

Commentary

What drives forest carbon storage? The ramifications of source–sink decoupling

As the climate changes and scientists seek to project its future course, an important uncertainty lies in the response of forests. Will rising atmospheric carbon dioxide (CO₂) and lengthening growing seasons relieve limitations to tree growth, allowing increased carbon (C) sequestration in long-lived woody tissues and providing a negative feedback to climate change? Or will increasing heat and drought stress reduce growth and increase mortality, resulting in a positive feedback to climate change? To answer this question, global C cycle models simulate photosynthesis under future conditions, using simple plant C allocation schemes to estimate the amount of C sequestered in woody growth vs that allocated to short-lived pools that are more rapidly respired back to the atmosphere as CO₂ (Fatichi *et al.*, 2014). However, there is growing evidence that these schemes are too simplistic, as wood production is frequently decoupled from photosynthesis (Delpierre *et al.*, 2016a,b; Etzold *et al.*, 2022), either through the passive limitation of woody tree growth by environmental conditions or active allocation prioritising other sinks. Needed, then, is an understanding of how woody growth is jointly shaped by photosynthesis (i.e. source limitation) and demand from various C sinks (i.e. sink limitation) across species and biomes (Körner, 2015). In this issue of *New Phytologist*, Martínez-Sancho *et al.* (2022; pp. 58–70) exemplifies the type of research needed to improve our ability to predict forest C sequestration under climate change, using an innovative approach to describe the seasonal course of C sequestration in tree stem growth and how it is affected by drought.

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Characterising the seasonal course of woody growth is challenging, even with frequent dendrometer measurements, because stems shrink and swell in relation to their hydraulic status, and because C sequestration associated with cell wall thickening lags behind radial growth (Cuny *et al.*, 2015; Martínez-Sancho *et al.*, 2022). To understand the timing of C sequestration, Martínez-Sancho *et al.*

collected weekly microcores from mature *Picea abies* trees to characterise the seasonal timing of wood formation, and then combined this information with a detailed analysis of wood anatomy and C stable isotopes (δ¹³C). In a nondrought year (2014), the rate of cell expansion peaked at the end of June, whereas rates of cell wall thickening and C sequestration peaked in early July, with all three variables displaying a unimodal peak. These patterns were consistent with other studies showing that tree stem growth rate peaks near the time of the summer solstice, with C sequestration lagging stem radial expansion (Cuny *et al.*, 2015; Dow *et al.*, 2022; Etzold *et al.*, 2022).

Extreme summer drought in 2015 resulted in dramatically different seasonal patterns of woody growth and C sequestration (Fig. 1; Martínez-Sancho *et al.*, 2022). During a 41-d period from mid-June to late July during which stem radial shrinkage indicated physiological water stress, rates of cell enlargement and thickening were slowed, resulting in bimodal growth and C sequestration curves with peaks before and after the drought. Overall, C sequestration was reduced 67% during the drought period. In addition, δ¹³C isotopes indicated increased C isotope discrimination, indicative of water limitation resulting in higher intrinsic

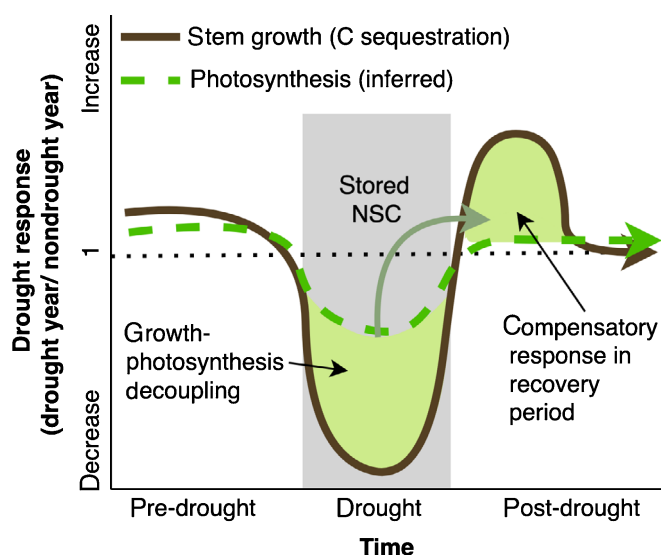


Fig. 1 Schematic summarizing the effects of a severe summer drought on seasonal patterns in CO₂ uptake (photosynthesis) and carbon (C) sequestration (woody growth). Schematic is based on the results of Martínez-Sancho *et al.* (2022; pp. 58–70) in this issue of *New Phytologist*, who combined weekly microcores with a detailed analysis of wood anatomy and C stable isotopes (δ¹³C) to understand the seasonal dynamics of C sequestration in four mature *Picea abies* trees in a Swiss valley. Strong reductions in stem growth during the drought resulted in nonstructural carbohydrate (NSC) stores that were used in a compensatory growth response following the drought, resulting in similar C sequestration in drought and nondrought years.

This article is a Commentary on Martínez-Sancho *et al.* (2022), 236: 58–70.

water use efficiency during the drought. The $\delta^{13}\text{C}$ drought signature appeared in wood formed after the drought, suggesting that, whereas sink limitations prevented the C fixed during the drought from contributing immediately to woody growth, this C was reserved and used to accelerate growth after the drought. Indeed, higher compensatory growth and C sequestration rates after the drought resulted in similar total C sequestration during the

drought and reference years (Martínez-Sancho *et al.*, 2022). Therefore, the study of intra-annual dynamics of wood formation revealed a drought impact on growth that would have gone undetected at the annual scale.

The fact that a severe drought coinciding with peak growing season had little effect on annual C sequestration is somewhat surprising in the context of other studies. Typically, annual growth

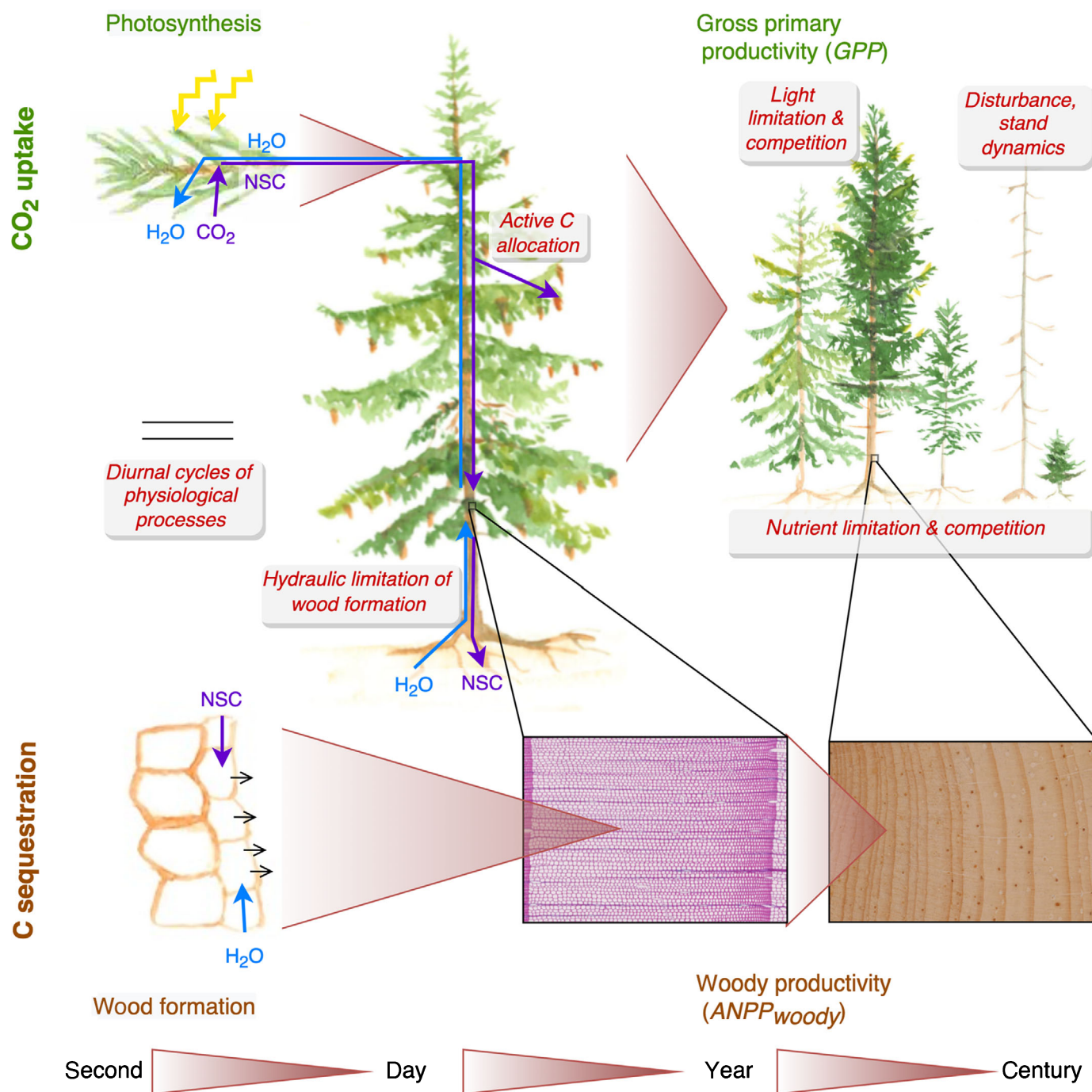


Fig. 2 Schematic summarizing sources of decoupling between CO₂ uptake and carbon (C) sequestration across various time scales. Across scales, various processes (text boxes) decouple C sequestration (wood formation or woody productivity, $\text{ANPP}_{\text{woody}}$, on the ecosystems scale) from CO₂ uptake (photosynthesis or gross primary productivity, GPP, on the ecosystems scale). Shaded wedges indicate integration across time and space. Tree ring images courtesy of Elisabet Martínez-Sancho (close-up of annual ring) and Steven A. Kannenberg (annual rings). Watercolour paintings by Kristina J. Anderson-Teixeira.

is quite responsive to drought or temperature stress during the peak season for woody growth (D'Orangeville *et al.*, 2018; Dow *et al.*, 2022; Kannenberg *et al.*, 2022). This is because cellular enlargement requires adequate turgor pressure and is therefore particularly sensitive to aridity (Delpierre *et al.*, 2016a; Zweifel *et al.*, 2021; Etzold *et al.*, 2022; Kannenberg *et al.*, 2022). In the Martínez-Sancho *et al.* study, a strong start to growth before the drought and strong postdrought compensatory response resulted in normal annual woody productivity. This was made possible by the relatively short duration of the drought; whereas short severe droughts can significantly impact annual growth, growth tends to be more sensitive to longer droughts (D'Orangeville *et al.*, 2018). The findings of Martínez-Sancho *et al.* point to the importance of the timing and length of drought in shaping C sequestration and highlight the need for improved understanding of the seasonal dynamics of CO₂ uptake and woody growth, including their decoupling.

The Martínez-Sancho *et al.* study adds to growing evidence that CO₂ uptake and woody production are decoupled across a range of time scales (Fig. 2). On time scales of seconds to hours, photosynthesis and stem growth are completely decoupled, with photosynthesis occurring during the day and most stem radial expansion occurring at night when stem hydration is maximal (Zweifel *et al.*, 2021). On time scales of days to months, stem growth is influenced by photosynthate availability, but is strongly constrained by temperature and soil moisture (Delpierre *et al.*, 2016a; Etzold *et al.*, 2022), being more sensitive to drought than gross primary productivity (GPP; Kannenberg *et al.*, 2022). On an annual time scale, woody aboveground net primary productivity (ANPP_{woody}) and GPP can be completely uncorrelated (e.g. Delpierre *et al.*, 2016a), implying significant annual variability in C allocation to woody growth vs other sinks (e.g. nonwoody tissues, reproduction, respiration, root exudation, nonstructural carbohydrate pools). In a cross-biome synthesis of available data, tree-ring widths were on average only weakly correlated with GPP ($r \leq 0.38$, Cabon *et al.*, 2022). An example of such decoupling of GPP and annual ANPP_{woody} occurs in temperate deciduous forests, where increased GPP in years with warm springs does not translate into increased stem growth (Dow *et al.*, 2022). Therefore, the preponderance of evidence demonstrates that forest CO₂ uptake and sequestration are decoupled on time scales ranging from seconds to years.

An important open question is the extent to which ANPP_{woody} and GPP are coupled on decadal to centennial time scales, and by extension, how global change drivers that alter GPP will affect ANPP_{woody}. Across broad climatic gradients where trees are largely adapted and acclimated to differences in climate, GPP and ANPP_{woody} vary roughly in proportion to one another (Banbury Morgan *et al.*, 2021). However, these processes may respond differently to global change drivers. While sustained decreases in GPP will inevitably decrease ANPP_{woody}, it remains unclear whether sustained *increases* in GPP will result in the corresponding increases in ANPP_{woody}. When GPP increased in response to 4 yr of experimental CO₂ fertilisation of a mature eucalypt forest, ANPP_{woody} remained unchanged, with the majority of extra C being allocated belowground and rapidly respired back to the atmosphere (Jiang *et al.*, 2020). Additional studies of C allocation

under altered environmental conditions are needed to understand the long-term coupling of GPP and ANPP_{woody}, and by extension how climate change will impact forest C sequestration.


The decoupling of ANPP_{woody} from GPP has important implications for our understanding of forest C sequestration under a changing climate. This is particularly true because decoupling is likely to increase in the future as it is driven, in part, by temperature and water stress. Most global C cycle models represent C allocation to ANPP_{woody} as a constant fraction of GPP (Friend *et al.*, 2019), and thereby effectively assume that long-term C sequestration in woody growth – the main variable of interest for climate change projections – parallels GPP. However, as reviewed above, this assumption is not accurate, with the implication that models may over- or underpredict forest sensitivity to global change drivers. For instance, models would be likely to overestimate the sensitivity of ANPP_{woody} to relatively short droughts (e.g. Martínez-Sancho *et al.*, 2022) but underestimate its sensitivity to longer droughts (Kannenberg *et al.*, 2022), while overestimating ANPP_{woody} of temperate deciduous forests under warming spring temperatures (Dow *et al.*, 2022). To reduce uncertainty regarding the future impact of global change on forest C sequestration, we need to develop comprehensive understanding regarding: (1) when, where and why decoupling occurs; (2) the spatial and temporal scales at which it operates; and (3) the implications for how we understand and model the forest C cycle. Given the complexity of tree physiology and forest C cycling, answering these open questions necessitates cross-scale and cross-methodology approaches, spanning from wood formation (Martínez-Sancho *et al.*, 2022) to dendroecology, eddy covariance and modelling.

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References

- Banbury Morgan R, Herrmann V, Kunert N, Bond-Lamberty B, Muller-Landau HC, Anderson-Teixeira KJ. 2021. Global patterns of forest autotrophic carbon fluxes. *Global Change Biology* 27: 2840–2855.
- Cabon A, Kannenberg SA, Arain A, Babst F, Baldocchi D, Belmecheri S, Delpierre N, Guerrieri R, Maxwell JT, McKenzie S *et al.* 2022. Cross-biome synthesis of source versus sink limits to tree growth. *Science* 376: 758–761.
- Cuny HE, Rathgeber CBK, Frank D, Fonti P, Mäkinen H, Prislan P, Rossi S, del Castillo EM, Campelo F, Vavřík H *et al.* 2015. Woody biomass production lags stem-girth increase by over one month in coniferous forests. *Nature Plants* 1: 15160.
- D'Orangeville L, Maxwell J, Kneeshaw D, Pederson N, Duchesne L, Logan T, Houle D, Arseneault D, Beier CM, Bishop DA *et al.* 2018. Drought timing and local climate determine the sensitivity of eastern temperate forests to drought. *Global Change Biology* 24: 2339–2351.
- Delpierre N, Berveiller D, Granda E, Dufrêne E. 2016a. Wood phenology, not carbon input, controls the interannual variability of wood growth in a temperate oak forest. *New Phytologist* 210: 459–470.
- Delpierre N, Vitasse Y, Chuine I, Guillemot J, Bazot S, Rutishauser T, Rathgeber CBK. 2016b. Temperate and boreal forest tree phenology: from organ-scale processes to terrestrial ecosystem models. *Annals of Forest Science* 73: 5–25.
- Dow C, Kim A, D'Orangeville L, Gonzalez-Akre E, Helcoski R, Herrmann V, Harley G, Maxwell J, McGregor I, McShea W *et al.* 2022. Warm springs alter timing but not total growth of temperate deciduous trees. *Nature* 608. doi: 10.1038/s41586-022-05092-3.
- Etzold S, Sterck F, Bose AK, Braun S, Buchmann N, Eugster W, Gessler A, Kahmen A, Peters RL, Vitasse Y *et al.* 2022. Number of growth days and not length of the growth period determines radial stem growth of temperate trees. *Ecology Letters* 25: 427–439.
- Fatichi S, Leuzinger S, Körner C. 2014. Moving beyond photosynthesis: from carbon source to sink-driven vegetation modeling. *New Phytologist* 201: 1086–1095.
- Friend AD, Eckes-Shephard AH, Fonti P, Rademacher TT, Rathgeber CBK, Richardson AD, Turton RH. 2019. On the need to consider wood formation processes in global vegetation models and a suggested approach. *Annals of Forest Science* 76: 49.
- Jiang M, Medlyn BE, Drake JE, Duursma RA, Anderson IC, Barton CVM, Boer MM, Carrillo Y, Castañeda-Gómez L, Collins L *et al.* 2020. The fate of carbon in a mature forest under carbon dioxide enrichment. *Nature* 580: 227–231.
- Kannenberg SA, Cabon A, Babst F, Belmecheri S, Delpierre N, Guerrieri R, Maxwell JT, Meinzer FC, Moore DJP, Pappas C *et al.* 2022. Drought-induced decoupling between carbon uptake and tree growth impacts forest carbon turnover time. *Agricultural and Forest Meteorology* 322: 108996.
- Körner C. 2015. Paradigm shift in plant growth control. *Current Opinion in Plant Biology* 25: 107–114.
- Martínez-Sancho E, Treydte K, Lehmann MM, Rigling A, Fonti P. 2022. Drought impacts on tree carbon sequestration and water use – evidence from intra-annual tree-ring characteristics. *New Phytologist* 236: 58–70.
- Zweifel R, Sterck F, Braun S, Buchmann N, Eugster W, Gessler A, Häni M, Peters RL, Walthert L, Wilhelm M *et al.* 2021. Why trees grow at night. *New Phytologist* 231: 2174–2185.

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