



Contents lists available at ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

Identifying differences in carbohydrate dynamics of seedlings and mature trees to improve carbon allocation in models for trees and forests

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ARTICLE INFO

Keywords:

Trees
Non-structural carbohydrates
Storage
Reserves
Source and sink limitation

ABSTRACT

Carbohydrates play a central role in plant functioning because they are building blocks and energy carriers for plant metabolic processes. Because plants are sessile organisms and cannot escape stressful environments they acclimate to unfavourable conditions by strategically allocating carbohydrate resources to overcome stress and promote survival, and build reserves for later use when demand is greater than supply from photosynthesis, like after defoliation. A mechanistic understanding of how plants and, in particular, long-lived organisms like trees allocate and remobilize stored carbohydrates is still very poor. Without such an understanding, however, integration of carbon dynamics from trees to ecosystems and to the globe becomes highly uncertain, especially under ongoing climate change.

Studies of carbohydrate dynamics in trees are often carried out on tree seedlings due to logistical and technical constraints and criticism has been raised whether results can be extrapolated to mature trees. Here we combine a literature review with a critical evaluation of using seedling studies on carbohydrate dynamics to infer mature tree responses that can subsequently be integrated at ecosystem level and beyond. Despite obvious differences between seedlings and mature trees with respect to carbohydrate dynamics, we propose that a combination of approaches, including seedling studies in controlled environments, measurements on mature trees in the field and ecosystem flux measurements, may provide sound estimates of carbohydrate dynamics at larger scales. We show how sensitive predictions of vegetation responses to disturbance are to changes in available reserves and argue that the implementation of more realistic representations of storage dynamics will likely improve simulations of vegetation responses to environmental stress.

1. Carbon allocation in plants: sources, sinks and priorities

Plants are like small factories. Carbohydrates produced during photosynthesis serve as building blocks and energy carriers for the construction of plant biomass. Carbohydrates are partitioned among different sinks and metabolic uses, like growth, life-maintaining functions (respiration, tissue repair/replacement, detoxification etc.), reproduction or storage (Chapin et al., 1990), or can be emitted as volatile organic compounds for communication and defence (Peñuelas and Llusà, 2004) and exported to symbionts or ecological partners like mycorrhiza, rhizobia or soil microbes (Bais et al., 2006; Smith, 1997; Smith and Smith, 2011; Van Rhijn and Vanderleyden, 1995). Sugars and other low-molecular non-structural carbohydrates (NSC) play a

central role in plant functioning not only because they are the substrates for synthesis of other compounds and energy sources for metabolic activities, but also because carbon (C) allocation is mediated by these mobile carbohydrates. Plants also form reserves, i.e. temporarily immobile forms of carbohydrates like starch or C-rich compounds like lipids (e.g., Höll, 1997), and these reserves can be mobilized and re-allocated to metabolic processes when photosynthetic gains are smaller than metabolic demand.

Unlike many other plant life forms, trees can live for centuries or even millennia and over these large temporal horizons the risk of experiencing unfavourable conditions (e.g., herbivore attack, drought) that cause reduced carbohydrate supply is very high (Hartmann and Trumbore, 2016). Carbohydrate storage is thus very important for tree

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<https://doi.org/10.1016/j.envexpbot.2018.03.011>

Received 28 September 2017; Received in revised form 12 March 2018; Accepted 12 March 2018

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survival and fitness, but our mechanistic understanding of how trees allocate and remobilize their resources, in particular stored C, is still very poor and limits our ability to realistically predict tree and ecosystem responses to environmental change (Dietze et al., 2014).

Carbon allocation generally appears to be a very intuitive process in plants. During early seedling development, for example, the radicle emerges in search for water, which is required for the expansion of the hypocotyl and cotyledons to be exposed to light. As the C reserve pool stored in the endosperm slowly depletes, the seed-leaves become the primary source of carbohydrates via photosynthesis. Both the above- and below-ground parts of plants are in what could be described as a functional equilibrium, where the amount of absorptive roots, acquiring nutrients and water, are in balance with the shoot and its associated leaf area providing carbohydrates and other metabolites for both the maintenance and growth of shoot and roots. Thus allocation of carbohydrates among plant organs appears to be a self-regulating process of relocation of resources – from sources to sinks (Gifford and Evans, 1981).

The allocation of carbohydrates among tree organs has been investigated for many decades (Kozlowski and Keller, 1966) and has given rise to hundreds of studies (Lacointe, 2000). C allocation comprises a highly complex set of interacting processes that are driven by organismic nutrient requirements and controlled by physiological, biogeochemical, and ecological constraints. Plants are sessile organisms that cannot escape stressful environments, so they must acclimate to challenging conditions by strategically allocating resources to overcome stress and promote survival. Stress may be imposed by abiotic factors (e.g., moisture and nutrient availability, temperature, and soil chemistry) or by biotic agents such as competition, herbivory, or diseases. Further the allocation of carbohydrates within a plant may be influenced by symbionts like mycorrhiza (Zhang et al., 2015), but also by environmental conditions that limit plant functions, like cold soils that limit root growth and resource uptake (Alvarez-Uria and Körner, 2007).

Changes in the pool size of different sinks in response to environmental cues can be measured as the change of mass of organs and reserves or as a net change in pool size over time to compute fluxes between pools (Poorter et al., 2012). C allocation may also refer to the distribution of carbohydrates between these pools/sinks in terms of their location (e.g., partitioning among leaves, stems, roots) or their function (e.g., the production of primary and secondary metabolites). Whole-tree carbon allocation studies in mature trees are rare and usually consider only a few components of the tree C balance (e.g., Andersen et al., 2010; Keel et al., 2006). Studies on mature trees comprising several components at the same time are very rare (but see Klein and Hoch, 2015) and usually rely on many assumptions and parameters from other studies. Due to the difficulty in studying mature trees, detailed flux investigations on seedlings and saplings are more common (e.g., Hartmann et al., 2015; Pumpanen et al., 2009), yet it remains uncertain how applicable results from these studies are to the responses of mature trees.

Allocation of carbohydrates in plants is thought to be controlled by the interplay of C sources and potentially competing sinks within in the plant. In general, allocation of C to a given sink may be limited by (1) the source strength, i.e. C supply from photosynthesis and/or remobilization of storage; (2) the rate of translocation of that C via the phloem; (3) the sink strength, i.e. the potential maximum C import rate of a sink when supply is not limiting (Wareing and Patrick, 1975), and (4) sink priority, i.e. “the preferential supply of available photosynthate between competing sinks” (p. 776, Minchin and Lacointe, 2005). When translocation is not limiting, the rate of C allocated to a sink will either be: (1) equal to its sink strength when sink < source strength (i.e. sink limitation) or (2) a function of source strength and sink priority when source < sink strength (i.e. source limitation), with lowest priority sinks being affected most by changes in C availability (Lacointe, 2000). Maintenance respiration is often assumed to have the highest priority,

followed by growth of the canopy and fruit development, then stem cambium and finally root growth (Minchin and Lacointe, 2005). By contrast, storage is often considered to be the lowest priority, with accumulation occurring only when other sinks are C saturated (Dickson, 1989; Minchin and Lacointe, 2005; Minchin and Thorpe, 1987). The physiological mechanisms by which sink priority is manifested are not well understood. Minchin et al. (1993) suggested that the relative position of sinks and sources along the transport pathway could determine hierarchy, with sinks closer to sources having higher priority. Alternatively, genetically regulated changes in sucrose transporters, cell-wall invertases, or in other proteins that affect phloem loading and unloading in sink tissues could be involved (Lemoine et al., 2013).

2. Tree seedlings are convenient for investigations but they're not small mature trees

Trees are impressive organisms; however, they are difficult to study, especially in investigations on processes that affect the whole organism over longer time periods; their great size (both below and above ground) hampers access to some organs (e.g., canopy, root system) and their long lifespan largely exceeds the life expectancy of the researcher. Hence, the temptation is great to use young trees (i.e. seedlings and saplings), and assume that they respond to environmental cues similar to a mature tree. However, these assumptions can be problematic; for example, past investigations on ozone effects on forest trees demonstrated that extrapolating results from seedlings to large trees led to an overestimation of observed ozone damage (Samuelson and Kelly, 2001).

While specific differences between seedlings and mature trees important for carbohydrate allocation will be discussed in later sections, it is obvious that simple allometric proportions (e.g., stem diameter to tree height) do not scale isometrically with tree size. Instead, allometric proportions are generally governed by laws of elasticity and stress resistance or hydraulic relationships that prevent breakage or allow sufficient water transport as trees grow larger (King, 2011; Ryan et al., 2006). Hence, seedlings are not simply small mature trees but change during maturation and this necessarily requires different allocation patterns. In addition, leaf and branch growth is usually constrained to early spring in most deciduous species whereas juveniles may exhibit continuous growth throughout the season (Kozlowski and Pallardy, 1997). This entails substantial seasonal differences in allocation patterns between seedlings and mature trees. In oak trees, for example, the photosynthetic capacity per unit leaf area increases three-fold during tree maturation (Cavender-Bares and Bazzaz, 2000), and this may be due to greater N content in leaves of mature trees (Mediavilla and Escudero, 2003). In other cases, growth and net assimilation rates may decline during tree maturation (Mencuccini et al., 2005). Hence, changes in allometry, photosynthetic capacity, and growth during maturation suggest that allocation of carbohydrates may be different between seedlings and mature trees and making their usefulness for extrapolation to mature trees questionable.

In models, allocation to growth is commonly attributed a higher priority than storage, and hence allocation to storage will largely be determined by the imbalance between source strength (net assimilation) and the sink strength of growth processes. However, the ratio of source to sink strength of growth may shift with tree development: For example it has been shown that the ratio of photosynthetic leaf mass (source) to total living biomass (source + sink) strongly declines with tree size (Poorter et al., 2012) and the ratio of heterotrophic (sink) to autotrophic (source) tissues increases with tree size (Ryan et al., 1995). By contrast, source:sink ratios may increase in field-grown trees with age when soil nutrient availability declines with stand maturation (Binkley et al., 1995; Frazer et al., 1990; Vitousek et al., 1989) and progressively reduces growth sink strength, as documented by slowly attenuating growth rates in elevated-CO₂ field trails on mature or taller trees (Ellsworth et al., 2017; Körner et al., 2005; Norby et al., 2010;

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