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Commentary

Carbon storage in trees: pathogens have their say

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The study of the role and dynamics of nonstructural carbohydrates (NSCs) in woody plants, and particularly in trees, has received renewed attention in the recent past (Sala et al. 2012, Dietze et al. 2014). There are several reasons for this increased interest but it seems clear that an important event was the publication of the McDowell et al. (2008) paper on the mechanism of drought-induced mortality in trees, in which the authors put forward the carbon-starvation hypothesis. According to this hypothesis, stomatal closure to prevent hydraulic failure under drought causes photosynthetic carbon uptake to diminish and, eventually, the plant may deplete its carbon reserves and starve as a result of continued metabolic demand for carbohydrates. This idea was not new (e.g., Waring 1987, Martínez-Vilalta et al. 2002, Bréda et al. 2006), but McDowell et al. (2008) presented it in a coherent and wider hydraulic framework, which made it compelling and influential. The carbon-starvation hypothesis implies that the amount and dynamics of carbohydrate storage in trees provide useful information on their drought responses. And off we went, many of us, to measure NSC concentrations in our field- and greenhouse-based studies of drought-induced tree mortality.

The carbon-starvation hypothesis was controversial from the beginning (McDowell and Sevanto 2010, Sala et al. 2010) and, although direct links between low NSC content and drought-induced tree mortality have been found in some cases (e.g., Galiano et al. 2011, Galvez et al. 2013), its overall importance in the tree-mortality process remains to be established. What is clear, however, is that these discussions have opened new perspectives into the study of plant responses to drought (McDowell 2011, Ryan 2011) and other stress factors, and, most importantly, they have bolstered the cross-communication between fields that had been rather disconnected in the recent past, including plant hydraulics, plant carbon economy and plant pathology. In addition, the renewed interest in the dynamics of NSCs has reopened an old debate on carbon allocation in plants and, in particular, on the role of carbon supply in limiting tree growth (Wiley and Helliker 2012, Fatichi et al. 2014, Palacio et al. 2014).

The classical view of the role of NSCs and their dynamics is based on a source–sink model and holds that carbon storage in plants is the result of the supply of newly assimilated carbon being higher than the overall demand at the sink tissues, including growth, respiration, defence and export (Kozlowski 1992). Although this view is consistent with different carbon allocation paradigms, it has frequently been taken to imply a passive storage, in which NSC builds up only when all the other demands have been satisfied. Under this paradigm, the fact that trees tend to have substantial amounts of NSC even under stressful conditions has been interpreted as implying that carbon availability does not limit tree growth (Körner 2003). However, NSCs may play a key role in maintaining hydraulic and osmotic functions and thus may not represent a simple overflow acting as a repository pool for future uses (McDowell 2011, Sala et al. 2012), in which case allocation to storage may be highly regulated (i.e., not passive) and may compete with growth at least under certain conditions (Chapin et al. 1990, Sala et al. 2012). From this perspective, the relatively high NSC levels in trees are not necessarily evidence of excess carbon and are compatible with carbon limiting, or co-limiting, tree growth (Wiley and Helliker 2012). This dispute is not trivial, as it has key implications on how we understand plant carbon economy and the way we model ecosystem carbon flows (Richardson et al. 2013, Dietze et al. 2014).

In this issue, Saffell et al. (2014) use a novel approach to study the relative priority of storage versus growth, taking advantage of the effects of Swiss needle cast (SNC, not to be confused with NSC) on Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). This disease is caused by an ascomycete (*Phaeocryptopus gäumannii* (Rohde) Petrak) that colonizes Douglas-fir foliage and causes stomatal blockage and, ultimately, leaf abscission. Interestingly, SNC occurs in wet environments, providing a natural experiment that is not complicated by the effects of drought stress. In agreement with previous studies, Saffell et al. (2014) find much lower radial growth in SNC-diseased trees with less functional leaf mass, presumably due to lower overall carbon uptake. However, the novelty of this study is the concurrent measurement of NSC dynamics and growth on infected trees. Their results show that NSC concentrations are unrelated to functional leaf mass (in twigs and foliage) or only decline slightly compared with growth (in the main trunk). This result is interpreted to imply that infected Douglas-fir maintains NSC levels, particularly in the crown, at the expense of stem growth, with important implications for the current debate between passive and active carbohydrate storage in trees.

The results by Saffell et al. (2014) are intriguing, but they also raise questions. An important one has to do with metrics. How should we measure the relative priority of storage versus growth? Ideally we should be able to monitor the carbon balance of whole, mature trees and all its components at relevant time scales. Unfortunately, this is a daunting task (see Dietze et al. 2014) and alternative measures of allocation priority are needed. Saffell et al. (2014) use the ratio of NSC concentration to basal area increment. This is an appealing measure mostly for practical reasons, as it combines the two most common ways of quantifying tree carbon storage and growth. However, it is only part of the story. Nonstructural carbohydrate concentration measures a (relative) content, whereas growth is a flux. A better index of relative priority would compare growth concurrently with the rest of the fluxes in and out the NSC compartment (or at least the changes in NSC content) (Ryan 2011), all expressed in the same or comparable units (Figure 1). Unfortunately, this is again challenging and brings us to yet another problem in plant carbon economy research. While it is reasonably easy to measure growth at the whole-tree level, even retrospectively using growth rings, estimating the total NSC content of an entire tree is exceedingly difficult and has only been done in very few studies (see Dietze et al. 2014). Nonstructural carbohydrate concentration varies among organs and tissues and a whole-tree assessment requires many measurements, as well as a precise quantification of the total biomass in each organ/tissue. And even that would not be enough, as repeated measurements would be required to assess changes in NSC.

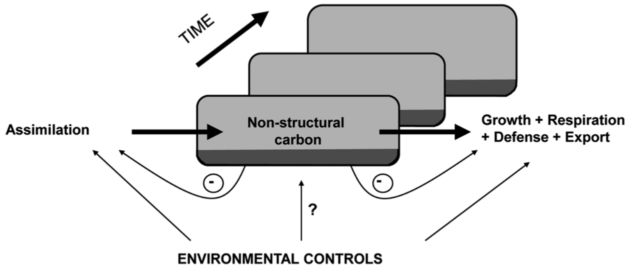

Figure 1. A possible view of nonstructural carbon (including NSC) as a pool resulting from the balance between carbon sources (assimilation) and sinks. Changes in this balance over time determine variation in the size of the pool. The dark grey area corresponds to nonstructural carbon serving immediate functions in osmotic regulation and vascular transport. The arrows with encircled minus signs indicate feedback and feedforward mechanisms by which sink and source activity is regulated. Environmental controls on source and sink activity illustrate the co-limitation between assimilation and other processes such as growth, which provides a middle ground between the extreme views of a purely carbon-limited growth and a 'growth-controlled' photosynthesis.

Another exciting aspect in Saffell et al. (2014) has to do with the role of pathogens. Fungal pathogens can establish very rich and diverse trophic interactions with trees, in which they may affect their carbon balance indirectly, as stressed in the Saffell et al. work, but also directly. *Phaeocryptopus gäumannii*, the fungal pathogen that causes SNC, is a biotroph, and as such it is able to obtain carbon directly from living leaf cells (Deacon 1997). This direct consumption, together with any carbon-expensive defence mechanisms or other hormonal responses that may be triggered, will have implications for the carbon balance of the affected leaves and elsewhere in the plant. Accounting for these effects is probably essential if we are to understand whole-tree carbon dynamics and its response to biotic and abiotic stress, as these two sources of stress appear to be intimately linked to each other (Desprez-Loustau et al. 2006, Jactel et al. 2011, Gaylord et al. 2013).

Clearly, elucidating the role of NSCs in trees will require additional research. We need to address the complexity of plant carbon economy and this can only be done if all the relevant disciplines come together into a common research framework and agenda. Saffell et al.'s (2014) study provides an example of a fruitful approach. Trophic (i.e., carbon-based) interactions between pathogens and trees are ubiquitous and it seems clear that a complete understanding of tree carbon dynamics will not be achieved until these interactions are explicitly accounted for. To find a common ground in disputes such as the role of carbon in limiting tree growth, we need to recognize the central importance of time scales in any discussion about carbon allocation (Dietze et al. 2014), and we need to be aware that data interpretation might be complicated by issues of definition. After all, what is storage? Chapin et al. (1990) define storage as resources that build up in the plant and can be mobilized in the future to support biosynthesis for growth or other plant functions. This definition highlights the role of storage as a pool/repository for future uses. But if NSCs have immediate functions in plant metabolism (osmotic regulation, maintaining vascular integrity; Sala et al. 2012), should we see them simply as storage? Do we need to view growth and NSC formation as competing flows or could we see NSCs simply as a pool from which different but interacting uses are possible (cf. Figure 1)? What is that we measure when we quantify NSC concentrations? I suspect that these important conceptual (and related technical) aspects will need to be resolved before current disputes are settled and a common view on plant carbon allocation emerges.

Conflict of interest

None declared.

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