



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

60

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 al.*,  
71 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  
119 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  
122 samples using the same methodology from 3-8 of the same individuals of each species ( $n = 147$

123 trees in total); this sampling was conducted between 27 July and 10 August 2015. A smaller  
124 subset of these sites was sampled in 2018 ( $n = 42$  trees in total), as discussed in the supporting  
125 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 Orłowski *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  $\delta^{18}\text{O}$  and  $\delta^2\text{H}$  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  $\leq 0.2$  ‰  $\delta^{18}\text{O}$  and  $\leq 0.4$  ‰  $\delta^2\text{H}$ . The standard deviation of an independent quality  
137 control standard used for analysis at ETH Zurich was 0.17 ‰  $\delta^{18}\text{O}$  and 0.62 ‰  $\delta^2\text{H}$ .

138

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

142

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

144

145 where  $\delta_x$  is the fractionation-compensated  $\delta^2\text{H}$  isotopic signature of xylem water, and  $\delta_{winterP}$ ,  
146  $\delta_{summerP}$ , and  $\delta_{annP}$  are the  $\delta^2\text{H}$  isotopic signatures of winter, summer, and volume-weighted  
147 annual precipitation at each study site. The  $\delta_x$  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 al.*  
150 (2019b). Projecting the xylem water values onto the meteoric water line means that the SOI  
151 values reported here are based on both the  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  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  $\delta^2\text{H}$  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**

176

177 The mean  $\delta^2\text{H}$  xylem water isotope ratios of all three tree species were more positive (7.1 to  
178 14.3‰ enriched) in 2019 compared to 2015 (**Figure S2; Table S3**). In contrast, the mean  $\delta^{18}\text{O}$   
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

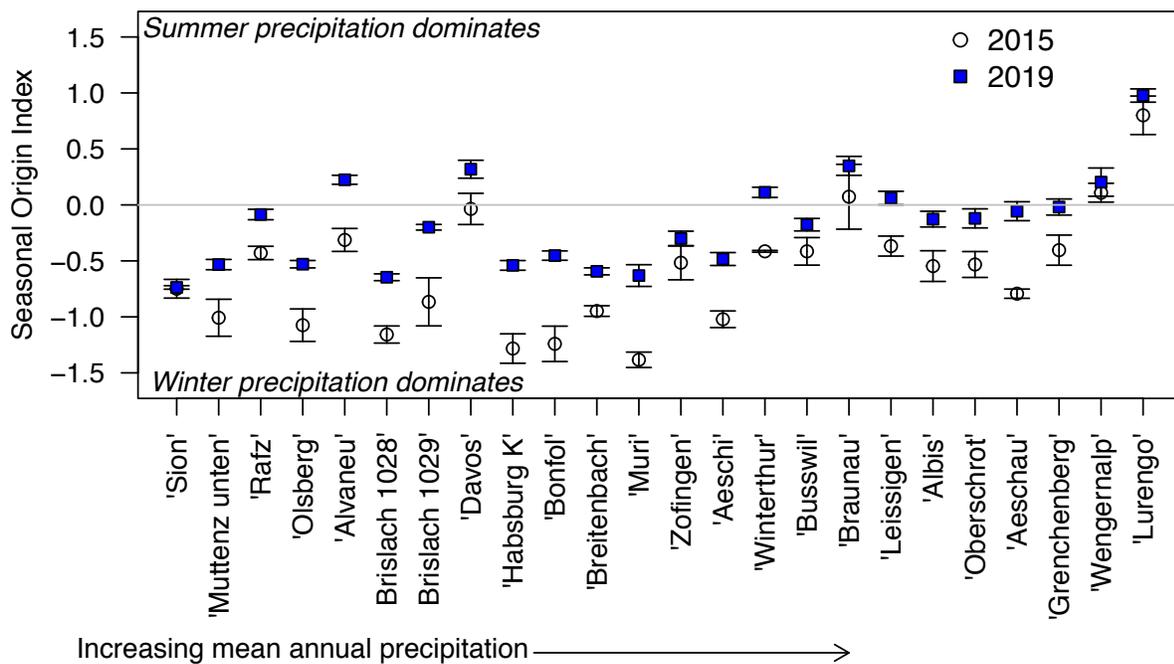
183 summer precipitation. Given that these measurements resulted from similar sample handling and  
184 analysis, analytical errors would likely apply similarly and thus not explain this difference.

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  
188 average standard deviation within plots was 7.61 ‰  $\delta^2\text{H}$  and 1.22 ‰  $\delta^{18}\text{O}$ . Average standard  
189 deviation within species within plots was generally smaller, ranging from 2.91 to 4.90 ‰  $\delta^2\text{H}$   
190 and 0.83 to 1.02 ‰  $\delta^{18}\text{O}$  (**Table S3**). Estimates of variation within tree crowns, among trees, and  
191 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



196

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<sup>-1</sup> at Sion) to highest (1791 mm yr<sup>-1</sup> at

199 Lurengo) mean annual precipitation. Data represent means ± SEM.

200

201 Mean site SOI was significantly more positive in 2019 compared to 2015, indicating a decrease  
202 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  
206 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  
212 significantly differed in SOI by  $0.43$  ( $f_{2,45} = 22.2$ ,  $p < 0.0001$ ,  $adj. r^2 = 0.47$ ; **Figure S4A**).  
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  
218 time ( $f_{3,44} = 10.4$ ,  $p < 0.0001$ ,  $adj. r^2 = 0.37$ ; **Figure S4B**). Collectively, these observations  
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.

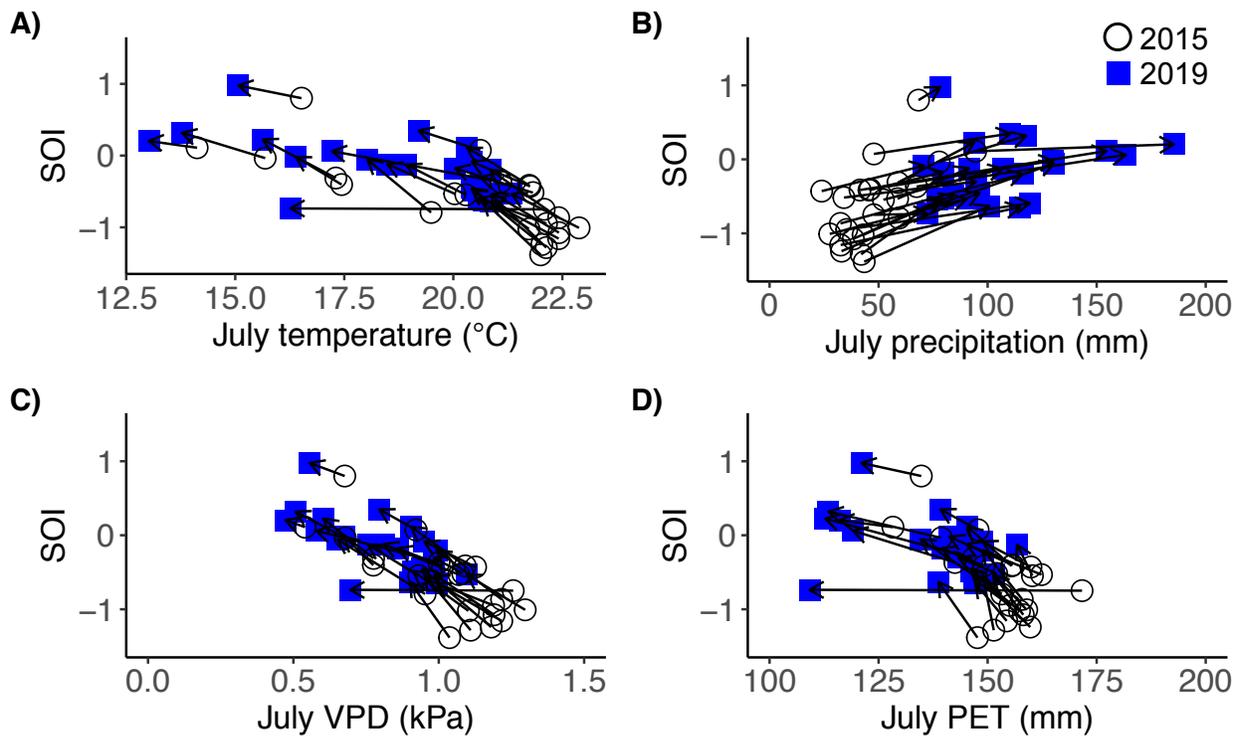
232

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

234

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

241



242

243 **Figure 2.** The change in the seasonal origin index of water at sites sampled in both 2015 and  
244 2019 as a function of the change in A) temperature, B) precipitation, C) vapor pressure deficit  
245 (VPD) and D) potential evapotranspiration (PET) in the month (July) prior to the sampling. The  
246 mean of the slopes (change in SOI per change in weather) significantly differed from zero for all  
247 four of the weather metrics.

248

249 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,  
251 whereas all sites showed higher SOI values in 2019 compared to 2015 (**Figure 2**). These patterns  
252 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  
254 significantly differed from zero;  $p < 0.0001$ ); this also held true for changes in SOI per change in  
255 other July weather indices, including temperature, VPD, and PET ( $p < 0.0001$ ). Interestingly,  
256 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  
258 there a statistically significant relationship with the year-to-year difference in annual  
259 precipitation ( $p = 0.92$ ).

260

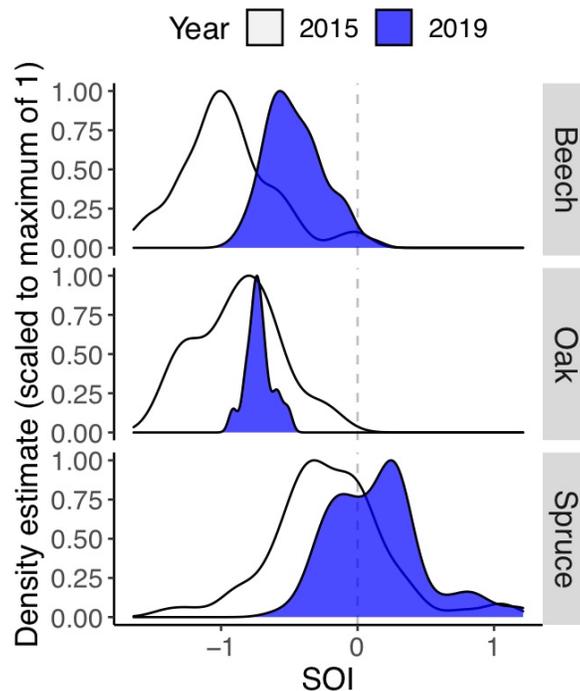
261 However, in spite of the consistent direction of the changes in weather with the change in SOI,  
262 the magnitude of the difference in SOI among sites between 2019 and 2015 was not correlated  
263 with the magnitude of the difference in temperature ( $\rho = -0.15$ ,  $p = 0.5$ ), precipitation ( $\rho = 0.18$ ,  
264  $p = 0.4$ ), vapor pressure deficit (VPD;  $\rho = -0.33$ ,  $p = 0.1$ ), or potential evapotranspiration (PET;  $\rho$   
265  $= 0.2$ ,  $p = 0.3$ ) in the month (July) prior to sampling (**Figure S6**). In other words, a greater  
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

277 Understanding how inter-annual differences in SOI vary with differences in precipitation and  
278 other weather metrics across sites can provide insights that add to our observations of first-order  
279 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

293 *Species Differences in Seasonal Origins of Water in Plants*



294  
295 **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,  $p <$   
304  $0.0001$ ). 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  
306 spruce demonstrated a decrease in the overrepresentation of winter precipitation in the wetter  
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)

330 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  
333 may be key to building upon our working first-order hypothesis – that SOI differences reflect  
334 different turnover times of root-zone soil water – and identifying how soil water transport,  
335 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  $\delta^2\text{H}$  of  
341 plant xylem water obtained by cryogenic vacuum distillation and the  $\delta^2\text{H}$  of steady-state  
342 transpiration of a known source water, Chen et al. (2020) identified a  $\delta^2\text{H}$  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  $\delta^2\text{H}$   
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  
367 in particular, the ability for a species to exploit summer precipitation when it becomes available,  
368 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

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

379

380 *Ecohydrology:* Partitioning the water sources that provision streamflow, evaporation,  
381 transpiration, and groundwater depends on our ability to develop models of how water transits  
382 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  
384 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**

395

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-](http://www-naweb.iaea.org/napc/ih/IHS_resources_gnip.html)  
398 [naweb.iaea.org/napc/ih/IHS\\_resources\\_gnip.html](http://www-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 <https://doi.org/10.5061/dryad.4j0zpc8dg>  
401 (Goldsmith *et al.*, 2022).

402

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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.

419

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