

## eXtra Botany

Insight

# Phloem: a missing link in understanding tree growth response in a changing environment

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This article comments on:

**Dusart N, Moulia B, Saudreau M, Serre C, Charrier G, Hartmann FP.** 2024. Differential warming at crown scale impacts walnut primary growth onset and secondary growth rate. *Journal of Experimental Botany* **75**, <https://doi.org/10.1093/jxb/erae360>

**Although the activities of various tree organs and tissues are under different environmental and internal constraints, they need to be coordinated to ensure whole-tree functioning. Dusart et al. (2024) conducted a heating experiment on branches of *Juglans regia* saplings during the entire growing season to examine the effect of temperature on primary (bud) and secondary (xylem) growth. They found that primary and secondary meristems responded asynchronously to elevated temperature, which suggests that lack of coordination mechanisms between primary and secondary growth at crown scale could have a potential impact on canopy and tree architecture.**

Growth of woody plants, which leads to an increase in their size and mass, occurs in specialized tissues, primary and secondary meristems, and involves the production of cells that differentiate into specialized tissues (Turley and Etchells, 2022). Growth is a very dynamic and plastic process that allows trees to adjust their growth forms to specific environmental conditions, which is reflected in altered tree architecture and morphology at any time throughout their life span (Agusti and Greb, 2013). Modified growth in response to environmental changes and external stimuli is thus of high adaptive significance for trees, but requires the coordination of complex developmental events to produce appropriate tissues and physiological outcomes (Spicer and Groover, 2010; Steppe et al., 2015; Singh et al., 2022).

In temperate and cold climates, primary and secondary meristems undergo seasonal cycles of activity and dormancy, which is an important adaptive mechanism for the survival of perennial plants to endure harsh environmental conditions during winter (Zhao et al., 2020). In addition to external environmental factors, various internal factors, such as hormones, sugars, and other metabolites, are involved in tree growth (Singh et al., 2022).

## Global warming could have a significant impact on tree architecture

Using an original warming experiment conducted on young walnut trees in a greenhouse, Dusart et al. (2024) shed further light on the effects of differential warming at the crown level on primary and secondary growth. A novel and ambitious approach combining phenological (bud phenology), cytological (intra-annual primary and secondary growth), and physiological analyses (water content determination and carbohydrate analysis) as well as data processing (radial growth modelling) brings new insights into fundamental research questions dealing with the impacts of temperature variations on tree growth.

They found that the resumption of primary growth of buds occurred earlier in response to elevated temperature, while the treatment had no effect on the primary growth rate (Dusart et al., 2024). In contrast, the resumption of secondary growth of xylem was not altered by temperature; however, the growth rate was increased. The cessation of primary and secondary growth was not affected by temperature. As a result, asymmetry was observed at the canopy level, with the warmed branches being longer and thicker than the control branches. The discrepancy in growth resumption and activity between primary and secondary meristems detected in the study by Dusart et al. (2024) provides compelling evidence that future rising temperature

associated with climate change will affect canopy and tree architecture. Temperature is not the only factor responsible for tree architecture, and further experiments on phenological, physiological, and structural responses of trees on other species of different ages and at the tree level are needed to better understand the relationships between different processes in different organs/tissues. Nevertheless, the findings of [Dusart et al. \(2024\)](#) provide an important insight into the meristems' (in) coordination in young walnut trees in relation to temperature variation and point to the lack of compensatory mechanisms at the crown level.

### Response of xylem and phloem to applied heating and cooling treatments may differ

The effect of specific environmental or other factors on the mechanisms of primary and secondary growth can be studied on trees growing in their natural environment or under experimentally controlled conditions ([Begum et al., 2013](#)). The application of elevated or decreased temperature has revealed differences in the response of cambium and cell differentiation patterns among different species of evergreen and deciduous habit or wood porosity ([Begum et al., 2013](#)) or tree age (dead bark thickness). The response also depends on the timing and duration of these treatments. The few studies that have taken phloem into account have shown a different response of phloem and xylem to applied elevated temperature ([Box 1; Fig. 1](#)) ([Gričar et al., 2006](#)). In addition to the tight connection of xylem and phloem vascular tissues through rays, the role of sieve tubes in the non-collapsed phloem in the long-distance transport of carbohydrates from the source tissues (leaves) to the sink tissues (meristems) is well known, so information on phloem formation and structure would contribute to a better understanding of the coordination mechanisms between primary and secondary growth ([Dusart et al., 2024](#)). In addition,

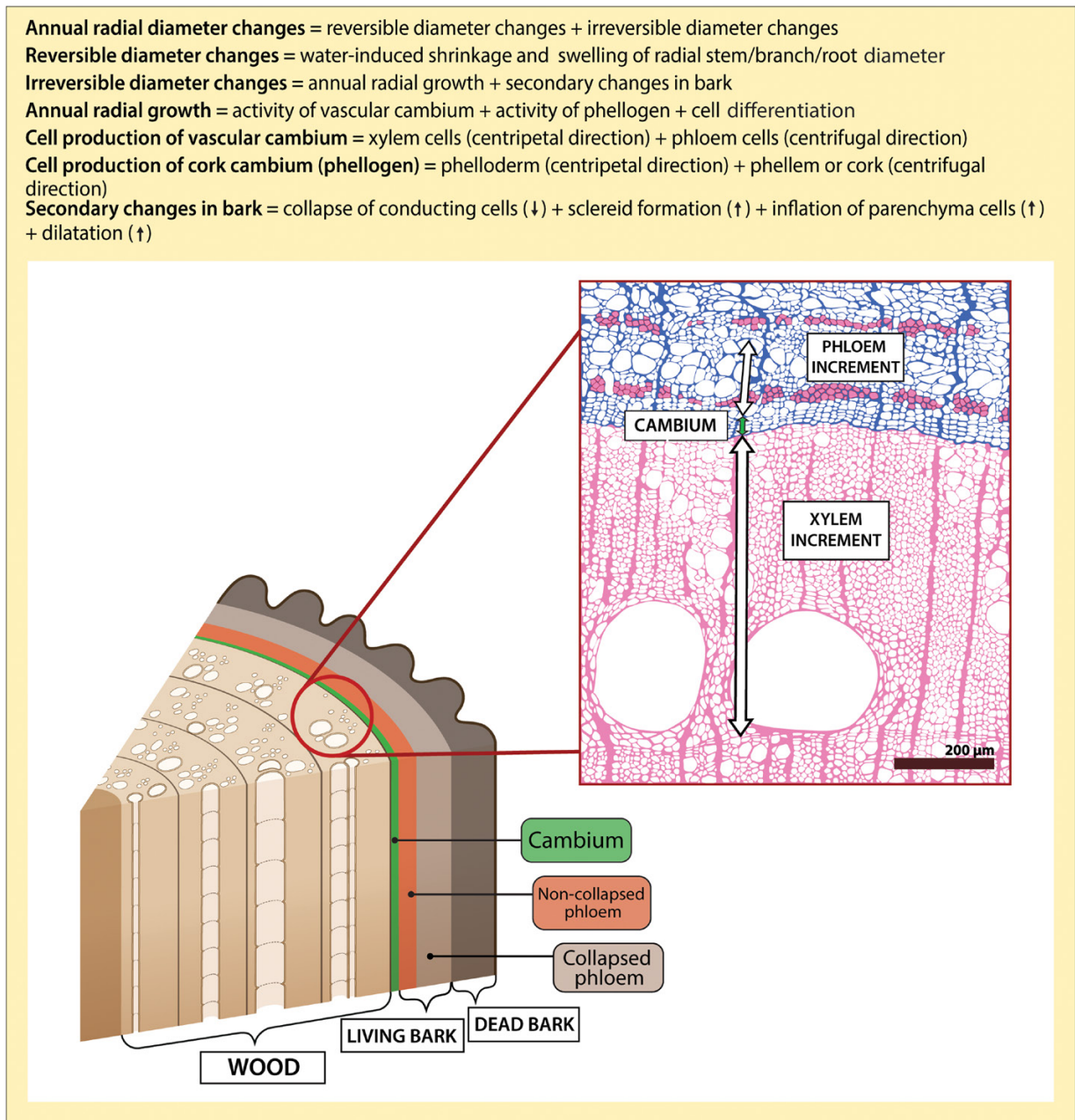
the response of xylem and phloem to external stimuli is not necessarily coordinated, which has been demonstrated in the case of heating and cooling experiments in *Picea abies* ([Gričar et al., 2006](#)) or post-fire response in the stems of *Quercus pubescens* ([Gričar et al., 2020](#)). In both cases, the phloem was the first to react to the increased temperature. The faster response of phloem can be explained by its more external position in a tree compared with xylem, which probably results in higher exposure to external stimuli and may lead to (i) higher tissue damage at very high temperatures (fire) or (ii) increased meristematic activity at higher temperatures that are favourable for tree growth.

### Link between primary and secondary growth also depends on wood porosity

Since the phenology of each organ/tissue is regulated by a combination of different environmental and internal factors ([Delpierre et al., 2016](#)), it is unclear how the interplay of these co-varying factors will affect primary and secondary growth and the ability of different tree species to adjust to environmental changes. In line with the findings of [Dusart et al. \(2024\)](#), other studies in different tree species have also shown that the timings of leaf and cambium phenology do not occur simultaneously, reflecting different environmental and internal constraints ([Gričar et al., 2020](#); [Yu et al., 2023](#)). In the case of boreal conifers, for example, primary growth and secondary growth are synchronous over the growing season after budburst, indicating that there may be an optimal mechanism simultaneously to allocate photosynthetic products and stored non-structural carbohydrates (NSCs) to the growth of different organs in trees ([Huang et al., 2014](#)). However, wood porosity affects tree phenology and physiology, and may also influence NCS distribution, dynamics, and availability ([Barbaroux et al., 2003](#)). In ring-porous species, which are unable to repair winter embolism, cambium growth resumes

#### Box 1. Radial growth of trees is not a synonym for xylem growth

Radial growth (i.e. secondary growth), which results in an increase in the volume of the conducting system and the formation of mechanical and protective tissues in stems, branches, and roots of woody plants, is often simplistically considered as xylem growth. However, the annual radial growth of trees is much more complex and involves the activity of two lateral meristems: the vascular cambium (in short, cambium) and cork cambium (phellogen) ([Fig. 1](#)). Both meristems are bifacial, producing cells in centripetal and centrifugal directions. Cambium produces secondary xylem (wood) centripetally and secondary phloem (bast) centrifugally ([Turley and Etchells, 2022](#)). Phellogen forms phellogen cells centripetally and phellem cells (cork) centrifugally. Together, they constitute secondary protective tissue (periderm). In trees with thick bark, sequential layers of periderm may anastomose (i.e. sequent periderms are connected and form a network), while their seasonal activity is still quite a mystery. In addition, numerous age-related secondary changes in older bark tissues, such as the collapse of sieve elements, sclereid formation, inflation of parenchyma cells, and dilatation, contribute to the irreversible diameter changes of stem branch or root, but the contribution of each of these processes in the bark to the intra-annual variation in tree girth is not known ([Gričar and Prislan, 2022](#)). However, this information would be particularly relevant when radial growth is monitored with continuous methods, such as dendrometers ([Zweifel et al., 2016](#)), and would improve data accuracy and the interpretation of the results ([Steppe et al., 2015](#)).



**Fig. 1.** Schematic representation of the anatomy of the secondary xylem and phloem in angiosperms. Upward-pointing arrows, which refer to the last definition of secondary changes in bark but are not shown in the figure, indicate an increase in cell/tissue dimensions, and a downward-pointing arrow indicates a decrease in dimensions.

before budbreak (Savage and Chuine, 2021), while in diffuse-porous species, budbreak occurs before or at the onset of stem radial growth. Consequently, in ring-porous species, the formation of initial earlywood vessels relies on NSCs produced in previous years and stored in the parenchyma cells. In diffuse-porous species, initial earlywood vessel development occurs after leaf expansion, so their formation largely depends on recent carbohydrates derived directly from photosynthesis (Barbaroux *et al.*, 2003). These linkages should therefore be further explored, including in

the context of climate change, to advance our understanding of tree physiology and carbon dynamics (Huang *et al.*, 2014).

### Non-structural carbohydrates are stored in xylem and phloem parenchyma

When performing a heating experiment, Dusart *et al.* (2024) measured carbohydrate and water content in different



parts of the branch to explore carbon and water balance during the experiment. They noted a difference in carbon and water remobilization at the end of bud ecodormancy under warming. NSCs are primarily stored in the parenchyma; these cells are therefore commonly used as a proxy to quantify and compare the potential storage reserve capacity in different tree tissues and organs. Although the majority of the studies that have focused on the parenchyma have been focused specifically on xylem (Morris *et al.*, 2016; Zhang *et al.*, 2022), the total xylem and bark axial and ray parenchyma fraction in a tree greatly depends on the species. Angiosperms have typically higher quantities of parenchyma than gymnosperms, whereby axial and ray parenchyma are abundant in the xylem in some tree species (Morris *et al.*, 2016). Gymnosperms generally have a negligible proportion of parenchyma in xylem, so bark parenchyma is crucial for the storage and transport of NSCs, nutrients, and water. To assess fully the involvement of NSCs in primary and secondary growth, the total NSC budget should be taken into account, namely seasonal photosynthate production rates and NSC storage pool sizes for all tree parts.

## Future research needs

Many short-term controlled experiments have been performed on seedlings, while experiments on adult trees are more complicated and are usually restricted to only a part of the tree. Experiments are undoubtedly crucial to understanding the response of radial growth patterns of trees to environmental stimuli better; however, it is not possible simply to extrapolate findings obtained from seedlings in the laboratory to mature trees in natural forests where, for instance, tree competition is a decisive factor driving tree growth and stand dynamics. Tree age affects its sensitivity to environmental conditions, which is generally greater in the juvenile phase than in the adult phase. Moreover, the temporal dynamics of radial growth patterns also largely depend on tree age or tree part, and is reflected in the structure of vascular tissues (Rossi *et al.*, 2009). To predict the response of different (adult) tree species and forests to anticipated environmental changes, their long-term adaptive responses and highly flexible resource allocation patterns should thus be considered (Meier and Leuschner, 2008). Finally, information on bark/phloem traits of different tree species, locations, and tree properties would allow more reliable prediction of intra- and interannual plasticity in cambial phenology and radial growth patterns as part of strategies of tree survival in changing environments.

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## Conflict of interest

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