



Tree carbon dynamics: what the age and availability of nonstructural carbohydrates can tell us about forest ecosystem resilience in a changing world[†]

Kyra A. Prats^{1,2}  and Morgan E. Furze^{1,2,3,*} 

¹Department of Botany and Plant Pathology, Purdue University, 915 Mitch Daniels Blvd, West Lafayette, IN 47907, USA

²Center for Plant Biology, Purdue University, West Lafayette, IN 47907, USA

³Department of Forestry and Natural Resources, Purdue University, 715 Mitch Daniels Blvd, West Lafayette, IN 47907, USA

*Corresponding author (mfurze@purdue.edu)

[†]This scientific commentary refers to 'Moisture stress limits radial mixing of non-structural carbohydrates in sapwood of trembling aspen' by Peltier et al. (<https://doi.org/10.1093/treephys/tpad083>).

Handling Editor: Sanna Sevanto

Trees are stationary, long-lived organisms that face fluctuations in environmental conditions over the span of their lifetime. In addition to experiencing favorable conditions, trees must endure stressful periods associated with both predictable (e.g., seasonality) and more unpredictable (e.g., drought and herbivory) events that require shifts in the allocation and use of resources to survive (Wiley and Helliker 2012, Wiley et al. 2017). Carbon (C) is the chemical backbone of many of these resources—ranging from carbohydrates to terpenes—that are central to plant function (Hartmann and Trumbore, 2016); therefore, how trees allocate and store C plays an important role in their response to changing environments. As trees navigate combined stresses along with the influence of climate change during the remainder of the 21st century, understanding C dynamics is critical for predicting tree resilience and the broader consequences for forest ecosystem function (Niinemets, 2010, Brüggemann et al. 2011, Anderegg et al. 2022).

In particular, for more than a century nonstructural carbohydrates (NSCs) have been the focus of study (Hartig, 1878, Fabricius, 1905) to understand their storage, allocation and use across diverse species and habitats. When trees take in carbon dioxide (CO₂) during photosynthesis, they produce NSCs (i.e., primarily sugars and starch) which then support processes such as growth, respiration, osmoregulation and defense (Dietze et al. 2014, Hartmann and Trumbore, 2016). Notably, while sugars support more immediate functions, starch can be stored for later use, with reserves buffering the differences between supply (photosynthesis) and demand (e.g., respiration and growth) (Chapin et al. 1990) and providing a potential resiliency mechanism to stress (Sala et al. 2012, O'Brien et al. 2014). Previous work has quantified the seasonal dynamics of NSCs in trees (e.g., Barbaroux et al. 2003, Hoch et al. 2003, Landhausser and Lieffers, 2003, Richardson et al. 2013), whole-tree NSC pools (e.g., Würth et al. 2005, Smith et al. 2017, Furze et al. 2018) and changes in NSC

concentrations and pools in response to environmental stress (e.g., Anderegg, 2012, Adams et al. 2013, Sevanto et al. 2014, Dickman et al. 2015, D'Andrea et al. 2021, Blumstein and Furze, 2022). However, far fewer studies have characterized the age (time since photosynthetic fixation) and availability (remobilization for metabolism) of NSCs, especially under stress, which leaves a pressing area for future study to improve our understanding of tree resilience (Figure 1).

The age of NSCs can be estimated by radiocarbon ($\Delta^{14}\text{C}$) measurements which make use of the ^{14}C bomb spike. Thermonuclear weapons testing in the 1950–60s nearly doubled $^{14}\text{CO}_2$ in the atmosphere and it has since continued to decline following a testing ban (Levin and Kromer, 2004, Levin et al. 2010). This curve has been co-opted by plant biologists to quantify the time since CO₂ was fixed into organic compounds through photosynthesis and thus to estimate the mean age of both structural (e.g., cellulose) and nonstructural (e.g., sugars and starch) C by comparing the ^{14}C signal in plant compounds with the curve (Schoor et al. 2016). We know from previous studies that NSC pools have different ages and turnover times (Richardson et al. 2013, 2015), that mixing in of younger NSCs into older stored reserves can occur in tree stems (Richardson et al. 2015, Trumbore et al. 2015, Hartmann and Trumbore, 2016) and that both new and old NSCs support functions such as growth and respiration, and even decades-old NSCs support these processes under certain conditions (Carbone et al. 2013, Muhr et al. 2013, 2016, 2018). Despite this knowledge, long-standing and prominent questions remain: (i) are older NSC reserves in deeper tissues available to support metabolism and to what extent can they be remobilized in response to stress (Sala et al. 2010, 2012, Hartmann and Trumbore, 2016); and (ii) how does environmental stress alter or constrain storage, turnover and remobilization dynamics of NSCs in trees and what are the implications for forest ecosystem resilience and function (Gessler and Treydte, 2016)?

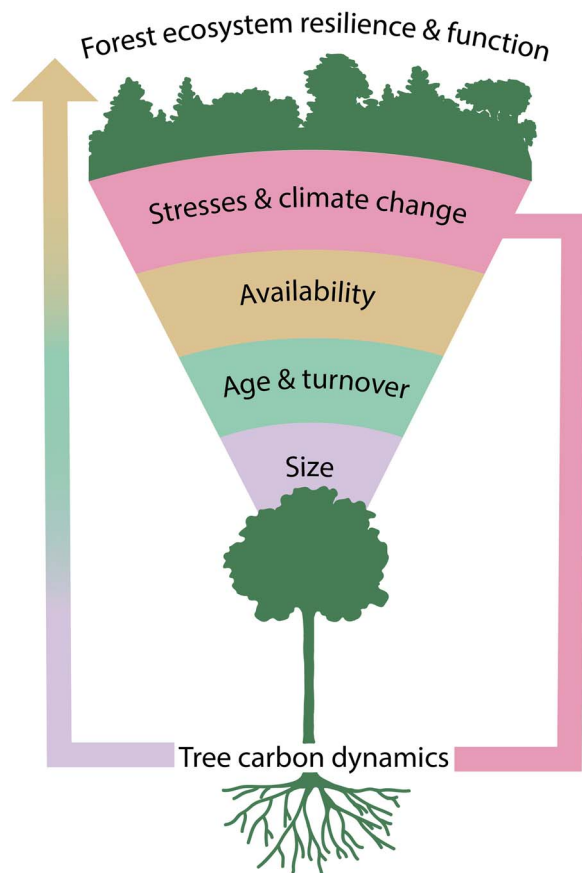


Figure 1. An overview of important NSC characteristics that comprise individual tree C dynamics, which when taken together have the ability to impact forest ecosystem resilience and function—a critical consideration in the face of global change. The NSC characteristics shown are size, age and turnover rates and availability. The pink portion of the arrow at right indicates that stresses and climate change have the potential to impact tree C dynamics. The gradient-colored portion of the arrow at left (with each color matching an NSC characteristic) indicates that individual tree C dynamics then have the potential to impact forest ecosystem resilience and function. While many studies have quantified the size and seasonal dynamics of NSC pools, NSC characteristics, like age, turnover and availability, represent major knowledge gaps in the field of tree ecophysiology. Understanding where different-aged NSCs are stored throughout trees and their metabolic availability are topics ripe for future study. Environmental stresses, particularly those induced by climate change, impact the ways in which NSC characteristics interact within trees and can thus determine the patterns of survival in the case of extreme, mortality-inducing stressors. The NSC dynamics at the scale of an individual tree or species can add up across a landscape to have cascading effects on the resilience of the ecosystem as a whole.

In this issue, the manuscript by Peltier et al. (2023c) makes use of a newly developed incubation-based ^{14}C method (Peltier et al. 2023b), which estimates the age of NSCs based on CO_2 respired by live tree tissues, to tackle such critical knowledge gaps about the age and availability of NSCs. Their work uniquely assesses these dynamics in the context of environmental stress and, more specifically, provides novel insight into how moisture stress influences the dynamics of NSC mixing and use in the sapwood of tree stems. Peltier et al. measured the isotopes (i.e., $\Delta^{14}\text{C}$ and $\delta^{13}\text{C}$ of respired CO_2 produced by NSC consumption) and NSC concentrations in the annual growth rings of *Populus tremuloides* growing at a wet site and a dry site that both experienced regional drought

5 years earlier. This allowed them to explore how moisture stress impacted the storage and radial mixing patterns of NSC pools in the stem sapwood and, therefore, to infer whether old or new NSCs were available to the trees. They hypothesized that NSC pools would be smaller and NSC mixing depth would be shallower with older NSCs being respired in the sapwood of trees at the dry site compared with the wet site.

They found that total NSC pools in the sapwood were 33–40% lower in dry site trees compared with wet site trees, which was consistent with their hypothesis and was suggestive of overall lower annual NSC storage. Additionally, dry site trees tended to store more sugars than starch, an interesting result, given the increased attention that sugars have recently received for their important non-metabolic functions, like osmoregulation, that provide a buffer to aridity (Long and Adams, 2023). In younger outer rings, NSCs were young (<1 year old) at both sites. In older deeper rings, NSC age increased and then leveled off with depth at the dry site, whereas NSC age gradually and then sharply increased with depth at the wet site despite the $\delta^{13}\text{C}$ data potentially suggesting a similar NSC mixing depth for trees at both sites in the sampling year. Their findings for radial trends in NSC age and mixing were more complicated than expected, yet established a helpful conceptual model to consider the interplay between NSC mixing depth, NSC consumption and moisture variability between years, which will be essential to test across species and environmental stresses in future studies. In brief, their framework posits that while wet site conditions enable deeper mixing that is consistent between years, chronic aridity limits the amount and depth of NSC mixing, yielding shallower mixing except in unusually favorable wet years when surplus NSCs may mix into deeper sapwood. Overall, they provide evidence that aridity may constrain NSC mixing into deep sapwood and increase the consumption of older NSCs.

Peltier et al.'s study is timely, given widespread tree mortality events across the globe (Allen et al. 2010, Hammond et al. 2022) and projected increases in stresses that could threaten forest ecosystem function, including C storage (Wang et al. 2021, Anderegg et al. 2022). Understanding tree resilience—and ultimately which forests will survive and persist—is crucial, and tree C dynamics, including the age and availability of NSCs, can help inform predictions. For example, understanding the function and availability of even older and deeper NSCs in trees as well as a tree's reliance on different-aged NSC pools during 'business as usual' and stressful conditions may impact whether a tree is more or less resilient (Hartmann et al. 2020, Peltier et al. 2023c). Further, the duration of stress can differentially alter the size and age of NSC pools, with potential repercussions for a tree's response to future stress (Peltier et al. 2023a). Findings from Peltier et al. will hopefully inspire much-needed research on how the mixing, consumption and availability of NSCs differ between species, biomes and environmental stresses, alone or in combination. For example, their framework of exploring a single tree species under variable moisture stress can be adapted to compare a diversity of forest trees, including angiosperms versus gymnosperms, tropical versus temperate versus boreal trees and those with contrasting wood anatomies and leaf habits; moreover, it can be expanded to study these comparisons under the influence of different abiotic and biotic stresses with both natural conditions and experimental manipulations. In particular, exploring NSC dynamics in foundation species that have the ability to govern ecosystem functioning within their

respective habitats (Ellison et al. 2005) would help address the implications that tree C dynamics have for forest ecosystem resilience.

Furthermore, methods to quantify the NSC characteristics (e.g., NSC pool size, age, turnover and availability) have the potential to improve predictive models (Dietze et al. 2014, Fang et al. 2020) and estimates of tree resilience in the face of climate change. Peltier et al.'s incubation-based ^{14}C method improves upon an earlier extraction-based method (Czimczik et al. 2014) in terms of cost and by only capturing nonstructural C that is metabolically available. These improvements will hopefully not only increase access to ^{14}C research for plant biologists through this method, but also its application has the potential to transform our ability to resolve metabolically available NSC dynamics in trees and consequently further the field in understanding under what stress conditions and to what extent different-aged NSC pools are available to support metabolism and tree survival.

Conflict of interest

None declared.

Funding

None declared.

Authors' contributions

K.A.P. and M.E.F. wrote the commentary. M.E.F. designed the figure with feedback from K.A.P.

Data availability

No new data were created or analyzed, and data sharing is not applicable to this commentary.

References

- Adams HD, Germino MJ, Breshears DD, Barron-Gafford GA, Guardiola-Claramonte M, Zou CB, Huxman TE (2013) Nonstructural leaf carbohydrate dynamics of *Pinus edulis* during drought-induced tree mortality reveal role for carbon metabolism in mortality mechanism. *New Phytol* 197:1142–1151.
- Allen CD, Macalady AK, Chenchouni H et al. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For Ecol Manage* 259:660–684.
- Anderegg WRL (2012) Complex aspen forest carbon and root dynamics during drought: a letter. *Clim Change* 111:983–991.
- Anderegg WRL, Chegwidden OS, Badgley G, Trugman AT, Cullenward D, Abatzoglou JT, Hicke JA, Freeman J, Hamman JJ (2022) Future climate risks from stress, insects and fire across US forests. *Ecol Lett* 25:1510–1520.
- Barbaroux C, Breda N, Dufrene E (2003) Distribution of above-ground and below-ground carbohydrate reserves in adult trees of two contrasting broad-leaved species (*Quercus petraea* and *Fagus sylvatica*). *New Phytol* 157:605–615.
- Blumstein MJ, Furze ME (2022) Interannual dynamics of stemwood nonstructural carbohydrates in temperate forest trees surrounding drought. *J For Res* 34:77–86.
- Brüggemann N, Gessler A, Kayler Z et al. (2011) Carbon allocation and carbon isotope fluxes in the plant-soil-atmosphere continuum: a review. *Biogeosciences* 8:3457–3489.
- Carbone MS, Czimczik CI, Keenan TF, Murakami PF, Pederson N, Schaberg PG, Xu X, Richardson AD (2013) Age, allocation and availability of nonstructural carbon in mature red maple trees. *New Phytol* 200:1145–1155.
- Chapin FS, Schulze ED, Mooney HA (1990) The ecology and economics of storage in plants. *Annu Rev Ecol Syst* 21:423–447.
- Czimczik CI, Trumbore SE, Xu XM, Carbone MS, Richardson AD (2014) Extraction of nonstructural carbon and cellulose from wood for radiocarbon analysis. *Bio-protoc* 4:e1169. <https://doi.org/10.21769/BioProtoc.1169>.
- D'Andrea E, Scartazza A, Battistelli A, Collalti A, Proietti S, Rezaie N, Matteucci G, Moscatello S (2021) Unravelling resilience mechanisms in forests: role of non-structural carbohydrates in responding to extreme weather events. *Tree Physiol* 41:1808–1818.
- Dickman LT, McDowell NG, Sevanto S, Pangle RE, Pockman WT (2015) Carbohydrate dynamics and mortality in a piñon-juniper woodland under three future precipitation scenarios. *Plant Cell Environ* 38:729–739.
- Dietze MC, Sala A, Carbone MS, Czimczik CI, Mantooth JA, Richardson AD, Vargas R (2014) Nonstructural carbon in woody plants. *Annu Rev Plant Biol* 65:667–687.
- Ellison AM, Bank MS, Clinton BD et al. (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front Ecol Environ* 3:479–486.
- Fabrizius L (1905) Untersuchungen über den Stärke- und Fettgehalt der Fichte auf der oberbayerischen Hochebene. *Naturwissenschaftliche Zeitung für Land- und Forstwirtschaft* 3:137.
- Fang J, Lutz JA, Shugart HH, Yan X (2020) A physiological model for predicting dynamics of tree stem-wood non-structural carbohydrates. *J Ecol* 108:702–718.
- Furze ME, Huggett BA, Aubrecht DM, Stolz CD, Carbone MS, Richardson AD (2018) Whole-tree nonstructural carbohydrate storage and seasonal dynamics in five temperate species. *New Phytol* 221:1466–1477.
- Gessler A, Treyde K (2016) The fate and age of carbon - insights into the storage and remobilization dynamics in trees. *New Phytol* 209:1338–1340.
- Hammond WM, Williams AP, Abatzoglou JT et al. (2022) Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests. *Nat Commun* 13:1761. <https://doi.org/10.1038/s41467-022-29289-2>.
- Hartig T (1878) Anatomie und Physiologie der Holzpflanzen Dargestellt in der Entstehungsweise und im Entwicklungsverlaufe der Einzelzelle, der Zellsysteme, der Pflanzenglieder und der Gesamtpflanze. Springer, Berlin, Germany.
- Hartmann H, Trumbore S (2016) Understanding the roles of nonstructural carbohydrates in forest trees - from what we can measure to what we want to know. *New Phytol* 211:386–403.
- Hartmann H, Bahn M, Carbone M, Richardson A (2020) Plant carbon allocation in a changing world - challenges and progress: introduction to a virtual issue on carbon allocation. *New Phytol* 227:981–988.
- Hoch G, Richter A, Korner C (2003) Non-structural carbon compounds in temperate forest trees. *Plant Cell Environ* 26:1067–1081.
- Landhauser SM, Lieffers VJ (2003) Seasonal changes in carbohydrate reserves in mature northern *Populus tremuloides* clones. *Trees* 17:471–476.
- Levin I, Kromer B (2004) The tropospheric $^{14}\text{CO}_2$ level in mid-latitudes of the northern hemisphere (1959–2003). *Radiocarbon* 46:1261–1272.
- Levin I, Naegler T, Kromer B et al. (2010) Observations and modelling of the global distribution and long-term trend of atmospheric $^{14}\text{CO}_2$. *Tellus B Chem Phys Meteorol* 62:26–46.
- Long RW, Adams HD (2023) The osmotic balancing act: when sugars matter for more than metabolism in woody plants. *Glob Chang Biol* 29:1684–1687.
- Muhr J, Angert A, Negrón-Juárez RI, Muñoz WA, Kraemer G, Chambers JQ, Trumbore SE (2013) Carbon dioxide emitted from live stems of tropical trees is several years old. *Tree Physiol* 33:743–752.
- Muhr J, Messier C, Delagrangé S, Trumbore S, Xu X, Hartmann H (2016) How fresh is maple syrup? Sugar maple trees mobilize carbon

- stored several years previously during early springtime sap-ascent. *New Phytol* 209:1410–1416.
- Muhr J, Trumbore S, Higuchi N, Kunert N (2018) Living on borrowed time – Amazonian trees use decade-old storage carbon to survive for months after complete stem girdling. *New Phytol* 220: 111–120.
- Niinemets Ü (2010) Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. *For Ecol Manage* 260:1623–1639.
- O'Brien MJ, Leuzinger S, Philipson CD, Tay J, Hector A (2014) Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. *Nat Clim Chang* 4:710–714.
- Peltier DMP, Carbone MS, McIntire CD et al. (2023a) Carbon starvation following a decade of experimental drought consumes old reserves in *Pinus edulis*. *New Phytol* 240:92–104.
- Peltier DMP, Lemoine J, Ebert C, Xu X, Ogle K, Richardson AD, Carbone MS (2023b) An incubation method to determine the age of available nonstructural carbon in woody plant tissues. *Tree Physiol* 1–12.
- Peltier DMP, Nguyen P, Ebert C, Koch G, Schuur EAG, Ogle K (2023c) Moisture stress limits radial mixing of non-structural carbohydrates in sapwood of trembling aspen. *Tree Physiol* <https://ejournal3.undp.ac.id/index.php/jamt/article/view/5101>. <https://doi.org/10.1093/treephys/tpad083>.
- Richardson AD, Carbone MS, Keenan TF, Czimczik CI, Hollinger DY, Murakami P, Schaberg PG, Xu X (2013) Seasonal dynamics and age of stemwood nonstructural carbohydrates in temperate forest trees. *New Phytol* 197:850–861.
- Richardson AD, Carbone MS, Huggett BA, Furze ME, Czimczik CI, Walker JC, Xu X, Schaberg PG, Murakami P (2015) Distribution and mixing of old and new nonstructural carbon in two temperate trees. *New Phytol* 206:590–597.
- Sala A, Piper F, Hoch G (2010) Physiological mechanisms of drought-induced tree mortality are far from being resolved. *New Phytol* 186: 274–281.
- Sala A, Woodruff DR, Meinzer FC (2012) Carbon dynamics in trees: Feast or famine? *Tree Physiol* 32:764–775.
- Schuur EAG, Druffel ERM, Trumbore S (2016) Radiocarbon and climate: mechanisms, applications and laboratory techniques. Springer, Switzerland.
- Sevanto S, McDowell NG, Dickman LT, Pangle R, Pockman WT (2014) How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. *Plant Cell Environ* 37:153–161.
- Smith MG, Miller RE, Arndt SK, Kasel S, Bennett LT (2017) Whole-tree distribution and temporal variation of non-structural carbohydrates in broadleaf evergreen trees. *Tree Physiol* 38:570–581.
- Trumbore S, Czimczik CI, Sierra CA, Muhr J, Xu X (2015) Non-structural carbon dynamics and allocation relate to growth rate and leaf habit in California oaks. *Tree Physiol* 35:1206–1222.
- Wang JA, Baccini A, Farina M, Randerson JT, Friedl MA (2021) Disturbance suppresses the aboveground carbon sink in north American boreal forests. *Nat Clim Chang* 11:435–441.
- Wiley E, Helliker B (2012) A re-evaluation of carbon storage in trees lends greater support for carbon limitation to growth. *New Phytol* 195:285–289.
- Wiley E, Casper BB, Helliker BR (2017) Recovery following defoliation involves shifts in allocation that favour storage and reproduction over radial growth in black oak. *J Ecol* 105:412–424.
- Würth MKR, Peláez-Riedl S, Wright SJ, Körner C (2005) Non-structural carbohydrate pools in a tropical forest. *Oecologia* 143: 11–24.