

1 **Cumulative growth and stress responses to the 2018-2019 drought in**
2 **a European floodplain forest**

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23 **Abstract**

24 Droughts increasingly threaten the world's forests and their potential to mitigate climate change.
25 In 2018-2019, Central European forests were hit by two consecutive hotter drought years, an
26 unprecedented phenomenon that is likely to occur more frequently with climate change. Here, we
27 examine trees' growth resistance and physiological stress responses (increase in carbon isotope
28 composition; $\Delta\delta^{13}\text{C}$) to this consecutive drought based on tree-rings of dominant tree species in a
29 Central European floodplain forest. Tree growth was not reduced for most species in 2018,
30 indicating that water supply in floodplain forests can partly buffer meteorological water deficits.
31 Drought stress in 2018 was comparable to former single drought years, but the cumulative drought
32 stress in 2019 induced drastic decreases in growth resistance and increases in $\Delta\delta^{13}\text{C}$ across all
33 species. Consecutive hotter droughts pose a novel threat to forests under climate change, even in
34 forest ecosystems with high levels of water supply.

35

36 **Introduction**

37 The frequency and intensity of droughts and corresponding surges of forest dieback events around
38 the globe are projected to increase in the 21st century^{1,2}. This critically endangers the world's
39 forests and the variety of ecosystem services they sustain, such as their potential to act as carbon
40 sink³ and as a nature-based solution for climate change mitigation⁴. Recent drought events,
41 moreover, belong to a new category, so called 'hotter droughts', where low precipitation coincides
42 with heat waves, which creates a positive feedback loop between soil-water depletion through
43 evapotranspiration and increased surface temperatures through reduced cooling by latent heat
44 production^{5,6}. In 2018-2019, Central Europe has been hit by two consecutive and hotter summer
45 drought events, a phenomenon unprecedented at least in the last 250 years but likely to occur more

46 frequently with intensifying climate change⁷. The 2018 hotter drought alone had already stronger
47 negative effects on European ecosystems than the formerly severest drought event in 2003⁵ and
48 induced widespread premature leaf senescence and tree mortality⁸. An increasing number of
49 studies has shown that droughts can affect tree growth and hence carbon cycling in forests for
50 years after the actual drought event and that such ‘legacy effects’ are widespread in forest
51 ecosystems^{9–13}. The consecutive hotter drought in 2019 may thus have critically amplified drought
52 stress as trees were hit that already had emptied carbon reserves, impaired hydraulic functioning
53 due to embolism and weakened defense systems^{8,13} and only access to emptied soil water reserves.
54
55 Drought effects on forests can be analyzed retrospectively through analyses of tree-rings, which
56 are an archive of past growing conditions including climate and water availability¹⁴. In
57 dendroecology the annual growth of trees (i.e. the width of tree rings formed each year) is a
58 principle indicator of drought effects, which can be analyzed through quantifying growth
59 resistance to drought (hereafter ‘growth resistance’)^{15,16}. Growth resistance quantifies the ability
60 of a tree to withstand drought stress through comparing growth in drought years with mean growth
61 in a reference period, i.e. years with ‘normal’ climate conditions prior to the drought event¹⁵. Such
62 growth resistance analyses may be especially suitable when rapid impact assessments are needed
63 and no data is available on the post disturbance period. Next to growth, the carbon isotope ratio of
64 ¹³C to ¹²C in wood – called $\delta^{13}\text{C}$ – is a widespread physiological indicator of a tree’s water status
65 and drought stress^{17–19}. The $\delta^{13}\text{C}$ composition in tissues of C₃ plants like most trees is a record of
66 the ratio between intercellular and ambient CO₂ concentration during the time of carbon fixation
67 that is modulated by both, CO₂ assimilation and stomatal aperture¹⁹. Under ample water supply
68 and fully open stomata, plants discriminate against the heavier ¹³C in favor of the lighter ¹²C.

69 However, under water shortage, stomatal conductance is stronger down-regulated than
70 assimilation, which induces an increase of $\delta^{13}\text{C}$ in the wood formed during drought^{17,19}. Thus,
71 drought stress can be quantified as increase in wood carbon isotope ratio ($\Delta\delta^{13}\text{C}$) between drought
72 and normal years. Hence, growth resistance and $\Delta\delta^{13}\text{C}$ combined provide a powerful tool to
73 quantify drought effects on trees.

74

75 Tree species vary greatly in their susceptibility to drought due to physiological and morphological
76 differences. Among other features such as cavitation resistance²⁰ two key factors that might drive
77 tree species reactions to drought are stomatal control and root system architecture^{21–23}. Stomatal
78 closure in response to water deficits enables plants to avoid critically low water potentials through
79 transpiration losses and thus hydraulic failure but species differ largely in their type of stomatal
80 control^{21,22}. Isohydric or water saving species close their stomata fast during water shortage, while
81 anisohydric or water spending species keep their stomata open and continue to transpire.
82 Consequently, the latter strategy necessitates continued water uptake via roots and carries an
83 increased risk for xylem cavitation²¹. While isohydric species may thus show earlier growth and
84 $\Delta\delta^{13}\text{C}$ responses, anisohydric species may face high cavitation risks during severe and prolonged
85 drought conditions characterized by very low soil moisture availability. Next to stomatal control,
86 root system architecture varies strongly between species^{23–25} and may influence drought responses
87 as shallow-rooting species likely lose access to soil water faster than deep-rooting species that can
88 access the deeper and still moist layers²⁶. Hence, for understanding and generalizing the effects of
89 consecutive droughts on forests, tree species should be examined that span a gradient in such traits.

90

91 The high tree species richness of floodplain forests²⁷ makes them ideally suited for comparative
92 studies of tree species reactions to consecutive droughts as they are one of the few systems where
93 coexisting mature trees spanning an entire gradient of hydraulic behaviors can be found.
94 Floodplain forests rank among the most rapidly disappearing ecosystems due to land conversion
95 and drainage^{23,28} and novel climatic conditions – like prolonged droughts – may amplify this trend
96 through changing the hydrological regimes on which these forests depend. For instance, sinking
97 groundwater levels may increase tree growth sensitivity to drought and susceptibility to drought-
98 induced dieback^{23,29} and this might bring these forests, which are among the most dynamic,
99 productive and diverse Central European habitats^{30,31}, closer to a tipping point. On the contrary,
100 the higher water availability in floodplain forests may buffer drought effects to a certain extent as
101 trees might have access to groundwater in addition to precipitation-derived moisture³². Hence, it
102 is conceivable that if drought effects on resistance and $\Delta\delta^{13}\text{C}$ were observed in floodplain trees,
103 other forest ecosystems might experience even stronger effects.

104

105 Here, we focus on the effect of the two consecutive drought years 2018-2019 characterized by
106 extremely hot and dry conditions (Fig. 1), as well as their cumulative effects, on tree growth
107 resistance and $\Delta\delta^{13}\text{C}$ as physiological stress response. To this end, we reconstruct the stress exerted
108 by this unprecedented event and compare it to past (single) drought events based on tree-ring
109 records from dominant tree species in the Leipzig floodplain forest, one of the few remaining and
110 thus highly protected floodplain forests in Central Europe^{33,34}. The studied species span a gradient
111 in stomatal control and root system architecture, with *Quercus robur* L. (hereafter oak) having
112 isohydric behavior^{35,36} and a deep reaching heart-sinker root system^{24,25}, *Acer pseudoplatanus* L.
113 (hereafter maple) having an intermediate (rather isohydric) stomatal control^{37,38} and rooting

114 depth²⁵ and *Fraxinus excelsior* L. (hereafter ash) having an anisohydric behaviour^{37,38} and an
115 allocation of most roots to shallow soil layers^{24,25}. This gradient allowed us to explore a broad
116 range of species response strategies to consecutive drought stress. We sampled trees in two
117 environmental strata representing topographic differences in distance to groundwater. We expect
118 the results for the hypotheses proposed below to be more pronounced in the dryer stratum.
119 Specifically, we tested the following hypothesis:

120

121 **H1** Drought stress in 2018 – measured as decreased growth resistance and a positive $\Delta\delta^{13}\text{C}$ – is
122 comparable to the stress experienced during former drought years. High groundwater levels in
123 floodplain forests buffer effects of such single drought years.

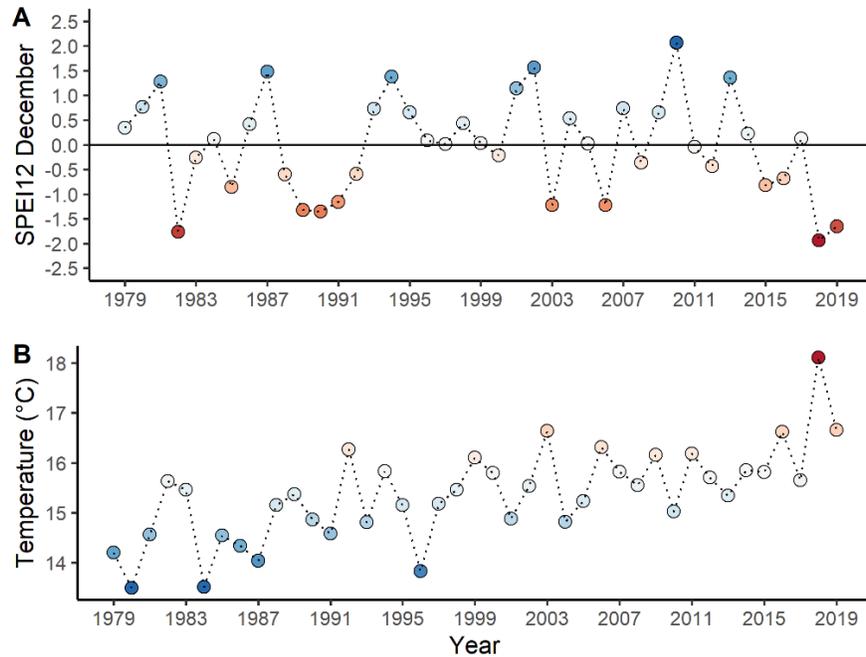
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125 **H2** The consecutive drought years 2018-2019 lead to a drastically decreased growth resistance and
126 a further increase in $\Delta\delta^{13}\text{C}$ in 2019.

127

128 **H3** Isohydric species respond faster to drought stress (already in 2018), while anisohydric species
129 react later but show stronger reactions to the consecutive drought in 2019.

130



131
132 Fig. 1 Annual standardized water balance of precipitation minus potential evapotranspiration (A, January-
133 December) and mean growing season temperature (B, April-September) per year from 1979-2019 in the
134 Leipzig floodplain forest. The water balance was calculated as Standardized Precipitation
135 Evapotranspiration Index (SPEI³⁹). Points are colored according to their value with deeper red indicating
136 increasing drought and heat wave severity. The horizontal line in (A) represents the long-term mean,
137 negative values indicate water deficits and positive values water surpluses. SPEI values below -1 and above
138 1 can be considered exceptionally dry and wet, respectively. See Supplementary Figs. 1-2 for additional
139 SPEI lengths, climatic and hydrological variables that we used to identify drought events.

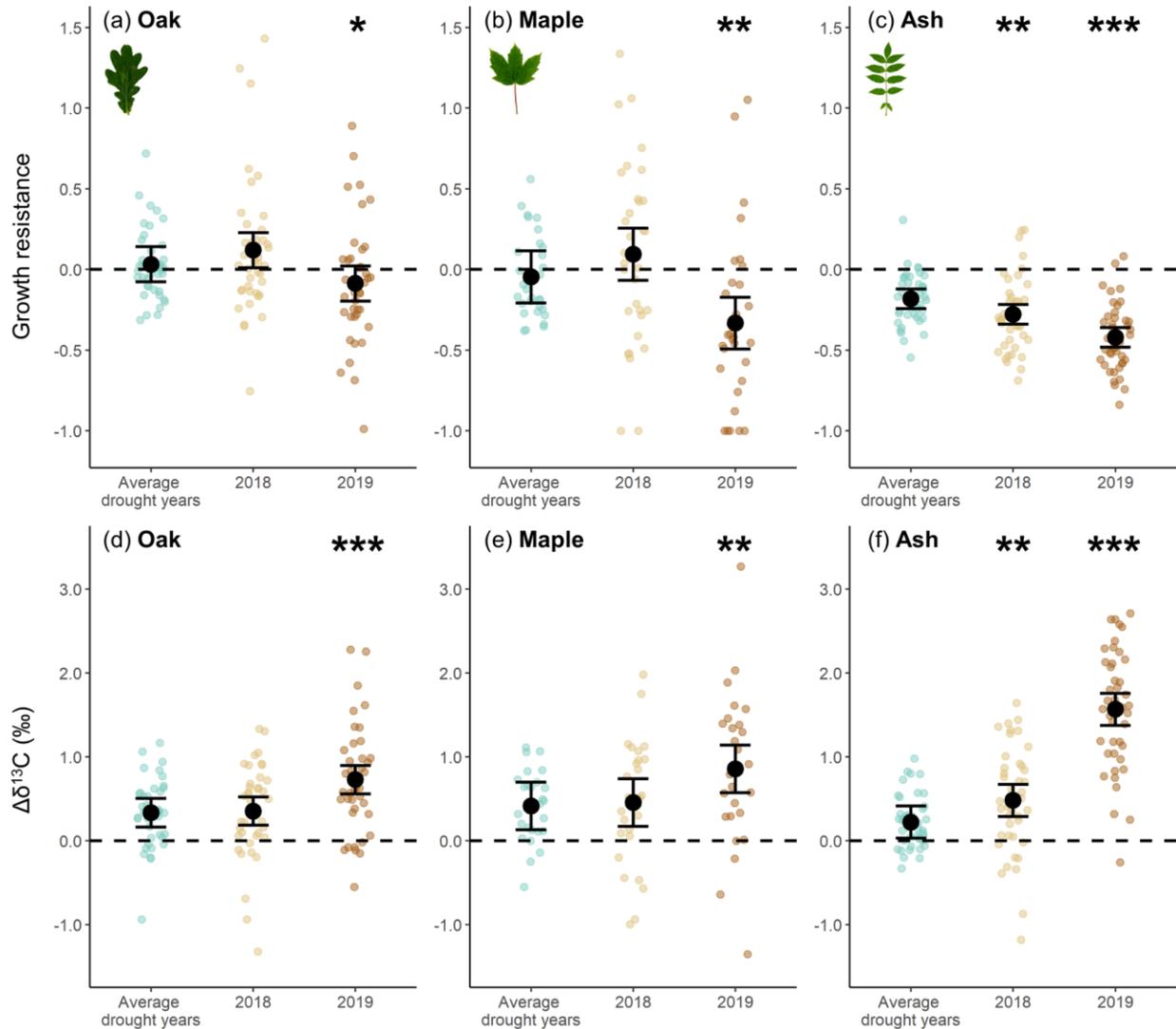
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141 Results

142 We found pronounced responses to drought stress in terms of tree growth and $\Delta\delta^{13}\text{C}$ across the
143 examined tree species, with strongest stress responses in the second of two consecutive drought
144 years (2019). Mean growth resistance in single drought years before the 2018-2019 consecutive

145 drought (hereafter ‘single drought years’) ranged around zero for oak and maple, while growth
146 resistance in ash tended to be below zero (Fig. 2a-c). This indicates a similar tree growth in single
147 drought years and in climatically ‘normal’ years for oak and maple but not for ash (drought year
148 classification based on the Standardized Precipitation Evapotranspiration Index (SPEI)³⁹; see
149 methods). Growth of oak and maple even tended to be higher in 2018 compared to normal years
150 (mean growth resistance above zero). The hotter drought in 2018 did not induce significant
151 reductions in growth resistance in oak and maple compared to single drought years ($P > 0.1$ for both
152 species) but growth resistance in ash decreased significantly ($t = -2.94$, $P = 0.004$; Fig. 2c;
153 Supplementary Table 1). In 2019, the second consecutive and extreme drought year, growth
154 resistance of all species dropped drastically in comparison to single drought years (oak $t = -2.00$,
155 $P = 0.049$; maple $t = -2.74$, $P = 0.008$; ash $t = -7.22$, $P < 0.001$; Fig. 2a-c; Supplementary Table 1) and in
156 comparison to 2018 (Supplementary Table 2). The trends in growth resistance were insensitive to
157 the type of growth data (raw or detrended) and reference period (1-year or pooled years) used
158 (Supplementary Figs. 3-4). Distance to groundwater had an overall small influence on the growth
159 resistance of the examined species (non-significant interaction of drought year and groundwater
160 level). Only for oak we found indications for a higher growth resistance on wet plots in 2019
161 (significant interaction of drought year and groundwater level, $P = 0.0413$). Among the three
162 analysed species, ash showed the highest growth sensitivity to drought (especially to SPEIs
163 indicating summer drought) while oak was the least sensitive (Supplementary Fig. 5).

164



165

166 Fig. 2 Growth resistance and increase in the carbon isotope ratio ($\Delta\delta^{13}\text{C}$) in wood of oak, maple and ash in

167 drought years. The figure shows growth resistance (upper panels) and $\Delta\delta^{13}\text{C}$ (lower panels) in the

168 consecutive hotter drought years 2018 and 2019 compared to the mean resistance and $\Delta\delta^{13}\text{C}$ in single

169 drought years (2003, 2006 and 2015). A value around 0 corresponds to a comparable growth and $\delta^{13}\text{C}$ in

170 drought and normal years. Black points show estimated marginal means and error bars the 95% confidence

171 intervals of linear mixed-effect model fits. Coloured points show growth resistance and $\Delta\delta^{13}\text{C}$ values per

172 tree and species (oak $n=40$, $n=39$; maple $n=32$, $n=26$; ash $n=42$, $n=42$) and are jittered to enhance visibility.

173 Growth resistance and $\Delta\delta^{13}\text{C}$ were calculated with Eq. 1 and Eq. 3, respectively. The tree ring-widths have

174 been detrended with a negative exponential function. Statistically significant differences in growth

175 resistance and $\Delta\delta^{13}\text{C}$ between the years 2018 and 2019 compared to single drought years are indicated by
176 asterisks over the respective year ('***' $p < 0.001$; '**' $p < 0.01$; '*' $p < 0.05$).

177

178 We found positive $\Delta\delta^{13}\text{C}$ values across all species and drought years, indicating tree physiological
179 stress responses to drought irrespective of drought type (single or consecutive; Fig. 2d-f).
180 However, the magnitude of $\Delta\delta^{13}\text{C}$ increases varied strongly between drought years and species.
181 For oak and maple, $\Delta\delta^{13}\text{C}$ was not significantly enhanced in 2018 compared to single drought
182 years ($P=0.85$ and $P=0.79$), while ash had significantly lower $\Delta\delta^{13}\text{C}$ values ($t=2.85$, $P=0.006$; Fig.
183 2f; Supplementary Table 1). Across all species, we found a drastic increase in $\Delta\delta^{13}\text{C}$ in 2019
184 compared to single drought years (oak $t=3.93$, $P<0.001$; maple $t=2.80$, $P=0.007$; ash $t=14.80$,
185 $P<0.001$; Fig. 2d-f; Supplementary Table 1) and in comparison to 2018 (Supplementary Table 2).
186 The $\Delta\delta^{13}\text{C}$ increase was strongest for ash. Distance to groundwater had no significant influence on
187 $\Delta\delta^{13}\text{C}$ for all examined species. Together these results indicate that drought stress in 2018 was,
188 except for ash, comparable to stress in former single drought years, while the second consecutive
189 drought year 2019 induced unprecedented growth reductions and increases in $\Delta\delta^{13}\text{C}$ across all
190 species.

191

192 **Discussion**

193 Using tree growth resistance and $\Delta\delta^{13}\text{C}$ as indicators of drought stress, we report a drastic increase
194 in drought-related stress in the second of two consecutive hotter drought years across all examined
195 species. Drought responses were strikingly consistent for both indicators (growth resistance and
196 $\Delta\delta^{13}\text{C}$; Fig. 2), but the timing and magnitude of responses were species-specific: Oak showed the
197 overall smallest stress response followed closely by maple with the strongest response in ash. The

198 2019 drought, although an extreme drought as well, was meteorologically less severe than the
199 preceding drought year 2018, as indicated by less negative SPEI values and lower growing season
200 temperature (Fig. 1). This indicates that the cumulative drought effect exerted by both years was
201 responsible for the stress increase in 2019. The 2018 hotter drought was the severest drought so
202 far recorded in Central Europe^{5,7,8}, but, as predicted, we found drought stress to be comparable to
203 former single drought years and tree growth to be largely within the range of climatically ‘normal’
204 years. Hence, the high water availability in floodplain forests may partly buffer tree stress
205 responses to single but not to consecutive drought years.

206
207 Our conclusion that the effects of single drought years were buffered to some extent contrasts with
208 the dramatic drought effects reported across European forests in 2018 that suffered widespread
209 defoliation, xylem hydraulic failure and mortality^{5,8} but is consistent with other floodplain forest
210 studies. For instance, the exceptionally high gross primary production during the warm spring in
211 2018 was found to compensate for losses later that year due to drought in a Czech floodplain
212 forest³¹. Similarly, tree growth recovered within two years after the 1976 drought for all herein
213 analyzed floodplain forest species, which was attributed to the drought buffering effect of water
214 availability in floodplain forests³². Nonetheless, we found physiological stress increases ($\Delta\delta^{13}\text{C}$)
215 in 2018 while tree growth in most species did not react. This confirms the view of more consistent
216 drought signals in $\Delta\delta^{13}\text{C}$ compared to tree ring-width¹⁸, potentially due to tree growth being
217 maintained from carbon reserves even under low soil water availability¹⁸.

218
219 This picture changed dramatically in 2019. As hypothesized, we observed drastic stress increases
220 in the second consecutive drought year, likely driven by the cumulative effect of both drought

221 years. Drought legacy effects⁹ were found to be widespread in forests and to effect tree growth and
222 $\Delta\delta^{13}\text{C}$ 1-5 years after the actual drought event^{9-13,15}. Hence, trees were likely still suffering from
223 2018 when the second drought year 2019 stroke. Results on drought legacies from former studies
224 are, however, only partially applicable to our case, as these focused on legacy effects in post
225 drought periods in which trees were already (partially) recovering. In such cases it is difficult to
226 disentangle drought legacy effects from other changes in a trees environment that may affect tree
227 growth and $\Delta\delta^{13}\text{C}$ ¹². In contrast, we focus here on two consecutive hotter drought years,
228 unprecedented in their severity at least since 250 years⁷, which left the trees no time to recover.
229 The few studies that studied prolonged droughts, moreover, did not examine the cumulative built-
230 up of drought effects from year-to-year as they used either mean tree growth across drought years
231 or growth in the last year of drought to calculate growth resistance¹⁶. In comparison, the strong
232 reactions we report for 2019 should be clearly attributable to legacies of 2018, as other changes in
233 the trees' environment like reduced competition for light are unlikely within a single year. In
234 addition, forest management can be excluded as potential cause as we did not sample trees in
235 stands that experienced recent interventions. Similarly, assessments of the 2018 hotter drought
236 found early signs of strong drought legacy effects^{5,8}.

237

238 Different meteorological conditions may have amplified this cumulative drought stress. The
239 increasing frequency of droughts and exceptionally hot years, especially since 2015⁸ (Fig. 1;
240 Supplementary Fig. 1), may have successively reduced the trees capacity to withstand drought¹³,
241 leaving them weakened when the 2018-2019 drought stroke⁵. Moreover, the second hotter drought
242 year 2019 started already with severe water shortages as the low winter and spring precipitation in
243 2018-2019 was not enough to refill soil water reservoirs (UFZ Drought Monitor/Helmholtz Centre

244 for Environmental Research). Finally, the severe drought conditions in both years coincided with
245 the main growth period of the trees (April-August)^{5,40} and thus exerted the highest possible stress.
246 Our sampling sites cover the whole gradient of groundwater conditions in the examined floodplain
247 forest but interestingly we found only small effects of groundwater level. The reasons remain
248 speculative. Differences in distances to the groundwater level may have been too small to induce
249 strong effects on tree performance or, alternatively, more intense rooting on dry plots may have
250 compensated for lower water availability²⁹. It is also possible that trees depended primarily on
251 water uptake from upper soil horizons that are fed through capillary rise from the groundwater
252 level^{24,41} which is broken under severe water shortage at all distances to the groundwater level.
253
254 Several physiological mechanisms could explain cumulative drought stress⁹. Drought-induced loss
255 of leaves and xylem cavitation may impair growth and transpiration (and thus effect $\Delta\delta^{13}\text{C}$)^{8,21}.
256 Under consecutive drought, this damage persists, while vulnerability to cavitation may continue
257 to increase under successive drought stress¹³. In the second drought year, less nonstructural
258 carbohydrates (NSC) reserves were likely left for xylem repair, growth and especially for keeping
259 up the trees defense system, which increases the susceptibility to pests and pathogens^{8,13,21,42}. Large
260 parts of the here examined stands suffered severe damages and mortality through sooty bark
261 disease, ash dieback and secondary beetle infestations in 2019, which points to depleted NSC
262 stores causing a collapse of the trees' immune system. We studied only the most vital tree
263 individuals of the population thus largely excluding disease effects from our sample. However, as
264 the majority of ash trees in the forest were affected to some degree⁴³, we cannot completely
265 disentangle whether the species intrinsic traits, incipient ash-dieback or their interaction caused
266 the strong stress response in this species. Finally, drought induces shifts in carbon allocation in

267 favor of the canopy and root system at the expense of radial growth¹¹ and, when photosynthesis is
268 insufficient to meet demands, NSC reserves are utilized to maintain autotrophic respiration, growth
269 and tissue repair^{42,44}. This enriches the reserve pool and tissues built from it in ¹³C as the
270 isotopically lighter ¹²C is turned over faster than ¹³C. Both processes may have further contributed
271 to the drastic decrease in tree-ring growth and increase in $\Delta\delta^{13}\text{C}$ in 2019 in addition to fractionation
272 through stomata closure.

273

274 The magnitude and timing of drought stress responses were species-specific, which may be related
275 to differences in species hydraulic traits. Oak has a deep reaching root system and may thus be
276 able to maintain water uptake during low precipitation periods^{24,29,45}, while its water saving
277 behavior (oak is isohydric^{35,36}) may have helped to avoid xylem cavitation during peak drought
278 periods²¹. In contrast, ash has roots mainly restricted to upper soil layers and is thus more
279 dependent on precipitation than oak^{23,24}. Its water spending behavior (ash is anisohydric^{37,38}),
280 moreover, carries a high risk for xylem cavitation if continued water uptake via roots is impaired²¹,
281 an especially risky strategy on the loamy Vega soils of our study site, which reached soil moisture
282 levels below the permanent wilting point of vegetation for clay soils⁴⁶ during the 2018 drought.
283 The intermediate stress reaction of maple is consistent with its stomatal control, which lies between
284 oak and ash^{37,38}. This partly confirms our third hypothesis in that anisohydric ash showed the
285 strongest reaction to consecutive drought, but we did not find faster reactions to drought in 2018
286 in isohydric species (oak and maple). The intermediate drought reaction of maple, which is often
287 considered drought sensitive³⁷, may also be related to its less exposed crown position (maple trees
288 were rather co-dominant) which can reduce irradiance and water pressure deficits⁴⁷. Finally, here
289 reported drought effects may be influenced through the naturally high tree species richness of

290 floodplain forests²⁷, as diverse tree communities may outperform species poor communities
291 through complementarity in water use such as water uptake from different soil layers^{24,48}.

292

293 The response of forests to the increasing frequency and intensity of droughts¹ will affect a variety
294 of ecosystem services and will determine if forests act as carbon sink or source in the 21st century.

295 Here, we show that the cumulative effect of two consecutive hotter drought years (2018-2019)

296 induces drastic drought-related tree stress responses in a Central European floodplain forest. We

297 found partly buffered tree stress responses, presumably because floodplain trees are fed by

298 groundwater in addition to precipitation, and examined only the most vital tree individuals of the

299 population. Our results thus show a ‘best-case scenario’ and more severe tree responses could be

300 expected if entire tree populations or other forest ecosystems were examined, as indicated by wide-

301 spread tree mortality observed in assessments of the 2018 drought^{5,8} and at our own site. Linking

302 responses in growth resistance and $\Delta\delta^{13}\text{C}$ to tree mortality and carbon ecosystem fluxes remains

303 challenging¹¹. Moreover, it remains unknown how the here observed responses will affect tree

304 recovery after and resilience^{15,16} to (future) droughts. The strong drought legacy effects we observe

305 in the second drought year (2019), the reported persistence of legacy effects for years⁹ and

306 successive declines in drought resistance under consecutive drought^{13,15} are worrisome. On the

307 other hand, a species like oak that combines a high tolerance to drought and flood⁴⁵, may remain

308 resilient, underlining its importance for floodplain forests. Consecutive hotter droughts are

309 projected to become more frequent⁷. Our ability to forecast forest responses to climate change

310 hinges on our ability to understand what drives tree responses to this novel stress.

311

312 **Methods**

313 **Study site**

314 In this study, we used data collected from a Central European floodplain forest ecosystem located
315 in the northwest of the city of Leipzig, Germany. The Leipzig floodplain forest is one of the few
316 remaining and thus highly protected floodplain forests in Central Europe^{33,34} and lies in the
317 transition zone between maritime and continental climate characterized by warm summers, with
318 an annual mean temperature of 9.6 °C and an annual precipitation sum of 525 mm (1979-2019;
319 DWD, Station Leipzig/Halle). Its main rivers Weiße Elster, Luppe, Pleiße and Parthe formed the
320 floodplain landscape, but their course and thus the floodplain forest itself has been strongly
321 influenced by human interventions over the last centuries⁴⁹. The straightening of rivers as well as
322 dike and canal constructions strongly influenced the hydrological regime of the floodplain forest,
323 which today does not experience regular flooding's anymore⁵⁰. The contemporary floodplain
324 forest ecosystem can be characterized as *Ficario-Ulmetum* Knapp ex Medwecka-Kornas 1952
325 (synonyms: *Fraxino-Ulmetum* Tüxen ex Oberdorfer 1953, *Querco-Ulmetum* Issler 1926 nom.
326 inval.) with oak, elm and ash being the dominant tree species⁵¹. The absence of flooding, however,
327 resulted in an on-going gradual shift to an oak-hornbeam forest (*Galium-carpinetum*
328 *stachyetosum*) and allowed other tree species (especially maple), which are intolerant to flooding,
329 to become dominant. Moreover, elm (*Ulmus minor*) largely disappeared from the tree canopy due
330 to the Dutch Elm Disease since the 1960s. Nowadays, the dominant tree species of Leipzig's
331 floodplain forest are *Quercus robur* L. (oak), *Acer pseudoplatanus* L. (maple) and *Fraxinus*
332 *excelsior* L. (ash)^{50,52}, on which we focus in the present study. The floodplain soils originated from
333 an accumulation of alluvial sediments, such as gravel, sand and loam, as result of several glacial
334 periods⁵⁰. These are nowadays covered by an alluvial clay layer with a thickness between 1-4 m,

335 rich in nutrients and with a high pH (around 6-7), whose deposition is closely linked to historic
336 human settlements and deforestation^{49,50}. The principal soil available to trees is thus a loamy Vega,
337 with partly gleyed conditions, above gravel and sand filled with groundwater.

338

339 **Drought year identification**

340 The definition and identification of drought is central to the analysis of drought effects. Here, we
341 define drought as period with water deficits compared to normal conditions, where ‘normal’ can
342 be quantified as a percentile of the long-term mean of meteorological or hydrological variables^{16,53}.
343 Following suggestions by Schwarz *et al*¹⁶ we selected drought years based on climatic and
344 hydrological information alone without considering tree growth reductions to avoid a biased
345 selection that could for example result in the exclusion of drought years without reduced growth.
346 We used the Standardized Precipitation Evapotranspiration Index (SPEI)³⁹ and river discharge data
347 to identify drought years. The SPEI is a commonly used drought index^{7,16,29} based on the
348 standardized monthly water balance of precipitation minus potential evapotranspiration. It can
349 quantify drought severity according to a droughts intensity and duration and can be calculated at
350 different time scales (e.g. 1-12 months)³⁹. Here, we used three different SPEI lengths that represent
351 the climatic water balance of the main vegetation period (SPEI for 3 months, Mai-July), the full
352 vegetation period (SPEI for 6 months, April-September) and the full year (SPEI for 12 months,
353 January-December) for each year and with a 40-year reference period (1979-2019; Supplementary
354 Fig. 1). SPEIs were calculated with the SPEI package⁵⁴ in R from monthly precipitation (mm) and
355 potential evapotranspiration (mm) data derived from the weather station located closest to the
356 study sites (DWD, Station Leipzig/Halle, ID 2932; Supplementary Fig. 1).

357

358 We classified years with SPEI values ≤ -1 as drought years, years with SPEI values ≥ 1 as
359 particularly wet and years with values between -1 and 1 as ‘normal’⁵⁵. To take into account the
360 hydrological regime of the floodplain forest, which is in addition to local precipitation strongly
361 influenced by its rivers, we compared the SPEI derived classification to river discharge calculated
362 for the same periods as the SPEIs (Supplementary Fig. 2). We considered only years without
363 particularly high discharge as drought years. Focusing on a 20-year period before the 2018-2019
364 consecutive drought, we selected 2005, 2009 and 2017 as reference years with normal climatic
365 conditions, while single drought years – in contrast to the 2018-2019 consecutive drought – were
366 2003, 2006 and 2015 (Fig. 1; Supplementary Figs. 1-2). We did not consider a longer period to
367 minimize the effect of past forest management and ground water fluctuation related influences on
368 tree growth. Both, the drought in 2018 and the one in 2019 were the most severe droughts in the
369 last 40 years (i.e. they had the lowest SPEI values), but 2018 had slightly lower SPEI values and
370 was especially characterized by an extreme heat wave during the vegetation period.

371

372 **Tree selection and increment core extraction**

373 We selected trees for extracting wood increment cores from permanent forest research plots of the
374 "Lebendige Luppe" (living Luppe river) project⁵⁶, which cover a gradient in topographic distances
375 to the groundwater level (Supplementary Fig. 6). The project features three distinct strata of
376 distance to groundwater: dry ($> 2\text{m}$), intermediate (1-2m) and wet ($\leq 1\text{m}$) plots, with 20 plots per
377 stratum each 0.25ha in size. Plots were not flooded since 1973 due to flood control measures
378 (dikes, river-straightening etc.), except for a relatively short period in winter 2011 and summer
379 2013, when the area of Leipzig experienced extreme flood events. We chose to sample trees on
380 dry and wet plots to cover both ends of the gradient of hydrological site conditions within the

381 floodplain forest (Supplementary Fig. 6). Across these plots, we extracted tree increment cores
382 from at least 40 tree individuals per species (20 trees per stratum) from each of the three dominant
383 tree species oak, maple and ash, amounting to 120 sampled trees. From each tree, we extracted
384 one increment core at a height of 80cm with a \emptyset 5mm increment corer (Suunto, Sweden) in
385 January-February 2020. Trees with diameters at breast height (dbh) > 20cm were selected
386 according to their dominance, past management history and health status. Competition for light is
387 a central determinant of tree growth and $\delta^{13}\text{C}$ that might complicate the detection of drought
388 effects¹⁷. We therefore sampled only dominant and co-dominant individuals, i.e. trees belonging
389 to category 1-2 according to the classification of Kraft⁵⁷, that were no direct competitors and
390 further excluded plots that showed signs of forest management in recent years. We further selected
391 only healthy appearing trees, excluding those ash trees visually affected by ‘ash dieback’
392 (*Hymenoscyphus fraxineus*) and those maple trees visually affected by the ‘sooty bark disease’
393 (*Cryptostroma corticale*). Both fungal pathogens had caused widespread tree damages and
394 diebacks in the Leipzig floodplain forest during the 2018-2019 consecutive drought and especially
395 very few ash trees were completely unaffected⁴³. We used the classification key of Lenz *et al.*⁵⁸
396 for ash dieback infestation and sampled only trees showing no to only little signs of infestation
397 (level 0-2 of infestation levels 0-5) based on annual infestation records for four years prior
398 sampling, while we sampled maple trees that showed no visual sign of sooty bark disease.
399 Importantly, our sample is thus representative for the most vital individuals of the entire
400 population. Since the number of trees fulfilling these strict criteria was too low within the plot
401 area, we sampled also oak and maple trees in the direct vicinity of the plots.

402

403 **Tree growth analysis**

404 Tree cores were dried at 70 °C for at least 3 days and then clamped in wooden alignment strips.
405 For surface preparation, we used a core microtome (WSL, Switzerland)⁵⁹ to enhance visibility of
406 tree ring boundaries. Tree ring-width was measured with a LINTAB 6 measuring table and the
407 TSAPWin Professional 4.64 program © 2002-2009 Frank Rinn / RINNTECH with an accuracy of
408 1/1000 mm. The measured sequences were cross-dated against a species-specific master
409 chronology developed in former works for the same area as well as against each other using
410 COFECHA⁶⁰. This allowed us to identify missing rings, which were more often found in maple
411 trees and in the consecutive drought years 2018-2019. Years without growth were included as zero
412 for the respective year. Sequences that could not be dated unequivocally were excluded from
413 further analysis. The final number of trees included for growth analysis was 114 trees instead of
414 the planned 120, including 40 oak, 32 maple and 42 ash trees from 11 wet and 15 dry plots.

415

416 Tree ring-width provides an integrated record of past growth conditions as influenced by
417 environmental factors including but not limited to climate and shows an inherent decrease in ring-
418 width with increasing tree size¹⁴. As we focus here on climatic influences on growth, we removed
419 age-related trends from the raw tree ring-width chronologies via a Negative Exponential curve⁶¹,
420 which provided the best compromise between removing long-term age trends and preserving
421 decadal variability in growth using the package `dpIR`^{62,63}. We assessed the climatic sensitivity of
422 tree growth through computing bootstrapped Pearson's correlation functions between species-
423 specific chronologies and monthly climatic variables (Supplementary Fig. 5), using the package
424 `treeclim`⁶⁴.

425

426 We used tree growth resistance to the consecutive drought years 2018 and 2019 as well as to single
427 drought years as indicator for tree growth responses to drought. Growth resistance for each
428 individual tree was calculated following Lloret *et al.*¹⁵ as:

429

$$430 \text{ Growth resistance} = \frac{Dr_{growth}}{PreDr_{growth}} - 1 \quad (1)$$

431

432 where Dr_{growth} is a tree's growth in drought year(s) and $PreDr_{growth}$ is a tree's growth in the
433 reference period characterized by normal climatic conditions. Growth resistance is thus
434 standardized around zero with positive values meaning higher and negative values lower growth
435 during drought year(s) compared to reference years. We calculated growth resistance for 2018,
436 2019 and for single drought years (using their mean growth resistance in all analysis). Recent
437 decades experienced an unprecedented surge in temperatures and drought events^{5,8}, making the
438 use of a continuous reference period of several years before drought events that is not influenced
439 by drought itself difficult. We therefore used the mean growth in three years (2005, 2009, 2017)
440 that were characterized by normal climatic conditions and not proceeded by a drought year (see
441 above; Supplementary Fig. 1) to calculate $PreDr_{growth}$. We used several years to calculate
442 $PreDr_{growth}$ and resistance in single drought years as this should reduce the influence of outliers
443 caused by individual tree reactions to other factors than climate (e.g. changes in competitive
444 interactions, waterlogging). However, as the choice of growth data and a reference period can
445 strongly influence results on tree growth resistance to drought¹⁶, we tested for the robustness of
446 here reported relationships. We examined tree growth dynamics and growth resistance in detail
447 based on raw and detrended ring-width and further compared resistance calculated with a 1-year
448 pre-period (2017 was the only climatically normal year before the 2018-2019 consecutive drought;

449 Supplementary Fig. 1) to resistance calculated with the mean reference period detailed above.
450 Trends in growth resistance between years were consistent for all species (Fig. 2a-c;
451 Supplementary Figs. 3-4).

452

453 **Carbon isotope analysis**

454 The stable carbon isotope composition ($\delta^{13}\text{C}$) in wood of the same cores was measured after
455 completing tree ring-width measurements. The tree rings of the herein analysed consecutive
456 drought years 2018-2019, of single drought years (2003, 2006, 2015) and of reference years (2005,
457 2009, 2017) were separated and their wood tissue homogenized. Some trees, especially maple
458 ones, did not form tree rings during the 2018-2019 consecutive drought, likely due to intense
459 drought stress. As their $\delta^{13}\text{C}$ could thus not be analysed, we excluded these trees from our isotope
460 analysis (6 maple and 1 oak tree). The homogenized material of the tree rings in reference years
461 (2005, 2009 and 2017) and single drought years (2003, 2006 and 2015), was pooled by mixing
462 equal shares of the material from each of the three years. The isotope analysis was done at the
463 BGC stable isotope laboratory of the Max Planck Institute for Biogeochemistry in Jena, Germany.
464 The results were expressed as isotopic ratio $\delta^{13}\text{C}$, calculated with the equation of Farquhar *et al.*¹⁹
465 as follows:

466

$$467 \quad \delta^{13}\text{C} = \left(\frac{\delta^{13}\text{C}(\text{sample})}{\delta^{13}\text{C}(\text{standard})} - 1 \right) * 1000\text{‰} \quad (2)$$

468

469 where $\delta^{13}\text{C}(\text{sample})$ and $\delta^{13}\text{C}(\text{standard})$ are the abundance ratios between ^{13}C and ^{12}C of the given
470 sample and Vienna PeeDee Belemnite international standard (VPDB). Isotope ratios were
471 expressed in δ -notation in per mil units (‰). We calculated the increase in $\delta^{13}\text{C}$ from reference to

472 drought years for each individual tree as indicator of a tree's physiological stress response to
473 drought as:

474

$$475 \quad \Delta\delta^{13}\text{C} = Dr_{\delta^{13}\text{C}} - PreDr_{\delta^{13}\text{C}} \quad (3)$$

476

477 where $Dr_{\delta^{13}\text{C}}$ is the isotope composition in drought year(s) and $PreDr_{\delta^{13}\text{C}}$ the isotope composition
478 in the reference years (see e.g. ref¹⁷). Positive values of $\Delta\delta^{13}\text{C}$ thus indicate higher and negative
479 values lower stress during drought year(s) compared to reference years. Drought and reference
480 years used to calculate $\Delta\delta^{13}\text{C}$ were the same as in the growth resistance analysis.

481

482 **Statistical analysis**

483 We used linear mixed-effect models (LMMs) to understand the effects of consecutive drought
484 years on tree growth resistance and $\Delta\delta^{13}\text{C}$ in comparison to single drought years. We were further
485 interested in understanding how these effects were modulated by changes in a trees distance to
486 groundwater. We fitted species-specific LMMs for growth resistance and $\Delta\delta^{13}\text{C}$ with the packages
487 `lme4`⁶⁵ and `lmerTest`⁶⁶ and a significance level of $\alpha=0.05$. Drought events (single droughts, 2018,
488 2019), groundwater level (dry > 2m, wet \leq 1m) and their interaction were modelled as fixed effects,
489 while tree identities nested within plots were used as nested random effects to account for
490 differences between plots and for repeated measurements on each individual tree. We selected the
491 most parsimonious model structure via backward model selection, first adjusting the fixed and
492 then the random effect structure, using the step function in `lmerTest`. The most parsimonious LMM
493 structure consistently retained only a fixed effect of drought event and tree identity nested within
494 plots as random effects, indicating that water table did not strongly influence observed

495 relationships. Only for the growth resistance LMM of oak we found a significant interaction
496 ($P=0.0413$) between drought event and groundwater level, which however disappeared when using
497 non-detrended growth data or a 1-year reference period. Therefore, to report only the most robust
498 relationships, we present all final LMMs with drought event as the only fixed effect. Final LMMs
499 (Supplementary Table 1) were fit using restricted maximum likelihood estimation (REML) and
500 marginal means and confidence intervals (95%) were predicted with the `ggeffects` package⁶⁷. We
501 used post-hoc pairwise comparisons with adjusted p-values for multiple comparisons (Tukey's
502 Honest Significant Difference) to compare differences between drought events using the `emmeans`
503 package⁶⁸ (Supplementary Table 2). Model assumptions (normality, independence and
504 homogeneity of variance) were visually checked through examining model residuals and through
505 quantile-quantile plots. All analyses were conducted in R version 4.0.3⁶⁹.

506

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517

518 **Author contributions**

519 C.W., F.S., R.A.E., A.K., R.R., C.S.-D. and G.S. conceived the idea and developed the concept of
520 the study. S.P., L.S., A.K., F.S., R.A.E. and C.S.-D. collected data. F.S., S.P, L.S. and G.S.
521 analyzed data. F.S., C.S.-D. and G.S. created figures. F.S. wrote the manuscript with contributions
522 from S.P. and L.S. All authors discussed the results and contributed substantially to revisions.

523

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