



## Commentary

# The fate and age of carbon – insights into the storage and remobilization dynamics in trees

The fate of carbon (C) in plants and terrestrial ecosystems has been an important topic for *New Phytologist* for a long time. Owen Atkin (2015) highlighted in a recent Editorial that *c.* 50 papers dealing with C allocation and cycling in plants have been published in this journal within a two-year period. Important experimental techniques used to assess this fate include  $^{13}\text{C}$  and  $^{14}\text{C}$  labelling experiments (Carbone *et al.*, 2007; Epron *et al.*, 2012) or the assessment of variations in the natural abundance of stable isotopes in different C pools and/or fluxes over time (Wingate *et al.*, 2010; Treydte *et al.*, 2014). Such applications are mainly suited to track transport and respiration of new assimilates within the plant and transfer to the mycorrhizosphere (Högberg *et al.*, 2010) over the short term. Furthermore they provide insight into the conversion of assimilates to structural compounds (Kagawa *et al.*, 2006), transfer to storage pools and mixing of new assimilates with older C pools (Keel *et al.*, 2007; Hartmann *et al.*, 2015).

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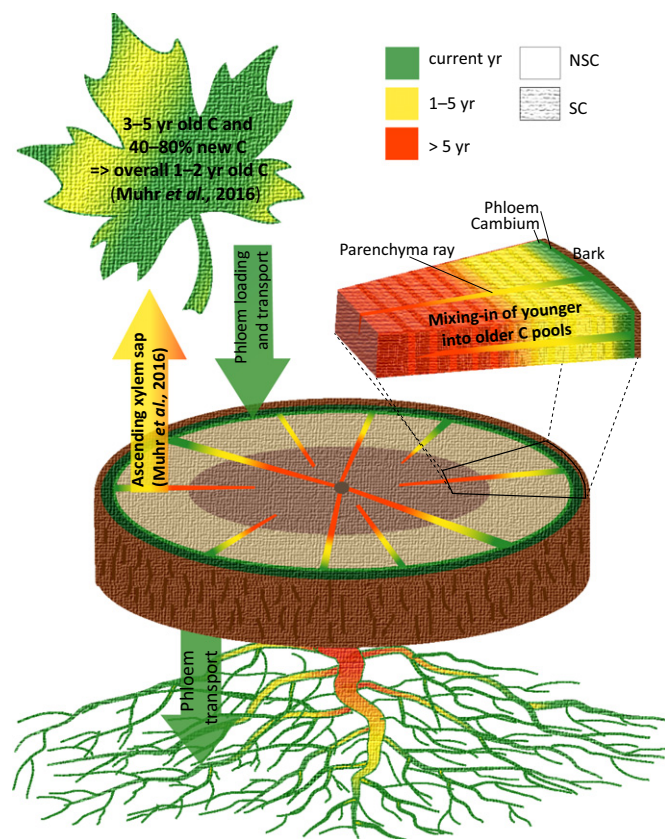
The application of the bomb-radiocarbon approach (e.g. Muhr *et al.*, 2013) to particular chemical compounds within the tree, or  $\text{CO}_2$  emitted from plant compartments, allows us to tackle the story from the other end. Rather than to track the fate of new assimilates this approach allows the age to be assessed and thus the origin of C used for particular metabolic processes. In this issue of *New Phytologist* Muhr *et al.* (2016; pp. 1410–1416) have characterized the C age of maple syrup, that is, of the sugars loaded into the ascending xylem sap before bud break and leaf expansion, at two different sites in Canada. Combining  $^{14}\text{C}$  and  $^{13}\text{C}$  analyses they could observe that the sugars in the maple xylem sap originate from a well mixed storage pool with a  $^{14}\text{C}$ -derived mean turn-over time of between 3 and 5 yr (Fig. 1). The finding that early-spring xylem loading does not directly and immediately depend on last year's photosynthesis and storage capacity indicates that maple sugar production is well buffered against single-year extreme events – such as drought or insect attacks – that might cause a reduction of

the assimilation capacity. The study is also a very good example of how the combination of different isotope approaches can add new information: whereas the  $^{14}\text{C}$  analysis indicates the turnover time of the remobilized C, the  $^{13}\text{C}$  analysis provides information on potential differences in the site conditions between the two stands examined.

Generally our knowledge of C storage and remobilization is increasing, for example it has been shown that deciduous trees can accumulate storage C that allows them to replace their whole foliage up to four times (Hoch *et al.*, 2003). Nevertheless there are still many unknowns especially concerning the dynamic regulation of C partitioning with varying, and potentially stressful, environmental conditions (Dietze *et al.*, 2014). Only recently Richardson *et al.* (2015) reported that the nonstructural carbon (NSC) pool in the parenchyma rays of the outermost tree rings originates from recent assimilates (< 1 yr old), whereas the older the tissue gets, the older is also the C storage pool (Fig. 1). However, the authors also observed that NSC was always younger than the structure of the storage tissue, thus pointing to mixing-in of younger NSC into older NSC pools; however, they did not find any indication of significant mixing-out of older into younger pools. These findings point to at least two NSC pools in the ray parenchyma (one with fast and one with slow turnover; Richardson *et al.*, 2013), which seem to be spatially separated.

Under 'normal' conditions during the growing season, when sufficient new assimilates are provided by photosynthesis, and phloem transport is fully functional, metabolic activity in heterotrophic tissues and growth will thus be mainly governed by recent assimilates. This assumption is supported by tree-ring stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ ) studies showing that the isotopic signal generated in the leaf is directly imprinted on the tree-ring cellulose or wood with some mixing, which just buffers diel and day-to-day fluctuations (Helle & Schleser, 2004; Gessler *et al.*, 2009, 2014). For  $\delta^{13}\text{C}$  of  $\text{CO}_2$  released from the trunk of trees, which is often seen to be a direct indicator of the  $\delta^{13}\text{C}$  of the metabolically active C pools, some recent research pointed to significant though time-lagged correlation with photosynthetic  $^{13}\text{C}$  discrimination (Wingate *et al.*, 2010). By contrast, also no relationship between  $\delta^{13}\text{C}$  of respired  $\text{CO}_2$  and  $\delta^{13}\text{C}$  of leaf sugars (Kodama *et al.*, 2008) was observed. This discrepancy points to our lack of understanding of C allocation and allocation priorities.

Spring is a particular period during a growing season where dynamic regulation of C allocation and the use of stored C is key, especially since in deciduous tree species new tissues are formed before assimilation has started. It is trivial to state that the production of the foliage in spring relies on stored C. But nevertheless there is no consensus on whether it is mainly last year's assimilates or also older C that is used. Gaudinski *et al.* (2009) concluded the C used for initial leaf growth in white and chestnut oak as well as in red maple was at a maximum 1 yr old, and thus only



**Fig. 1** The fate and age of carbon (C) in trees. An overview of the estimated age/turnover time (colour code) of structural carbon (SC) and nonstructural carbon (NSC) in trees. The arrows indicate transported sugars, in roots and leaves the age of SC is indicated. The inflated trunk section indicates the age of the SC of the tree ring and the NSC in the parenchyma ray (starch and sugars) and in the phloem (sugars). For clarity the size of the parenchyma rays has been strongly increased and does not represent the real scale. (From data from Muhr *et al.* (2016, this issue of *New Phytologist*, pp. 1410–1416), Richardson *et al.* (2015) and Gaudinski *et al.* (2009).)

slightly older than the C used for fine root production. Muhr *et al.* (2016) hypothesize that initial leaf growth in sugar maple is supported by C of the same age as they found in the xylem (i.e. 3–5 yr) and that 40–80% of the leaves' final biomass is made up from new assimilates; this results in the overall C of the leaves to be 1–2 yr old. This finding points to either species-specific differences or to the impact of the previous year(s) environmental conditions, which allowed more or less accumulation of NSC. We might also assume that the strong xylem loading with sugars in sugar maple is a special situation. In most tree species the transport of C to new developing leaves occurs via the phloem and thus sugars most probably originate from storage tissues close to the cambium with young NSC. In the diffuse porous sugar maple, however, the ascending xylem sap might be able to tap the older NSC stored in the inner section of the parenchyma rays of the stem wood (Fig. 1).

In deciduous trees growth of early wood in spring is also ensured by remobilized storage compounds (Helle & Schleser, 2004) and there is evidence from  $^{13}\text{C}$  labelling studies, and observation of autocorrelation within tree-ring  $\delta^{13}\text{C}$  data (Monserud & Marshall, 2001), that storage from the previous year could be a main C

source. We, however, also know that tree radial growth in summer (i.e. late wood), which is normally achieved by recent assimilates, can be driven by stored and remobilized C under extreme heat and drought conditions thus resulting in uncoupling of the  $\delta^{13}\text{C}$  tree-ring signal from actual leaf level physiology (Hentschel *et al.*, 2015).

What we lack is the mechanistic understanding of how stress factors such as drought and heat, which impair photosynthesis and thus the supply of new assimilates, can modify the storage and remobilization patterns in old-grown trees on the short- and long-term and how the turnover times of storage pools will be affected by such stress. This also has clear implications for isotope-based dendroclimatology and dendroecology: in a dry and hot summer, the tree-ring isotopic signature might not be predictive for the actual climate and the tree response to it. A combination of  $^{13}\text{C}$  and  $^{14}\text{C}$  analysis in whole wood or cellulose might, however, help to detect the incorporation of older C into the late wood and thus help to increase the explained variance in tree-ring isotope records.

Long-term exposure to drought might also trigger reoccurring needs to use stored C compounds for sustaining vital processes such as maintenance respiration, root and/or seed production thus depleting the storage pools and decreasing the resistance towards C starvation (McDowell, 2011). At present, however, it is hardly known how such stressors acting on the long-term scale modify the storage and remobilization of C in mature trees. Thus we are strongly impaired in our knowledge to predict if C starvation plays a role in tree mortality and forest dieback (Sala *et al.*, 2010). Without such understanding of the processes, however, tree and forest mortality predictions under changing climates cannot be achieved. Bomb radiocarbon analyses such as conducted by Muhr *et al.* (2016) are an important tool to address these issues. They might be applied to sugar transport as done by Muhr *et al.* (2016), for NSC storage pools and for structural tissues under different disturbance regimes. Combining such  $^{14}\text{C}$  analysis with  $^{13}\text{C}$  isotopic pulse labelling approaches will definitely improve our understanding of the fate of new assimilates within the plant (and the soil interface) and of the origin of the C used for tissue formation and metabolic activities under variable and extreme environmental conditions.

Arthur Gessler\* and Kerstin Treydte

Swiss Federal Research Institute WSL, Zürcherstr. 111, 8903, Birmensdorf, Switzerland

(\*Author for correspondence: tel +41 44 7392 818; email arthur.gessler@wsl.ch)

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**Key words:** <sup>13</sup>C and <sup>14</sup>C, bomb-radiocarbon approach, carbon storage and remobilization, drought, metabolic activity, nonstructural carbon pool, old-grown trees.



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