



Editorial: Part of an invited issue on carbon allocation

Introduction to the invited issue on carbon allocation of trees and forests

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Introduction

Carbon (C) allocation is a major issue in plant ecology, controlling the flows of C fixed in photosynthesis between respiration and biomass production, and between short- and long-lived and aboveground and belowground tissues. Incomplete knowledge of C allocation currently hinders accurate modelling of tree growth and forest ecosystem metabolism (Friedlingstein et al. 1999, Gower et al. 2001, Landsberg 2003, Ryan et al. 2004, Litton et al. 2007), and thus predictions of the effects on C cycling of variations in environmental conditions, soil fertility, tree and forest age, species composition and global change. Allocation to reproduction versus above- and belowground vegetative parts (Mund et al. 2010) is closely related to seed production and survival. Allocation also plays an important role for acquisition of resources (light, nutrients and water) that often limit forest productivity (Litton et al. 2007). The harvest index, the distribution of resources between the harvested parts of the plants and the remaining biomass, is a key parameter in agriculture and forestry. While photosynthetic capacities of plants determine the overall C acquisition and then biomass production, only a part goes to the harvested organs (Navarro et al. 2008). In trees, only 10–30% of the C fixed in photosynthesis is used for wood production (Litton et al. 2007), and wood production is perhaps the biomass component most sensitive to environment and nutrition.

Allocation of assimilated C among organs is affected by the environment, phenology and ontogeny, and this affects tree

growth, the contribution of each organ to autotrophic respiration, C transfer to the rhizosphere and C sequestration in the ecosystem because of differences in lifespan and decomposition rates among tree organs (Körner 2003). This editorial highlights the major findings that are reported in this invited issue and other related papers recently published in *Tree Physiology*, as well as their implications for future research.

Modelling allocation

Soil–vegetation–atmosphere transfer models (e.g., MuSICA; Domec et al. 2012, this issue) are key tools for predicting the interactions between climate and ecosystem–atmosphere C exchange. These models are yet to incorporate a mechanistically based scheme for C allocation because we lack information on the controls of allocation (Cannell and Dewar 1994, Friedlingstein et al. 1999, Lacoite 2000, Mäkelä et al. 2000). Novick et al. (2012, this issue) adapted a conceptual model for belowground C partitioning (Palmroth et al. 2006) and predicted the interactive effects of elevated CO₂ and soil fertility on C allocation to resin production as the balance between the rate of carbohydrate production and the rate at which available carbohydrates are used in primary growth processes. Franklin et al. (2012, this issue) review modelling approaches for estimating C and N allocation in forest ecosystems, and identified several classes of approaches to model partitioning of assimilated C (or N) to each organ. Among them, empirical approaches based on fixed ratio or allometric relationships

assume partitioning to be in a steady state at stand level, and thus lack of allocation response to environmental changes. Other approaches are based on more mechanistic representations of the allocation process: functional-balance approaches maintain an optimal partitioning of internal resources (e.g., Reynolds and Chen 1996) while eco-evolutionarily based models (e.g., King 1993, McMurtrie and Dewar 2011) link partitioning to all other physiological processes because this is the integrated whole-plant performance that is optimized and subjected to selection. However, assessing the adaptive nature of any trait is challenging, as is assessing fitness. For these and for all models, predictions need to be evaluated against empirical data (Mäkelä 2012, this issue).

Carbon balance approach

C allocation in trees can be estimated using a C mass-balance approach, coupling measurements of standing biomass derived from allometric relationships, litterfall with CO₂ efflux from soil and tree organs (Ryan et al. 1996). Three articles in this issue used this approach to investigate the relationship between soil fertility and the amount of C that trees allocate to wood production in high productive *Eucalyptus grandis* (W. Hill ex Maiden) plantations in Brazil. Epron et al. (2012b, this issue), expanding on research by Laclau et al. (2009), found that potassium deficiency strongly decreases the wood production of eucalypt plantations by decreasing leaf longevity, leaf area index, and gross primary production (GPP), and by increasing the partitioning of GPP to roots. Interestingly, applying a low dose of sodium partly alleviates the effect of potassium deficiency on how trees allocate their C (Epron et al. 2012b).

Nouvellon et al. (2012, this issue) showed that a mixture of eucalypts and nitrogen (N)-fixing trees (*Acacia mangium* Willd.) had lower wood production than the eucalypt monoculture. The lower wood production was related to shifts in partitioning from wood growth to litter production, and from aboveground wood growth to belowground flux (probably a response to low water availability that offset any benefits of biological N fixation by the *Acacia*). Campoe et al. (2012, this issue) found that both gross primary production and partitioning between aboveground growth and belowground flux caused changes in stem wood production along a soil nutrient–water availability gradient. These three papers and others (Ryan et al. 2010, Stape et al. 2010) demonstrate that soil fertility and water availability affect aboveground wood production through changes in both GPP and C partitioning between aboveground and belowground flux.

Climate change and carbon allocation

While water availability controls productivity, little is known about the effect on productivity of trees' ability to redistribute and, thus, use water from deep soil layers under future climate

conditions characterized by a higher evaporative demand. Deep root water uptake and hydraulic redistribution from deep soil layers to shallow layers can supply water to forest ecosystems during drought, sustaining photosynthesis and increasing net ecosystem exchange in loblolly pine stands. Domec et al. (2012, this issue) examine the role of hydraulic redistribution under climate change using a soil–plant–atmosphere model (MuSICA; Ogée et al. 2003). The model predicted higher GPP under an altered climate (temperature = +3 °C; CO₂ concentration = 600 μmol mol⁻¹) and N fertilization, but an increase in night transpiration in warmer nights will reduce the effect of hydraulic redistribution on tree water balance and C fluxes.

Temperature is predicted to rise in the northern boreal region where tree growth is considered to be temperature limited (Way and Oren 2010). Pumpanen et al. (2012, this issue) observed that root biomass and the rate of photosynthesis for silver birch, Norway spruce and Scots pine seedlings increased with higher soil temperature, but a simultaneous increase in both photosynthesis and respiration rates resulted in no change in net CO₂ exchange and seedling biomass. Interactive effects between temperature, tree genotype and prevailing O₃ level on C allocation were observed in silver birch (Kasurinen et al. 2012, this issue). Elevated temperature delayed leaf abscission, enhancing leaf biomass, while ozone accelerated leaf senescence and stimulated mycorrhizal root growth and sporocarp production. While warming is supposed to shift allocation from belowground to aboveground (Way and Oren 2010), the response depends on other environmental and biotic factors.

Novick et al. (2012, this issue) showed that elevated CO₂ enhanced resin production in pine trees, suggesting that they may be better protected from bark beetle attacks in the future. The effect of atmospheric CO₂ on resin production varies with soil N availability, with more resin production on less fertile sites. Fertilization of forest plantations or N deposition may thus stimulate wood production but reduce the positive effect of elevated CO₂ on resin production and resistance to bark beetle attacks.

Carbohydrate storage

Partitioning of photosynthesis to storage and defence may be a key element in tree tolerance to drought and susceptibility to insect attacks (McDowell et al. 2011). Carbon investment in storage may provide safety margins to allow long-lived trees to maintain hydraulic transport and metabolism during episodes of severe stress. Mobilization of carbohydrates from reserves also facilitates dormancy release and re-sprouting from buds, which might be an important survival mechanism for trees exposed to frequent disturbances (Regier et al. 2010). Carbohydrates from reserves sustain growth of fine roots allowing a recovery in water uptake after a summer drought (Genet et al. 2010), help

maintain tree growth after defoliation (Eyles et al. 2009) and supply early wood growth in ring-porous species prior to budburst and carbohydrate supply from photosynthesis (Barbaroux and Bréda 2002, El Zein et al. 2011).

Despite the important roles identified for stored carbohydrates, little is known about the mechanisms that control carbohydrate storage and release. Is carbohydrate storage a low-priority, passive process that accumulates only when C is in excess and indicates the status of the tree's C balance (Körner 2003)? Or, is tree carbohydrate storage a high-priority, active process (Silpi et al. 2007, Chantuma et al. 2009) that accumulates C at the expense of competing sinks, as suggested by Sala et al. (2012, this issue)? How much of the carbohydrate stored is available and how much is sequestered, perhaps permanently, and what regulates this (Millard and Grelet 2010)? Is growth controlled by factors other than the carbohydrate supply (Navarro et al. 2008, Mund et al. 2010)? What are the factors that regulate input to and output from storage? What roles, besides those identified above, does carbohydrate supply from storage play in tree physiology? Sala et al. (2012, this issue) proposed a framework for answering these questions. Sala et al. (2012, this issue) also suggested that trees invest a large amount of C in storage that often acts as an active sink, and that these pools may be used to maintain hydraulic transport during episodes of severe stress. Given the potential importance of carbohydrate storage in trees, the lack of fundamental information about mechanism and control is distressing.

Pulse labelling

Pulse labelling of trees with stable or radioactive C isotopes has received renewed interest in the last few years to trace the fate of recently assimilated C inside the tree, and to the soil and the atmosphere. In their review of the literature, Epron et al. (2012a, this issue) highlighted a rather fast transfer of recent assimilates belowground despite species differences in transport velocity. The transfer rate can be strongly related to environmental conditions, decreasing as temperature and soil water content decrease (Plain et al. 2009). However, light levels do not affect the rate of C transfer in pine (Warren et al. 2012, this issue). Pulse-labelling experiments have revealed that C allocation patterns are highly dynamic and change with the seasons, but disentangling the effects of phenology, i.e., driven by biological controls, from those mediated by environmental factors remains a challenge. Pulse labelling potted silver birch saplings revealed that ozone exposure shifts C allocation belowground at the expense of leaves (Kasurinen et al. 2012, this issue). The importance of stored carbohydrates in trees (Sala et al. 2012, this issue) suggests that more field-labelling experiments will be required to understand the mechanisms that control storage and release, the contribution of stored carbohydrates to metabolism and respiration, and the

contribution of storage to growth (e.g., fine roots in spring, Endrulat et al. 2010; wood formation in ring-porous and diffuse-porous species, Palacio et al. 2011).

Future research

Ecophysiologicalists have long highlighted the need for a better understanding of the response of C allocation to the environment (Landsberg et al. 1991, Trumbore 2006). For some aspects, we have moved remarkably close to this goal. A recent review (Litton et al. 2007) and the mass-balance studies cited above show that all three components of C allocation (flux, partitioning and biomass) respond similarly to changes in resource availability. Increased resources (water, nutrients) increase GPP and decrease partitioning belowground, resulting in higher flux and partitioning to wood production. These responses occur across both sites and species, and within a site for a single species. We also now know that the transport of carbohydrates from the canopy to belowground is remarkably quick (Högberg et al. 2008, Dannoura et al. 2011, Epron et al. 2011).

Despite these successes, three areas seem to us to deserve intense research focus. First, the mechanism and function of carbohydrate storage need to be understood for timescales relevant for tree performance and survival (Sala et al. 2012, this issue). Examining fluxes to and from storage (rather than simply concentration changes) in response to resource variability would increase understanding and tie storage in with what we understand about C balance. Moreover, understanding interactions between N and C storage and remobilization are required to predict the response of trees to environmental change (Millard and Grelet 2010). Secondly, the relationship between short-term (diurnal), seasonal and annual patterns of flux and partitioning are not yet fully understood. Pulse-labelling experiments show that diurnal and seasonal flux and partitioning vary considerably. How are these variations integrated with more easily obtained annual estimates, and what is the relationship between the measurements at the different timescales? Development of models that account for variations in the natural abundance of stable isotopes of C and N, thus constraining transfer rates of C and N between plants and soil, might help link these temporal scales (Hobbie and Ouimette 2009, Ogée et al. 2009, Wingate et al. 2010). Finally, what are the feedbacks between C sinks (growth, respiration) and the other components of C balance (photosynthesis, storage and respiration)? Most models (and probably most ecophysiologicalists) assume that one can estimate photosynthesis knowing leaf area integrated photosynthetic capacity and environment, but sinks such as cell division and growth are much more sensitive to the environment than photosynthesis (Körner 2003). Any sink-source feedback is likely to involve C allocation processes. Studies coupling measurements of cell division and expansion with

measurements of photosynthesis, respiration and storage changes will aid in understanding these potentially important, but neglected, feedbacks.

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