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RESEARCH ARTICLE

Water potential gradient, root conduit size and root xylem hydraulic conductivity determine the extent of hydraulic redistribution in temperate trees

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Abstract

1. Hydraulic redistribution (HR) of soil water through plant roots is widely described; however its extent, especially in temperate trees, remains unclear. Here, we quantified HR of five temperate tree species. We hypothesized that both, HR within a plant and into the soil increase with higher water-potential gradients, larger root conduit diameters and root-xylem hydraulic conductivities as HR driving factors.
2. Saplings of conifer (*Picea abies*, *Pseudotsuga menziesii*), diffuse-porous (*Acer pseudoplatanus*) and ring-porous species (*Castanea sativa*, *Quercus robur*) were planted in split-root systems, where one plant had its roots split between two pots with different water-potential gradients (0.23–4.20 MPa). We quantified HR via deuterium labelling.
3. Species redistributed 0.39 ± 0.14 ml of water overnight (0.08 ± 0.01 ml/g root mass). Higher pre-dawn water-potential gradients, hydraulic conductivities and larger conduits significantly increased HR quantity. Hydraulic conductivity was the most important driving factor on HR amounts, within the plants (0.03 ± 0.01 ml/g) and into the soil (0.06 ± 0.01 ml/g).
4. Additional factors as soil-root contact should be considered, especially when calculating water transfer into the soil. Nevertheless, trees maintaining high-xylem hydraulic conductivity showed higher HR amounts, potentially making them valuable 'silvicultural tools' to improve plant water status.

KEYWORDS

diffuse-porous temperate trees, drought, hydraulic redistribution driving factors, hydraulic redistribution quantity, ring-porous temperate trees, split-root experiment, stable water isotope labelling (^{2}H/deuterium), temperate conifer trees

1 | INTRODUCTION

Hydraulic redistribution (HR) describes the passive flux of water through plants and their roots, for example from moist to dry soil layers. Roots that span soil layers across a soil water-potential (Ψ) gradient, take-up, redistribute and release water overnight, when transpiration is virtually absent. Initially described for (semi-) arid regions (e.g. Burgess, Adams, Turner, & Ong, 1998; Caldwell & Richards, 1989; Richards & Caldwell, 1987), HR has also been demonstrated in mesic environments (Dawson, 1993) and is now considered a general phenomenon occurring across different climates and ecosystems (e.g. Quijano & Kumar, 2015; Sardans & Peñuelas, 2014).

Hydraulic redistribution of soil water can facilitate plant health and growth in multiple ways. For example, roots in dry soil layers may stay alive, maintaining root life span (Bauerle, Richards, Smart, & Eissenstat, 2008) and functionality (Scholz et al., 2008) in suboptimal growing conditions. If water is released into the rhizosphere (Emerman & Dawson, 1996), roots may retain soil contact (Ryel, Leffler, Peek, Ivans, & Caldwell, 2004), and consequently, access to nutrients (Caldwell, Dawson, & Richards, 1998; Querejeta, Egerton-Warburton, & Allen, 2003). Additionally, higher rates of transpiration, photosynthesis and hence growth can occur as a result of HR, prolonging plant growth throughout a season (Brooks, Meinzer, Coulombe, & Gregg, 2002; Howard, Van Iersel, Richards, & Donovan, 2009). However, a critical point remains under debate; what factors play the greatest role in determining the magnitude of redistributed water? For temperate tree species in particular, it is currently unclear which driving factors influence the amount of water that is hydraulically redistributed the most, both, within the root system and into the rhizosphere soil. Therefore, we have yet to understand which plant and environmental circumstances must be given that facilitative HR effects occur (Ammer et al., 2018; Pretzsch et al., 2014).

While a number of suggested factors drive HR, including 'external' environmental and 'internal' plant factors (Neumann & Cardon, 2012), a mechanistic understanding of the role each factor plays in determining the quantity of HR is still lacking. Reported 'external' factors include soil texture, soil Ψ gradients and atmospheric vapour pressure deficit (VPD), while plant-driven 'internal' factors affecting HR include xylem vessel conductivity (Quijano & Kumar, 2015), rates of (night-time) transpiration (Dawson et al., 2007; Howard et al., 2009) and water refilling of plant storage tissues (Yu et al., 2018). In addition, root characteristics such as bark thickness (Bauerle et al., 2008) or the regulation of aquaporins (Li, Santoni, & Maurel, 2014; Prieto, Armas, & Pugnaire, 2012) might affect the amount of redistributed water. Potential seasonal shifts in 'external' and 'internal' factors could also help to explain seasonal shifts in the magnitude of HR (Hultine, Scott, Cable, Goodrich, & Williams, 2004; Priyadarshini et al., 2016). However, a large variability in the quantification of HR (Neumann & Cardon, 2012) exemplifies the need to tease apart the aforementioned 'internal' and 'external' factors. In this study, we aimed to quantify both, the amounts of water that saplings of five common temperate tree species redistributed within their root system and the amounts of HR water these saplings released into the rhizosphere soil. We hypothesized that more water would be redistributed following an increasing Ψ gradient between dry and moist root branches of the same plant ('external' driving factor for HR). Furthermore, we hypothesized that the amount of redistributed water would increase with increasing root conduit diameter and, potentially more accurate, with increasing 'actual' (unflushed) xylem hydraulic conductivity of the roots, as it accounts for potential native embolisms in the conduits due to drought conditions ('internal' driving factors). We chose two conifer-, one diffuse-porous and two ring-porous, species to cover a range of root conduit diameter sizes and, therefore, potential root-xylem hydraulic conductivities. Trees were planted in split-root systems that enabled us to create and control different Ψ gradients between dry and moist roots for each species and to quantify HR through deuterium labelling.

2 | MATERIALS AND METHODS

2.1 | Plants and growth conditions

In December 2015, trees were planted into split-root systems (Figure 1), where two pots (10 L each) were bolted together with one centrally located tree's (split-root plant, SRP) root system split equally between a 'dry' and a 'moist' pot (Figure 1). Additional 'reference' trees for water potential and hydraulic conductivity contrasts were planted in each of the pots (plant in the dry pot, 'DP' and plant in the moist pot, 'MP', respectively, Figure 1). Therefore, each complete split-root system was composed of three trees of the same species. Replicate systems were composed of 2- to 4-year-old saplings of *Picea abies* (L. Karst.), *Pseudotsuga menziesii* ((Mirb.) Franco, planted in December 2016), *Acer pseudoplatanus* (L.), *Quercus robur* (L.) and *Castanea sativa* (Mill.). A soil-filled foam-sleeve was placed around the root collar of the SRP to prevent root desiccation after planting. The sleeve and the soil within were removed several weeks before the experiment. We aimed for seven replicate systems per species; however, as the split-root setup displayed a stressful environment for some SRPs, not all plants survived and therefore the number of replicate systems deviated between the species (Table 1). Over all species, the height of the studied SRPs ranged from 50 to 95 cm and root biomass in the 'dry' pot from 3.0 to 18.8 g. While most species were very similar in size, *C. sativa* trees had larger root systems (Table 2). We used a potting soil (mixture of topsoil, compost, turf and lava (20% organic matter); Wurzer Umwelt GmbH, Eitting, Germany), mixed with 10% of soil retrieved from forest-stands dominated by the respective species to provide species-specific mycorrhizal inoculum. All trees were well-watered and grown in a greenhouse in Freising, Germany (48°23′57.98″N, 11°43′00.99″E) under ambient climate conditions until July 2017 to ensure establishment.

The experiment was conducted in two 7.7 m^2 growth chambers at the 'TUMmesa' research facility (Technical University of Munich – Model EcoSystem Analyser; http://www.tummesa.de/home) to

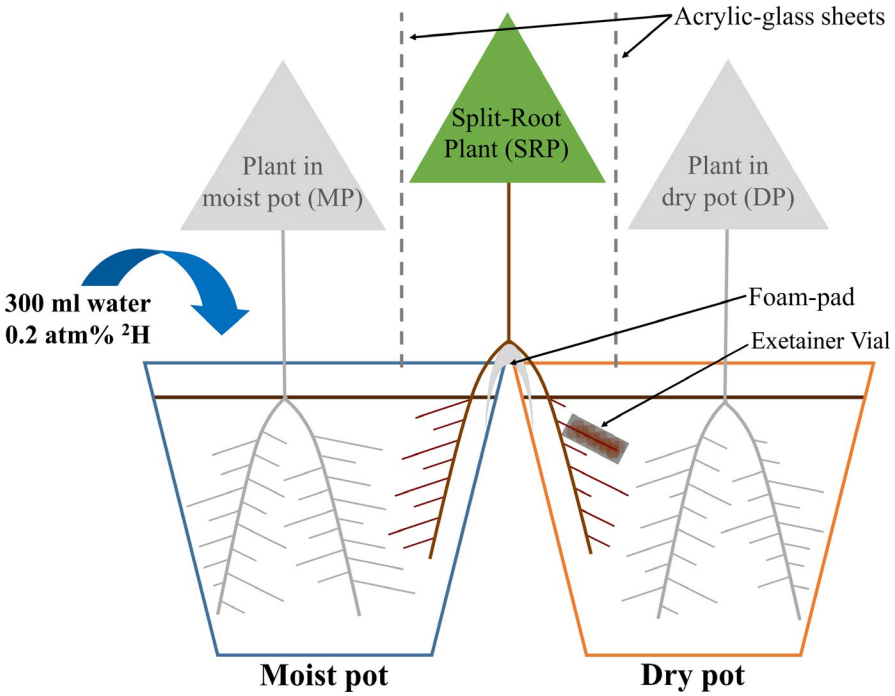

FIGURE 1 Scheme of the split-root system. Split-root systems consisted of one centrally located tree's (split-root plant, SRP) root system split equally between a 'moist' and a 'dry' pot. A foam-pad was placed between the roots of the SRP and the pot edges to minimize injury to the roots. Additional reference trees were planted completely within each of the pots ('MP' and 'DP', respectively). Acrylic-glass sheets were placed vertically on the pots, to prevent canopy contact between the plants. One root branch of the SRP in the dry pot was inserted into an exetainer vial, including rhizosphere soil. The root and the soil were harvested in separate exetainer vials upon labelling

TABLE 1 Intersecting set of analysed split-root systems and respective driving factors soil water content (SWC), pre-dawn water potential (Ψ_{PD}) and actual root-xylem hydraulic conductivity (k_{sa})

	Isotope analysis	SWC	Ψ_{PD}	k_{sa}
	n			
Picea abies	7	7	6	3
Pseudotsuga menziesii	7	7	7	5
Acer pseudoplatanus	3	3	0	2
Quercus robur	4	4	4	2
Castanea sativa	6	6	4	4

provide strictly controlled environmental conditions. Plants were acclimated to growth chamber conditions for at least 3 weeks before the experiment started. Day/night hours were maintained at 15/9 hr with corresponding temperatures of 25/15°C. Relative humidity (rH) was 89 ± 0% (1 *SE*) during the night to limit potential night-time transpiration and decreased to 60 ± 0% (1 *SE*) during the day. During the day, the mean photosynthetically active photon flux density at canopy level was 305 ± 4 µmol m^{-2} s^{-1} (1 *SE*) with a plateau of 434 ± 0 µmol m^{-2} s^{-1} (1 *SE*) that lasted for 7 hr. Temperature and light were gradually increased and decreased during morning and evening hours respectively.

2.2 | Soil water content and leaf water potentials

Volumetric soil water content (SWC) was recorded in both pots when the experiment started with a TDR probe spanning the depth of the pots (i.e. 15 cm; TDR100, Campbell Scientific). Additionally, we measured pre-dawn water potential (Ψ_{PD}) in leaves of most of the DP, MP and SRP (Table 1) with a Scholander-type pressure bomb (1505D pressure chamber, PMS Instrument Company). *A. pseudoplatanus* trees were excluded from Ψ_{PD} measurements due to the heavy exudation of milky sap from the petioles. At pre-dawn, the whole sapling water potential can be assumed to be in equilibrium, that is between leaves and roots. The moisture gradient within the SRP between the roots in the moist and dry pots was calculated as the difference in Ψ_{PD} between the SRP and the DP and will be referred to as 'Ψ_{PD} difference' in the following paragraphs.

2.3 | Experimental setup

Because of limited space in the growth chambers, the experiment was conducted in four campaigns from July to September 2017. All replicates of a maximum of two species were studied in parallel in one campaign (timing of the experiment did not influence the amounts of HR water, $p = .2$). Replicates of each species were equally split between both growth chambers. First, we initiated different soil moisture gradients between replicates of the two pots. Irrigation was limited to different extents from the 'dry' pot, resulting in SWCs ranging from 6.6 to 19.9 vol%. The 'moist' pot was well-watered, with SWCs ranging from 11.0 to 41.7 vol% (Table 3). In order to capture all HR water of a root, without losing any amount to the bulk soil or neighbouring trees, c. 1 week before the experiment, we carefully excavated a single root branch of the SRP (average 0.28 ± 0.06 g (1 *SE*) dry mass, Table 2, c. 9 cm length). This root branch with its attached rhizosphere soil (average dry mass of 5.3 ± 0.2 g (1 *SE*), Table 2) was put into an exetainer vial (Labco) and buried back

TABLE 2 Basic tree characteristics of the studied split-root plants (SRP; means ± 1 *SE*)

		SRP dry pot					
	Tree height (cm)	Root biomass (g)	Root biomass exetainer (g)	Root water content (ml)	Root water exetainer (ml)	Mass rhizosphere exetainer (g)	Water rhizosphere exetainer (ml)
Picea abies	57 ± 2^{ab}	4.6 ± 0.9^{a}	0.16 ± 0.02^{a}	7.7 ± 1.7^{ab}	0.27 ± 0.04^{ab}	4.5 ± 0.3^{a}	1.0 ± 0.1^{a}
Pseudotsuga menziesii	67 ± 1^{a}	3.0 ± 0.7^{a}	0.11 ± 0.01^{a}	4.6 ± 1.0^{a}	0.16 ± 0.01^{ab}	6.4 ± 0.4^{b}	0.8 ± 0.1^{a}
Acer pseudoplatanus	66 ± 3^{ab}	5.8 ± 1.1^{ab}	0.31 ± 0.05^{ab}	6.4 ± 0.9^{ab}	0.35 ± 0.03^{ab}	5.0 ± 0.4^{ab}	1.1 ± 0.2^{ab}
Quercus robur	67 ± 3^{a}	3.8 ± 1.0^{a}	0.14 ± 0.04^{a}	3.7 ± 1.0^{a}	0.14 ± 0.04^{a}	5.6 ± 0.3^{ab}	0.8 ± 0.1^{a}
Castanea sativa	49 ± 7^{b}	18.8 ± 4.0^{b}	0.68 ± 0.22^{b}	20.5 ± 5.2^{b}	0.67 ± 0.19^{b}	4.8 ± 0.4^{a}	1.6 ± 0.2^{b}

Note: Different letters indicate significant differences between the species per parameter.

TABLE 3 Soil water content (SWC) in the moist and dry pots of the split-root systems when the experiment started (means ± 1 *SE*)

	SWC moist pot (vol%)	SWC dry pot (vol%)	SWC difference (vol%)
Picea abies	29.6 ± 4.2^{a}	12.2 ± 1.6^{***a}	17.5 ± 3.7^{a}
Pseudotsuga menziesii	20.1 ± 1.4^{a}	8.5 ± 0.4^{***a}	11.6 ± 1.5^{a}
Acer pseudoplatanus	25.4 ± 5.2^{a}	10.3 ± 0.8^{*a}	15.1 ± 5.0^{a}
Quercus robur	22.3 ± 4.1^{a}	10.6 ± 0.5^{*a}	11.7 ± 3.6^{a}
Castanea sativa	21.7 ± 3.9^{a}	9.0 ± 0.5^{***a}	12.7 ± 3.7^{a}

Note: Letters indicate significant differences between the species; asterisks give significant differences between the moist and dry pot (*< 0.05, ***< 0.001).

into the dry pot soil (Figure 1). We took care that only entire root branches that were vital in their appearance and therefore representative for the whole root system were buried in the vials. Before labelling, we sampled bulk soil with a metal core (diameter c. 1 cm), placed the soil into a plastic bag, gently mixed the soil and transferred a subsample into an exetainer vial. These soil samples served as reference for soil and root samples after the labelling (Hafner et al., 2017). Additional xylem sap samples, extracted prior to labelling from branches with the bark removed, confirmed isotopic equality between unlabelled soil and plant xylem sap (p = .3, xylem sap and respective soil measured in nine pots; data not shown).

On the labelling day, 300 ml of deuterium-enriched water (0.2 atom-%) was carefully added to the soil of the moist pot. During this time, the dry pot was covered with aluminium foil to prevent contamination. Then, the moist soil was covered with foil and acrylic-glass sheets were placed vertically on the pots, to prevent canopy contact between the plants (Figure 1). Deuterium labelling was performed at midday to ensure the optimal uptake of label by the moist pot's SRP roots before any potential HR was initiated. Subsequent soil sampling took place as described above before dawn on the following day, minimizing the chance that redistributed water in the dry pot was taken up again by the SRP for transpiration. In parallel, we harvested the single root branch of the SRP in the dry pot, removed it from the buried exetainer vial—leaving the rhizosphere soil—and quickly put it into a separate exetainer vial. Both vials were sealed and all isotope samples were stored at −18°C until further processing. All samples on the dry side were taken before the soil samples on the moist, labelled side to avoid contamination. The water was extracted by cryogenic vacuum distillation for 2 hr (West, Patrickson, & Ehleringer, 2006) and mass difference revealed sample water content. Additionally, we determined the dry mass for all soil samples to calculate the relative water content (in mass%), revealing no difference between bulk and rhizosphere soil (p = .3, data not shown).

All water samples were analysed for their δ^2H with an isotope-ratio mass-spectrometer (IRMS, Isoprime 100, Elementar Analysensysteme GmbH) coupled to a multiflow system (222 XL Liquid Handler, Gilson) or a cavity ring-down spectrometer (CRDS, L2120-i, Picarro) coupled to a vaporizer module (A0211, Picarro). Cross measurements of soil and root-xylem samples revealed no statistical differences between both instruments (p = .9; regression: R^2 = .99, p < .001) or putative contamination with organic compounds (West, Goldsmith, Brooks, & Dawson, 2010). Measurement precision was determined against two laboratory standards ('heavy': δ^2H of 133.3 ± 1.7 ‰ [1 *SD*] and 'light': δ^2H of −159.4 ± 1.9 ‰ [1 *SD*]) and was better than ±0.8 ‰ (1 *SE*) for the IRMS and ±1.9 ‰ (1 *SE*) for the CRDS respectively.

2.4 | Assessment of root characteristics

We recorded the fresh and dry mass of the harvested root systems of the SRPs in the dry pot, after the experiment ended to calculate root water content (Table 2). Roots were separated into root mass inside the exetainer vials and root mass of the remaining root system. Additional root samples (length c. 1 cm, diameter 1.9 ± 0.2 mm (1 *SE*), n = 3–9 per species) of parallel plant individuals, not used for the labelling experiment but of the same age and grown under the same environmental conditions, were dried in ethanol (Hafner et al., 2017) and subsequently cut with laser ablation tomography (Chimungu,

Brown, & Lynch, 2014). Pictures of the root slices photographed with a resolution of 25,400 dpi were analysed for xylem conduit diameters. All xylem conduits on three representative sample areas (0.5 mm^2 each) of each cross section were marked by hand with GIMP (GNU Image Manipulation Program, Version 2.10.2, The GIMP Team, https://www.gimp.org/) and conduit area was determined with ImageJ (Version 1.47t, Wayne Rasband, National Institutes of Health; Figure S1). Following Scholz, Klepsch, Karimi, and Jansen (2013), the equivalent circle diameter was calculated.

Finally, we calculated the 'actual' and maximum root-xylem hydraulic conductivity for the SRP and the neighbour plants in the dry pots. To this end, we measured hydraulic conductance with a 'xylem embolism meter' (XYL'EM, Bronkhorst France S.A.S.). Roots of experimental SRPs plus additional SRPs of the same age and grown under the same environmental conditions (Table 1, n = 5 per species) were cut several times under water. Resulting root parts had a diameter of 2.6 ± 0.7 mm (1 *SE*) and a length of 2.7 ± 0.6 cm (1 *SE*). Subsequently, the bark was removed on the side that was inserted into the XYL'EM apparatus. First, the 'actual' (unflushed) hydraulic conductance was measured (K_{act}, in kg MPa^{-1} s^{-1}) at c. 0.007 MPa with degassed, filtered (0.2 µm) water with 10 mM KCl and 1 mM $CaCl_2$ added (Barigah et al., 2013). After the measurement of K_{act}, we obtained maximum hydraulic conductance (K_{max}, in kg MPa^{-1} s^{-1}) by flushing the sample several times at c. 0.12 MPa for 10 min, until no further increase in conductance occurred. Subsequently, the length was measured and the conductive area (A_{cond}) was assessed by analysing a picture of each cross section photographed under a stereomicroscope with ImageJ. Actual and maximum specific xylem hydraulic conductivity (k_{sa} and k_{sm} in kg s^{-1} m^{-1} MPa^{-1}) were then calculated as:

$$k_{s\,a/m} = \frac{K_{act/max} \times \text{length}}{A_{cond}}. \quad (1)$$

The fraction of k_{sa} from k_{sm} revealed the percent loss of conductivity (PLC) of the respective species:

$$\text{PLC} = \frac{k_{sm} - k_{sa}}{k_{sm}} \times 100\,(\%). \quad (2)$$

2.5 | Mixing model calculations

The relative fractions (in %) and absolute amounts (in ml) of the redistributed labelled water (further referred to as 'HR water') were calculated as a mixture of two end-members for each single split-root system. We assumed the isotopic composition of the water in the SRP roots to be a mixture of soil water retrieved from the soil in the dry pot and HR water from the moist pot:

$$\text{HR}_{SRP} = \frac{\delta^2H\left(\text{SRP}_{\text{root dry\_L}}\right) - \delta^2H\left(\text{soil}_{\text{dry\_BL}}\right)}{\delta^2H\left(\text{soil}_{\text{moist\_L}}\right) - \delta^2H\left(\text{soil}_{\text{dry\_BL}}\right)} \times 100\,(\%), \quad (3)$$

with HR_{SRP}: Fraction of HR water in the SRP root in the dry pot, δ^2H ($SRP_{root\ dry\_L}$): Delta value of the SRP root in the dry pot upon labelling, δ^2H ($soil_{moist\_L}$): Delta value of the soil in the moist pot upon labelling and δ^2H ($soil_{dry\_BL}$): Delta value of the soil in the dry pot before labelling.

Correspondingly, the HR water in each rhizosphere soil of the SRP root in the dry pot was calculated as:

$$\text{HR}_{\text{rhizosphere}} = \frac{\delta^2H\left(\text{SRP}_{\text{rhizosphere\_L}}\right) - \delta^2H\left(\text{soil}_{\text{dry\_BL}}\right)}{\delta^2H\left(\text{soil}_{\text{moist\_L}}\right) - \delta^2H\left(\text{soil}_{\text{dry\_BL}}\right)} \times 100\,(\%), \quad (4)$$

with $HR_{rhizospere}$: Fraction of HR water in the rhizosphere soil of the SRP root in the dry pot and δ^2H ($SRP_{rhizosphere\_L}$): Delta value of the rhizosphere soil of the SRP root in the dry pot upon labelling.

We calculated the absolute amount of HR water in the single root systems (in ml, $HR_{a\,SRP}$) by multiplying each corresponding relative fraction of HR water (Equation 3) with the respective water content of the SRP root system in the dry pot (Table 2). We first calculated the amount of HR water in each exetainer vial ($HR_{a\,exetainer}$) for rhizosphere soils and SRP roots, by multiplying the relative fraction of HR water (Equations 3 and 4) with the water content of the sample (wc_{sample}) in the exetainer vial (Table 2):

$$\text{HR}_{\text{a exetainer rhizosphere/SRP}} = \text{HR}_{\text{rhizosphere/SRP}} \times \text{wc}_{\text{sample rhizosphere/SRP}}\ (\text{ml}). \quad (5)$$

We then calculated the ratio of HR water in the exetainer vial between rhizosphere soil and SRP root ($R_{rhizosphere/SRP}$):

$$R_{\text{rhizosphere/SRP}} = \frac{\text{HR}_{\text{a exetainer rhizosphere}}}{\text{HR}_{\text{a exetainer SRP}}}. \quad (6)$$

By multiplying the ratio with the absolute amount of HR water in the SRP root ($HR_{a\,SRP}$), and assuming this ratio was consistent for the whole root system of the SRP, we calculated the absolute amount of HR water in the rhizosphere ($HR_{a\,rhizosphere}$) per pot:

$$\text{HR}_{\text{a rhizosphere}} = R_{\text{rhizosphere/SRP}} \times \text{HR}_{\text{a SRP}}\ (\text{ml}). \quad (7)$$

Finally, we added the absolute amount of HR water in the SRP root to the absolute amount of HR water in the rhizosphere to calculate total HR of one plant during one night and then averaged the amounts for each species. To put the redistributed amount of water into a comparable context, we also calculated the ratio between HR water in the roots and rhizosphere and the dry root mass of the SRP in the dry pot (Table 2) to get the amount of HR water per root mass (HR_r):

$$\text{HR}_{r\,\text{SRP/rhizosphere}} = \frac{\text{HR}_{\text{a SRP/rhizosphere}}}{\text{root mass}_{\text{SRP}_{\text{dry}}}}\ (\text{ml/g}). \quad (8)$$

To verify our results on the fractions of redistributed water, we also ran the calculations with a mixing model accounting for uncertainty errors when calculating with average isotope values ('Iso Error', Phillips & Gregg, 2001). Applying the model on the average δ^2H values of the respective end-members per tree species gave the same values as our calculations.

2.6 | Statistics

All isotope data were checked for significant ($p < .05$) increases of δ^2H upon labelling. The pot identities served as random factor nested over the respective growth chamber identities in a linear mixed effect model (R package NLME, version 3.1-137) where the δ^2H values of the different samples (soil, root) were tested individually for increases (day and species as independent variables). Increase of δ^2H upon labelling and differences between the species were revealed with the lsmeans post-hoc test (R package LSMEANS, version 2.27-62). Residuals of the model data were checked for normal distribution (shapiro.test) and the data, where necessary, were transformed to meet residual normal distribution. Model data were checked for variance homogeneity (Levene test; R package CAR, version 2.1-2). The same model and tests were applied to check for the differences between the species in the amount of HR water and driving factors (Ψ_{PD}, conduit diameters, $k_{s\ a/m}$). Correlations between driving factors and mixing model outputs were performed via a multiple factor linear regression on split-root systems, where respective data were completely available (Table 1, i.e. amount of HR water and measured driving factors Ψ_{PD} difference and k_{sa}). Additional single factor linear models were calculated for each determining factor to gain slope, intercept, R^2 and p-value of the correlation. Finally, as we did not measure root anatomy of the SRPs that were analysed for their amount of HR water, the average mixing model output was correlated with the average conduit diameter per species. Mean values are shown ±1 *SE*. All statistical analyses were performed with R version 3.3.1 (R Development Core Team, 2018) in RStudio version 1.1.447 (RStudio Team, 2015).

3 | RESULTS

3.1 | Soil water content and leaf water potentials

For all species, SWC in the dry pot (mean: 10.1 ± 0.5 vol%) was significantly lower than in the moist pot (mean: 23.8 ± 1.7 vol%) and not different between the species (Table 3). Also, the SWC difference between the moist and dry pot (mean of 13.8 ± 1.5 vol%) did not differ across species (Table 3). This difference in soil moisture between the moist and dry pot resulted in a mean Ψ_{PD} difference between the SRP and the DP of 1.71 ± 0.24 MPa, with the maximum difference found in *Q. robur* (Table 4). For all species, a range of Ψ_{PD} differences, and therefore in the 'external' HR driving factor, of at least 1.03 MPa per species was established between the moist and dry pot (Table 4). Pre-dawn Ψ of the SRP was not different to Ψ_{PD} of the MP ($p > .8$), while the DP showed a significantly lower Ψ_{PD} than MP or SRP ($p < .001$, each, Table S1).

3.2 | Conduit diameters and root hydraulic conductivities

The potential 'internal' HR driving factors root conduit diameter and k_{sa}, were largest and highest in stem ring-porous *C. sativa* and *Q. robur* (average over both species: 40.53 ± 0.84 µm and 0.55 ± 0.06 kg s^{-1} m^{-1} MPa^{-1}, respectively). Stem diffuse-porous *A. pseudoplatanus* had a smaller diameter but similar k_{sa} (Table 5), while the conifers—limited to tracheids—showed the smallest diameter and lowest k_{sa} (mean: 10.61 ± 0.10 µm and 0.30 ± 0.03 kg s^{-1} m^{-1} MPa^{-1}, respectively). All deciduous species formed embolisms (mean PLC in the SRPs: 64 ± 4%) in the roots growing in the dry pots, whereas no difference between k_{sa} and k_{sm} was present in the conifers (Table 5). Percent loss of conductivity was significantly higher in stem ring-porous *C. sativa* and *Q. robur* than in *A. pseudoplatanus*.

3.3 | Isotopic enrichment upon labelling

Upon labelling, we found a significant ^2H enrichment in the soil of the moist pot across all species (Table 6) with an average value of 1,835 ± 203 ‰. The roots of the SRP in the dry pot were significantly ^2H enriched upon labelling in *C. sativa*, *P. menziesii* and *Q. robur* trees ($p < .001$, each), whereas, despite several samples being clearly enriched (i.e. δ^2H after labelling was at least 10 ‰ higher than before labelling in seven of 10 samples), average δ^2H values in *A. pseudoplatanus* ($p = .08$) tended to be and *P. abies* ($p = .2$) were not significantly increased above the unlabelled reference (Table 6).

TABLE 4 Pre-dawn water potential (Ψ_{PD}) differences between split-root plants and plants grown in the dry pots when the experiment started (means ± 1 *SE* and min and max values respectively)

	Ψ_{PD} difference (MPa)	Min difference (MPa)	Max difference (MPa)	Difference range (max–min) (MPa)
Picea abies	0.74 ± 0.15[a]	0.26	1.29	1.03
Pseudotsuga menziesii	1.54 ± 0.26[a]	0.62	2.71	2.09
Acer pseudoplatanus	NA	NA	NA	NA
Quercus robur	3.17 ± 0.40[b]	2.30	4.20	1.90
Castanea sativa	2.01 ± 0.62[ab]	0.23	3.12	2.89

Note: Min and Max differences in Ψ_{PD} were set to differ by at least 1 MPa per species to generate higher and lower 'external' driving factors for each species. The range in Ψ_{PD} differences per species is given in the last column. Letters indicate significant differences between the species. Note that *A. pseudoplatanus* trees were excluded from the measurements due to heavy milky sap exudation from petioles.

TABLE 5 Conduit diameters and hydraulic conductivity (k_s; separated into 'actual' k_{sa}, i.e. considering drought-induced xylem embolism and maximum k_{sm}, i.e. full conductivity without embolism) of the split-root plants in the dry pot (means ± 1 *SE*)

	Conduit diameter		k_{sa}	k_{sm}
	n (conduit diameter)	μm	kg s^{-1} m^{-1} MPa^{-1}	
Picea abies	6	9.96 ± 0.73^{a}	0.27 ± 0.02^{a}	0.27 ± 0.02^{a}
Pseudotsuga menziesii	3	11.25 ± 0.43^{a}	0.34 ± 0.08^{ab}	0.34 ± 0.08^{a}
Acer pseudoplatanus	9	27.42 ± 1.12^{b}	0.61 ± 0.10^{bc}	1.18 ± 0.18^{b}
Quercus robur	9	34.99 ± 1.45^{bc}	0.64 ± 0.09^{c}	2.01 ± 0.21^{***b}
Castanea sativa	9	44.22 ± 5.81^{c}	0.46 ± 0.08^{abc}	2.28 ± 0.48^{***b}

Note: Letters indicate significant differences between the species; asterisks give significant differences between k_{sa} and k_{sm} (*** < 0.001).

TABLE 6 Deuterium isotope signals (δ^2H) of soils and roots (roots of split-root plants in the dry pot) of the split-root system (means ± 1 *SE*)

	Before labelling	After labelling	Before labelling	After labelling		
	Soil moist	Soil moist	Soil dry	Soil dry	Rhizosphere soil dry	SRP root dry
	δ^2H (‰)					
Picea abies	−61 ± 1^{a}	1,846 ± 271^{***a}	−55 ± 2^{a}	−55 ± 3^{a}	−40 ± 2^{***a}	−43 ± 3^{a}
Pseudotsuga menziesii	−61 ± 1^{a}	2,033 ± 386^{***a}	−53 ± 2^{a}	−53 ± 3^{a}	−42 ± 2^{***ab}	−19 ± 11^{***ab}
Acer pseudoplatanus	−66 ± 3^{a}	1,224 ± 402^{***a}	−61 ± 2^{a}	−61 ± 2^{a}	−49 ± 2$^{°ab}$	−40 ± 9$^{°a}$
Quercus robur	−59 ± 3^{a}	893 ± 154^{***a}	−58 ± 2^{a}	−56 ± 2^{a}	−48 ± 2^{ab}	18 ± 30^{***b}
Castanea sativa	−68 ± 0^{a}	2,524 ± 591^{***a}	−67 ± 2^{a}	−66 ± 4^{a}	−58 ± 4$^{°b}$	−43 ± 4^{***a}

Note: Letters indicate significant differences between the species; asterisks give significant increases above reference values after the labelling (° ≤ 0.1, *** < 0.001).

TABLE 7 Hydraulically redistributed water in roots, rhizosphere soils and combined total amount of the split-root plants (means ± 1 *SE*) for the whole root system (in ml) and per root dry mass (in ml/g)

	SRP root		Rhizosphere		Total	
	ml	ml/g	ml	ml/g	ml	ml/g
Picea abies	0.06 ± 0.02^{a}	0.01 ± 0.00^{a}	0.29 ± 0.13^{a}	0.06 ± 0.02^{a}	0.35 ± 0.13^{a}	0.07 ± 0.02^{ab}
Pseudotsuga menziesii	0.07 ± 0.02^{a}	0.03 ± 0.01^{a}	0.13 ± 0.04^{a}	0.05 ± 0.01^{a}	0.19 ± 0.04^{a}	0.08 ± 0.02^{ab}
Acer pseudoplatanus	0.11 ± 0.03^{ab}	0.02 ± 0.01^{ab}	0.20 ± 0.05^{a}	0.04 ± 0.01^{a}	0.31 ± 0.02^{a}	0.06 ± 0.02^{ab}
Quercus robur	0.29 ± 0.12^{b}	0.08 ± 0.03^{b}	0.27 ± 0.10^{a}	0.11 ± 0.06^{a}	0.56 ± 0.15^{a}	0.19 ± 0.07^{a}
Castanea sativa	0.17 ± 0.04^{ab}	0.01 ± 0.00^{a}	0.42 ± 0.24^{a}	0.02 ± 0.01^{a}	0.59 ± 0.23^{a}	0.04 ± 0.01^{b}

Note: Letters indicate significant differences between the species.

The rhizosphere soil in the dry pot was significantly enriched in *P. abies* ($p < .001$) and *P. menziesii* ($p < .01$), whereas the δ^2H tended to be significantly enriched in *A. pseudoplatanus* ($p = .09$) and *C. sativa* ($p = .08$). No enrichment was detected in *Q. robur* ($p = .16$, again despite two of four samples being clearly enriched). The bulk soil in the dry pot did not increase in δ^2H after one night (Table 6).

3.4 | Amounts of HR water in the SRP roots and in the rhizosphere soil

After one night, the root systems of stem ring-porous *C. sativa* and *Q. robur* redistributed more water (average over both species of 0.22 ± 0.05 ml) than stem diffuse-porous *A. pseudoplatanus* (0.11 ± 0.03 ml, not significant though) and significantly more than the conifer species (average of *P. abies* and *P. menziesii* of 0.06 ± 0.01 ml, $p < .05$, Figure S2). All species released similar amounts of HR water into the rhizosphere soil as they redistributed within their respective root systems (Table 7). When comparing the combined roots and rhizosphere amounts of HR water by the SRP, total HR was not different between the species. Total HR of stem ring-porous *C. sativa* and *Q. robur* trees (0.59 ± 0.23 ml and 0.56 ± 0.15 ml respectively, Table 7) tended to have the highest average values ($p = .08$ vs. conifers, see Figure S2). The amount of HR water in the root system per root dry mass was significantly higher in *Q. robur* trees (0.08 ± 0.03 ml/g) than in the conifers

and *C. sativa* (Table 7). Per root dry mass, species did not deviate in the amount of released water into the rhizosphere (average: 0.06 ± 0.01 ml/g), but for total HR water by root dry mass, *Q. robur* redistributed more than *C. sativa* ($p < .01$), while the other species were in between (Table 7).

3.5 | Dependence of HR on 'external' and 'internal' factors

In a single factor regression, we found a positive correlation in both the amount of HR water in the SRP roots and the total HR water in the dry pot when a Ψ_{PD} difference existed between the pots in our systems, indicating that higher Ψ_{PD} differences resulted in higher amounts of redistributed water across the observed species (Figure 2a). Regression and significance level were higher for HR water in the roots ($R^2 = .2$, $p < .05$) than for total HR water ($R^2 = .1$, $p = .07$). The same pattern was true for the amount of water that was redistributed per root dry mass. The regression was the same for root water only ($R^2 = .2$, $p < .05$), while for total HR water no significant correlation was found ($R^2 = .1$, $p = .16$; Figure 2b). Although not significant, a distinct trend in the correlation between the amount of HR water and Ψ_{PD} difference was also observed on the single species level. However, the range of respective Ψ_{PD} differences and the number of replicates per species were too few for a significant regression (e.g. *P. menziesii* that had a relatively wide range and seven replicates: $R^2 = .3$, $p = .10$ for the amount of HR water in the SRP roots vs. the Ψ_{PD} difference).

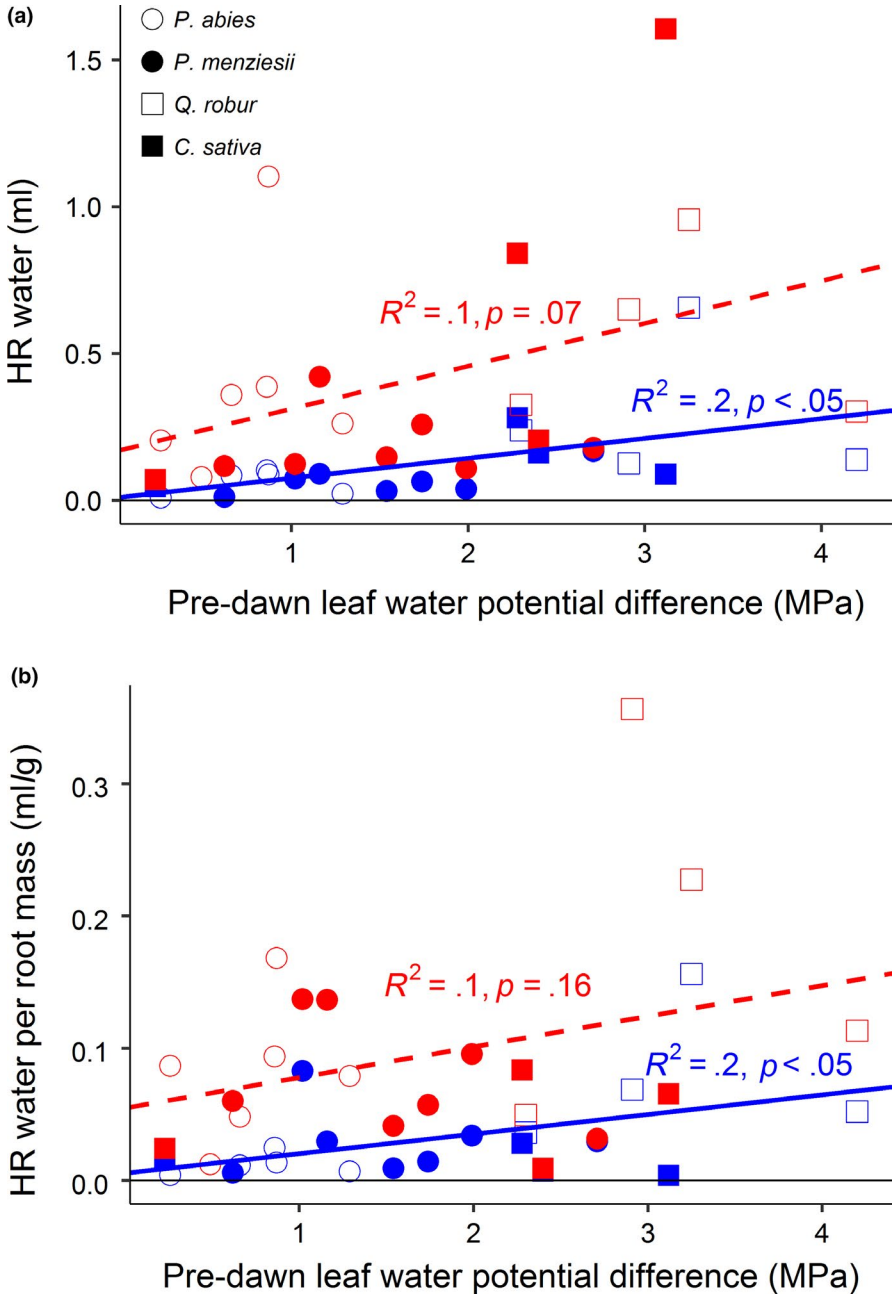

FIGURE 2 Correlation of pre-dawn water potential (Ψ_{PD}) difference with the amount of HR water (a: whole root system and b: per root dry mass; blue: amount in the roots, red: total amount). Note that *Acer pseudoplatanus* trees were excluded from the measurements due to heavy milky sap exudation. For number of replicates per species, see Table 1

With increasing conduit size, the amount of HR water increased for both, HR water found in SRP roots and total HR water (Figure 3a). The correlation (R^2 = .2, p < .01) for HR water found in SRP roots was slightly better compared to the total amount of HR water (R^2 = .1, p < .05). However, we did not find a correlation between either the root or total amount of HR water per root dry mass and the conduit size (Figure 3b). A strong positive correlation was found for both, HR water within the SRP and total HR water, when correlated with k_{sa} of the respective root system (R^2 = .4, p < .01 for the SRP root and R^2 = .3, p < .05 for total HR, respectively, Figure 4a). A positive relationship was also found between the amounts of water that were redistributed per root dry mass; regression and significance level were the same for HR within the root system, while the R^2 was slightly lower but still significant for total HR (R^2 = .2, p < .05, Figure 4b). On a single species level, respective k_{sa} values were too narrow and replicates were too few to determine significant correlations (for *C. sativa* a positive correlation with R^2 = .3 was found, though not significant).

When combining Ψ_{PD} difference and k_{sa} in a multifactor model, a positive correlation for the HR water inside the root system was found, both for the HR water in the whole root system (R^2 = .5, p < .05) and per root dry mass (R^2 = .4, p < .05). Within the model, k_{sa} had a significant influence on the outcome (p < .05), while the influence of Ψ_{PD} difference was not significant. A positive trend between HR amounts and the combined driving factors was also found for both, total HR water across the whole root system and total HR water per root dry mass (R^2 = .2, p = .1, each). Within the model, k_{sa} had a significant impact on the total amount of HR water per root dry mass (p < .05). A positive trend (p = .07) of k_{sa} on total HR amounts across the whole root system was also detected. The impact of Ψ_{PD} difference on total HR amounts was again not

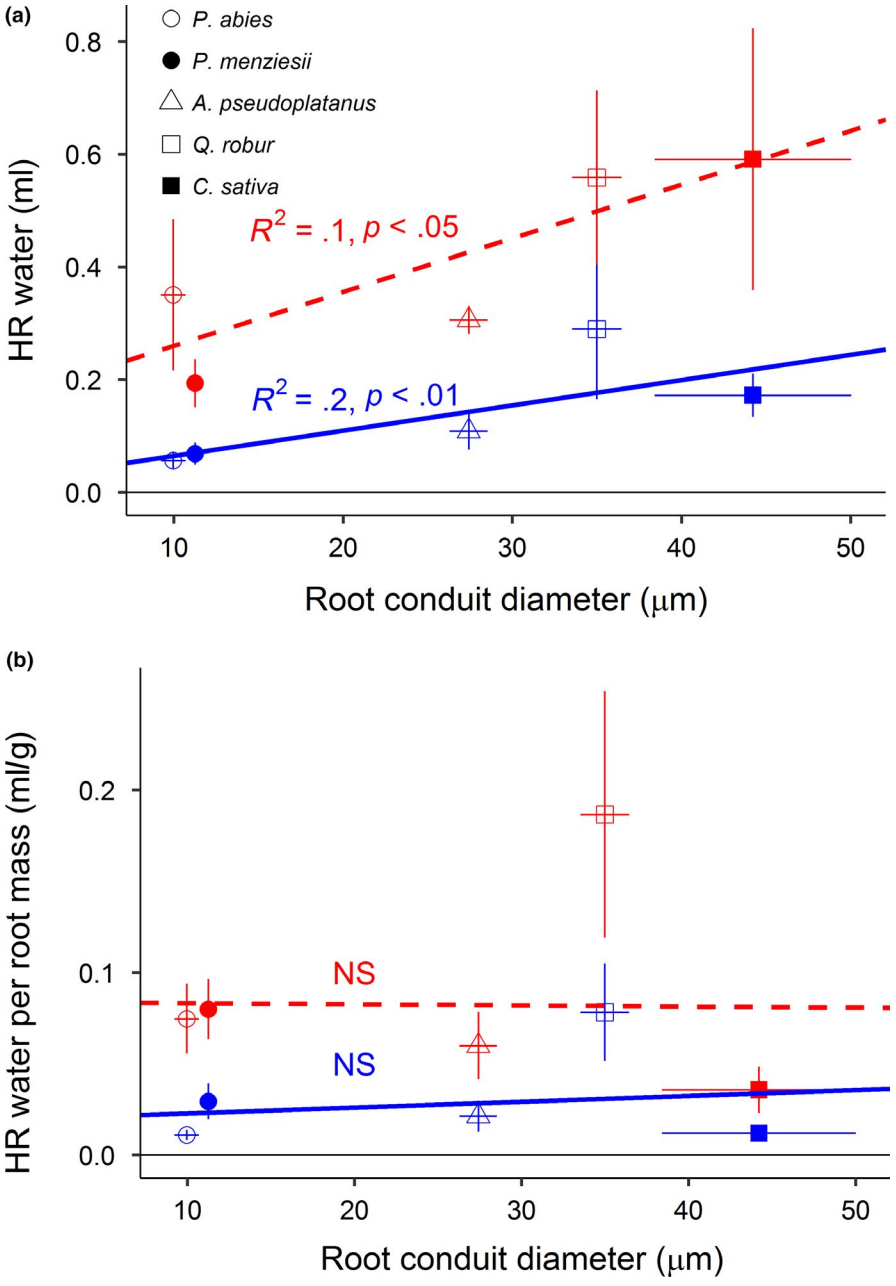

FIGURE 3 Correlation of mean root conduit diameters with the average amount of HR water (a: whole root system and b: per root dry mass; blue: amount in the roots, red: total amount)

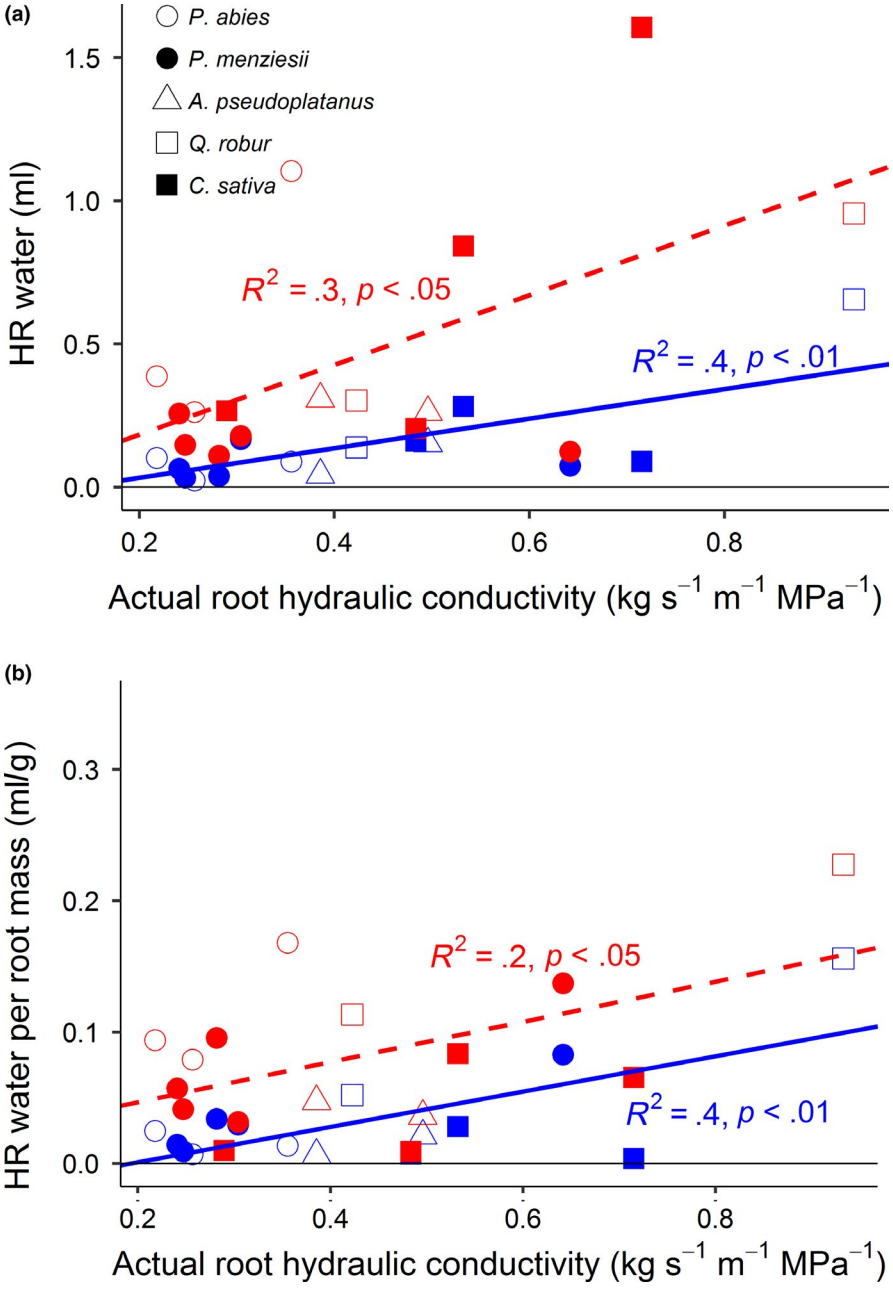

FIGURE 4 Correlation of 'actual' (unflushed) root hydraulic conductivity (i.e. conductivity considering drought-induced xylem embolism; k_{sa}) with the amount of HR water (a: whole root system and b: per root dry mass; blue: amount in the roots, red: total amount). For number of replicates per species, see Table 1

significant. Therefore, most of the variation in HR by the plants in our systems was explained by the variation of the 'internal' driving factor k_{sa}.

4 | DISCUSSION

On average, within a single night, saplings of five temperate tree species redistributed 0.39 ± 0.14 ml (0.08 ± 0.01 ml/g root dry mass) of water, with 0.13 ± 0.03 ml (0.03 ± 0.01 ml/g) of HR water held within the roots, and 0.26 ± 0.06 ml (0.06 ± 0.01 ml/g) released into the soil. These amounts represent the minimum quantities of water transferred via HR over one night. The actual amounts of transferred water might be larger, as unlabelled water still present in the roots of the SRP in the dry pot was redistributed first and could not be detected with our approach. We found significant evidence to support our hypotheses that plants redistribute more water with increasing Ψ_{PD} differences, with larger root conduit diameters and higher root-xylem hydraulic conductivity. The influence of k_{sa} was greater than that of the Ψ_{PD} difference or root conduit diameters and, therefore presented the main driver for variation in water redistribution over one night within our systems.

We note an analogy to Ohm's law in electricity, where a 'tension' (here: Ψ_{PD} difference) and 'resistors' (here: conduit diameter, xylem hydraulic conductivity) define the extent of the 'current' (here: HR).

By establishing a range of Ψ_{PD} differences between the roots in the moist and dry pots of the split-root systems, we created different

'external' HR driving 'tensions'. We found a positive correlation between the Ψ_{PD} differences and the amount of HR water across all species, supporting our hypothesis. While perhaps intuitive that a moisture difference is an important prerequisite and driving factor for HR (Caldwell et al., 1998; Yu, Feng, Si, Xi, & Li, 2013), this study shows that the magnitude of external 'tensions' relates to how much water is redistributed within a root system. As the amount of HR water increased with the increase in the Ψ_{PD} difference, HR and its benefits to trees might increase in those regions where more frequent summer drought events are forecasted (Flato et al., 2013; Orth, Zscheischler, & Seneviratne, 2016).

There was a positive correlation between xylem conduit size as k_{sa} and the amount of HR water. In light of the 'resistor' concept, species with smaller xylem conduits showed lower conductance for HR than species with larger conduits and higher k_{sa}. Root conduit anatomy (Hafner et al., 2017) and xylem hydraulic conductivity (Quijano & Kumar, 2015) reflected the magnitude of the internal 'resistor' of different species for HR, confirming our hypothesis that HR increases with increasing root conduit diameter and root-xylem hydraulic conductivity. Because the deciduous species of our study had embolism formation in their roots by the end of the experiment (Table 5; Figure 5), the correlation between the amount of HR water and k_{sa} as surrogate for conductivity was more accurate and resulted in better correlations than the regression with xylem conduit diameter.

There was a lack of a correlation for total HR water, as additional factors may influence water efflux into the soil. For example, depending on species and respective root bark thickness, suberized cells in the periderm may serve as a barrier for the water flow into the soil (Brunner, Herzog, Dawes, Arend, & Sperisen, 2015). Moreover, water transport could be limited by the regulation and number of aquaporins in the root cell membranes (Maurel et al., 2015). Additionally, for the angiosperm species, the maximum vessel length (not shown) was higher than the length of the segment we analysed. Therefore, total root conductivity of angiosperm species could deviate from the values estimated here, although we found a positive correlation between k_{sa} and root conduit diameters (R^2 = .3, p < .001; not shown). Moreover, within the root's conduit system, warts inside the vessel, pit aperture, vessel tapering or the architecture of perforation plates could additionally affect the amount of water being moved (Hesse, Hafner, & Grams, 2019). There is also indication that finer roots have a different water transport capability than larger roots (Dawson, 1997; Hesse et al., 2019). Hence, additional experiments on the hydraulic conductivity of whole root systems should be considered. Finally, poor root–soil contact in dry soils (Carminati, Vetterlein, Weller, Vogel, & Oswald, 2009) may prevent the movement of HR water into the rhizosphere (Ryel et al., 2004). At similar soil water potentials, species-specific root branching or number of tips may affect root–soil contact differently (Pregitzer et al., 2002). Therefore, the Ψ_{PD} presented in this study cannot easily be translated into soil Ψ but rather represent the Ψ experienced by the roots, including overall loss of root–soil contact. As k_{sa} is a parameter that combines root architecture (conduit diameters, representing maximum xylem hydraulic conductivity) with environmental conditions (Ψ gradient, reflected through PLC in the roots), it proved to be a robust driving factor with a strong influence on HR over the one night frame used in our systems.

4.1 | Potential of the 'exetainer-setup'

We recognize that placing root branches together with their rhizosphere soil directly into exetainer vials was an uncommon approach and, therefore, subjected to potential bias. There was no significant difference between the water content of the bulk soil and the rhizosphere soil inside the exetainer vials, suggesting that we did not influence the amount of HR due to altered soil moisture

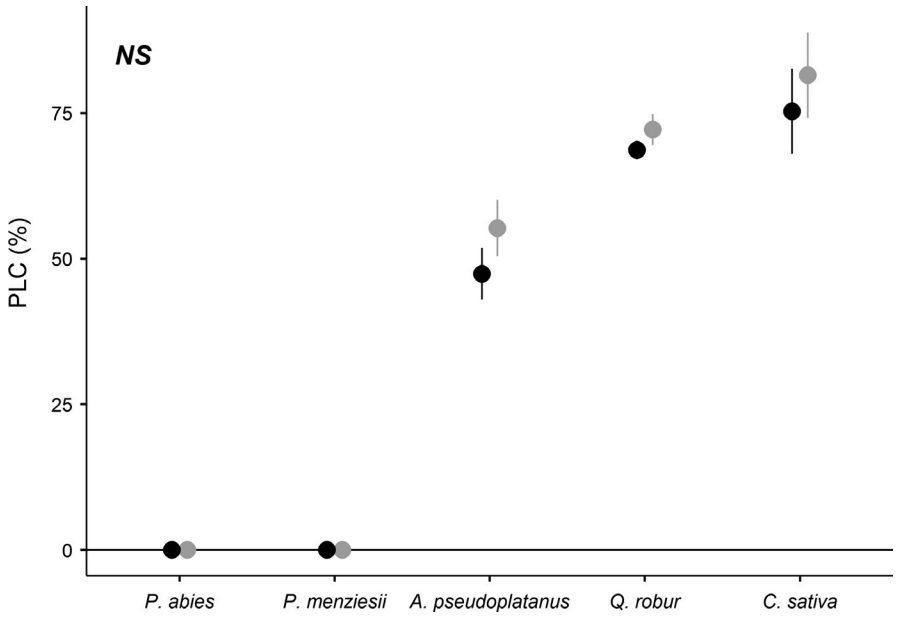

FIGURE 5 Percent loss of conductivity (PLC) assessed for the five study species in the split-root plant (SRP, black) and the reference plant with its root system only in the dry pot (DP, grey). The conifers did not show embolism while the deciduous trees showed average PLC of 64 ± 4% (1 *SE*; SRP) and 70 ± 4% (1 *SE*; DP; not significantly different, though)

conditions. Although the root systems were treated with great care, we cannot exclude that root–soil contact was affected. Thus, the difference in Ψ_{PD} might not necessarily translate into the gradient experienced by the 'exetainer' root branches. Additionally, Ψ_{PD} difference was calculated between SRP and DP and not within the root system of the SRP. The difference experienced by the SRP could therefore slightly deviate, potentially explaining why the regression with Ψ_{PD} difference was weak compared to k_{sa}. Moreover, the presented amounts of HR water in the rhizosphere soil represent minimum amounts, as more water could potentially be released in an 'undisturbed' root–soil system. Effectively, the exetainer-setup proved very beneficial, as it allowed us to obtain all water redistributed by a single root branch in one night. The minimal chance for water evaporation from the vial and the set-up ensured that no water penetrated further into the bulk soil or was taken up by neighbouring plants.

4.2 | Benefits to the SRP

Plants may maintain transpiration and 'safe' water potentials even with only parts of their conductive area (Dietrich, Hoch, Kahmen, & Körner, 2018), and only a portion of their root system hydrated, potentially explaining why we did not find a difference in Ψ_{PD} between the SRP and MP. Furthermore, redistributing water within their root system and releasing it into the soil can be beneficial to the plant (Prieto et al., 2012; Ryel et al., 2004). In our system, the additional water held inside the roots due to HR proved to have a positive impact. When we compared PLC of the SRP to their neighbouring plants with roots only in the dry pots, PLC was always lower in the SRP (Figure 5). This is in line with several studies reporting fewer embolisms to occur or embolisms likely to be repaired through HR (Domec et al., 2006; Domec, Warren, Meinzer, Brooks, & Coulombe, 2004; Prieto & Ryel, 2014). In addition to the benefit of maintaining well-hydrated roots via HR, these roots can also live longer, thereby reducing carbon-costs to the plant (Bauerle et al., 2008).

5 | CONCLUSIONS

The amount of water, the temperate tree species in our study redistributed through their root systems towards dry soil during one night was significantly dependent on an external driving 'tension', that is Ψ_{PD} difference and on internal 'resistors', that is root conduit diameter and especially k_{sa}. The amount of HR water, that is, 0.08 ± 0.01 ml/g root dry mass appears rather small. However, if one scales this number to mature forest trees with dry root masses of c. 100 kg, HR amounts could be in the range of 4–20 L per tree per day. Daily transpiration in 'typical' Central European forests may reach 30 L per tree per day (Larcher, 1994). Therefore, HR would account for c. 10%–70% of total daily transpiration. The amounts presented here result from a strictly controlled environment, therefore we emphasize this approximation should be treated with care. However, if applicable, HR would contribute substantially to the water cycle in temperate forests, as already indicated for tropical regions (Lee, Oliveira, Dawson, & Fung, 2005). With anticipated precipitation shifts in the future, HR could become more relevant in temperate forests facing increasing drought periods and thus greater soil-moisture gradients. Tree species that retained higher root k_{sa} under the drought conditions in our experiment clearly had a higher 'internal' potential for HR, predestinating them for selective planting if HR is to be used as a 'silvicultural tool' to improve plant water status in future forests.

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AUTHORS' CONTRIBUTIONS

B.D.Ha. and T.E.E.G. designed the study. B.D.Ha. and B.D.He. collected and analysed the data. B.D.Ha., T.L.B. and T.E.E.G. interpreted the data. B.D.Ha. drafted the manuscript. All the authors critically revised the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.tmpg4f4v3 (Hafner, Hesse, Bauerle, & Grams, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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