Received: 14 August 2023 | Revised: 5 January 2024 | Accepted: 21 February 2024

DOI: 10.1002/eco.2641

RESEARCH ARTICLE

WILEY

Isotopic evidence for seasonal water sources in tree xylem and forest soils

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Funding information
Waldlabor Project Grant, Grant/Award Number: 4.20.P01

Abstract

Forest trees greatly influence both the routing of water downward into the subsurface and the re-routing of water upward through water uptake and transpiration. To reveal how the subsurface soil water pools used by trees change across seasons, we analysed 2 years of stable isotope ratios of precipitation, soil water from different depths (using both bulk sampling and suction-cup lysimeters), and xylem in a mixed beech and spruce forest. Precipitation as well as mobile and bulk soil waters all showed a distinct seasonal signature; the seasonal amplitude decreased with depth, and mobile soil waters fluctuated less than bulk soil waters. Xylem water signatures in both tree species were similar to the bulk soil water signatures and rather different from the mobile soil water signatures. The beech and spruce trees had different isotope ratios, suggesting the use of different water sources, and these differences were larger under dry antecedent conditions than wet antecedent conditions. Despite these differences, both species predominantly transpired waters with a winter-precipitation isotopic signature throughout the summer, including during wet conditions when more recent precipitation was available. Over most of the sampling dates, the fraction of recent precipitation (i.e. from the preceding 30 days) in xylem water was low, despite both species typically demonstrating the use of both shallow and deeper soil waters. These results provide evidence that the soil water storages used by these trees are largely filled in winter and bypassed by recent precipitation, implying long residence times.

KEYWORDS
end-member mixing, forest water cycle, new water fractions, seasonality, soil water, stable water isotopes, tree water sources, tree water uptake

1 | INTRODUCTION

Plants drive water cycling at local to global scales, with their uptake from subsurface water storages accounting for the majority of terrestrial evapotranspiration (Nelson et al., 2020). Understanding the dynamics of how these plant-available subsurface water storages are recharged and extracted can improve our ability to predict transpiration fluxes and drought vulnerability. Stable isotope ratios of water are widely used to identify water sources to plants (White, 1989), and the combined use of plant and soil water isotope data has revealed useful (and sometimes counterintuitive) findings concerning plant–soil–water interactions (Kirchner et al., 2023). For example, Dawson and Ehleringer (1991) found that the xylem signature of riparian trees was different from that of streamflow, suggesting that some trees use soil water held in tension even when streamwater is available. Brooks et al. (2010) showed that infiltrating precipitation can pass through soils and reach streams with apparently little mixing with the stored water that supplies trees. Isotope measurements by Allen, Kirchner, et al. (2019) and Allen, von Freyberg, et al. (2019) imply that recent precipitation can reach streams even when soil water deficits exist, and that trees can access water from previous seasons even when more recent water should be available. Such processes generally conflict with conceptual models in which new inputs refill antecedent deficits, rather than bypassing those water-depleted storages. Our study builds on such findings, seeking to understand how such hydrologic behaviour occurs, when and where it is expected to occur, and what implications it has for precipitation inputs supplying transpiration.

Seasonal signals in precipitation, with isotopically heavier precipitation in summer and lighter precipitation in winter, allow us to track the relative abundance of precipitation from each season in groundwaters (Jasechko, 2019; Jasechko et al., 2014), streamflow (Allen, von Freyberg, et al., 2019) and plants (Allen, Kirchner, et al., 2019; Goldsmith et al., 2022; Martin et al., 2018; Sprenger et al., 2022). Soils carry the isotopic signature of many previous precipitation events in any given layer, and trees may take up water from multiple soil layers in different proportions (Warren et al., 2007). Despite this mixing, greater reliance on one seasons' precipitation versus another can be observed. These observations have been made both in regions with dry growing seasons (Brooks et al., 2010; Rempe & Dietrich, 2018) and in regions with year-round precipitation (Allen, Kirchner, et al., 2019; Goldsmith et al., 2022;). However, an important unknown is how new precipitation inputs (precipitation that is 'new' since the last sampling) are used (or not used) by forest trees. Shifts in water uptake depths during water limitations have been observed for crops and trees (Rothfuss & Javaux, 2017; Sun et al., 2022). But what happens when dry periods are interrupted by new precipitation inputs? Is there a rapid shift in sources to favour the use of those new inputs?

Here we use a 2-year dataset of precipitation, soil water and xylem water isotopes to identify how trees' water sources vary across seasons and wetness conditions. Our analysis focusses on two widespread species in Europe, Norway spruce (*Picea abies*) and European beech (*Fagus sylvatica*), which account for 44% and 18% of the total Swiss forest inventory. Using these data, we address the following research questions:

1. What soil water sources are being used by forest trees? This is assessed by comparing isotopic signals in xylem water to those of precipitation, mobile soil waters and bulk soil waters across the whole observation period and for single sampling dates.
2. How do seasonal and event precipitation mix with water stored in soils, by depth and across varying antecedent conditions?
3. Does water from specific depths, precipitation from individual events, or precipitation from specific seasons dominate the mixture of water used by trees and, if so, does that dominance vary throughout the year?

2 | STUDY SITE AND METHODS

2.1 | Sampling and data collection

Our WaldLab Forest Experimental Site is a small 0.3 km^2 catchment along a mixed forested hillslope dominated by spruce and beech trees at a mean elevation of 510 m a.s.l. in Zurich, Switzerland (Figures 1 and S1). The site is part of the larger 'Waldlabor' Zürich (www.waldlabor.ch) initiative. The mean annual temperature of the site is 9.3°C, and mean annual precipitation is 1134 mm. Since March 2020, we have measured and sampled various waters along the hillslope: precipitation after each event, bulk and mobile soil waters, as well as beech and spruce (and young spruce) xylem waters. The soil is a luvisol of approximately 100-cm depth on top of $\sim$ 6 m moraine material from the last glacial maximum. The dominant soil structure is silty sand with clay fractions below 10%. The subsurface is unsaturated at all depths down to at least 7 m.

Major climate parameters are recorded outside the forest with a compact all-in-one weather station (Atmos41, METER Group, Inc.) at 10-min resolution approximately 150 m outside the forest. At the same location, we also collected precipitation samples for isotope analysis with a funnel into a glass bottle through a syringe to avoid evaporation as described in von Freyberg, Allen, et al. (2020). Bottles were emptied after each event larger 3 mm, typically on the same day or the morning of the next day. Only five out of the 175 precipitation events in the observation period (1 April 2020 through 31 March 2022) were snowfall events. We sampled mobile soil water (the fraction of soil water that has no direct surface contact with the soil grains, thus is held cohesively and can move freely) and bulk soil water (including the fraction of soil water that is stored in hydration spheres of clay minerals or held tightly inside the capillary spaces). We sampled mobile soil water (SW_{mobile}) at 10-, 20-, 40- and 80-cm depths at two sites (Figure 1) with suction lysimeters (Slim Tube Soil Water Sampler, Soil Moisture Equipment Corp). We applied a suction of 0.7 bar on Mondays and Thursdays and emptied the samplers twice a week on the following Thursdays and Mondays. In addition, we sampled bulk soil (SW_{bulk}) at two locations (Figure 1) at 10, 20, 40 and 80 cm depths with a 2-cm wide auger every 3 weeks and extracted the bulk soil water cryogenically. However, we began sampling mobile and bulk soil water at 80 cm only in June 2021. On 19 sampling dates, roughly every 3 weeks from July 2020 through the end of October 2021, we sampled beech (two branches each from three to four trees, resulting in $n = 119$ samples), spruce (one to two branches from two trees, resulting in $n = 57$) and young spruce (one to two branches from two trees, resulting in $n = 70$), by cutting branches for cryogenic water extraction. Samples were collected around midday; the branches were collected based on accessibility from the ground, but the relatively low sampling elevation (up to a maximum of 8 m) is still expected to be representative (see Bernhard et al., 2023, where we showed that uncertainties regarding the sampling height are small at a close-by site). Immediately after cutting the branches, bark and phloem were peeled off and the remaining wood was placed in

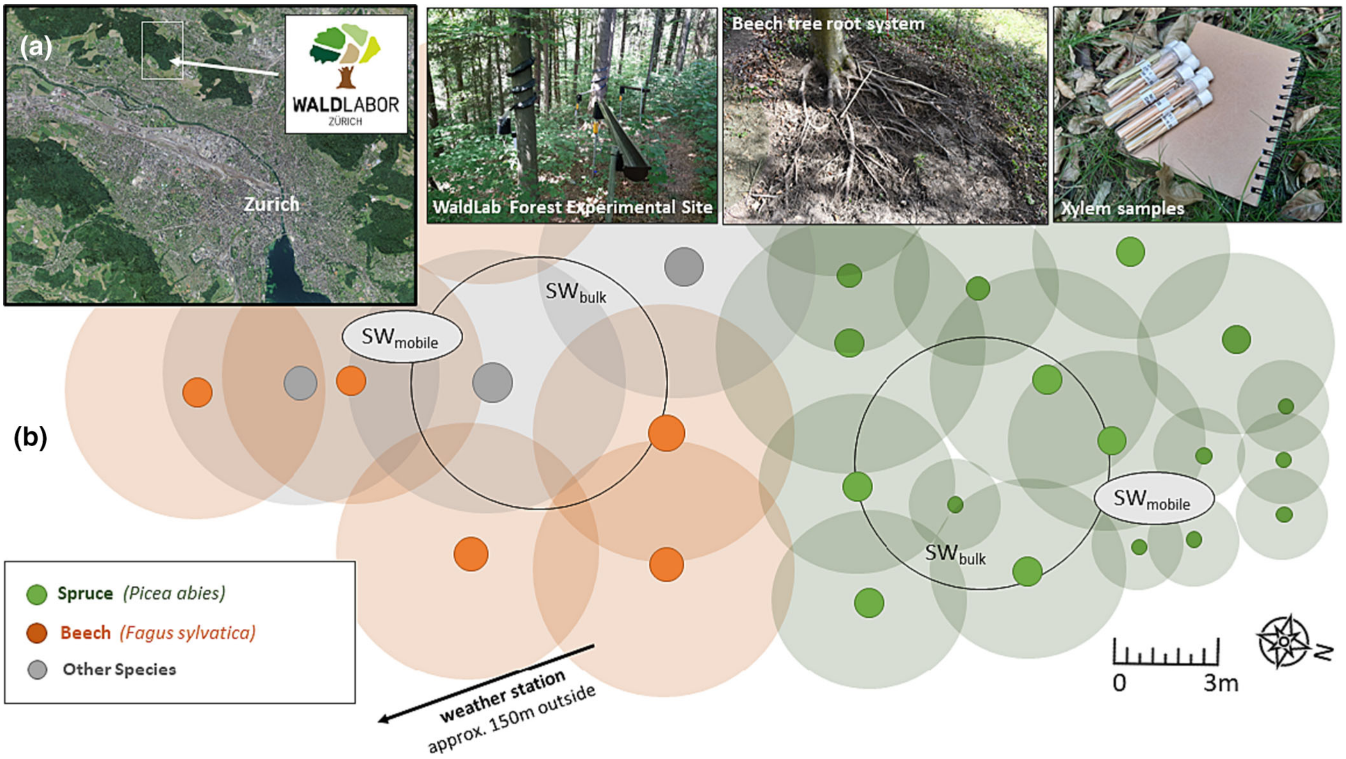


FIGURE 1 (a) Location of the WaldLab Forest experimental site study site in Zurich, Switzerland, scheme of the tree locations as well as the (b) locations of mobile (SW_{mobile}) and bulk (SW_{bulk}) soil water sampling. Precipitation for isotope analysis was sampled outside the forest perimeter at the weather station, at approximately 150-m distance from the site.

exetainers (12 mL Exetainer, Labco Ltd., Ceredigion, UK). Both the xylem and bulk soil samples were stored in those containers at -18°C until extraction. Cryogenic vacuum distillation was performed in the Institute of Agricultural Sciences stable isotope lab at ETH Zurich, using the equipment and protocol described in Sun et al. (2022).

The ^{18}O and ^{2}H isotopic composition of xylem water isotopes was analysed with a high-temperature–conversion elemental analyser (TC/EA) connected to a Delta Plus XP isotope ratio mass spectrometer via a ConFlo III interface (Thermo Fisher Scientific, Bremen, Germany). All other samples (precipitation and soil waters) were analysed with a triple isotope water analyser (Los Gatos – TIWA-45-EP). Both instruments are reported to have precisions of 1 ‰ for δ^{2}H and 0.2 ‰ for δ^{18}O.

2.2 | Isotope data evaluation and the seasonality index

We present the data in time series in δ notation in per-mil units (‰) relative to V-SMOW (Vienna Standard Mean Ocean Water). We focus on δ^{2}H, although figures using δ^{18}O data can be found in the supplement and in dual isotope plots. The local meteoric water line (LMWL) in the dual isotope plot is calculated by reduced major axis regression (described in Harper, 2016) instead of linear regression. This approach is used because classic linear regression assumes that the *x*-axis has no error/uncertainty, but in the case of a dual isotope plot, there is uncertainty on both axes.

To assess the seasonality of waters, we use the seasonal origin index (SOI), introduced and described in Allen, Kirchner, et al. (2019):

$$\mathrm{SOI} = \begin{cases} \frac{\delta_x - \delta_{\text{annP}}}{\delta_{\text{summerP}} - \delta_{\text{annP}}}, \text{if } \delta_x > \delta_{\text{annP}} \\ \frac{\delta_x - \delta_{\text{annP}}}{\delta_{\text{annP}} - \delta_{\text{winterP}}}, \text{if } \delta_x < \delta_{\text{annP}} \end{cases}, \qquad \text{(Equation1)}$$

The SOI expresses the isotopic signature of soil and xylem water (δ_x) relative to the seasonal cycle of precipitation, using amount-weighted annual precipitation (δ_{annP}), summer precipitation (δ_{summerP}, defined as the peak of a fitted sine curve representing seasonal cycles of precipitation), and winter precipitation (δ_{winterP}, defined as the trough of the same fitted sine curve). A SOI close to -1.0 indicates that the water mostly originates from winter precipitation, whereas a SOI close to 1.0 indicates that the water mostly originates from summer precipitation.

To analyse how much of xylem water is composed of recent precipitation (i.e. precipitation falling between each pair of xylem sampling dates), we calculated the fraction of new water (F_{new}) as suggested in Kirchner (2019):

$$F_{\text{new}} = \frac{\delta xyl_i - \delta xyl_{i-1}}{\delta P - \delta xyl_{i-1}} \qquad (2)$$

where δxyl_i is the xylem water signature of the most recent sampling date, δxyl_{i-1} is the xylem water signature of the previous sampling date, and δP is the volume-weighted average of precipitation between the two sampling dates (typically 3-week intervals).

To assess the fractions of xylem water for each sampling date ($Xyl_{[t=2]}$) consisting of bulk soil waters and recent precipitation, we used a simple mixing model that calculates the relative contribution of two different sources ($f1$ and $f2$):

$$Xyl_{(t=2)} = f1^{*}\, bulksoil_{(t=1)} + f2^{*}\, P_{(t1 \geq t2)} \qquad (3)$$

where $bulksoil_{(t=1)}$ is the isotopic composition of water in the bulk soil at the previous timestep and $P_{(t1 \geq t2)}$ is the volume weighed isotopic composition of precipitation that fell between the previous and most recent xylem sampling dates (typically the last 3 weeks).

3 | RESULTS AND DISCUSSION

3.1 | Isotopic variation of precipitation, soil waters and xylem water

From April 2020 to March 2022, we observed seasonal cycles in isotope ratios (shown for δ^2H in Figure 2 and for δ^{18}O in Figure S2) in incoming precipitation that corresponded with transitions between summer and winter seasons. Isotope ratios were lighter in winter and heavier in summer, with volume-weighted annual precipitation δ^2H averaging −63.9 ‰ (and δ^{18}O averaging −9.5 ‰), as shown by the dashed lines in Figure 2b–d. Mixtures of precipitation in soil or plants that lie above that line (Figure 2) contain more summer precipitation than annual precipitation does (i.e. summer precipitation is over-represented in those soil and xylem samples), and mixtures below that line contain more winter precipitation than annual precipitation does (i.e. winter precipitation is over-represented in those soil and xylem samples).

Mobile and bulk soil waters showed a seasonal cycle in δ^{18}O, similar to that of precipitation but with a dampened amplitude (Figures 2c,d); however, the beech, spruce and young spruce samples did not show a clear seasonal cycle (Figures 2b and S1b). Readers should note that several of the collection dates occurred during the dormant season for beech, during which some of the highest and most variable xylem δ^2H values were observed. Overall, most of the bulk soil samples plotted below the mean precipitation line, indicating that they over-represent winter precipitation; in contrast, the mobile soil water samples were quite evenly distributed around the mean precipitation signatures, suggesting that they, on average, reflect a less directionally biased mixture of precipitation. The mean mobile soil water δ^2H (−64.8 ± 0.5 ‰, mean ± standard error) was similar to the mean annual precipitation δ^2H (−63.9 ± 2.5 ‰), whereas the mean bulk soil water δ^2H was substantially lighter (−79.2 ± 0.7 ‰). Given the consistency among soil water samplers and close tracking of precipitation fluctuations, mobile soil waters seemed to reflect recent precipitation more than bulk soil waters did.

3.2 | Event-based evaluation of isotope signatures in precipitation, soil and xylem waters

We calculated the fraction of recent precipitation (precipitation from the preceding 30 days – further on called 'new' precipitation or F_{new}) that can be found in the xylem waters of beech, spruce and young spruce (Figure 3). For beech δ^2H, only 6 out of 19 sampling dates showed the xylem water to be composed of more than 30% new precipitation; for spruce and young spruce, those values were 5 and 2 out of 19 sampling dates, respectively. Higher values of F_{new} occurred during fall and spring (i.e. during September through November and April through June); at other sampling dates, xylem signatures in beech, spruce and young spruce mostly showed no detectable influence by recent precipitation.

We used a simple mixing model to calculate how much precipitation water vs. bulk soil water across all soil depths (10, 20, 40 and 80 cm), shallow bulk soil water (10 and 20 cm) and deep bulk soil water (40 and 80 cm) can be found in the xylem waters of beech, spruce and young spruce (Figure 4). We excluded results for beech during the dormant season (November to April), as beech are not actively transpiring, and xylem signatures are more likely to represent enrichment of waters stored in the stem. We found that for many of the xylem sampling dates, beech, spruce and young spruce xylem contained a mixture of soil waters rather than recent precipitation (grey bars in Figure 4a, c, and e). More explicitly, xylem water δ^2H lay between the δ^2H of shallow and deep bulk soil water (i.e. 6, 10 and 12 times out of 19 samplings for beech, spruce and young spruce; see Table 1). Only a few xylem samples carried the signature of soil layers shallower than 20 cm (1, 2, and 0 times for beech, spruce and young spruce); beech xylem samples carried the signature of soil layers deeper than 40 cm on 5 out of 19 sampling dates. However, during fall and spring (i.e. April, May, September, October, and November; see Table 1), xylem signatures were closer to recent precipitation than soil water, suggesting that these samples were dominated by recent precipitation (2, 4 and 4 times for beech, spruce and young spruce). Xylem waters were enriched in heavy isotopes during December and February, yielding isotope signatures that were much heavier than the waters found in the soil (10 to 40 cm) or recent precipitation. This is expected because during times when trees are not using water, evaporative enrichment in the stem will lead to heavier isotopic signatures (marked in orange in Table 1).

We examined one xylem sampling date (27 July 2021) in the peak growing season in more detail to highlight the importance of winter precipitation for soil water storage and tree water uptake (Figure 5). We here show data for 27 July 2021 as this date represents the peak growing season without major water limitations; similar results for all sampling dates are shown in Figure S4. Xylem and bulk soil waters were isotopically similar, whereas most precipitation during the preceding three summer months (April through June; yellow boxplots) was isotopically heavier. Thus, the major source of xylem water in the peak growing season of 2021 was a mixture of stored soil waters from previous months and seasons, so it is important to clarify the relative

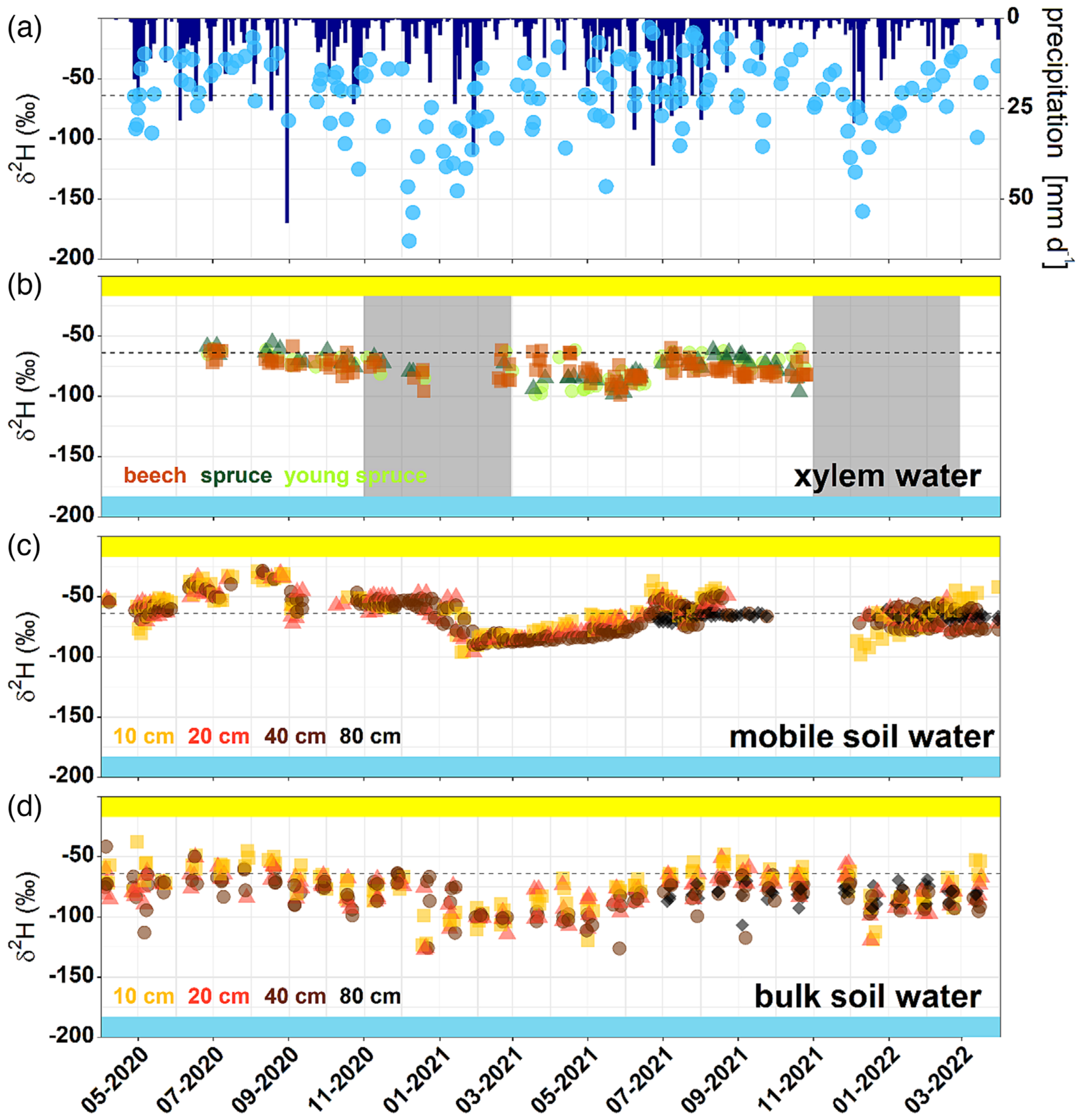
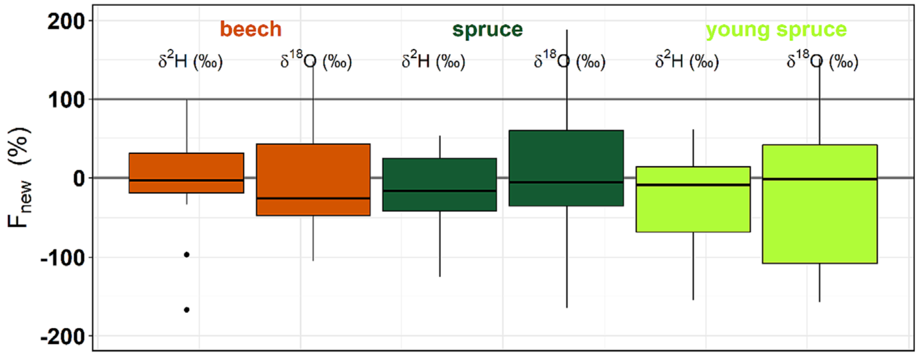


FIGURE 2 (a) Time series of precipitation rate and δ^2H isotopic composition, (b) xylem water isotopic composition in beech, spruce and young spruce trees, and (c) mobile and (d) bulk soil water isotopic composition at 10-, 20-, 40- and 80-cm depth from April 2020 until March 2022. We show time series of δ^2H; similar results for δ^{18}O are shown in Figure S2. The yellow and blue lines indicate summer and winter precipitation signatures, respectively. Grey shadings in Figure 2b indicate the dormant season (from November to March).

FIGURE 3 Fraction of new precipitation (from the 30 days preceding the xylem water sampling date – F_{new}) found in xylem water of beech (orange), spruce (dark green) and young spruce (light green) as calculated from δ^2H and δ^{18}O.



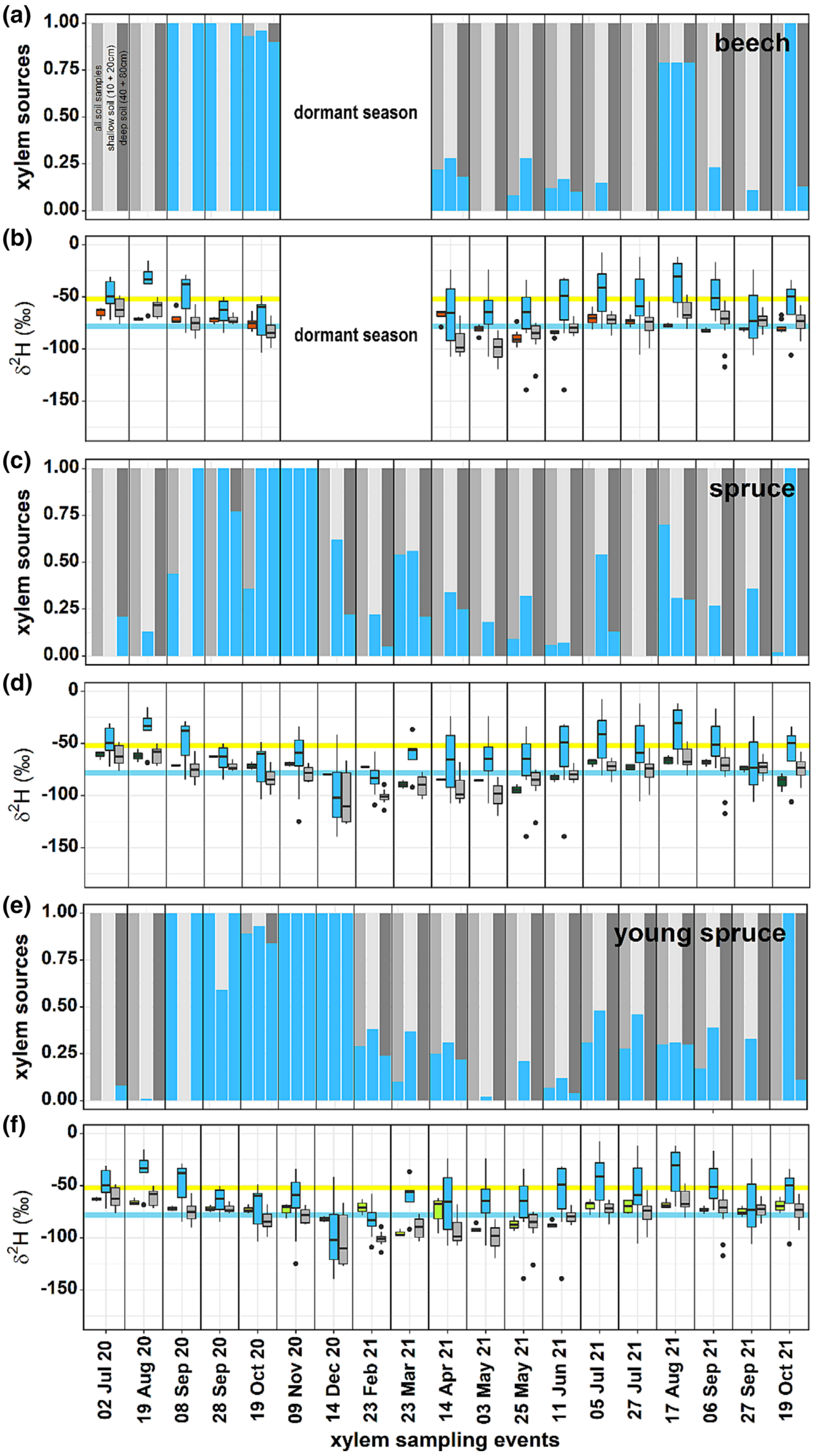


FIGURE 4 Results of mixing calculations assessing the mixture of water from recent precipitation (from the last 30 days before sampling, shown in light blue) and bulk soil water (sampled at the day of xylem sampling) for all depths (in grey), shallow soil water (10 and 20 cm, in light grey) and deep soil water (40 and 80 cm, in dark grey) for (a) beech, (c) spruce (c) and (e) young spruce. Distributions of isotope ratios in xylem, precipitation and bulk soil water samples for each sampling date for (b) beech, (d) spruce and (f) young spruce (f). The coloured lines indicate the mean precipitation signatures for summer and winter precipitation in light blue and yellow, respectively. Dual isotope plots showing the distribution of the isotopic signals in mobile and bulk soil waters compared to those in xylem waters can be found in Figure S5.

importance of winter and summer precipitation as sources for soil water storage.

Results from the mixing model suggest that beech trees typically used deeper water sources than spruce (and young spruce), which is in line with the expected differences in their rooting depths. While beech trees have heart roots, with most roots occupying the top 40 cm, spruce species have distributed roots in the shallow soil up to around 25 cm (Schmid & Kazda, 2002). Previous studies found that

TABLE 1 Mean δ^2H isotopic composition of precipitation in the 30 days preceding the xylem sampling (P) of bulk soil water in the shallow soil (soil$_{shal}$ – 10 and 20 cm) and deep soil (soil$_{deep}$ – 40 to 80 cm), as well as in beech, spruce and young spruce xylem, with a qualitative assessment of the likely main water sources found in xylem waters. Please note that bulk soil sampling at 80 cm only started on 5 July 2021.

Date	P δ^2H_{mean}	Soil$_{shal}$ δ^2H_{mean}	Soil$_{deep}$ δ^2H_{mean}	Beech δ^2H_{mean}	Beech qualitative assessment	Spruce δ^2H_{mean}	Spruce qualitative assessment $_n$	Young spruce δ^2H_{mean}	Young spruce qualitative assessment
02 Jul	−48.08	−59.81	−64.13	−64.98	**Deeper than 40 cm**	−60.83	Between shallow and deep	−62.80	Between shallow and deep
19 Aug	−32.80	−56.90	−68.12	−71.23	**Deeper than 40 cm**	−61.97	Between shallow and deep	−65.76	Between shallow and deep
08 Sep	−67.26	−71.53	−83.48	−69.93	Between 10 and 20 cm	−70.95	Between 10 and 20 cm	−72.05	Between shallow and deep
28 Sep	−77.42	−70.80	−74.15	−72.27	Between shallow and deep	−62.28	More recent Precipitation	−72.19	Between shallow and deep
19 Oct	−72.18	−79.70	−89.75	−75.68	More recent Precipitation	−71.86	More recent Precipitation	−72.99	More recent Precipitation
09 Nov	−72.08	−80.16	−75.89	−72.87	Dormant season	−69.78	More recent Precipitation	−73.32	More recent Precipitation
14 Dec	*−128.35*	*−100.76*	*−99.12*	−84.77	Dormant season	*−79.56*	*Evaporative enrichment*	*−82.18*	*Evaporative enrichment*
23 Feb	*−78.17*	*−100.94*	*−101.63*	−78.60	Dormant season	*−72.59*	*Evaporative enrichment*	*−70.82*	*Evaporative enrichment*
23 Mar	−62.16	−87.06	−99.39	−70.44	Dormant season	−89.37	Between shallow and deep	−89.37	Between shallow and deep
14 Apr	−75.39	−88.67	−101.11	−68.00	Dormant season	−84.53	Between 10 and 20 cm	−75.04	More recent Precipitation
03 May	−73.39	−96.03	−104.10	−81.49	More recent Precipitation	−85.47	More recent Precipitation	−90.89	More recent Precipitation
25 May	−58.90	−82.10	−97.40	−89.22	Between shallow and deep	−94.16	Between shallow and deep	−87.01	Between shallow and deep
11 Jun	−51.52	−77.68	−83.21	−84.38	**Deeper than 40 cm**	−82.53	Between shallow and deep	−87.69	**Deeper than 40 cm**
05 Jul	−39.41	−67.28	−78.49	−70.79	Between shallow and deep	−68.31	Between shallow and deep	−69.44	Between shallow and deep
27 Jul	−57.19	−68.13	−81.88	−73.58	Between shallow and deep	−72.81	Between shallow and deep	−70.16	Between shallow and deep
17 Aug	−52.87	−58.36	−73.65	−77.57	**Deeper than 40 cm**	−66.11	Between shallow and deep	−68.06	Between shallow and deep
06 Sep	−42.41	−63.81	−83.72	−82.29	Between shallow and deep	−68.05	Between shallow and deep	−73.07	Between shallow and deep
27 Sep	−57.33	−68.47	−77.89	−80.93	**Deeper than 40 cm**	−74.18	Between shallow and deep	−74.93	Between shallow and deep
19 Oct	−58.91	−68.43	−80.08	−69.17	Between shallow and deep	−81.79	**Deeper than 40 cm**	−69.17	Between shallow and deep

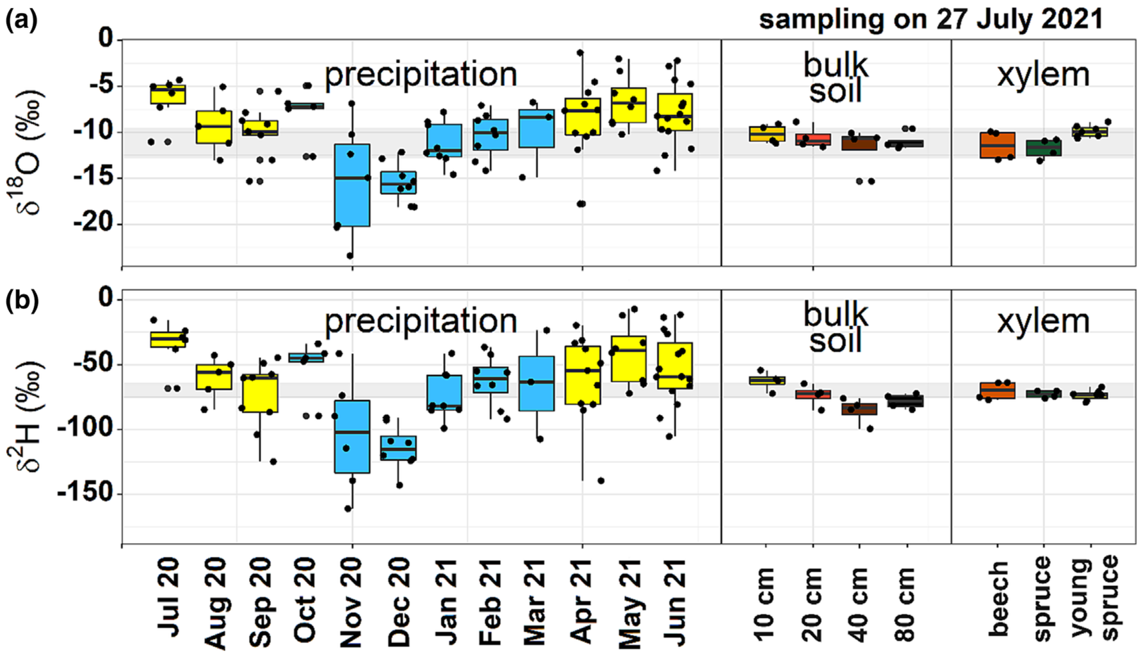


FIGURE 5 Isotope signature of precipitation in the 12 months prior to the bulk soil (from left to right: 10, 20, 40 and 80 cm) and xylem sampling (from left to right: beech, spruce, young spruce) on 27 July 2021 for (a) ^{18}O and (b) ^{2}H. The blue and yellow boxes indicate winter and summer precipitation, respectively. The boxplots (here and in all upcoming dual isotope plots) indicate the interquartile range for each species; the line indicates the median. The points surrounding the boxplots indicate the single measurements; the grey horizontal bar in the background marks the interquartile range of xylem isotope signatures across all three species.

beech took up waters from deeper layers (Meißner et al., 2012), especially when water closer to the surface was limited (Brinkmann et al., 2019). However, caution is warranted as there are other factors that may complicate interpretation of such data. For example, in mixed beech and spruce plots, root development and spatial distribution of roots were different than at sites where only beech grew, even in places where water resources were typically not limited (Cahill et al., 2010; Schmid et al., 2015). So at our site where beech and spruce coexist, we would expect that their root systems occupy separate soil layers to avoid competition for water resources (Meißner et al., 2012). Although we found that that root water uptake depths were quite similar for both beech and spruce (see Table 1 and results in Martinetti et al., 2023), differences between the two species exist. Spruce took up water from shallower layers, which is in line with the spruce water uptake depth of 10 to 20 cm reported by Bishop and Dambrine (1995).

3.3 | Seasonality of precipitation, soil and xylem waters

We separately examined the data from each of the winter and the summer halves of the years, November through April and May through October, respectively. We excluded dormant-season beech xylem signatures, because these are likely to reflect stem evaporative enrichment rather than the source waters. Figure 6 shows that the xylem signatures of beech (in summer) and spruce and young spruce (in both winter and summer) resembled winter precipitation. This is also confirmed by the non-significant differences between winter precipitation and xylem waters as calculated from Mann–Whitney *U* tests (Table 2). Xylem waters were isotopically much lighter than summer precipitation, implying that throughout the year, tree xylem at our site mostly contained winter precipitation, despite Zurich typically receiving more precipitation during the summer months than during the winter months. During our 2-year observation period, the total volume of precipitation falling during summer (May through October) was twice the volume of precipitation falling during winter (November through April).

We calculated the SOI (Allen, Kirchner, et al., 2019) for all xylem samples (beech, spruce and young spruce) and the mobile and bulk soil water samples. Figure 7 shows the distribution of SOI for the summer half of the year (May through October, in colours) and the winter half of the year (November through April, in grey). Most xylem isotope samples (Figure 7a–c) had an SOI < 0, indicating that they are mixtures dominated by winter precipitation.

SOI values for mobile soil water in winter and summer showed distinct variation across the different depths. At 10-, 20-, and 40-cm depths, most summer soil water had SOI > 0 (indicating a predominantly summer source), whereas winter soil water was a mixture dominated by winter sources. The fraction of samples with SOI < 0 increased with depth, with winter soil waters at 40 cm mostly having SOI < 0. At 80 cm, mobile soil waters sampled in both winter and

FIGURE 6 Dual-isotope plot for tree xylem (beech, spruce, and young spruce shown by orange, dark green, and light green, respectively) and summer versus winter precipitation (light and dark blue, respectively). Boxplots show distributions of isotopic signals in precipitation and xylem waters for winter (November through April) and summer (May through October). The xylem water signatures in both winter and summer are more consistent with winter precipitation. Winter xylem isotopes are not shown for beech because beech does not actively transpire during winter. The black line indicates the local meteoric water line (LMWL) fitted to all precipitation data in the observation period by reduced major axis regression.

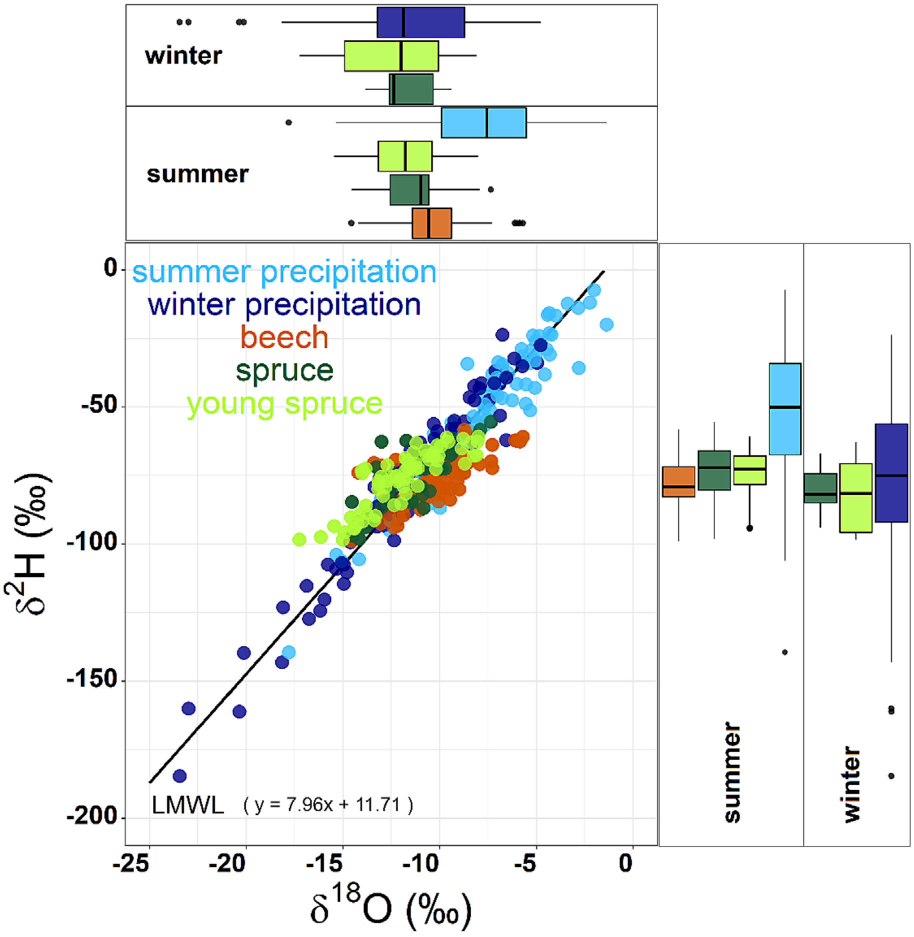


TABLE 2 Mann–Whitney *U* tests comparing isotopic signals in beech, spruce and young spruce xylem water versus winter and summer precipitation.

	Beech		Spruce		Young spruce	
P	δ^{18}O	δ^{2}H	δ^{18}O	δ^{2}H	δ^{18}O	δ^{2}H
Summer	***	***	***	***	***	***
Winter	**	*ns*	*ns*	*ns*	*ns*	*ns*

Note: *ns*, non-significant.
*******p*-value 0.001–0.05.
********p*-value < 0.001.

summer were well mixed between winter and summer precipitation (based on less than 1 year of samples because sampling at this depth only started in June 2021).

Bulk soil waters in summer at 10 cm depth were almost evenly distributed around SOI = 0, with larger fractions of winter precipitation with increasing depth. However, in the winter half of the year (and for both winter and summer soil water samples at 80-cm depth), most bulk soil water samples were predominantly composed of winter precipitation (with the most samples with SOI > 0 at 10-cm depth).

Looking at the overall seasonality signals in xylem waters (Figures 6), we found temporal disconnections between the water in xylem and precipitation, that is, the beech and spruce forest trees contained winter precipitation throughout the year. This has been shown across Switzerland in previous work by Allen, Kirchner, et al. (2019) and Goldsmith et al. (2022), but those studies were based on snapshot sampling dates in summer, whereas our study shows that these observations may also hold across the year (Figures 6 and 7). Although our site typically receives more precipitation during the summer months than during the winter months (ratio of approximately 67% to 33% for May through October and November through April, respectively, for our 2-year observation period), soils were typically drier during the summer months. This presumably reflects a greater fraction of summer precipitation being evaporated back to the atmosphere and thus never reaching the deeper soil layers where it would be available for forest trees (i.e. deeper than 10 cm). Also in summer, water in the top layer might be consumed by forest floor vegetation (i.e. shrubs and grasses) that roots in the upper layers of the soil.

A second potential explanation for the relative scarcity of summer precipitation in summer xylem samples might be interception processes in the forest canopy and the forest-floor litter layer. The fraction of summer precipitation that is available for trees for water uptake may be very small due to canopy and forest floor interception, which may be reducing soil water recharge by ~40% (Floriancic et al., 2022; Gerrits et al., 2010) compared to what it would have

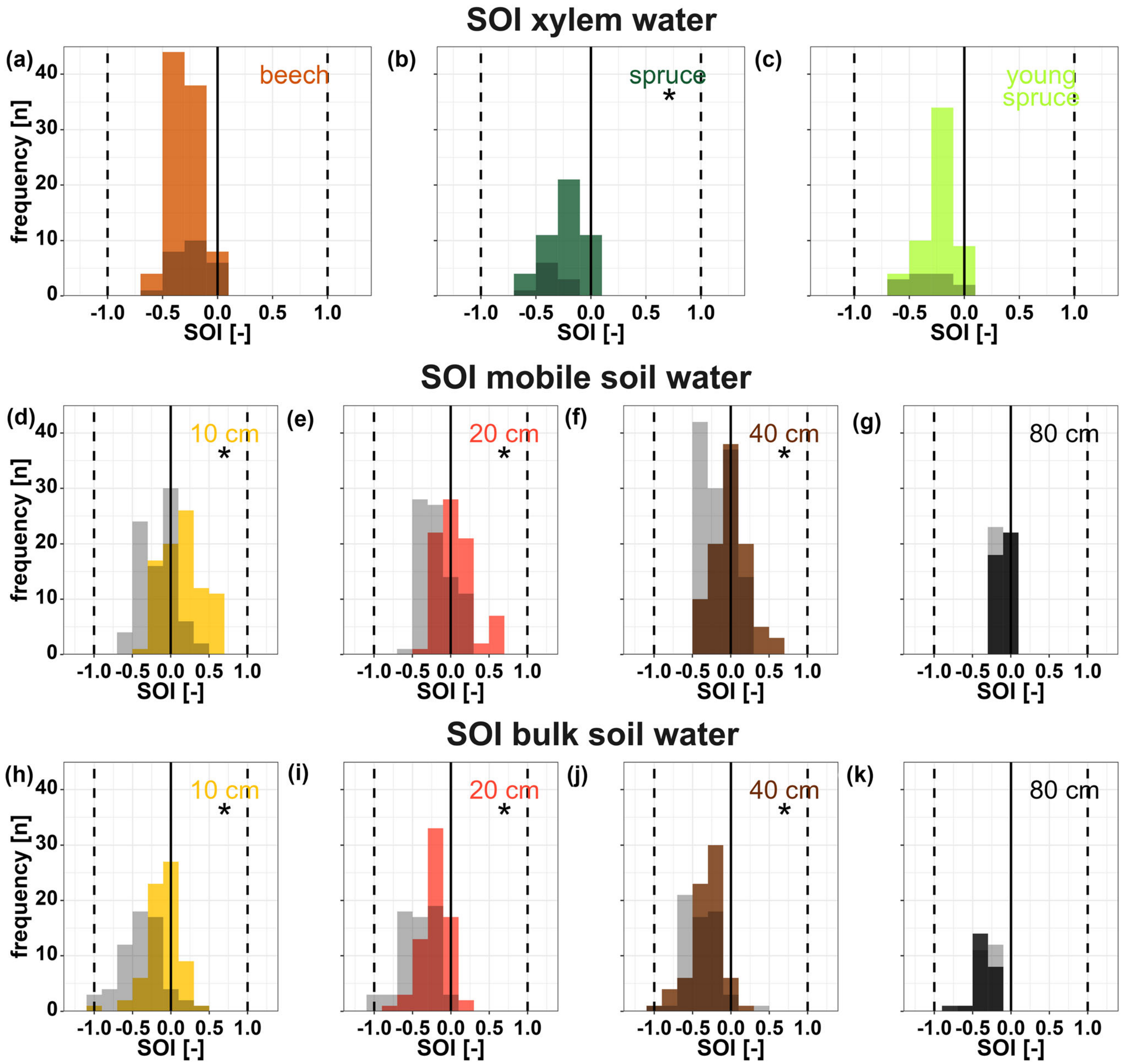


FIGURE 7 Frequency distribution of the seasonal origin index (SOI) for (a) beech, (b) spruce and (c) young spruce xylem (upper row), mobile soil waters at (d) 10, (e) 20, (f) 40 and (g) 80 cm (middle row), and bulk soil waters at (h) 10, (i) 20, (j) 40 and (k) 80 cm (bottom row). The coloured bars indicate the distribution for the summer half of the year (May through October); the grey bars indicate the distribution for the winter half of the year (November through April). Asterisks indicate that there are significant ($p < 0.05$, *t*-test) differences between SOI in summer and winter.

otherwise been; much of the remainder may also be evaporated from soils or taken up by understory plants before reaching tree roots. Overall, we recorded an average of 306 mm of precipitation in the summer months (May through October), from which we assume that only around 60% or 183 mm are reaching the forest soils (see, Floriancic et al., 2022). Thus, the net precipitation remaining accessible to tree roots following other evaporation processes may explain why winter precipitation dominates tree water sources even if it accounts for less than half of annual precipitation. Indeed, Figure 2d shows that bulk soils deeper than 10–20 cm rarely show summer-like precipitation signatures, even in summer; however, this evidence does not clarify whether the first or second potential reason is more relevant. Although soil texture might play an important role in the storage capacities of soils, similar seasonality signals across larger scales; that is, studies covering a large variety of soil types (Allen, Kirchner, et al., 2019; Goldsmith et al., 2022) indicate that the dominance of winter precipitation is more likely to be related to a lack of summer precipitation reaching rooting-depth soils, rather than to soil storage capacities.

Some previous (in situ) isotope studies have documented trees taking up recent precipitation (i.e. summer precipitation in summer months). For example, Gessler et al. (2022) found that a beech tree took up most of its xylem water from the topsoil (filled with recent precipitation), and did not shift water uptake to deeper (most likely older) water pools during dry periods. However, the experiment was carried out during the severe 2018 drought at a single tree outside of a forest, which might not reflect the competition for water that trees experience in a dense forest stand. However, these and similar findings point to the importance of looking at both the seasonal signals in the bulk xylem isotopes and the relationships between precipitation and xylem isotopes during individual sampling dates.

Another reason for the seasonal disconnection between isotope signals in precipitation and xylem lies in the aggregation of the data (i.e. looking at clusters of summer vs. winter isotopic signatures). We saw a seasonal cycle in precipitation isotopes, as evident from Figure 2a, with a significant difference ($p < 0.05$) in both δ^{18}O and δ^{2}H between summer and winter. Distributions of winter and summer precipitation isotopes were still fairly symmetrical (Pearson median skewness between −0.3 and 0.3). However, individual precipitation events occurring during the winter half of the year were isotopically heavier than typical winter precipitation, and individual summer precipitation events were isotopically lighter than typical summer precipitation. This results in partial overlaps between the distributions of summer and winter precipitation isotopes (see Figures 2a and overlap of the boxplots in Figure 6); however the overall effects of this are small, as our results hold looking at both bulked data across 2 years (Figures 6 and 7) and single sampling campaigns (Figure S4). A limitation of SOI analysis is that xylem or soil water values are compared to the mean precipitation isotope ratio which, for a relatively short time series like ours, includes precipitation that has not yet fallen. Thus, it is assumed that the 2-year record represents long-term precipitation, and thus also approximates values of precipitation that fell prior to any collected soil or xylem water samples. While this is a potential source of uncertainty that cannot be quantified, we assume that uncertainty to be small compared to the >8 ‰ δ^{2}H often associated with gridded precipitation isotope products (Allen et al., 2018), which have been the primary source for precipitation end-members in SOI analyses.

3.4 | Seasonality patterns in wet growing seasons

While the summer of 2020 received normal amounts of precipitation, the summer half of the year 2021 was unusually wet, that is, 607 and 752 mm for the summer half precipitation in 2020 and 2021, respectively. Previous studies (Goldsmith et al., 2022; Guo et al., 2018; Williams & Ehleringer, 2000) have reported that discrepancies between summer precipitation and summer xylem waters are smaller in wet years; thus, a wet summer like the one observed in 2021 should have led to more summer precipitation transpired by trees in summer, as a result of greater input of recent precipitation to the soil. We tested this by replotting SOI as shown in Figure 7 for the summer half of the year (May through October) for the wettest half of sampling dates (in colours) and the driest half of sampling dates (in shades), splitting the dataset by precipitation sums in the 30 days prior to xylem and soil sampling (Figure 8). We observed that the differences between the driest and wettest halves of the sampling dates were rather small in xylem water signatures, with mean SOI varying from −0.27 to −0.25, −0.28 to −0.20, and −0.28 to −0.20, for beech, spruce and young spruce, respectively (Figure 8a–c). Similarly, small differences were observed for mobile and bulk soil water SOI: mean SOI across all depths shifted from −0.09 to −0.04 and −0.31 to −0.28 for mobile and bulk soil waters, respectively. Generally, we found that in campaigns with less antecedent precipitation, summer mobile waters contain more summer precipitation, but that trend was minimally apparent in xylem and bulk soil water signatures (Figure 8).

Our results suggest that although mean annual precipitation affects the lag between precipitation seasonality and xylem seasonality (Goldsmith et al., 2022; Guo et al., 2018; Williams & Ehleringer, 2000), antecedent wetness (precipitation in 30 days prior to the sampling dates) appears to have no significant effect (Figure 8). Thus, we hypothesize that overall root structures of the trees at a specific site, which are probably adapted to the average precipitation that a location receives, are dominantly affecting the lag between precipitation seasonality and xylem seasonality. This is supported by a recent study from our site, where Martinetti et al. (2023) showed that during an exceptionally dry summer, tree transpiration was limited although deep roots were not water limited, thus trees could not sustain full transpiration with the root architecture adopted to typical climatic conditions. Short-term (i.e. last 30 days) moisture availability had little effect on the seasonal signals in the xylem; thus, we infer no shifts in the accessed water pools and uptake depths at our site for these two non-drought years. However, this might not hold for exceptionally dry years, as previous studies showed that trees might shift their water uptake depths during water limitations (e.g., Brinkmann et al., 2019; Gartner et al., 2009; Meißner et al., 2012). Another possibility can also be that trees' rooting architectures (especially in moderate climates) are more adapted to the overall soil depth, texture and nutrient availability.

3.5 | Methodological limitations of xylem and soil water signal interpretation

Although we took regular bulk soil samples with an auger, we did not see a change in the bulk soil signal (see Figure 2) resulting from the artificial creation of preferential flow paths through drilling (von Freyberg, Knapp, et al., 2020). Recent studies have pointed to potential extraction bias when using cryogenic vacuum extraction (e.g. Chen et al., 2020). Whereas for bulk soil water extractions, the bias is potentially negligible (Newberry et al., 2017); Chen et al. (2020) clearly documented δ^{2}H offsets in xylem waters. These offsets were attributed to the exchange of ^{2}H in the wood tissue with waters in the xylem. However, in a more recent study, Diao et al. (2022) showed

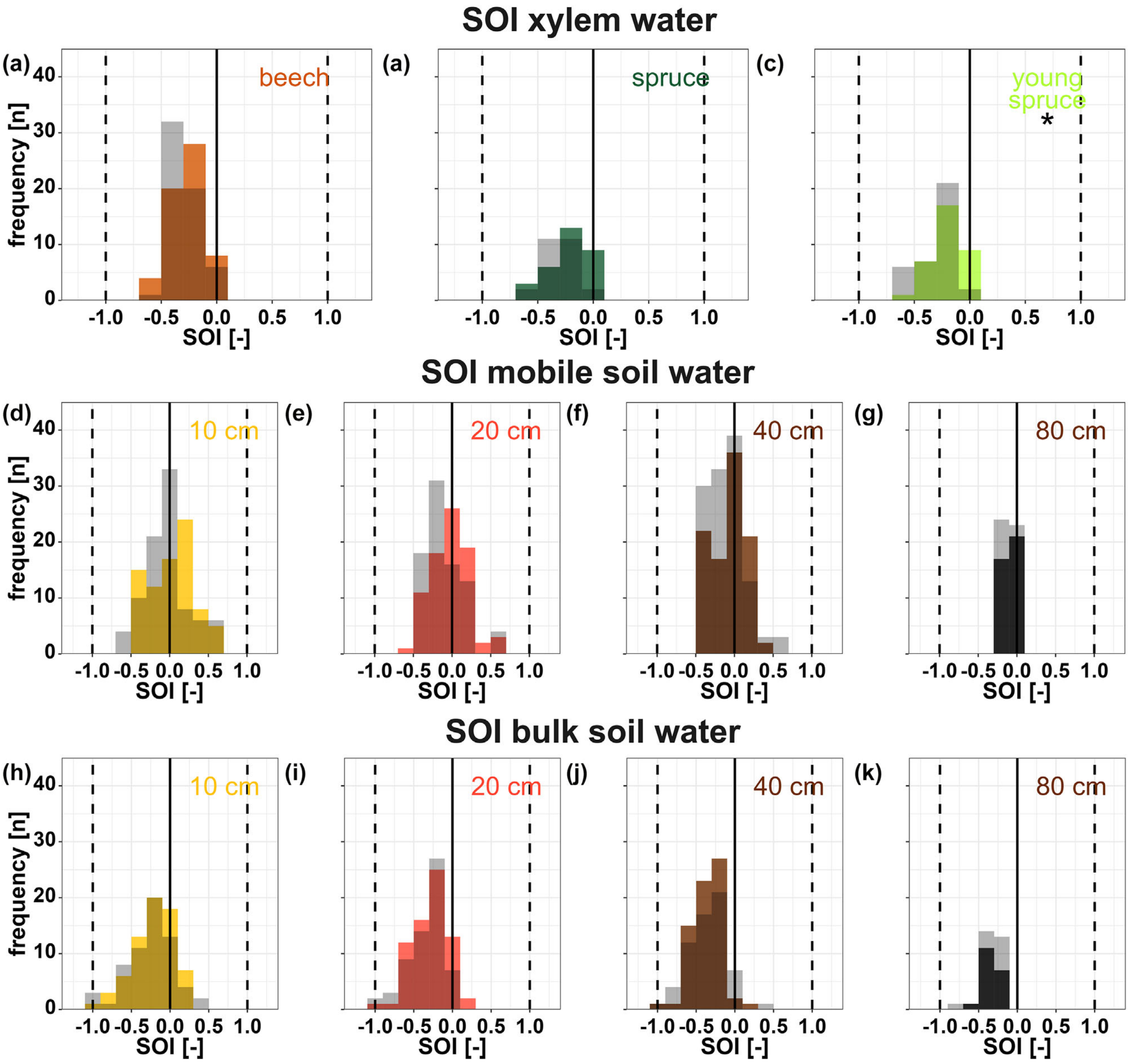


FIGURE 8 Frequency distributions of the seasonal origin index (SOI) for the summer half of the year (May through October) for (a) beech, (b) spruce and (c) young spruce xylem (upper row), mobile soil waters in (d) 10, (e) 20 cm and (f) 40 cm (middle row) and bulk soil waters in (g) 10, (h) 20, (i) 40 cm (bottom row). The coloured and grey bars indicate the distributions for campaigns with low and high antecedent precipitation, respectively, in the 30-day period prior sampling. The asterisk indicates that there are significant differences ($p < 0.05$, t-test) between SOI in dry and wet antecedent conditions.

that these offsets are potentially small when large volumes of water (i.e. > 600 μL) were extracted. This was true for most of the xylem samples (>95%) we presented in the study, where we typically extracted > 1 mL of xylem water. Another effect on the xylem signal can originate from water that is stored in xylem but not actively contributing to transpiration. In a recent study, Barbeta et al. (2022) used a cavitron centrifuge at specific spinning rates to specifically extract sap water from xylem and intra-cellular water stored in the xylem tissue. Barbeta et al. (2022) found that the sap xylem water matched the irrigation water (with no effects of isotopic fractionation during root water uptake), but the water extracted from xylem tissue storage was always depleted in δ^2H; this depletion could potentially also influence our results. However, we calculated the effect of the potential offset by δ^2H depletion, that is, a bias of −6.1 ‰, (Allen & Kirchner, 2022), and found that our major conclusion derived from Figure 6 does not change and forest trees (at our site) were indeed containing a mixture of water dominated by winter precipitation throughout the entire year (see Figure S3). Therefore, our main conclusions are robust against the potential biases introduced by water extraction that have been described elsewhere.

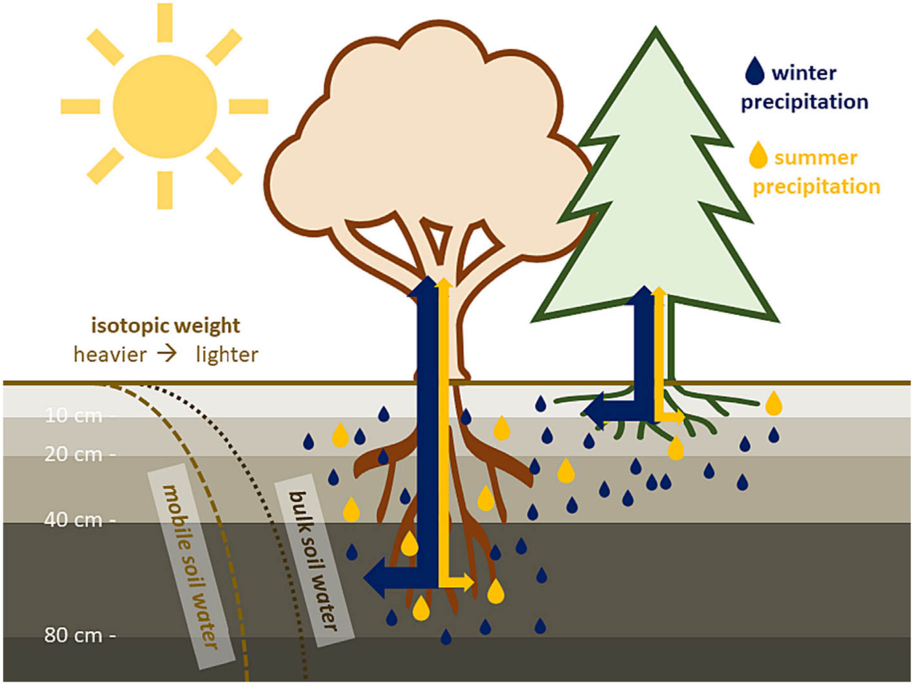


FIGURE 9 Conceptualization of the water signals and seasonality patterns across the forest water cycle. During most of the year, the xylem water signatures are more consistent with winter precipitation signatures.

4 | CONCLUSION

Based on 2 years of stable water isotope measurements in precipitation, mobile and bulk soil waters, and beech and spruce xylem waters at our mixed forest site, we documented the seasonal signals and patterns of tree water uptake across the forest water cycle (Figure 9). We found that mobile and bulk soil waters exhibit distinct seasonal signals, with amplitudes that decrease with depth.

Recent precipitation was only dominant in a few xylem samples, collected predominantly in fall and spring. Recent precipitation made up a larger fraction of mobile soil waters than bulk soil waters; however, isotopic signals of bulk soil waters up to 40-cm depth also exhibit a seasonal cycle similar to precipitation. Mobile soil waters sampled at the same spots (using lysimeters) throughout the whole observation period fluctuated less than bulk soil waters (which necessarily come from different soil volumes each time, because the sampling is destructive). We found that xylem and bulk soil exhibited smaller differences than mobile soil water between dry and wet antecedent conditions. Mobile soil waters sampled during summer contained more summer precipitation when sampled following drier antecedent conditions.

Peak growing season xylem signatures matched bulk soil signatures well, indicating that bulk soil waters are plausibly the major source of tree water uptake. Mixing calculations revealed that the isotope ratios in xylem water were a mixture of shallow (10 to 20 cm depth) and deep (40 to 80 cm depth) bulk soil waters for most sampling dates. Beech and spruce trees predominantly sourced water from depths between 40 to 80 cm and 10 to 40 cm, respectively. Xylem waters exhibited a winter precipitation signature in both summer and winter, suggesting that trees at our site preferably use winter precipitation for transpiration. This holds also after potential uncertainties from δ^{2}H depletion originating from cryogenic vacuum distillation or xylem water storage are accounted for.

In summary, beech and spruce forest trees at our site do not typically transpire recent precipitation but instead rely on a mixture of bulk soil waters dominated by winter precipitation.

ACKNOWLEDGEMENTS

The project was funded through Waldlabor Project Grant 4.20.P01 awarded to Marius Floriancic. We thank the Waldlabor Zürich (Martin Brüllhardt – www.waldlabor.ch) as well as the forest owner Jakob Heusser for their cooperation and support. Further information on the WaldLab Forest Experimental Site can be found here: https://hyd.ifu.ethz.ch/ecohydlab/waldlab.html. We acknowledge support during data collection and laboratory work from the technical staff and student helpers working at the WaldLab Forest Experimental Site (Lena Straumann, Anna Lena Könz, Maria Grundmann, Lara Virsik, Elisa Hage, Stefano Martinetti, Fabian Strittmatter, Adrian Kreiner, Livio Steiger and Lucien Biolley). We thank Tracy Napitupulu and Björn Studer for isotope analyses and Annika Ackermann, Roland A. Werner and Nina Buchmann for sharing the cryogenic extraction laboratory. Open access funding provided by Eidgenossische Technische Hochschule Zurich.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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

How to cite this article: Floriancic, M. G., Allen, S. T., & Kirchner, J. W. (2024). Isotopic evidence for seasonal water sources in tree xylem and forest soils. *Ecohydrology*, e2641. https://doi.org/10.1002/eco.2641