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Mapping wood formation across scales: Models, methods and experiments

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Perspective

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Abstract

The formation of xylem and phloem by the vascular cambium is a cellular process that is influenced by biotic and abiotic factors at sub-seasonal timescales. However, the significance of cambial activity extends across space (up to ecosystems) and time (up to centuries). This relates to the functional importance of xylem and phloem and the extremely long persistence of woody tissues, which are also a major carbon sink. Hence, studying this phenomenon involves a wide variety of approaches and methods that fundamentally vary in their temporal and spatial scales. From global vegetation dynamics to maple syrup production, the articles in the special collection 'Advances in Xylem and Phloem Formation Research' well reflect this diversity. Collectively, they reveal the complexity of underlying mechanisms and the potential for implementation of simpler schemes into global models.

Given the global abundance of woody biomass, even minor variations in its properties have widespread consequences on forest ecosystem functioning and the global carbon cycle. In a proof-of-concept study, Voss et al. (2026) illustrate the impact of accounting for environmentally driven, locally emergent wood density, which can influence the individual's carbon allocation, growth rates and height, and thus influence the entire forest dynamics and structures. This has implications for improving dynamic global vegetation models by accounting for the environmental dependence of wood density. In some cases, treating wood density as a dynamic rather than a static variable significantly alters predictions regarding forest stand structure and carbon storage. This highlights that there is large potential when considering these small-scale processes and their resulting wood anatomy in larger-scale ecosystem models.

However, studying the underlying processes can prove challenging. The cambium and the developing xylem and phloem are located in a narrow zone under the bark, making direct *in vivo* observation difficult, particularly when compared to apical meristems. Two articles in this collection represent advances in addressing these methodological challenges. The article by Adikurnia and Rathgeber (2025) provides a detailed analysis of the limitations of using automatic tape dendrometers to study wood phenology. Although these instruments are easy to use and non-destructive, their output integrates both xylem and phloem growth, as well as fluctuations in water content. This highly complex signal can be combined with a logistic model to effectively describe wood formation dynamics, especially during the peak growing season. However, it is more difficult to deduce the onset and cessation dates of xylem formation from this data, when growth is very slow and obscured by other processes. In this context, micro-coring, despite being more labour-intensive, offers more precise and reliable estimates of growth dynamics.

In another methodological article, Marchand et al. (2026) propose recommendations for the analysis of xylogenesis in angiosperms. While extensive global coordination efforts have led to common protocols for gymnosperms, similar harmonization work remains to be finalized for angiosperms. This article significantly contributes to this effort, providing detailed and well-illustrated guidelines. Ecological modelling requires large databases including angiosperms, which constitute the vast majority of tree species. This calls for coordinating and standardizing studies.

To gain a detailed understanding of the physiology and ecology of xylogenesis, observation alone—even in highly contrasting situations—may not be sufficient. Direct and controlled manipulations of wood formation often allow for a deeper exploration of the mechanisms involved (Buttò et al., 2025). Three articles in this collection take this approach.

In their study on a drought-resistant eucalyptus species, *E. cladocalyx*, Gama et al. (2025) imposed cyclic droughts. The treated individuals did not respond to all drought cycles, indicating a form of acclimation. The authors trained a random forest classifier and applied it to tissue samples to categorize cells into fibres or vessels. Cell production rates were estimated from cell

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counts, cell diameters and growth rates. One of the most striking findings is the cambium's resilience to water stress, in terms of cell production rates. The response to drought is primarily manifested by a reduction in vessel area. Nevertheless, the analysis of anatomical properties is complex in this experiment, due to differences in intensity between drought cycles and genetic diversity among individuals.

A more drastic manipulation of tree physiology was carried out by Camarero et al. (2026) on Spanish junipers growing in a semi-arid environment. A branch from each individual was girdled, which blocks the transport of assimilates between the leaves and the sinks below the girdle. The authors observed increased starch and NSC content in the leaves of the girdled branches, but no difference in the sapwood. Part of the leaves' starch reserves may have been hydrolysed and osmolytes may have been stored in the phloem and bark. This would explain why the girdled branches exhibited greater fluctuations in diameter. The near absence of growth in the year of girdling nevertheless made it impossible to observe the effects on wood formation. This article, like that of Gama et al. (2025), illustrates both the potential and the difficulties of direct manipulations of secondary growth.

The last article to mention is also the sweetest and the most focused on commercial applications of tree physiology. The pressure building up in wood vessels moving sap is a fascinating biophysical phenomenon, long exploited by Canada's Indigenous peoples to harvest maple sugar. Maple syrup production is now of great economic and cultural importance to Quebec. However, what are the impacts of tapping on wood formation? The article by McNulty et al. (2025) provides answers by exploring growth performance and associated wood anatomical traits after tapping and sap collection. While tapping can reduce diameter growth at the northern limit of the species, the effect on the hydraulic function of the formed wood is marginal. In addition to providing practical guidance for the sustainable management of sugar maples, these findings offer insights into the trade-off between mechanical strength and hydraulic efficiency under stress.

Despite the wide range of topics covered by this special collection, one notable gap remains: the relative lack of studies explicitly addressing phloem dynamics. This tissue remains a neglected area of research on secondary growth, despite its importance in trees' physiological responses to external stimuli (Gričar, 2024). The coordination between xylem and phloem formation, including under stress, is undoubtedly a fruitful avenue of research to explore in the near future.

From a methodological perspective, the limited integration of phloem into studies of secondary growth also reflects technical constraints. Phloem tissues are more difficult to sample, preserve and analyse than xylem, and their rapid turnover further complicates temporal analyses. As a result, many large-scale datasets and modelling frameworks rely almost exclusively on xylem-derived variables, potentially overlooking key aspects of tree physiology. Addressing this imbalance will require the development of standardized protocols for phloem observation and quantification, as well as their incorporation into existing monitoring networks and databases.

Finally, data syntheses that move beyond single case studies are key to bridging spatial and temporal scales. In this regard, the development of new databases will enable both to improve the standardization of data collection and reporting and fast track their use in a broader context or to inform models that can, in turn, be used to make inferences on large-scale vegetation functioning and biogeochemical cycles.

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