The proximal end was then attached to a tubing system and perfused at a pressure of 6 kPa with filtered (0.22  $\mu\text{m}$ ) solution of HCl (pH 2). The hydraulic pressure head was adjusted to avoid any refilling of embolized tracheids. The rate of efflux was measured in a 1-ml-graduated pipette. When the flow was steady, the time required for the meniscus to cross five consecutive graduation marks (0.5 ml) was recorded. Specific conductivity was calculated as the mass flow rate of the perfusion solution divided by the pressure gradient across the root segment, normalized by the xylem cross-sectional area. Native embolism was determined by comparing the initial (or native) conductivity ( $k_{s(i)}$ ) of root segments to the maximum conductivity ( $k_{s(\text{max})}$ ) after removal of air emboli by soaking the samples in perfusion solution under vacuum for 48 h. Percentage loss of conductivity (PLC) was computed as  $\text{PLC} = 100(1 - k_{s(i)} / k_{s(\text{max})})$ .

### Root xylem vulnerability to embolism

The air injection method (Sperry and Saliendra 1994) was used to measure vulnerability of root xylem to water-stress-induced embolism. The air-injection method is based on the assumption that the xylem tension required to pull air into a conduit and cause embolism is equal in magnitude to the positive air pressure required to push air into the conduit when the xylem water is at atmospheric pressure. Root segments were collected in the field as described above, and air emboli were removed by soaking the samples in perfusion solution under vacuum for 48 h. The segments were inserted into the air-injection chamber with both ends protruding and attached to the tubing system for measuring  $k_s$  as described above. A vulnerability curve was generated by first pressurizing the air chamber to 0.05 MPa to avoid water extrusion from lateral root scars, and allowing the system to equilibrate for 3 min. Water flow through the root was initiated and  $k_{s(\text{max})}$  was measured as described above. A pressure of 0.5 MPa was then applied and held constant for 2 min. After equilibration, the air chamber pressure was reduced to 0.05 MPa, and  $k_{s(0.5)}$  measured. This process was repeated for

pressures ranging from 0.5 to 4.0 MPa, or until the conductivity of the segment was negligible.

### Relative water content

The relative water content (RWC) of each sample used for determination of native embolism and xylem vulnerability was calculated as

$$\text{RWC} = \frac{(M_f - M_d)}{(M_{\text{Sat}} - M_d)} \times 100 \quad (1)$$

where  $M_f$ ,  $M_d$  and  $M_{\text{Sat}}$  are the root fresh mass, dry mass, and mass at full saturation, respectively. For some analyses, root water content was expressed as relative water deficit ( $\text{RWD} = 100 - \text{RWC}$ ). To characterize the relationship between RWC and embolism,  $M_{\text{Sat}}$  was determined initially after vacuum infiltration in perfusion solution to remove emboli, then  $M_f$  was recorded after each pressurization during generation of vulnerability curves, and  $M_d$  was determined by oven-drying the sample following the final pressurization. Native RWC was also determined on 12–20 fine roots (1.1–1.8 mm diameter) collected at each site concurrent with sampling of larger roots for determination of native embolism.

### Soil water potential and volumetric water content

Soil water potential ( $\Psi_{\text{soil}}$ ) was measured using individually calibrated screen-cage thermocouple psychrometers (PST-55, Wescor, Logan, Utah, USA) installed between May and June 2002 at multiple depths in three to four locations at each site. Measurements were recorded every 30 min with a data logger (CR7X, Campbell Scientific, Logan, Utah, USA). Means of measurements made at 20 and 30-cm depth are reported here because these depths encompassed the mean depth at which root samples were collected. Soil volumetric water content ( $\theta$ ,  $\text{m}^3 \text{m}^{-3}$ ) was measured at the same depths using annular frequency domain capacitance sensors (Sentek, Adelaide, Australia) placed in PVC access tubes (Paltineanu and Starr 1997) installed in the vicinity of the soil psychrometers. Values of  $\theta$  were recorded every 10 min with a data logger (RT6, Sentek, Adelaide). The total daily water use ( $\text{mm day}^{-1}$ ) in the 20–30 cm layer was calculated as the difference between the daily maximum and minimum  $\theta$ , and net water use ( $\text{mm day}^{-1}$ ) was calculated as the difference between the maximum  $\theta$  between 2 consecutive days. HR was calculated as the difference between the total and the net water use, and was normalized by the total daily water use (Brooks et al. 2002; Meinzer et al. 2004).

### Tree water potential and stomatal conductance

Predawn and midday water potentials of upper canopy leaves ( $\Psi_L$ ) were determined on individual needles (ponderosa pine) or twigs (Douglas-fir) with a Scholander-type pressure chamber (PMS, Corvallis, Ore., USA). Water potential values were corrected to ground level using the height at which the samples were obtained and a standing gravitational gradient of 0.01  $\text{MPa m}^{-1}$ . In addition, daily mean maximum values of  $g_s$  of exposed, upper to mid-canopy foliage were determined with a null balance porometer (LI-1600, Li-Cor, Lincoln, Neb., USA). Maximum values of  $g_s$  usually occurred between 0900 and 1100 hours when the mean vapor pressure deficit was 1.4±0.1 kPa and 2.5±0.2 kPa in the Douglas-fir and ponderosa pine stands, respectively. Water potential and  $g_s$  were measured on the same day that roots were collected for determination of native embolism on three individual fascicles or twigs from three ponderosa pine and four Douglas-fir trees. Canopy access was provided by towers in the 24-year-old Douglas-fir stand and the old-growth pine stand, and by the Wind River Canopy Crane in the old-

growth Douglas-fir stand. The young pine canopy was accessible from the ground.

#### Statistical analyses

Vulnerability curves were fitted by the least squares method based on a sigmoidal function:

$$PLC = \frac{100}{(1 + e^{a(\Psi - b)})} \quad (2)$$

where the parameter  $a$  is an indicator of the slope of the linear part of the vulnerability curve and  $b$  is the pressure at which 50 PLC occurred ( $P_{50}$ , MPa). The minimum root xylem water potentials were estimated using the vulnerability curves determined in the laboratory and the PLC measured in the field. The maximum PLCs without HR were determined using the predicted  $\Psi_{soil}$  without HR, the relationships between  $\Psi_{soil}$  and root xylem water potentials, and the vulnerability curves. Differences in hydraulic parameters and field measurements between old-growth and young trees and between species were determined using a one-way ANOVA and to assess the difference at each date, a two-way ANOVA with one repeated measure factor was made. All statistical procedures were conducted with Statistical Analysis Systems' software (SAS 1999).

## Results

### Root $k_s$ and xylem vulnerability

Values of  $k_{s(max)}$  for a given age class and species did not vary seasonally, fluctuating around overall means ranging from  $3.4 \pm 0.1$  to  $4.9 \pm 0.3 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$  (Table 2). The overall mean  $k_{s(max)}$  for both age classes of Douglas-fir was 15% lower than for ponderosa pine ( $P=0.02$ ). For both species,  $k_{s(max)}$  was lower in roots of young than in old trees ( $P<0.02$ ).

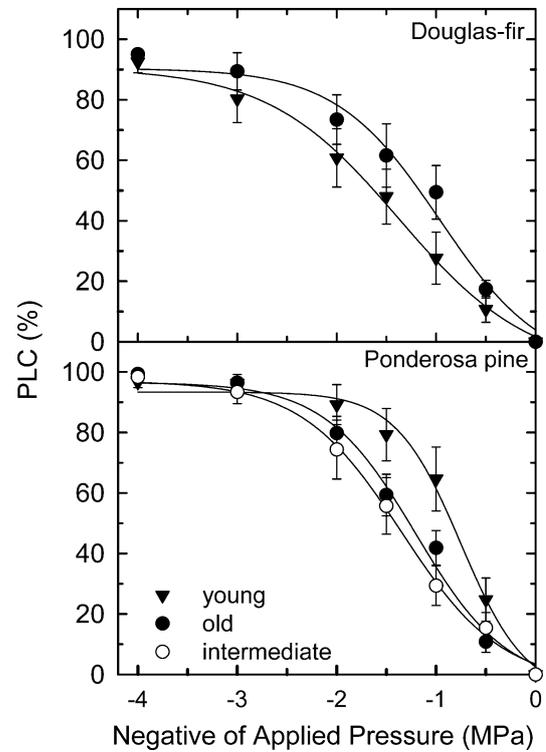
Root xylem vulnerability curves were steep, with PLC increasing sharply above 0.5 MPa applied pressure in both species (Fig. 1). The PLC reached 80 at  $-2.0$  MPa in ponderosa pine and  $-3.0$  MPa in Douglas-fir. Values of  $P_{50}$  ranged from  $-0.7$  MPa in roots of young ponderosa pine to  $-1.4$  MPa in roots of young Douglas-fir (Table 2). Based on their  $P_{50}$  value of  $-0.7$  MPa, roots of young ponderosa pine trees were significantly more vulnerable to embolism than those of intermediate ( $P_{50}=-1.3$  MPa) and old-growth ( $P_{50}=-1.2$  MPa) trees. However,  $P_{50}$  did not differ significantly among roots of young and old Dou-

glas-fir trees, and among roots of Douglas-fir and old-growth and intermediate ponderosa pine.

There was a sigmoidal relationship between RWC and the applied pressure, with no significant species- or age-related differences in slopes (data not shown).

### Native root embolism

In both species, shallow roots of young trees were more embolized at the end of the summer than when measurements began (Fig. 2). In roots of young Douglas-fir, embolism increased significantly ( $P=0.02$ ) from 20 PLC in July to 55 PLC in September. Similarly, in young ponderosa pine root embolism increased significantly ( $P=0.01$ ) from 45 PLC in June to 75 PLC in August and



**Fig. 1** Vulnerability curves showing the percentage loss of hydraulic conductivity (PLC) versus the negative of applied air pressure for Douglas-fir and ponderosa pine medium root xylem ( $n=6$ ) of young trees (triangles), intermediate trees from old-growth site (open circles) and old-growth trees (filled circles). Error bars are standard errors

**Table 2** Total diameter, xylem diameter, maximum specific conductivity ( $k_{s(max)}$ ), and the negative of applied pressure at which 50% loss of  $k_{s(max)}$  is reached ( $P_{50}$ ) of roots sampled from

	Ponderosa pine			Douglas-fir	
	Old-growth	Intermediate	Young	Old-growth	Young
Mean total diameter (mm)	$3.3 \pm 0.3$ a	$3.4 \pm 0.2$ a	$3.5 \pm 0.3$ a	$3.6 \pm 0.2$ a	$3.6 \pm 0.2$ a
Mean xylem diameter (mm)	$2.0 \pm 0.1$ a	$2.0 \pm 0.1$ a	$2.1 \pm 0.1$ a	$2.0 \pm 0.1$ a	$1.9 \pm 0.1$ a
$k_{s(max)}$ ( $\text{kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ )	$4.9 \pm 0.3$ a	$4.2 \pm 0.2$ b	$3.7 \pm 0.2$ bc	$4.0 \pm 0.2$ b	$3.4 \pm 0.1$ c
$P_{50}$ (MPa)	$-1.2 \pm 0.1$ a	$-1.3 \pm 0.2$ a	$-0.7 \pm 0.1$ b	$-1.0 \pm 0.3$ ab	$-1.4 \pm 0.1$ a

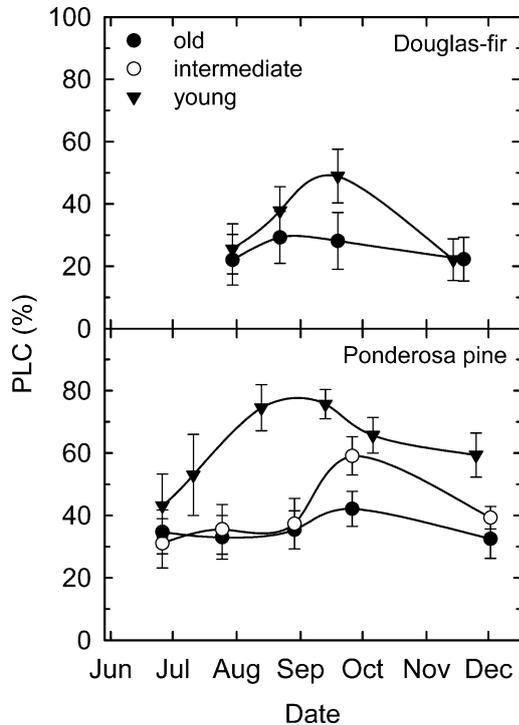
ponderosa pine and Douglas-fir trees of different ages. Values are means ( $\pm$ SE) for  $n=6$  roots. Values with different letters within a row are significantly different ( $P<0.05$ )

September. In roots of the intermediate trees at the old-growth ponderosa pine site, embolism also increased significantly ( $P=0.01$ ) from 30 PLC at the end of June to 59 PLC at the end of September. In contrast, roots of the old-growth trees never experienced more than 30 and 40 PLC for Douglas-fir and ponderosa pine, respectively (Fig. 2).

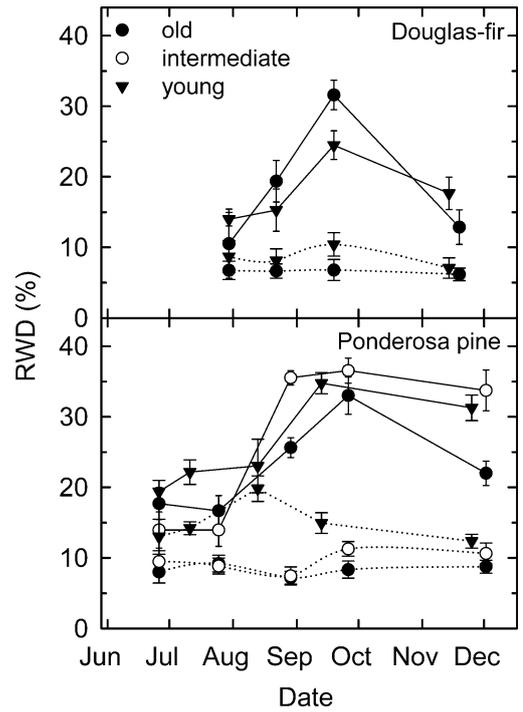
The seasonal trend in RWD of medium (2–4-mm diameter) roots (Fig. 3) followed that of native PLC. Medium roots of the old-growth trees lost less than 15% of their RWC compared to 20% for the young ponderosa pine trees. In contrast, fine (1.1–1.8 mm diameter) roots experienced higher seasonal RWD than medium roots in both old and young trees ( $P<0.05$ ), with maximum values of 25–30% RWD in Douglas-fir and 30–35% RWD in ponderosa pine. For both medium and fine roots, the initial RWD was not zero at the beginning of the growing season, but ranged from 8 to 18% (Fig. 3). PLC and RWD were strongly related and appeared to be independent of species and age classes (Fig. 4). Based on the relationship in Fig. 4 and seasonal courses of root RWD (Fig. 3), fine roots in all sites were likely to have experienced at least 80 PLC at the peak of the summer drought.

#### Soil water status and HR

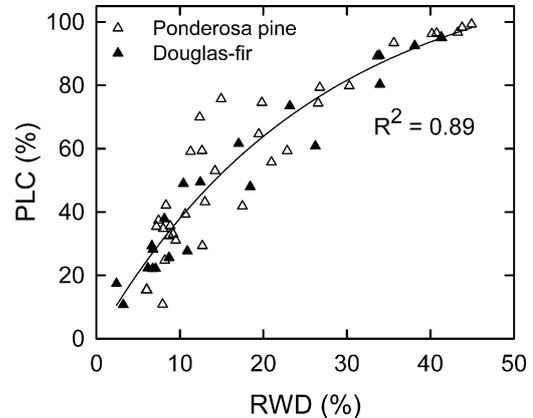
At the beginning of the study in June, mean  $\theta$  of the 20–30 cm layer ranged from 0.20 to 0.25  $\text{m}^3 \text{m}^{-3}$  in the



**Fig. 2** Seasonal percentage loss of xylem hydraulic conductivity (PLC) in Douglas-fir and ponderosa pine medium roots ( $n=8-10$ ) of young trees (triangles), intermediate trees from old-growth site (open circles) and old-growth trees (filled circles). Error bars are standard errors



**Fig. 3** Seasonal relative water deficit (RWD) in Douglas-fir and ponderosa pine for fine roots (<2-mm diameter,  $n=5$ ; solid lines) and medium roots (2–4-mm diameter,  $n=8-10$ ; dotted lines) of young trees (triangles), intermediate trees from old-growth site (open circles) and old-growth trees (filled circles). Error bars are standard errors



**Fig. 4** Percent loss of conductivity (PLC) versus the relative water deficit (RWD) for Douglas-fir (solid triangles) and ponderosa pine (open triangles) medium root samples

Douglas-fir stands and from 0.15 to 0.17  $\text{m}^3 \text{m}^{-3}$  in the ponderosa pine stands (Fig. 5a,b). Between June and October, gradual soil drying occurred in the ponderosa pine stands, with  $\theta$  falling to ca. 0.07  $\text{m}^3 \text{m}^{-3}$  by the end of October. However, about half of the seasonal decline in  $\theta$  in the ponderosa pine stands had occurred by the end of July. In the Douglas-fir stands,  $\theta$  had fallen to ca. 0.12  $\text{m}^3 \text{m}^{-3}$  by mid-September, when light rain events caused a transient partial recovery of  $\theta$ . Maximum daily net water use in the 20–30 cm layer ranged between 0.2 and 0.4  $\text{mm day}^{-1}$  in the Douglas-fir stands and between

0.1 and 0.2 mm day<sup>-1</sup> in the ponderosa pine stands (Fig. 5c,d). By the time  $\theta$  reached its seasonal minimum value, net water use had declined to ca. 0.03 mm day<sup>-1</sup> in the Douglas-fir stands and ca. 0.01 mm day<sup>-1</sup> in the ponderosa pine stands.

Soil  $\Psi$  in the 20–30 cm layer was close to zero in all sites at the beginning of the study period and showed little change until late July to mid-August in the Douglas-fir stands and early to mid-July in the ponderosa pine stands (Fig. 6a–d). The seasonal decline in  $\Psi_{\text{soil}}$  was slower in the old-growth Douglas-fir stand, where  $\Psi_{\text{soil}}$  never dropped below  $-0.8$  MPa, than in the young Douglas-fir stand, where  $\Psi_{\text{soil}}$  dropped to  $-1.4$  MPa by September (Fig. 6). Both ponderosa pine sites experienced severe drought in the upper soil with  $\Psi_{\text{soil}}$  dropping to  $-2.0$  MPa at the old-growth site and  $-2.9$  MPa at the young site.

In all sites, HR was not detected until threshold values of  $\Psi_{\text{soil}}$  had been attained (Fig. 6e,f). Soil  $\Psi$  thresholds for the onset of HR ranged from ca.  $-0.05$  MPa in the old-growth stands to ca.  $-0.6$  MPa in the young stands. The mean  $\Psi_{\text{soil}}$  threshold for the onset of HR among all stands was  $-0.33 \pm 0.16$  MPa, and 50% of seasonal maximum HR was attained at a mean  $\Psi_{\text{soil}}$  of  $-0.64 \pm 0.10$  MPa. Normalized HR in the 20–30 cm layer did not appear to reach its maximum values until  $\Psi_{\text{soil}}$  in the same layer had fallen below predawn  $\Psi_L$ . In the Douglas-fir stands, overnight HR replaced a maximum of 60% of the previous day's soil water utilization until a precipitation event in September temporarily eliminated HR. In the old-growth ponderosa pine stand where the greatest absolute values of HR were observed (0.06 mm day<sup>-1</sup>), overnight partial recharge of soil water remained at 60–80% between August and October. The predicted seasonal decline in  $\Psi_{\text{soil}}$  in the absence of HR was substantially greater than the observed decline in all sites (Fig. 6a–d). However, significant deviation of predicted and observed  $\Psi_{\text{soil}}$  did

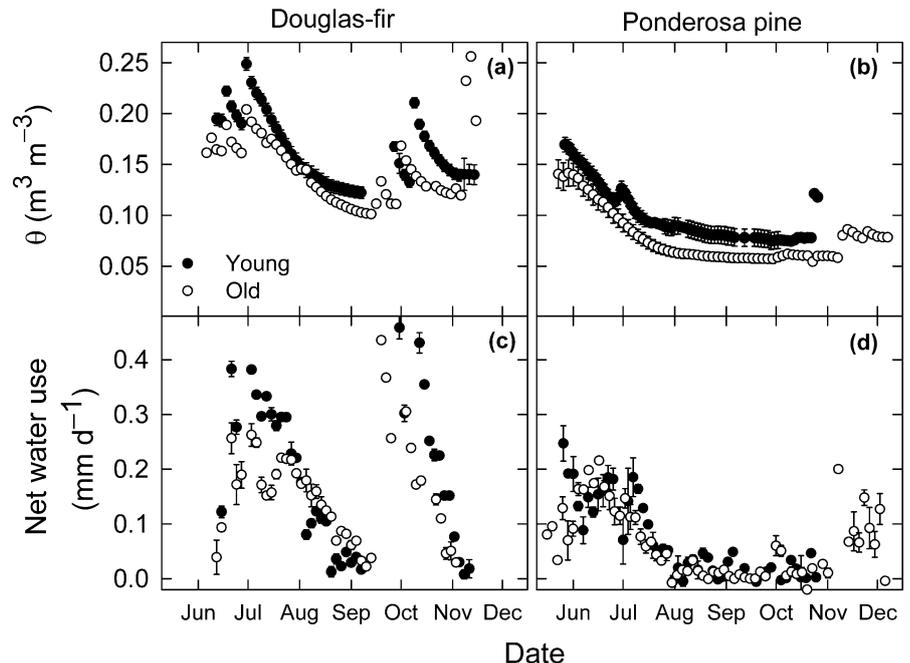
not occur until  $\Psi_{\text{soil}}$  had fallen below thresholds for the onset of HR. The deviation of predicted from observed time courses of  $\Psi_{\text{soil}}$  was greatest in the old-growth ponderosa pine stand where in the absence of HR  $\Psi_{\text{soil}}$  at 20–30 cm would have fallen below  $-4.0$  MPa (Fig. 6d).

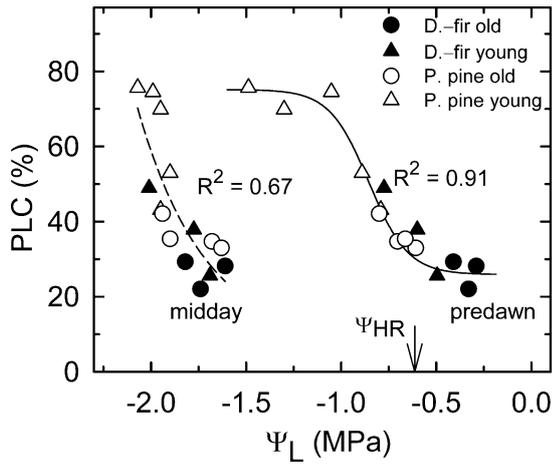
#### Mitigation of seasonal embolism and stomatal closure by HR

The relationship between seasonal variation in PLC and  $\Psi_L$  corrected to ground level appeared to be identical across species and age classes (Fig. 7). PLC remained nearly constant as predawn  $\Psi_L$  decreased from  $-0.25$  to  $-0.60$  MPa, then began to increase sharply as predawn  $\Psi_L$  fell below  $-0.60$  MPa, which corresponded to the mean  $\Psi_{\text{soil}}$  at which HR attained approximately 50% of its seasonal maximum (cf. Fig. 6). As predawn  $\Psi_L$  decreased from  $-0.6$  to  $-1.0$  MPa, PLC increased from 25 to 70%, and then remained constant as predawn  $\Psi_L$  decreased further to  $-1.5$  MPa. Despite the large seasonal variation in predawn  $\Psi_L$  and PLC, the variation in midday  $\Psi_L$  was relatively small, with midday  $\Psi_L$  remaining nearly constant at  $-2.0$  MPa once PLC had reached its seasonal maximum.

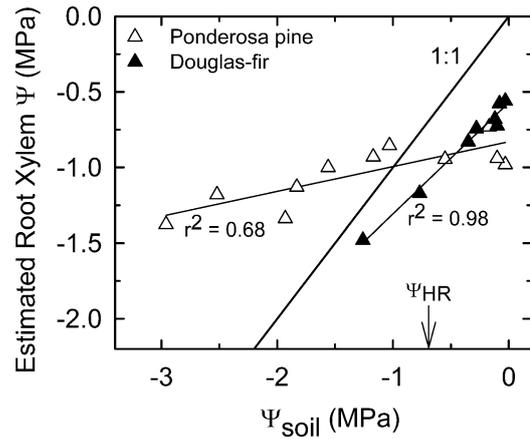
The estimated root xylem  $\Psi$ , determined from the vulnerability curves and native PLC, decreased linearly with  $\Psi_{\text{soil}}$  measured on the same day the roots were collected (Fig. 8). In ponderosa pine, estimated root  $\Psi$  was lower than  $\Psi_{\text{soil}}$  early in the season, but then became higher than  $\Psi_{\text{soil}}$  over a range of  $\Psi_{\text{soil}}$  corresponding to the onset of HR. In Douglas-fir, estimated root  $\Psi$  was always lower than  $\Psi_{\text{soil}}$ , but extrapolation of the linear relationship between  $\Psi_{\text{soil}}$  and estimated root  $\Psi$  suggested that continued seasonal decline in  $\Psi_{\text{soil}}$  may have eventually resulted in root  $\Psi$  becoming less negative than that of the

**Fig. 5a–d** Time courses of soil volumetric water content ( $\theta$ ; **a** and **b**) and net water use (**c** and **d**) between 20 and 30 cm in young and old-growth Douglas-fir and ponderosa pine stands during the dry season





**Fig. 7** Percent root loss of conductivity (*PLC*) versus midday and predawn leaf water potentials ( $\Psi_L$ ) corrected for the gravitational component in young and old-growth Douglas-fir and ponderosa pine trees. The vertical arrow represents the mean  $\Psi_{soil}$  at which HR reached 50% of its seasonal maximum ( $\Psi_{HR}$ )

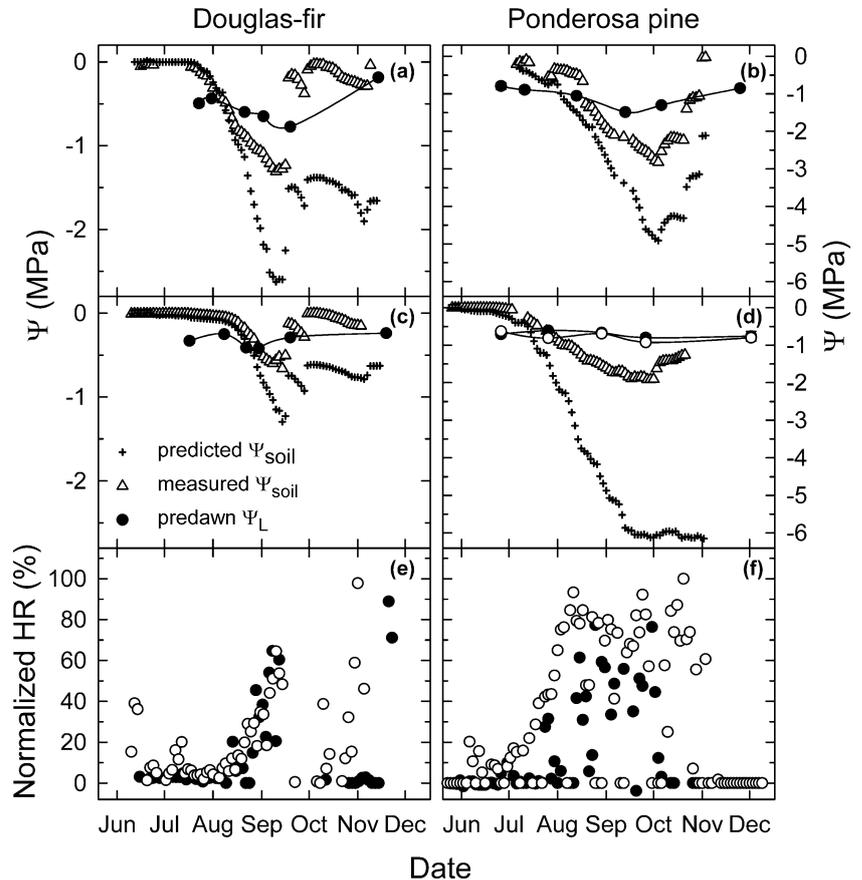


**Fig. 8** Estimated root xylem water potentials versus soil water potentials ( $\Psi_{soil}$ ) in young and old-growth Douglas-fir (*filled symbols*) and ponderosa pine (*open symbols*) stands. The estimated root water potential was determined using the measured native root embolism and the vulnerability curves. The vertical arrow represents the mean  $\Psi_{soil}$  at which HR reached 50% of its seasonal maximum ( $\Psi_{HR}$ )

soil. In both ponderosa pine and Douglas-fir stands, redistributed water originally taken up by deeper roots thus appeared to partially uncouple the  $\Psi$  of shallow roots from that of the surrounding soil. Seasonal minimum values of  $\Psi_{soil}$  at 1-m depth were  $-0.1$  to  $-0.3$  MPa, indicating greater water availability to deeper roots in these stands (data not shown).

In all of the sites, the seasonal maximum root PLC in the absence of HR was predicted to be substantially greater than observed values (Table 3). In the old-growth sites, the PLC without HR was predicted to be approximately twice the measured PLC, whereas in the younger stands the predicted increase in PLC without HR was between 11 and 21%.

**Fig. 6a-f** Time courses of soil and predawn water potentials ( $\Psi$ ) in young (a and b) and old-growth (c and d) Douglas-fir and ponderosa pine stands and normalized hydraulic redistribution (Normalized HR; e and f) between 20 and 30 cm. The predicted time course of soil water potential was calculated in the absence of nightly partial recovery due to HR. At the old-growth ponderosa pine site, predawn water potentials from old-growth trees (*closed circles*) and intermediate trees (*open circles*) are represented. In e and f, *open* and *closed circles* represent old-growth and young sites, respectively



**Table 3** Soil water potential between 20 and 30 cm ( $\Psi_{\text{soil}}$ ), predawn leaf water potential corrected to ground level ( $\Psi_{\text{L}}$ ), estimated root xylem water potential and maximum percent loss of root conduc-

tivity (PLC) measured and estimated assuming no hydraulic redistribution (HR) in ponderosa pine and Douglas-fir stands

	Ponderosa pine			Douglas-fir	
	Old-growth	Intermediate	Young	Old-growth	Young
Minimum $\Psi_{\text{soil}}$ at 20–30 cm (MPa)	$-1.8 \pm 0.3$	$-1.8 \pm 0.3$	$-2.7 \pm 0.4$	$-0.5 \pm 0.1$	$-1.4 \pm 0.2$
Minimum predawn $\Psi_{\text{L}}$ (MPa)	$-0.8 \pm 0.1$	$-0.9 \pm 0.1$	$-1.6 \pm 0.1$	$-0.4 \pm 0.1$	$-0.8 \pm 0.1$
Minimum root xylem $\Psi$ (MPa)	$-1.1 \pm 0.2$	$-1.6 \pm 0.2$	$-1.4 \pm 0.2$	$-0.7 \pm 0.1$	$-1.5 \pm 0.1$
Observed maximum PLC (%)	$42 \pm 5$	$59 \pm 6$	$76 \pm 5$	$29 \pm 7$	$49 \pm 8$
Predicted maximum PLC without HR (%)	$81 \pm 6$	$73 \pm 6$	$87 \pm 7$	$68 \pm 4$	$70 \pm 6$

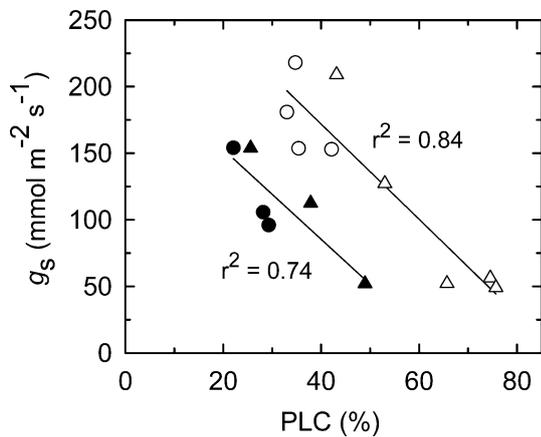
Daily  $g_s$  decreased linearly with increasing PLC for both species with all age classes following similar patterns within a species (Fig. 9). Although  $g_s$  was greater in ponderosa pine at a given value of PLC, the slopes of the linear relationships were similar ( $P=0.46$ ).

## Discussion

We found compelling evidence that partial overnight replenishment of soil water by HR in ponderosa pine and Douglas-fir stands diminished loss of shallow root function during seasonal drought periods. As moisture near the soil surface became depleted, transfer of water from moist, deeper soil layers prevented  $\Psi_{\text{soil}}$  from falling to levels that would have induced complete loss of water transport capacity in shallow roots. In roots of the old-growth trees, PLC never exceeded 45% throughout the entire dry season (Fig. 2). In the old-growth ponderosa pine stand,  $\Psi_{\text{soil}}$  in the 20–30 cm layer did not fall below  $-2$  MPa, whereas without HR,  $\Psi_{\text{soil}}$  would likely have reached values as low as  $-4$  to  $-6$  MPa, causing more than 80% embolism (Table 3). Root embolism in ponderosa pine is not predicted to reach 100% at even these low soil water potentials because root xylem water potential is greater than that of the soil below  $-1$  MPa (Fig. 8). Although greater soil water storage in the wetter old-growth

Douglas-fir stand allowed  $\Psi_{\text{soil}}$  to remain above  $-1$  MPa, HR still played an important role in maintaining  $\Psi_{\text{root}}$  and  $\Psi_{\text{soil}}$  above levels that would have provoked substantially greater PLC than that observed (Fig. 6, Table 3). In the younger stands, minimum  $\Psi_{\text{root}}$  was lower and maximum PLC greater than in the old-growth stands, implying that HR was not as effective in maintaining  $\Psi_{\text{soil}}$  above thresholds associated with rapidly increasing PLC in these stands. It should be noted that our predictions of PLC in the absence of HR (Table 3) are extremely conservative because  $\Psi_{\text{root}}$  was estimated from relationships between  $\Psi_{\text{soil}}$  and  $\Psi_{\text{root}}$  determined in the presence of HR. Without HR, it is likely that shallow  $\Psi_{\text{root}}$  would have been more closely coupled to  $\Psi_{\text{soil}}$  as the soil dried, leading to full embolism in most of the stands. One of the primary consequences of HR thus appears to be protection of shallow roots from total hydraulic dysfunction through delayed drying of the upper portion of the soil profile.

The loss of root conductivity was strongly related to predawn and midday  $\Psi_{\text{L}}$ , with common relationships found among all four sites, despite differences in species, tree size and soil type (Fig. 7). Embolism increased rapidly below a threshold predawn  $\Psi_{\text{L}}$  of  $-0.6$  MPa, which also corresponded to the mean  $\Psi_{\text{soil}}$  at which HR reached 50% of its seasonal maximum. This concordance suggests that despite probable differences in soil texture among sites and in maximum rooting depth and water use among the trees studied, there was a degree of convergence in the plant and soil water potential thresholds at which root embolism accelerates and HR begins to regulate  $\Psi_{\text{soil}}$ , thereby delaying loss of root conductivity (Hacke et al. 2000). Native PLC was 24% in Douglas-fir roots and 36% in ponderosa pine roots early in the season when  $\Psi_{\text{soil}}$  was still near zero. However, predawn plant  $\Psi$  and  $\Psi_{\text{soil}}$  in the 20–30 cm layer were only briefly in equilibrium in all four sites (Fig. 6a–d). At the beginning of the dry season, mean predawn  $\Psi_{\text{L}}$  was  $-0.42$  MPa in the Douglas-fir stands and  $-0.74$  MPa in the ponderosa pine stands. Using these values as estimates of root xylem  $\Psi$  to predict PLC from the vulnerability curves, initial PLC values of 13 and 32% were obtained for Douglas-fir and ponderosa pine, respectively, which were consistent with the native PLC of roots collected from the sites. The disequilibrium between plant and soil  $\Psi$  early in the season was probably attributable to nocturnal transpiration or incomplete overnight rehydration of the aboveground portion of the trees



**Fig. 9** Stomatal conductance ( $g_s$ ) versus percent root loss of conductivity (PLC) in young and old-growth Douglas-fir and ponderosa pine trees. Symbols are as in Fig. 7

(Donovan et al. 2001,2003). Later in the season, when  $\Psi_{\text{soil}}$  at 20–30 cm became more negative than predawn  $\Psi_L$  (Fig. 6a–d), HR resulting from reverse flow of sap through roots (Brooks et al. 2002; Scholz et al. 2002) reversed the normal root/soil  $\Psi$  gradient, keeping the  $\Psi$  of shallow roots above that of the soil.

Our results suggest a link between root PLC and regulation of stomatal conductance (Fig. 9). Root xylem embolism acted in concert with stomata to limit water loss, thereby maintaining minimum  $\Psi_L$  above critical values to prevent further xylem embolism (Sperry 2002). In the present study, seasonal variation in predawn  $\Psi_L$  was roughly twice that of midday  $\Psi_L$  and variation in midday  $\Psi_L$  decreased sharply as maximum values of root PLC were reached (Fig. 7). Stomata thus appeared to more tightly regulate midday  $\Psi_L$  as opposed to predawn  $\Psi_L$  because midday  $\Psi_L$  remained nearly constant at around  $-2.0$  MPa despite variation in predawn  $\Psi_L$  and  $\Psi_{\text{soil}}$  during soil drying (Tardieu and Davies 1993). It has been shown that avoidance of extensive embolism through the isohydric control of minimum  $\Psi_L$  is governed by a feedback between stomatal conductance and  $\Psi_L$  (Saliendra et al. 1995). Below a threshold midday  $\Psi_L$  of ca.  $-1.7$  MPa, a sharp increase in root embolism was associated with a stomatal closing response that maintained midday  $\Psi_L$  above  $-2.0$  MPa (Meinzer and Grantz 1990; Cochard et al. 2002).

Triggering of stomatal closure by embolism in root xylem may be a means of preventing catastrophic xylem failure in the aerial portions of the plant. Stomatal responses to experimental manipulations of whole-plant hydraulic conductance involving root pruning (Meinzer and Grantz 1990), root pressurization (Saliendra et al. 1995), and chilling of roots (Cochard et al. 2000) are consistent with this proposed mechanism of preventing catastrophic xylem failure. The consequences of partial embolism during drought may be less serious in roots because their function may be more readily restored after drought, either by refilling of embolized conduits with the advent of soil and root rewetting (Jaquish and Ewers 2001; J. Irvine, personal communication), or growth of new roots (Kolb and Sperry 1999). Critical values of plant  $\Psi$  could also be linked to root death and regeneration. It has been shown in several conifer seedlings that no root regeneration occurred below a predawn  $\Psi_L$  of  $-1.3$  MPa, and below this threshold value root mortality was close to 100% (Girard et al. 1997). This value of plant  $\Psi$  corresponds to about 80 PLC in our study (Fig. 7), and may correspond to the turgor threshold below which new root growth is inhibited (Zou et al. 2000).

Seasonal courses of PLC (Fig. 2) indicated that embolized tracheids were partially or completely refilled by late fall before the soil had been fully recharged by precipitation. Because of the size of the roots studied, it is unlikely that reduced PLC in the late fall reflected the production of new, non-embolized roots. Embolized tracheids may readily refill when water is available, even in the absence of positive pressures (Borghetti et al. 1991). As shown by the relationship between RWD and PLC

(Fig. 4), a relatively small amount of water can markedly increase root conductivity. The mechanism responsible for refilling of embolized xylem conduits is still unknown, but refilling is faster when embolism is artificially induced by air pressure than when it is naturally induced by drought (Hacke and Sperry 2003). Refilling of embolized tracheids in Douglas-fir and ponderosa pine roots may have been facilitated during periods of HR that increased the water content of shallow roots by reversing the direction of water flow. Reverse flow has previously been documented in both Douglas-fir and ponderosa pine roots (Brooks et al. 2002). Because low soil temperature severely reduces root water uptake during winter (Oertli 1996), refilling of roots in the absence of fall rains may furnish an ecological advantage to trees growing in climates with cold winters by allowing the roots to become fully functional before the snow melts in the spring.

Values of  $k_{\text{smax}}$  for Douglas-fir and ponderosa pine roots were higher than those previously reported for stems of the same species (Domec and Gartner 2001,2003). Values of  $k_{\text{smax}}$  for Douglas-fir roots were similar to those reported for excised seedling roots (Coleman et al. 1990), but  $k_{\text{smax}}$  of ponderosa pine roots was lower than that reported in an earlier study (Gladwin et al. 1998). Although Douglas-fir and ponderosa pine roots have higher conductivity than stems, they are more vulnerable to embolism than stems (Domec and Gartner 2001,2003). Greater conductivity and higher vulnerability to embolism in roots generally parallels the presence of wider and longer conduits in roots than in stems (Ewers 1985). These data suggest that roots can transport water more easily when the soil and plant-water status are favorable, but their lower resistance to embolism may limit plant water use during drought, and therefore play a critical role for stomatal regulation of plant water status.

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