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Title: Cross-biome synthesis of source versus sink limits to tree growth

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43 **Abstract:** Uncertainties surrounding tree carbon allocation to growth are a major limitation to
44 projections of forest carbon sequestration and response to climate change. The prevalence and
45 extent to which carbon assimilation (source) or cambial activity (sink) mediate wood production
46 is fundamentally important and remains elusive. Here we quantify source-sink relations across
47 biomes by combining eddy-covariance gross primary production with extensive on-site and
48 regional tree-ring observations. We find widespread temporal decoupling between carbon
49 assimilation and tree growth, underpinned by contrasting climatic sensitivities of these two
50 processes. We elucidate substantial differences in assimilation-growth decoupling between
51 angiosperms and gymnosperms and stronger decoupling with canopy closure, aridity, and
52 decreasing temperatures. Our results reveal pervasive sink control over tree growth that is likely
53 to be increasingly prominent under global change.

54 **One-Sentence Summary:** Cross-biome correlation analysis shows pervasive decoupling
55 between carbon assimilation and tree growth.
56

57 **Main Text:**

58 Forest ecosystems currently constitute a net carbon (C) sink that offsets around 25% of
59 yearly anthropogenic C emissions, thus actively mitigating climate change (1). C allocation to
60 aboveground wood biomass is the largest contributor to vegetation C storage over climate-
61 relevant time scales. However, wood C allocation is poorly understood and is a major uncertainty
62 for projections of future forests' C storage potential (2). The common representation of wood
63 growth as a linear function of C assimilation has been identified as a major structural limitation
64 of current vegetation models (3, 4). The development of improved C allocation schemes
65 currently lacks a solid empirical and mechanistic basis (5). Thus, there is an urgent need to
66 illuminate the relationship between C assimilation and tree growth.

67 A fundamental debate revolves around the degree to which C assimilation via
68 photosynthesis (source limitation) versus direct environmental limitations to cambial cell
69 development (sink limitation) controls wood growth (6). As reflected by C allocation schemes in
70 the vast majority of vegetation models, source limitation has been the dominant paradigm for
71 decades (4). Yet, a growing body of literature indicates that cambial activity is typically more
72 sensitive than photosynthesis to a range of environmental conditions, including low water
73 availability, temperature, and nutrient availability (7–11). The prevalence of source vs sink
74 limitations to tree growth has far-reaching implications for forest dynamics under climate
75 change, because these processes will likely respond differently to global change (6–9),
76 potentially shifting C allocation away from the stem. Substantial indirect evidence supports the
77 hypothesis that C sink limitations may be particularly important in cold, dry, and late-
78 successional forests. For example, elevated non-structural C (e.g., starch and sugars)
79 concentrations are frequently observed in colder environments or during drought (8, 12).
80 Additionally, Free Air CO₂ Enrichment (FACE) experiments tends to show that increasing [CO₂]
81 improves tree growth in early-stage forests but often not in mature forests, perhaps because of
82 stronger nutrient limitations (13–15). But the relatively small scale and replication of FACE
83 experiments, especially in mature forests, prevents general conclusions regarding the linkage
84 between C source and sink dynamics in trees.

85 Co-located assessments of gross primary productivity (GPP) and tree growth theoretically
86 enable the evaluation of the coupling between tree C assimilation and growth increment. Past
87 studies adopting such an approach were nevertheless limited by dataset size (site number ≤ 5) and

88 yielded contrasting findings, with no clear explanation of observed differences (16–21). The
89 advent of large-scale, long-term networks of flux towers measuring C exchange across a diverse
90 assemblage of biomes, in combination with a growing number of both on-site and global tree-
91 ring datasets, opens new opportunities to characterize C source–sink relationships at larger
92 temporal and spatial scales. Here, we compile a new dataset comprising GPP records at 78 forest
93 flux sites (**Table S1**), together with on-site tree ring width chronologies at a subset of 31 sites
94 ($RW_{\text{on-site}}$), as well as 1800 nearby regional ring width chronologies (RW_{region}). GPP and RW
95 records were detrended, in order to remove low frequency signals (e.g., stand structure, tree age
96 and size), and aggregated such that records were representative of year-to year variations of
97 stand C assimilation and aboveground woody growth, respectively (22). This C assimilation and
98 tree growth dataset extends across most of Europe and North America, encompassing a variety
99 of forested biomes from semi-arid to boreal, and representing both angiosperm and gymnosperm
100 tree species (**Fig. 1, Fig. S1, Table S2**). Leveraging this dataset, we (i) quantify the strength, (ii)
101 identify the seasonality, and (iii) explore environmental drivers of tree C source–sink
102 relationships across biomes.

103 We first characterized C source and sink relationships at the regional scale by statistically
104 accounting for the decrease of the correlation between GPP and RW_{region} (r_{region}) with increasing
105 geographic and climatic distances, as well as with an index of species dissimilarity between sites
106 (22) (**Fig. S2**). As expected from reported tree growth synchrony over large distances (23) we
107 observed sustained correlations up to ~500 km. We thus built on this widespread ecological
108 feature to derive robust regional estimates of tree C assimilation and growth correlation, $r_{D=0}$, for
109 theoretical co-located sites of identical climate and species composition (i.e., spatial distance,
110 climatic distance and species dissimilarity of 0), integrating over multiple timescales. We then
111 complemented regional-scale analyses with paired GPP and on-site tree-ring correlations ($r_{\text{on-site}}$,
112 see annual GPP and RW series in **Fig. S3**). The latter dataset has a lower sample size compared
113 to the regional network but is model-free and therefore reduces the risk of methodological
114 artifacts.

115 Both on-site and regional correlations showed an overall weak association between tree C
116 assimilation and growth, $r_{\text{on-site}}$ and $r_{D=0}$ reaching maxima of 0.26 and 0.38, respectively (**Fig 2A–**
117 **B**). The observed difference between on-site and regional estimates could be offset by setting
118 species dissimilarity to the average encountered for $RW_{\text{on-site}}$, resulting in a maximum regional

119 correlation of 0.27 (22). RW_{region} observations partially build on the international tree ring data
120 bank, where sampling is often biased towards dominant and climate sensitive trees (24).
121 However, we find that this is unlikely an issue here, as dominant trees account for most of stand
122 GPP and we statistically corrected for differences in climate (22). Overall, similar regional and
123 on-site results show the suitability of regional RW data to quantify local GPP–RW correlations
124 and broad agreement between the two approaches, which both suggest a substantial decoupling
125 between C assimilation and tree growth across multiple biomes.

126 On-site and regional GPP–RW correlations exhibited a similar temporal structure (22),
127 with correlation magnitude increasing with the length of the GPP integration period and
128 maximum correlations being found at the 10- and 12-months scales for $r_{\text{on-site}}$ and r_{region} ,
129 respectively (**Fig. 2**). This supports the often-implicit assumption that annual tree-ring
130 increments are most strongly related to annual carbon assimilation (21). Overall, RW was best
131 correlated to GPP integrated over the period spanning previous Sep or Nov to current Aug,
132 consistent with a previous study (20), indicating a short temporal lag between C assimilation and
133 tree growth. This result suggests that, despite estimated low C source limitation of tree growth
134 overall, excess photosynthates are stored over winter following radial growth cessation and
135 allocated to the next year’s growth. This phenomenon is often cited as a potential explanation for
136 delayed climatic effects on tree growth and growth auto-correlation (25, 26). Analysis of multi-
137 year trends (**Table S4**) nevertheless indicates weak association of RW and GPP at this scale,
138 contrary to the hypothesis that C storage might lead to the convergence of tree growth and C
139 assimilation over the long term (27).

140 We found large spatial variations in the strength of GPP–RW coupling (**Fig. 3**).
141 Weighted deciles of maximum on-site r ranged from -0.08 to 0.60 , consistent with previously
142 reported values (16–21). These spatial variations imply a range of source vs. sink limitations. We
143 estimate that because of approximations and measurement errors, RW–GPP correlations between
144 0.7 and 0.9 would be expected under strong source control of tree growth (22). The high end of
145 the observed correlation range ($0.6 \leq r_{\text{on-site}} \leq 0.9$: 10% of observations) thus appears reflective of
146 substantial source limitation of tree growth at the corresponding sites, whereas the majority of
147 sites display evidence consistent with sink limitations. We did not observe a biome effect on on-
148 site correlations but regional-scale r was significantly related to several environmental factors
149 (**Fig. 3B**). Specifically, gymnosperm proportion had a positive effect on current year r_{region} but a

150 negative one on previous year r_{region} , suggesting that gymnosperm growth relies more directly on
151 current and less on previous year C assimilation than angiosperms, reflecting fundamental
152 physiological differences between these two clades. A small but positive effect of species
153 richness on r_{region} suggests a link between species diversity and C use efficiency (i.e., the ratio
154 between net and gross primary production), which may arise as a result of increased
155 complementarity with structural and functional heterogeneity (28). Decreasing r_{region} with
156 increasing leaf area index indicates that closed canopy forests, which under a given climate tend
157 to be older and more nutrient-limited than open canopy forests, are prone to stronger decoupling
158 between C source and sink activity. This result agrees with the observations that CO₂ growth
159 fertilization tends to fade in older, nutrient-limited forests (15). Last, r_{region} was found to be
160 positively related to site temperature and water availability, consistent with known biophysical
161 controls of cambial activity and the ensuing prediction that sink limitations are stronger under
162 colder and drier conditions (6–9). These combined results draw a clear picture that increasing
163 resource limitation, aridity, and low temperatures promote C source-sink decoupling across a
164 broad range of biomes.

165 Finally, decoupled C assimilation and tree growth was further revealed by diverging
166 climate sensitivities of these two processes (22) (**Fig. 4**). As anticipated from C assimilation and
167 wood formation literature, GPP and RW both responded positively to temperature and water
168 availability but were weakly correlated with photosynthetically active radiation (hereafter
169 radiation) (29, 30). However, their seasonal variability differed markedly, indicating that
170 fundamentally different physiological processes may limit C assimilation and tree growth. GPP
171 responded mostly to spring and fall temperatures, as well as to summer water availability,
172 suggesting an important role of temperature-triggered leaf phenology controlling annual GPP
173 (31). In contrast, RW appeared to be most strongly related to year-round water availability, with
174 a weak positive temperature effect peaking in summer. This agrees with previous observations
175 that tree growth is primarily and increasingly water-limited in the study regions (29) and is
176 consistent with the central role of cell turgor in controlling cambial cell division and expansion
177 (7, 11). Overall, this analysis shows the large but contrasting climate sensitivity of the tree
178 growth and photosynthesis proxies used here. This is contrary to the expectation that RW and
179 GPP would have weaker but similar climate sensitivity if low RW–GPP were due primarily to
180 large measurement errors. These results instead strongly suggest that weak control of C

181 assimilation over tree growth is underpinned by fundamentally contrasting source and sink
182 processes with diverging environmental sensitivities (6).

183 Taken together, our results provide consistent evidence for the pervasive influence of
184 non-photosynthetic processes on tree radial growth. This conclusion has major implications in
185 terms of projections of forest dynamics and feedbacks with the global C cycle and climate
186 change, as most global vegetation models essentially simulate forest productivity and C
187 sequestration as a linear function of C assimilation (3, 4). Because sink processes are relatively
188 more sensitive to water availability than temperature constrains compared to C assimilation (**Fig.**
189 **4**) and are not directly dependent on atmospheric [CO₂], unaccounted for and widespread sink
190 limitations could lead to overestimating the positive effect of warming and CO₂ fertilization
191 while underestimating the negative effect of increasing water stress on forest productivity.
192 Overall, accounting for sink limitations of tree growth may lower projections of future forest C
193 sequestration in many regions and could thus potentially compromise forests' potential for
194 climate change mitigation. Based on these considerations, our results underscore that
195 incorporation of sink-limited carbon allocation schemes in global vegetation models is urgently
196 needed (3, 4).

197 Our results nevertheless indicate a certain degree of interaction between C source and
198 sink activities, as suggested by the weak but significantly positive correlations observed between
199 GPP and RW, as well as their temporal and spatial variations. Such dynamic coupling between C
200 assimilation and tree growth potentially reconciles contrasting observations of the prevalence of
201 source vs sink limitations (15) and provides a bridge between current source-centered
202 representations of tree growth and sink-driven schemes. Variations in the prevalence of source vs
203 sink limitations to tree growth further highlights the importance of understanding their drivers
204 (5). Here we show that across biomes, the occurrence of sink limitations is highly consistent with
205 known biophysical controls of cambial cell division, notably turgor-driven growth. Because
206 turgor is a central mechanism of growth across scales and has a large potential for both
207 integration of several relevant processes and parameter-parsimonious upscaling (32), the turgor-
208 driven growth framework appears to be a promising way forward to developing mechanistic
209 sink-limited schemes in vegetation models.

210 Key remaining uncertainties include whether our results can be generalized to other
211 biomes such as tropical forests, which are central to the global C cycle, and quantifying the

212 dynamic nature of source and sink interactions. Likewise, characterizing the degree of C source
213 and sink decoupling at decadal to centennial scales is relevant regarding climate change but
214 currently remains elusive due to the temporal depth of C assimilation measurements. Source–
215 sink decoupling over both short and longer timescales implies less C limitation of tree growth.
216 Weak C limitation of tree growth under certain conditions nonetheless raises the question of the
217 fate of excess C. Closing trees' C budget and elucidating drivers of C allocation to different
218 sinks, specifically stem vs underground growth and C storage thus emerges as a critical way
219 forward (14).

220

221 **Figure legends:**

222

223 **Fig 1. Spatial distribution of gross primary production (GPP) and regional ring width**

224 **(RW_{region}) sites used in this study.** RW_{region} sites are indicated by crosses and GPP sites by

225 circle. The number of RW_{region} site-year observations associated with each flux tower is denoted

226 by circle size. GPP sites that further include on-site RW are colored in yellow, and in red

227 otherwise.

228

229 **Fig 2. Temporal structure of gross primary productivity (GPP) vs. ring width (RW)**

230 **correlations.** (A) Seasonal on-site correlations ($r_{\text{on-site}}$). Each cell corresponds to the average

231 correlation calculated between on-site RW and GPP summed over a time-period defined by a

232 window onset (from previous year Jan to current Dec) and length (from 1 to 12 months). (B)

233 Regional-based estimates of null distance correlations ($r_{D=0}$) modelled by Eq. S1 (see **Fig. S2**

234 for an illustration of the 12-months case from current year Jan). Significant correlation values

235 are displayed on top of corresponding cells (lightface: p -value < 0.05 ; bold: p -value < 0.01).

236

237 **Fig 3. Spatial variations and environmental drivers of gross primary productivity (GPP) vs.**

238 **ring width (RW) correlations.** (A) Effect of biome on on-site correlations ($r_{\text{on-site}}$) observed on

239 the period with highest correlation average (previous Nov–current Oct; non-significant). Boxes

240 represent the median, the 1st and the 3rd quartiles. Whiskers represent 1.5 times the inter-quartile

241 range. Dots represent individual r values and dot size is proportional to the underlying number

242 of observations. (B) Effect of stand structure and climatic variables on current and previous year

243 regional-based estimates of null distance correlations ($r_{D=0}$). Error bars represent SE. All effects

244 are highly significant ($p < 0.001$: gymnosperm proportion, species richness, mean annual

245 climatic water deficit – MACWD, mean annual temperature – MAT) except for that of leaf area
246 index (LAI) on current year correlations (ns).

247

248 **Fig 4. Gross primary production (GPP) and regional ring width (RW) climatic sensitivity.**

249 Climate-corrected partial correlations between GPP and regional RW and three climate
250 variables (from the top to the bottom: mean temperature – T_{mean} , Palmer’s drought severity index
251 – PDSI, and radiation – Rad) at the three-monthly scale, over the period 1990–2015 (to the
252 extent of series span). Error bars correspond to SE. Statistical significance of estimated
253 coefficients is denoted as: * – $p < 0.05$; ** – $p < 0.01$; *** – $p < 0.001$.

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316 Methodology: AC, WA, SK

317 Data contributions: All co-authors

318 Investigation: AC, WA, SK

319 Visualization: AC

320 Funding acquisition: WA

321 Writing – original draft: AC, WA, SK

322 Writing – review & editing: All co-authors

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324

325 **Data and materials availability:** All processed data used for the analyses are available on
326 Dryad (DOI: 10.5061/dryad.15dv41nzt) and the code is available on Zenodo (DOI:
327 10.5281/zenodo.6033963).

328 **Supplementary Materials**

329 Materials and Methods

330 Fig S1 to S5

331 Tables S1 to S4

332 References (52–67)

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