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Drought-induced decoupling between carbon uptake and tree growth impacts forest carbon turnover time

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1 **Title**

2 Drought-induced decoupling between carbon uptake and tree growth impacts forest carbon
3 turnover time

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25

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27 GPP, legacy effect, resilience, resistance, tree rings

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38 **Abstract**

39 The ability of forests to withstand, and recover from, acute drought stress is a critical
40 uncertainty regarding the impacts of climate change on the terrestrial carbon (C) cycle, but it is
41 unclear how drought responses scale from individual trees to whole forests. Here, we
42 assembled a dataset of tree-ring chronologies co-located within the footprint of eddy covariance
43 towers across North America and Europe, with the aim of quantifying the sensitivity of tree
44 radial growth versus gross primary productivity (GPP) during and following drought. We found
45 that drought induced a large decoupling across C cycle processes, whereby GPP was relatively
46 resistant to water stress despite large reductions in tree-ring widths. This decoupling also
47 occurred in the year following drought (i.e., a 'drought legacy effect'), and was similar in
48 magnitude in response to both summer and winter droughts. By modeling whole-forest C
49 turnover time, we show that a radial growth-GPP decoupling has important ramifications for the
50 forest C cycle, especially if the C not used to support radial growth is instead allocated towards
51 pools with short residence times. Our results demonstrate that quantifications of drought
52 impacts that rely solely on C uptake are missing this fundamental pathway through which
53 drought alters the forest C cycle and the resulting feedbacks to the climate system.

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58

59 **Introduction**

60 Forests store nearly half of the carbon (C) in terrestrial ecosystems and take up ~25% of
61 all anthropogenic C emissions (Bonan, 2008; Pan et al., 2011). However, the capacity of forests
62 to assimilate and store C is threatened by an increase in the frequency and severity of droughts
63 (Cook et al., 2015; Dai, 2013; McDowell et al., 2020). The drought resistance (ability to maintain
64 function) and resilience (ability to recover function) of these processes in future climates is a
65 major uncertainty in the terrestrial C cycle (Sippel et al., 2018) yet exerts a significant influence
66 on the climate change mitigation potential of forests worldwide (Anderegg et al., 2020).

67 Current efforts to quantify the resistance and resilience of forests to drought stress have
68 largely been undertaken using tree-ring chronologies (Camarero et al., 2018; Lloret et al., 2011;
69 Merlin et al., 2015). These approaches are invaluable towards understanding the climatic,
70 topographic, and biological mechanisms that underpin the responses of tree growth to drought.
71 However, radial tree growth is only one aspect of a complex forest C cycle, and the relationship
72 between growth and whole-ecosystem fluxes of C is indirect. Thus, several studies have
73 quantified the drought resistance and resilience of C uptake using broader-scale metrics of
74 forest C cycling such as gross primary productivity (GPP) derived from flux towers (He et al.,
75 2018; Shen et al., 2016; Yu et al., 2017). Recent evidence suggests that drought may drive a
76 large decoupling between these processes, whereby structural tree growth is much more
77 sensitive to drought than GPP (Delpierre et al., 2016; Kannenberg et al., 2020b, 2019b).

78 While this decoupling is intuitive at the tissue-level given the higher drought sensitivity
79 of turgor-driven cell expansion than photosynthesis (Hsiao, 1973) and the plasticity of plant C

80 allocation in response to environmental stress (Epron et al., 2012), evidence at the stand- or
81 ecosystem -scale is scarce due to the paucity of co-located measurements of tree growth and
82 GPP (Babst et al., 2021, though see Cabon et al., 2022 and Krejza et al., 2022). Therefore, our
83 knowledge of the degree of coupling between growth and GPP rests entirely on either case
84 studies from a single drought (Kannenberget al., 2019b), or GPP proxies from models or remote
85 sensing products that may not fully capture both the magnitude of drought impacts or any
86 lagged recovery processes (Anderegg et al., 2015; Kolus et al., 2019; Stocker et al., 2019). Given
87 this lack of evidence, it is unsurprising that most large-scale vegetation models represent
88 allocation to woody tissues as a constant percentage of GPP (Fatichi et al., 2019). Additional
89 uncertainties regarding these processes arise due to the high species-specificity of drought
90 responses, which are underlain by variability in key functional traits. Uncovering the traits that
91 underlie tree drought responses, as well as the coupling between GPP and growth, has the
92 potential to lead us to an improved predictive understanding of how drought impacts the forest
93 carbon cycle.

94 Divergent drought impacts on tree growth versus GPP have vast implications for our
95 understanding of the terrestrial C cycle. Large shifts in allocation from tree boles to pools with
96 shorter residence times (Doughty et al., 2015, 2014; Kannenberg et al., 2019b) have
97 consequences for the turnover time of forest C, the magnitude of which is a major uncertainty in
98 current vegetation models (Carvalhais et al., 2014; Friend et al., 2014; Pugh et al., 2020).
99 Quantifying the differential sensitivity of drought resistance and resilience across distinct C cycle
100 processes and scales could provide valuable insights regarding whether drought impacts are
101 likely to be most apparent through decreased C uptake and productivity, and/or through a
102 shortened C turnover time.

103 Here, we seek to directly test the hypothesis that drought decouples tree radial growth
104 from ecosystem C uptake. To do so, we amassed a dataset of 38 tree ring chronologies
105 (spanning 31 common gymnosperm and angiosperm species) collected at 16 different eddy
106 covariance tower sites (277 total site-years) that have experienced a severe drought. These
107 chronologies represented the majority of the species present within these towers' footprints,
108 enabling direct comparisons between the resistance and resilience of tree growth and stand-
109 scale GPP. We then explored the implications of a decoupling between growth and GPP for the
110 forest C cycle using a 'box model' that includes fluxes in and out of the main pools of tree
111 structural C. We ask:

- 112 1) Are drought resistance and resilience decoupled across C cycle processes?
- 113 2) What traits shape variability in resistance and resilience, and what controls the
114 degree of decoupling of these indices across scales?
- 115 3) What are the implications of a decoupling between tree radial growth and GPP for
116 whole-forest C turnover?

117

118 **Materials and methods**

119 *Sites and eddy covariance data*

120 We compiled a dataset of 38 tree-ring chronologies collected near or within the
121 footprint of 16 different eddy covariance towers (Fig. 1, Table S1). These sites, located across
122 North America and Europe, spanned a wide variety of ecosystem types and were largely
123 representative of various temperate and arid woodland biomes (Fig. 1), yet all experienced a

124 severe summer or winter drought within the flux record (see below for drought definition). All
125 sites are included in either the FLUXNET2015 Tier 1 (Pastorello *et al.* 2020,
126 fluxnet.org/data/fluxnet2015-dataset) or AmeriFlux (ameriflux.lbl.gov, downloaded January 6,
127 2021) datasets.

128 For the 10 sites in the AmeriFlux network (representing 30 chronologies), net ecosystem
129 exchange data (NEE) was gapfilled using the 50th percentile Ustar distribution and then
130 partitioned into GPP using the nighttime method (Reichstein *et al.*, 2005) as implemented in the
131 R package *REddyProc* (Wutzler *et al.*, 2018). Data that were gapfilled by site PIs were
132 preferentially used, if available. If the NEE variable was not available, turbulent CO₂ flux (FC) was
133 used instead. The meteorological data used for partitioning were taken from the primary sensor
134 (the _1_1_1 suffix). During some periods, there were not enough incoming shortwave radiation
135 data to properly gapfill NEE. In these cases, incoming photosynthetically active radiation (if
136 available) was converted to shortwave, under the assumption that half of the incoming solar
137 irradiance is photosynthetically active radiation (Britton and Dodd, 1976). Data from US-UMB
138 from AmeriFlux are aggregated into both 30-minute (years 2007 – 2019) and 60-minute (years
139 2000 – 2014) increments. For this site, we used the full 30-minute record for 2007 – 2019 and
140 the 60-minute record for 2000 – 2006. For FLUXNET sites, we used the nighttime partitioned,
141 variable 50th percentile distribution Ustar GPP product (i.e., GPP_NT_VUT_REF), which is the
142 data product most comparable to our AmeriFlux partitioning approach. We confirmed that our
143 partitioning approach was comparable to the FLUXNET2015 data by comparing a subset of 6
144 sites that were included in both datasets (and thus partitioned independently). At these sites,
145 monthly sums of our GPP product closely matched FLUXNET2015 ($r^2 = 0.98$, slope not
146 significantly different from one).

147 Some gaps remained even after gapfilling due to sensor malfunction, maintenance, or
148 other long-term gaps. Years with large gaps in GPP during the growing season were excluded
149 from analysis, and the site-years that remained all had < 5% of GPP records missing.

150 In order to make GPP (typically aggregated at 30- or 60-minute resolutions) comparable
151 to detrended tree-ring widths (annual resolution, see below for tree-ring detrending methods),
152 we normalized the GPP time series by summing GPP for each site-year and calculating the
153 anomaly for each annual GPP sum (i.e., the percentage deviation from mean GPP at that site). At
154 11 sites, annual GPP increased or decreased over time, which would bias our calculations of
155 drought responses depending on the year in which the drought occurred. For sites that had a
156 statistically significant (via linear regression, $P < 0.05$) increase or decrease in annual GPP over
157 time, we detrended the GPP time series by taking the residuals of the linear model and
158 normalizing them as above. This quantification of normalized and detrended annual GPP was
159 used for all subsequent analysis.

160

161 *Tree ring data*

162 Canopy dominant or co-dominant trees of the common species at each flux site have
163 been previously cored, processed, measured, and crossdated using standard
164 dendrochronological procedures (Speer, 2012; Stokes and Smiley, 1999). Crossdated ring width
165 measurements were detrended using a spline with a 50% frequency cutoff set at two-thirds of
166 the mean sample length (Klesse, 2021), and species-level chronologies (ring width indices, RWI)
167 were built using a bi-weight robust mean-value approach in the R package *dplR* (Bunn, 2008).
168 The distance of each cored tree to the flux tower varied, but all cores were sampled within 1 km

169 of the tower. At least 5 trees were cored for each species at each site, though the average
170 number of cores per site was 55 ± 8.0 (mean \pm standard error). Chronology lengths ranged from
171 30 to 300 years, and the average chronology length was $112.9 \text{ years} \pm 9.8$ (mean \pm standard
172 error). The average expressed population signal (EPS, which quantifies the signal-to-noise ratio
173 of the time series) for our chronologies was 0.87 ± 0.01 (mean \pm standard error). Our results
174 were robust to removing chronologies with an EPS lower than the commonly-used threshold of
175 0.85 (Fig. S1). However, given that this threshold is arbitrary (Buras, 2017) and a low EPS may
176 simply be indicative of less synchronous tree growth within a stand (a dynamic worth capturing
177 in our study), we elected to not remove chronologies with low EPS for subsequent analyses.
178 Chronology information and statistics are available in Table S2.

179 We also compiled species composition estimates for all cored tree species at each site
180 (Table S3). These estimates were obtained from the published literature where possible. If
181 published data were not found, species composition estimates were taken from site webpages
182 or obtained directly from site research teams. We used plot-based basal area measurements
183 where possible, but needed to use biomass or canopy cover estimates at a small subset of sites.
184 Citations and data sources for these estimates are available in Table S3. When multiple tree
185 species were present at a flux tower site, we calculated a community-weighted mean RWI using
186 these data, in order to increase comparability to whole-ecosystem measurements of GPP.

187

188 *Forest and plant trait data*

189 Site information of location, elevation, mean annual temperature, mean annual
190 precipitation, and IGBP biome were taken from the respective site pages on the AmeriFlux or

191 FLUXNET2015 websites. Functional traits were collected from a variety of different datasets for
192 each of our sampled tree species, including: wood density from the Global Wood Density
193 Database (Chave et al., 2009), specific leaf area and maximum photosynthetic rate from Maire
194 et al. (2015), and hydraulic traits (P50, the water potential at which 50% of xylem conduits are
195 embolized, and the P50 safety margin, which is the difference between P50 and the minimum
196 water potential observed) from the Xylem Functional Traits database (Gleason et al., 2016). Trait
197 data for the analyzed species are available in Table S4.

198 Drought responses in GPP likely reflect the integrated signal of all constituent species in
199 the tower footprint. Therefore, we aggregated plant trait data to the stand scale in a number of
200 ways: the mean trait value of all cored species, the standard deviation of all cored species, and
201 the mean of all cored species weighted by species composition.

202

203 *Climate data*

204 Standardized Precipitation Evaporation Index v2.6 (SPEI) data for all site-years were
205 used to quantify drought severity (Vicente-Serrano et al., 2010). SPEI data were extracted for
206 two relevant time scales in order to capture the differential effects of growing season versus
207 winter droughts: June – August (hereafter, “Summer”) and the previous October – March
208 (hereafter, “Winter”).

209 We calculated mean site climatic water deficit (CWD) as potential evapotranspiration
210 (PET) minus actual evapotranspiration (AET), using data from the TerraClimate dataset
211 (Abatzoglou et al., 2018). Monthly values CWD were extracted for all sites, and these values
212 were summed to get annual CWD. Mean site CWD was calculated over the period 2000 – 2019

213 in order to reflect climatic conditions during the years when most of our flux tower data were
214 present.

215

216 *MODIS data*

217 MODIS leaf area index (LAI) over 8-days windows (MCD15A2H, 500 m pixel size) were
218 obtained for each site from 2002 – 2019 using the R package *MODISTools* (Tuck et al., 2014). In
219 order to make MODIS data comparable to annual GPP sums in ecosystems that experience large
220 annual variation in LAI (e.g., deciduous forests), we limited LAI data to the growing season in
221 each year using a previously published method (Kannenberget al., 2020a). We considered the
222 start of the growing season to be the first day at which a smoothed curve of daily GPP sums
223 crossed a threshold of mean winter GPP + 30% of the annual smoothed GPP amplitude, and the
224 end of the growing season to be the last time point when smoothed GPP fell below this
225 threshold. Annual growing season LAI means were used in the calculation of drought indices
226 (detailed below), while growing season LAI was also averaged over the entire time interval (2002
227 – 2019) to calculate mean site LAI and thus quantify the typical canopy cover at each site.

228

229 *Calculation of drought indices*

230 To quantify the responses of RWI, GPP, and LAI to severe drought, we calculated metrics
231 of drought resistance and resilience. First, we identified severe drought years within the eddy
232 covariance record at each site. We defined a severe drought as a < -1.5 anomaly in SPEI during
233 two different periods: summer (June – August, the peak growing season) and winter (the

234 previous October – March, the start of the hydrological year to early spring). These two periods
235 were chosen to capture any differential effects of a hotter, acute growing season drought (i.e.,
236 summer drought) versus a longer-term anomaly in early season moisture storage (i.e., winter
237 drought). Our results were nearly identical when defining a summer drought as the full growing
238 season (April – September), due to significant overlap between the drought years identified with
239 each method (Fig. S2). Any multi-year droughts (i.e., two sequential winter or summer drought
240 years < -1.5 SPEI) were identified and not considered in our analyses to avoid any bias
241 introduced by a few anomalously severe droughts. Likewise, multi-drought years (i.e., a winter
242 and summer drought in the same year) were not included in the analysis (see Table S1 for the
243 drought site-years that were included in our analyses). The selected threshold of drought
244 severity was chosen to represent a severe drought that impacts forest function, yet also be
245 common enough to have a reasonable sample size in our dataset. The threshold of -1.5 SPEI,
246 which corresponds to a return period of 20 years across all sites in our dataset (range = 10 to 33-
247 year return period), is comparable with other studies that have quantified severe drought
248 resistance and resilience (Anderegg et al., 2015; Kannenberg, Maxwell, et al., 2019). Our main
249 results were robust to relaxing our threshold to -1.2 SPEI (roughly a drought every 8 years, Fig.
250 S3). When increasing our threshold to -2 SPEI (a once per century event), our sample size
251 decreased drastically to only 4 drought events across all sites (Fig. S4).

252 Once these severe drought years were identified, we calculated drought resistance (R_t)
253 and resilience (R_s) for the community-weighted RWI (hereafter referred to as “RWI”), annual
254 normalized GPP, and mean growing season LAI as follows:

255
$$R_t = X_{Drought} / \underline{X_{Non-drought}}$$

256
$$R_s = X_{Drought+1} / \underline{X_{Non-drought}}$$

257 Where $X_{Drought}$ represents the process of interest (i.e., RWI, GPP, LAI) during the
258 drought year itself, $X_{Drought+1}$ represents the process of interest in the year following a
259 drought, and $\underline{X_{Non-drought}}$ represents the mean of that process in all non-drought years. Thus,
260 these indices are analogous to effect sizes, where R_t represents the impact of each drought on
261 the process of interest relative to normal conditions, and R_s represents the degree to which that
262 process recovered in the year following the drought. These metrics are a slight modification of
263 those developed by Lloret *et al.* (2011), intended to remove noise related to variability in the
264 pre-drought year (Kannenberget al., 2019b). Finally, the degree of decoupling between GPP and
265 RWI (denoted ΔR_t or ΔR_s) was calculated as R_t or R_s in GPP minus R_t or R_s in RWI.

266

267 *C turnover time model*

268 In order to quantify the impact of C reallocation away from stem growth and towards
269 other structural tissues, we modeled the mean turnover time of whole-forest structural C using
270 a simple four-pool vegetation C model under a range of different scenarios, whereby the C not
271 allocated to stem growth during the drought year and following year (i.e., R_t and R_s) was re-
272 allocated entirely to leaf, coarse root, or fine root pools instead. Due to the large uncertainties
273 regarding the residence times and allocation dynamics of reproductive tissues and non-
274 structural pools (e.g., sugars/starches, root exudates, respiratory losses), we elected to
275 constrain our analyses to non-reproductive structural components.

276 To do so, we compiled data for total biomass C density (aboveground and belowground
277 biomass in Mg C ha⁻¹) for the year 2010 from the 300 m grid cell containing all the flux tower
278 sites using the dataset of Spawn *et al.* (2020). These biomass estimates are almost entirely
279 reflective of tree cover (as opposed to understory vegetation or seedlings) since the underlying
280 dataset for forest biomass is largely based on observations of saplings and mature trees.

281 After converting to total biomass C within each grid cell (Mg C), that biomass C was
282 partitioned out to each sampled species using our species composition estimates (Table S3). We
283 then allocated that C to leaf, aboveground woody biomass (AWB), coarse root, and fine root
284 pools for each species using allometry derived from the Biomass And Allometry Database
285 (BAAD, Falster *et al.* (2015), Table S5). For our species, all entries in BAAD that had
286 measurements of total plant mass were considered after entries associated with greenhouse
287 and growth chamber studies were excluded to avoid biases associated with the allometry of
288 seedlings and saplings. From these data, mean percent of biomass contained in leaves, AWB
289 (boles and branches), coarse roots, and fine roots were calculated. Many of our species were
290 not present in this dataset, and thus data were aggregated to the family level or to the plant
291 functional type level (i.e., deciduous angiosperm, deciduous conifer, or evergreen conifer). In
292 some cases, our allometric estimates across tissues had a sum greater than one (expected since
293 these tissue-specific estimates are many times drawing on different data sources). In those
294 cases, values were scaled to sum to one. In order to account for tissue-specific differences in C
295 content, we then scaled these estimates by the percentage of C contained in each tissue.
296 Percent C (by dry mass) data for each tissue were obtained for all species from the TRY database
297 (Kattge *et al.* 2020, Table S6), and gaps were filled using family-level and then functional type-
298 level means as above.

299 The effect of drought on AWB was estimated by quantifying the reduction in basal area
300 increment (BAI) in each species during the drought year itself and in the year after (i.e., R_t and
301 R_s). BAI chronologies were constructed using the ‘inside-out’ approach in the R package *dpIR*
302 (Bunn, 2008). We used this method because diameter measurements were not available for
303 many of our sites.

304 Reductions in total aboveground woody C (AWC) were estimated by multiplying total
305 AWC by the reduction in stand basal area (the sum of chronology BAI) C represented by the $R_t +$
306 R_s tree rings. We then simulated the impacts of a re-allocation of AWC on whole-forest C
307 turnover time by adding that lost AWC entirely to leaf, coarse root, or fine root pools.

308 Whole-forest C turnover time was calculated as follows. First, tissue-specific C density
309 data were converted into a turnover flux (F_{tissue} , in $Mg\ C\ yr^{-1}$) by dividing the total C in each tissue
310 for each species at each site by the mean lifespan (in years) of that tissue (Table S7). Leaf, fine
311 root, and coarse root lifespan data were directly available from TRY, and AWB life span was
312 considered as the mean plant age. Leaf lifespan data for deciduous species were considered to
313 be one year. Tissue lifespan data were aggregated from TRY for each species, and gaps in tissue
314 lifespan data were filled by family and then functional type means. Then, we weighted each
315 tissue-specific F_{tissue} by that species’ allometry in order to derive a whole-tree turnover flux, F_{tree} .

$$316 \quad F_{tree} = \sum (F_{tissue} \times Frac_{tissue})$$

317 Where F_{tissue} represents the turnover flux of each structural tissue (leaves, AWB, coarse
318 roots, and fine roots) and $Frac_{tissue}$ represents the proportion of total tree biomass contained in
319 each tissue. F_{tree} was then scaled to the whole forest by weighting the F_{tree} of each species by its
320 fractional of total stand basal area.

321
$$F_{forest} = \sum (F_{tree} \times Frac_{species})$$

322 Where $Frac_{species}$ represents the proportion of total species composition for each species
323 at each site. Whole-forest C turnover time, τ (in years), was then calculated as the ratio of
324 whole-forest total C density (C_{forest}) to F_{forest} (Pugh et al., 2020; Sierra et al., 2017).

325
$$\tau = \frac{C_{forest}}{F_{forest}}$$

326 Finally, we derived a percent change in τ for each of our tissue allocation scenarios,
327 compared to a scenario where there was no reduction in AWC due to drought (i.e., R_t and R_s
328 were 1). Note that this percentage represents the change in whole-forest τ due entirely to
329 allocation shifts in structural C during the drought year itself and the year after, not changes to τ
330 over longer time scales.

331

332 *Statistical analysis*

333 Comparisons between categorical variables were conducted using two-tailed t-tests or
334 via pairwise Tukey's HSD for multiple comparisons. Trait correlations were assessed using
335 ordinary least squares regression. For these regressions, normality and homoscedasticity of
336 residuals were confirmed using quantile-quantile and residual plots and were natural log or
337 square root transformed if necessary. All analyses were conducted in the R 4.0 computing
338 environment (R Core Team 2021).

339

340 **Results**

341 Drought resistance (R_t) and resilience (R_s) in radial tree growth varied widely across
342 species and sites (Fig. S5-S6). Averaged across all drought occurrences, drought reduced
343 community-weighted RWI by 25.4% during the year of the drought itself (i.e., resistance) and by
344 21.1% in the year after (i.e., resilience, Fig. 2). Lagged drought effects on growth were apparent
345 only one year, with the exception that RWI was significantly reduced for two years following a
346 summer drought (Fig. S7). R_t and R_s were also comparable in response to winter versus summer
347 droughts (Fig. 2). Contrary to the large observed reductions in RWI during and post-drought,
348 annual GPP and growing season LAI remained relatively unchanged, as R_t and R_s were not
349 significantly reduced below one (Fig. 1, Fig. S8-S10).

350 In general, R_t was correlated with various plant- and site-level traits while R_s was not,
351 though in some cases these relationships differed for summer versus winter droughts (Fig. 3, Fig.
352 S11). R_t calculated from RWI was highest in gymnosperm species and associated with low
353 specific leaf area (SLA) and wood density (WD), though the correlation with WD was not
354 significant following winter droughts. No traits were found to be correlated with R_s calculated
355 from RWI. The traits that predicted R_t and R_s were less consistent for indices derived from GPP.
356 For example, mean P50, mean site precipitation, and mean site water deficit were strong
357 predictors of R_t in response to summer droughts, while there were no significant correlations
358 with R_s . In contrast, R_t in response to winter droughts was best predicted by mean SLA, SLA
359 variability, and P50 variability, while R_s in response to winter droughts was strongly correlated
360 with mean maximum photosynthetic capacity (A_{max}) and mean LAI.

361 The degree of decoupling between RWI and GPP R_t during a summer drought was best
362 explained by broad site factors such as elevation ($P < 0.05$, $R^2 = 0.25$) and gymnosperm fraction
363 ($P < 0.05$, $R^2 = 0.20$) instead of plant traits (Fig. 4), though these factors were less successful in

364 explaining the decoupling in Rs. No correlations were found between the degree of RWI-GPP
365 decoupling and any site factors or plant traits following a winter drought.

366 As a way of estimating the C cycle impacts of the observed decoupling between RWI and
367 GPP, we modeled changes to whole-forest C turnover time (τ) under a range of scenarios,
368 whereby the C not allocated to tree-ring widths was instead allocated to other structural pools.
369 We found ubiquitous decreases in τ across all allocation scenarios (Fig. 5, all $P < 0.01$). Declines
370 in τ were particularly pronounced if C was allocated to leaves (mean change in $\tau = -3.3\%$), due to
371 the large amount of biomass held in foliage and its short lifespan. Decreases in τ were present,
372 but smaller, if C was allocated belowground (-1.2%), due to the small percentage of total
373 biomass held in fine roots (mean = 4.5% of total biomass) and the longer lifespan of coarse roots
374 (mean = 13.75 yrs).

375

376 **Discussion**

377 *Drought decouples GPP and growth*

378 We found that drought induced a striking decoupling between community-weighted
379 tree growth and stand-scale C dynamics, whereby RWI was significantly reduced in the year of,
380 and the year after, drought, while total annual GPP and mean LAI were unchanged. While RWI,
381 GPP, and LAI have been known to covary in some cases (Campioli et al., 2016; Teets et al., 2017;
382 Xu et al., 2017), our results add to growing evidence that radial growth and canopy-scale C
383 processes are commonly decoupled (Cabon et al., 2022; Delpierre et al., 2016; Mund et al.,
384 2010; Pappas et al., 2020; Rocha et al., 2006; Seftigen et al., 2018).

385 We also found the magnitude of R_t and R_s in radial growth to be comparable in
386 response to both summer and winter droughts. Given the strong temperature seasonality at
387 most of our sites, the impacts of winter droughts are likely manifest through reductions in spring
388 water balance and/or an increase in freeze-thaw induced root embolism due to decreased soil
389 insulation from snowpack (Love et al., 2019; Venturas et al., 2017). While many studies on
390 drought responses focus on droughts that occur in the growing season, our results point to the
391 large potential for winter droughts to alter forest C cycling in both arid and mesic forests.

392 Correlations between drought indices and plant- or site-level traits were generally
393 sparse, though we did find a significant linkage between R_t in radial growth and factors
394 pertaining to investment in tissue longevity such as SLA and WD. Consequently, gymnosperm
395 species had the highest R_t in RWI. There is a robust literature documenting the relationship
396 between investment into leaf longevity and tolerance to environmental stressors, including
397 drought (Wright et al., 2004). Thinner leaves (and leaves in angiosperms generally) are less of a
398 C investment for a tree, and are indicative of a life history strategy more tuned towards fast
399 growth in favorable environmental conditions, whereas higher leaf C investment (as in most
400 gymnosperms) is indicative of more long-lived, stress tolerant species (Greenwood et al., 2017;
401 Grime, 1979). However, contrary to previous work (Anderegg et al., 2015; Vitasse et al., 2019)
402 we found that R_s was not lower for gymnosperm species. High latitude coniferous forests
403 feature more prominently in our dataset than previous studies, and thus this result may indicate
404 a greater ability of gymnosperms in northern or mesic forests to recover from drought stress.
405 The factors underlying the high R_t in GPP were less clear, though we did confirm previous
406 evidence that found embolism resistance (P_{50}), site aridity, and drought severity to mediate the

407 responses of whole-forest C fluxes to drought (Anderegg et al., 2015; Schwalm et al., 2017; Wu
408 et al., 2018), with lower R_t observed in drier forests and in those with lower mean P50.

409 There is a growing interest in incorporating key plant functional traits to improve the
410 predictive capacity of terrestrial biosphere models (Fatichi et al., 2019; Fisher et al., 2018;
411 Kennedy et al., 2019). However, it stands to reason that different mechanisms control different
412 C cycle processes, and our results confirm that the functional traits underlying drought
413 responses in growth versus C uptake likely differ. Recognizing this nuance is an important factor
414 to consider towards trait-based vegetation modeling.

415 Multiple mechanisms for the decoupling between RWI and GPP have been proposed
416 (reviewed in Kannenberg *et al.* 2020b). A buffering of GPP during drought due to understory
417 species is one such mechanism, though emerging evidence indicates that these species are
418 frequently equally or more drought sensitive than canopy dominant species (Kannenberg et al.,
419 2019b; Rollinson et al., 2021). An abundance of research indicates that a major factor driving
420 this decoupling is likely the weakening of the link between C source activity and radial growth
421 sink dynamics due to: 1) the greater sensitivity of xylogenesis than photosynthesis to aridity, and
422 2) dynamic C allocation processes (Kannenberg et al., 2019b; Körner, 2015; Mund et al., 2010;
423 Pappas et al., 2020; Peters et al., 2021; Rocha et al., 2006). For example, radial growth is often
424 more sensitive to drought than GPP (Delpierre et al., 2016; Martin-StPaul et al., 2017; Peters et
425 al., 2021), and thus the different sensitivities of these processes could result in radial growth
426 reductions without concomitant declines in GPP. Radial growth is likely also actively reduced
427 during and following drought, whereby C is allocated elsewhere such as non-structural carbon
428 (Körner, 2015), root structural and exudate pools (Phillips et al., 2016), or reproductive efforts
429 (Hacket-Pain et al., 2018).

430 *Allocation shifts impact turnover time*

431 No matter if the decoupling between RWI and GPP was due to passive or active
432 mechanisms, the C that was fixed yet not used for radial growth necessarily went towards some
433 other structural or non-structural pools. Allocation of C away from long-lived aboveground
434 woody biomass pools could impart profound changes on the forest C cycle irrespective of any
435 drought-induced decline in GPP, because that C is very likely to be allocated towards tissues or
436 compounds with shorter turnover times (Pappas et al., 2020). We estimated that no matter
437 what structural pool C was allocated to, whole-forest C turnover time (τ) was significantly
438 reduced, and this decline was notably large in the foliar allocation scenario. Given that our
439 drought threshold of -1.5 SPEI represented a roughly 20-year drought frequency, our upper-
440 bound estimate of mean τ (where C was allocated to foliar tissue following a summer drought)
441 implies a 0.39% reduction in τ over the lifespan of the forest assuming steady-state vegetation
442 dynamics. The magnitude of this estimate is striking as it is roughly a sixth of the current trend in
443 forest τ (-2.3%) due to increasing tree mortality (Yu et al., 2019). While significant foliar
444 allocation shifts due to drought have been observed at some of our sites (Kannenberg et al.,
445 2019b), widespread canopy allocation across sites seems unlikely given that we did not observe
446 a significant decrease in R_t or R_s derived from MODIS LAI.

447 These changes in τ are likely a conservative estimate since we only modeled non-
448 reproductive structural C components, which have relatively long residence times. If C were
449 allocated to respiratory fluxes or non-structural compounds, which generally can turn over
450 within days or weeks (Carbone et al., 2007; Muhr et al., 2016), declines in τ would be even more
451 sizeable. Likewise, large-scale allocation to reproductive efforts (e.g., masting events) frequently
452 occurs during or following drought (Hackett-Pain et al., 2018), and is a plausible mechanism for

453 the decoupling between RWI and GPP that would likely reduce τ . Though, the magnitude of this
454 reduction in turnover τ would be highly species-dependent given the high variability in
455 reproductive allocation and tissue residence time across species (Wenk and Falster, 2015). We
456 also note that our model did not include any decomposition dynamics due to uncertainties in
457 decomposition rate over time and across species. Despite these uncertainties, our results
458 provide a first-order approximation of the impacts of drought-induced allocation shifts on the
459 forest C cycle across a range of scenarios. Crucially, our τ modeling reveals that the degree to
460 which the decoupling between RWI and GPP impacts the forest C cycle hinges on where that C is
461 allocated. Further efforts in model development, coupled with increased measurement of
462 allometry and C allocation during and after drought, are necessary steps towards refining our
463 estimates of how this decoupling will impact the ability of forests to mitigate climate change.

464 *Conclusions*

465 Drought is likely to cause consequential impacts to the terrestrial C cycle through
466 changes in C uptake, forest structure, and mortality rates (Saatchi et al., 2013; Yang et al., 2018;
467 Yu et al., 2019). Here, we document widespread and direct evidence of an additional, and
468 underappreciated, impact of drought on the forest C cycle: a fundamental disconnect between
469 the responses of tree radial growth versus whole-forest C uptake. We estimate that a drought-
470 induced allocation of C away from radial growth leads to decreases in whole-forest C turnover
471 time. This evidence indicates that drought impacts on terrestrial C cycling may be significantly
472 mediated by C allocation processes, irrespective of C uptake. Crucially, satellite-based estimates
473 of drought impacts or vegetation models driven by photosynthetic or productivity dynamics may
474 be missing key pathways through which the C cycle will be altered in a changing climate with
475 more frequent and severe drought.

476

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487

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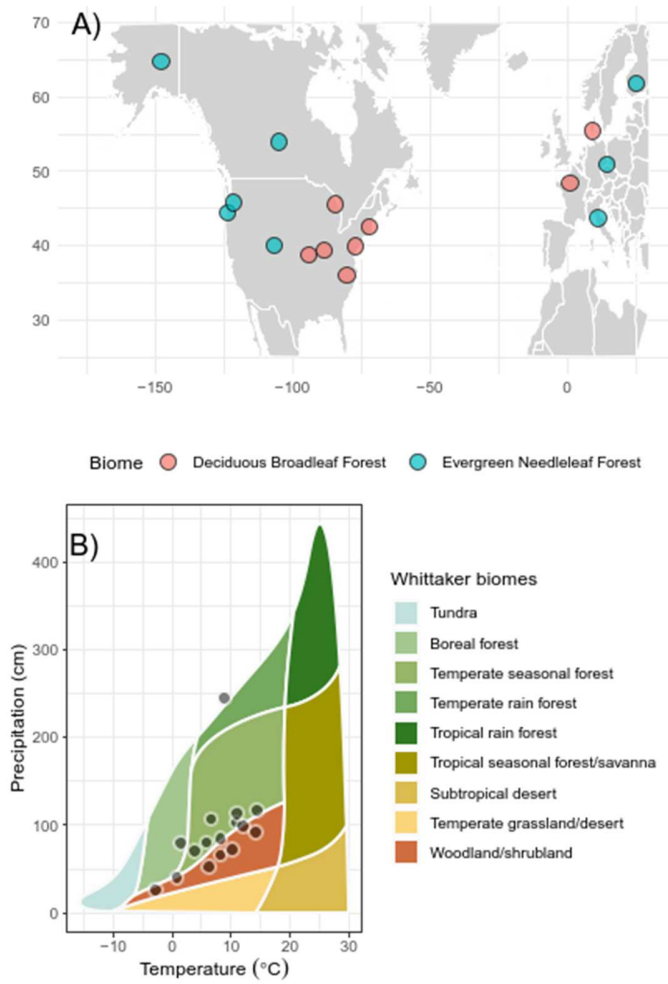
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931 **Figures**

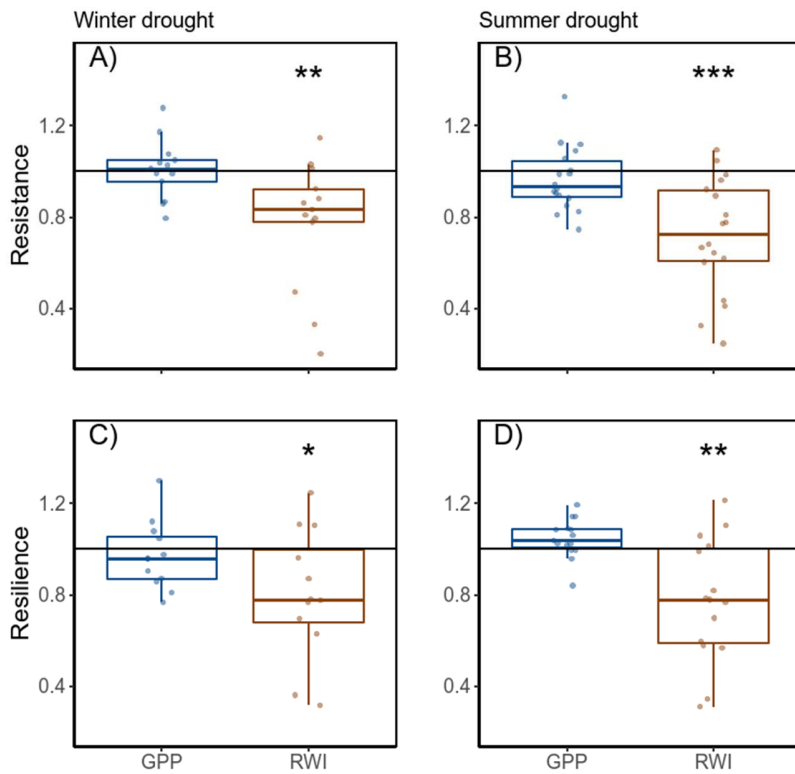


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933 Figure 1. Map of all eddy covariance towers where tree-ring chronologies were collected (panel

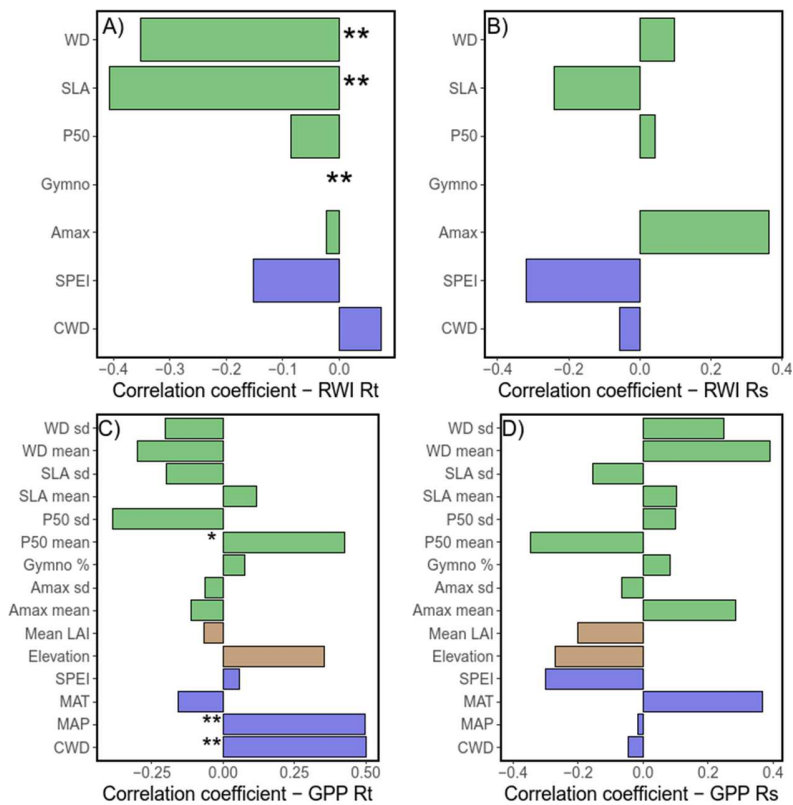
934 A), along with the climate space and biome that our sites represented (panel B).

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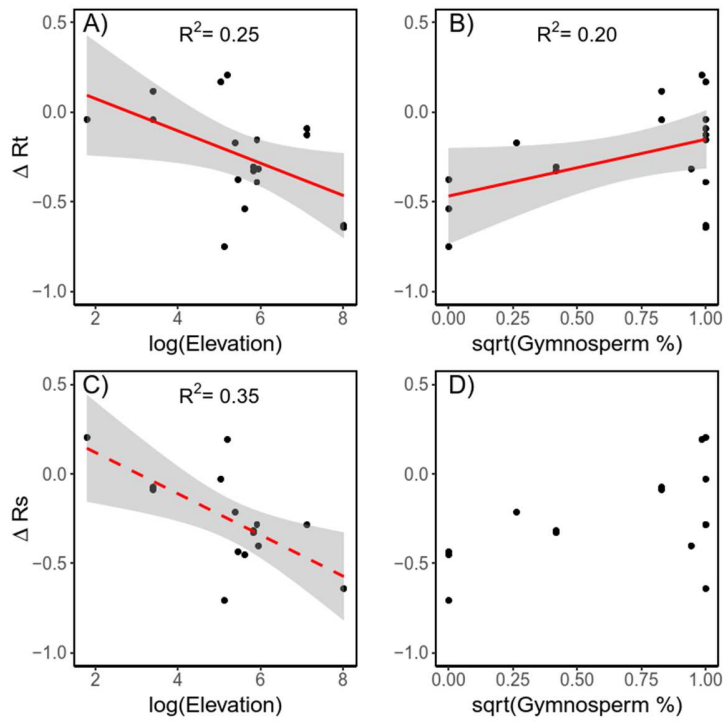
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937 Figure 2. Resistance (R_t , panels A and B) and resilience (R_s , panels C and D) in normalized gross
 938 primary productivity (GPP) and weighted tree-ring width (RWI) in response to two drought
 939 periods: winter (October – March, panels A and C) and summer (June – August, panels B and D).
 940 The horizontal line represents a value of one, which represents no response to drought. The *
 941 symbol indicates a p-value < 0.05 for a t-test from one, ** indicates a p-value < 0.01, and ***
 942 indicates a p-value < 0.001.



943

944 Figure 3. Pearson's correlation coefficients between Rt (panels A and C) and Rs (panel B and D)
 945 in weighted ring width (RWI, panels A and B) and normalized gross primary productivity (GPP,
 946 panels C and D) in response to summer droughts for all plant- and site-level traits, including
 947 maximum photosynthetic capacity (Amax), mean site climate water deficit (CWD), elevation,
 948 taxa (gymnosperm/angiosperm, or % gymnosperm species presence), mean annual
 949 temperature/precipitation (MAT/MAP), mean site leaf area index (Mean LAI), the water
 950 potential at 50% loss of conductivity (P50), specific leaf area (SLA), SPEI during the drought
 951 (SPEI), and wood density (WD). Bar color represents the type of trait: plant (green), climate
 952 (blue), or site (brown). The * symbol indicates a p-value < 0.1, while ** indicates a p-value <
 953 0.05. Correlation coefficients are not present for the 'Gymno' trait as these relationships were
 954 assessed with t-tests.



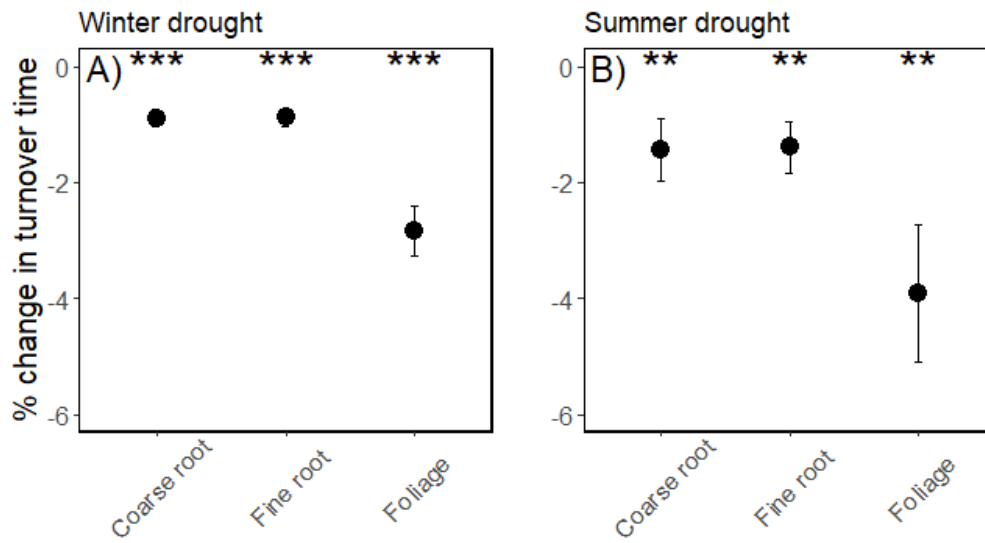
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956 Figure 4. Relationships between tree-and site-level traits and ΔR_t (panels A and B) or ΔR_s (panels
 957 C and D) in response to summer drought. Solid trendlines are present for significant
 958 relationships ($p < 0.05$) and dotted lines represent moderately significant relationships ($p < 0.1$).

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963 Figure 5. Change in whole-forest C turnover time in response to winter (panel A) and summer
 964 (panel B) droughts based on simulations where the losses of tree ring C during, and following,
 965 drought (i.e., R_t and R_s), are allocated entirely to coarse roots, fine roots, or leaves. Dots
 966 represent the tissue mean and error bars represent standard error. The * symbol indicates a p-
 967 value < 0.05 for a t-test from 0, ** indicates a p-value < 0.01, and *** indicates a p-value <
 968 0.001.