Climatic influences on summer use of winter precipitation by trees

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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.

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19	Key points
20	
21	We determined the representation of water originating from winter versus summer precipitation
22	in the xylem of common Swiss trees.
23	
24	Water originating from winter precipitation was observed in trees at most sites, even at the height
25	of summer, but varied among species.
26	
27	Climate and species appear to be key controls over spatial and inter-annual variations in the
28	seasonal origins of water used by trees.
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30	

31 Abstract

32

33 Trees in seasonal climates may use water originating from both winter and summer precipitation. 34 However, the seasonal origins of water used by trees have not been systematically studied. We 35 used stable isotopes of water to compare the seasonal origins of water found in three common 36 tree species across 24 Swiss forest sites sampled in two different years. Water from winter 37 precipitation was observed in trees at most sites, even at the peak of summer, although the 38 relative representation of seasonal sources differed by species. However, the representation of 39 winter precipitation in trees decreased with site mean annual precipitation in both years; 40 additionally, it was generally lower in the cooler and wetter year. Together, these relationships 41 show that precipitation amount influenced the seasonal origin water taken up by trees across both 42 time and space. These results suggest higher turnover of the plant-available soil-water pool in 43 wetter sites and wetter years.

44

45 Plain Language Summary

46

47 In the middle of a hot and dry summer, we often think that a large rain event can "rescue" a 48 forest from drought. However, it is not clear whether trees can or do consistently use the water 49 from summer rains. A growing body of research indicates that over the course of the summer 50 growing season, trees take up significant amounts of water that originated as winter snow or rain. 51 We studied the seasonal origins of the water taken up by three common tree species (beech, oak 52 and spruce) in forest sites across Switzerland in two different years. Our results demonstrate that 53 trees at most sites use some water from winter snow and rain, even at the height of summer, 54 although there were differences among species and sites. The water sources used by trees likely 55 reflect a combination of the amount and timing of winter and summer precipitation, the rate at 56 which that precipitation moves through the soil, and the distribution of the tree roots that take up 57 the water. Determining the seasonal origin of water used by trees, as well as why it may vary 58 over time and space, can help us better anticipate the effects of global climate change. 59

61 Introduction

62

63 In ecosystems with seasonal growth, it could be expected that growing season precipitation 64 should serve as the primary water source for plants when their water demand is high. However, 65 many stable isotope studies have shown that the water used by trees during the growing season 66 often originates primarily from winter rather than summer precipitation (Phillips & Ehleringer, 67 1995; Hu et al., 2010; Kerhoulas et al., 2013; Martin et al., 2018; Allen et al., 2019b; 68 Berkelhammer et al., 2020). For instance, using an index of the seasonal origins of water taken 69 up by trees, we previously found that common tree species from 182 sites across Switzerland 70 mostly used water from winter precipitation at the height of an extremely dry summer (Allen et 71 al., 2019b). In that study, however, trees in more humid sites used relatively less winter 72 precipitation, and the proportions of summer versus winter precipitation in tree xylem varied by 73 species (see also Williams & Ehleringer, 2000; Guo et al., 2018). These differences must reflect 74 an interplay between root distributions, soil-water storage, and recharge dynamics. Resolving the 75 controls over such patterns can improve our understanding of the vulnerability of vegetation to 76 hydroclimatic disturbances.

77

78 The consistency, over space and time, in the seasonal origins of water used by trees, as well as 79 how they are shaped by weather and climate, remain unresolved. We used stable isotopes of 80 hydrogen and oxygen as tracers to study the seasonal origin of water in three common tree 81 species in 24 long-term forest monitoring plots in Switzerland, bringing together observations 82 made on the same trees in two different summers. Our objectives were 1) to determine whether 83 the seasonal origins of water in trees varies consistently among species and across sites during 84 two different growing seasons and 2) to test how variation in weather and climate factors may 85 explain the observed differences. We hypothesized that our original observations demonstrating 86 less reliance of trees on winter precipitation at wetter sites (Allen *et al.*, 2019b) would also apply 87 to wetter years, and thus that the hot and dry conditions in which we made our original 88 observations may have resulted in atypically high use of winter precipitation. Our results provide 89 insights relevant for a number of important questions, including how to reconstruct climates in 90 the past, how water resources are partitioned within ecosystems in the present, and what sources 91 of water may be critical for plants in the future.

92

93 Methods

94

95 *Climatological context:* The first sampling, carried out in 2015, occurred in the context of an 96 unusually warm and dry summer (Table S1). Summer air temperatures were >2 °C higher and 97 precipitation amounts were 20-40% below the long-term climate norm (1981-2010) in much of 98 Switzerland, but up to 45% above the long-term norm in the southern and western Swiss Alps 99 (MeteoSchweiz, 2015). These unusual conditions raised questions of whether or not the patterns 100 that we previously observed – specifically, that winter precipitation contributes strongly to 101 summer evapotranspiration (Allen et al., 2019a,b) – were likely to also hold in more typical 102 summers. Many subsequent years have also continued to be warm and dry. In particular, a small 103 subset of sites were resampled in the summer of 2018, which was the most extreme drought on 104 record in central Europe (Schuldt et al., 2020). A larger set of sites were resampled in the 105 summer of 2019, which was similarly hot; however, precipitation was more normal 106 (MeteoSchweiz, 2019). 107 108 Field sampling: Our study was carried out in the context of a long-term forest health monitoring 109 program that includes nearly 200 sites (Braun et al., 2017, 2020). Each site contains at least one 110 of three key tree species: beech (Fagus sylvatica L.), spruce (Picea abies (L.) H. Karst.), and oak 111 (Quercus robur L.). General site characteristics are described in Allen et al., (2019b) and in 112 Figure S1 and Table S2. 113 114 Between 22 July and 3 August 2019, we collected samples from 8 individuals of each species at

115 24 sites (n = 258 trees in total; one site has 10 individuals of a species). Fully sunlit branches

116 were collected, using pole pruners, by a technician suspended below a helicopter. Samples were

117 returned to the ground, immediately enclosed in a black plastic trash bag to suppress

118 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

120 longitude included in the monitoring network as a whole. Here we compare our observations in

121 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.

126

127 *Sample processing:* For each sample, the bark and vascular cambium were removed from a fully 128 suberized piece of the branch, the remaining xylem was sealed in a glass vial, and the vial was 129 frozen until water extraction. Water extraction was carried out via cryogenic vacuum distillation 130 at the Paul Scherrer Institute (2015) and at ETH Zurich (2019) on manifolds with an identical 131 design as described in Orlowski et al. (2013). Branch samples were extracted under a 0.03 hPa 132 vacuum for 2 h at 80 °C and the evaporated water was frozen in a liquid nitrogen trap. Samples 133 were then analyzed for δ^{18} O and δ^{2} H by TC/EA-IRMS at the Paul Scherrer Institute (2015) and 134 at ETH Zurich (2019). All values are presented per mil (‰) relative to V-SMOW. The standard 135 deviation of an independent quality control standard used for analysis at the Paul Scherrer 136 Institute was $\leq 0.2 \ \% \ \delta^{18}$ O and $\leq 0.4 \ \% \ \delta^{2}$ H. The standard deviation of an independent quality 137 control standard used for analysis at ETH Zurich was 0.17 $\% \delta^{18}$ O and 0.62 $\% \delta^{2}$ H. 138

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:

143
$$SOI = \begin{cases} \frac{\delta_x - \delta_{annP}}{\delta_{summerP} - \delta_{annP}}, & \text{if } \delta_x > \delta_{annP} \\ \frac{\delta_x - \delta_{annP}}{\delta_{annP} - \delta_{winterP}}, & \text{if } \delta_x < \delta_{annP} \end{cases}$$
Eq. 1

144

145 where δ_x is the fractionation-compensated δ^2 H isotopic signature of xylem water, and $\delta_{winterP}$, 146 $\delta_{summerP}$, and δ_{annP} are the δ^2 H isotopic signatures of winter, summer, and volume-weighted 147 annual precipitation at each study site. The δ_x values in Eq. 1 were compensated for evaporative 148 fractionation by projecting dual-isotope measurements of xylem water to local meteoric water 149 lines along theoretical evaporation-line slopes, using the method described in detail in Allen et 150 al. (2019b). Projecting the xylem water values onto the meteoric water line means that the SOI 151 values reported here are based on both the δ^2 H and δ^{18} O of the xylem samples, and thus that Eq.

152 1 would yield similar results for either isotope. Isotopic signatures of precipitation were 153 estimated using data from the two years prior to sampling (i.e., August 2013-July 2015 for the 154 2015 xylem samples, and August 2017-July 2019 for the 2019 xylem samples), as inputs to a 155 previously described and validated model (Allen *et al.*, 2018). The site mean δ^2 H of precipitation 156 in the two years prior to sampling in 2019 was enriched by 8.96 ‰ compared to 2015. The 157 seasonal origin index (SOI) provides a measure of the overrepresentation of a season's 158 precipitation in xylem relative to the representation of that season's precipitation in the annual 159 precipitation amount. Negative values of SOI suggest an overrepresentation of winter 160 precipitation in xylem and positive values suggest an overrepresentation of summer precipitation 161 in xylem. The SOI will be near -1.0 for soil and plant water samples derived entirely from 162 winter precipitation and near 1.0 for samples derived entirely from summer precipitation.

163 To study how the seasonal origin of water in trees varies as a function of mean annual 164 precipitation amount between years, we used analysis of covariance. To study how variation in 165 summer precipitation amount and other meteorological factors may contribute to the observed 166 differences in the seasonal origin of water in trees between the sample years, we determined the 167 change in SOI between years as a function of the change in temperature, precipitation, vapor 168 pressure deficit and potential evapotranspiration at each site in the month prior to sampling and 169 compared the mean of these slopes to zero using one sample t-tests. Similarly, we determined the 170 magnitude of the difference in SOI at a given site between years and the magnitude of the 171 differences in the same weather variables in the month prior to sampling at that site and 172 correlated the measures using Spearman's Rank Correlations. Daily climate data were generated 173 from a geospatial model using weather station data (Meteotest, Bern, Switzerland).

174

175 **Results and Discussion**

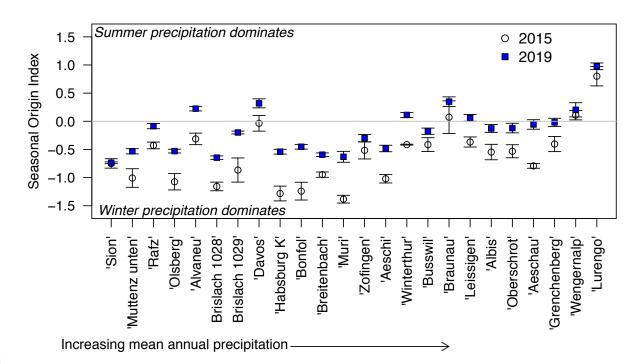
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177 The mean δ^2 H xylem water isotope ratios of all three tree species were more positive (7.1 to 14.3‰ enriched) in 2019 compared to 2015 (**Figure S2; Table S3**). In contrast, the mean δ^{18} O 179 xylem isotope ratios of all three species were similar in 2019 compared to 2015 (from -0.1‰ 180 depleted to 1.1‰ enriched). Summer precipitation across our sites averaged 86 mm more in 2019 181 than in 2015. Xylem water also plotted closer to the meteoric water line in 2019 than in 2015 182 (**Figure S2**), suggesting greater soil surface evaporation in 2015 from a pool that contained less

- 183 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.
- 185
- 186 The within-plot and species-within-plot variation in xylem water isotopes can be evaluated using
- 187 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
- 189 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;
- 192 von Freyberg *et al.*, 2020).
- 193

194 First-Order Controls on Seasonal Origins of Water in Plants

195



197 **Figure 1.** The seasonal origin index of water in xylem at sites sampled in both 2015 and 2019.

- 198 Sites are ordered left to right from lowest (690 mm yr⁻¹ at Sion) to highest (1791 mm yr⁻¹ at
- 199 Lurengo) mean annual precipitation. Data represent means \pm SEM.
- 200

201 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 =

203 23, p < 0.0001, Figure 1). However, the SOI of water in trees was <0 in both 2015 (mean and

204 median of sites = -0.60 and -0.54) and 2019 (mean and median of sites = -0.17 and -0.15),

205 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

207 of the same sites as 2015, using the same approach, also show overrepresentation of winter

- 208 precipitation (Figure S3).
- 209

210 The SOI of water in trees increased linearly as a function of precipitation in both years at a 211 common slope of 0.12 (unitless SOI) per 100 mm precipitation, but with intercepts that significantly differed in SOI by 0.43 ($f_{2,45} = 22.2, p < 0.0001$, adj. $r^2 = 0.47$; Figure S4A). 212 213 Previous research in temperate semi-arid ecosystems has also observed that vegetation in wetter 214 sites consistently uses more summer precipitation (Williams & Ehleringer, 2000; Guo et al., 215 2018). Both the slopes and intercepts significantly differed between the years when considering 216 the relationship between the SOI of water in trees and precipitation in the month (July) before 217 sampling, indicating that the effects of summer precipitation amount were not consistent over time ($f_{3,44} = 10.4$, p < 0.0001, adj. $r^2 = 0.37$; Figure S4B). Collectively, these observations 218 219 indicate that annual precipitation amounts impose a first-order control on the seasonal origin of 220 water used by plants. We hypothesize that greater inputs to a given volume of soil water storage 221 should drive greater turnover of the water in that volume, and thus increase the proportion of 222 recent precipitation within it. However, this mechanism assumes that the incoming precipitation 223 either displaces existing soil water or re-fills soil storage depleted through evapotranspiration. If, 224 alternatively, summer precipitation bypasses soil water storage in summer (e.g., when those 225 pores may be filled by winter precipitation; Brooks et al., 2010), then we would expect the driest 226 soils to show more responsiveness to changes in summer precipitation. The effects of 227 precipitation amount on soil water turnover should apply across both time and space, which is 228 consistent with our observation of higher representation of summer water in trees at wetter sites 229 in both years and the generally higher representation of summer precipitation in the wetter year. 230 While the flow processes involved remain unclear, our new findings make it clearer that dry 231 conditions result in higher relative use of, and perhaps reliance on, stored winter precipitation.

233 Second-Order Controls on Seasonal Origins of Water in Plants

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232

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.

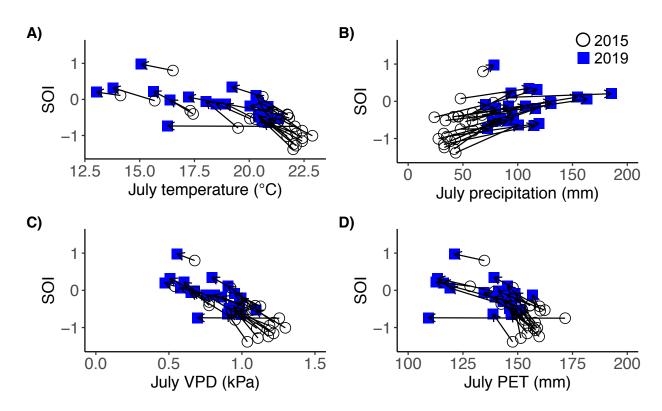




Figure 2. The change in the seasonal origin index of water at sites sampled in both 2015 and
2019 as a function of the change in A) temperature, B) precipitation, C) vapor pressure deficit
(VPD) and D) potential evapotranspiration (PET) in the month (July) prior to the sampling. The
mean of the slopes (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

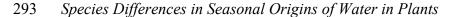
- 250 month (July) prior to sampling in 2019, compared to the month prior to sampling in 2015,
- whereas all sites showed higher SOI values in 2019 compared to 2015 (Figure 2). These patterns
- were consistent within species (Figure S5). Consequently, the mean change in SOI per change in
- 253 July precipitation 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
- 257 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
- 259 precipitation (p = 0.92).
- 260

261 However, in spite of the consistent direction of the changes in weather with the change in SOI, 262 the magnitude of the difference in SOI among sites between 2019 and 2015 was not correlated 263 with the magnitude of the difference in temperature ($\rho = -0.15$, p = 0.5), precipitation ($\rho = 0.18$, p = 0.4), vapor pressure deficit (VPD; $\rho = -0.33$, p = 0.1), or potential evapotranspiration (PET; ρ 264 = 0.2, p = 0.3) in the month (July) prior to sampling (Figure S6). In other words, a greater 265 266 difference in temperature, precipitation, VPD, or PET between the two years was not correlated 267 with a greater difference in SOI. All three species exhibited similar correlations between year-to-268 year SOI differences and year-to-year differences in weather indices, although spruce exhibited a 269 significant correlation ($\rho = -0.61$, p = 0.02) between SOI differences and VPD differences. The 270 correlation between SOI differences and precipitation differences was not strengthened by 271 excluding small precipitation events (< 5 mm), which probably would not have infiltrated into 272 the soil. Finally, we found no evidence for a significant correlation of by-site slopes (change in 273 SOI per change in weather metric) with site mean annual precipitation (p > 0.1). Thus, we were 274 unable to explain the relative magnitudes of changes in SOI among sites, even if the average 275 change in SOI per change in (only) previous-month weather differences was highly significant. 276

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

280 precipitation used by trees may relate to interactions between climate and rooting depths. For 281 instance, if plants in wetter environments have shallow rooting depths, then the available storage 282 for plant-available water would be smaller and we would have expected greater SOI sensitivities 283 to precipitation in the wetter environments; we did not observe that. An alternative second-order 284 control may relate to differences in how precipitation infiltrates and percolates through soils in 285 wetter versus drier conditions. If all of July precipitation entered the soil profile and became 286 available to roots, we would expect the drier soils in drier environments to have been more 287 sensitive to increased inputs, resulting in greater changes in SOI per changes in July precipitation 288 amount; however, we also did not observe this to be the case (Figure S6). While inter-annual 289 differences in weather and SOI were widespread across sites, changes in magnitude in SOI were 290 not well explained by any variable across the sites, such that there was a lack of evidence that 291 second-order controls over the seasonal origins of plant-water are consistent among sites.

292



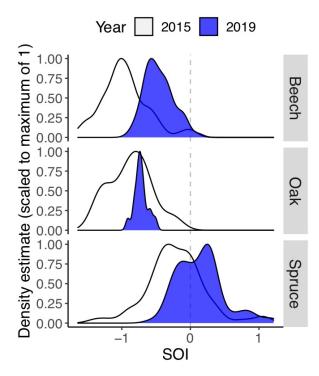


Figure 3. Probability density functions (scaled to maximum of 1) of the seasonal origin index

- 296 (SOI) of water in the xylem of A) beech, B) oak and C) spruce in summer 2015 (white) and 2019
- 297 (blue). Sample sizes are in Table S3.
- 298

299 The mean SOI values were shifted significantly higher in 2019 compared to 2015 for beech (t-300 test; t = -10.4, df = 89, p < 0.0001, difference of mean SOI = 0.50) and spruce (t-test; t = -6.0, df 301 = 124, p < 0.0001, difference of mean SOI = 0.35), but not oak (paired t-test; t = -1.7, df = 13, p 302 = 0.1, difference of mean SOI = 0.15) (Figure 3). The distributions of SOI values also 303 significantly differed between years for beech and spruce (Kolmogorov-Smirnov tests, p < p304 0.0001). In both sample years, we observed that beech had the highest, and spruce the lowest, 305 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 306 307 compared to the drier sampling year. Results from oak must be interpreted cautiously as they are 308 from only two sites.

309

310 Previous research has demonstrated that plant species differ in their use of winter versus summer 311 precipitation (Williams & Ehleringer, 2000; Guo et al., 2018), as well as differ in the elasticity of 312 their use of summer precipitation when more becomes available (West *et al.*, 2007). The 313 differences observed among beech, spruce, and oak are likely to partially result from how the 314 predominant climate conditions shape root distributions and therefore the ability for species to 315 exploit summer precipitation events (Fan et al., 2017). Spruce occurs in wetter environments in 316 Switzerland and has more shallow roots (Schmid & Kazda, 2002), which may enable them to use 317 small episodic summer precipitation events. Beech occupies intermediate environments and oak 318 the driest environments in Switzerland. Our results indicate that the mean change in SOI per 319 change in July precipitation between years was higher in spruce (0.008) and beech (0.010) than 320 oak (0.003), which lends some support to the idea that spruce and beech rooting patterns may 321 make them more sensitive to summer precipitation than oak. We also previously posited that the 322 strong overrepresentation of winter precipitation in beech in 2015 may have been because those 323 trees used water from soil layers that were not recharged during dry summer conditions because 324 any new summer precipitation bypassed those soil layers due to preferential flow (Allen et al., 325 2019b). Our new findings show that even the beech forests at drier sites increase in their use of 326 summer precipitation when more is available.

327

328 Our study was not designed to understand how much water trees use from particular precipitation 329 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

331 (Jasechko & Taylor, 2015) or preferential flow through the subsurface (Buttle & McDonald,

332 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.

336

337 Considerations of Key Uncertainties

338

339 In addition to environmental influences on SOI, our interpretation may be confounded by 340 methodological artifacts associated with cryogenic vacuum distillation. By comparing the δ^2 H of 341 plant xylem water obtained by cryogenic vacuum distillation and the $\delta^2 H$ of steady-state 342 transpiration of a known source water, Chen et al. (2020) identified a δ^2 H extraction bias that 343 they attributed to some combination of isotopic exchange of hydrogen in wood tissue with water 344 in wood tissue and/or water stored in the xylem that is not participating in transpiration. We 345 recalculated SOI, following the procedures of Allen and Kirchner (2022), by assuming that $\delta^2 H$ 346 was biased by -6.1‰, based on the average cryogenic extraction offset identified among 30 347 species in 6 different studies (Goldsmith & Allen, 2021; Figure S7). Applying this offset shifts 348 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 349 how this extraction bias varies among species, and if it arises from water stored in xylem that is 350 not participating in transpiration (Barbeta et al., 2020), then it may also differ between the two 351 sample years. Re-interpreting plant xylem source water in light of a potential extraction bias 352 must be done with caution, as its magnitude and its causes (and therefore its application to 353 specific species in specific contexts) remain unresolved.

354

355 Conclusions

356

357 During midsummer many plants use water that originated during winter, implying that winter

358 precipitation may play an important role in governing growing season dynamics, particularly in

359 the context of shifting seasonal precipitation inputs projected to occur with climate change

360 (Zeppel et al., 2014). Thus, projected changes in precipitation amount, the seasonal distribution

361 of that precipitation, or the event sizes could all change the seasonal sources of water used by

362 trees. Resolving the seasonal origins of water used by plants, as well as their controls, therefore

363 has relevance for plant function ecology, (isotope) dendrochronology, and ecohydrology. We

364 conclude by highlighting a few key examples:

365

366 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.*,

369 2007). Of particular interest is whether species can shift between winter and summer

370 precipitation sources over inter-annual timescales, (e.g., Roden & Ehleringer, 2007) and

371 therefore keep pace with a changing climate.

372

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.

379

380 *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

383 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.

385

386 By sampling the same trees at the same forest sites in two different summers, we were able to

387 observe how weather and climate influence the seasonal origins of water used by three common

388 tree species. Our results indicate that water from winter precipitation was consistently

389 represented in tree xylem at the peak of summer. However, the representation of winter vs.

390 summer precipitation varied consistently as a function of species, site characteristics, and year-

391	to-year weather differences. Our results provide insights into how the sources of water used by
392	trees may change as the frequency, intensity and duration of drought changes in the future.
393	
394	Data Availability Statement
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396	The precipitation isotope data used for modeling SOI are available from
397	https://www.bafu.admin.ch/bafu/de/home.html and from http://www-
398	naweb.iaea.org/napc/ih/IHS_resources_gnip.html. Precipitation volume data are available from
399	https://www.meteoswiss.admin.ch/home.html. The tree xylem water isotope and site
400	weather/climate characteristics data, are available from <u>https://doi.org/10.5061/dryad.4j0zpc8dg</u>
401	(Goldsmith <i>et al.</i> , 2022).
402	
403	Acknowledgements
404	
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413	
414	Author Contributions
415	
416	GG conceptualized the project. GG, SB, and RTWS designed methodology and carried out the
417	investigation. GG and STA curated data, carried out formal analysis, and wrote original draft. All
418	authors contributed to subsequent editing.
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