Opinion

Diel growth dynamics in tree stems: linking anatomy and ecophysiology

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Impacts of climate on stem growth in trees are studied in anatomical, ecophysiological, and ecological disciplines, but an integrative framework to assess those impacts remains lacking. In this opinion article, we argue that three research efforts are required to provide that integration. First, we need to identify the missing links in diel patterns in stem diameter and stem growth and relate those patterns to the underlying mechanisms that control water and carbon balance. Second, we should focus on the understudied mechanisms responsible for seasonal impacts on such diel patterns. Third, information on stem anatomy and ecophysiology should be integrated in the same experiments and mechanistic plant growth models to capture both diel and seasonal scales.

Tree stem growth has huge implications but is poorly understood

Forests cover 30% of Earth's land surface, store 45% of terrestrial carbon, and are responsible for 50% of the terrestrial net primary production [1,2]. Forest productivity has increased globally over the past decades, which has been attributed to the positive effect of increasing CO_2 on tree growth, thus far offsetting negative impacts of warming and drought [3,4]. However, the long-term impacts on trees and forests of increasing CO_2, rising temperatures, and drought remain highly uncertain [5–7]. Another uncertainty is the role of trees in mitigating rising ambient CO_2 [8] and global warming by sequestering carbon in stems [1,2]. We argue that such ecological uncertainties can be only tackled by developing an understanding of the stem growth of individual trees that is based on underlying anatomical and ecophysiological principles, which are currently represented by separate scientific domains.

In this opinion article, we briefly present an overview of the major fluxes and pools of water and carbon inside a stem segment of a tree. We then examine the diel dynamics in radial stem growth and underlying water and carbon mechanisms under wet and dry conditions. We also elucidate the possible processes affecting stem growth across a wet and dry growing season, integrating seasonal trends in stem anatomy and ecophysiology. We distinguish between major known patterns and processes and more speculative ones. All of these discussions are based on observations in the different research disciplines but also result from mechanistic plant models aiming at integration. Based on this, we show the missing pieces that are critical to building an integrative theory to understand the causes and consequences of tree stem growth on diel and seasonal scales. Addressing the key missing pieces of information is very much needed to understand and predict the impacts of a changing climate on annual tree growth patterns and the future production and carbon sequestration potential of forests.

Carbon and water fluxes in stem segments

Water is transported upward in the sapwood, downward in the phloem, and radially between sapwood and phloem and is stored in both sapwood and phloem (Figure 1, fluxes/pools steps 1–4). Carbon is transported downward in the phloem in the form of sugars (Figure 1, step 2) and those sugars are used for maintenance of living cells in sapwood, cambium, and phloem (Figure 1, step 6), for growth in the cambium and developing cells (Figure 1, step 5), or for storage in the form of starch (Figure 1, step 11). Some carbon released as CO_2 by respiring cells in the tree stem diffuses directly into the atmosphere (Figure 1, step 7a,b,c), whereas another substantial portion of this respired CO_2 remains inside the stem (Figure 1, step 8a,b,c) where it dissolves in xylem sap and is transported away from the site of origin (Figure 1, step 7d). Some CO_2 slowly diffuses in the axial direction (Figure 1, step 9). The amount of CO_2 escaping into the atmosphere (measured efflux; Figure 1) is further reduced when respired CO_2 is refixed in sugars through photosynthesis within the stem (Figure 1, step 10). Below we discuss diel patterns in these water and carbon fluxes and their consequences for stem growth (see also Figure 2) and provide an overview of the current state-of-the-art technology and methods used to quantify these fluxes (Figure 1 and Boxes 1 and 2).

Stem dynamics in water fluxes and storage

Large forest trees lose up to 99% of their acquired water through leaf transpiration, whereas less than 1% is

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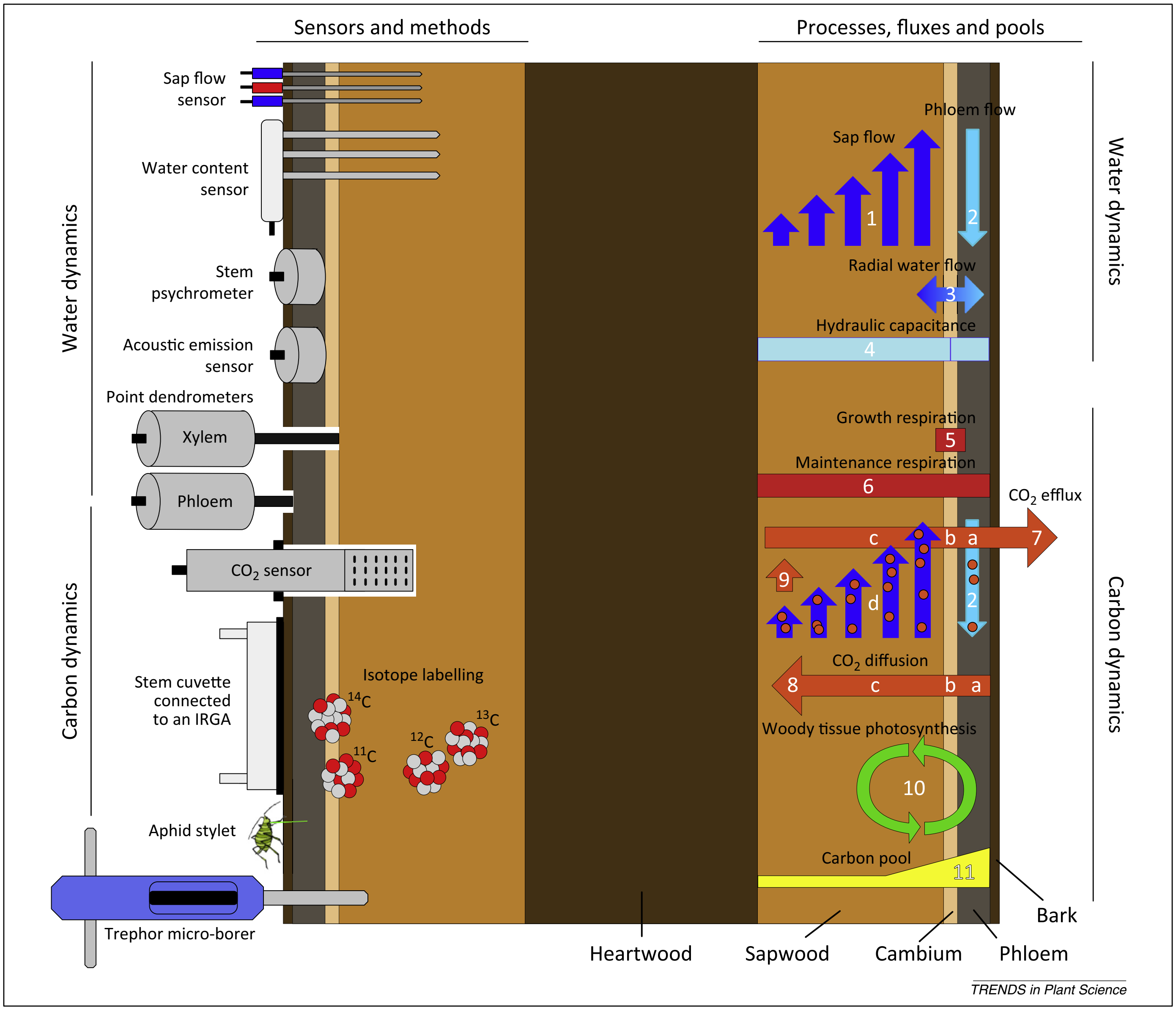

Figure 1. Schematic of important processes, fluxes, and pools of water and carbon inside a stem segment of a tree (right): (1) sap flow in the xylem (or transpiration stream), transporting part of the dissolved CO_2 (7d); (2) phloem sap flow, transporting sugars and dissolved CO_2; (3) radial exchange of internally stored water between living cells in xylem and phloem and the transpiration stream; (4) hydraulic capacitance, defining the capacity of living cells to store water and release it into the transpiration stream; (5) growth respiration; (6) maintenance respiration; (7) diffusion of CO_2 out of the stem from phloem (a), cambium (b), and xylem ray cells (c) or imported in xylem sap (d); (8) CO_2 diffusing into the transpiration stream from phloem (a), cambium (b), or xylem ray cells (c); (9) axial CO_2 diffusion along air-filled spaces in the wood; (10) CO_2 fixation by woody tissue photosynthesis, which can utilize CO_2 from all four sources (a, b, c, d) above; (11) carbon pool, which comprises recently assimilated sugars transported in the phloem (2), locally refixed CO_2 in photosynthetic tissue (10), and local starch reserves. Adapted from [40,41]. Details of the technology and methods used for quantifying the diel dynamics in water, carbon, and stem growth (left) can be found in Box 1 and 2.

retained in biomass [9]. On a sunny summer day, an adult tree may lose and acquire several hundred liters of water. Leaf transpiration typically starts minutes to hours earlier than water flow in stem and roots, because transpiration is also supported by water from internal water storage [10]. The daily amount of water withdrawn from storage contributes 5–22% to the total daily water loss [11–13] and its diel dynamics affect radial stem growth. On cloudy or rainy days, internally stored water may even contribute more to the amount of lost water [14]. The typical diel patterns in water relations at the stem level for a fully exposed canopy tree during a sunny day after a wet period (unstressed conditions with ample soil water reserves) and a dry period are shown in Figure 2. We distinguish between well-established patterns and more speculative patterns in green and red, respectively. For simplicity, we do not deal with cloudy or rainy days, which may provide different patterns.

On a sunny day in unstressed conditions, a strong symmetric, hump-shaped pattern of sap flow in the tree stem is observed (Figure 2B), leading to large day/night differences in water potential and changes in internally stored water in xylem and phloem (Figure 2C). Embolisms in the xylem [15], which can be detected by acoustic emissions (Figure 2B), occur in concert with the decrease in stem water potential and reduce xylem hydraulic conductivity. The embolisms also release water into the transpiration stream and can thus be considered as a source of