

Commentary

Plant carbon allocation in a changing world – challenges and progress: introduction to a Virtual Issue on carbon allocation

Current challenges in research on plant allocation

Plants are sessile organisms that, once germinated, have to cope with *in situ* environmental conditions for the rest of their life span. These conditions may be favourable for growth and development but may also be constraining or even harmful for their survival. Hence plants must employ available resources most strategically to optimize growth and development and to avoid stress and reduce harm or damage. In this context carbon (C) plays a central role as it is one of the most abundant and most versatile elements involved in plant metabolism. During photosynthesis carbon dioxide (CO₂) is taken up from the air and converted to nonstructural carbohydrates (NSC) that serve as both energy carrier and as a building block for anabolic processes like growth, defence or exchanges with other organisms (Hartmann & Trumbore, 2016).

The partitioning of the primary products of photosynthesis into different functional pools is termed carbon (C) allocation and has been subject of investigations for many decades. For example, early botanists studied plant allocation responses as changes in growth patterns following manipulations like branch removal (Hartig, 1878). Several conceptual frameworks were developed decades ago to describe plant allocation strategies in terms of a functional equilibrium between aboveground and belowground organ biomass (Brouwer, 1963). Allocation has also been described as a trade-off in resource partitioning between different functional sinks, like growth and defence in the presence of herbivores and pathogens (Herms & Mattson, 1992). Mooney (1972) stated almost 50 years ago that ‘through a quantitative understanding of how different plants gain and allocate their resources it will be possible to make predictions as to their success in any given physical environment in combination with any competitor and predator’. Understanding how C allocation is regulated is thus key for predicting plant responses to environmental changes (Dietze *et al.*, 2014) and consequences for ecosystem functioning (Brüggemann *et al.*, 2011). Yet, almost 50 years after Mooney (1972) our knowledge of the regulatory mechanisms of C allocation is still poor due the complexity in assessing important C allocation

components, in particular fluxes among metabolic processes, like photosynthesis, respiration or root exudation, and between different biomass pools, like primary and secondary metabolites (Poorter *et al.*, 2012).

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NSC are of particular interest as they are the dominant currency of C allocation. Several recent papers have investigated seasonal patterns of NSC distributions in different tree organs (e.g. Hoch *et al.*, 2003; Würth *et al.*, 2005; Martínez-Vilalta *et al.*, 2016; Smith *et al.*, 2017). However, integration of such observations of C dynamics at the whole tree level and to entire forests could shed light on seasonal ecosystem NSC dynamics but is still sparse in the literature. A better mechanistic understanding of how the build-up and the use of NSC and NSC storage are regulated, in particular during environmental stress, is also still lacking. The review by (Hartmann & Trumbore, 2016) raises several of such knowledge gaps in research on NSC dynamics in forest trees and provides suggestions for future progress. For example, tree organs may contain decade old NSC reserves in the parenchyma of deeper cell layers of roots, stems and branches, but to what extent and under what conditions these reserves can be mobilized and used in metabolism remains uncertain (Hartmann & Trumbore, 2016). In most vegetation models NSC reserves are assumed to be stored and used in the current year of simulation without substantial temporal carry-over, and NSC storage merely is the balance between photosynthetic production minus respiratory losses and allocation to growth (Dietze *et al.*, 2014). NSC reserves are thus often considered a sort of overflow reservoir only to be filled when other plant functions are satiated. However, in long-lived organisms like trees, allocation to NSC reserves at the expense of other functions like growth may be a safer strategy to ensure long-term survival during the many stressful periods a tree may encounter during its long life span (Sala *et al.*, 2012; Wiley & Helliker, 2012). Whether NSC reserves merely accumulate when production outweighs demand or reserve formation has a high allocation priority and competes with other sinks is important for realistically simulating plant responses to environmental change (Hartmann *et al.*, 2018). Whole-plant investigations assessing all major C sinks, not only NSC storage pools, are needed to provide support for either strategy but are still rather rare. Another important knowledge gap that is

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closely related is whether, and to what degree, tree growth is limited by the supply of C (C-source limitation) or growth processes themselves (C-sink limitation) (Fatichi *et al.*, 2014, 2019; Friend *et al.*, 2019). While most vegetation models run under the assumption that plant metabolism is source driven, sink limitation by environmental factors, like water or nutrient availability, may be more constraining for growth and development than C availability (Körner, 2015). The optimum partitioning theory predicts that allocation to belowground organs increases when soil water availability declines, however, such a response may not be feasible during strong drought when transport of C to support belowground growth is slowed (Ruehr *et al.*, 2009) and roots become increasingly isolated from aboveground organs (Hartmann *et al.*, 2013). Drought impacts on C allocation are thus still far from being well understood. Furthermore, belowground processes, in particular export of C from roots to the rhizosphere are yet another important aspect of C allocation of which our knowledge is still sparse because processes taking place belowground are much harder to investigate than aboveground.

The current collection addresses these areas of interest: (1) spatial-temporal dynamics and regulation of NSC storage in plants, (2) source vs sink controls on C allocation, (3) drought and temperature effects on C allocation, and (4) C allocation to symbiotic rhizosphere interactions. Many of these papers were presented during the session on C allocation at the 2018 annual meeting of the European Geosciences Union (EGU) in Vienna (Austria). To better highlight recent progress that has been achieved in research on C allocation we have also included other relevant papers that have been published in *New Phytologist* in recent years.

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Spatio-temporal dynamics of NSC and regulation of C storage in plants

The integration of NSC measurements at the whole tree and ecosystem level was addressed by Furze *et al.* (2019). They measured NSC concentrations in five tree species at high-temporal resolution over a year. Scaling up to the whole tree level was done using allometric models, and to the whole ecosystem level using forest inventory data. Temporally, they found that seasonal depletion of NSC at the whole tree level was minimal, yet substantial depletion occurred within branches in the spring. The overall size of the branch NSC storage pool was surprisingly comparable to that of the root storage pool. Whole-tree and

ecosystem-level NSC estimates showed that models consistently overestimate NSC storage. This work is important because it improves our understanding of within-tree NSC organ dynamics, and provides solid species-specific and ecosystem-level NSC pool estimates, which can be used to evaluate and improve C cycle models.

Klein & Hoch (2015) addressed the difficult task of partitioning seasonal ecosystem C dynamics in a forest stand in Israel into tree physiological processes using a mass balance approach. Their study integrated different data sources including eddy covariance ecosystem flux data, tree-scale measurements of C fluxes like assimilation and respiration, C pools in structural biomass and NSC storage, as well as partitioning rules derived from theory and corroborated by field measurements. The study provides an excellent template for spatio-temporal down-scaling of ecosystem fluxes to physiological processes of individual trees and provides insights on how trees manage NSC resources as both 'cash flow' (sugars) and NSC storage (starch) over the growing season.

Trees store large amounts of NSC in all organs, enough to replace their foliage approximately four times over (Hoch *et al.*, 2003). In the woody biomass of branches, stems and roots, parenchyma cells remain alive for decades and NSC stored within these cells can also be decades old (Muhr *et al.*, 2013). The question whether old NSC reserves can be used for metabolism or if they are simply sequestered and unavailable for metabolic uses has been debated repeatedly in the scientific community (Körner, 2003; Sala *et al.*, 2012). Radiocarbon is a useful tool to assess the mean age of NSC stored in tissues, and the time lag between photosynthesis and allocation to growth and metabolism and the following investigations have used radiocarbon analyses and derived C ages to infer NSC allocation patterns. Muhr *et al.* (2016) analyse the C age of springtime sap of sugar maple (*Acer saccharum* Marsh.) and find that sugars that are mobilized before bud break had been produced during the previous three to five growing seasons. They estimate that c. 40% of newly-formed leaf biomass is made from these older reserves which highlights the need to include a temporal C storage component in vegetation models. The study by Carbone *et al.* (2013) shows that cellulose in stem wood of red maple (*Acer rubrum* L.) is produced from a 0.9-year-old mix of newly-assimilated and older NSC reserves and regrowth of stem sprouts from stumps can be fuelled by very old (up to c. 17 years) NSC reserves. This study underscores the potential utility of old reserves for general plant functional processes and even more so for plant survival following disturbance. Such older reserves are not spatially stationary, as Richardson *et al.* (2015) document. They show a strong mixing of reserves across the youngest tissues (most recent five growth rings) in white pine and red oak while the mixing of young reserves into older tissues is rather limited. These results are important as they provide an empirical basis for more realistic simulation of tree C reserves using pools of different turnover times, i.e. fast vs slow (Richardson *et al.*, 2013). Herrera-Ramirez *et al.* (2020) used C ages to constrain two C allocation models to estimate storage age and pool turnover times in *Pinus halepensis* Mill., *Acer rubrum* L. and *Pinus taeda* L. They find that in particular NSC fluxes to storage and growth in roots influences C reserve turnover times but also that C age distributions vary across species indicating different

allocation strategies. The papers by Richardson *et al.* (2013) and Herrera-Ramirez *et al.* (2020) are excellent examples of how C allocation models constrained by NSC reserve ages can provide insights into whole-tree C dynamics that concentration measurements alone cannot offer.

The question whether NSC concentrations in plant tissues are a reliable indicator of the C balance has attracted considerable attention in recent years (Hoch, 2015). Weber *et al.* (2019) conducted a 3-year experiment to investigate the impact of C limitation treatments (deep shade) on NSC storage in saplings of a range of temperate tree species varying in shade tolerance. Shading substantially reduced growth and initially also NSC concentrations by 50% relative to the control treatment. However, at the end of the 3-year experiment there was no difference in NSC concentrations between treatments. A potential explanation for these results is that in the shaded treatment, the storage of NSC was prioritized over growth, although the authors caution that this should not be viewed as a 'strategic decision' but rather the outcome of a complex of processes operating simultaneously. Regardless, an important conclusion of this study is that drawing inferences about whole-tree C status solely on the basis of NSC concentrations could lead to erroneous or misleading conclusions. By contrast, a study run by the same group found that depletion of stored NSC via shading below *c.* 15% of seasonal 'normal' (i.e. light-control) levels led to tree death in several angiosperm and gymnosperm tree species, likely from NSC starvation (Weber *et al.*, 2018). NSC levels of trees that would not recover following re-exposure to light were considered thresholds of starvation, a parameter that was so far unknown.

As mentioned earlier, it is currently not known whether NSC reserve formation in trees is dependent on C availability (Sala *et al.*, 2012). Huang *et al.* (2019a) conducted an experiment in which ambient CO₂ was reduced as a means of manipulating C availability. They found that trees prioritize long-term survival via maintenance of C storage and defence capacity over current growth when C availability was severely reduced. The study is one of the first to document that NSC storage is not merely an overflow process, although reduced sink activity may liberate resources for NSC storage. Future research agendas should ideally manipulate both source and sink activity including defence to further address NSC storage regulatory processes (Gessler & Grossiord, 2019). Based on the observed prioritization of allocation to defence Huang *et al.* (2019b) call for a broader view of C dynamics in trees as changes in C partitioning under stress may be relevant for long-term forest dynamics via reduced tree defence metabolism. They underscore the importance of implementing such mechanistic detail in large-scale vegetation simulators to improve forecasting of future forest dynamics including interactions with biotic agents like bark beetles.

Allocation from sources to sinks – what controls these fluxes?

Whether reduced growth can be attributed to C-source limitation was investigated by Schmid *et al.* (2017) who conducted an experiment using defoliation and CO₂ reduction/enrichment.

They hypothesized that if C-source limitation is the driving factor, then plants grown under high-CO₂ treatment should exhibit less growth reduction than plants grown under lower CO₂ treatments. Before defoliation, growth was reduced by low CO₂. However, reductions in relative growth after defoliation were not related to CO₂ treatment, leading to rejection of the C-source limitation hypothesis. Furthermore, NSC reserves were not fully depleted after defoliation, and indeed even in the lower CO₂ treatments, reserves were fully re-established by the end of the growing season. Various interpretations of these results are possible, including simultaneous C-source and C-sink limitation of wood growth, and prioritization of NSC storage over growth processes (e.g. Silpi *et al.*, 2007; Sala *et al.*, 2012; Wiley & Helliker, 2012).

To date most process-based models of forest growth are based on the C-source limitation hypothesis and therefore rely on the assumption that growth is purely driven by photosynthesis. Guillemot *et al.* (2017) demonstrate that predictions of forest growth with the process-based model CASTANEA can be significantly improved by accounting for lagged effects of water stress on C allocation to wood and by including a direct environmental control on wood sink demand. This work suggests that explicitly considering sink-demand fluctuations in modelling increases the capacity to predict the spatial and year-to-year variability of aboveground forest growth. It thereby highlights the need to move from purely C-source driven growth models to a better representation of C allocation mechanisms related to sink control (Friend *et al.*, 2019). The work by Abadie *et al.* (2018) underscores sink control even for metabolic pathways by investigating allocation of newly-assimilated C between photosynthetic (chlorogenate, sugars) and photorespiratory (amino acids) intermediates in sunflower in response to changing proportions of CO₂ to O₂ in the atmosphere. Such changes may occur during drought when plants respond to low water availability and/or high water vapour pressure deficit with stomatal closure and further fixation of CO₂ reduces the CO₂ : O₂ ratio (Osmond *et al.*, 2000). Abadie *et al.* (2018) show that C fluxes through metabolic pathways are not proportional to net photosynthesis but depend on interactions between C and nitrogen (N) metabolism, as the accumulation of photorespiratory intermediates requires an additional demand for N assimilation and is thus sink-limited. Such findings are important and corroborate recent paradigm shifts in vegetation modelling that a direct causal link from C assimilation to plant growth may be an over-simplification (Fatichi *et al.*, 2014).

Tree C allocation in response to environmental change

The optimal partitioning theory predicts that allocation to belowground organs is favoured over aboveground allocation during soil resource limitation as to release constraints imposed by the most limiting resource (Bloom *et al.*, 1985). Mackay *et al.* (2020) used a model-based analysis to investigate mechanisms associated with conifer resilience to drought, with results then evaluated against data from a drought/heat field experiment. The modified TREES model simulates C acquisition, allocation, and storage of NSC reserves, as well as soil-plant hydraulics. The analysis shows that trees rely on bedrock groundwater during hot

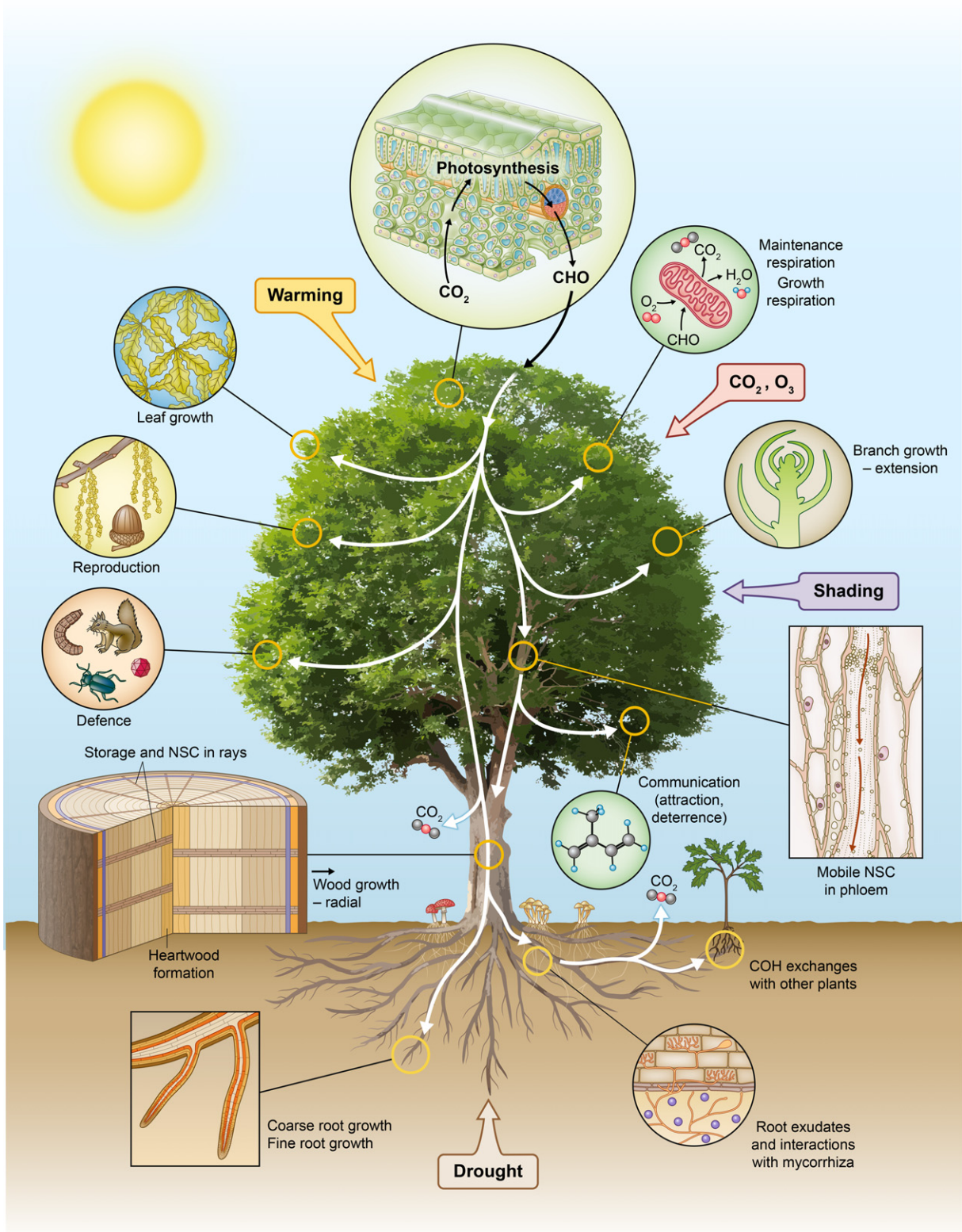


Fig. 1 Plant carbon allocation in a changing world. Plants allocate carbohydrates produced during photosynthesis to support maintenance, growth, development, and reproduction as well as defence and communication. Environmental parameters, like temperature, precipitation and atmospheric CO_2 or ozone concentrations, influence these processes either directly (e.g. heat damage) or by influencing the availability of carbohydrates (e.g. reduction of photosynthetic rates). Plants respond to changes in environmental conditions by shifting the partitioning of available carbon among organs (e.g. aboveground vs belowground growth, reproduction) and/or functional metabolites (e.g. synthesis of cellulose for growth vs production of defence compounds). Such plant responses define allocation strategies, most of which are still not well understood in the context of climate change. NSC, nonstructural carbohydrates.

and dry conditions (and on soil water following rain events), but that allocation to fine roots to support bedrock water uptake must be already initiated before the onset of drought stress. The explicit coupling between C allocation and hydraulics is a novel aspect of this work, which highlights the importance of realistic model representation of both the costs (carbon) and benefits (water) of fine roots. The study thus refines the optimal partitioning theory by including a temporal dimension to the allocation response. Ledo *et al.* (2018) present results from an analysis of root : shoot ratios based on a global data set of more than 3400 trees. The meta-analysis aims to identify which factors, like environmental conditions (e.g. temperature, precipitation), management type, or intrinsic factors (e.g. tree size, species), influence the proportion of belowground vs aboveground biomass as indicators of long-term allocation patterns (Fig. 1). They show that not only aridity but also tree size is an important driver of belowground allocation which nicely complements the optimal partitioning theory (Bloom *et al.*, 1985).

Aboveground wood production was not affected by reduced water availability from experimental rainfall exclusion in a *Quercus ilex* stand (Gavinet *et al.*, 2019). However, aboveground net primary productivity (ANPP) declined with lower leaf and acorn production indicating a proportional increase in C allocation to wood. Reducing stand density by thinning lowered stand transpiration and increased water use efficiency and thereby buffered effects of spring drought on C allocation to components of ANPP. Similarly, Drake *et al.* (2019b) found that experimental warming and drought in young Eucalyptus trees increased C allocation aboveground to respiration and growth but decreased C allocation belowground. A side-effect of increased C allocation to aboveground growth was that growth respiration was enhanced but maintenance respiration acclimated to elevated temperature. This work is interesting because it shows that warming had measurable impact on allocation aboveground, yet drought may not have comparable impact on belowground allocation to roots. The study underscores the need to better understand how increased allocation aboveground in a warming world may be influenced by limiting factors, such as water and soil nutrients, as well as how it may feedback on ecosystem C balance. From the same group and also based on a warming experiment Drake *et al.* (2019a) conducted a study using $^{13}\text{CO}_2$ pulse-chase labelling to determine how respiration was partitioned into aboveground and belowground Eucalyptus tree components. They found that warming alone had no effect on allocation to respiration, and surprisingly very little, only 10%, of the label was respired aboveground. The study highlights the role of leaf-level respiration acclimation during warming, and suggests autotrophic respiration may not be as sensitive to warming as many models predict.

Carbon allocation to rhizosphere symbiotic interactions

The amount of C deposited by roots to the rhizosphere has been estimated to be more than 10% of the photosynthetic C input, e.g. for grasslands (Pausch & Kuzyakov, 2018). The C demand

function related to root exudation and the C transfer to mycorrhizal symbionts and endophytes has rarely been considered in the context of C source–sink relationships and their implications for C allocation. A $^{13}\text{CO}_2$ pulse labelling experiment in grassland showed that a massive reduction in canopy photosynthesis by experimental shading had much stronger effects on aboveground compared to root carbon dynamics, and that the transfer of recent C to fungal communities and gram-negative bacteria remained sustained in spite of a strong depletion of NSC levels in leaves (Bahn *et al.*, 2013). This reflects the strategy of grassland plants to ensure survival by preferentially allocating C belowground and demonstrates a surprisingly stable sink activity of the rhizosphere in spite of an interrupted C source activity.

Several recent studies have highlighted the importance of C allocation to roots and the rhizosphere for plant and ecosystem responses to drought. In a mountain grassland, drought reduced the amount of C allocation to roots to a similar degree as photosynthesis, and increased the investment of recent assimilates to storage and to a pool of osmotically active compounds (Hasibeder *et al.*, 2015). The effects of drought on the partitioning of recent C between belowground storage and respiration differed between grasslands dominated by fast- or slow-growing plants and consequently changed in response to land-use change (Ingrisch *et al.*, 2020). Drought also altered C allocation to the rhizosphere, where transfer of recent C from plants was significantly reduced for bacteria, while it remained sustained for fungi (Fuchslueger *et al.*, 2014). This suggests that grasslands dominated by slow-growing plants, which are associated with a higher proportion of fungal communities, are more drought resistant than grasslands characterized by fast-growing plant species associated with bacterial communities, which favour more rapid recovery from drought by speeding up N cycling after rewetting (Karlowsky *et al.*, 2018). Williams & de Vries (2020) take this finding one step further and highlight the potential role of root exudation for plant and ecosystem responses to drought. They suggest that fast-growing plants modify their root exudates to recruit beneficial microbes that facilitate their regrowth after drought, with cascading impacts on their abundance and on ecosystem functioning. De Vries *et al.* (2019) provide an experimental test for potential effects of root exudation on rhizosphere respiration. They found that while drought reduced the amount of root exudation of two common grassland species, it also affected the quality of root exudates and increased their capacity to stimulate microbial activity. By increasing nutrient availability, this could in turn facilitate plant regrowth after drought. Taken together, these studies provide evidence that belowground C allocation and its role in plant–microbe interactions in the rhizosphere can have major impacts on the plant and ecosystem resistance and recovery from extreme climatic events such as droughts.

Carbon allocation to fungal communities also plays an important role for nutrient acquisition and C sequestration in boreal forests, where ectomycorrhizal (ECM) fungi enhance the capacity to decompose soil organic matter (SOM) and mobilize organic N ('ECM decomposition'). Baskaran *et al.* (2017) developed a model to test how N availability affects the C

allocation to ECM and their role in SOM decomposition. They demonstrate that under low N availability increased mining for N by ECM promotes forest growth and that an optimal allocation of photosynthetic C to ECM fungi can therefore maximize forest productivity. They also point out that future work should account more explicitly for the relative role of ECM vs saprotrophs and their competition for nutrients, which may have cascading consequences for nutrient availability to plants. There is increasing evidence that mycorrhizal networks can also play a role in transporting recently assimilated C between trees (e.g. Klein *et al.*, 2016). Based on a ^{13}C tracer experiment on small Douglas fir seedlings Pickles *et al.* (2017) found that most C allocated belowground was transferred to rhizosphere mycorrhizal fungi, while only small amounts of photosynthates were exchanged between Douglas fir seedlings via the hyphal network. The study shows that the belowground transfer of NSC was in some cases more pronounced between neighbouring siblings with a shared parent (kinship effect), but that it was overall a very minor source of C.

Progress and perspectives in research on C allocation

Carbon allocation can be viewed from different angles: as biomass proportions, as fluxes between the biomass pools and the partitioning of available C into different pools (i.e. gross primary productivity (GPP), Litton *et al.*, 2007). In the past, biomass proportions have been studied most intensively and have provided valuable insights into plant adaptive or acclimatory responses to changes in environmental conditions (Poorter *et al.*, 2012). Short-term plant responses and allocation dynamics can be better investigated with fluxes but they are also much more challenging to assess. The use of isotopic tracers has allowed substantial progress in providing information on such short-term allocation responses, in particular when pools with rapid turnover times, like metabolic pathways or processes are of interest (e.g. Abadie *et al.*, 2018; Drake *et al.*, 2019a). Recent approaches presented in this collection combine biomass measurements, flux assessments and estimates of GPP to produce a more holistic budgeting of C allocation (e.g. Klein & Hoch, 2015; Huang *et al.*, 2019a) and consideration of additional functional pools, like secondary metabolites and their synthesis pathways, may further complement our understanding of plant allocation responses to environmental change (Huang *et al.*, 2019b).

The studies compiled in this Virtual Issue highlight some important advances in our understanding of the C allocation in plants and ecosystems, including the following:

- Process-based models are moving away from a purely C source-driven perspective and increasingly account for sink controls on C allocation. By coupling C allocation and respiration with hydraulic mechanisms this new generation of models has increased the capacity of projecting plant and ecosystem C allocation responses to environmental change, including drought;
- NSC reserves in trees can be decades old. There seems to be a well-mixed functional NSC pool in tissues that is at most a couple of years old and this pool fuels metabolism during normal growth conditions. Following disturbance older NSC reserves can be

mobilized. Such temporal dynamics of the storage pool have been used to constrain C allocation models and allowed defining species-specific C allocation strategies;

- Allometric scaling and top-down mass balance approaches have been shown to produce estimates of ecosystem-scale allocation dynamics for entire forests;
- Trees can survive extended periods with very little NSC reserves left in their organs; however, C starvation occurs before NSC reserves are completely depleted;
- NSC reserve formation and allocation to defence have a high allocation priority and are supplied with C even when there is no excess C available;
- Trees can acclimate respiratory demands to elevated temperatures, belowground allocation to produce root biomass to maintain water uptake must be initiated early during drought;
- Belowground C allocation to the rhizosphere, including root exudation and C transfer to mycorrhizas can constitute an important C sink function and can contribute to promoting drought resistance and recovery.

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