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Friendly neighbours: Hydraulic redistribution accounts for one quarter of water used by neighbouring drought stressed tree saplings

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Abstract

Hydraulic redistribution (HR) can buffer drought events of tree individuals, however, its relevance for neighbouring trees remains unclear. Here, we quantified HR to neighbouring trees in single- and mixed-species combinations. We hypothesized that uptake of HR water positively correlates with root length, number of root tips and root xylem hydraulic conductivity and that neighbours in single-species combinations receive more HR water than in phylogenetic distant mixed-species combinations. In a split-root experiment, a sapling with its roots split between two pots redistributed deuterium labelled water from a moist to a dry pot with an additional tree each. We quantified HR water received by the sapling in the dry pot for six temperate tree species. After 7 days, one quarter of the water in roots (2.1 ± 0.4 ml), stems (0.8 ± 0.2 ml) and transpiration (1.0 ± 0.3 ml) of the drought stressed sapling originated from HR. The amount of HR water transpired by the receiving plant stayed constant throughout the experiment. While the uptake of HR water increased with root length, species identity did not affect HR as saplings of *Picea abies* ((L.) Karst) and *Fagus sylvatica* (L.) in single- and mixed-species combinations received the same amount of HR water.

KEYWORDS

drought, *Fagus sylvatica*, hydraulic redistribution to neighbours, mixed species forests, *Picea abies*, root length, split-root experiment, stable water isotope labelling (^{2}H/deuterium), temperate tree species

1 | INTRODUCTION

Hydraulic redistribution (HR) is the passive reallocation of water through roots and other tissues of plants along a water potential (ψ) gradient (Nadezhdina et al., 2010). In the soil, roots with access to moist layers redistribute water towards dry layers when the plants are not transpiring, usually overnight (Richards & Caldwell, 1987). The water can subsequently be released into the dry rhizosphere (Emerman & Dawson, 1996; Hafner, Hesse, Bauerle, & Grams, 2020).

Under drought, HR may facilitate plant growing conditions, by for example, easing rhizosphere soil re-wetting or even prolonging the growing season (Brooks, Meinzer, Coulombe, & Gregg, 2002; Howard, Van Iersel, Richards, & Donovan, 2009). Hydraulic redistribution may increase water use of plants, whole stands or ecosystems by up to 50% (Domec et al., 2010), and simultaneously improve water use efficiency and plant carbon assimilation (Amenu & Kumar, 2008). Previous studies have suggested that HR may have a beneficial impact on neighbouring plants. Namely, under drought, neighbouring trees may take up HR water released by plants with root access to moist soil layers (Brooks et al., 2002; Hafner et al., 2017). The additional water acquired by neighbouring plants was hypothesized to support higher stomatal conductance and growth (Dawson, 1993; Magh et al., 2018), with up to nine times higher biomass production in dry regions (Bogie et al., 2018), increasing drought resistance and to potentially improve survival (Pang et al., 2013).

With anticipated reductions of tree vitality (Allen et al., 2010; Bréda, Huc, Granier, & Dreyer, 2006; Clark et al., 2016) under severe and prolonged summer droughts (D'Orangeville et al., 2018; Flato et al., 2013; Orth, Zscheischler, & Seneviratne, 2016), the question arises to what extent HR to neighbouring trees may improve the water balance of temperate species (Ammer et al., 2018; Goldstein et al., 2008; Pretzsch et al., 2014)? Therefore, it is important to not only quantify the amount of HR water neighbours receive and use for tissue rehydration and transpiration but also to unravel the mechanisms by which HR water becomes available and is taken up by neighbouring plants. As probably a major fraction of HR water is transported from plant to plant via close root contact, root grafts or a common mycorrhizal network (CMN, Warren, Brooks, Meinzer, & Eberhart, 2008; Prieto et al., 2016), longer root systems with a high number of root tips of the neighbouring trees could be favourable parameters. Additionally, root hydraulic conductivity (k_s) could be a factor influencing the amount of uptake of HR water by neighbouring plants. There is evidence that roots retaining higher k_s under drought redistribute more water (Hafner et al., 2020; Quijano & Kumar, 2015) and are also able to take up water faster after re-wetting (North & Nobel, 1998) than roots with lower k_s. Therefore, higher k_s in drought stressed neighbouring plants could also increase the amount of HR water they take up.

Redistribution of water to neighbours may differ if the neighbour is of the same species or another. Hydraulic redistribution has been suggested to majorly contribute to increased growth and resistance against abiotic and biotic stressors in mixed species communities compared to single-species combinations (Metz et al., 2016; Morin, Fahse, Scherer-Lorenzen, & Bugmann, 2011; Pretzsch et al., 2010). Especially for *Fagus sylvatica* (L.) and *Picea abies* ((L.) Karst.), admixture of both species promises increased stability under prolonged drought conditions (Neuner et al., 2015; Pretzsch et al., 2014). While HR by *F. sylvatica* (Hafner et al., 2017) and *P. abies* (Nadezhdina, Cermák, Gaspárek, Nadezhdin, & Prax, 2006) has been demonstrated in single species compositions, it now seems worthwhile to explore uptake of HR water by neighbours in mixed-species combinations. It has been shown that species that are phylogenetically close, exchange more carbon via connected root systems or a CMN than rather distant species (Klein, Siegwolf, & Körner, 2016; Rog, Rosenstock, Körner, & Klein, 2020). Therefore, the redistribution of water between trees might be higher within the same species as well.

In this study, we quantify how much HR water drought stressed neighbouring saplings of six common temperate tree species received from a redistributing tree in a growth chamber split-root experiment. We hypothesized that the amount of received HR water increases with more favourable root characteristics of drought stressed saplings, that is, higher root length, number of root tips or k_s. Additionally, we hypothesized that flux of HR water to neighbour trees is higher within individuals of the same species than across species for phylogenetically distant *F. sylvatica* and *P. abies* trees.

2 | MATERIAL AND METHODS

2.1 | Plant material and establishment

Saplings of *Acer pseudoplatanus* (L.), *F. sylvatica*, *Castanea sativa* (Mill.), *Quercus robur* (L.), *P. abies* and *Pseudotsuga menziesii* ((Mirb.) Franco), between 2–4-year-old, were planted in December 2015 (*P. menziesii* in December 2016) into split-root systems (SRS, Figure 1, Figure S1). Species were chosen to cover a range of xylem-conduit diameters and hence hydraulic conductivities from conifers (*P. abies* and *P. menziesii*) to diffuse porous (*A. pseudoplatanus* and *F. sylvatica*) to ring porous species (*C. sativa* and *Q. robur*). Further, species are either economically important for Central European forestry or seen as potentially well suited to become important among future climate conditions (Pretzsch et al., 2014; Rais, van de Kuilen, & Pretzsch, 2014; Thurm et al., 2018). Saplings were planted in a potting soil mixture (consisting of topsoil, compost, turf and lava) including 20% organic matter (Wurzer Umwelt GmbH, Eitting, Germany). Additionally, we added a native soil (10%) taken from forest-stands dominated by mature trees of the study species, to provide species-specific mycorrhizal inoculum to the SRS. Each SRS (Table **1**) consisted of three trees with one central split-root plant ("SRP") that had its roots equally split between two pots (10 L each), that contained one additional tree each (Figure 1, Figure S1). Eight different types of SRS were set up, either as single-specific or *P. abies*/*F. sylvatica* mixed SRS (Table 1). Trees were established in the pots until July 2017 in a greenhouse in Freising, Germany (48°23′57.98" N, 11°43′00.99″ E).

2.2 | Experimental setup

We conducted the experiment from July to September 2017 at the TUMmesa facility (Technical University of Munich—Model EcoSystem Analyser; http://www.tummesa.de/home) in two parallel growth chambers (7.7 m^2 each) with 15 hr of daytime and 9 hr of nighttime. Temperature, photosynthetic photon flux density (PPFD) and relative humidity (RH) were incrementally increased or decreased during morning and evening hours. The corresponding day/night temperatures were 24.9 ± 0.3/15.0 ± 0.1°C (1 *SD*), day/night RH was 60.0 ± 0.3/88.9 ± 2.4% (1 *SD*) and PPFD at canopy level reached 434.2 ± 10.7 $\mu mol\ m^{-2}\ s^{-1}$ (1 *SD*) for 7 hr during mid-day. Nighttime RH was high intentionally to facilitate HR and prevent nighttime transpiration by the plants (Howard et al., 2009). In addition, relatively high RH (>85%) occurs frequently in nights throughout the growing season in the region (Weihenstephan-Dürnast weather station of the German Meteorological Service, DWD), therefore representing natural conditions.

Once the plants were inside the growth chambers, we established a soil moisture gradient between the two pots by reducing irrigation from one pot ("dry pot" with the "DP") while keeping the other pot well-

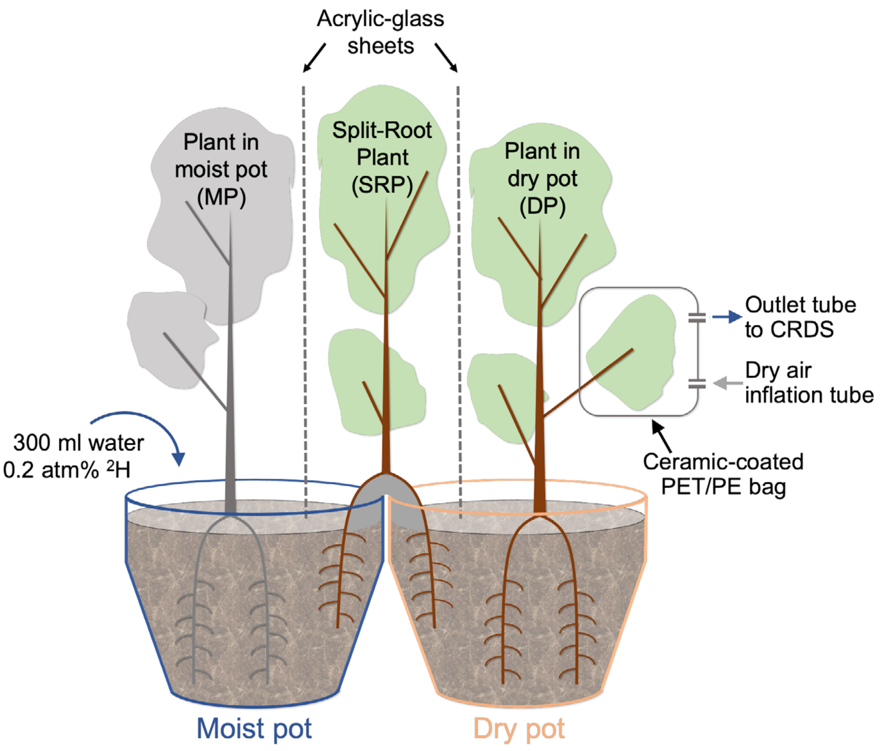


FIGURE 1 Scheme of the split-root systems (SRS) with one tree's (split-root plant, SRP) root system split equally between a "moist" and "dry" pot. A foam-pad was placed between the roots of the SRP and the pot to prevent injuries. Additional trees were planted in both pots ("MP" and "DP," respectively). Vertical acrylic-glass sheets prevented canopy contact between the plants. Foliated twigs of the DP were placed in transparent ceramic-coated PET/PE chambers that were inflated with dry air. Outlet air went via PVC tubes to a cavity-ring-down-spectrometer (CRDS) for ^{2}H isotopic analysis [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Types of split-root systems (SRS) analysed in this study

	n	n DP transpiration	MP	SRP	DP
P. abies	7	3	*P. abies*	*P. abies*	*P. abies*
P. abies mix	7	5	*F. sylvatica*	*F. sylvatica*	*P. abies*
P. menziesii	7	4	*P. menziesii*	*P. menziesii*	*P. menziesii*
A. pseudoplatanus	7	3	*A. pseudoplatanus*	*A. pseudoplatanus*	*A. pseudoplatanus*
F. sylvatica	7	3	*F. sylvatica*	*F. sylvatica*	*F. sylvatica*
F. sylvatica mix	5	4	*P. abies*	*P. abies*	*F. sylvatica*
C. sativa	7	1	*C. sativa*	*C. sativa*	*C. sativa*
Q. robur	7	3	*Q. robur*	*Q. robur*	*Q. robur*

Note: The SRS consisted of one tree grown in a moist pot (MP), one tree in a dry pot (DP) and one tree with its root system split between both pots (SRP; see also Figure **1** and Figure S1). In total eight types of SRS were set up: six single-specific SRS and two mixed SRS with mixtures of *P. abies* and *F. sylvatica* trees. Between 5 and 7 replicates were studied. In the case of DP transpiration, 1–5 replicates were assessed, each.

watered ("moist pot" with the "MP," Figure **1**, Figure S1) over the course of approx. 1 month. Volumetric soil water content (SWC) was assessed via time domain reflectometry (TDR) measurements at the start of the experiment (15 cm probe; TDR100, Campbell Scientific, Shepshed, UK). We also measured water potentials in leaves of the MP and DP predawn (ψ_{leaf}) using a pressure bomb (1505D pressure chamber, PMS Instrument, Albany, OR). As *A. pseudoplatanus* trees exuded a lot of milky sap from the petioles, we discarded them from ψ_{leaf} measurements.

2.3 | ^{2}H labelling, plant sampling, and isotope analysis

Prior to ^{2}H labelling, we sampled initial reference bulk soil from both dry and moist pot using a metal core (diameter of 1 cm) and transferred a subsample into an exetainer vial (Labco, Lampeter, UK). We then carefully labelled the soil of the moist pot with 300 ml of deuterated water (0.2 atom-% ^2H_2O), while the soil in the neighbouring dry pot was covered with aluminium foil to prevent contamination. Afterwards, also the soil in the moist pot was covered with foil to minimize evaporation, and acrylic-glass sheets were installed, preventing canopy contact between plants (Figure 1, Figure S1). The experiment ended 7 days after the deuterium labelling. Stem xylem and roots of DPs and SRPs were sampled, DPs before highly ^{2}H enriched SRPs to avoid contamination. Before dawn, all trees were cut at the root collar and a c. 5 cm long subsample of the lower stem xylem, with the bark removed, was taken. Root branches (0.84 ± 0.04 g (1 *SE*) dry mass, representing 30 ± 3% (1 *SE*) of whole root system mass) of the DPs and SRPs each were randomly collected as representative subsamples of the whole respective root systems.

The roots were quickly but carefully freed from rhizosphere soil, and transferred into exetainer vials. All samples were stored at −18°C until water was extracted by cryogenic vacuum distillation (2 hr, West, Patrickson, & Ehleringer, 2006).

We used an isotope-ratio-mass-spectrometer (IRMS, Isoprime 100, Elementar Analysensysteme GmbH, Langenselbold, Germany) connected to an autosampler system (222 XL Liquid Handler; Gilson, Middleton, WI) and a cavity-ring-down-spectrometer (CRDS, L2120-i; Picarro Inc., Santa Clara, CA) connected to a high-precision vaporizer (A0211; Picarro Inc.) to analyse the samples for their δ^2H. Sample cross measurements between both instruments showed no statistical differences ($p = .9$; regression: $R^2 = 0.99$, $p < .001$) or possible organic compound contamination of the CRDS (Hafner et al., 2020; West, Goldsmith, Brooks, & Dawson, 2010). We used two working standards ("light": δ^2H of −159.4 ± 1.9 ‰ (1 *SD*) and "heavy": δ^2H of 133.3 ± 1.7 ‰ (1 *SD*)) to determine measurement precision that was better than ±0.8 ‰ (1 *SE*, IRMS) and ± 1.9 ‰ (1 *SE*, CRDS), respectively.

2.4 | Assessment of leaf transpiration

Up to five DP replicates per type of SRS were assessed for δ^2H of leaf transpiration (Table **1**). About half of total DP leaf mass per sapling was placed in transparent 3 L plastic bag chambers (ceramic-coated PET/PE mix of approx. 115 μm thickness, Long Life for Art, Eichstetten, Germany; Figure 1, Figure S1) and sealed at the bottom with Terostat-IX (Henkel AG & Co. KGaA, Düsseldorf, Germany). Chambers were continuously flushed with dry air with a flow rate of 1 L/min and outlet air was connected to a CRDS (L2120-I; Picarro Inc.) via a 16-Port Distribution Manifold (A0311; Picarro Inc.), switching every 10 min between the 16 different chambers. Vapour and isotope concentrations stabilized after c. 5 min, and the last 2 min of each interval were averaged. To best meet isotopic steady-state conditions, δ^2H of transpiration water was recorded during mid-day, when environmental conditions and rate of transpiration were constant. Δ2H values were calibrated against two working standards and corrections for vapour concentration offsets were performed (see supplements).

Using a two end-member mixing model, we calculated the δ^2H of the transpired water as the difference to the vapour concentration and isotope signal of an empty reference chamber:

$$\delta^2 H_T = \frac{\left(\delta^2 H_C * ppm_C - \delta^2 H_{EC} * ppm_{EC}\right)}{\left(ppm_C - ppm_{EC}\right)} \tag{1}$$

with

$\delta^2 H_T$: δ^2H of the DP transpiration,

$\delta^2 H_C$: δ^2H in the foliated chamber,

ppm_C : Volumetric water vapor concentration in the foliated chamber,

$\delta^2 H_{EC}$: δ^2H in the empty reference chamber and.

ppm_{EC} : Volumetric water vapor concentration in the empty reference chamber.

Similarly, the vapour concentration of the transpired water (ppm_T) was calculated as difference between the vapour concentration of the foliated chamber and of the empty chamber:

$$ppm_T = ppm_C - ppm_{EC} \tag{2}$$

From ppm_T we calculated the absolute humidity (aH_T, in ml/m^3) of the transpired water:

$$aH_T = \frac{ppm_T * M * \rho * 0.1}{R * T} \tag{3}$$

with

M: Molar mass of water (18.02 g/mol),

ρ Atmospheric pressure (in mbar).

R Molar gas constant (8.3144598 J/mol K) and.

T Temperature (in K).

By interpolating linearly across measurement steps (each chamber was measured 13 times per day), we calculated the amount of daily transpired water (T, in ml) of the plants by:

$$T = \sum_{0}^{i} \Delta t * Q * aH_T * \frac{total\ leaf\ area}{leaf\ area\ in\ chamber} \tag{4}$$

with

Δ t: Time difference between measurement steps and

Q: Flow rate (1 L/min).

For upscaling to whole-tree transpiration, leaf area (inside and outside the chamber) was assessed. A conversion factor of 3.2 (*P. abies*, Homolova et al., 2012) and 2.32 (*P. menziesii*, Barker, 1968) was used to calculate total needle area from projected area for the conifers.

2.5 | Root characteristics

Fresh and dry mass of DP root branches, DP rootstocks and DP stems were recorded. Individual root segments ($n = 5$ per type of SRS; average mass: 0.42 ± 0.05 g (1 *SE*)) were scanned (1,200 dpi, Epson Perfection 4,990 Photo) and images analysed with WinRhizo (WinRHIZO Reg 2013e, Regent Instruments Inc., Quebec, Canada) for determination of root length and number of tips. Specific root length (SRL, the ratio of root length to dry mass of the root) was calculated and used to estimate total root length per tree. Total number of root tips was linearly scaled from the fraction of the analysed root segment to the total root system.

Finally, we measured native k_s of the DPs with a "xylem embolism meter" (XYL'EM, Bronkhorst France S.A.S., Montigny-Les-Cormeilles, France). DP roots ($n = 5$ per species, $n = 8$ for *P. abies*) were cut several times under water and their barks gently peeled on the sides that were inserted into the XYL'EM (measured pieces had a diameter of 2.5 ± 0.1 mm (1 *SE*) and a length of 2.7 ± 0.1 cm (1 *SE*)). Hydraulic conductance was measured (K_{act}, in kg MPa^{-1} s^{-1}) at approx.

0.007 MPa (i.e., without removing native embolisms) using degassed, filtered (0.2 μm) water, additionally containing 10 mM KCl and 1 mM $CaCl_2$ (Barigah et al., 2013; Hesse, Hafner, & Grams, 2019). Length and conductive area (A_{cond}) of the root sample were measured and k_s (in kg s^{-1} m^{-1} MPa^{-1}) was calculated as:

$$k_s = \frac{K_{act} * \text{Length}}{A_{cond}} \tag{5}$$

2.6 | Model calculations

We calculated the relative fractions (in %) and absolute amounts (in ml) of HR water in roots, stems and transpiration for each DP using two end-member mixing models. For the DP root, we assumed the δ^2H in the root water to be a mixture of soil water in the dry pot and redistributed labelled water released by the SRP:

$$HR_{DP\_root} = \frac{\delta^2 H(DP_{root}) - \delta^2 H(Soil_{dry\_BL})}{\delta^2 H(SRP_{root}) - \delta^2 H(Soil_{dry\_BL})} * 100\,(\%) \tag{6}$$

with

HR_{DP_root} : Fraction of HR water in the DP root,

$\delta^2 H(DP_{root})$: δ^2H of the DP root 7 days after labelling,

$\delta^2 H(Soil_{dry\_BL})$: δ^2H of the soil in the dry pot before labelling and.

$\delta^2 H(SRP_{root})$: δ^2H of the SRP root in the dry pot 7 days after labelling.

Similarly, we calculated the isotopic composition of water in the DP stem as:

$$HR_{DP\_stem} = \frac{\delta^2 H(DP_{stem}) - \delta^2 H(Soil_{dry\_BL})}{\delta^2 H(SRP_{root}) - \delta^2 H(Soil_{dry\_BL})} * 100\,(\%) \tag{7}$$

with

HR_{DP_stem} : Fraction of HR water in the DP stem and.

$\delta^2 H(DP_{stem})$: δ^2H of the DP stem 7 days after labelling.

To assess daily transfer dynamics, we calculated fractions of HR water in the transpiration for all days between labelling and harvesting the plants (i.e., day 1 to day 6). As end-members, we used the unlabelled soil δ^2H value before labelling and the δ^2H value of the SRP root of the respective day after the labelling (day 1 to day 6). For the SRP root that released the HR water, we linearly interpolated between the δ^2H from day 1 (Hafner et al., 2020) and day 7 after labelling, assuming a steady increase from day 1 to day 7 (Table S1):

$$HR_{DP\_transpiration\_day\_x} = \frac{\delta^2 H(DP_{transpiration\_day\_x}) - \delta^2 H(Soil_{dry\_BL})}{\delta^2 H(SRP_{root\_day\_x}) - \delta^2 H(Soil_{dry\_BL})} * 100\,(\%) \tag{8}$$

with

$HR_{DP\_transpiration\_day\_x}$: Fraction of HR water in the DP transpiration on day *x* (i.e., day 1–6 after labelling),

$\delta^2 H(DP_{transpiration\_day\_x})$: δ^2H of the DP transpiration on day *x* (i.e., day 1–6 after labelling) and

$\delta^2 H(SRP_{root\_day\_x})$: δ^2H of the SRP root in the dry pot x days (i.e., day 1–6) after labelling.

We used these relative fractions to compare uptake of HR water between single species and mixed SRS. Finally, to gain the absolute amounts of HR water per tree, the respective fractions of HR water were multiplied with the amounts of water in DP roots, DP stems and total DP transpiration of the respective days (1–6; Equation (4)).

We also ran the mixing model calculations (Equation (6)–(8)) using the average δ^2H values per type of SRS with a mixing model accounting for uncertainty errors ("Iso Error," Phillips & Gregg, 2001), giving the same results as our single-value based calculations.

2.7 | Statistics

The statistical analyses were conducted in R (version 3.3.1, R Development Core Team, 2018) using the RStudio environment (version 1.1.447, RStudio Team, 2015). The isotope data were checked for significant ($p < .05$) increases in δ^2H after labelling. We used the pots as random factors nested over respective growth chamber identities in a linear mixed effect model (R package nlme, version 3.1-137, Pinheiro, Bates, DebRoy, Sarkar, & Team, 2018). We tested the δ^2H values of the samples (SRP root, DP root, DP stem and DP transpiration) individually for increases (using day and type of SRS as independent variables). Increases in and differences between the δ^2H values of the types of SRS were revealed with the lsmeans post-hoc test (R package lsmeans, version 2.27-62, Lenth, 2016). Model data were checked for residual normal distribution (shapiro.test) and variance homogeneity (leveneTest; R package car, version 2.1-2, Fox & Weisberg, 2019). Where necessary, values were transformed to meet residual normal distribution. Differences between the types of SRS in the amounts and fractions of HR water and between plant or soil characteristics (biomass, root length, leaf area, ψ_{leaf}, SWC, k_s) were checked using the same model and tests. We performed a multiple linear regression to determine a potential dependency of our mixing model outputs from the three independent root characteristic parameters tested (root length, number of tips, k_s). For the model, dependent and independent parameters were standardized with the normalize function (R package BBmisc, version 1.11, Bischl et al., 2017). Mean values are given ±1 standard error (1 *SE*).

3 | RESULTS

3.1 | Plant and soil characteristics

Volumetric soil water content in the dry pot ranged between 8.5 ± 0.4 vol% (*P. menziesii*) and 16.8 ± 2.5 vol% (*P. abies* mix, Table 2) and was significantly lower for all types of SRS than in the moist pot (average in the moist pot: 28.7 ± 1.4 vol%). Consequently, the average moisture gradient between moist and dry pot was 16.8 ± 1.1 vol% (not shown). Pre-dawn ψ_{leaf} of the DP ranged from −0.8 ± 0.1 MPa in

P. abies to significantly lower −2.8 ± 0.7 and −3.5 ± 0.4 MPa in *C. sativa* and *Q. robur*, respectively (Table 2). The difference in pre-dawn ψ_{leaf} between DP and MP was greatest in *Q. robur* (2.97 ± 0.33 MPa), while *P. abies* combinations had the smallest difference (0.47 ± 0.15 MPa, Table 2). The root systems of *C. sativa* were significantly heavier (27.7 ± 4.4 g) and longer (149 ± 25 m) than the systems of all other species (Table 3). With 25 ± 6 m, *Q. robur* DPs had the shortest average root length, while the other species were in a range between 40 ± 19 m (*F. sylvatica* mix) and 62 ± 24 m (*F. sylvatica*) but not significantly different from each other (Table 3). Accordingly, the stems of *C. sativa* had the highest biomass (14.4 ± 1.9 g), while stems of *P. abies* trees (1.6 ± 0.1 g in single and 1.2 ± 0.1 g in mix SRS) had a significantly lower biomass than all other species (Table 3). Root hydraulic conductivity (k_s) was highest in *A. pseudoplatanus* and *F. sylvatica* mix (0.64 ± 0.08 kg s^{-1} m^{-1} MPa^{-1} and 0.64 ± 0.02 kg s^{-1} m^{-1} MPa^{-1}, respectively) and lowest in *P. abies*, *P. menziesii* and *C. sativa* (0.28 ± 0.07 kg s^{-1} m^{-1} MPa^{-1}, 0.29 ± 0.03 kg s^{-1} m^{-1} MPa^{-1} and 0.33 ± 0.08 kg s^{-1} m^{-1} MPa^{-1}, respectively, Table 3). Root systems of *Q. robur* had the highest number of root tips (1850 ± 424), while *P. menziesii* trees had the lowest number of tips (287 ± 63). Total leaf area was highest in *C. sativa* (1,648 ± 261 cm^2) and *Q. robur* (993 ± 173 cm^2), while all other species had significantly smaller leaf areas (between 89 ± 18 cm^2 in *P. abies* mix and 389 ± 101 cm^2 in *A. pseudoplatanus*, Table 3).

TABLE 2 Volumetric soil water content (SWC) in dry pots, measured pre-dawn leaf water potentials (ψ_{leaf}) of plants in the dry pots, measured after labelling and difference in ψ_{leaf} between the plant in the dry and in the moist pot (means ±1 *SE*)

	swc (vol-%)	DP ψ_{leaf} (MPa)	Δ ψ_{leaf} (MPa)
P. abies	11.2 ± 1.8^{ab}	−0.9 ± 0.3^{a}	0.73 ± 0.25^{a}
P. abies mix	16.8 ± 2.5^{a}	−0.8 ± 0.1^{a}	0.47 ± 0.15^{a}
P. menziesii	8.5 ± 0.4^{b}	−2.0 ± 0.3^{ab}	1.54 ± 0.26^{a}
A. pseudoplatanus	11.1 ± 0.6^{ab}	*NA*	*NA*
F. sylvatica	11.9 ± 1.1^{ab}	−1.6 ± 0.5^{ab}	1.12 ± 0.47^{a}
F. sylvatica mix	16.7 ± 2.6^{a}	−0.9 ± 0.1^{a}	0.62 ± 0.15^{a}
C. sativa	9.0 ± 0.4^{b}	−2.8 ± 0.7^{bc}	2.01 ± 0.62^{ab}
Q. robur	11.2 ± 0.7^{ab}	−3.5 ± 0.4^{c}	2.97 ± 0.33^{b}

Note: Letters indicate significant ($p < .05$) differences between the types of split root systems. Note that ψ_{leaf} of *A. pseudoplatanus* trees could not be assessed due to heavy milky sap formation.

3.2 | Enrichment in ^{2}H upon labelling

Before labelling, δ^2H was at −59 ± 1 ‰ across all SRS. On day 7 upon labelling, δ^2H of the SRP roots in the dry pots were significantly increased in all types of SRS ranging from −14 ± 7 ‰ in *C. sativa* to 168 ± 68 ‰ in *P. menziesii* (average value of 54 ± 14 ‰, Table 4), confirming a translocation of labelled water within the SRP from the labelled, moist to the dry pot. The DP roots showed significantly increased values in all types of SRS except for *F. sylvatica* mix (−51 ± 3 ‰) and *Q. robur* (−46 ± 3 ‰) with the same tendency (p = .05). In the stems, all DP were significantly enriched in δ^2H with the exception of again *F. sylvatica* mix (−42 ± 4 ‰, p = .07) and *Q. robur* (−51 ± 2 ‰). Finally, the δ^2H of the transpired water increased after the labelling in almost all species (Table 4). On day 6 it was significantly enriched when compared to δ^2H values before the labelling in *P. abies* (single & mix), *P. menziesii*, *F. sylvatica* (single & mix) and *Q. robur* (Table 4); no enrichment in transpired water was found on any day after the labelling in *A. pseudoplatanus* and *C. sativa* (δ^2H on day 6: −58 ± 1 ‰ and – 69 ‰, respectively, Table 4).

3.3 | Amounts of HR water in roots, stems and transpiration of DP in single-specific SRS

Seven days after labelling, the DP roots growing in single-specific SRS contained on average 2.26 ± 0.48 ml of HR water (i.e., 25 ± 4% of total root water; see blue bars in Figure 2). The absolute amount was highest in *P. abies* trees (5.07 ± 1.82 ml) and significantly higher than in *Q. robur* and *F. sylvatica* with the lowest amounts of 0.43 ± 0.22 ml and 0.72 ± 0.36 ml, respectively (Table 5). The results were consistent also for the fractions of HR water in total root water, with highest fractions in *P. abies* (50 ± 13%) and lowest in *Q. robur* roots (9 ± 3%,

TABLE 3 Characteristics of plants in the dry pots (DP), i.e., root and stem biomass, total root length, number of root tips, native hydraulic conductivity (k_s) and whole-tree leaf area (means ±1 *SE*)

	Root biomass (g)	Stem biomass (g)	Root length (m)	Root tips	k_s (kg s^{-1} m^{-1} MPa^{-1})	Leaf area (cm^2)
P. abies	7.0 ± 1.1^{a}	1.6 ± 0.1^{a}	46 ± 12^{a}	828 ± 165^{abc}	0.28 ± 0.07^{a}	299 ± 56^{a}
P. abies mix	2.8 ± 0.8^{a}	1.2 ± 0.1^{a}	42 ± 23^{a}	478 ± 151^{abc}	0.34 ± 0.04^{ab}	89 ± 18^{a}
P. menziesii	5.6 ± 0.8^{a}	3.8 ± 0.1^{b}	59 ± 13^{ab}	287 ± 63^{a}	0.29 ± 0.03^{a}	300 ± 45^{a}
A. pseudoplatanus	8.1 ± 1.3^{a}	4.4 ± 0.2^{b}	59 ± 17^{ab}	1,176 ± 373^{abc}	0.64 ± 0.08^{b}	389 ± 101^{a}
F. sylvatica	5.0 ± 2.3^{a}	3.0 ± 0.7^{b}	62 ± 24^{ab}	1,493 ± 460^{bc}	0.49^{ab}	255 ± 45^{a}
F. sylvatica mix	2.4 ± 0.7^{a}	3.6 ± 0.2^{b}	40 ± 19^{ab}	1,377 ± 544^{abc}	0.64 ± 0.02^{b}	146 ± 44^{a}
C. sativa	27.7 ± 4.4^{b}	14.4 ± 1.9^{c}	149 ± 25^{b}	453 ± 74^{ab}	0.33 ± 0.08^{a}	1,648 ± 261^{b}
Q. robur	4.8 ± 0.8^{a}	4.1 ± 0.3^{b}	25 ± 6^{a}	1850 ± 424^{c}	0.57 ± 0.06^{ab}	993 ± 173^{b}

Note: Letters indicate significant ($p < .05$) differences between the different types of split-root systems.

TABLE 4 δ^2H (‰) of soil water before labelling (d0), of roots of the split-root plant (SRP) growing in the dry pot (d7) and of roots and stems of the plant in the dry pot (DP) at day 7 and of DP transpiration on days 1–6 (means ±1 *SE*)

	DP	SRP	DP	DP	DP	DP	DP	DP	DP	DP
	Soil	Root	Root	Stem	Transpiration					
	d0	d7	d7	d7	d1	d2	d3	d4	d5	d6
P. abies	−57 ± 1^{ab}	21 ± 35 ^{***a}	−40 ± 3 ^{***ac}	−46 ± 2 ^{*ab}	−60 ± 2^{abc}	−48 ± 0^{abc}	−55 ± 2^{abc}	−50 ± 2^{abc}	−50 ± 3^{abc}	−42 ± 2 ^{**a}
P. abies mix	−57 ± 2^{ab}	4 ± 18 ^{***a}	−41 ± 1 ^{***ac}	−47 ± 3 ^{*ab}	−50 ± 2^{bc}	−54 ± 2^{bc}	−59 ± 4^{a}	−52 ± 3^{a}	−53 ± 2^{abc}	−46 ± 2 ^{*a}
P. menziesii	−53 ± 2^{a}	168 ± 68 ^{***a}	−28 ± 8 ^{***a}	−40 ± 5 ^{*a}	−47 ± 3^{bc}	−37 ± 2 ^{*a}	−40 ± 4 $^{\circ bc}$	−36 ± 4 ^{*bc}	−41 ± 4 $^{\circ bc}$	−28 ± 3 ^{***d}
A. pseudoplatanus	−63 ± 1^{ab}	86 ± 46 ^{***a}	−40 ± 9 ^{***abc}	−55 ± 2 ^{*b}	−67 ± 5^{ac}	−61 ± 3^{b}	−66 ± 5^{a}	−53 ± 4^{ac}	−53 ± 5^{abc}	−58 ± 1^{bc}
F. sylvatica	−60 ± 1^{ab}	48 ± 29 ^{***a}	−43 ± 3 ^{***abc}	−50 ± 3 ^{*ab}	−50 ± 3 ^{*abc}	−51 ± 3 ^{*abc}	−57 ± 2^{abc}	−51 ± 3 ^{*abc}	−53 ± 1^{abc}	−51 ± 1 ^{*ab}
F. sylvatica mix	−55 ± 2^{ab}	33 ± 45 ^{**a}	−51 ± 3^{bc}	−42 ± 4 $^{\circ ab}$	−70 ± 7^{a}	−48 ± 2^{abc}	−56 ± 4^{ac}	−52 ± 3^{ac}	−56 ± 4^{ac}	−41 ± 2 ^{*a}
C. sativa	−66 ± 2^{b}	−14 ± 7 ^{***a}	−55 ± 1 ^{***b}	−50 ± 1 ^{***ab}	−60^{abc}	−69^{bc}	−69^{ac}	−63^{a}	−73^{a}	−69^{c}
Q. robur	−57 ± 2^{ab}	76 ± 17 ^{***a}	−46 ± 3 $^{\circ abc}$	−51 ± 2^{ab}	−44 ± 6^{b}	−40 ± 7^{ac}	−35 ± 6 ^{*b}	−34 ± 4 ^{*b}	−36 ± 6 ^{*b}	−26 ± 1 ^{**d}

Note: Letters indicate significant ($p < .05$) differences between the types of split-root systems, and asterisks give significant enrichment in^{2}H above d0 soil water (° ≤ 0.1, * < 0.05, ** < 0.01, *** < 0.001).

Table 5). In DP stems, we found 0.79 ± 0.19 ml of HR water over all species (i.e., fraction of 17 ± 3% of total stem water; green bars in Figure 2). The absolute amount was significantly higher in *C. sativa* (3.18 ± 0.50 ml) than in all other species (Table 5). The relative fractions were highest in *P. abies* and *C. sativa* (30 ± 8% and 35 ± 5%, respectively), while the lowest fractions were found in *P. menziesii* and *Q. robur* (8 ± 2% and 4 ± 1%, respectively; Table. 5).

In total daily transpiration, HR water amounted to 0.99 ± 0.33 ml (fraction of 22 ± 6% of 3.57 ± 0.58 ml total transpired water) on day 6 after the labelling over all single-specific SRS. Two individuals almost entirely transpired HR water (see open symbols close to the 1:1-line, Figure 3). *C. sativa* did not transpire HR water and also the fraction in *A. pseudoplatanus* was very low (4 ± 0.4%). However, both species had the lowest daily transpiration of about 1.3 ml (Figure 3). The amount of HR water that trees transpired each day were constant from day 1 to day 6 after the labelling (Figure 3).

In a multiple linear regression, we found that root length, number of tips and k_s significantly influenced the absolute amounts of HR water in roots ($R^2 = 0.8$, $p < .001$) and stems ($R^2 = 0.5$, $p < .01$), but not in transpiration ($R^2 = 0.2$, $p = .29$; Table 6). Within the model, root length was significantly positively correlated with the amount of HR water in roots and stems and was the most important driving factor on HR amounts (Table 6). Combining the amounts of HR water found in roots and stems, *C. sativa*, that had the longest roots, also contained the highest amounts of HR water, while *Q. robur* with significantly shorter root lengths also had less HR water in roots and stems (Figure 4). In the roots, also number of tips and the interaction of root length and number of tips were positively correlated with amounts of HR water (Table 6). Opposing to our expectation, k_s had a negative effect on the quantity of labelled HR water in the roots, either as single factor ($p < .01$) or in interaction with root length ($p < .01$) or number of tips ($p < .01$; Table 6).

3.4 | Amounts of HR water in mixed SRS

In the mixed SRS, DP roots of *P. abies* contained 2.51 ± 0.75 ml (i.e., 45 ± 11% of 7.30 ± 3.00 ml total root water) of HR water redistributed by *F. sylvatica* SRPs. Conversely, DP roots of *F. sylvatica* received 0.20 ± 0.07 ml (i.e., 6 ± 2% of 3.14 ± 0.92 ml total root water, Figure 2) from *P. abies* SRPs. In the DP stems we found 0.27 ± 0.10 ml (29 ± 11% of 0.93 ± 0.04 ml total stem water) of redistributed water in *P. abies*, whereas 1.46 ± 0.64 ml (47 ± 20% of 3.11 ± 0.20 ml total stem water) of the water in *F. sylvatica* DPs originated from the other species (Figure 2). The transpired water on day 6 contained 0.63 ± 0.18 ml (30 ± 9% of 2.61 ± 0.55 ml total transpired water) of HR water in *P. abies* DPs and 1.41 ± 1.13 ml (49 ± 25% of 2.45 ± 1.16 ml total transpired water) in *F. sylvatica* DPs in mixture (Table **5**). Two *F. sylvatica* DPs almost entirely transpired HR water (see closed symbols close to the 1:1-line, Figure **3**). For *P. abies*, the highest fractions of HR water were found in roots in both, single- and mixed-species combinations, while the highest fractions of HR water were measured in the transpiration of *F. sylvatica* single-and mixed-species combinations (Figure 5; not significantly for both, though). When comparing single- and mixed-species SRS (Figure **5**), there was no difference for both species in the fractions of HR water in roots, stems and transpiration whether the neighbour was the same or another species (Table 5).

4 | DISCUSSION

Hydraulic redistribution (HR) functioned as an important supply of water for the drought stressed saplings of all tested temperate tree species. On average, one quarter of the water in the DPs originated from HR. Root length was the best predictor of variations in HR water amounts, supporting our first hypothesis, that more favourable root characteristics increase HR amounts. Among *F. sylvatica* and *P. abies*, it was insignificant whether the SRP was of the same or another species. Therefore, our second hypothesis that DP in single-specific SRS take up higher amounts of HR water than in mixed SRS was not supported by our findings.

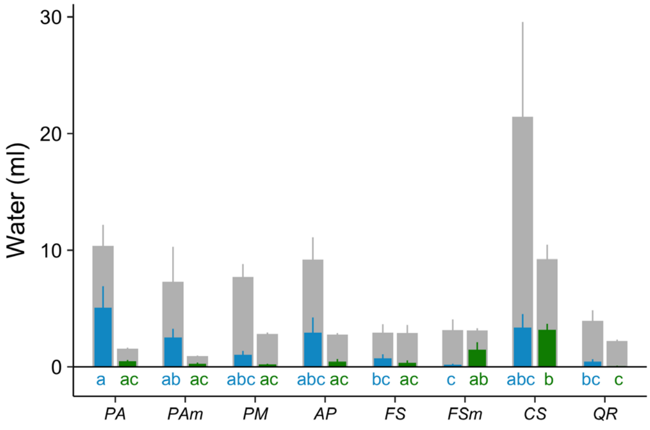


FIGURE 2 Amount (in ml) of HR water in roots (blue) and stems (green) in plants grown in the dry pots of the different types of split-root systems (SRS). Species are *P. abies* (*PA*), *P. abies* mix (*PAm*), *P. menziesii* (*PM*), *A. pseudoplatanus* (*AP*), *F. sylvatica* (*FS*), *F. sylvatica* mix (*FSm*), *C. sativa* (*CS*) and *Q. robur* (*QR*). Grey bars give total water in tissues and letters indicate significant ($p < .05$) differences in roots and stems between the types of SRS [Colour figure can be viewed at wileyonlinelibrary.com]

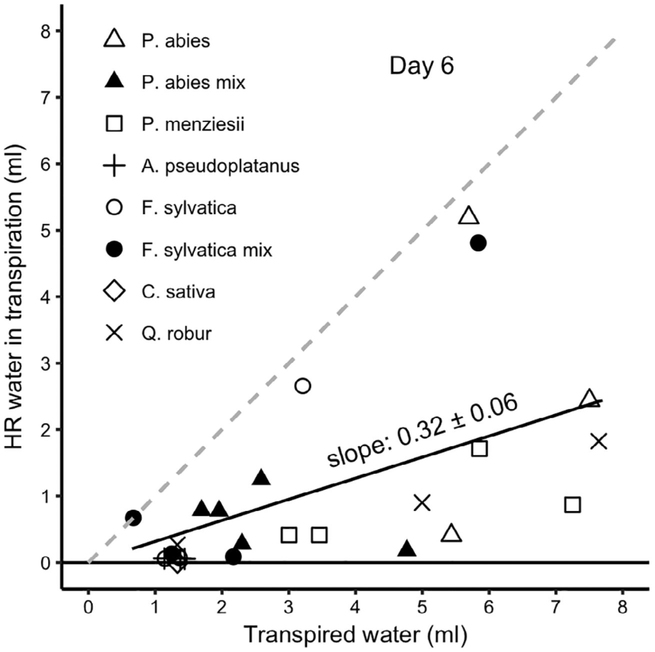
4.1 | Root length as a driver of HR towards neighbouring trees

We found HR water in the DPs of all types of SRS, confirming the general occurrence of the effect in woody species (Brooks et al., 2002; Hafner et al., 2017; Muler, van Etten, Stock, Howard, & Froend, 2018). The contribution of HR to either plant tissue- or transpiration water was different for the species: In *Q. robur* and *F. sylvatica*, we hardly found HR water in roots or stems (Figure 2). These species used the HR water directly in their transpiration (Figure 3), as the amounts of daily transpired HR water were high (21 ± 2% in *Q. robur* and 31 ± 26% in *F. sylvatica*, respectively). Conversely, *A. pseudoplatanus* and *C. sativa* hardly transpired but largely kept the HR water within their roots and stems. For these species, HR water potentially played a bigger role for refilling of internal water storages (Yu et al., 2018) as transpiration rates were rather low. In fact, decoupling of sap flow and transpiration and using tissue storage water for transpiration has been reported as a strategy for some species to survive temporal droughts (Klein et al., 2016). Another reason for the differences between the species was revealed when looking at their root characteristics. Within the multiple linear regression model, the amount of HR water taken up by neighbouring DPs was especially dependent on their root length and the interaction of root length and number of tips. Concurring with our expectations, species with shorter roots (e.g., *Q. robur*, Table 3) also showed the lowest amounts of HR water in roots and stems, while the species with the highest root length, *C. sativa*, also had most HR water in roots and stems (Figure 4). It has been reported that HR water amounts increase with higher root densities (Aanderud & Richards, 2009). Distribution and proximity of roots has been suggested as an important driving factor for HR between species, with higher root contact increasing HR

TABLE 5 Amounts (ml) and fractions (%) of redistributed water in roots, stems and transpiration in the different types of split-root systems (SRS; means ±1 *SE*) 7 days (transpiration: 6 days) after labelling

	Root		Stem		Transpiration	
	ml	%	ml	%	ml	%
P. abies	5.07 ± 1.82 ^{a}	50 ± 13^{a}	0.46 ± 0.12 ^{ac}	30 ± 8^{ab}	2.64 ± 1.40 ^{a}	44 ± 25^{a}
P. abies mix	2.51 ± 0.75 ^{ab}	45 ± 11^{ab}	0.27 ± 0.10 ^{ac}	30 ± 11^{ab}	0.63 ± 0.18 ^{a}	30 ± 9^{a}
P. menziesii	1.05 ± 0.31 ^{abc}	14 ± 3^{abc}	0.21 ± 0.06 ^{ac}	8 ± 2^{ab}	0.77 ± 0.28 ^{a}	17 ± 4^{a}
A. pseudoplatanus	2.93 ± 1.31 ^{abc}	35 ± 17^{abc}	0.44 ± 0.23 ^{ac}	15 ± 8^{ab}	0.06 ± 0.00 ^{a}	4 ± 0^{a}
F. sylvatica	0.72 ± 0.36 ^{bc}	22 ± 7^{abc}	0.35 ± 0.20 ^{ac}	12 ± 7^{ab}	0.92 ± 0.85 ^{a}	31 ± 26^{a}
F. sylvatica mix	0.20 ± 0.07 ^{c}	6 ± 2^{c}	1.46 ± 0.64 ^{ab}	47 ± 20^{ab}	1.41 ± 1.13 ^{a}	49 ± 25^{a}
C. sativa	3.38 ± 1.14 ^{abc}	23 ± 5^{abc}	3.18 ± 0.50 ^{b}	35 ± 5^{a}	0.00 ^{a}	0^{a}
Q. robur	0.43 ± 0.22 ^{bc}	9 ± 3^{bc}	0.09 ± 0.02 ^{c}	4 ± 1^{b}	1.00 ± 0.46 ^{a}	21 ± 2^{a}

Note: Letters indicate significant differences between the types of SRS.



Day	Transpired HR water (ml/day)	Regression slope (i.e. predicted % of HR water in transpiration)	r^2
Day 1	1.07 ± 0.31	0.23 ± 0.04 ***	0.6
Day 2	1.59 ± 0.46	0.36 ± 0.06 ***	0.6
Day 3	0.81 ± 0.27	0.21 ± 0.03 ***	0.6
Day 4	0.96 ± 0.26	0.24 ± 0.04 ***	0.7
Day 5	0.77 ± 0.25	0.22 ± 0.04 ***	0.5
Day 6	**1.03 ± 0.30**	**0.32 ± 0.06 *** **	**0.5**

FIGURE 3 Amount of transpired HR water versus total daily transpired water (in ml) of the plants grown in the dry pots on day 6 after labelling. The dotted line indicates equality. Mixed species compositions are highlighted as filled symbols. The slope of the regression predicts the fraction of HR water in the transpiration. The table gives amounts and fractions of transpired HR water between day 1 and day 6 after labelling. Amounts were not different from each other. Asterisks indicate *P*-values for the regression slopes of the different models (*** < 0.001). r^2 give the adjusted correlation coefficients of the models

TABLE 6 Output parameters of a 3-factor linear model for regression between amounts of HR water (in ml) found in roots, stems and transpiration of the plants grown in the dry pots (DP) with root length, number of tips and hydraulic conductivity (k_s) of the DPs

	HR water in roots			**HR water in stems**			**HR water in transpiration**		
	Coefficient	***t* value**	***p* value**	**Coefficient**	***t* value**	***p* value**	**Coefficient**	***t* value**	***p* value**
Root length	0.7985	5.15	**<.001**	1.070	4.72	**<.001**	0.4015	0.66	.53
Tips	0.2669	2.19	**<.05**	0.1525	0.86	.40	0.1464	0.55	.60
k_s	−0.3666	−3.06	**<.01**	0.1724	0.99	.34	−0.2167	−0.65	.54
Root length × tips	0.3722	2.47	**<.05**	0.3386	2.54	.15	−0.8341	−1.24	.25
Root length × k_s	−0.5672	−3.81	**<.01**	−0.1063	−0.49	.63	0.0369	0.07	.94
Tips × k_s	−0.4232	−3.53	**<.01**	0.0684	0.39	.70	−0.1918	−0.55	.60
Root length × tips × k_s	−0.2391	−1.57	.14	0.4642	2.08	.06	−1.016	−1.47	.18
Adjusted R^2			.77			.50			.18
p value			**<.001**			**<.01**			.29

Note: The linear model includes interactions between the independent variables. Data were standardized so that coefficients with a greater difference to zero indicate relatively bigger weights of the respective independent variables on the model outcome. *T*-values describe the coefficient divided by its *SE*. The greater the difference from the *t*-value to zero, the greater the evidence that the coefficient does not equal zero. Coefficients of determination and *p* values are each given for the whole models for roots, stems and transpiration. Significant correlations are highlighted in bold.

amounts (Hultine, Williams, Burgess, & Keefer, 2003; Scholz et al., 2008; Schoonmaker, Teste, Simard, & Guy, 2007). Some species seem to avoid contact with other roots, to reduce (self-) competition (Falik, Reides, Gersani, & Novoplansky, 2003; Maina, Brown, & Gersani, 2002), while others show increased growth when root systems are in close vicinity with their neighbours (Armas & Pugnaire, 2011). We detected less HR water with higher root k_s in our statistical model (Table 6). Potentially, labelled HR water was transported faster from roots to stems and then transpired in plants with higher k_s, reducing the labelling signal. There was no significant correlation of root length, number of tips or root k_s with HR amounts in DP transpiration. For HR water in transpiration, potentially additional driving factors have to be considered that also influence plant stomatal conductance and transpiration rate, for example, vapour pressure deficit or leaf abscisic acid concentrations (Lange, Lösch, Schulze, & Kappen, 1971; Whitehead, 1998; Will, Wilson, Zou, &

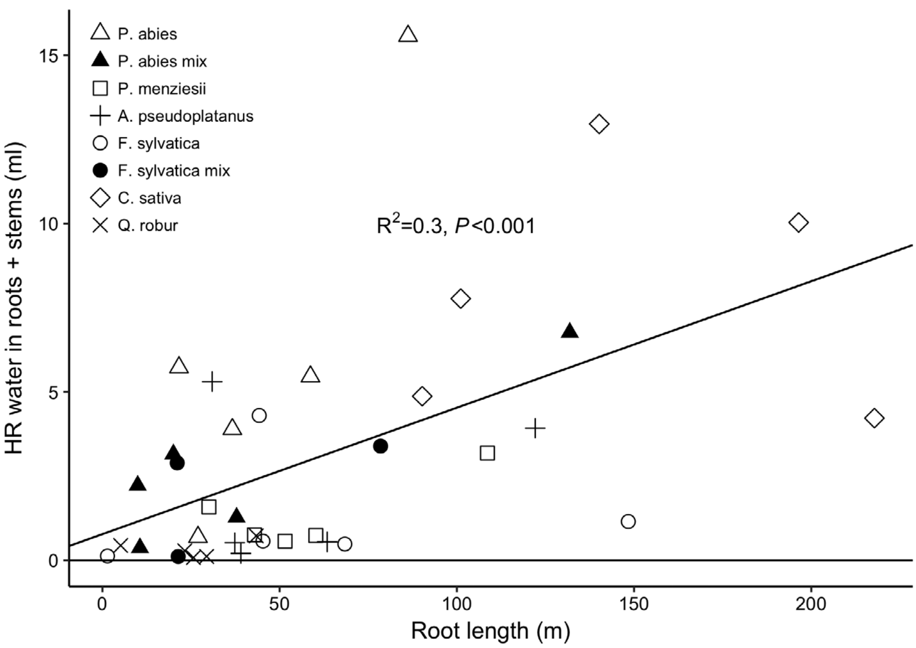


FIGURE 4 Correlation of root length (m) of the plants in the dry pot (DP) with the accumulated amount of HR water in roots and stems (ml) of the DP

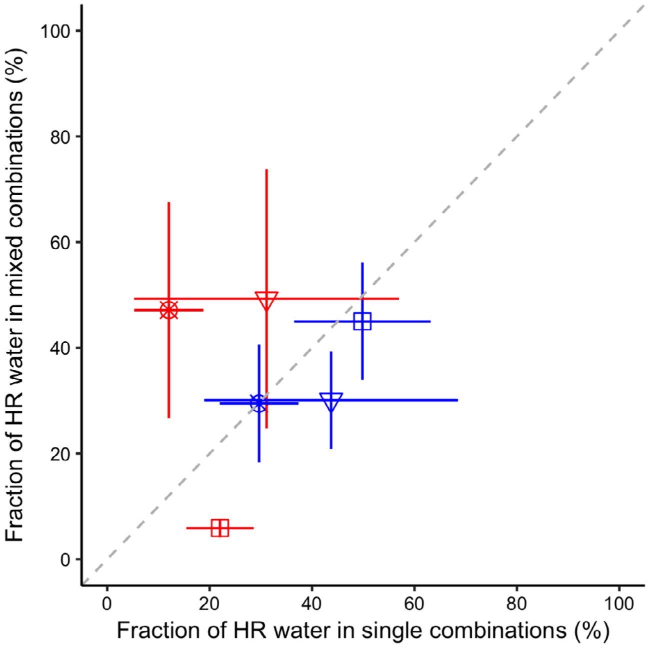


FIGURE 5 Fractions (in %) of HR water in roots (squares), stems (crossed circles) and transpiration (triangles) in plants grown in the dry pots of *P. abies* (blue) and *F. sylvatica* (red) in single-species combinations (X-axis) versus mixed combinations (Y-axis). The dotted diagonal indicates equality. No statistical differences were found for both species between single and mixed combinations. All values are means ±1 *SE* (Note that for *F. sylvatica* mix the error bar for root HR water is smaller than the symbol size) [Colour figure can be viewed at wileyonlinelibrary.com]

Hennessey, 2013). The δ^2H values in the transpiration of the trees increased from day 1 to day 6 after the labelling in almost all species (Table 4). This is in line with previous time-series observations in soil water ^{2}H excess due to HR after deuterium labelling (Töchterle et al., 2020). However, the amount of daily transpired HR water was constant (Figure 3). Hydraulic redistribution is a mostly passive process, driven by external factors (ψ gradient) and regulated by plant internal characteristics (e.g., k_s, bark thickness) (Hafner et al., 2020; Neumann & Cardon, 2012). As these factors were constant during the experiment, it appears plausible that redistribution by SRPs and uptake of HR water by DPs was similar every day. Although it has been shown that more water is redistributed among higher ψ gradients (Hafner et al., 2020; Neumann & Cardon, 2012), uptake of HR water by plants under low soil ψ may be limited. For instance in a previous study with moderate drought, we found that neighbouring trees receiving HR water contained up to 80% of HR water in their roots (Hafner et al., 2017). Here, neighbouring species received lower fractions, while experiencing drought conditions that were at the edge of their reported survival, as for example, ψ_{leaf} values lower than −3.5 MPa have been reported to cause 88% embolism in *Q. robur* conduits (Cochard, Bréda, & Aussenac, 1992; Tyree & Cochard, 1996). Therefore, there may be a trade-off between the amount of redistributed water among a higher water potential gradient and the level of drought stress causing plants to close their stomates and thus limited water uptake.

Interestingly, coniferous *P. abies* trees, where root length or number of tips were not significantly different to the other species, showed the highest amounts of HR water in roots and transpiration (Table 5). Also, SRPs of *P. abies* did not redistribute more water from the moist to the dry pot than the other species (Hafner et al., 2020). Given the low k_s and conduit diameter, amounts of HR water are expected to be rather low in *P. abies* (Hafner et al., 2020). It has, however, been shown that *Picea* trees tend to increase root branching when growing with neighbours (Paya, Silverberg, Padgett, & Bauerle, 2015). Therefore, the high amounts of HR water in *P. abies*

DPs might be explained by closer root proximity of *P. abies* trees to its neighbours. However, no clear hierarchical pattern or mechanistic background on root proximity is known yet (Armas & Pugnaire, 2011).

4.2 | Mixed combinations

In contrary to our hypothesis, DPs grown in single-specific SRS did not receive more HR water than in mixed SRS, at least for the tested combinations of *F. sylvatica* and *P. abies* (Figure 5). Preconditions for HR such as SWC, root length or leaf area were not different between saplings in single- and mixed-species SRS, allowing for direct comparison between the two (Table 3). We did not quantify mycorrhization or determine mycorrhizal morphotypes; however, we frequently observed invested root tips of both, *P. abies* and *F. sylvatica* during harvest. It has been described that, although phylogenetically distant, *P. abies* and *F. sylvatica* are partially colonized by the same mycorrhizae (Nickel et al., 2018; Rog et al., 2020; Trappe, 1962), therefore potentially allowing for a HR-pathway via a CMN. The role that mycorrhizae may play in HR has been accentuated in previous studies (Egerton-Warburton, Querejeta, & Allen, 2007; Plamboeck et al., 2007; Prieto et al., 2016; Querejeta, Egerton-Warburton, & Allen, 2003), but should be further investigated, especially between (phylogenetically) different species. However, the influence of species mixture on either benefit or competition on HR water seems to vary widely with involved species, as water can be provided to or drained from neighbours (Prieto, Armas, & Pugnaire, 2012) and might even change from facilitation to competition across a growing season (Muler et al., 2018; Priyadarshini et al., 2016). Our results demonstrate, that *P. abies* and *F. sylvatica* both can profit from HR in mixture with each other. However, these results should not be transferred into a mature forest easily. It has been shown that rooting depths and therefore access to water resources vary in mixed *P. abies*—*F. sylvatica* stands. While *P. abies* roots are predominantly present in shallow soil layers, roots of *F. sylvatica* tend to grow deeper, in particular in mixture (Goisser et al., 2016; Schmid & Kazda, 2001; Zwetsloot, Goebel, Paya, Grams, & Bauerle, 2019). Therefore, *F. sylvatica* may redistribute more water to the benefit of *P. abies* trees than vice versa. Both species may co-habit with *Q. robur* that develops a tap root, capable of lifting deep soil water (Zapater et al., 2011). Also *P. menziesii* saplings can profit from HR by neighbouring mature *P. menziesii* trees (Brooks, Meinzer, Warren, Domec, & Coulombe, 2006; Nadezhdina et al., 2009) but were observed to grow also well with *F. sylvatica* (Thurm & Pretzsch, 2016). Hydraulic redistribution may be part of this facilitative mixed-species interaction. Occurrence and seasonality of HR in grown mixed-species forest should be further investigated to estimate the relevance of water redistribution for different species in mixture under field conditions.

4.3 | Conclusions

All observed species benefited from HR, either by refilling water storages or for transpiration, irrespective of growing in mixture or in single-specific SRS. Rooting patterns, especially root proximity between same and different species need to be investigated as close proximity and even direct contact might have an important influence on the amount of HR water neighbouring trees take up. Our results support the assumption that HR may be an important mechanism for forest growth and stability (Ammer et al., 2018; Pretzsch et al., 2014). This may be true in particular among species with different rooting depths, where one species redistributes water from moist soil layers that another species may not reach with its root system. The actual relevance of HR in temperate forests needs to be tested to determine to what extent the considerable benefit, found in this study, also translates into the field. The importance of HR will likely increase as a mechanism to improve drought resistance of temperate forests, especially when water limitations become more frequent under ongoing climate change.

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CONFLICT OF INTEREST

All authors declare that they have no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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