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

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

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

**Main Text:**

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

A fundamental debate revolves around the degree to which C assimilation via photosynthesis (source limitation) versus direct environmental limitations to cambial cell development (sink limitation) controls wood growth (*6*). As reflected by C allocation schemes in the vast majority of vegetation models, source limitation has been the dominant paradigm for decades (*4*). Yet, a growing body of literature indicates that cambial activity is typically more sensitive than photosynthesis to a range of environmental conditions, including low water availability, temperature, and nutrient availability (*7–11*). The prevalence of source vs sink limitations to tree growth has far-reaching implications for forest dynamics under climate change, because these processes will likely respond differently to global change (*6–9*), potentially shifting C allocation away from the stem. Substantial indirect evidence supports the hypothesis that C sink limitations may be particularly important in cold, dry, and late-successional forests. For example, elevated non-structural C (e.g., starch and sugars) concentrations are frequently observed in colder environments or during drought (*8*, *12*). Additionally, Free Air $CO_2$ Enrichment (FACE) experiments tends to show that increasing $[CO_2]$ improves tree growth in early-stage forests but often not in mature forests, perhaps because of stronger nutrient limitations (*13–15*). But the relatively small scale and replication of FACE experiments, especially in mature forests, prevents general conclusions regarding the linkage between C source and sink dynamics in trees.

Co-located assessments of gross primary productivity (GPP) and tree growth theoretically enable the evaluation of the coupling between tree C assimilation and growth increment. Past studies adopting such an approach were nevertheless limited by dataset size (site number ≤5) and yielded contrasting findings, with no clear explanation of observed differences (*16–21*). The advent of large-scale, long-term networks of flux towers measuring C exchange across a diverse assemblage of biomes, in combination with a growing number of both on-site and global tree-ring datasets, opens new opportunities to characterize C source–sink relationships at larger temporal and spatial scales. Here, we compile a new dataset comprising GPP records at 78 forest flux sites (**Table S1**), together with on-site tree ring width chronologies at a subset of 31 sites ($RW_{on\text{-}site}$), as well as 1800 nearby regional ring width chronologies ($RW_{region}$). GPP and RW records were detrended, in order to remove low frequency signals (e.g., stand structure, tree age and size), and aggregated such that records were representative of year-to year variations of stand C assimilation and aboveground woody growth, respectively (*22*). This C assimilation and tree growth dataset extends across most of Europe and North America, encompassing a variety of forested biomes from semi-arid to boreal, and representing both angiosperm and gymnosperm tree species (**Fig. 1, Fig. S1**, **Table S2**). Leveraging this dataset, we (i) quantify the strength, (ii) identify the seasonality, and (iii) explore environmental drivers of tree C source–sink relationships across biomes.

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

Both on-site and regional correlations showed an overall weak association between tree C assimilation and growth, $r_{on\text{-}site}$ and $r_{D=0}$ reaching maxima of 0.26 and 0.38, respectively (**Fig 2A–B)**. The observed difference between on-site and regional estimates could be offset by setting species dissimilarity to the average encountered for $RW_{on\text{-}site}$, resulting in a maximum regional correlation of 0.27 (*22*). $RW_{region}$ observations partially build on the international tree ring data bank, where sampling is often biased towards dominant and climate sensitive trees (*24*). However, we find that this is unlikely an issue here, as dominant trees account for most of stand GPP and we statistically corrected for differences in climate (*22*). Overall, similar regional and on-site results show the suitability of regional RW data to quantify local GPP–RW correlations and broad agreement between the two approaches, which both suggest a substantial decoupling between C assimilation and tree growth across multiple biomes.

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

We found large spatial variations in the strength of GPP–RW coupling (**Fig. 3**). Weighted deciles of maximum on-site *r* ranged from –0.08 to 0.60, consistent with previously reported values (*16*–*21*). These spatial variations imply a range of source vs. sink limitations. We estimate that because of approximations and measurement errors, RW–GPP correlations between 0.7 and 0.9 would be expected under strong source control of tree growth (*22*). The high end of the observed correlation range ($0.6 \leq r_{on\text{-}site} \leq 0.9$: 10% of observations) thus appears reflective of substantial source limitation of tree growth at the corresponding sites, whereas the majority of sites display evidence consistent with sink limitations. We did not observe a biome effect on on-site correlations but regional-scale *r* was significantly related to several environmental factors (**Fig. 3B**). Specifically, gymnosperm proportion had a positive effect on current year $r_{region}$ but a negative one on previous year $r_{region}$, suggesting that gymnosperm growth relies more directly on current and less on previous year C assimilation than angiosperms, reflecting fundamental physiological differences between these two clades. A small but positive effect of species richness on $r_{region}$ suggests a link between species diversity and C use efficiency (i.e., the ratio between net and gross primary production), which may arise as a result of increased complementarity with structural and functional heterogeneity (*28*). Decreasing $r_{region}$ with increasing leaf area index indicates that closed canopy forests, which under a given climate tend to be older and more nutrient-limited than open canopy forests, are prone to stronger decoupling between C source and sink activity. This result agrees with the observations that $CO_2$ growth fertilization tends to fade in older, nutrient-limited forests (*15*). Last, $r_{region}$ was found to be positively related to site temperature and water availability, consistent with known biophysical controls of cambial activity and the ensuing prediction that sink limitations are stronger under colder and drier conditions (*6–9*). These combined results draw a clear picture that increasing resource limitation, aridity, and low temperatures promote C source-sink decoupling across a broad range of biomes.

Finally, decoupled C assimilation and tree growth was further revealed by diverging climate sensitivities of these two processes (*22*) (**Fig. 4**). As anticipated from C assimilation and wood formation literature, GPP and RW both responded positively to temperature and water availability but were weakly correlated with photosynthetically active radiation (hereafter radiation) (*29*, *30*). However, their seasonal variability differed markedly, indicating that fundamentally different physiological processes may limit C assimilation and tree growth. GPP responded mostly to spring and fall temperatures, as well as to summer water availability, suggesting an important role of temperature-triggered leaf phenology controlling annual GPP (*31*). In contrast, RW appeared to be most strongly related to year-round water availability, with a weak positive temperature effect peaking in summer. This agrees with previous observations that tree growth is primarily and increasingly water-limited in the study regions (*29*) and is consistent with the central role of cell turgor in controlling cambial cell division and expansion (*7*, *11*). Overall, this analysis shows the large but contrasting climate sensitivity of the tree growth and photosynthesis proxies used here. This is contrary to the expectation that RW and GPP would have weaker but similar climate sensitivity if low RW–GPP were due primarily to large measurement errors. These results instead strongly suggest that weak control of C assimilation over tree growth is underpinned by fundamentally contrasting source and sink processes with diverging environmental sensitivities (*6*).

Taken together, our results provide consistent evidence for the pervasive influence of non-photosynthetic processes on tree radial growth. This conclusion has major implications in terms of projections of forest dynamics and feedbacks with the global C cycle and climate change, as most global vegetation models essentially simulate forest productivity and C sequestration as a linear function of C assimilation (*3*, *4*). Because sink processes are relatively more sensitive to water availability than temperature constrains compared to C assimilation (**Fig. 4**) and are not directly dependent on atmospheric [$CO_2$], unaccounted for and widespread sink limitations could lead to overestimating the positive effect of warming and $CO_2$ fertilization while underestimating the negative effect of increasing water stress on forest productivity. Overall, accounting for sink limitations of tree growth may lower projections of future forest C sequestration in many regions and could thus potentially compromise forests' potential for climate change mitigation. Based on these considerations, our results underscore that incorporation of sink-limited carbon allocation schemes in global vegetation models is urgently needed (*3*, *4*).

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

Key remaining uncertainties include whether our results can be generalized to other biomes such as tropical forests, which are central to the global C cycle, and quantifying the dynamic nature of source and sink interactions. Likewise, characterizing the degree of C source and sink decoupling at decadal to centennial scales is relevant regarding climate change but currently remains elusive due to the temporal depth of C assimilation measurements. Source–sink decoupling over both short and longer timescales implies less C limitation of tree growth. Weak C limitation of tree growth under certain conditions nonetheless raises the question of the fate of excess C. Closing trees' C budget and elucidating drivers of C allocation to different sinks, specifically stem vs underground growth and C storage thus emerges as a critical way forward (*14*).

**Figure legends:**

**Fig 1. Spatial distribution of gross primary production (GPP) and regional ring width ($\mathrm{RW}_{\mathrm{region}}$) sites used in this study.** $\mathrm{RW}_{\mathrm{region}}$ sites are indicated by crosses and GPP sites by circle. The number of $\mathrm{RW}_{\mathrm{region}}$ site-year observations associated with each flux tower is denoted by circle size. GPP sites that further include on-site RW are colored in yellow, and in red otherwise.

**Fig 2. Temporal structure of gross primary productivity (GPP) vs. ring width (RW) correlations**. (**A**) Seasonal on-site correlations ($r_{\text{on-site}}$). Each cell corresponds to the average correlation calculated between on-site RW and GPP summed over a time-period defined by a window onset (from previous year Jan to current Dec) and length (from 1 to 12 months). (**B**) Regional-based estimates of null distance correlations ($r_{D=0}$) modelled by Eq. S1 (see **Fig. S2** for an illustration of the 12-months case from current year Jan). Significant correlation values are displayed on top of corresponding cells (lightface: p-value < 0.05; bold: p-value < 0.01).

**Fig 3. Spatial variations and environmental drivers of gross primary productivity (GPP) vs. ring width (RW) correlations**. (**A**) Effect of biome on on-site correlations ($r_{\text{on-site}}$) observed on the period with highest correlation average (previous Nov–current Oct; non-significant). Boxes represent the median, the 1st and the 3rd quartiles. Whiskers represent 1.5 times the inter-quartile range. Dots represent individual *r* values and dot size is proportional to the underlying number of observations. (**B**) Effect of stand structure and climatic variables on current and previous year regional-based estimates of null distance correlations ($r_{D=0}$). Error bars represent SE. All effects are highly significant ($p < 0.001$: gymnosperm proportion, species richness, mean annual climatic water deficit – MACWD, mean annual temperature – MAT) except for that of leaf area index (LAI) on current year correlations (ns).

**Fig 4. Gross primary production (GPP) and regional ring width (RW) climatic sensitivity**. Climate-corrected partial correlations between GPP and regional RW and three climate variables (from the top to the bottom: mean temperature – $T_{mean}$, Palmer's drought severity index – PDSI, and radiation – Rad) at the three-monthly scale, over the period 1990–2015 (to the extent of series span). Error bars correspond to SE. Statistical significance of estimated coefficients is denoted as: * – $p<0.05$; ** – $p<0.01$; *** – $p<0.001$.

## References:

1. P. Friedlingstein *et al.*, *Earth Syst. Sci. Data*. **12**, 3269–3340 (2020).
2. T. A. M. Pugh *et al.*, *Biogeosciences*. **17**, 3961–3989 (2020).
3. A. D. Friend *et al.*, *Ann. For. Sci.* **76**, 49 (2019).
4. S. Fatichi, S. Leuzinger, C. Körner, *New Phytol.* **201**, 1086–1095 (2014).
5. F. Babst *et al.*, *Trends Plant Sci.* **26**, 210–219 (2021).
6. C. Körner, *Curr. Opin. Plant Biol.* **25**, 107–114 (2015).
7. T. C. Hsiao, *Annu. Rev. Plant Physiol.* **24**, 519–570 (1973).
8. B. Muller *et al.*, *J. Exp. Bot.* **62**, 1715–1729 (2011).
9. R. L. Peters *et al.*, *New Phytol.* **229**, 213–229 (2021).
10. I. Cornut *et al.*, *For. Ecol. Manage.* **494**, 119275 (2021).
11. A. Cabon, R. L. Peters, P. Fonti, J. Martínez-Vilalta, M. De Cáceres, *New Phytol.* **226**, 1325–1340 (2020).
12. G. Hoch, C. Körner, *Glob. Ecol. Biogeogr.* **21**, 861–871 (2012).
13. T. Klein *et al.*, *J. Ecol.* **104**, 1720–1733 (2016).
14. M. Jiang *et al.*, *Nature*. **580**, 227–231 (2020).
15. A. P. Walker *et al.*, *New Phytol.* **229**, 2413–2445 (2021).
16. A. V. Rocha, M. L. Goulden, A. L. Dunn, S. C. Wofsy, *Glob. Chang. Biol.* **12**, 1378–1389 (2006).
17. F. Babst *et al.*, *New Phytol.* **201**, 1289–1303 (2014).
18. N. Delpierre, D. Berveiller, E. Granda, E. Dufrêne, *New Phytol.* **210**, 459–470 (2016).
19. C. Pappas *et al.*, *Agric. For. Meteorol.* **290**, 108030 (2020).
20. A. Teets *et al.*, *Agric. For. Meteorol.* **249**, 479–487 (2018).
21. M. Lempereur *et al.*, *New Phytol.* **207**, 579–590 (2015).
22. Materials and methods are available as supplementary materials on Science Online.
23. M. del Río *et al.*, *For. Ecol. Manage.* **479**, 118587 (2021).
24. S. Klesse *et al.*, *Nat. Commun.* **9**, 1–9 (2018).
25. R. Zweifel, F. Sterck, *Front. For. Glob. Chang.* **1**, 1–9 (2018).
26. A. Gessler, K. Treydte, *New Phytol.* **209**, 1338–1340 (2016).
27. C. M. Gough, C. S. Vogel, H. P. Schmid, H. B. Su, P. S. Curtis, *Agric. For. Meteorol.* **148**, 158–170 (2008).
28. S. Mensah, R. Veldtman, A. E. Assogbadjo, R. Glèlè Kakaï, T. Seifert, *Ecol. Evol.* **6**, 7546–7557 (2016).
29. F. Babst *et al.*, *Sci. Adv.* **5**, eaat4313 (2019).
30. N. Delpierre *et al.*, *Agric. For. Meteorol.* **154–155**, 99 (2012).
31. J. Xia *et al.*, *Proc. Natl. Acad. Sci. U. S. A.* **112**, 2788–2793 (2015).
32. A. Potkay, T. Hölttä, A. T. Trugman, Y. Fan, *Tree Physiol.* **42**, 229–252 (2022).

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Data contributions: All co-authors

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

**Supplementary Materials**

Materials and Methods

Fig S1 to S5

Tables S1 to S4

References (*52–67*)