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

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### 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 analyzed two 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 varied 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 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 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.

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### 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 analyzed two 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 varied 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 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 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.

## 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. Allen *et al.* (2019a & 2019b) showed 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 behavior 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 *et al.* , 2019a) and plants (Martin *et al.* , 2018; Allen *et al.* , 2019b; Goldsmith *et al.* , 2022; 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 and Dietrich, 2018) and in regions with year-round precipitation (Allen *et al.* , 2019b; Goldsmith*et al.* , 2022;). However, an important unknown is how new precipitation inputs are used (or not used) by forest trees. Shifts in water uptake depths during water limitations have been observed for crops and trees (Rothfuss and 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 favor 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 focuses 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?

## Study Site and Methods

### Sampling and data collection

Our experimental field 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. 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 & mobile soil waters, as well as beech and spruce (and young spruce) xylem waters.

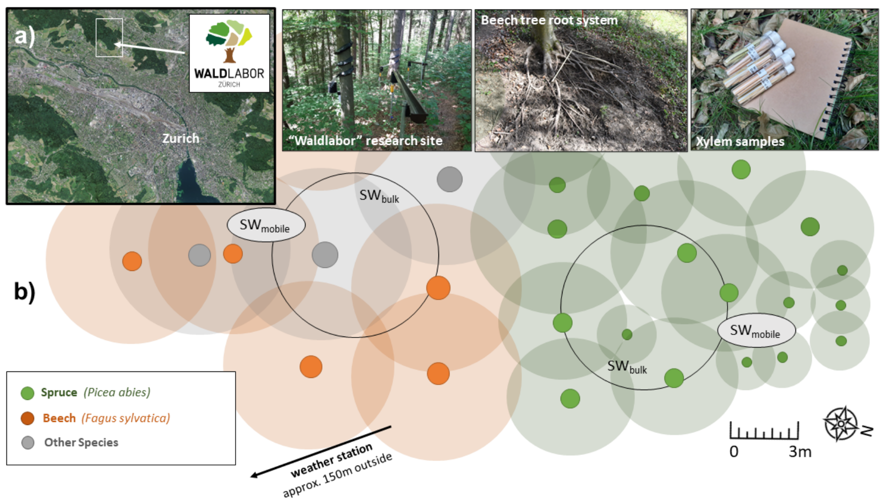


**Figure 1:** Location of the "Waldlabor" study site in Zurich, Switzerland **(a)** , scheme of the tree locations as well as the locations of mobile ($SW_{mobile}$ ) and bulk ($SW_{bulk}$ ) soil water sampling. Precipitation for isotope analysis was sampled outside the forest perimeter at the weather station, at approximately 150 m distance from the site.

Major climate parameters are recorded outside the forest with a compact all-in-one weather station (Atmos41, METER Group, Inc.) at 10-minute resolution. We sampled mobile soil water (the fraction of soil water that has no direct surface contact with the soil, 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 three 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 three weeks from July 2020 through the end of October 2021, we sampled beech (two branches each of three to four trees, resulting in n = 119 samples), spruce (one to two branches of two trees, resulting in n = 57) and young spruce (one to two branches of two trees, resulting in n = 70), by cutting branches for cryogenic water extraction. Samples were collected around midday. Immediately after cutting the branches, bark and phloem were peeled off and the remaining wood was placed in 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 analyzed with a high-temperature-conversion elemental analyzer (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, soil waters) were analyzed with a triple isotope water analyzer (Los Gatos – TIWA-45-EP). Both instruments are reported to have precisions of 1 $\delta^2H$ and 0:2

**Isotope data evaluation and the seasonality index**

We present the data in timeseries in δ-notation in per mil units (relative to V-SMOW (Vienna Standard Mean Ocean Water). We focus on $\delta^2H$, although figures using $\delta^{18}O$ data can be found in the supplement and in dual isotope plots. Please note that the regression lines in the dual isotope plot are 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 *et al.* (2019):

$$\mathrm{SOI} = \begin{cases} \dfrac{\delta_x - \delta_{\mathrm{annP}}}{\delta_{\mathrm{summerP}} - \delta_{\mathrm{annP}}}, & \text{if } \delta_x > \delta_{\mathrm{annP}} \\[2ex] \dfrac{\delta_{\mathrm{x}} - \delta_{\mathrm{annP}}}{\delta_{\mathrm{annP}} - \delta_{\mathrm{winterP}}}, & \text{if } \delta_x < \delta_{\mathrm{annP}} \end{cases},$$

The SOI expresses the isotopic signature of soil and xylem water ($\delta_{\xi}$ ) relative to the seasonal cycle of precipitation, using amount-weighted annual precipitation ($\delta_{\mathrm{annP}}$), summer precipitation ($\delta_{\mathrm{summerP}}$, defined as the peak of a fitted sine curve representing seasonal cycles of precipitation), and winter precipitation ($\delta_{\mathrm{winterP}}$, defined as the trough of the same fitted sine curve). An 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 analyze how much of xylem water is composed of recent precipitation (from the time between two xylem sampling dates) we calculated the fraction of new water ($F_{new}$ ) as suggested in Kirchner (2019):

$$F_{\mathrm{new}} = \frac{\delta\xi\psi\lambda_i - \delta\xi\psi\lambda_{i-1}}{}$$

greek$\delta P -$ xyl$_{i-1}$

Whereas $\delta\xi\psi\lambda_\iota$ is the xylem water signature of the most recent sampling date, $\delta\xi\psi\lambda_{\iota\text{-}1}$ is the xylem water signature of the previous sampling date, and $\delta\Pi$ is the volume-weighted average of precipitation between the two sampling dates (typically three-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$f2$ ):

$$Xyl_{(t=2)} = f1 * bulksoil_{(t=1)} + f2 * P_{(t1->t2)}$$

Where $bulksoil_{(t=1)}$ is the isotopic composition of water in the bulk soil at the previous timestep and$P_{(t1->ts)}$ is the volume weighed isotopic composition of precipitation that fell between the previous and most recent xylem sampling dates (typically the last three weeks).

## Results and discussion

### Isotopic variation of precipitation, soil waters and xylem water

From April 2020 to March 2022, we observed seasonal cycles in isotope ratios (shown for $\delta^2$H in Figure 2 and for $\delta^{18}$O in the supplementary material Figure S1) 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 $\delta^2$H averaging -63.9 (and $\delta^{18}$O averaging -9.5 by the dotted lines in Figure 2 b-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 $\delta^{18}$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 (Figure 2b; Figure 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 $\delta^2$H 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 $\delta^2$H (-64.8 $\pm$ 0.5, mean $\pm$ standard error) was similar to the mean annual precipitation $\delta^2$H (-63.9 $\pm$ 2.5), whereas the mean bulk soil water $\delta^2$H was substantially lighter (-79.2 $\pm$ 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.

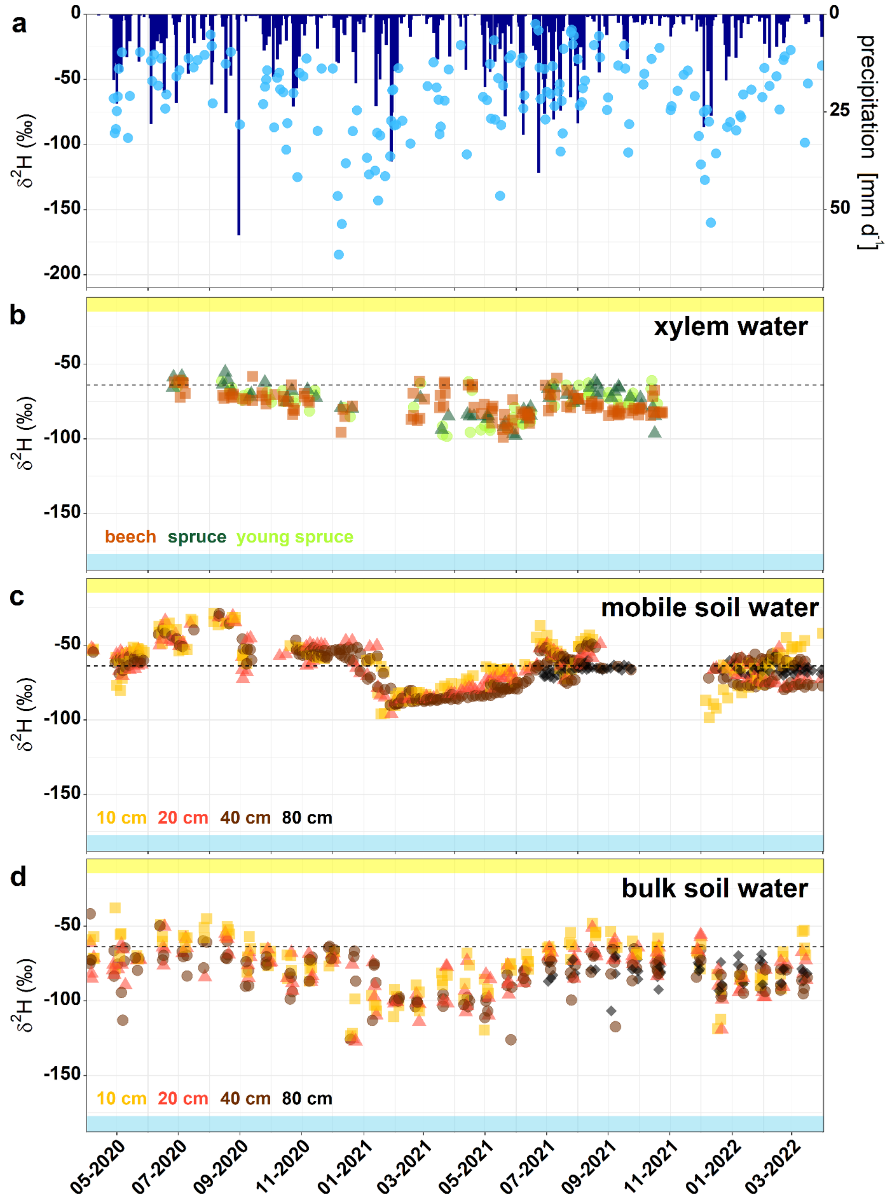


**Figure 2:** Timeseries of precipitation rate and $\delta^2$H isotopic composition **(a),** xylem water isotopic composition in beech, spruce and young spruce trees**(b)** , and mobile **(c)** and bulk **(d)** soil water isotopic composition at 10, 20, 40 and 80cm depth from April 2020 until March 2022. We show timeseries of $\delta^2$H; similar results for $\delta^{18}$O are shown in the supplementary material Figure S1.

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

We calculated the fraction of new or recent precipitation (precipitation from the preceding 30 days - $F_{new}$ ) that can be found in the xylem waters of beech, spruce and young spruce (Figure 3). For beech $\delta^2$H, 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 value 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.

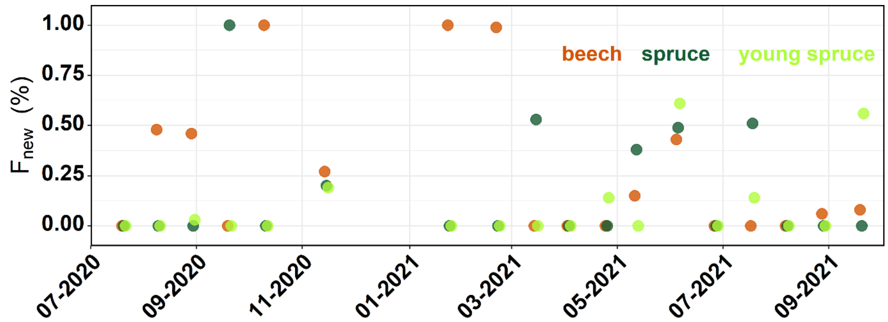


**Figure 3:** Fraction of new precipitation (from the 30 days preceding the xylem water sampling date - $F_{new}$ ) found in xylem water of beech (orange), spruce (dark green) and young spruce (light green) as calculated from $\delta^2$H**.**The results for $F_{new}$ from $\delta^{18}$O are shown in supplementary Figure S2.

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 (gray bars in Figures 4a, 4c, and 4e). More explicitly, xylem water $\delta^2$H lay between the $\delta^2$H 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).

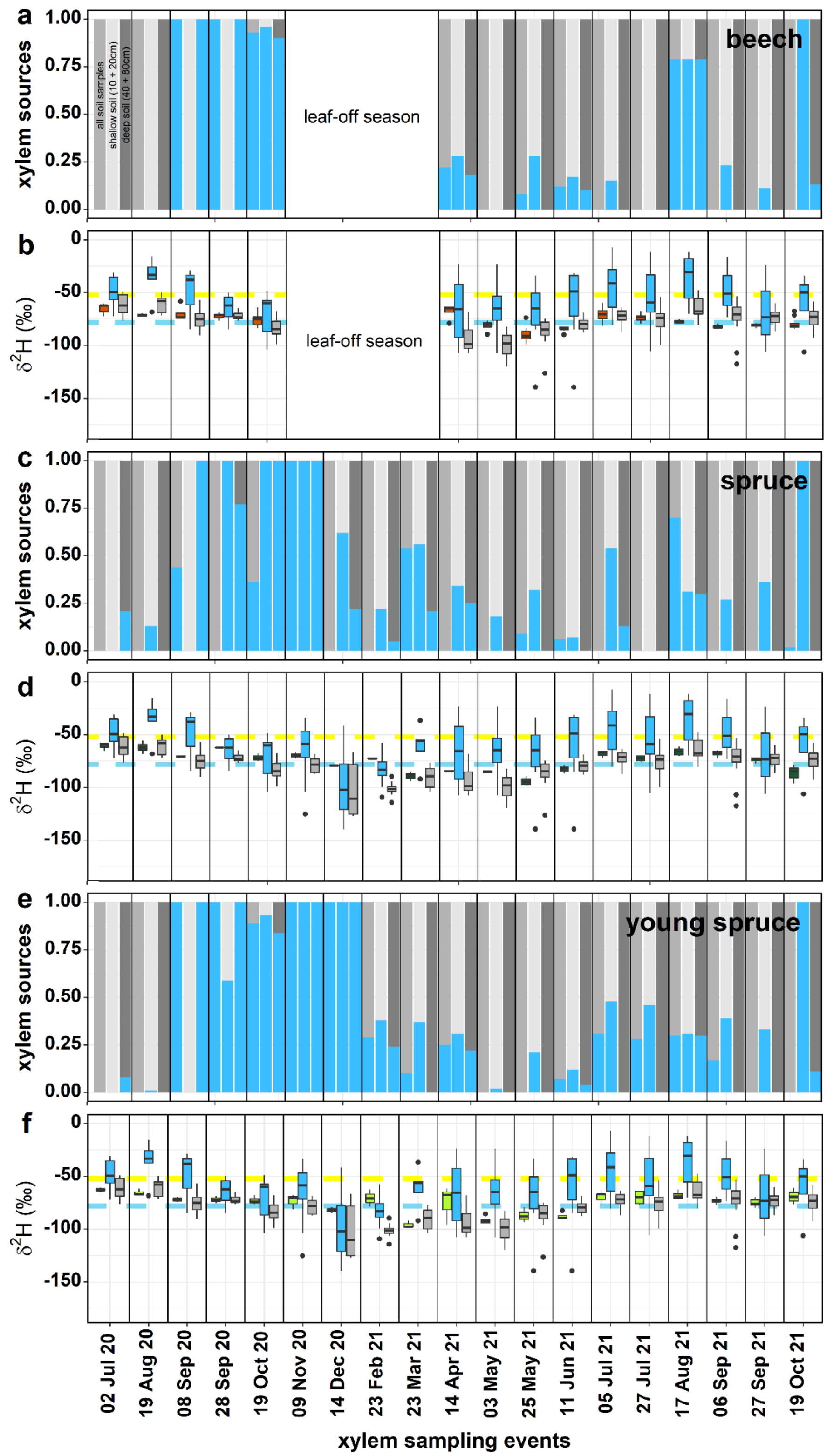


**Figure 4:** Results of mixing calculations assessing the mixture of water from recent precipitation (from

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 beech **(a)** , spruce **(c)** and young spruce**(e).** Distributions of isotope ratios in xylem, precipitation and bulk soil water samples for each sampling date for beech**(b)** , spruce **(d)** and young spruce **(f)** . The dashed lines indicate the mean precipitation signatures for summer and winter precipitation in light blue and yellow, respectively.

**Table 1:** Mean $\delta^2$H isotopic composition of precipitation in the 30 days preceding the xylem sampling (P), bulk soil water in the shallow (soil$_{shal}$ - 10 and 20 cm) and deep soil (soil$_{deep}$ - 40 to 80cm), 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 80cm only started on 05$^{th}$ July 2021.

| **date** | **Π $\delta^2$H$_{\mu\varepsilon\alpha\nu}$** | **σοιλ$_{\sigma\eta\alpha\lambda}$ $\delta^2$H$_{\mu\varepsilon\alpha\nu}$** | **σοιλ$_{\delta\varepsilon\varepsilon\pi}$ $\delta^2$H$_{\mu\varepsilon\alpha\nu}$** | **beech $\delta^2$H$_{\mu\varepsilon\alpha\nu}$** | **beech qualitative assessment** | **spruce $\delta^2$H$_{\mu\varepsilon\alpha\nu}$** | **spruce qualitative assessment n** | **young spruce $\delta^2$H$_{\mu\varepsilon\alpha\nu}$** | **yo sp qu tiv ass me** |
|---|---|---|---|---|---|---|---|---|---|
| 02 Jul | -48.08 | -59.81 | -64.13 | -64.98 | **deeper than 40 cm** | -60.83 | between shallow & deep | -62.80 | bet sha dee |
| 19 Aug | -32.80 | -56.90 | -68.12 | -71.23 | **deeper than 40 cm** | -61.97 | between shallow & deep | -65.76 | bet sha dee |
| 08 Sep | -67.26 | -71.53 | -83.48 | -69.93 | **between 10 & 20cm** | -70.95 | **between 10 & 20cm** | -72.05 | bet sha dee |
| 28 Sep | -77.42 | -70.80 | -74.15 | -72.27 | between shallow & deep | -62.28 | **more recent precipitation** | -72.19 | bet sha dee |
| 19 Oct | -72.18 | -79.70 | -89.75 | -75.68 | **more recent precipitation** | -71.86 | **more recent precipitation** | -72.99 | **mo rec pr tat** |
| 09 Nov | -72.08 | -80.16 | -75.89 | -72.87 | leaf-off season | -69.78 | **more recent precipitation** | -73.32 | **mo rec pr tat** |
| *14 Dec* | *-128.35* | -100.76 | -99.12 | -84.77 | leaf-off season | -79.56 | *evaporative enrichment* | -82.18 | *eve enr me* |
| *23 Feb* | *-78.17* | -100.94 | -101.63 | -78.60 | leaf-off season | -72.59 | *evaporative enrichment* | -70.82 | *eve enr me* |
| 23 Mar | -62.16 | -87.06 | -99.39 | -70.44 | leaf-off season | -89.37 | between shallow & deep | -89.37 | bet sha & |
| 14 Apr | -75.39 | -88.67 | -101.11 | -68.00 | leaf-off season | -84.53 | **between 10 & 20cm** | -75.04 | **mo rec pr tat** |

| date | **Π $\delta^2H_{\mu\epsilon\alpha\nu}$** | **$\sigma o\iota\lambda_{\sigma\eta\alpha\lambda}$ $\delta^2H_{\mu\epsilon\alpha\nu}$** | **$\sigma o\iota\lambda_{\delta\epsilon\epsilon\pi}$ $\delta^2H_{\mu\epsilon\alpha\nu}$** | **beech $\delta^2H_{\mu\epsilon\alpha\nu}$** | **beech qualitative assessment** | **spruce $\delta^2H_{\mu\epsilon\alpha\nu}$** | **spruce qualitative assessment n** | **young spruce $\delta^2H_{\mu\epsilon\alpha\nu}$** | **yo sp qu tiv ass me** |
|---|---|---|---|---|---|---|---|---|---|
| 03 May | -73.39 | -96.03 | -104.10 | -81.49 | **more recent precipitation** | -85.47 | **more recent precipitation** | -90.89 | **mo rec pr tat** |
| 25 May | -58.90 | -82.10 | -97.40 | -89.22 | between shallow & deep | -94.16 | between shallow & deep | -87.01 | bet sha & |
| 11 Jun | -51.52 | -77.68 | -83.21 | -84.38 | **deeper than 40 cm** | -82.53 | between shallow & deep | -87.69 | **de th cm** |
| 05 Jul | -39.41 | -67.28 | -78.49 | -70.79 | between shallow & deep | -68.31 | between shallow & deep | -69.44 | bet sha & |
| 27 Jul | -57.19 | -68.13 | -81.88 | -73.58 | between shallow & deep | -72.81 | between shallow & deep | -70.16 | bet sha & |
| 17 Aug | -52.87 | -58.36 | -73.65 | -77.57 | **deeper than 40 cm** | -66.11 | between shallow & deep | -68.06 | bet sha dee |
| 06 Sep | -42.41 | -63.81 | -83.72 | -82.29 | between shallow & deep | -68.05 | between shallow & deep | -73.07 | bet sha & |
| 27 Sep | -57.33 | -68.47 | -77.89 | -80.93 | **deeper than 40 cm** | -74.18 | between shallow & deep | -74.93 | bet sha dee |
| 19 Oct | -58.91 | -68.43 | -80.08 | -69.17 | between shallow & deep | -81.79 | **deeper than 40 cm** | -69.17 | bet sha dee |

We examined one xylem sampling date (27 July 2021) in the peak growing season in more detail to reveal the discrepancies between seasonal signals and event-scale xylem / precipitation signals for precipitation of the last 12 months prior to xylem sampling (Figure 5). Xylem and bulk soil waters were isotopically similar, whereas most precipitation during the preceding three summer months (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, so it is important to clarify the relative importance of winter and summer precipitation as sources for soil water storage.

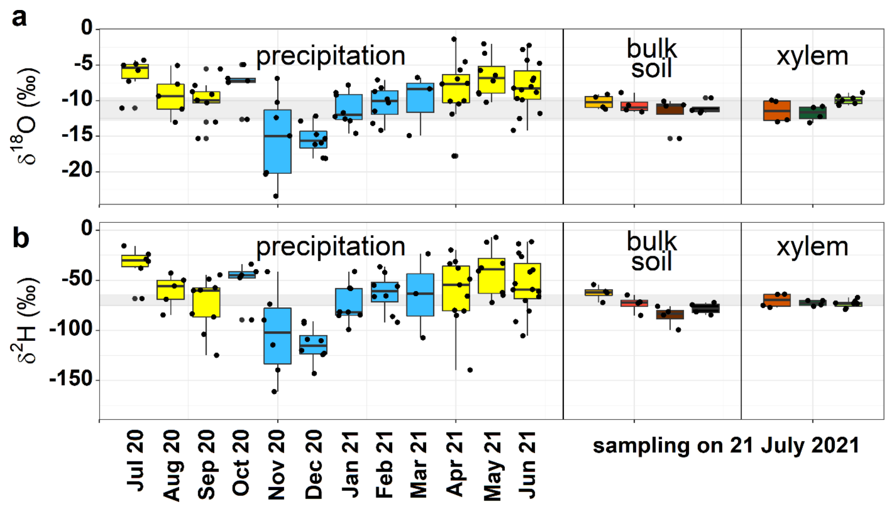


**Figure 5:** Isotope signature of precipitation in the 12 months prior to the bulk soil (10, 20, 40 and 80cm) and xylem sampling (beech, spruce, young spruce) on 27 July 2021 for $^{18}$O**(a)** and $^{2}$H **(b)** . The blue and yellow boxes indicate winter and summer precipitation, respectively. The 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.

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 roots 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 and Kazda, 2002). Previous studies found that 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 were 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'd expected that their root systems occupy separate soil layers to avoid competition for water resources (Meißner *et al.* , 2012). 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).

**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 Wilcoxon signed rank 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 two-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).

**Table 2:** Wilcoxon signed rank tests comparing isotopic signals in winter and summer xylem versus winter and summer precipitation.

| | beech | beech | spruce | spruce | young spruce | young spruce |
|---|---|---|---|---|---|---|
| **P** | **δ^18O** | **δ^2H** | **δ^18O** | **δ^2H** | **δ^18O** | **δ^2H** |
| **summer** | *** | *** | *** | *** | *** | *** |
| **winter** | *leaf-off season* | *leaf-off season* | ns | ns | ns | ns |

** $p$ -value 0.001 – 0.05 *** $p$ -value < 0.001*ns* -> non-significant

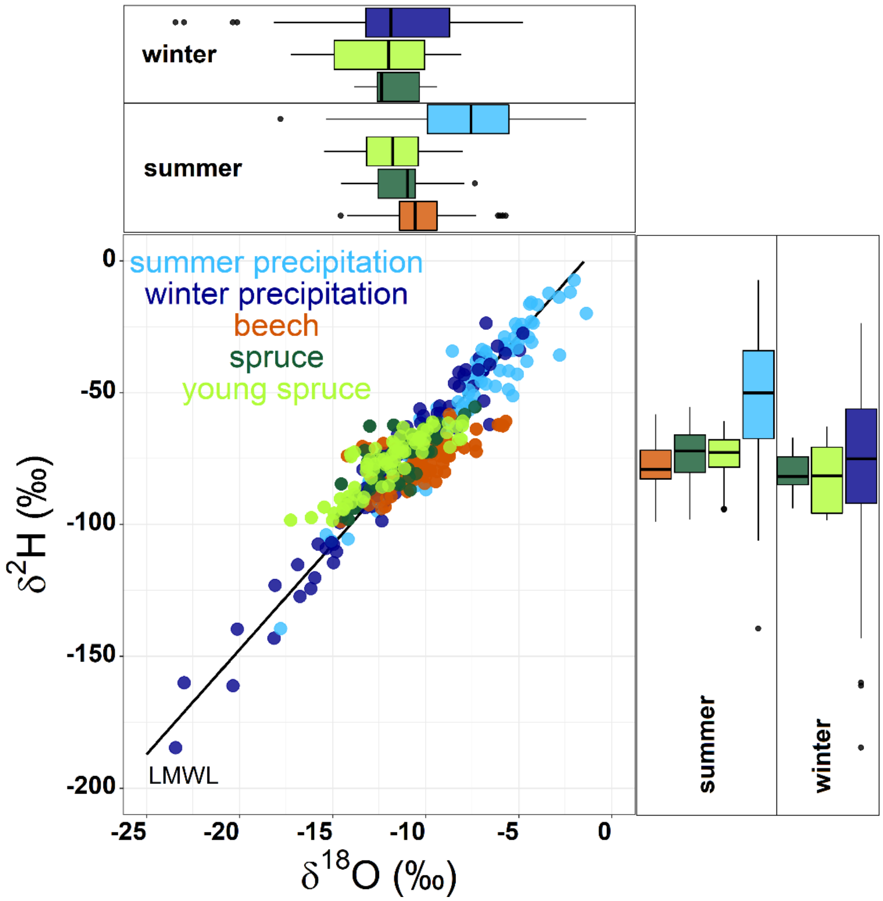


**Figure 6:** Dual-isotope plot for tree xylem (beech, spruce, and young spruce shown by orange, dark green, and light green, respectively) and summer vs. winter precipitation (light and dark blue, respectively). Boxplots show distributions of isotopic signals in precipitation and xylem waters for winter (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.

We calculated the seasonal origin index SOI (Allen *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 colors) and the winter half of the year from (November through April, in gray). Most xylem isotope samples (Figure 7a-c) had an SOI < 0, indicating that they are mixtures dominated by winter precipitation. This was especially evident in spruce and young spruce xylem, and less obvious in beech, where samples seem to be quite evenly distributed around a SOI of 0. Surprisingly, the few samples of beech xylem water from the winter months were dominated by SOI > 0, suggesting that they were dominated by summer precipitation (or because there is no transpiration in winter months, that they were evaporatively enriched while stored in the branches).

SOI values for mobile soil water showed distinct variation across the different depths: whereas at 10 cm, 20 cm and 40 cm depth most summer soil water had SOI > 0 (indicating a predominantly summer source) winter soil water was well mixed between summer and winter. 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 summer were well mixed between winter and summer precipitation (based on less than one year of samples because sampling at this depth only started in June 2021).

Bulk soil waters in summer were almost evenly distributed around SOI = 0, with slightly 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).

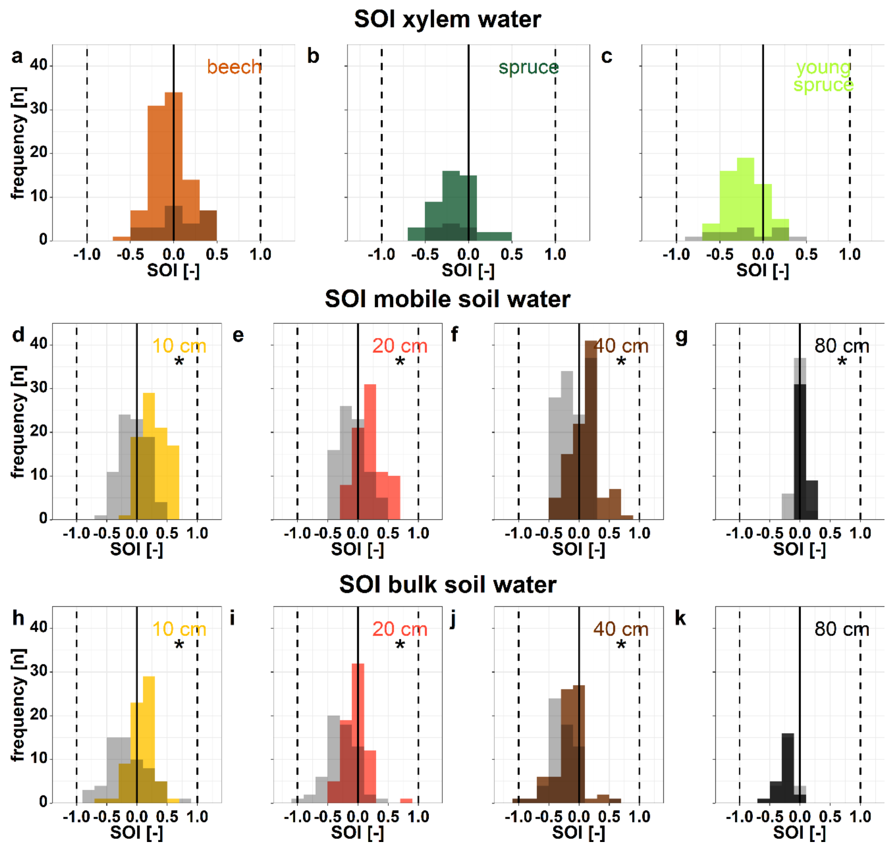


**Figure 7:** Frequency distribution of the seasonal origin index (SOI) for beech **(a)** , spruce **(b)** and young spruce xylem**(c)** (upper row), mobile soil waters at 10 cm **(d)** , 20 cm **(e)** , 40cm **(f)** and 80 cm **(g)** (middle row) and bulk soil waters at 10 cm **(h)** , 20 cm **(i)** , 40cm**(j)** and 80 cm **(k)** (bottom row). The colored bars indicate the distribution for the summer half of the year (May through October), the gray 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 the SOI in summer and winter.

Looking at the overall seasonality signals in xylem waters (Figures 6) we found temporal disconnections between the water in xylem and precipitation, i.e., the beech and spruce forest trees contained winter precipitation throughout the year. This has been shown across Switzerland in previous work by Allen *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. 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 two-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 otherwise been; much of the remainder may also be evaporated from soils or taken up by understory plants before reaching tree roots. 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 reasons is more relevant.

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 $\delta^{18}$O and $\delta^{2}$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).

**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 i.e., 607 mm and 752 mm for the summer half precipitation in 2020 and 2021, respectively. Previous studies (Goldsmith *et al.* , 2022; Guo *et al.* , 2018; Williams and 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 colors) 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 0.00 to -0.07, -0.15 to -0.04, and -0.24 to -0.15, for beech, spruce and young spruce respectively (Figure 8a-c). Similarly small differences were observed for bulk soil water SOI: mean SOI across all depths shifted from -0.08 to -0.03. But we saw a larger shift in mobile soil water SOI, from 0.21 to 0.12, across all depths between the drier and wetter summer sampling dates. The largest differences were observed in 10 cm ($p < 0.05$) and 40 cm (not significant) depths (SOI shift of -0.09), however, observed shifts between subsets were only significant for 10 and 80 cm (indicated by asterisks in Figure 8). 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).

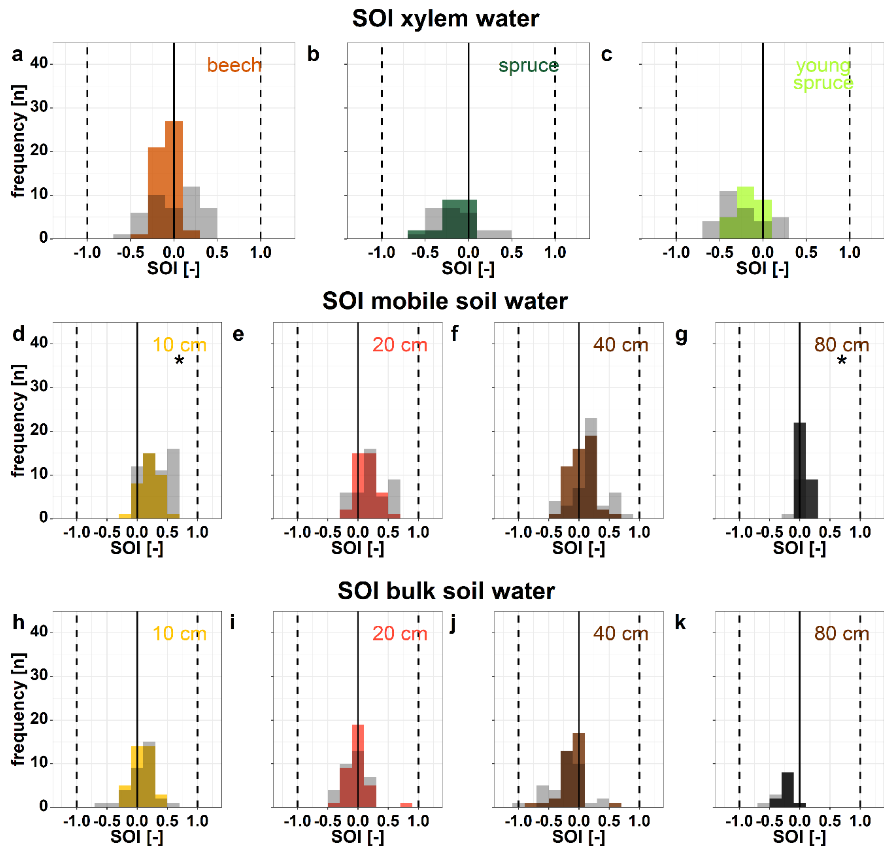


**Figure 8:** Frequency distributions of the seasonal origin index (SOI) for the summer half of the year (May through October) for beech**(a)** , spruce **(b)** and young spruce xylem **(c)**(upper row), mobile soil waters in 10 cm **(d)** , 20 cm**(e)** and 40cm **(f)** (middle row) and bulk soil waters in 10 cm **(g)** , 20 cm **(h)** , 40cm **(i)** (bottom row). The colored and gray 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.

Our results suggest that although mean annual precipitation has impact on the lag between precipitation seasonality and xylem seasonality (Goldsmith *et al.* , 2022; Guo *et al.* , 2018; Williams and 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. 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).

### 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 *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 small and thus negligible (Newberry *et al.* , 2017), Chen *et al.* (2020) clearly documented $\delta^2H$ offsets in xylem waters. These offsets were attributed to the exchange of $^2H$ in the wood tissue with waters in the xylem. However, in a more recent study, Diao *et al.* (2022) showed that these offsets are potentially small when large amounts (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 stored in xylem 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 $\delta^2H$; this depletion could potentially also influence our results. However, we calculated the effect of the potential offset by $\delta^2H$ depletion, i.e., a bias of -6.1 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 Supplementary Material – Figure S3). Therefore, our main conclusions are robust against the potential biases introduced by water extraction that have been described elsewhere.

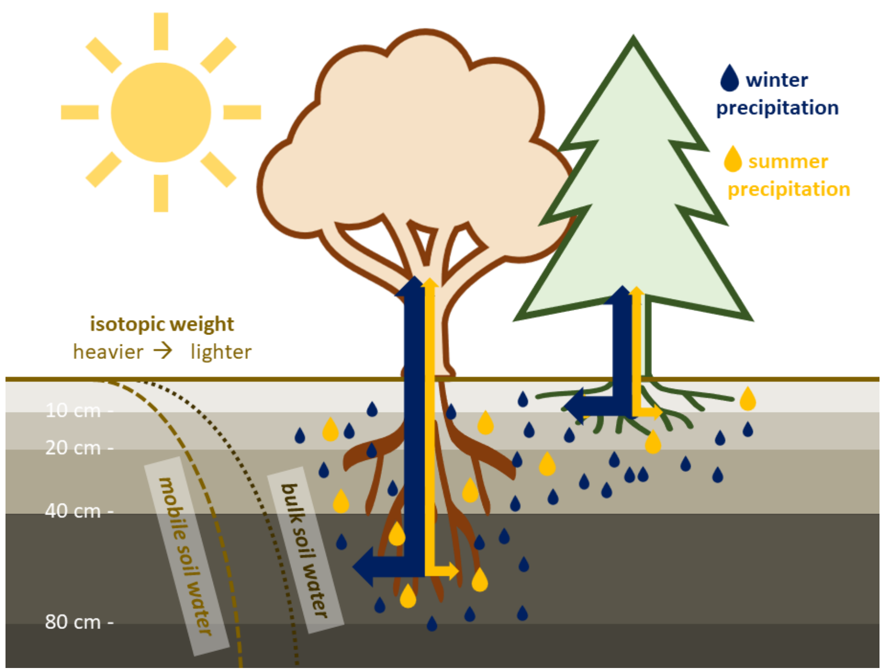


**Figure 9:** Conceptualization of the water signals and seasonality patterns across the forest water cycle. During most of the year the xylem water signatures are more consistent with winter precipitation signatures.

### Conclusion

Based on two 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 (Figure 2).

Recent precipitation was only dominant in a few xylem samples, collected predominantly in fall and spring (Figure 3). Recent precipitation made up a larger fraction of mobile soil waters than bulk soil waters (Figure 7); however, isotopic signals of bulk soil waters up to 40 cm depth also exhibit a seasonal cycle similar to precipitation (Figure 2). Mobile soil waters sampled at the same spot from lysimeters throughout the whole observation period were less variable compared to bulk soil waters (Figure 2). 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 (Figure 8).

Peak growing season xylem signatures match 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 (Figure 4; Table 1). Beech trees predominantly sourced water from depths between 40 to 80 cm and spruce trees from 10 to 40 cm. Xylem waters exhibited a winter precipitation signature in both summer and winter, suggesting that trees at our site preferably use winter precipitation for transpiration (Figure 6; Figure 9). This holds also after potential uncertainties from $\delta^2$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 consume recent precipitation, but instead a mixture of bulk soil waters dominated by winter precipitation (Figure 9).

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