Climatic influences on summer use of winter precipitation by trees

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Abstract

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Key points

We determined the representation of water originating from winter versus summer precipitation in the xylem of common Swiss trees.

Water originating from winter precipitation was observed in trees at most sites, even at the height of summer, but varied among species.

Climate and species appear to be key controls over spatial and inter-annual variations in the seasonal origins of water used by trees.
Abstract

Trees in seasonal climates may use water originating from both winter and summer precipitation. However, the seasonal origins of water used by trees have not been systematically studied. We used stable isotopes of water to compare the seasonal origins of water found in three common tree species across 24 Swiss forest sites sampled in two different years. Water from winter precipitation was observed in trees at most sites, even at the peak of summer, although the relative representation of seasonal sources differed by species. However, the representation of winter precipitation in trees decreased with site mean annual precipitation in both years; additionally, it was generally lower in the cooler and wetter year. Together, these relationships show that precipitation amount influenced the seasonal origin water taken up by trees across both time and space. These results suggest higher turnover of the plant-available soil-water pool in wetter sites and wetter years.

Plain Language Summary

In the middle of a hot and dry summer, we often think that a large rain event can “rescue” a forest from drought. However, it is not clear whether trees can or do consistently use the water from summer rains. A growing body of research indicates that over the course of the summer growing season, trees take up significant amounts of water that originated as winter snow or rain. We studied the seasonal origins of the water taken up by three common tree species (beech, oak and spruce) in forest sites across Switzerland in two different years. Our results demonstrate that trees at most sites use some water from winter snow and rain, even at the height of summer, although there were differences among species and sites. The water sources used by trees likely reflect a combination of the amount and timing of winter and summer precipitation, the rate at which that precipitation moves through the soil, and the distribution of the tree roots that take up the water. Determining the seasonal origin of water used by trees, as well as why it may vary over time and space, can help us better anticipate the effects of global climate change.
Introduction

In ecosystems with seasonal growth, it could be expected that growing season precipitation should serve as the primary water source for plants when their water demand is high. However, many stable isotope studies have shown that the water used by trees during the growing season often originates primarily from winter rather than summer precipitation (Phillips & Ehleringer, 1995; Hu et al., 2010; Kerhoulas et al., 2013; Martin et al., 2018; Allen et al., 2019b; Berkelhammer et al., 2020). For instance, using an index of the seasonal origins of water taken up by trees, we previously found that common tree species from 182 sites across Switzerland mostly used water from winter precipitation at the height of an extremely dry summer (Allen et al., 2019b). In that study, however, trees in more humid sites used relatively less winter precipitation, and the proportions of summer versus winter precipitation in tree xylem varied by species (see also Williams & Ehleringer, 2000; Guo et al., 2018). These differences must reflect an interplay between root distributions, soil-water storage, and recharge dynamics. Resolving the controls over such patterns can improve our understanding of the vulnerability of vegetation to hydroclimatic disturbances.

The consistency, over space and time, in the seasonal origins of water used by trees, as well as how they are shaped by weather and climate, remain unresolved. We used stable isotopes of hydrogen and oxygen as tracers to study the seasonal origin of water in three common tree species in 24 long-term forest monitoring plots in Switzerland, bringing together observations made on the same trees in two different summers. Our objectives were 1) to determine whether the seasonal origins of water in trees varies consistently among species and across sites during two different growing seasons and 2) to test how variation in weather and climate factors may explain the observed differences. We hypothesized that our original observations demonstrating less reliance of trees on winter precipitation at wetter sites (Allen et al., 2019b) would also apply to wetter years, and thus that the hot and dry conditions in which we made our original observations may have resulted in atypically high use of winter precipitation. Our results provide insights relevant for a number of important questions, including how to reconstruct climates in the past, how water resources are partitioned within ecosystems in the present, and what sources of water may be critical for plants in the future.
Methods

Climatological context: The first sampling, carried out in 2015, occurred in the context of an unusually warm and dry summer (Table S1). Summer air temperatures were >2 °C higher and precipitation amounts were 20-40% below the long-term climate norm (1981-2010) in much of Switzerland, but up to 45% above the long-term norm in the southern and western Swiss Alps (MeteoSchweiz, 2015). These unusual conditions raised questions of whether or not the patterns that we previously observed – specifically, that winter precipitation contributes strongly to summer evapotranspiration (Allen et al., 2019a,b) – were likely to also hold in more typical summers. Many subsequent years have also continued to be warm and dry. In particular, a small subset of sites were resampled in the summer of 2018, which was the most extreme drought on record in central Europe (Schuldt et al., 2020). A larger set of sites were resampled in the summer of 2019, which was similarly hot; however, precipitation was more normal (MeteoSchweiz, 2019).

Field sampling: Our study was carried out in the context of a long-term forest health monitoring program that includes nearly 200 sites (Braun et al., 2017, 2020). Each site contains at least one of three key tree species: beech (Fagus sylvatica L.), spruce (Picea abies (L.) H. Karst.), and oak (Quercus robur L.). General site characteristics are described in Allen et al., (2019b) and in Figure S1 and Table S2.

Between 22 July and 3 August 2019, we collected samples from 8 individuals of each species at 24 sites (n = 258 trees in total; one site has 10 individuals of a species). Fully sunlit branches were collected, using pole pruners, by a technician suspended below a helicopter. Samples were returned to the ground, immediately enclosed in a black plastic trash bag to suppress transpiration, and left in a refrigerated cooler until further processing (< 24 h). Sites were selected to be broadly representative of the ranges of temperature, precipitation, elevation, and longitude included in the monitoring network as a whole. Here we compare our observations in 2019 to observations in the same 24 sites from our original sampling in 2015, where we collected samples using the same methodology from 3-8 of the same individuals of each species (n = 147
trees in total); this sampling was conducted between 27 July and 10 August 2015. A smaller subset of these sites was sampled in 2018 (n = 42 trees in total), as discussed in the supporting information.

**Sample processing:** For each sample, the bark and vascular cambium were removed from a fully suberized piece of the branch, the remaining xylem was sealed in a glass vial, and the vial was frozen until water extraction. Water extraction was carried out via cryogenic vacuum distillation at the Paul Scherrer Institute (2015) and at ETH Zurich (2019) on manifolds with an identical design as described in Orlowski et al. (2013). Branch samples were extracted under a 0.03 hPa vacuum for 2 h at 80 °C and the evaporated water was frozen in a liquid nitrogen trap. Samples were then analyzed for δ¹⁸O and δ³H by TC/EA-IRMS at the Paul Scherrer Institute (2015) and at ETH Zurich (2019). All values are presented per mil (‰) relative to V-SMOW. The standard deviation of an independent quality control standard used for analysis at the Paul Scherrer Institute was ≤ 0.2 ‰ δ¹⁸O and ≤ 0.4 ‰ δ³H. The standard deviation of an independent quality control standard used for analysis at ETH Zurich was 0.17 ‰ δ¹⁸O and 0.62 ‰ δ³H.

**Analytical approach:** To determine the seasonal origin of the precipitation in trees, we used an index of the isotopic signature of plant xylem water relative to seasonal cycles of isotopes in precipitation (Allen et al., 2019b). This seasonal origin index can be described as follows:

\[
SOI = \begin{cases} 
\frac{\delta_x - \delta_{\text{annP}}}{\delta_{\text{summerP}} - \delta_{\text{annP}}}, & \text{if } \delta_x > \delta_{\text{annP}} \\
\frac{\delta_x - \delta_{\text{annP}}}{\delta_{\text{annP}} - \delta_{\text{winterP}}}, & \text{if } \delta_x < \delta_{\text{annP}}
\end{cases}
\]  

Eq. 1

where \(\delta_x\) is the fractionation-compensated δ³H isotopic signature of xylem water, and \(\delta_{\text{winterP}}, \delta_{\text{summerP}}, \text{and } \delta_{\text{annP}}\) are the δ³H isotopic signatures of winter, summer, and volume-weighted annual precipitation at each study site. The \(\delta_x\) values in Eq. 1 were compensated for evaporative fractionation by projecting dual-isotope measurements of xylem water to local meteoric water lines along theoretical evaporation-line slopes, using the method described in detail in Allen et al. (2019b). Projecting the xylem water values onto the meteoric water line means that the SOI values reported here are based on both the δ³H and δ¹⁸O of the xylem samples, and thus that Eq.
would yield similar results for either isotope. Isotopic signatures of precipitation were estimated using data from the two years prior to sampling (i.e., August 2013-July 2015 for the 2015 xylem samples, and August 2017-July 2019 for the 2019 xylem samples), as inputs to a previously described and validated model (Allen et al., 2018). The site mean \( \delta^2H \) of precipitation in the two years prior to sampling in 2019 was enriched by 8.96‰ compared to 2015. The seasonal origin index (SOI) provides a measure of the overrepresentation of a season’s precipitation in xylem relative to the representation of that season’s precipitation in the annual precipitation amount. Negative values of SOI suggest an overrepresentation of winter precipitation in xylem and positive values suggest an overrepresentation of summer precipitation in xylem. The SOI will be near -1.0 for soil and plant water samples derived entirely from winter precipitation and near 1.0 for samples derived entirely from summer precipitation.

To study how the seasonal origin of water in trees varies as a function of mean annual precipitation amount between years, we used analysis of covariance. To study how variation in summer precipitation amount and other meteorological factors may contribute to the observed differences in the seasonal origin of water in trees between the sample years, we determined the change in SOI between years as a function of the change in temperature, precipitation, vapor pressure deficit and potential evapotranspiration at each site in the month prior to sampling and compared the mean of these slopes to zero using one sample t-tests. Similarly, we determined the magnitude of the difference in SOI at a given site between years and the magnitude of the differences in the same weather variables in the month prior to sampling at that site and correlated the measures using Spearman’s Rank Correlations. Daily climate data were generated from a geospatial model using weather station data (Meteotest, Bern, Switzerland).

Results and Discussion

The mean \( \delta^2H \) xylem water isotope ratios of all three tree species were more positive (7.1 to 14.3‰ enriched) in 2019 compared to 2015 (Figure S2; Table S3). In contrast, the mean \( \delta^{18}O \) xylem isotope ratios of all three species were similar in 2019 compared to 2015 (from -0.1‰ depleted to 1.1‰ enriched). Summer precipitation across our sites averaged 86 mm more in 2019 than in 2015. Xylem water also plotted closer to the meteoric water line in 2019 than in 2015 (Figure S2), suggesting greater soil surface evaporation in 2015 from a pool that contained less
summer precipitation. Given that these measurements resulted from similar sample handling and analysis, analytical errors would likely apply similarly and thus not explain this difference.

The within-plot and species-within-plot variation in xylem water isotopes can be evaluated using data from 2019. For plots with 2 different tree species (i.e., 8 plots with 16 individuals), the average standard deviation within plots was 7.61 ‰ $\delta^{2}$H and 1.22 ‰ $\delta^{18}$O. Average standard deviation within species within plots was generally smaller, ranging from 2.91 to 4.90 ‰ $\delta^{2}$H and 0.83 to 1.02 ‰ $\delta^{18}$O (Table S3). Estimates of variation within tree crowns, among trees, and across plots are limited and can be used to better inform study design (Goldsmith et al., 2018; von Freyberg et al., 2020).

First-Order Controls on Seasonal Origins of Water in Plants

![Graph: Seasonal Origin Index vs. Mean Annual Precipitation](image)

**Figure 1.** The seasonal origin index of water in xylem at sites sampled in both 2015 and 2019. Sites are ordered left to right from lowest (690 mm yr$^{-1}$ at Sion) to highest (1791 mm yr$^{-1}$ at Lurengo) mean annual precipitation. Data represent means ± SEM.
Mean site SOI was significantly more positive in 2019 compared to 2015, indicating a decrease in the overrepresentation of water from winter precipitation in trees (paired t-test; t = -10.2, df = 23, p < 0.0001, Figure 1). However, the SOI of water in trees was <0 in both 2015 (mean and median of sites = -0.60 and -0.54) and 2019 (mean and median of sites = -0.17 and -0.15), indicating that winter precipitation was overrepresented in late-summer tree xylem water in both sample years. Data sampled and analyzed in 2018 (which was another drought year) from seven of the same sites as 2015, using the same approach, also show overrepresentation of winter precipitation (Figure S3).

The SOI of water in trees increased linearly as a function of precipitation in both years at a common slope of 0.12 (unitless SOI) per 100 mm precipitation, but with intercepts that significantly differed in SOI by 0.43 (f²,45 = 22.2, p < 0.0001, adj. r² = 0.47; Figure S4A). Previous research in temperate semi-arid ecosystems has also observed that vegetation in wetter sites consistently uses more summer precipitation (Williams & Ehleringer, 2000; Guo et al., 2018). Both the slopes and intercepts significantly differed between the years when considering the relationship between the SOI of water in trees and precipitation in the month (July) before sampling, indicating that the effects of summer precipitation amount were not consistent over time (f³,44 = 10.4, p < 0.0001, adj. r² = 0.37; Figure S4B). Collectively, these observations indicate that annual precipitation amounts impose a first-order control on the seasonal origin of water used by plants. We hypothesize that greater inputs to a given volume of soil water storage should drive greater turnover of the water in that volume, and thus increase the proportion of recent precipitation within it. However, this mechanism assumes that the incoming precipitation either displaces existing soil water or re-fills soil storage depleted through evapotranspiration. If, alternatively, summer precipitation bypasses soil water storage in summer (e.g., when those pores may be filled by winter precipitation; Brooks et al., 2010), then we would expect the driest soils to show more responsiveness to changes in summer precipitation. The effects of precipitation amount on soil water turnover should apply across both time and space, which is consistent with our observation of higher representation of summer water in trees at wetter sites in both years and the generally higher representation of summer precipitation in the wetter year. While the flow processes involved remain unclear, our new findings make it clearer that dry conditions result in higher relative use of, and perhaps reliance on, stored winter precipitation.
**Second-Order Controls on Seasonal Origins of Water in Plants**

While trees at most sites demonstrated an overrepresentation of precipitation originating from winter in both years, we also observed compelling differences in the representation of winter versus summer precipitation in trees between years. The general positive shift in SOI from 2015 to 2019 corresponded with a general positive shift towards more humid conditions in July, but the magnitudes of those SOI shifts by site were not well explained by the magnitudes of weather changes by site.

**Figure 2.** The change in the seasonal origin index of water at sites sampled in both 2015 and 2019 as a function of the change in A) temperature, B) precipitation, C) vapor pressure deficit (VPD) and D) potential evapotranspiration (PET) in the month (July) prior to the sampling. The mean of the slopes (change in SOI per change in weather) significantly differed from zero for all four of the weather metrics.
All sites showed a lower temperature, higher precipitation, lower VPD, and lower PET in the month (July) prior to sampling in 2019, compared to the month prior to sampling in 2015, whereas all sites showed higher SOI values in 2019 compared to 2015 (Figure 2). These patterns were consistent within species (Figure S5). Consequently, the mean change in SOI per change in July precipitation between years had a significant positive value (i.e., the mean of site slopes significantly differed from zero; \( p < 0.0001 \)); this also held true for changes in SOI per change in other July weather indices, including temperature, VPD, and PET (\( p < 0.0001 \)). Interestingly, these statistically significant relationships did not hold true when the changes in any of the four weather indices were calculated for the two months (June + July) prior to sampling, nor was there a statistically significant relationship with the year-to-year difference in annual precipitation (\( p = 0.92 \)).

However, in spite of the consistent direction of the changes in weather with the change in SOI, the magnitude of the difference in SOI among sites between 2019 and 2015 was not correlated with the magnitude of the difference in temperature (\( r = -0.15, p = 0.5 \)), precipitation (\( r = 0.18, p = 0.4 \)), vapor pressure deficit (VPD; \( r = -0.33, p = 0.1 \)), or potential evapotranspiration (PET; \( r = 0.2, p = 0.3 \)) in the month (July) prior to sampling (Figure S6). In other words, a greater difference in temperature, precipitation, VPD, or PET between the two years was not correlated with a greater difference in SOI. All three species exhibited similar correlations between year-to-year SOI differences and year-to-year differences in weather indices, although spruce exhibited a significant correlation (\( r = -0.61, p = 0.02 \)) between SOI differences and VPD differences. The correlation between SOI differences and precipitation differences was not strengthened by excluding small precipitation events (< 5 mm), which probably would not have infiltrated into the soil. Finally, we found no evidence for a significant correlation of by-site slopes (change in SOI per change in weather metric) with site mean annual precipitation (\( p > 0.1 \)). Thus, we were unable to explain the relative magnitudes of changes in SOI among sites, even if the average change in SOI per change in (only) previous-month weather differences was highly significant.

Understanding how inter-annual differences in SOI vary with differences in precipitation and other weather metrics across sites can provide insights that add to our observations of first-order controls on the seasonal origins of water in trees. Second-order controls on the source of
precipitation used by trees may relate to interactions between climate and rooting depths. For instance, if plants in wetter environments have shallow rooting depths, then the available storage for plant-available water would be smaller and we would have expected greater SOI sensitivities to precipitation in the wetter environments; we did not observe that. An alternative second-order control may relate to differences in how precipitation infiltrates and percolates through soils in wetter versus drier conditions. If all of July precipitation entered the soil profile and became available to roots, we would expect the drier soils in drier environments to have been more sensitive to increased inputs, resulting in greater changes in SOI per changes in July precipitation amount; however, we also did not observe this to be the case (Figure S6). While inter-annual differences in weather and SOI were widespread across sites, changes in magnitude in SOI were not well explained by any variable across the sites, such that there was a lack of evidence that second-order controls over the seasonal origins of plant-water are consistent among sites.

Species Differences in Seasonal Origins of Water in Plants

Figure 3. Probability density functions (scaled to maximum of 1) of the seasonal origin index (SOI) of water in the xylem of A) beech, B) oak and C) spruce in summer 2015 (white) and 2019 (blue). Sample sizes are in Table S3.
The mean SOI values were shifted significantly higher in 2019 compared to 2015 for beech (t-test; \( t = -10.4, \text{df} = 89, p < 0.0001 \), difference of mean SOI = 0.50) and spruce (t-test; \( t = -6.0, \text{df} = 124, p < 0.0001 \), difference of mean SOI = 0.35), but not oak (paired t-test; \( t = -1.7, \text{df} = 13, p = 0.1 \), difference of mean SOI = 0.15) (Figure 3). The distributions of SOI values also significantly differed between years for beech and spruce (Kolmogorov-Smirnov tests, \( p < 0.0001 \)). In both sample years, we observed that beech had the highest, and spruce the lowest, overrepresentation of winter precipitation, with oak showing intermediate use. Both beech and spruce demonstrated a decrease in the overrepresentation of winter precipitation in the wetter compared to the drier sampling year. Results from oak must be interpreted cautiously as they are from only two sites.

Previous research has demonstrated that plant species differ in their use of winter versus summer precipitation (Williams & Ehleringer, 2000; Guo et al., 2018), as well as differ in the elasticity of their use of summer precipitation when more becomes available (West et al., 2007). The differences observed among beech, spruce, and oak are likely to partially result from how the predominant climate conditions shape root distributions and therefore the ability for species to exploit summer precipitation events (Fan et al., 2017). Spruce occurs in wetter environments in Switzerland and has more shallow roots (Schmid & Kazda, 2002), which may enable them to use small episodic summer precipitation events. Beech occupies intermediate environments and oak the driest environments in Switzerland. Our results indicate that the mean change in SOI per change in July precipitation between years was higher in spruce (0.008) and beech (0.010) than oak (0.003), which lends some support to the idea that spruce and beech rooting patterns may make them more sensitive to summer precipitation than oak. We also previously posited that the strong overrepresentation of winter precipitation in beech in 2015 may have been because those trees used water from soil layers that were not recharged during dry summer conditions because any new summer precipitation bypassed those soil layers due to preferential flow (Allen et al., 2019b). Our new findings show that even the beech forests at drier sites increase in their use of summer precipitation when more is available.

Our study was not designed to understand how much water trees use from particular precipitation events, although this is of interest given projected changes in event size (Vautard et al., 2014).
and the greater likelihood that high precipitation intensities correspond with greater recharge
(Jasechko & Taylor, 2015) or preferential flow through the subsurface (Buttle & McDonald,
2002). Pairing fine temporal resolution sampling with a large spatial domain that spans climates
may be key to building upon our working first-order hypothesis – that SOI differences reflect
different turnover times of root-zone soil water – and identifying how soil water transport,
recharge, and root-extraction processes vary over time and space.

Considerations of Key Uncertainties

In addition to environmental influences on SOI, our interpretation may be confounded by
methodological artifacts associated with cryogenic vacuum distillation. By comparing the $\delta^2$H of
plant xylem water obtained by cryogenic vacuum distillation and the $\delta^2$H of steady-state
transpiration of a known source water, Chen et al. (2020) identified a $\delta^2$H extraction bias that
they attributed to some combination of isotopic exchange of hydrogen in wood tissue with water
in wood tissue and/or water stored in the xylem that is not participating in transpiration. We
recalculated SOI, following the procedures of Allen and Kirchner (2022), by assuming that $\delta^2$H
was biased by -6.1‰, based on the average cryogenic extraction offset identified among 30
species in 6 different studies (Goldsmith & Allen, 2021; Figure S7). Applying this offset shifts
the mean SOI among sites from −0.60 to −0.25 in 2015 and −0.17 to 0.16 in 2019. It is not clear
how this extraction bias varies among species, and if it arises from water stored in xylem that is
not participating in transpiration (Barbeta et al., 2020), then it may also differ between the two
sample years. Re-interpreting plant xylem source water in light of a potential extraction bias
must be done with caution, as its magnitude and its causes (and therefore its application to
specific species in specific contexts) remain unresolved.

Conclusions

During midsummer many plants use water that originated during winter, implying that winter
precipitation may play an important role in governing growing season dynamics, particularly in
the context of shifting seasonal precipitation inputs projected to occur with climate change
(Zeppel et al., 2014). Thus, projected changes in precipitation amount, the seasonal distribution
of that precipitation, or the event sizes could all change the seasonal sources of water used by trees. Resolving the seasonal origins of water used by plants, as well as their controls, therefore has relevance for plant function ecology, (isotope) dendrochronology, and ecohydrology. We conclude by highlighting a few key examples:

**Functional ecology:** Identifying the seasonal origins of water used by different plant species, and in particular, the ability for a species to exploit summer precipitation when it becomes available, has implications for understanding plant function in the context of global change (West et al., 2007). Of particular interest is whether species can shift between winter and summer precipitation sources over inter-annual timescales, (e.g., Roden & Ehleringer, 2007) and therefore keep pace with a changing climate.

**Isotope Dendrochronology:** Accurate reconstruction of past climate using stable isotopes of oxygen in tree rings depends on understanding the isotopic values of source water incorporated into the tree rings (Treydte et al., 2014). Studying the seasonal origins of water used by trees can better constrain estimates of source water, particularly when multiple chronologies are brought together from different sites (Saurer et al., 2008), as well as prevent misinterpretation of climate signals.

**Ecohydrology:** Partitioning the water sources that provision streamflow, evaporation, transpiration, and groundwater depends on our ability to develop models of how water transits through the critical zone (Brooks et al., 2010; Kirchner & Allen, 2020). Studying the seasonal origins of water used by trees provides an important means for source-water partitioning, and for inferring the transit, mixing, and use of water in critical zones.

By sampling the same trees at the same forest sites in two different summers, we were able to observe how weather and climate influence the seasonal origins of water used by three common tree species. Our results indicate that water from winter precipitation was consistently represented in tree xylem at the peak of summer. However, the representation of winter vs. summer precipitation varied consistently as a function of species, site characteristics, and year-
to-year weather differences. Our results provide insights into how the sources of water used by
trees may change as the frequency, intensity and duration of drought changes in the future.

Data Availability Statement

The precipitation isotope data used for modeling SOI are available from
https://www.bafu.admin.ch/bafu/de/home.html and from http://www-
naweb.iaea.org/napc/ih/IHS_resources_gnip.html. Precipitation volume data are available from
https://www.meteoswiss.admin.ch/home.html. The tree xylem water isotope and site
weather/climate characteristics data, are available from https://doi.org/10.5061/dryad.4j0zpc8dg
(Goldsmith et al., 2022).

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Author Contributions

GG conceptualized the project. GG, SB, and RTWS designed methodology and carried out the
investigation. GG and STA curated data, carried out formal analysis, and wrote original draft. All
authors contributed to subsequent editing.

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