

1 **Functional traits explain growth resistance to successive hotter droughts**
2 **across a wide set of common and future tree species in Europe**

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6 **Submitted to:** Plant biology: special issue (Impacts of Droughts and Drought Legacies on
7 Plants and Ecosystems)

8 **Abstract**

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- 10 • In many regions worldwide, forests suffer from climate change-induced droughts.
11 The ‘hotter drought’ in Europe in 2018 with the consecutive drought years 2019 and
12 2020 caused large-scale growth declines and forest dieback. We investigated if tree
13 growth responses to the 2018–2020 drought can be explained by tree functional
14 traits related to drought tolerance, growth, and resource acquisition.
 - 15 • We assessed growth resistance, that is, growth during drought compared to pre-
16 drought-conditions, in 71 planted tree species using branch shoot increments. We
17 leveraged gap-filled trait data related to drought tolerance (P50, stomata density and
18 conductivity), growth and resource acquisition (SLA, LNC, C:N, A_{max}) and wood
19 density from the TRY database to explain growth resistance for gymnosperms and
20 angiosperms.
 - 21 • We found significantly reduced growth during drought across all species. Legacy
22 effects further decreased growth resistance in 2019 and 2020. Gymnosperms showed
23 decreasing growth resistance with increasing P50 and acquisitiveness, such as high
24 SLA, LNC, and A_{max} . Similar results were found for angiosperms, however, with less
25 clear pattern. Four distinct response types emerged: ‘Sufferer’, ‘Late sufferer’,
26 ‘Recoverer’ and ‘Resisters’, with gymnosperms predominately falling into the
27 ‘Sufferer’ and ‘Late sufferer’ categories.
 - 28 • Our study provides evidence for significant growth reductions and legacy effects in
29 response to consecutive hotter droughts, which can be explained by functional traits
30 across a wide set of tree species. The a posteriori classification into response types
31 revealed the diversity of temporal responses to a prolonged drought. We conclude
32 that high drought tolerance bolsters growth resistance, while acquisitive species
33 suffer stronger under drought.

33

34 **Keywords:** climate change, forest, drought tolerance traits, shoot growth, ARBOfun

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47

48 **Introduction:**

49 In many regions of the world forest productivity decreases, as trees suffer from more
50 intense and frequent drought events caused by climate change (Allen et al., 2010; IPCC,
51 2014; McDowell et al., 2020). Negative impacts on forests are particularly pronounced for
52 so-called ‘hotter droughts’ which are compound events characterized by low precipitation
53 and simultaneous heat waves (Allen et al., 2015). Such hotter droughts cause enhanced soil-
54 water depletion and increases in canopy temperature, potentially surpassing physiological
55 tolerance thresholds and thereby inducing strong growth reductions (Allen et al., 2015;
56 Buras, Rammig, & Zang, 2020). Such growth declines often precede large-scale tree mortality
57 events, eventually being amplified by climate change-induced insect and pathogen
58 outbreaks. (Allen et al., 2015; McDowell et al., 2020). Thus, hotter droughts negatively
59 impact many ecosystem functions and services of forests, such as carbon sequestration
60 (Buras, Rammig, & Zang, 2020; Senf et al., 2020) and transpirative cooling (Richter et al.,
61 2021), and may induce strong changes in species compositions (Schuldt et al., 2020).
62 However, we thus far have only a limited understanding of how intense drought events
63 cause growth reductions across a wide range of tree species. We further lack knowledge on
64 functional properties of tree species which help to develop trait-based models to generalize
65 responses to hotter drought across wide taxonomic gradients and to parametrize models
66 predicting growth responses and eventually mortality risks (Adams et al., 2017).

67 In the year 2018, Central Europe experienced a hotter drought, which was climatically
68 the most extreme drought since the beginning of climatic records in Europe (Schuldt et al.,
69 2020; Zscheischler & Fischer, 2020). The hotter drought conditions persisted in the year
70 2019 and in many Central European regions continued even until 2020 (Rakovec et al.,
71 2022). These three consecutive drought years (hereafter referred to as the ‘2018–2020
72 drought’) may mark the beginning of a new era of compound climate extremes which is in
73 line with models of climate change that project hotter, drier and more extreme climatic
74 conditions, particularly in summer months, for Central Europe during the 21st century (IPCC,
75 2014; Reichstein et al., 2013; Samaniego et al., 2018; Trenberth et al., 2014; Zscheischler &
76 Seneviratne, 2017). Such consecutive and hotter droughts induce prolonged stress, amplified
77 reductions in tree growth and eventually large-scale forest dieback, especially when
78 interacting with fungal pathogen and insect outbreaks (Hari et al., 2020; Kleine et al., 2021;
79 Schnabel et al., 2022; Thonfeld et al., 2022).

80 Here we aim to understand tree growth responses across a broad range of native and
81 introduced Central European tree species to the 2018–2020 drought. We included
82 introduced species from North America and Asia, based on their current relevance in Central
83 Europe as future tree species under climate change. Growth resistance in this context is
84 defined as the ratio of the growth during the drought years and the growth prior to the
85 drought. Especially interesting are potential growth reactions during the second and third
86 consecutive drought year (2019 and 2020), as droughts can still affect trees negatively one
87 to five years after the actual drought event, which is known as drought legacy effect
88 (Anderegg et al., 2015; Anderegg, Kane, et al., 2013; Bigler et al., 2006; Gazol et al., 2020;
89 Kannenberg et al., 2018; Schnabel et al., 2022). Legacy effects of the 2018 drought, such as
90 associated damages to the water transport system of trees (Anderegg, Plavcová, et al.,

91 2013), may limit their capacity to deal with and recover from the subsequent drought years.
92 Moreover, growth reductions may be amplified by a cumulative build-up of soil water
93 deficits. Hence, one may expect a lower growth resistance in the consecutive drought years
94 2019 and 2020, which is, for instance, consistent with recent reports of a lower growth
95 resistance in 2019 compared to 2018 in a Central European floodplain forest (Schnabel et al.,
96 2022). However, observational forest studies are typically restricted to relatively few tree
97 species making it complicated to test for the trait-based mechanisms driving legacy effects
98 and to generalize these across regional tree floras.

99 The recent years have seen a surge of studies exploring the trait-based mechanisms
100 underpinning drought effects on tree growth (Bose et al., 2020; Larysch et al., 2022; Liu et
101 al., 2022). These studies are typically restricted to few tree species in single sites or combine
102 observations from different sites that vary in environmental conditions. Under water
103 shortage, plants are facing a trade-off between carbon gain and water loss (Cowan &
104 Farquhar, 1977). Thus, the physiological key processes that cause growth reductions are
105 either carbon starvation or partial hydraulic failure, but the relative balance between both
106 processes varies strongly between tree species and with growing conditions (Adams et al.,
107 2017; McDowell et al., 2008; Sala et al., 2010; Schuldt et al., 2020; Sevanto et al., 2014). It
108 emphasizes the importance to observe growth responses under drought in a single site
109 under comparable conditions. Traits related to drought tolerance, such as P50 (pressure,
110 where 50 % of the hydraulic system's conductivity has been lost (Adams et al., 2017;
111 Guillemot et al., 2022)), or stomatal control traits, may help to understand growth
112 reductions caused by those two mechanisms (Schnabel et al., 2021, 2022). One may expect
113 that tree species whose functional traits indicate a high drought tolerance, such as a low P50
114 indicating a high tolerance to negative water potentials (Jarbeau et al., 1995; Choat et al.,
115 2018), show a higher growth resistance. Moreover, high stomata density can be caused by
116 lower stomata size, but also may be related to specific spatial distribution (Klein, 2014;
117 Lawson & Blatt, 2014), both possibly indicating a faster or more precise stomata control and,
118 thus a better adaptation to drought under drought conditions. The stomata control is also
119 expected to link to different adaptation strategies under drought of anisohydric and
120 isohydric species (Klein, 2014; N. McDowell et al., 2008). Traits related to stomatal control
121 are complex and depend on tree hydraulics, such as xylem and leaf water potential, but also
122 on the photosynthetic rate. Isohydric species, for example, close their stomata earlier i.e., at
123 lower water potentials or water pressure deficit, often have reduced mean stomata
124 conductance to avoid hydraulic failure during drought and thus are considered water-savers.
125 In contrast, as anisohydric species close their stomata late and thus often have higher mean
126 stomata conductance, they are considered water-spenders (Klein, 2014; N. McDowell et al.,
127 2008). Along this gradient of stomatal behaviour, we would expect that species with lower
128 stomatal conductance are less susceptible to drought. Next to drought-tolerance traits,
129 growth and resource acquisition related traits, such as traits of the leaf economics spectrum
130 representing the slow-fast gradient of plant growth (Guillemot et al., 2022; Reich, 2014) may
131 explain growth resistance to drought. First, tree species with LES trait expressions of the leaf
132 economic spectrum (LES, Díaz et al., 2016) related to conservative resource use and slow
133 growth, such as a high carbon to nitrogen ration (C:N), may feature a higher growth
134 resistance to drought (Choat et al., 2015; Reich, 2014; Wright et al., 2004). This view is

135 consistent with reports of a high correlation of these traits with traits related to cavitation
136 resistance such as P50 (Guillemot et al., 2022; Reich, 2014; Schnabel et al., 2021). In
137 contrast, LES traits related to acquisitive resource use and fast growth, such as high specific
138 leaf area (SLA), leaf nitrogen content (LNC), and light-saturated maximum photosynthetic
139 rate (A_{max}), may feature a lower growth resistance to drought (Wright et al., 2004; Reich,
140 2014; Díaz et al., 2016; Greenwood et al., 2017). In addition, wood density combines various
141 wood properties and is associated with mechanical strength and water transport of the stem
142 (Chave et al., 2009; Zanne et al., 2010). Divergent effects were found before. While some
143 found that species with high wood density have lower mortality rates during drought
144 (Greenwood et al., 2017) and higher growth resistance (Serra-Maluquer et al., 2022), others
145 found for temperate angiosperms higher canopy dieback with high wood density (Hoffmann
146 et al., 2011). Still, slow-growing species tend to have denser wood (Chave et al., 2009; L.
147 Poorter, 2008), thus we would expect growth resistance to increase along with wood
148 density.

149 To guide management decisions and to improve the predictive capacities of forest
150 models it is important to understand the response of all Central European tree species to the
151 2018–2020 drought, i.e. not only of those dominating today, but also the many subordinate
152 or biogeographically neighboring tree species that may form the forest under future climate
153 regimes. Currently, establishing the relationship between functional properties of tree
154 species and their responses to the novel climate situation is challenging. To gain enhanced
155 understanding, we have to exploit the unique sequence of climate events since 2018 and
156 find means to reconstruct tree responses for as many tree species with relevance for Central
157 Europe, including the native tree flora and common non-native tree species. For this
158 purpose, national forest inventories are of limited use for two reasons: (i) they do not
159 possess the necessary temporal resolution to capture the sequence of growth responses
160 (initial resistance, legacy effects, potential recovery), (ii) the Central European managed
161 forest landscape is dominated by few merchantable tree species such as Norway Spruce
162 (*Picea abies*), Scots Pine (*Pinus sylvestris*), European Beech (*Fagus sylvatica*) and Pedunculate
163 Oak (*Quercus robur*), which make up 73.5% of the forest area according to the last German
164 national forest inventory (BWI 2012). In contrast, rare species with large potential for
165 forestry under drier and hotter climates, such as the Checker Tree (*Sorbus torminalis*) and
166 Downy Oak (*Quercus pubescens*) are hardly captured (Buras & Menzel, 2019; Kunz et al.,
167 2018). For instance, three species, as reported by Schnabel et al. (2022), showed reduced
168 growth resistance and drought legacy effects in 2019 compared to 2018, but such
169 observational studies are typically restricted to few tree species making it difficult to derive
170 generalizable conclusions on the trait-based mechanisms across tree species which may
171 explain this drought legacy effect.

172 Here, we examine the effects of the three consecutive drought years 2018–2020 on a
173 large set of 71 planted tree species (Table S1) under experimental conditions in the research
174 arboretum ARBOfun. The arboretum contains 100 species including gymnosperms and
175 angiosperms as well as native and common exotic species. Each species is 5 times replicated
176 in a wide stand with no competition and grown under similar soil conditions. ARBOfun was
177 designed to study responses to climate variability for a large number of tree species. Taking
178 advantage of this unique design, we here aim to provide new insights into the growth

179 resistance of an unprecedented set of tree species and to test if the strength and type of
180 growth responses can be predicted by tree functional traits related to drought tolerance and
181 resource acquisition capacity. We hypothesized that:

182 (1) The 2018-2020 drought reduced tree growth, with a greater reduction in growth
183 resistance in the years 2019 and 2020 due to legacy effects.

184 (2) Tree species whose functional traits indicate drought tolerance show a higher
185 growth resistance to drought stress than drought intolerant species.

186 (3) Tree species whose resource acquisition traits favour rapid growth are more
187 susceptible to drought and show a lower growth resistance during drought than tree species
188 with traits indicating a conservative resource use.

189

190 **Material and Methods:**

191 Experimental design and study site

192 The ARBOfun research arboretum is located south of Leipzig (Saxony, Germany, 51°16'N,
193 12°30'E). The experiment was established in 2012 on 2.5 ha of former extensively used
194 arable land with the soil type Luvisol. In 2012 a set of 69 species were planted, and 31
195 additional species were added in 2014, totalling 100 tree species. Each species is randomly
196 replicated 5 times within a block design, where each block contains one individual per
197 species (Figure 1). The tree individuals are arranged in a checkerboard-pattern with a wide
198 spacing 5.8 m to prevent competition in the early years of the experiment. Due to mortality,
199 predominantly unrelated to drought (e.g. vole damage to roots), not all species have five replicates.
200 The meadow between the trees is mown twice per year. The selected tree species represent
201 the diversity of woody species native to Europe, originating from the gradient from hemi-
202 boreal to sub-mediterranean forests and, in addition, includes selected species from North-
203 America and Asia frequently planted in forest plantations or cities (Table S1).

204 The study site is located at an elevation of 150 m a.s.l. in the transition zone from
205 maritime to continental climate. At the area the mean annual precipitation is approximately
206 520 mm, and mean annual temperature is 9.7 °C (1980-2020; DWD Climate Data Center
207 [CDC], Station Leipzig/Halle, ID 2932). In 2018–2020 a period of consecutive drought and
208 heat occurred all over Central Europe. To characterise the climatic conditions at our study
209 site, we examined monthly temperature and precipitation as well as the standardized water
210 balance of precipitation minus potential evapotranspiration using the Standardized
211 Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano, et al. 2010). SPEI is an often-
212 used drought index (Hari et al., 2020; Schwarz et al., 2020) which quantifies drought severity
213 according to a drought's intensity and duration across time scales (Vicente-Serrano et al.,
214 2010). We calculated three different SPEI lengths with the SPEI package (Beguería & Vicente-
215 Serrano, 2017) in R: SPEI3 capturing the water balance during the main vegetation period
216 (Mai–July), SPEI6 during the full vegetation period (April–September) and SPEI12 during the
217 entire year (January–December). Monthly climate data were derived from the weather
218 station located closest to the experiment that featured complete records (DWD Climate Data
219 Center [CDC], Station Leipzig/Halle, ID 2932). Potential evapotranspiration was calculated

220 with the FAO-56 Penman-Monteith equation (Beguería & Vicente-Serrano, 2017) using the
221 following DWD data: monthly means of daily minimum temperature, daily maximum
222 temperature, wind speed, cloud cover, atmospheric surface pressure, relative humidity,
223 vapor pressure as well as station elevation and latitude.

224 Tree sampling and trait measurements

225 For the present study, we measured shoot increments for a total set of 71 tree species
226 (Table S1). The measurements took place in spring 2021. We used the scars of bud scales to
227 retrospectively measure the shoot increments of three lateral branches per tree from the
228 year 2020 back to the year 2016 (Figure S1). For the measurement of the lateral branches,
229 first, the lateral branch that was south-facing and at about ¼ total tree height was selected
230 and measured. Additionally, a second lateral branch was selected anti-clockwise around the
231 tree 120° angle from the first branch, while a third lateral branch was selected in the same
232 way starting from the second branch. For the present study, we included only species with at
233 least 2 replicates each with a minimum of 2 branch measurements which could at least be
234 dated back until the year 2017. This leaves us with a total of 850 measured branches on 284
235 tree individuals.

236 Species resistance is defined as the lack of an ecological performance reduction during
237 disturbance or stress conditions (Kaufman, 1982; MacGillivray & Grime, 1995). We used
238 resistance as indicator for drought stress of the trees and calculated it as the ratio of
239 performance during the disturbance/stress and before the disturbance/stress according to
240 (Lloret et al., 2011).

$$\text{Resistance} = \frac{\text{Drought}}{\text{PreDrought}}$$

241 ‘Drought’ corresponds to growth during one or all of the drought years 2018, 2019, or 2020,
242 while ‘PreDrought’ correspond to the growth before the drought, which we calculated as the
243 mean of the reference years 2016 and 2017 (growth for 2016 was only available for 81 % of
244 the branches). We calculated growth resistance as:

$$\text{GR}_{dr.y} = \frac{b_{dr.y}}{b_{pre.dr.y}}$$

245 Where, GR is the growth resistance, b the length of the branch increment, while $dr.y$ is the
246 drought year and $pre.dr.y$ the pre-drought reference. Note, that values of $\text{GR}_{dr.y} > 1$, also
247 indicate resistance even though the growth rates exceed the pre-drought performance.

248 We selected eight different functional traits that we, based on the literature (Anderegg
249 et al., 2019), expected to be key traits for growth resistance and that are available in the TRY
250 database for a large number of species (Kattge et al., 2020): (1) P50, (2) stomata density, (3)
251 stomatal conductance, (4) specific leaf area (SLA), (5) leaf nitrogen content (LNC), (6) , leaf
252 carbon to nitrogen ratio (C:N), (7) maximal photosynthetic rate (A_{\max}), and (8) wood density.
253 (1) P50 (MPa) describes the xylem pressure, where 50 % of the hydraulic system’s
254 conductivity has been lost. If the xylem pressure falls below that, the plant is exposed to a
255 high risk of lethal embolism (Brodribb & Cochard, 2009; Sperry & Tyree, 1988).

256 (2) Stomata density (mm^{-2}) is the number of stomata per leaf area and can be linked to
257 stomata size and distribution, but also indicates stomatal control and conductance (Klein,
258 2014).

259 (3) Mean stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$) is the conductivity for water vapor per leaf
260 area per time of the stomata and can be linked to tree hydraulics and leaf water potential,
261 but also to the photosynthetic rate and with that mechanistically to an acquisition strategies
262 (Garcia-Forner et al., 2016).

263 (4) Specific leaf area (SLA, $\text{mm}^2 \text{mg}^{-1}$) is leaf area gain per invested leaf biomass. It is
264 suggested to be negatively related to plant performance under drought (H. Poorter et al.,
265 2009). Further it is a key trait representing resource acquisition and a fast growth and
266 resource acquisition of the plant economic spectrum (Reich, 2014; Wright et al., 2004).

267 (5) Leaf nitrogen content (LNC, mg g^{-1}) is a major component of photosynthetic compounds
268 such as the enzyme Rubisco and thus directly affects the photosynthetic capacity of leaves
269 (Evans, 1989; Reich et al., 1995) and is also one of the traits representing a fast growth and
270 resource acquisition of the plant economic spectrum (Reich, 2014; Wright et al., 2004).

271 (6) The leaf carbon to nitrogen ratio (C:N) is, beside others functions, linked to growth, but
272 also stress responses (Hessen et al., 2004). A high C:N indicates a low N concentration, thus
273 slow growth as mentioned before, but also a high C concentration, which can also indicate
274 thicker cell wall, which makes the species more resistant to drought stress (Reich, 2014;
275 Wright et al., 2004).

276 (7) Light-saturated maximum photosynthetic rate (A_{max} , $\mu\text{mol g}^{-1} \text{s}^{-1}$) is the maximum carbon
277 assimilation rate under normal water conditions as an index of photosynthetic capacity
278 (Anderegg et al., 2018; Zhu et al., 2018), and associated with fast resource acquisition
279 (Lambers & Poorter, 2004).

280 (8) Wood density (g cm^{-3}) combines diverse wood properties, such as mechanical strength,
281 water storage and transport (Chave et al., 2009; Zanne et al., 2010). In general, the wood
282 density strongly depends on the porosity group, however, we would expect an overall trend
283 that species with high wood density are more resistant against drought.

284 Statistical analysis

285 All statistical analysis were done with the statistical software R (R Core Team, 2020).
286 We used linear mixed-effects models (lme function in nlme package, (Pinheiro et al., 2023)
287 to predict growth resistance across tree species. We used drought year (2018, 2019 and
288 2020) coded as factor as a fixed effect. We log-transformed tree growth resistance to fulfil
289 model assumptions (normality and homogeneity of variance) and used branch ID nested
290 within tree ID as a nested random effect structure. As reference of tree growth under
291 'normal' climatic conditions, we used the mean growth in 2016 and 2017 (which were
292 neither exceptionally wet nor dry years, nor were the years before, which could have caused
293 legacy effects in 2016 and 2017). We used a post-hoc test for comparisons between the
294 years (emmeans function in the emmeans R package, (Lenth, 2023), corrected for multiple
295 comparisons with first order autocorrelation structure (corAR1) with the year as covariate.
296 We also ran linear mixed-effects models in the same way for gymnosperms and angiosperms
297 separately and for every single species.

298 We used available trait data from the TRY Plant Trait Database (Kattge et al., 2020).
299 Since the available data do not compile a complete dataset, we conducted a gap-filling to
300 predict trait values for those traits and species that were not available. For the gap-filling we
301 used a hierarchical Bayesian implementation of probabilistic matrix factorization (BHPMF,
302 Schrodte et al., 2015). In a first step we cleaned the available data on TRY, excluded non-
303 vascular species, juveniles, and non-healthy plants. We further excluded outlier values with a
304 distance of > 5 standard deviations from taxonomic or functional group means (Kattge et al.,
305 2011, 2020) and A_{\max} and stomatal conductance measured under conditions of CO_2 not
306 ambient (300-450 ppm), unsaturated light conditions ($< 800 \mu\text{mol m}^{-2} \text{s}^{-1}$) and temperature
307 outside 20 and 30 °C. Then we z-transformed the data and ran the gap-filling with the
308 BHPMF approach. In a post-processing we back-transformed the data and excluded data of
309 the 25% quantile with highest standard deviation per prediction of a trait record (Fazayeli et
310 al., 2014). We excluded data with a distance of > 3 standard deviations from taxonomic and
311 functional group means.

312 With the gap-filled data we ran linear mixed-effects models (lme function in nlme
313 package (Pinheiro et al., 2023), to predict growth resistance by each individual trait
314 interaction with drought year (2018, 2019 and 2020, coded as factor). We again used the
315 branch nested in the tree as random factor and the mean growth in 2016 and 2017 as a
316 reference. We also ran principal component analyses (PCA). For the PCAs we could include
317 53 species with full trait coverage, 18 gymnosperms and 35 angiosperms. The PCAs were
318 conducted with the prcomp function. We also used the loadings of PCA axes 1 and 2 as
319 predictors in the same way to predict growth resistance with linear mixed effect models. We
320 used Fisher's exact test for contingency table data for analysing different response types
321 within the clades.

322

323 **Results:**

324 Climate

325 We observed consecutive hotter drought conditions from 2018-2020, with climatic drought
326 severity declining slightly from 2018 over 2019 to 2020 (SPEI12 values of -2.06, -1.76, -1.53,
327 respectively, Figure 2A). All three years were among the driest in the last 40 years when
328 considering the peak vegetation period (May-July), the full vegetation period (April-
329 September), and the entire year (Figure 2 and Figure S2)). However, especially the
330 coincidence of high temperatures (Figure 2B) and low precipitation (Figure 2C) as well as the
331 consecutive nature of these droughts marked the 2018-2020 drought as exceptional.

332 Growth resistance of all species

333 The lowest growth resistance of 0.018 was measured for *Crataegus monogyna* in 2020,
334 while the highest growth resistance of 6.962 was measured for *Fraxinus excelsior* also in
335 2020. Median growth resistance per species varied from 0.318 (*Juglans regia*) up to 1.314
336 (*Castanea sativa*, Figure 3), while the gymnosperm with lowest median growth resistance of
337 0.436 was *Tsuga canadensis* and with highest median growth resistance of 1.143 was *Pinus*
338 *mugo*.

339 We found that the growth resistance across all species was significantly reduced in the
340 years 2018 ($p < 0.001$), 2019 ($p < 0.001$), and 2020 ($p < 0.001$) compared to the mean growth of
341 the reference years 2016 and 2017 (Figure 4). The between-years comparison showed that
342 growth resistance was significantly lower in 2019 ($p < 0.001$) and 2020 ($p < 0.001$) than in 2018,
343 while the growth resistance in 2020 did not significantly differ from 2019. The same was true
344 if we looked at clades of angiosperms and gymnosperms separately, however, for the
345 gymnosperms the between-years comparison showed in addition a significant difference
346 between 2019 and 2020 with growth resistance being lower in 2020 ($p = 0.031$; Figure 4).

347 Functional trait responses

348 Looking at the effects of the single traits on the growth resistance, we found significant
349 evidence for relationships within the gymnosperms as well as in the angiosperms (Figure 5,
350 Table 1). Within the gymnosperms, we found that P50 had a significant negative effect on
351 the growth resistance in 2019 ($p < 0.005$; Figure 5, Table 1). Stomatal conductance had a
352 significant negative effect on the growth resistance of gymnosperms in all three years
353 ($p = 0.004$, < 0.001 , $= 0.008$, respectively). Also SLA, LNC and A_{\max} had significant negative
354 effects on the growth resistance of gymnosperms in all three years ($p < 0.001$, for all), while
355 the C:N significantly increased growth resistance in all three years ($p = 0.007$, 0.029 , < 0.001 ,
356 respectively). These models explained between 17–27 % of variation in growth resistance,
357 through their fixed effects (marginal R^2 (R^2_m)) and 42–48 % through their fixed and random
358 effects (conditional R^2 (R^2_c), Table 1).

359 For the angiosperms we found that P50 had a negative effect on the growth resistance
360 in the year 2018 ($p = 0.005$) and in 2019 ($p = 0.011$; Figure 5, Table 1). A_{\max} had a negative
361 effect on the growth resistance for angiosperms in 2018 ($p = 0.003$) and in 2020 ($p = 0.005$) and
362 wood density positively affected growth resistance in 2020 ($p = 0.003$). These models
363 explained between 7–27 % of variation in growth resistance through their fixed (R^2_m) and 28–
364 48 % through their fixed and random effects (R^2_c , Table 1).

365 Trait spaces

366 The principal component analysis (PCA) of all species within the trait space showed a
367 clear separation between gymnosperms and angiosperms (Figure S3). Key drivers are the
368 traits: SLA, LNC, C:N and A_{\max} that clearly separated the two clades. Due to the strong
369 separation in the trait space between the clades, we ran separate PCAs for both clades.
370 When looking at the PCA for the gymnosperms only, we found that LES traits from the fast-
371 slow-gradient are mainly associated with the first PCA axis (38 %; Figure 6), such as SLA, LNC,
372 C:N, and A_{\max} . The first principal component (PC1) for gymnosperms as predictor, showed
373 significant positive effects on the growth resistance for all three drought years ($p < 0.001$,
374 respectively; $R^2_m = 24$ %, $R^2_c = 47$ %), meaning that gymnosperms with conservative traits
375 featured a higher growth resistance (Figure 7, Table 1), which is in line with the single trait
376 responses. The PCA of the angiosperms, also showed LES traits (SLA, LNC and C:N) mainly
377 associated with the first PCA axis (31.54 %; Figure 6), but the PC1 as predictor did not
378 significantly affect growth resistance (Figure 7, Table 1).

379 For the gymnosperms, the traits P50 and wood density formed a gradient in opposing
380 directions, thus higher P50 was associated with lower wood density. For the angiosperms,

381 the two-dimensional trait space showed that P50 and wood density both load on PC2 in
382 positive direction. However, when including PC4, P50 and wood density clearly showed an
383 opposing pattern (Figure S4), that we also can see in the single trait responses (Figure 5).
384 Stomata density and stomatal conductance also point, in both clades, in opposing direction
385 and form a gradient of higher stomata density with lower stomatal conductance, which is for
386 the gymnosperms on PC1 and for the angiosperms for PC2.

387 Response types

388 With the single species models, we found recurring patterns that allowed us to classify
389 the species *a posteriori* based on their drought responses over the three consecutive
390 drought years into four main response classes: ‘Sufferer’, ‘Late sufferer’, ‘Resister’ and
391 ‘Recoverer’ (Figure 8, Figure S5). As ‘Sufferers’ we defined species with a significant negative
392 growth resistance in all three years 2018, 2019, and 2020. ‘Late sufferers’ are species that
393 had no significantly reduced growth resistance initially in 2018 but then a significantly
394 reduced growth resistance latest in 2020. Species defined as ‘Resisters’ had no significantly
395 reduced growth resistance in 2018, 2019, and 2020. The ‘Recoverers’ are species that had
396 significantly negative growth resistance in 2018 or/and 2019; and had no significantly
397 reduced growth resistance in 2020 (Figure 8). The full decision tree behind this classification
398 is shown in Figure S5, while the classification for every single species is listed in Table S1.

399 We observed clear patterns of how these response types are distributed over the
400 phylogenetic clades and that they are statistically independent from each other (Figure 9;
401 $p=0.149$). The 23 gymnosperms did mainly show a growth pattern of ‘Sufferer’ (8 species)
402 and ‘Late sufferer’ (10 species), and had only 2 species counting as ‘Recoverer’ and 3
403 ‘Resister’ species. Within the 48 angiosperms we found 11 ‘Sufferer’ and 13 ‘Late sufferer’,
404 but also 13 ‘Recoverer’ and 11 ‘Resister’. However, we did not detect an apparent pattern of
405 the four response types within the trait spaces of gymnosperms and angiosperms (Figure
406 S6).

407

408 **Discussion**

409 Tree growth resistance across species

410 Over the three consecutive drought years 2018–2020, we found evidence for significant
411 growth reductions in our analysis of 71 tree species growing at a single site under the
412 controlled experimental conditions of the research arboretum ARBOfun. Overall, we
413 confirmed our first hypothesis that the 2018–2020 drought caused a growth reduction over
414 the whole drought period, but growth reductions were greater in 2019 and 2020. During
415 drought, trees lack water and face the trade-off between carbon gain and water loss. Thus,
416 growth reduction is a reaction to maintain physiological key processes which prevent the
417 tree from carbon starvation and hydraulic failure, as the two major reasons for tree
418 mortality during droughts (Adams et al., 2017; N. McDowell et al., 2008; Sala et al., 2010;
419 Schuldt et al., 2020; Sevanto et al., 2014). In contrast to most previous studies (but see Liu et
420 al. (2022)), the use of shoot increments as a growth indicator enabled us to precisely
421 measure tree growth even though the trees at our study site are relatively young and thus

422 not suitable for taking tree cores for standard dendrochronological analysis. Given that
423 climatic drought severity was lower in the consecutive drought years 2019 and 2020 (Figure
424 2), the stronger growth reduction in 2019 and 2020 is likely the result of drought legacy
425 effects. Especially the 23 species of the response type 'Late sufferer' emphasize the
426 progressive deterioration of growing conditions under consecutive drought due to legacy
427 effects, since they did not show reduced growth during the first drought year (2018), while
428 they had reduced growth in the later years (2019/2020; Table S1). Legacy effects, such as
429 damages to the tree's water transport system, are known to effect trees and forests
430 negatively up to five years after the drought (Anderegg et al., 2013; Anderegg et al., 2015;
431 Bigler et al., 2006; Gazol et al., 2020; Kannenberg et al., 2018; Schnabel et al., 2022). We also
432 found that the growth resistance for the gymnosperms was more strongly reduced
433 compared to the angiosperms in all three years (Figure 4). This is also supported by the
434 response type classification where most gymnosperm species (>75 %), except for five
435 species, suffered during the consecutive drought years and were therefore classified either
436 as 'Sufferer' or as 'Late sufferer', while of the angiosperms only 50 % were classified as
437 'Sufferer' or 'Late sufferer' (Figure 9, Table S1). Already others found evidence that
438 gymnosperms suffer more strongly during drought, since for gymnosperms reinvesting into
439 damaged leaves is costly (Anderegg et al., 2020; Larysch et al., 2022; Song et al., 2022).
440 However, also equally high mortality risks during drought were found for angiosperms and
441 gymnosperms worldwide (Anderegg et al., 2016).

442 Drought-tolerance traits and wood density

443 For the drought tolerance trait P50, which we expected to be negatively related to
444 growth resistance, we found a significantly negative effect on growth resistance of
445 gymnosperms in 2019 and of angiosperms in 2018 and 2019 (Figure 5). Thus, we could
446 confirm our second hypothesis as we found that species whose functional traits indicate
447 increasing drought tolerance by the P50 trait show an increase in embolism resistance and,
448 hence, also growth resistance (Guillemot et al., 2022; Petruzzellis et al., 2022).

449 For angiosperms, increasing wood density increased growth resistance in 2020, as we
450 expected, but we did not observe this relationship for gymnosperms, which might be due to
451 a much smaller range of wood densities within the gymnosperms ($0.40\text{-}0.65\text{ g cm}^{-3}$)
452 compared to angiosperms ($0.43\text{-}0.98\text{ g cm}^{-3}$). For gymnosperms, wood density was
453 negatively related to P50 (PC2, Fig. 6), similarly a strong negative correlation between wood
454 density and P50 existed for angiosperms (albeit on PC4, Table S2). Thus, a low P50, meaning
455 high embolism resistance, links to high wood density, causing increased growth resistance.
456 This supports previous evidence, that wood density is associated with other drought
457 tolerance traits such as hydraulic safety margin and P50 (Oliveira et al., 2021; Rosner, 2017).
458 In addition, we found that wood density and P50 formed a separate axis independent to the
459 leaf economics spectrum (LES, Díaz et al., 2016). Although the overall effect of wood density
460 on growth resistance is still debated (Chave et al., 2009; L. Poorter, 2008), our study provides
461 evidence that wood density is associated with enhanced growth resistance.

462 For gymnosperms and angiosperms, stomata density and stomatal conductance loaded
463 in opposing directions in the PCAs (Figure 6), which implies that species with low stomata
464 density have high stomatal conductance, most likely due to few but large stomata. As

465 expected, gymnosperms with lower stomatal conductance had a higher growth resistance.
466 Moreover, for the gymnosperms, effects of stomatal conductance on growth resistance
467 were similar as for the LES traits (SLA, LNC, C:N, A_{max}), which is likely related to stomata
468 density and stomatal conductance being associated with these LES traits in trait space (PC1,
469 Fig. 6), an association which has been reported previously albeit for angiosperms in the
470 subtropics (Kröber et al., 2014). Thus, we expect a high stomatal conductance to be
471 associated with acquisitive resource use. However, for angiosperms, we did not find such
472 close association between stomata traits and LES traits nor with hydraulic traits (P50).

473 Leaf economics spectrum traits

474 In gymnosperms, LES trait expressions associated with conservative resource use and
475 slower growth increased growth resistance during the drought (Figure 5, Table 1). In
476 addition, these LES traits formed an important axis of functional variation on the first axis
477 (i.e., SLA, LNC, C:N, A_{max}), ranging from fast to slow strategies. As expected, PC1 was
478 positively related to growth resistance within all three years (Figure 7, Table 1). For
479 angiosperms, we found significantly negative growth responses for A_{max} in 2018 and 2020
480 (Figure 5, Table 1), showing that species with a high light-saturated maximum
481 photosynthetic rate - usually associated with fast growth - have a low growth resistance.
482 Also, for angiosperms, most of the LES traits loaded on the first PCA axis (i.e., SLA, LNC, and
483 C:N, Figure 6). Thus, we confirmed hypothesis 3 for gymnosperms and angiosperms (albeit
484 weaker associations of LES traits were observed). This means species with resource
485 acquisition traits favouring rapid growth are more susceptible to drought and show a
486 stronger reduction in growth resistance during consecutive drought years. Earlier studies
487 suggested that LES trait expressions related to conservative resource use and slow growth
488 are related to (1) a lower drought mortality across biomes (Greenwood et al., 2017), and (2)
489 a higher drought tolerance in the tropics (Guillemot et al., 2022). Similarly to our findings, a
490 study in subtropical experimental tree communities reported recently that acquisitive
491 species had reduced growth resistance under drought conditions (Schnabel et al., 2024),
492 albeit based on fewer tree species. The weaker trend for the angiosperms in our study could
493 be caused by the fact that 50 % of the angiosperms did not suffer substantially during the
494 entire drought period. Thus, according to our response type classification, 27 % of the
495 angiosperms recover already during the drought, while 23 % resist the drought in their
496 growth response (Figure 9, Table S1). Further, our study shows that even though we found a
497 legacy effect in the growth resistance in 2019 and 2020, the LES trait control was directly
498 present from the first drought year of 2018 onwards. For the first time, we report clear
499 evidence for LES traits driving tree growth resistance for a wide species set under nearly
500 identical growing conditions and extreme drought conditions, causing legacy effects.

501 Management

502 Trees in the arboretum ARBOfun were planted at a wide spacing, which prevented tree-
503 tree interactions. Thus, our results can be interpreted as the intrinsic, trait-driven response
504 of the species to climatic conditions without influences of competition, competitive
505 reduction or facilitation (Forrester & Pretzsch, 2015), which are otherwise present in forests
506 and shape effects of functional traits on ecosystem functioning (Trogisch et al., 2021). Our
507 study thus captures 'pure' trait-driven responses of a wide set of Central European tree

508 species to consecutive drought years including species dominating today's forests but also
509 those which may dominate under a future climate regime such as currently subordinate or
510 biographically neighbouring tree species. The traits and trait syndromes (such as P50 and the
511 LES) we observed to influence growth resistance can thus inform management decisions on
512 tree species choice and be used to improve the predictive capacity of forest models. The
513 identification of the four response types helps to recognize growth resistance pattern across
514 species, but also gives important insights for single key species. The two currently
515 economically most relevant tree species in Central European managed forest, *P. abies* and *P.*
516 *sylvestris*, together making up, for instance, 47.7 % of Germany's managed forest (BWI
517 2012), suffered strongly the last years (Senf et al., 2020). They showed a drought response of
518 'Late sufferer', which indicates that they likely strongly suffer in the coming century facing
519 more regular and more intense droughts caused by climate change (IPCC, 2014). Similar
520 negative predictions were also found by others (Buras & Menzel, 2019; Kölling & Mette,
521 2022; Wessely et al., 2024). In contrast, the angiosperms *F. sylvatica* and *Q. robur*, currently
522 accounting for 25.8% of Germany's managed forests (BWI 2012), showed response types of
523 'Recoverer' and 'Resister', respectively. Also Kölling & Mette (2022) and Buras & Menzel
524 (2019) classified those two species as more resistance against climate change. While the
525 drought resistance of *F. sylvatica* is under debate (Kunz et al., 2018), we could reinforce
526 evidence for it. Two species of currently minor merchantable value, but with potential to
527 gain in economic importance for Central European forests in the future are *S. torminalis* and
528 *Q. pubescens* (Buras & Menzel, 2019; Kunz et al., 2018). We also classified those as the
529 response type of 'Recoverer' and 'Resister', respectively. Thus, our response type
530 classification approach, helps to depict single species responses, even though we did not find
531 clear patterns of the response types within the trait spaces (Figure S6), pointing to the fact
532 that similar responses may be achieved by different but equivalent trait configurations which
533 warrants further investigation.

534 Reflection

535 We did not explicitly correct for phylogeny, since the separation of clades (angiosperms
536 and gymnosperms) already captures a large portion of the phylogenetic signal (see Figure
537 S3). Further, we also did not control for tree size. One would expect larger fast-growing trees
538 to root deeper and thus have better water access, however we found fast-growing species
539 are less growth resistant. The gap-filling of the trait data from the TRY database is a helpful
540 and indispensable tool to be able to investigate many traits for a wide set of species.
541 However, it has the weakness that traits for different species in TRY have been measured
542 with different methods, at different times and places, which can, dependent on the species
543 and the trait, induce a high amount of variation due to strong plasticity. Moreover,
544 particularly P50, which is a key trait for drought tolerance (Choat et al., 2012), is difficult to
545 measure, especially in ring-porous species with very long vessels. Therefore, we excluded
546 P50 values larger than -0.5, as suggested by (Sergent et al., 2020), due to unrealistically high
547 values. However, we decided against excluding P50 values smaller than leaf turgor loss point
548 (P_{tlp}) values, as suggested by (Guillemot et al., 2022), due to the fact, that the available trait
549 data on those two traits in the TRY database came mainly from different studies and did not
550 cover all our species. Overall, our trait-based models explained only moderate shares of
551 variation in growth resistance with a higher predictive capacity for gymnosperms compared

552 to angiosperms (Table 1), but we expect that with more and particularly in-situ measured
553 traits such models are likely to increase in their predictive capacity. Similarly, with such an
554 enhanced trait coverage, we might eventually be able to derive trait-based predictions for
555 the assignment of species to the observed response types.

556

557 **Outlook and conclusion**

558 For future studies, we plan for in-situ functional trait measurements which likely have
559 the potential to improve growth predictions under consecutive hotter droughts. Moreover,
560 besides the drought tolerance and LES traits we studied here, other hydraulic traits such as
561 turgor loss point or hydraulic safety margin, but especially also belowground traits may be
562 important predictors of growth resistance to drought. Belowground traits such as specific
563 root length, root tissue density or root C:N, which capture a conservation, a collaboration
564 and a plant size gradient (Bergmann et al., 2020; Comas et al., 2013; Weigelt et al., 2021)
565 were already found to affect above- and belowground plant productivity under drought
566 (Brunner et al., 2015; Comas et al., 2013). Thus, future studies should consider more and
567 especially belowground traits. The importance of drought tolerance and LES traits for growth
568 resistance, and the recovery of some species under consecutive drought as we have shown,
569 suggest that functional traits might also explain growth resilience. Some species, such as *F.*
570 *sylvatica*, *Quercus rubra* or *S. torminalis* did already recover during the drought, even though
571 an overarching legacy effect was visible. However, we do not know whether and when the
572 species of 'Sufferers', such as *Larix decidua* or *Ulmus laevis* and the 'Late sufferers', such as
573 *Acer campestre*, *P. abies* or *P. sylvestris* do recover over time. Hence, studying growth
574 resilience and recovery including also the recent wetter years 2023 or even 2024 is hence of
575 high interest at our study site. Overall, we are planning on future studies looking at tree
576 growth expression over pre-drought, consecutive hotter drought and post-drought years,
577 studying resistance, recovery and resilience to these contrasting climatic conditions and to
578 further explore the underlying, trait-based mechanisms by including in-situ measured trait
579 data capturing both, above- and belowground trait gradients.

580 In conclusion, we observed significantly reduced growth across the 71 tree species
581 during the consecutive hotter drought years 2018–2020 with legacy effects further reducing
582 growth resistance during 2019 and 2020. Drought-tolerance and LES traits were important
583 predictors of growth resistance, with lower growth resistance observed in species featuring
584 trait expressions indicative of low drought tolerance (high P50), fast growth and acquisitive
585 resource use (high SLA, LNC, and A_{max}). Trait-growth resistance relationships were clearer for
586 gymnosperms than for angiosperms. We expect these findings to facilitate the development
587 of management strategies for forests under a future climate regime characterized by more
588 frequent, severe and prolonged droughts through supporting tree species choice and the
589 improvement of forest models.

590 **Acknowledgement:** We thank the TRY database for the provision of trait data.

591 **Author Contributions:** LK formal analysis, visualization, writing – original draft preparation;
592 FS conceptualization, formal analysis, methodology, supervision, writing – review & editing;
593 RR conceptualization, formal analysis, writing – review & editing; AR investigation, writing –

594 review & editing; **JK** methodology, formal analysis, writing – review & editing; **KA** formal
595 analysis, writing – review & editing; **AK** investigation, writing – review & editing; **TK**
596 investigation, writing – review & editing; **CW** idea, conceptualization, supervision, funding
597 acquisition, project administration, writing – review & editing

598 **Date Availability Statement:** We plan to publish the data at iBID (iDiv).

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Figures, Tables

Figures

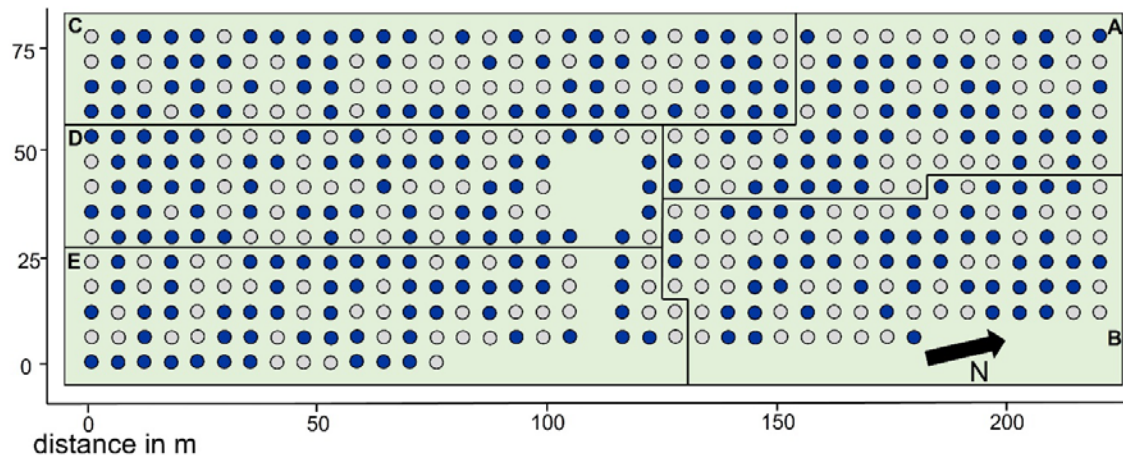


Figure 1: Study site. Top view on the ARBOfun study site. The points represent the 100 species, each randomized within 5 blocks (A-D). The dark blue colour marks the trees used for this study. The planting distance between trees is 5.8 m.

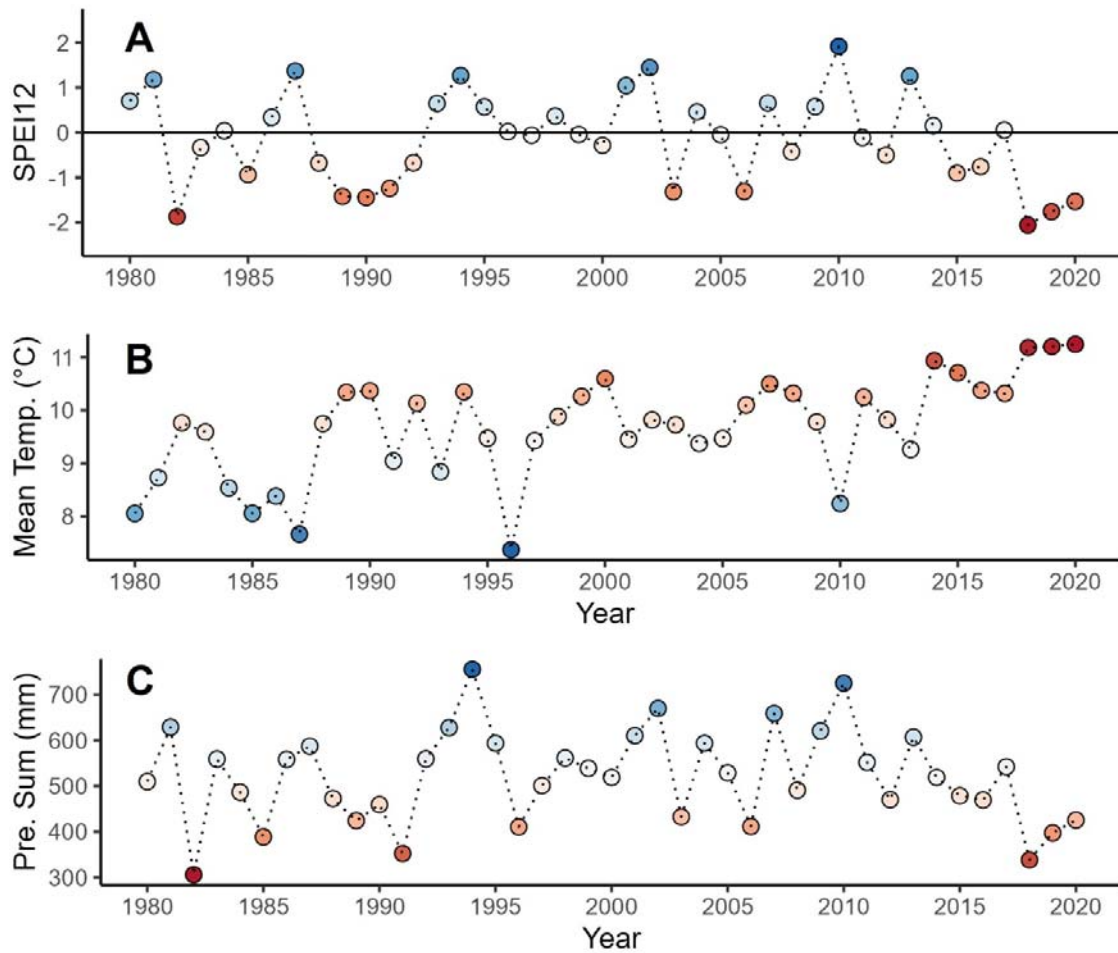


Figure 2: Standardised Precipitation-Evapotranspiration Index (SPEI), mean annual temperature and annual precipitation sum. The SPEI12 is calculated for the whole year from January to December. The zero line is the reference period 1981–2010. Blue coloured dots indicate positive SPEI values, while red coloured dots show negative SPEI values. The mean temperature and precipitation sum are calculated over the whole year. Also, here, the blue and red colour indicates higher and lower values compared to the reference period, respectively.

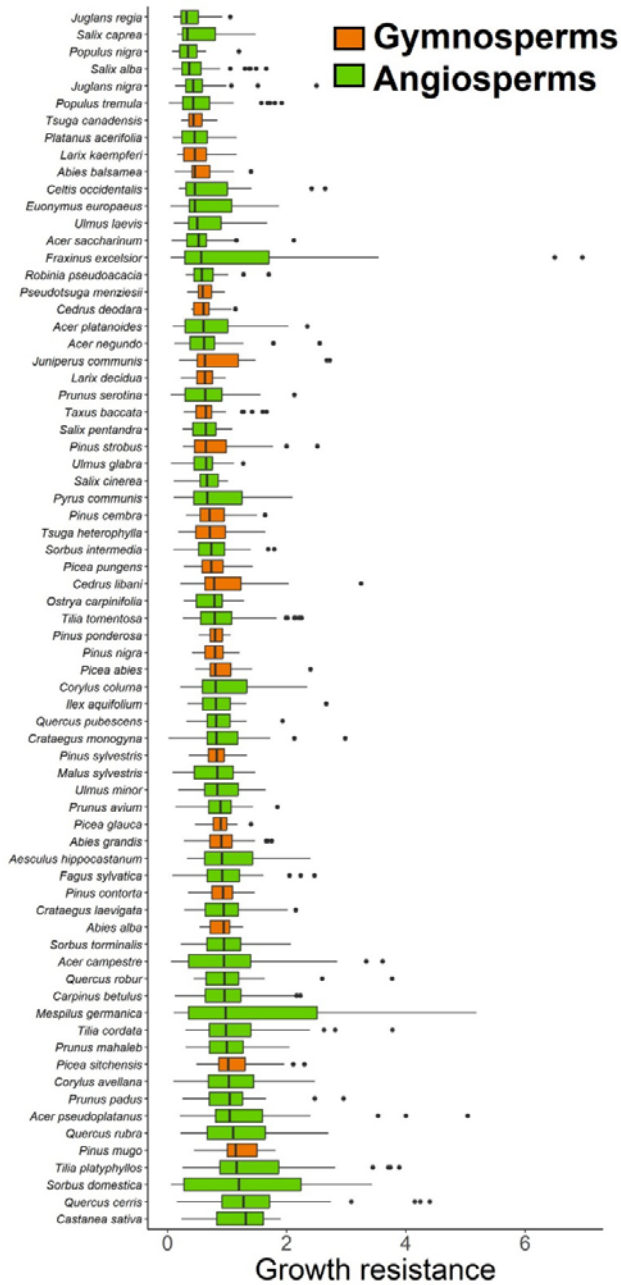


Figure 3: Growth resistance of all tree species, sorted by the median growth resistance per species.

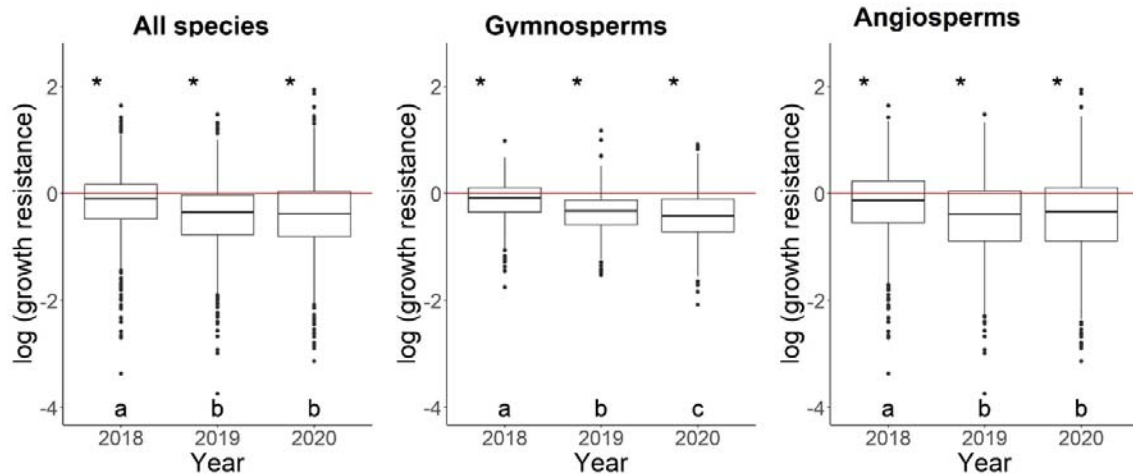
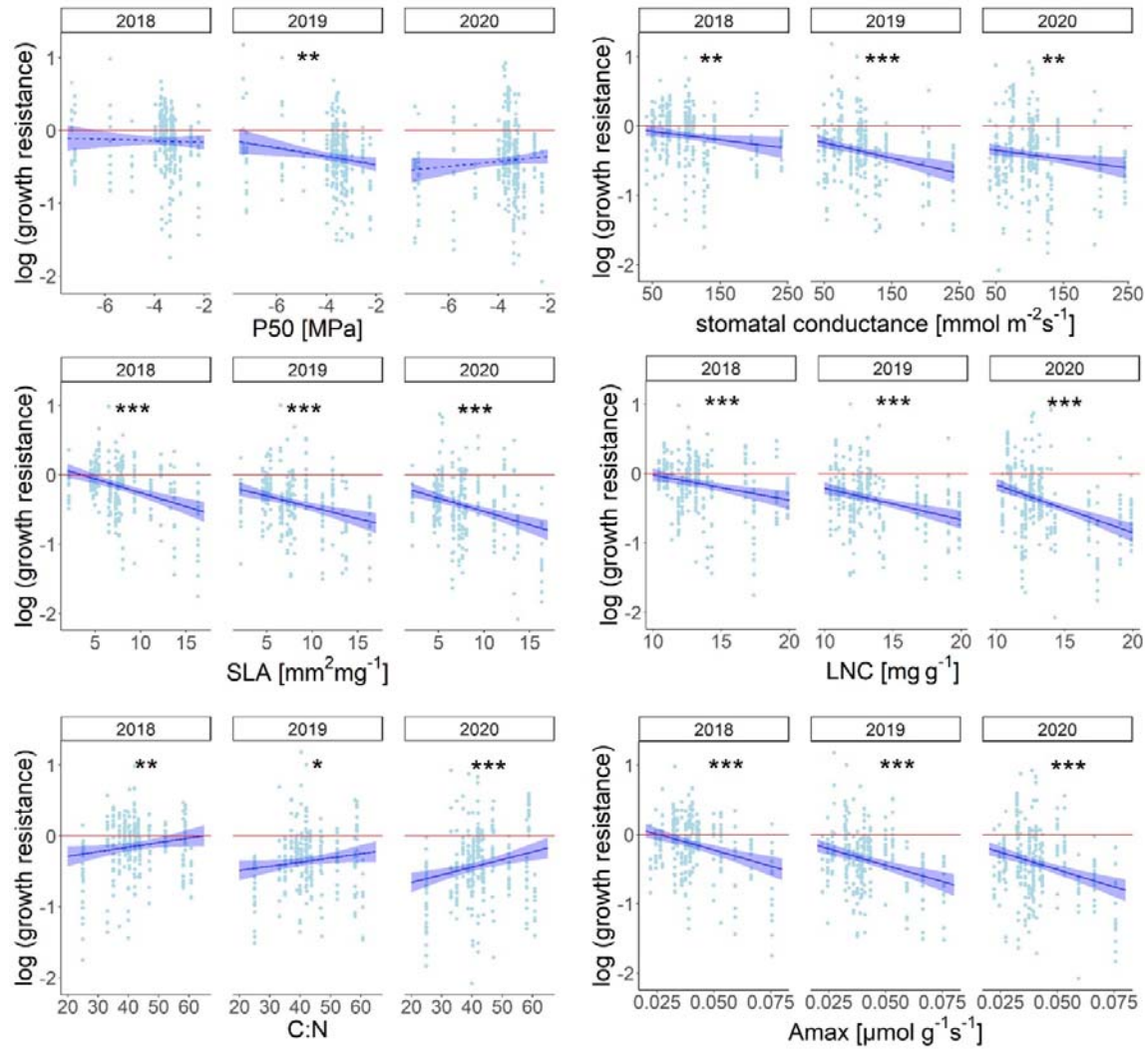


Figure 4: Growth resistance. Boxplots show the growth resistance of trees during the drought years 2018–2020 compared to the growth in the reference years (mean of 2016 and 2017) shown as red zero-line. Across species a significant ($p < 0.05$) reduction in growth resistance, indicated with the asterisks, compared to the growth in the reference years was observed. The significant differences between the years were tested with a post-hoc test and are indicated by the characters (a, b, c). Similarly, significant ($p < 0.05$) reductions in growth resistance were found when analysing the gymnosperms and the angiosperms separated.

Gymnosperms



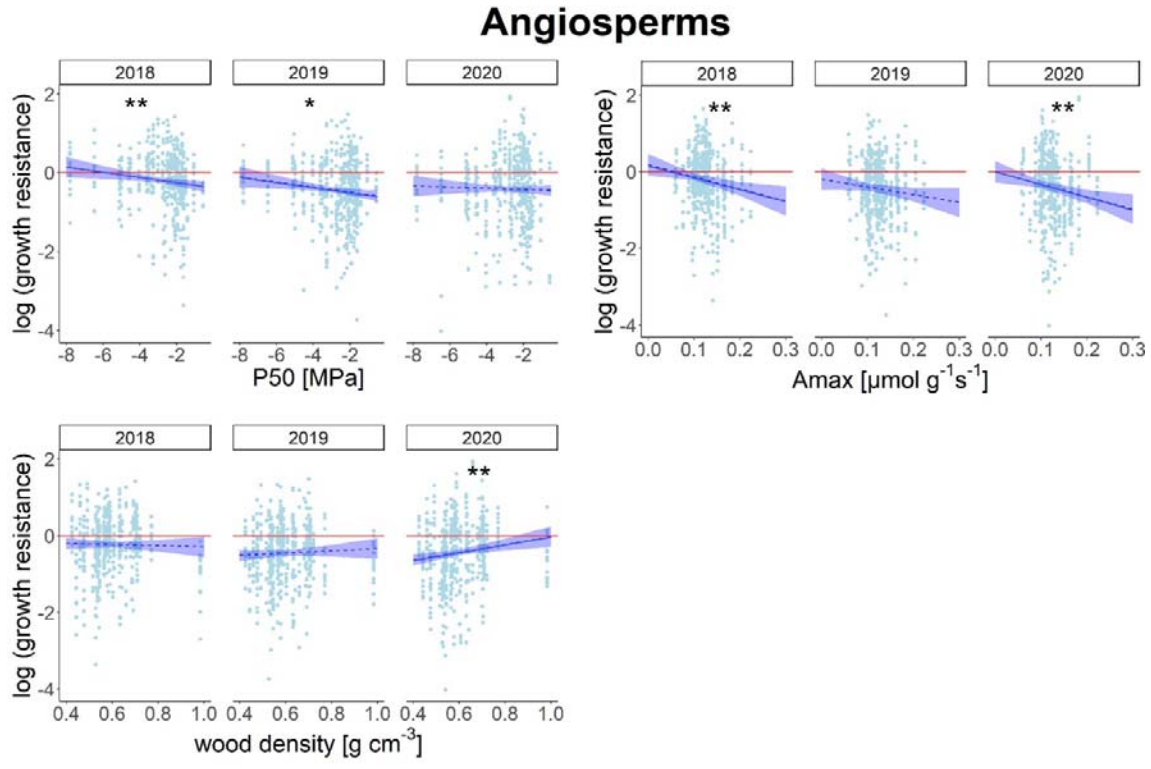


Figure 5: Trait-driven responses in growth resistance for gymnosperms and angiosperms. Shown are relationships between functional traits and the growth resistance of gymnosperm and angiosperm trees during the drought years 2018–2020 based on linear mixed-effects model fits. Growth resistance is depicted compared to tree growth in the reference years (mean of 2016 and 2017) shown as red zero-line. The asterisks indicate significant relationships (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$), while a dashed line symbolizes a non-significant relationship. Shaded bands show a 95% confidence interval.

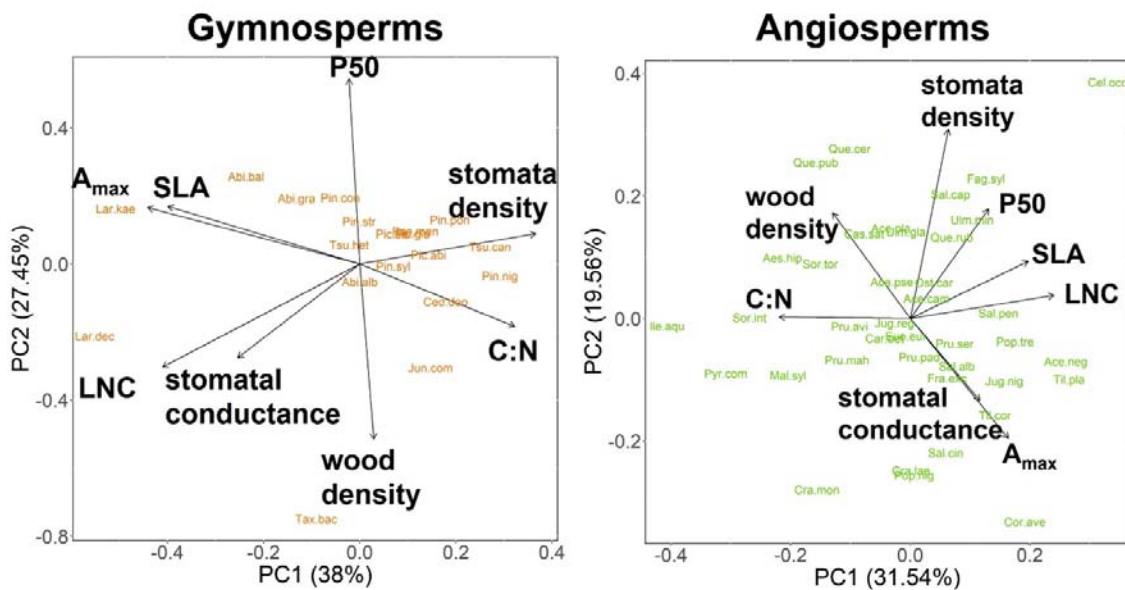


Figure 6: PCAs of gymnosperms and angiosperms depicting the trait space of the continuous traits P50, stomatal density, stomatal conductance, SLA, LNC, C:N, A_{max} , and wood density.

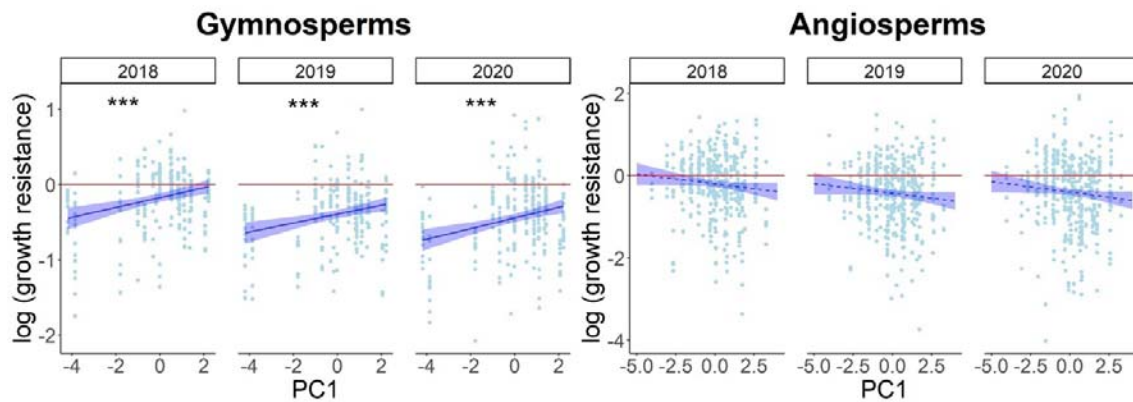


Figure 7: Principal components as predictors of tree growth resistance for gymnosperms and angiosperms. Shown are relationships between the principal component 1 (PC1) and growth resistance of gymnosperm and angiosperm trees during the drought years 2018–2020 based on linear mixed-effects model fits. Growth resistance is depicted compared to tree growth in the reference years (mean of 2016 and 2017) shown as red zero-line. The asterisks indicate significant relationships (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$), while a dashed line symbolizes non-significant relationships. Shaded bands show a 95% confidence interval.

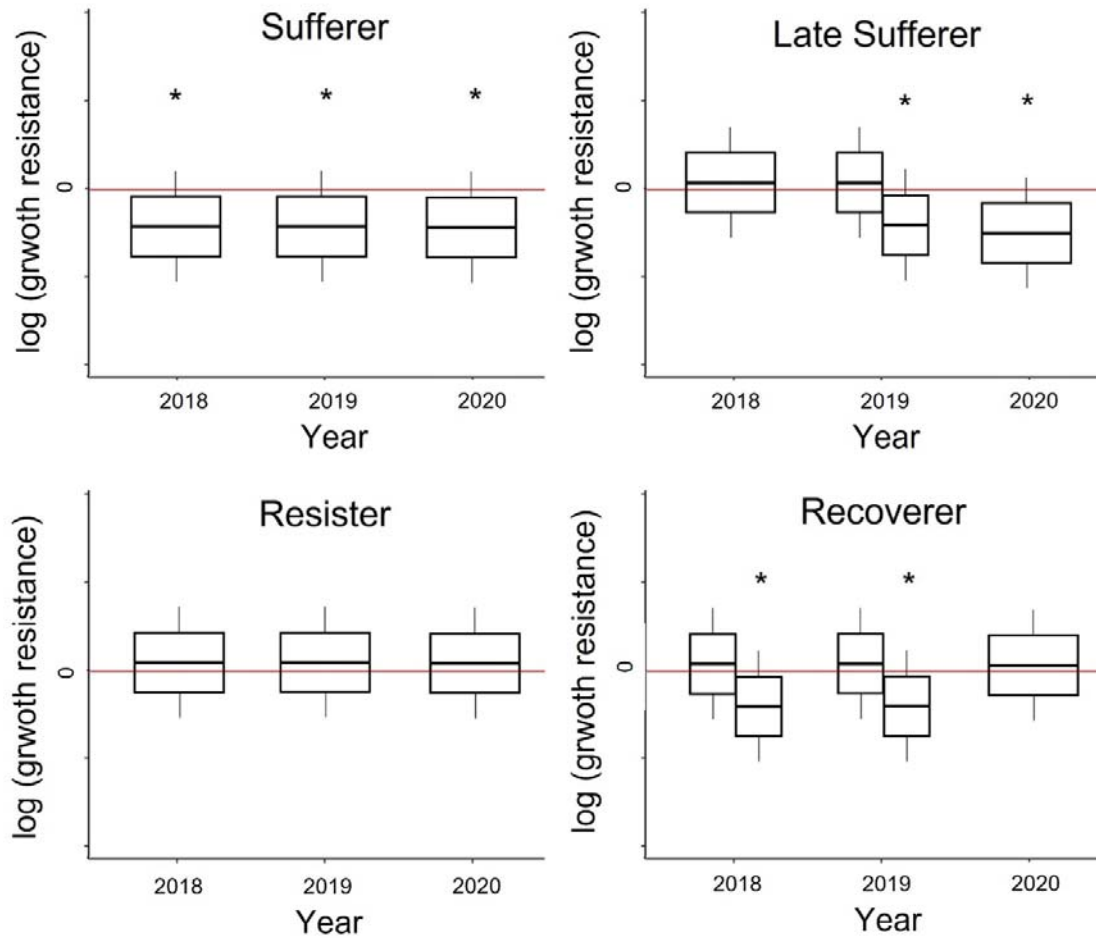


Figure 8: Response type classification. Growth response patterns over the three drought years 2018–2020 for the four response types classified due to the decision tree in Figure S4. The boxplots above the red reference zero line represent positive or not significant resistance and the ones below the red zero line negative resistance values with asterisks indicating a significant response in growth resistance. The divided boxplot for the Late Sufferer in 2019 and for the Recoverer in 2018 and 2019 show positive and not significant (1st boxplot) or significant negative (2nd boxplot) effects, since they represent two divergent paths of the decision tree (Figure S5). In addition, for the Recoverer, either 2018 or 2019 or both years needed to be significantly negative as shown in the decision tree (Figure S5).

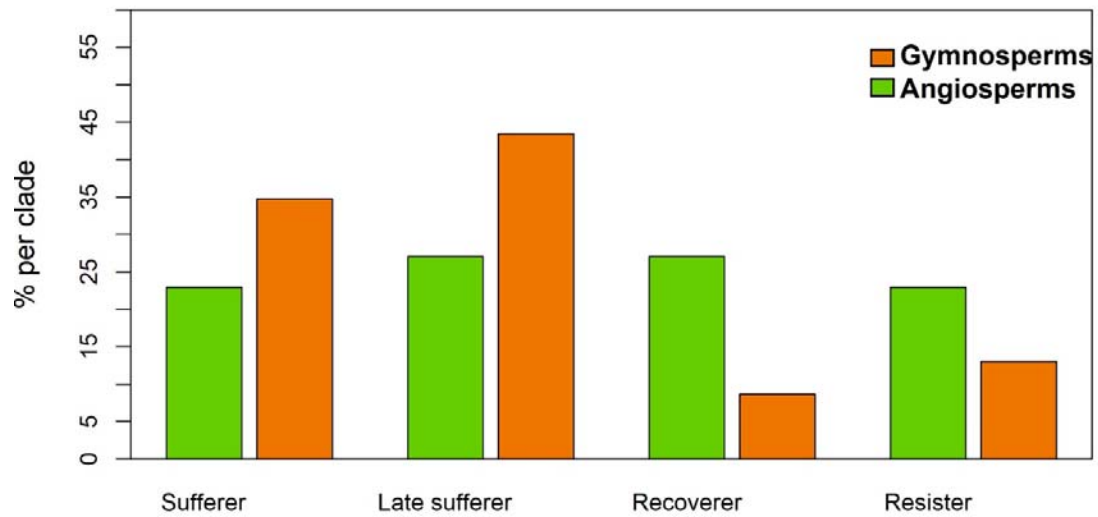


Figure 9: Distribution of clades into response types. 'Sufferer', 'Late sufferer', 'Recoverer', and 'Resister' separated for the clades of angiosperms and gymnosperms. Fisher's exact test showed significant differences between clades and response types ($p=0.149$).

Tables

Table 1: Growth resistance explained by the single traits and the principal component 1 (PC1) for the drought years 2018–2020 for gymnosperms and angiosperms. Species number is the number of species include in the model for the single trait. Growth resistance is the slope of the relationship, with green and red indicating positive and negative relationships based on linear-mixed effects model fits, respectively. The marginal R^2 (R^2_m) shows the variation explained by fixed and the conditional R^2 (R^2_c) the variation explained by fixed and random effects. The asterisks indicate significant relationships (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

| | Gymnosperms | | | | | | | | | |
|-----------------------------|-------------|------------------|------------------|------------------------|------|------------------------|------|------------------------|------|--|
| | spec no. | R ² m | R ² c | growth resistance 2018 | sig. | growth resistance 2019 | sig. | growth resistance 2020 | sig. | |
| P50 | 23 | 0.18 | 0.43 | -0.010 | | -0.057 | ** | 0.034 | | |
| stomata density | 23 | 0.17 | 0.42 | <0.001 | | <0.001 | | 0.001 | | |
| stomatal conductance | 23 | 0.20 | 0.43 | -0.001 | ** | -0.002 | *** | -0.001 | ** | |
| SLA | 21 | 0.27 | 0.48 | -0.040 | *** | -0.033 | *** | -0.039 | *** | |
| LNC | 22 | 0.25 | 0.48 | -0.036 | *** | -0.045 | *** | -0.069 | *** | |
| C:N | 23 | 0.19 | 0.43 | 0.006 | ** | 0.006 | * | 0.011 | *** | |
| A_{max} | 23 | 0.23 | 0.44 | -9.227 | *** | -9.424 | *** | -9.998 | *** | |
| wood density | 23 | 0.17 | 0.42 | -0.030 | | -0.030 | | -0.572 | | |
| PC1 | 19 | 0.24 | 0.47 | 0.066 | *** | 0.059 | *** | 0.071 | *** | |
| | Angiosperms | | | | | | | | | |
| | spec no. | R ² m | R ² c | growth resistance 2018 | sig. | growth resistance 2019 | sig. | growth resistance 2020 | sig. | |
| P50 | 43 | 0.08 | 0.29 | -0.065 | ** | -0.064 | * | -0.015 | | |
| stomata density | 45 | 0.07 | 0.28 | <0.001 | | <0.001 | | <0.001 | | |
| stomatal conductance | 45 | 0.07 | 0.29 | <0.001 | | <0.001 | | <0.001 | | |
| SLA | 46 | 0.27 | 0.48 | -0.003 | | -0.008 | | -0.003 | | |
| LNC | 44 | 0.07 | 0.29 | 0.004 | | 0.001 | | -0.010 | | |
| C:N | 45 | 0.07 | 0.28 | 0.002 | | 0.001 | | 0.007 | | |
| A_{max} | 46 | 0.08 | 0.29 | -3.166 | ** | -2.023 | | -3.258 | ** | |
| wood density | 46 | 0.08 | 0.30 | -0.142 | | 0.297 | | 1.013 | ** | |
| PC1 | 39 | 0.07 | 0.29 | -0.048 | | -0.047 | | -0.051 | | |