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Employing stable isotopes to determine the residence times of soil water and the temporal origin of water taken up by *Fagus sylvatica* and *Picea abies* in a temperate forest

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Summary

- We (i) assessed how the seasonal variability of precipitation $\delta^2\text{H}$ and $\delta^{18}\text{O}$ is propagated into soil and xylem waters of temperate trees; (ii) applied a hydrological model to estimate the residence time distribution of precipitation in the soil; and (iii) identified the temporal origin of water taken up by *Picea abies* and *Fagus sylvatica* over four growing seasons.
- Residence times of precipitation in the soil varied between a few days and several months and increased with soil depth. On average, 50% of water consumed by trees throughout a growing season had precipitated in the same growing season, while 40% had precipitated in the preceding winter or even earlier. Importantly we detected subtle differences with respect to the temporal origin of water used by the two species throughout a growing season.
- We conclude that not only growing season precipitation but also winter precipitation is important for the water supply of temperate trees and that winter precipitation could buffer impacts of spring or summer droughts.
- Our study additionally provides the means to obtain realistic estimates of source water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values for trees from precipitation isotope data, which is essential for improving model-based interpretations of $\delta^{18}\text{O}$ and $\delta^2\text{H}$ values in plants.

Key words: *Fagus sylvatica*, GNIP, *Picea abies*, residence time, soil water, stable isotopes, temporal origin, xylem water

Introduction

The availability of water is fundamental for plants to remain turgid, to allow cell expansion and growth, and to keep stomata open for gas exchange. Water can be acquired by plants from various sources such as ground water, snow and rain, or fog water (Dawson, 1998; Ehleringer *et al.*, 2000; Tang & Feng, 2001; Goldsmith *et al.*, 2012). In most terrestrial ecosystems, the main water source of plants is, however, soil water that originates from precipitation. Numerous studies have assessed the spatial origin of plant source water in the soil, in particular with respect to the depth from which plants acquire their water (White *et al.*, 1985; Meinzer *et al.*, 1999; Yang *et al.*, 2015; Volkman *et al.*, 2016). In addition, several investigations have assessed the use of distinct moisture pools in the ground by plants such as soil vs. ground water (Dawson & Pate, 1996; Bertrand *et al.*, 2014) or soil vs. stream water (Dawson & Ehleringer, 1991). In contrast to the spatial origin, very little is known on the temporal origin of water that plants use (but see Ehleringer *et al.* (1991)). In particular in temperate ecosystems, the temporal origin of precipitated water in the soil that is used by different tree species as source water is mostly unknown (Sprenger *et al.*, 2016; Volkman *et al.*, 2016). Resolving the temporal origin of water in the soil and identifying when the water that plants take up throughout the growing season had precipitated is yet key to understand how plants utilize and partition this essential resource and to anticipate how climate change induced shifts in seasonal precipitation patterns will affect the availability of water for plants in temperate ecosystems (Moberg *et al.*, 2006; IPCC, 2013; Evaristo *et al.*, 2015; Fischer *et al.*, 2015).

Resolving the temporal origin of precipitation in the soil and in the xylem water is also important to better understand the drivers of stable hydrogen (H) and oxygen (O) isotope compositions ($\delta^2\text{H}$ and $\delta^{18}\text{O}$, respectively) in plants. $\delta^2\text{H}$ and $\delta^{18}\text{O}$ of water and organic materials in plants have been recognized as valuable natural tracers in ecological, biogeochemical, hydrological and paleo-climate research and even in forensic sciences. $\delta^2\text{H}$ and $\delta^{18}\text{O}$ in tree-rings and leaf wax lipids are, for example, used for climate reconstructions (McCarroll & Loader, 2004; Treydte *et al.*, 2006; Sachse *et al.*, 2012), and $\delta^2\text{H}$ and $\delta^{18}\text{O}$ in plant-transpired vapor have been used to partition evapotranspiration fluxes in ecosystems (Bowling *et al.*, 2003; Good *et al.*, 2015). $\delta^2\text{H}$ and $\delta^{18}\text{O}$ of water and organic compounds in plants depend on the isotope composition of the plant's source water (Tang & Feng, 2001). Most studies assume that there is no fractionation during source water uptake by plants via roots (Wershaw *et al.*, 1966; Dawson & Ehleringer, 1991; Newberry *et al.*, in press; but also

see Lin & Sternberg, 1994; Ellsworth & Williams, 2007). As such, the xylem water in plants is typically identical in its isotope composition to the water that a plant has taken up from the soil (Ehleringer & Dawson, 1992). In addition, water becomes enriched in the heavier ^2H and ^{18}O isotopes during transpiration in the leaves because water composed of the lighter ^1H and ^{16}O isotopes evaporates more easily. This generates a distinct leaf water isotope signal that is ultimately imprinted into the organic compounds that are synthesized in plants and into the water vapor transpired by plants (Roden *et al.*, 2000; Kahmen *et al.*, 2011; Kahmen *et al.*, 2013; Cernusak *et al.*, 2016).

In the past, sophisticated leaf water models have been developed that allow to predict the evaporative ^2H and ^{18}O enrichment of leaf water above the plant's source water with high precision (Craig & Gordon, 1965; Flanagan *et al.*, 1991; Farquhar & Lloyd, 1993; Barbour, 2007). Comparable mechanistic insight into what determines variability in the isotope composition of a plant's source water does, however, not exist. The approximation of a plant's source water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ from precipitation isotope databases as the GNIP data base (Kanner *et al.*, 2013; Managave, 2014; Dee *et al.*, 2015) or derived products such as the online isotope calculator for precipitation (OIPC)(Bowen & Wilkinson, 2002; Richter *et al.*, 2008) is therefore still difficult and can introduce large uncertainties in the interpretation of H and O isotopes in plants.

To resolve these uncertainties, we assessed the variability of hydrogen and oxygen isotopes in precipitation, soil water at different depths, and xylem water of *Fagus sylvatica* and *Picea abies* in a temperate forest over the course of four years. We used these data to determine (1) how the seasonal variability of $\delta^2\text{H}$ and $\delta^{18}\text{O}$ in precipitation is integrated in soil water within the soil profile; (2) what the residence time of precipitation in the soil at different soil depths is; (3) how seasonal patterns in precipitation $\delta^2\text{H}$ and $\delta^{18}\text{O}$ is reflected in xylem water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values of *F. sylvatica* and *P. abies*; and (4), what the temporal origin of a trees source water is, i.e. determine when the water had precipitated that is taken up by *P. abies* and *F. sylvatica* throughout a growing season?

Materials and Method

Study site and environmental data

We performed our study at the temperate forest Lägeren near the town of Wettingen, Switzerland (47°28'42.0"N, 8°21'51.8"E). The site is located at 682 m a.s.l. on a south-facing slope at the transition from the Swiss Plateau to the Swiss Jura mountains. The vegetation is a

diverse mixed forest, with an average tree age of 105 to 185 years. The overstory vegetation is dominated by *F. sylvatica* with the companion species *P. abies*, *Fraxinus excelsior*, *Abies alba* and *Acer pseudoplatanus* (Eugster *et al.*, 2007). The main soil types are rendzic leptosols (or rendzinas) and haplic cambisols (Heim *et al.*, 2009). Bedrocks of limestone and marl start 0.6-1 m below the soil surface. The climate at the site during the reference period 1981-2010 is characterized by a mean annual precipitation of 1110 mm (MeteoSwiss reference stations Dietikon and Otelfingen) and a mean annual air temperature of 9.4°C (MeteoSwiss stations Zürich Reckenholz and Zürich Fluntern SMA).

We recorded continuous half-hourly atmospheric data of air temperature, short-wave incoming radiation and wind speed with data loggers (CR10X and CR1000, Campbell Scientific Inc., Logan, UT, USA) on the top of an eddy covariance tower that is installed at our research site. In addition, precipitation was measured on the second platform of the tower at canopy height. Dielectric soil moisture probes (Decagon ECH₂O EC-20, Pullman, WA, USA) measured the volumetric soil moisture content at -0.1 m, -0.2 m and -0.3 m soil depths. These data were recorded with a CR1000 data logger (Campbell Scientific Inc., Logan, UT, USA) at 10-min intervals from 2012 to 2015.

Water isotope sample collection

$\delta^2\text{H}$ and $\delta^{18}\text{O}$ values of precipitation were obtained from GNIP data from the Buchs/Suhr station which is within 25 km distance from our research site. We compared the isotope composition of precipitation at the GNIP site to the isotope composition of precipitation that we collected at our research site for the years 2012 – 2014. For this purpose, we collected precipitation during the growing season in 2012, 2013, and 2014 using five precipitation collectors built after Prechsl *et al.* (2015). We stored the collected precipitation samples cool at 4°C in 1.5 ml airtight glass vials (Macherey-Nagel GmbH, Düren, Germany) until analysis. Water from the collectors was sampled nominally once a month for isotope analyses.

From 2012 to 2015, we collected soil water 5 to 9 times throughout the year. On each sampling date, six replicate soil cores were taken with a Pürkhauer soil corer with a diameter of 28 mm (Goecke GmbH & Co. KG, Schwelm, Germany). Soil cores were separated into eight different depths (0-0.05 m, 0.05-0.1 m, 0.1-0.2 m, 0.2-0.3 m, 0.3-0.4 m, 0.4-0.5 m, 0.5-0.6 m, 0.6-0.7 m; n=6 each). From each soil core 3-5 g of soil from each depth was transferred into a 12 ml airtight exetainer (Labco, Lampeter, UK) immediately after the soil

core was taken. The samples were stored on crushed ice in the field and put in a freezer at -23°C in the laboratory until further extraction.

To assess the isotope composition of xylem water of *P. abies* and *F. sylvatica*, we collected twigs in the tree crown with the help of tree climber 5 to 9 times throughout the 2012 to 2015 growing seasons. Samples of *P. abies* were collected in three seasons (2012 to 2014), while samples of *F. sylvatica* were collected in four seasons (2012 to 2015). Sample collection started in spring after leaf flush and ended just before litter fall in autumn. After removing bark and phloem of the twigs, xylem samples were transferred into 12 ml airtight exetainers (Labco, Lampeter, UK) and stored in a -23°C freezer in the laboratory until cryogenic water extraction. We sampled all four cardinal directions for both species in 2012 and 2013. However, we reduced the sample size in 2014 and 2015 to two cardinal directions (south and west), as no significant differences in xylem water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values among the four sample directions were found during the first sampling campaigns (data not shown).

Samples of precipitation, soil and xylem waters were all collected on the same dates. Whenever possible, precipitation collectors were sampled more frequently.

Cryogenic water extraction and stable water isotope analysis

To extract the water from soil and xylem samples, we used a cryogenic water extraction line that was built after (Ehleringer *et al.*, 2000). A detailed description of the extraction line can be found in Kahmen *et al.* (2008). For the $\delta^2\text{H}$ and $\delta^{18}\text{O}$ analysis of precipitation, soil and xylem water samples, we used a high-temperature conversion/elemental analyzer (TC/EY; Finnigan MAT, Bremen, Germany), which was connected to a Delta Plus XP isotope ratio mass spectrometer via a ConFlo III interface (Finnigan MAT; Werner *et al.* (1999)) For $\delta^{18}\text{O}$ analyses, water was converted to CO with the carbon reduction method after Gehre *et al.* (2004). Samples and laboratory standards were positioned after the concept of Werner and Brand (2001). All post-run offline calculations (i.e., offset, memory effect, and drift corrections) were done according to Werner and Brand (2001). The long-term quality of our control laboratory standard water (WP-0503-Z0010B) was $\pm 0.48\text{‰}$ for $\delta^2\text{H}$ and $\pm 0.17\text{‰}$ for $\delta^{18}\text{O}$ over all measurements.

Modelling residence time distributions of water in the soil, root water uptake and temporal origin of xylem water

We used a modified Hydrus-1D version (Simunek *et al.*, 2008; Stump *et al.*, 2012) to simulate the infiltration of precipitation into the soil and to determine the residence time

distribution (RTD) and the mean residence time (MRT) of precipitation water in the soil for the years 2012–2015. The residence time of water in the soil is the time span between the precipitation of the water and the observation of the water at a given depth node in the soil. As the soil water at a given depth consists of water that had originated from multiple precipitation events, the RTD describes the age distribution of these different precipitation sources at a given soil depth and MRT describes the mean of all residence times at a given depth.

Hydrus-1D additionally allows to calculate root water uptake (RWU), which is the water taken up by a tree from the soil at a given point in time. Assuming that water storage within the tree is negligible on the timescale of interest (i.e. weeks to months), the water described by RWU is equivalent to the water flowing through the xylem of a tree and used for transpiration. By combining RWU patterns with the computed soil water RTDs for each depth node, we could determine the RTDs of RWU and thus the age distributions of root water uptake for any given day of the growing season. Ultimately, this allowed to calculate the age distributions of cumulative root water uptake for an entire growing season and to determine the temporal origin of precipitation water taken up by a tree from the soil.

The standard version of Hydrus-1D is not designed to simulate the transport of stable water isotopes. We employed, however, an isotope-enabled modification of the original Hydrus-1D software for our study in order to simulate the isotope composition of soil and xylem water (Sprenger *et al.*, 2015b) and to validate the model against measured isotope composition of soil and xylem water. The isotope-enabled version of Hydrus-1D follows the approach of Stumpp and Hendry (2012) to simulate isotope/solute transport in the soil. Previous applications of this modified Hydrus-1D version can be found in the works of Stumpp and Hendry (2012); Stumpp *et al.* (2012); Huang *et al.* (2015); Sprenger *et al.* (2015a). Fractionations by soil evaporation are not considered in the isotope-enabled version of Hydrus-1D as they are generally limited to the forest floor in dense temperate forests as the one investigated here (Schulze *et al.*, 1994; Kelliher *et al.*, 1995).

A detailed description of the model and the parameters used in the model is provided in the supporting information of this paper (see Methods S1).

Statistical analyses

We used orthogonal regressions and their 95% confidence intervals for the local meteoric water lines (LMWLs) for Lägeren and the Buchs/Suhr GNIP station, as well as all regressions displayed in Fig. 1 (soil water and xylem water) and Table S1. The variation of

the measured soil water isotopes at different soil depths explained by the modelled soil water isotopes at the same soil depths was calculated by orthogonal regression using the same R package as above (Table S2). The above approach was also used for calculating the variation of measured xylem water of both tree species explained by the modelled xylem water isotopes using orthogonal regressions (Table S3). For all data processing, statistical analysis and graphics we used R version 3.1.2 (R Core Team, 2014).

Results

Annual precipitation was 966 mm, 843 mm, 812 mm and 628 mm in 2012, 2013, 2014 and 2015, respectively, and was thus considerably lower than the long-term mean (1110 mm). Precipitation during the main growing season (i.e. May 1st – September 30th) differed substantially among the four investigated years. While growing season precipitation was 536 mm and 457 mm in 2012 and 2014, respectively, it was 375 mm and 354 mm in 2013 and 2015, respectively. This illustrates that our investigations were conducted during years with two wet summers and two exceptionally dry summers (Orth *et al.*, 2016).

Precipitation $\delta^2\text{H}$ values varied between -29.0‰ and -157.6‰ and precipitation $\delta^{18}\text{O}$ values between -4.4‰ and -20.8‰ at the Buchs/Suhr GNIP station over the years 2012 - 2015 (Fig. 1, Fig. 2). The precipitation $\delta^2\text{H}$ values that we collected during the growing season at the Lägeren research site varied between -39.1‰ and -107.6‰, and $\delta^{18}\text{O}$ values varied between -6.2‰ and -15.0‰ (Fig. 1). As expected, $\delta^2\text{H}$ and $\delta^{18}\text{O}$ in precipitation were at both locations enriched in the heavier isotopes in the summer and depleted during winter during all years (Fig. S1). The slope of the LMWL was 8.00 for Buchs/Suhr and 8.03 for the Lägeren research site (Fig. 1). From this, and the identical seasonal patterns at both locations we conclude that the isotope composition of precipitation at the GNIP site Buchs/Suhr is indistinguishable from the isotope composition of precipitation at the Lägeren research site. We thus used the data from the GNIP database for our study as model input variables because these data were available for all four years of our investigation (as compared to only three years of data directly measured at our research site).

Soil water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values followed the seasonal trends that we observed in precipitation with ^2H - and ^{18}O -enriched soil water in summer and ^2H - and ^{18}O -depleted soil water in winter (Fig. 2 a,b, Fig. S1). The amplitude of this seasonal trend was similar to the amplitude of precipitation in the shallow soil but declined with soil depth. Specifically, soil water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values measured in the shallowest soil layer (0.0 - 0.05 m) varied

between -42.2‰ and -120.0‰ in $\delta^2\text{H}$ and between -5.5‰ and -15.8‰ in $\delta^{18}\text{O}$ across all study years. The isotopic composition of soil water at the deepest soil layer (0.6 - 0.7 m) varied between -60.8‰ and -97.0‰ and between -9.5‰ and -13.7‰ for $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values, respectively. To test for differences between the regression lines resulting from $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values of soil water at different depths and the LMWL of precipitation at the Buchs/Suhr GNIP station, we used the 95% confidence interval of the slope of the orthogonal regression of the Buchs/Suhr GNIP station (Table 1) and compared it to the 95% confidence interval of the slope of soil water at each single soil depth (Table 2). We found that the 95% confidence interval of the slope of Buchs/Suhr overlapped with the 95% confidence interval of the slopes of soil water at any soil depth (Fig. 1, Table 1, Table 2). This indicates that the isotope ratios of soil water from all soil layers were indistinguishable from the LMWL and that evaporative ^2H - and ^{18}O -enrichment had no significant effect on the isotope composition of soil water at our research site.

Xylem water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values of *P. abies* varied across all years between -45.9‰ and -99.4‰ and between -6.3‰ and -13.5‰, respectively (Fig. 1, Fig. S1). Xylem water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values of *F. sylvatica* varied across all years between -57.2‰ and -89.0‰ and between -7.4‰ and -12.0‰, respectively (Fig. 1, Fig. S1). Xylem water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values of *P. abies* are indistinguishable from the LMWL, while those of *F. sylvatica* plot slightly below the LMWL (Fig. 1). The 95% confidence interval of the slope of xylem water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values of *P. abies* or *F. sylvatica* overlapped with the confidence intervals of the slope of the soil water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values (Table 1, Table 2).

Simulated soil water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values were in good agreement with measured soil water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values (Fig. 2 a,b). Orthogonal regressions of measured soil water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ over simulated soil water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ resulted in R^2 values that ranged between 0.71 and 0.91 for $\delta^2\text{H}$ and between 0.72 and 0.92 for $\delta^{18}\text{O}$ (Table S2). Simulated xylem water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values were also in good agreement with measured values. Here orthogonal regressions of measured xylem water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ over simulated xylem water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ resulted in R^2 values of 0.61 and 0.57 for $\delta^2\text{H}$ and $\delta^{18}\text{O}$ of *P. abies* and of 0.75 and 0.73 for $\delta^2\text{H}$ and $\delta^{18}\text{O}$ for *F. sylvatica* (Table S3). Simulated and measured soil moisture content also agreed well, with R^2 s of 0.85, 0.86 and 0.87 for soil moisture at 10 cm, 20 cm and 30 cm depth, respectively over all four study years (Fig. S2).

Simulated MRT of soil water for the years 2012 – 2015 increased generally with increasing soil depth (Fig. 3). The median MRT at 0.05 m soil depth across all years was 41 days, but varied slightly among seasons: it was on average 47 ± 26 days in winter (December,

January, February), 58 ± 21 days in spring (March, April, May), 42 ± 13 days in summer (June, July, August) and 35 ± 9 days in autumn (September, October, November). The median MRT at 0.35 m soil depth across all years was 100 days. During winter, the median MRT was 94 ± 23 days, in spring 113 ± 26 days, in summer 115 ± 31 days, and in autumn 98 ± 31 days. At 0.65 m soil depth, the median residence time of soil water across all years was 176 days. During winter, median MRT was 161 ± 52 days, and in spring 180 ± 39 days, whereas summer and autumn showed even longer MRTs of 207 ± 48 and 209 ± 78 days, respectively.

Fig. 4 illustrates how to best read the simulated age distributions of root water uptake (RWU) displayed in Fig. 5: In Fig. 4, the youngest 20% of water taken up by trees on day X had precipitated in the time period Y days before day X. Likewise, the youngest 80% of the water taken up by trees on day X had precipitated in the time period Z days before day X. In general, steep curves indicate a larger fraction of water taken up by trees from recent precipitation events. Each line in Fig. 5 can be interpreted accordingly and indicates thus the cumulative age distribution of water taken up by trees on a respective day of the year. Note that RWU only occurred when the atmosphere was sufficiently dry to allow transpiration. While the age distribution of root water uptake was simulated for the entire year for the evergreen species *P. abies* (Fig. 5a), it was simulated only for the growing season (i.e. May to October) for the deciduous species *F. sylvatica* (Fig. 5b). To simplify the very detailed information on the age distribution of RWU contained in Fig. 5 a,b, we computed the average age distribution of water cumulatively taken during each of the months March to October 2012 - 2015 for *P. abies* and during each of the months May to October 2012 - 2015 for *F. sylvatica* (Fig. 6). These were the months where >95% of the annual transpiration occurred for the respective tree species (Fig. 5 a,b).

We found that across May-October the youngest 20% of the water cumulatively taken up by *P. abies* was between 0 and 8 days old and between 0 and 9 days for *F. sylvatica* (Fig. 6). The youngest 80% of the water cumulatively taken up by *P. abies* across May-October was between 0 and 149 days old and between 0 and 165 days old for *F. sylvatica*. On average, water taken up in the summer was older than water taken up in spring and autumn. This is illustrated by an average maximum age of 181 and 174 days for the youngest 80% of the water cumulatively taken up by *P. abies* or *F. sylvatica*, respectively across the four years in May and an average maximum age of 104 and 123 days for the youngest 80% of the water cumulatively taken up by *P. abies* or *F. sylvatica*, respectively across the four years in August. In addition, our results show that in dry summers, such as July, August, September

and October 2013 and 2015, *P. abies* and *F. sylvatica* took up water that was older than water that was taken up in summer months of the wetter years 2012 and 2014 (Fig. 6). Interestingly, the simulated age distribution of water cumulatively taken up in the dry summers of 2013 and 2015 differs between *F. sylvatica* and *P. abies* (Fig. 7, Fig. S3). In July, August and September of the dry years 2013 and 2015, the youngest 30 to 80% of the water cumulatively taken up by *F. sylvatica* was between 10 and 100 days older than the water cumulatively taken up by *P. abies*. In August 2012 and June 2014, both of which were dry months, there was also a tendency that the water cumulatively taken up *F. sylvatica* was older than the water taken up by *P. abies* (Fig. 7, Fig. S3).

We computed the age distributions of water that was cumulatively taken up by the trees during an entire growing season. This allowed us to describe the temporal origin of precipitation that was taken up by a tree from the soil throughout an entire growing season. We defined the growing season (and thus cumulated water uptake) for the evergreen conifer *P. abies* to last from October 1st of the previous year to September 30th of the current year and for the deciduous *F. sylvatica* from May 1st to September 30th (Fig. 8). Our results show that when averaged across all four years 43% (*P. abies*) and 49% (*F. sylvatica*) of the water was cumulatively taken up by the two tree species throughout a growing season (i.e. between May and October) originated from precipitation events that occurred during the same growing season (Fig. 8 a,c). Additional 45% and 41% of the water taken up by *P. abies* and *F. sylvatica* during a growing season originated from precipitation that occurred in the preceding autumn or winter, and 12% and 10% originated even from the previous growing season (or before). The contribution of different precipitation events to the total water used by trees throughout a growing season is, however, not equally distributed throughout the year, but shows a bimodal distribution. Precipitation occurring in the months of April to August of the current growing season and precipitation occurring in October to December prior to the current growing season (i.e. of the previous year) contribute proportionally larger fractions to the cumulative seasonal source water of trees than precipitation occurring in the months of January to March of the current year (Fig. 8b,d). This bimodal distribution is likely a direct consequence of the yearly precipitation patterns at our site, where little precipitation occurred from December to March throughout all four years of the study (Fig. 1, Fig. 2). We found marked differences in the temporal origin of precipitation that was taken up by *P. abies* and *F. sylvatica* during a growing season. In general, *P. abies* used more water that originated from precipitation that occurred during the preceding autumn or winter than *F. sylvatica*. In

contrast, *F. sylvatica* utilized more water that originated from precipitation that occurred during the same growing season (Fig. 8e).

Discussion

Temporal origin of water taken up by P. abies and F. sylvatica

Our study shows that the water that is cumulatively taken up by *P. abies* and *F. sylvatica* throughout a growing season is a mix of young water that had precipitated only days or a few weeks before water uptake, and older water that had precipitated several months before water uptake (Fig. 6, Fig. 8). While it is well known that the water supply of vegetation in seasonally dry ecosystems depends on precipitation from different times of the year (Ehleringer *et al.*, 1991; Brooks *et al.*, 2010), the temporal origin of water used by trees in temperate ecosystems was previously unknown. Our results now indicate that autumn and winter precipitation and even precipitation from the previous growing season contribute substantially to the water supply of temperate trees. This finding is important as it suggests that winter precipitation could buffer the impacts of summer drought on temperate forests. Conversely, it suggests that reduced precipitation in autumn and winter months could amplify the impact of dry spells or drought for the functioning of temperate forest trees in the summer.

Interestingly, the age distribution of water taken up by *P. abies* and *F. sylvatica* in the months May to October differed between two species (Fig. 7, Fig. S3). In particular in the months of the dry summers of 2013 and 2015, *F. sylvatica* took up more old water than *P. abies* while both species show a very similar age distribution of water taken up in the summer months of the wet year 2014. Differences between *P. abies* and *F. sylvatica* with respect to the age distribution of water taken up during dry months are likely the consequence of different root distributions of the two species, in particular in deeper soil layers, where roots of *P. abies* are absent (Leuschner *et al.*, 2001; Schmid & Kazda, 2001)(Fig. S4). Brinkmann *et al.* (in prep) showed that *P. abies* and *F. sylvatica* both utilize soil water from the upper soil layers when abundant water is available for plant uptake in these layers. However, in dry periods when water supply in the upper soil layers declines, *F. sylvatica* is able to access water from deeper soil layers, while *P. abies* is not able to access this water. Given increasing residence times of soil water with in deeper soil layers (Fig. 3), the different abilities of the two species to access deeper soil water during dry periods consequently explains the larger fraction of old water taken up by *F. sylvatica* in dry summer months as compared to *P. abies*.

We also found differences between *P. abies* and *F. sylvatica* with respect to the temporal origin of water that is cumulatively taken up throughout a growing season (Fig. 8). When averaged across all four years, *P. abies* used more water that originated from precipitation that occurred in the preceding autumn or winter, while *F. sylvatica* utilized more water that originated from precipitation that occurred in the same growing season (Fig. 8e). In contrast to the deciduous *F. sylvatica*, the evergreen tree *P. abies* is able to take up water in autumn and winter. Since water taken up at any given moment contains a substantial fraction of recently precipitated water (Fig. 6), water cumulatively taken up throughout a growing season will thus contain more winter precipitation for *P. abies* than for *F. sylvatica*. In addition, *F. sylvatica* has higher transpiration rates than *P. abies* in the summer months (Fig. 5). Again, as water taken up at any given moment contains a substantial fraction of recently precipitated water, higher summer transpiration rates will lead to an increased uptake of recently precipitated water by *F. sylvatica*. Differences in growing season length of the two species, amplified by higher summer transpiration rates of *F. sylvatica* compared to *P. abies* can thus explain the species-specific differences in the temporal origin of water that is cumulatively taken up by two species throughout the growing season (Fig. 5).

Niche complementarity with respect to the use of different water sources has to date largely focused of the spatial arrangement of different niches in the soil or on the exploitation of distinct moisture pools by plants such as soil vs. ground water (Dawson & Pate, 1996; Bertrand *et al.*, 2014) or soil vs. stream water (Dawson & Ehleringer, 1991). Only few studies have shown, that different co-existing plant species can utilize moisture sources of different temporal origin (Ehleringer *et al.*, 1991). Here we show, that the two most common tree species in temperate European forests are partly complementary with respect to the temporal origin of water that they utilize throughout a growing season. Our finding thus provides one mechanistic explanation for the recently detected positive relationships between tree diversity and ecosystem function (Grossiord *et al.*, 2014; Musavi *et al.*, 2017).

The influence of MRT on variability in the temporal origin of water taken up by trees

Precipitation input, transpirational water loss and infiltration rates of water into the soil strongly influence the MRTs of soil water and thus the age distribution of water taken up by the trees. This can be nicely seen in Fig. 3 where intensive rain events, e.g., in May 2015, caused an immediate decrease in MRT over the whole soil profile we consider here. This suggests that MRTs of soil water are generally shorter in years with high precipitation inputs and high transpiration rates. In fact, MRTs of soil water were particularly long in the second

half of the year 2015, which can be attributed to the extremely hot and dry 2015 summer (MeteoSchweiz, 2016; Orth *et al.*, 2016). As a consequence of the long soil water MRTs triggered by the hot and dry 2015 summer, the age distribution of water taken up by *P. abies* and *F. sylvatica* between June and October 2015 also shifted to water with higher ages in both species as compared to the other years that were wetter (Fig. 6). These patterns are in line with Sprenger *et al.* (2016), who also identified that precipitation amount and precipitation intensity (defined as the ratio of the precipitation amount over the number of days with precipitation (Hrachowitz *et al.*, 2009)) are key drivers of soil water MRTs.

Linking precipitation, soil and xylem water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values

The age distribution of water taken up by *P. abies* and *F. sylvatica* throughout a growing season has also important implications for estimating the source water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ of temperate trees and consequently for the interpretation of tree ring $\delta^{18}\text{O}$ chronosequences or sedimentary leaf wax $\delta^2\text{H}$ records (Treydte *et al.*, 2006; Rach *et al.*, 2017). Our study shows that source water of trees is not directly coupled to precipitation as often assumed, but consists instead of a mix of different precipitation events that had occurred weeks or months before the water was actually taken up by the tree. Considering such age distributions will be critical for estimating source water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values from the GNIP data-base or from the online isotope calculator for precipitation (OIPC) (Bowen & Wilkinson, 2002). This is in particular relevant if contributions of past precipitation events to the cumulative seasonal source water follow a bimodal or even more complex distribution pattern as we have shown here (Fig. 7). Otherwise, the source water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values of trees will likely be over- or under-estimated, which could impair the interpretation of tree ring $\delta^{18}\text{O}$ chronosequences or sedimentary leaf wax $\delta^2\text{H}$ records.

Model performance and evaluation of model assumptions

Hydrus-1D was optimized with soil moisture values as well as with soil water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values. The simulated soil water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values can explain a substantial fraction of the variability that we observed in measured soil and xylem water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values (Fig. 2, Table S2, Table S3). In addition, the modelled soil moisture also agrees well with empirically determined soil moisture at the site for all years of the study (Fig. S2). Following optimization, Hydrus-1D was independently validated with xylem water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values, which also yielded 75% and 73% explained variance, respectively (measured in *F. sylvatica*), and 61% and 57% of the values for *P. abies*, respectively (Table S3). In general, this

illustrates that the model with our parameterization allowed to simulate hydrological processes for our site with high precision.

Importantly, Hydrus-1D simulated the isotope composition of soil and xylem water under the assumption that no isotope fractionation of soil water occurs during soil water evaporation at the soil surface at our forest site. In contrast to this assumption, previous studies have reported that soil water isotopic ratios, in particular those measured in shallow soil layers, that deviate from the LMWL, indicating kinetic isotope fractionation associated with evaporative water losses from the soil surface (Zimmermann *et al.*, 1967; Hsieh *et al.*, 1998; Meinzer *et al.*, 2001; Gazis & Feng, 2004; Eggemeyer *et al.*, 2009; Brooks *et al.*, 2010; Song *et al.*, 2011). However, the slopes of all soil water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values that we measured in this were indistinguishable from the slopes of the LMWL (Fig. 1). This suggests that evaporative water loss from the soil surface and associated ^2H - and ^{18}O -enrichment of soil water plays no important role at our research site and supports the assumption we made for the model. Our finding is in agreement with previous work by Schulze *et al.* (1994) and Kelliher *et al.* (1995) who suggested that the contribution of soil evaporation to whole ecosystem evapotranspiration becomes negligible in ecosystems with a leaf area index of three or larger (such as the temperate forest that we investigated), since available energy at the soil surface is low in dense forests.

Hydrus-1D is also based on the assumption that water at a given depth in the soil is well mixed in the pore space and that all water is available for root water uptake. This model assumption of one homogenous soil water pool is in contrast to recent studies that have suggested that soil water is often split into two isotopically distinct pools: one pool (the mobile soil water pool) consists of precipitation water that is not affected by evaporation and feeds the ground water and river recharge discharge. The second pool (the immobile soil water pool) consists of water that is ^2H - and ^{18}O -enriched by evaporation and resides in the capillary spaces of the soil where it is partially available for plant water uptake. Given that the two proposed soil water pools are differently affected by evaporation, they can be distinguished in $\delta^2\text{H}$ and $\delta^{18}\text{O}$ dual isotope space, where water from the mobile water pool which feed river and groundwater discharge plots on the LMWL and water from the immobile and evaporatively ^2H - and ^{18}O -enriched soil water pool which is used by plants plots below the LMWL (Brooks *et al.*, 2015; Evaristo *et al.*, 2015; Good *et al.*, 2015). In contrast to the findings that lead to the suggested “two water worlds”, the slopes of $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values in dual isotope space are indistinguishable for precipitation, soil and xylem water in our study (Fig. 1, Table 1, Table 2, Table S1). This suggests that for the investigated forest,

no such two water worlds exist but that in agreement with our model assumption soil water at a given depth is well mixed in the pore space.

Conclusions

The mean residence time of precipitation in the soil as well as the age distribution of water taken up by *P. abies* and *F. sylvatica* provides important new insights into the link between precipitation, plant water uptake and thus ecohydrological dynamics of temperate ecosystems. Our study shows that the water taken up by trees in a temperate forest is a mix of young water that had precipitated during the actual growing season but that autumn and winter precipitation and even precipitation from the previous growing season also contribute substantially to the water supply of temperate trees. In addition, both investigated tree species differ and are thus partly complementary with respect to the temporal origin of water that they utilize throughout a growing season. Resolving the temporal dynamics of the source water origin of trees is essential to predict how water as a critical resource is used in a temperate forest. In addition, it allows to anticipate how future changes in precipitation patterns will impact the functioning of temperate ecosystems. Resolving the age distribution patterns of water taken up by trees throughout a growing season also provides the means to weigh monthly precipitation $\delta^2\text{H}$ and $\delta^{18}\text{O}$ and to obtain thus more realistic estimates of source water $\delta^2\text{H}$ and $\delta^{18}\text{O}$. In turn, this will improve the model-based interpretation of tree ring $\delta^{18}\text{O}$ chronosequences or sedimentary leaf wax $\delta^2\text{H}$ records.

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Author Contributions

This study was designed by Ansgar Kahmen and Markus Weiler. Research was performed by Nadine Brinkmann and Stefan Seeger as well as collecting and analyzing the data. Data interpretation was done by all authors as well as writing the manuscript. All input and output data can be found under DOI: [10.3929/ethz-b-000202251](https://doi.org/10.3929/ethz-b-000202251) upon acceptance of this manuscript.

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Figure legends:

Fig. 1 $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values of precipitation (Lägeren research site and Buchs/Suhr GNIP station), soil water at different depths (0-0.05 m, 0.05-0.1 m, 0.1-0.2 m, 0.2-0.3 m, 0.3-0.4 m, 0.4-0.5 m, 0.5-0.6 m, 0.6-0.7 m) and xylem water of *F. sylvatica* and *P. abies* at the Lägeren research site for all study years. Global meteoric water line (GMWL) is defined as $\delta^2\text{H}=8\delta^{18}\text{O}+10\text{‰}$ (Dansgaard, 1964). GMWL and the local MWL for Lägeren research site and Buchs/Suhr are displayed in all panels as lines. All orthogonal relationships are highly significant at $p < 0.001$. Intercepts, slopes, R^2 s and p-values for the regression lines as well as the confidence intervals for precipitation, soil- and xylem water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values are provided in Tables S1-S3.

Fig. 2 (a) $\delta^2\text{H}$ and (b) $\delta^{18}\text{O}$ values of precipitation and soil water at 0.0 to 0.7 m soil depth at the Lägeren research site in 2012-2015. The color gradient indicates the isotopic composition of precipitation and soil water. Vertical rectangles display measured isotope values. Values outside the rectangles are Hydrus-1D simulated values.

Fig. 3 Precipitation and mean residence time of soil water at 0.0 to 0.7 m soil depth for the four study years (2012-2015). The color gradient indicates the mean residence time of soil water in days. Dashed lines indicate constant mean residence times of soil water of 30, 60, 120, 240 and 360 days.

Fig. 4 Schematic explanation of the cumulative age distributions of root water uptake (RWU) displayed in Fig. 5. The youngest 20% of water that has been taken up by the trees on day x (between 0.8 and 1.0 cumulative fraction of RWU) originates from the period y (indicated by the horizontal arrow). The youngest 80% of water that has been taken up by the trees on day x (between 0.2 and 1.0 cumulative fraction of RWU) originates from the time period z.

Fig. 5 Cumulative age distributions of root water uptake (RWU) for the four study years at Lägeren research site. Each line indicates a day when water was taken up by a beech or spruce tree. During days with high atmospheric humidity or during precipitation events, Hydrus-1D assumed no transpiration stream and thus no water uptake from the soil. The different colors indicate the month were water has been taken up by (a) *P. abies* and (b) *F. sylvatica*.

Fig. 6 Cumulative age distributions of root water uptake (RWU) by *P. abies* and *F. sylvatica* aggregated for each month in the growing season from May to October (2012-2015) at the Lägeren research site. Displayed are values for individual years and the mean cumulative curve across all four years.

Fig. 7 Monthly averages of RWU age differences between *P. abies* and *F. sylvatica*. Positive values indicate that *F. sylvatica* is taking up older water than *P. abies*. The colored lines show differences for specific months, while the black lines show the months' values averaged over the four years.

Fig. 8 Temporal origin of the cumulative growing season RWU (i.e. the cumulative source water) of *P. abies* (a,b) and *F. sylvatica* (c,d) for an entire growing season. RWU is displayed as cumulative curve (a,c) and percentage (b,d) starting at the end of each year's growing season (indicated by shaded area). (d) Difference between the temporal origin of the cumulative growing season RWU curve of *F. sylvatica* and *P. abies*. Displayed are values for individual years and the mean across all four years.

Supporting Information

Fig. S1 $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values of precipitation (GNIP station Buchs/Suhr and Lägeren), soil water at different soil depths and xylem water of *P. abies* and *F. sylvatica* in 2012-2015.

Fig. S2 Simulated versus observed volumetric soil moisture content.

Fig. S3 Monthly averages of RWU ages differences between *P. abies* and *F. sylvatica* in 2012-2015.

Fig. S4 Normalized relative fine root densities for *P. abies* and *F. sylvatica*.

Fig. S5 Illustration of residence time modelling with a storage matrix.

Fig. S6 Root water uptake model after Feddes *et al.* (1978) as used within Hydrus-1D.

Table S1 Orthogonal regressions of measured precipitation $\delta^2\text{H}$ and $\delta^{18}\text{O}$ of Lägeren and Buchs/Suhr GNIP station.

Table S2 Orthogonal regressions of measured soil water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ over simulated soil water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ for differing soil depths in 2012 to 2015.

Table S3 Orthogonal regressions of measured xylem water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ over simulated xylem water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ for *P. abies* and *F. sylvatica*.

Table S4 Hydrus-1D model parameters.

Methods S1 Modelling residence time distributions of water in the soil, root water uptake and temporal origin of xylem water using HYDRUS 1D.

Tables

Table 1 Orthogonal regressions of measured soil water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ at different soil depths. All linear relationships had a p-value < 0.001.

Soil depth [m]	R ²	Intercept	Intercept C.I. 95%		Slope	Slope C.I. 95%	
			Lower	Upper		Lower	Upper
0-0.05	0.98	5.71	0.88	11.27	7.89	7.37	8.49
0.05-0.1	0.99	7.07	3.00	11.60	7.92	7.50	8.38
0.1-0.2	0.98	9.90	4.57	15.99	8.04	7.53	8.63
0.2-0.3	0.99	9.32	3.96	15.42	7.89	7.41	8.44
0.3-0.4	0.98	8.23	2.26	15.15	7.68	7.15	8.30
0.4-0.5	0.97	10.55	3.84	18.43	7.79	7.21	8.49
0.5-0.6	0.93	11.75	0.67	26.28	7.83	6.88	9.07
0.6-0.7	0.94	14.72	3.90	28.68	8.08	7.16	9.27

Table 2 Orthogonal regressions of measured xylem water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ from *P. abies* and *F. sylvatica*. All linear relationships had a p-value < 0.001.

Xylem water data	R ²	Intercept	Intercept C.I. 95%		Slope	Slope C.I. 95%	
			Lower	Upper		Lower	Upper
<i>F. sylvatica</i>	0.92	-6.36	-10.12	-2.17	7.06	6.69	7.48
<i>P. abies</i>	0.96	2.28	-0.03	4.75	7.45	7.21	7.70

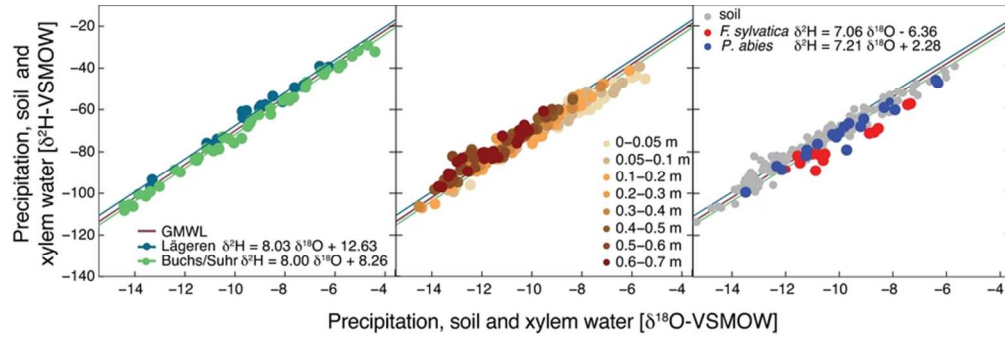


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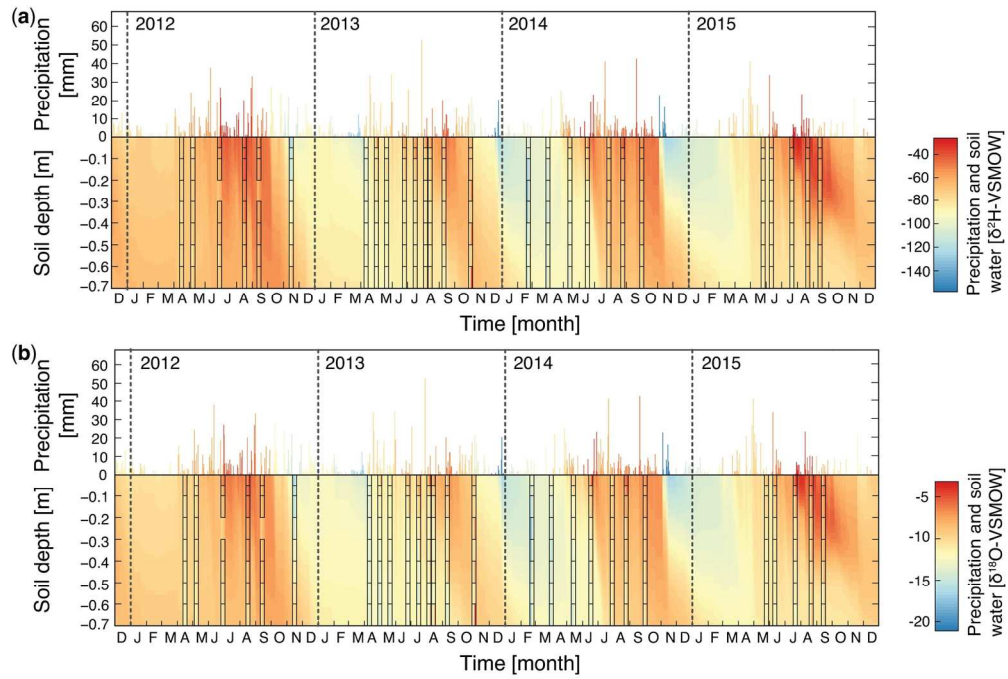


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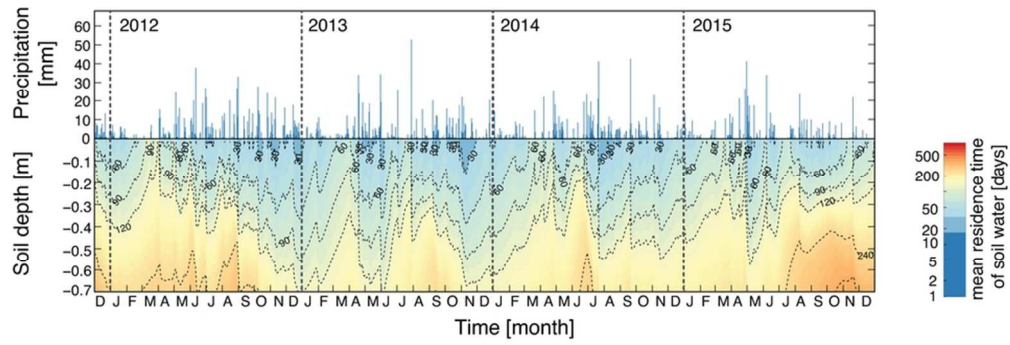


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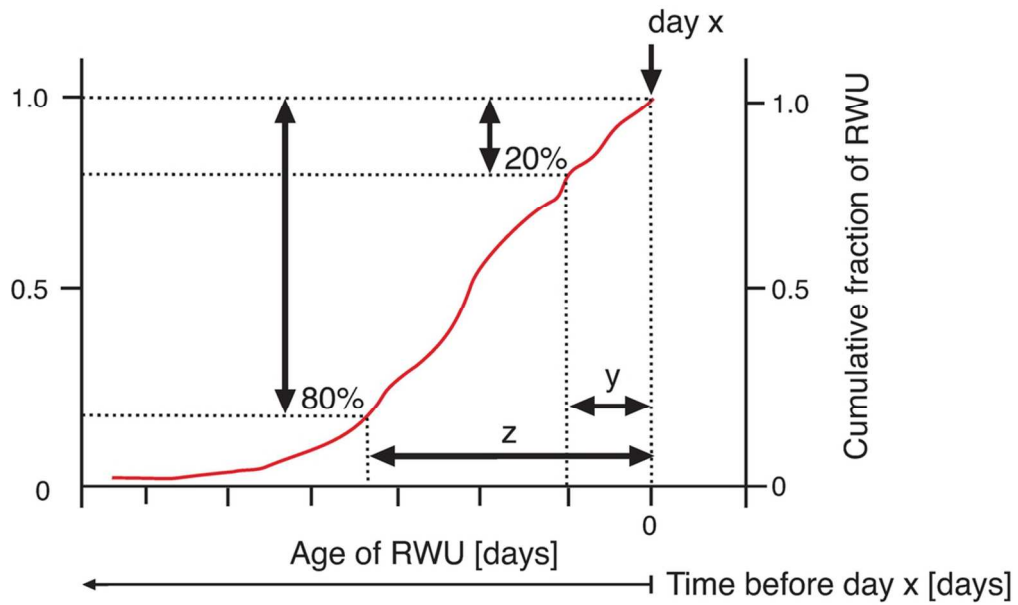


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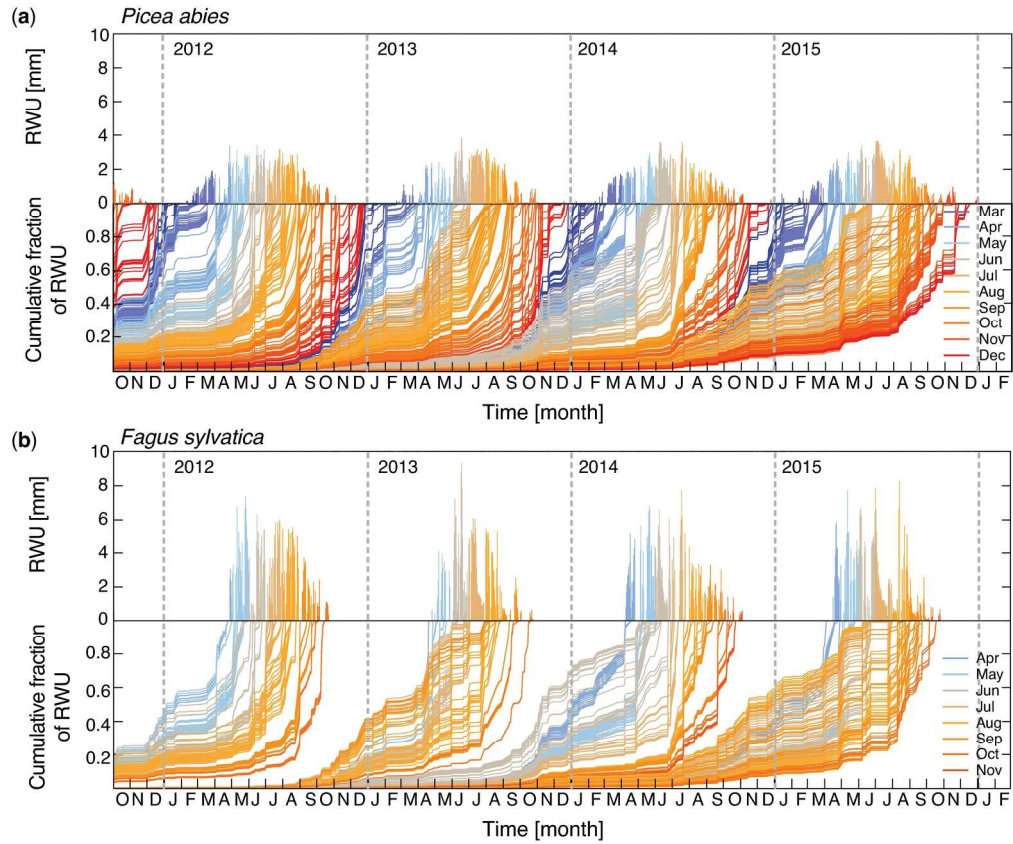


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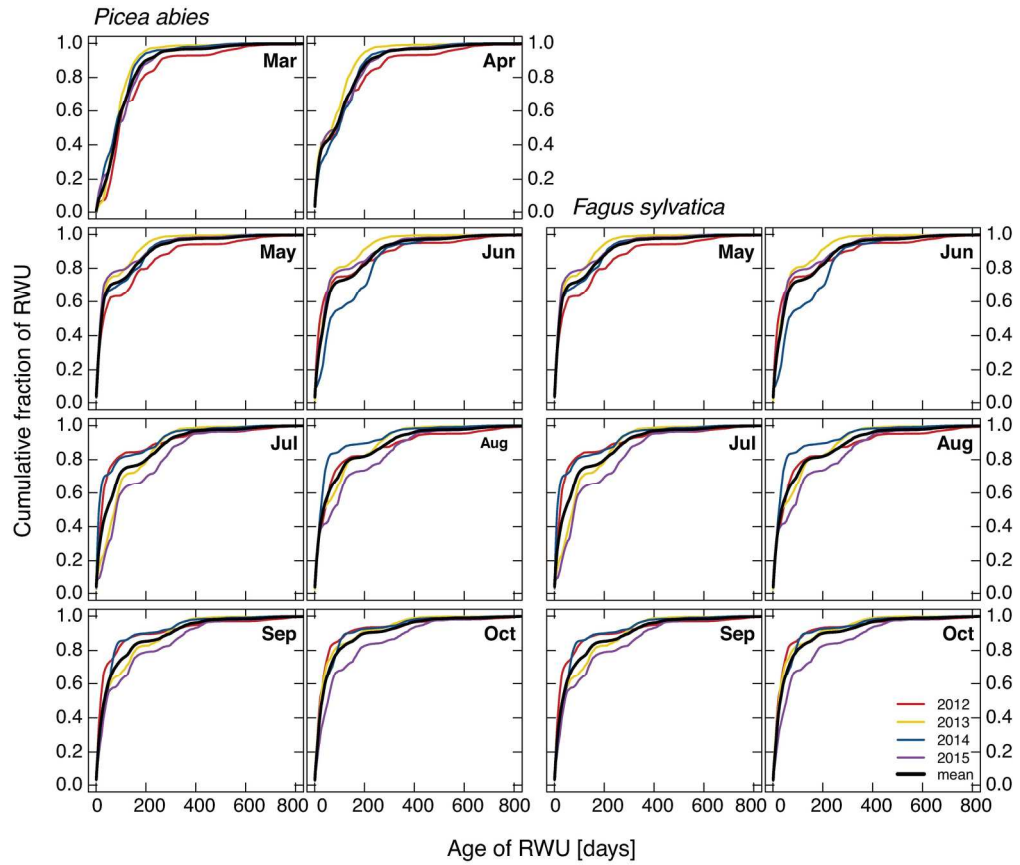


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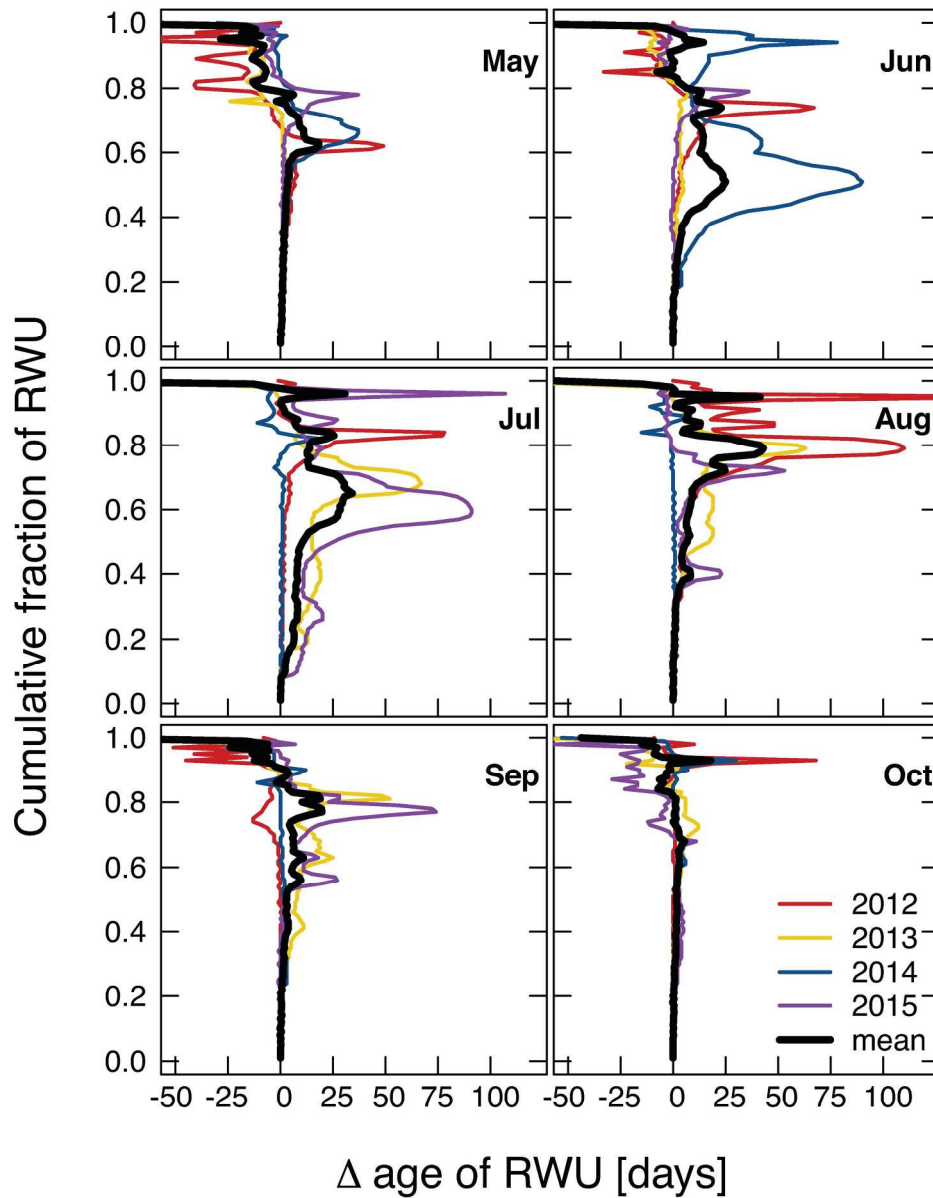


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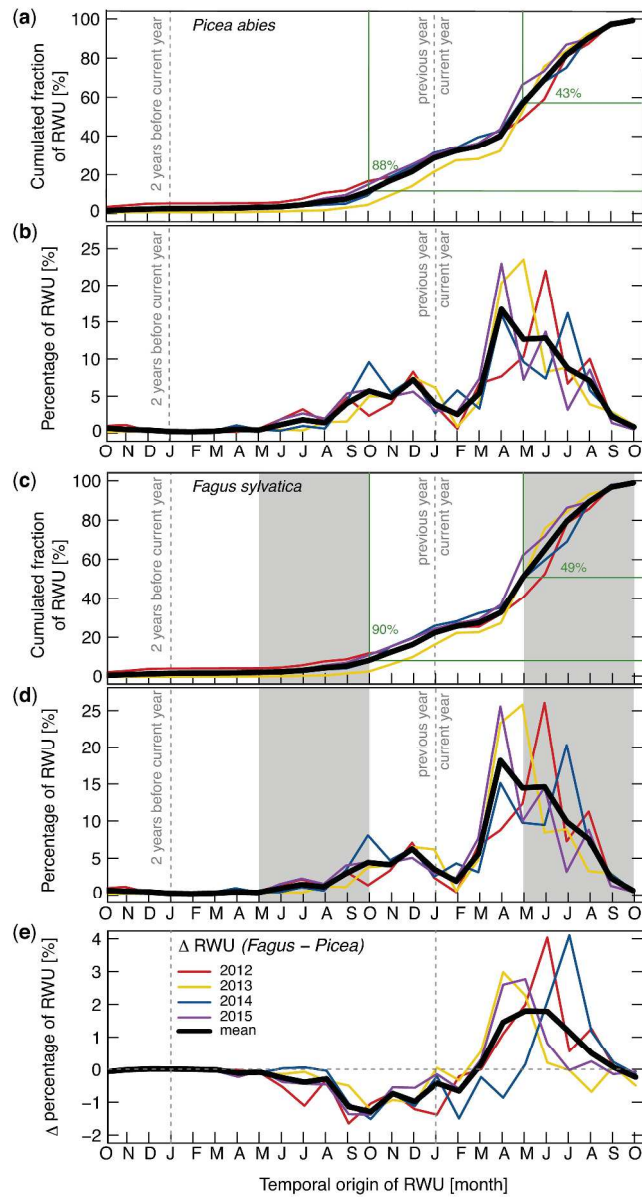


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