



Tansley review

Modelling carbon sources and sinks in terrestrial vegetation

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Summary

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The increase in atmospheric CO₂ in the future is one of the most certain projections in environmental sciences. Understanding whether vegetation carbon assimilation, growth, and changes in vegetation carbon stocks are affected by higher atmospheric CO₂ and translating this understanding in mechanistic vegetation models is of utmost importance. This is highlighted by inconsistencies between global-scale studies that attribute terrestrial carbon sinks to CO₂ stimulation of gross and net primary production on the one hand, and forest inventories, tree-scale studies, and plant physiological evidence showing a much less pronounced CO₂ fertilization effect on the other hand. Here, we review how plant carbon sources and sinks are currently described in terrestrial biosphere models. We highlight an uneven representation of complexity between the modelling of photosynthesis and other processes, such as plant respiration, direct carbon sinks, and carbon allocation, largely driven by available observations. Despite a general lack of data on carbon sink dynamics to drive model improvements, ways forward toward a mechanistic representation of plant carbon sinks are discussed, leveraging on results obtained from plant-scale models and on observations geared toward model developments.

I. Introduction

In a world where plants are the only natural agent recycling carbon (C) from its low-energy form (atmospheric CO₂) back to its high-energy form (carbohydrates), understanding the limitations of this process is of utmost importance; and this is even more so because,

within the lifetime of an individual tree planted in the middle of the 19th century, the availability of one of the reactants of the aforementioned process, atmospheric CO₂ concentration [CO₂], will have doubled from 285 ppm in 1850 to > 500 ppm within the coming decades. Moreover, the terrestrial C cycle, and the associated C stored by vegetation through plant growth (terrestrial

C sink), remains the least constrained component of the current global C cycle (Le Quéré *et al.*, 2018), resulting also in uncertain projections of future [CO₂] (Friedlingstein, 2015). Indeed, changes in C stored in the soil and vegetation feed back to ongoing climatic change with an uncertainty range of up to 300 ppm of [CO₂] by the end of the century (Friedlingstein *et al.*, 2014). While some of this uncertainty is related to land management and land-use scenarios (e.g. Arneth *et al.*, 2017), a fundamental question in our current understanding of the vegetation C cycle globally is whether (1) C assimilation through photosynthesis, (2) plant growth, and (3) plant C sequestration are limited by the availability of [CO₂]. Importantly, point (1) does not imply point (2), and nor does point (2) imply point (3). Box 1 summarizes the terminology used in the literature and in this review for describing C sources and sinks depending on the spatial level of organization (plant or ecosystem) and the perspective (plant, ecosystem, or atmosphere). The C budget at the plant or ecosystem level is the net result of the balance between C sources and sinks. The variability of C sources and sinks at the plant level affects ecosystem-level C dynamics and the resulting global C budget. While we recognize the importance of forest demography (e.g. Bunker *et al.*, 2005) and soil biogeochemical processes in determining the terrestrial C sink (e.g. Thornton *et al.*, 2007), in this review we deliberately focus only on vegetation physiological processes.

In recent years, the literature has adopted the terms ‘source limitation’ for C source-limited plant growth, vs ‘sink limitation’ for plant growth limited by factors other than C assimilation (Körner *et al.*, 2007; Box 1). While most of the experimental evidence supports the prevalence of sink-limited plant growth (e.g. Millard *et al.*, 2007; Körner, 2015), analyses of the global C budget suggest that some of the human-emitted C may have stimulated plant growth, possibly leading to enhanced C storage in the phytomass or soil (e.g. Keenan *et al.*, 2016). This, however, can only be true if, across considerable spatial scales, source limitation dominated in the last decades. Here, we review this apparent discrepancy by discussing (1) the mechanisms of source vs sink limitation in plant growth, (2) the controversy about the CO₂-driven terrestrial C sinks and (3) how our understanding of sink- vs source-limited plant growth is reflected (or not) in terrestrial biosphere models.

Historically, considerable research efforts investigating the plant C budget have focused predominantly on C sources (e.g. Bernacchi *et al.*, 2013; Evans, 2013) rather than considering also the role of building C pools and C outputs; for example, respiration and tissue turnover (Millard *et al.*, 2007; Friend *et al.*, 2014; Körner, 2017). Perhaps the most basic, yet intuitive, justification for the need to consider all the components making up the C budget of a plant is the fact that C is just one of many ingredients needed for plant growth. Using a building construction site analogy, the source is represented by the availability of bricks and the sink is represented by the capacity of using these bricks to construct the building (the plant; Fig. 1). Bricks (i.e. C) are only one of the resources that are required to facilitate plant growth. It is unlikely that focusing only on brick delivery can explain the overall time of construction of the building, since other materials (e.g. fixtures and mortar, equivalent to nutrients in our analogy) or factors such as brick transport

Box 1 Plant- and ecosystem-level C sources and sinks.

Plant C budget

The balance between plant C sources and sinks determines the resulting C stock of the plant, while turnover of plant tissues provides the material for ecosystem-level heterotrophic respiration R_h .

C source and source-limited plant growth

Plant C source refers to gross primary production (GPP); that is, the C fixed through photosynthesis (carboxylation minus photorespiration; Wohlfahrt & Gu, 2015). Source limitation implies that GPP is limiting plant growth; that is, a higher GPP leads to enhanced growth. Plant growth here is defined as net primary productivity minus the C exported to mycorrhiza or exudated through roots; that is, GPP minus autotrophic respiration R_a , minus the sum of C exports. Autotrophic respiration sums up all the C respired from living plant tissues. These fluxes are looked at annual or multi-annual time scales, and in this definition the changes in C reserves are part of plant growth.

C sinks and sink-limited plant growth

Plant C sinks include C investment in plant growth (tissue expansion and meristematic activity, C allocated to reproduction), R_a , and C exported to mycorrhiza or through root exudation. Sink-limited plant growth refers to environmental (e.g. temperature, water, nutrient controls) or plant internal (e.g. ontogenetic) controls that determine plant tissue formation regardless of the amount of assimilated C.

Ecosystem C source and sinks

Focusing on vegetated ecosystems and assuming that lateral flows of C are negligible, GPP is the main C source to the ecosystem, and ecosystem respiration R_{eco} (the sum of R_a and R_h) and C losses via disturbances (e.g. fires, biomass harvesting) are the main C outputs. The balance between C source and outputs represent the ecosystem C budget and, for short time scales, equals the net ecosystem production (NEP = GPP - R_{eco}). If NEP is consistently positive, the ecosystem is a C sink.

Atmospheric C budget

From an ‘atmospheric’ perspective, similar terminology is used but with reversed signs of the C source and sinks to the atmosphere; that is, net ecosystem exchange of C between the land surface and atmosphere (under certain simplifications) is equal to -NEP (Chapin *et al.*, 2006). In this case, the residual between GPP minus C respiration and other C losses is the terrestrial C sink or source, depending on the sign.

(C transport), working conditions (temperature and water availability), and possible construction failures and unforeseen events (disturbances and competition) are all contributing to the final product (plant growth). To a certain extent, ‘brick trading’ may be possible in return for other materials (e.g. C investments in root growth to facilitate nutrient or water uptake), but only under specific conditions, and it will unlikely compensate for major deficiencies in other resources.

Knowledge of photosynthesis is fundamental for analyses of C budgets (e.g. Bernacchi *et al.*, 2013), and it is a natural component to start with in any C budget study because it defines the quantity of

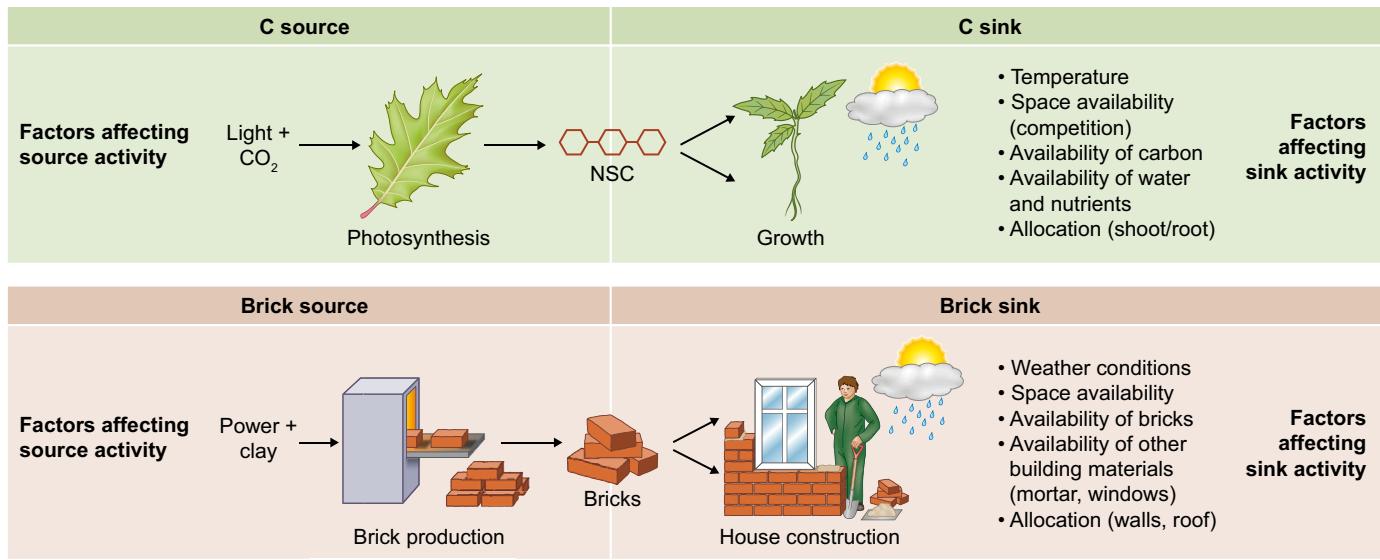


Fig. 1 The construction site analogy of carbon (C) source and sink limitation in plant growth. The build-up of C in a growing plant is ultimately governed by the provisioning of C (C source; left side of the figure), and its investment into plant tissues (C sink; right side of the figure). These processes and the factors driving them can be exemplified with the construction site analogy, where C, or bricks in our analogy, forms the key ingredient. The C source activity is mainly driven by the availability of light and atmospheric CO_2 (i.e. photosynthesis), or power and clay (i.e. brick production). Yet, for the C sink activity, where plant tissues (or buildings) are formed, the provisioning of C (or bricks) becomes only one of many limiting factors. Apart from C, favourable temperature and water availability, at least 14 other macro- and micronutrients are required (and hence can limit) the C sink strength (Körner, 2015). Often, these additional resources cannot be acquired by investing C. In the construction site analogy, these are other building materials (mortar, windows, etc.). Just like a plant is not entirely made up of C, a house is not just made of bricks and bricks cannot be easily traded for windows. While temperature affects both the C source and the sink, it systematically limits the C sink strength before the C source (Parent *et al.*, 2010). Further, processes like competition, C allocation and translocation to different plant tissues, and defence mechanisms can affect the C sink directly and the source only indirectly. Overall, this makes the C sink both much more complex to describe and model and also more likely to be limiting for plant growth. It is also obvious that the nonstructural carbohydrates (NSCs, the bricks before they are used for building) play a central role in the balance between C source and C sink activity. For example, the NSCs supply should be relatively low where the source (brick delivery) is limiting, but the opposite should be true where sink strength is limiting.

C entering into the plants. However, the reason for a prominent photosynthetic-centred perspective on the plant C budget is likely the ease with which leaf gas exchange became measurable in the second half of the last century (Körner, 2015). By contrast, C-sink-related processes, such as C allocation to different plant organs aboveground and especially belowground, are inherently difficult to measure and to describe analytically. Field data have therefore typically focused on leaf-level net assimilation (Ainsworth & Rogers, 2007) or changes in C stocks mostly aboveground (e.g. Brienen *et al.*, 2015; Doughty *et al.*, 2015), often disregarding harder to estimate C fluxes (respiratory losses, C exudates) and pools (nonstructural carbohydrates (NSCs), fine and coarse roots). Concurrently, there has been a focus on eddy covariance flux tower observations (e.g. Aubinet *et al.*, 2011), which are ideally suited to measure whole ecosystem exchange of C between the land surface and the atmosphere (net ecosystem exchange; Box 1), but upscaling those remains problematic (Friend *et al.*, 2007; Baldocchi, 2008; Medlyn *et al.*, 2017; Zscheischler *et al.*, 2017). Furthermore, eddy covariance data and atmospheric CO_2 -inversion (e.g. Schimel *et al.*, 2015) summarize the net effect (i.e. net ecosystem exchange) of two large but not individually measurable fluxes: gross primary production (GPP) and ecosystem respiration R_{eco} , making it difficult to constrain individual processes (Reichstein *et al.*, 2005; Lasslop *et al.*, 2010). Observations of carbonyl sulphide fluxes can help to disentangle photosynthetic CO_2 uptake from respiration

(Asaf *et al.*, 2013; Wehr *et al.*, 2016), but with high uncertainties (Wohlfahrt *et al.*, 2012). Remote-sensing approaches are based on light absorption and reflection and, therefore, are proxies of photosynthesis; for example, Moderate Resolution Imaging Spectroradiometer GPP (Yang *et al.*, 2013), fluorescence-based indices (Zhang *et al.*, 2016; Sun *et al.*, 2017) or leaf area index (LAI) (e.g. Global Inventory Monitoring and Modeling System, Zhu *et al.*, 2013). Therefore, although they may capture some of the variability in vegetation biomass (e.g. Myneni *et al.*, 2001; Pappas *et al.*, 2017), they contribute to the plant C source perspective, which has been prevalent in the literature.

Direct observations of growth are mostly limited to aboveground (e.g. Keeling & Phillips, 2007; Babst *et al.*, 2014), and there is not much information on growth at high temporal resolution; for example, by using high-frequency dendrometer observations (Deslauriers *et al.*, 2007) or sub-monthly wood microcores estimating xylogenesis (Cuny *et al.*, 2015; Delpierre *et al.*, 2016a; Rossi *et al.*, 2016). In addition, plant phenological patterns are well studied for leaves but remain poorly characterized for other components, such as roots or NSCs, with a few exceptions (e.g. Richardson *et al.*, 2013; McCormack *et al.*, 2014; Delpierre *et al.*, 2016b). Therefore, important knowledge gaps in characterizing plant sink function remain. Plant resource allocation strategies including the regulation of passive and active C storage and transport are poorly understood (Franklin *et al.*, 2012; Sala *et al.*,

2012; Steppe *et al.*, 2015). The available datasets originate from few experiments, making generalizations and broader process understanding challenging (e.g. sparse and sporadic NSC data; Martínez-Vilalta *et al.*, 2016).

Historically, the aforementioned observation-driven focus on plant C assimilation rather than growth is reflected in terrestrial biosphere models (TBMs, here used in the broadest sense; e.g. Fatichi *et al.*, 2016a), which mostly concentrate on photosynthesis and, in comparison, have simplified representation of plant respiration, sink activities and C turnover rates (Fatichi *et al.*, 2014; Pugh *et al.*, 2016). The C-source perspective in models is further reinforced by the existence of an elegant, robust and mathematically tractable framework for modelling leaf-level C assimilation (e.g. Farquhar *et al.*, 1980; Bonan *et al.*, 2011), for which there is no analogy in describing other plant processes. It is therefore not surprising that there have been only few attempts for a ‘balanced’ modelling of plant C sinks and sources, assigning adequate importance to both mechanisms. Although essential modelling frameworks of combined source and sink controls on plant growth were conceptualized early on (Thornley, 1991; Dewar, 1993), they have never been included in TBMs. This is because of their idealized nature and lack of adequate parameterization and validation for multiple plant functional types required by TBM applications. Only recently, following a growing focus on NSCs, plant mortality and effects of elevated CO₂ (eCO₂), attempts have been made to include sink limitation in TBMs (e.g. Leuzinger *et al.*, 2013; Fatichi *et al.*, 2014; Guillemot *et al.*, 2017). However, some of those approaches have remained at the proof-of-concept stage, while a systematic implementation in TBMs will require better generalization and confirmation with ground data. Concurrently, progress has been made in developing detailed tree-level plant hydraulic and C models (Hölttä *et al.*, 2006; De Schepper & Steppe, 2010; Schiestl-Aalto *et al.*, 2015), which offer a promising foundation for a mechanistic inclusion of plant C source and sink processes into TBMs. Despite these advancements, we are still far from having a mechanistic, or even a conceptual but extensively tested, implementation of C sink controls in TBMs. A representation of source–sink relations in models is likely fundamental to get the right answer for the right reason in plant responses to environmental changes (Leuzinger & Thomas, 2011; Fatichi *et al.*, 2014). For instance, we can expect that a more mechanistic and balanced description of C source–sink dynamics in plants will shed light on one of the longstanding controversies; namely, the discrepancy between consistently positive trends in terrestrial C uptake in global-scale observations in contrast to plot-scale observations, which suggest limited or no CO₂ stimulation of plant growth (e.g. Peñuelas *et al.*, 2011; Schimel *et al.*, 2015; see Section II). Changes in C stocks in soils may partially explain this discrepancy, but we argue that properly including C sink controls in TBMs has the potential to transform our understanding of biosphere–atmosphere feedbacks, which will likely impact on atmospheric CO₂ projections and their uncertainties. If measuring processes like phloem transport or

instantaneous plant growth was as easy as, for instance, measuring leaf gas exchange or remotely sensed GPP, such projections would have likely been different.

II. Discrepancy in predicting the effects of rising [CO₂] on the terrestrial C sink

Leaf-level photosynthesis of C₃ plants is C limited at current level of [CO₂], whereas for C₄ plants it is close to saturation (Drake *et al.*, 1997; Ainsworth & Rogers, 2007). This is supported by various studies including Free-Air CO₂ Enrichment experiments (e.g. Bader *et al.*, 2010; Ellsworth *et al.*, 2012). Therefore, if acclimation is limited, leaf-level C assimilation of C₃ plants increases with rising [CO₂]. However, different data sources are currently generating an important controversy on the evolution of the terrestrial C with increasing [CO₂]. From [CO₂] measurements and global C budgets, the existence of a C sink is evident (Pan *et al.*, 2011; Schimel *et al.*, 2015; Le Quéré *et al.*, 2018). The terrestrial C sink is continuously increasing or even accelerating, likely due to the pause in warming (Keenan *et al.*, 2016; Ballantyne *et al.*, 2017), reaching up to 3.0 Pg C yr⁻¹ in the latest years (Le Quéré *et al.*, 2018), even though this number is the residual term of other, more easily measurable pools and fluxes rather than a measured flux itself. How much of this amount of C is indeed taken up by plants is difficult to quantify, and it is unclear how much the increased [CO₂] is directly responsible for this outcome and how much is due to indirect effects such as changes in soil moisture (Fatichi *et al.*, 2016a), air temperature (Forkel *et al.*, 2016) or other environmental drivers (Huntingzinger *et al.*, 2017). Note that rising [CO₂] mainly affects photosynthesis; and whereas higher temperature may affect photosynthesis, it affects ecosystem respiration even more. Furthermore, processes such as landfill, lake deposition, organic-C river transport and regrowth of young forests can reduce the global intact land sink (Regnier *et al.*, 2013). However, the globally estimated C sink corresponds to an average of 20–30 g C that are stored each year for each square metre of vegetated land. Despite difficulties in direct attributions, recent studies suggest that the terrestrial C sink can be related to an increase in GPP, with a GPP growth of c. 31% in the 20th century, based on carbonyl sulphide observations (Campbell *et al.*, 2017). Similar results are obtained analysing the seasonal cycle of [CO₂] (Forkel *et al.*, 2016) or using water use efficiency (i.e. the ratio of C assimilation to transpiration) as a constraint of the C budget (Cheng *et al.*, 2017). To support this view, remote-sensing observations of vegetation reflectivity indexes show an increase in leaf area (greening) in the last decades, which has been largely attributed to increased [CO₂] (e.g. Donohue *et al.*, 2013; Zhu *et al.*, 2016). Observational evidence from undisturbed sites also supports the occurrence of such a strong terrestrial C sink due to increased [CO₂] (e.g. Keenan *et al.*, 2013; Fernández-Martínez *et al.*, 2017). In summary, from those studies and from corresponding TBM simulations (e.g. Schimel *et al.*, 2015; Keenan *et al.*, 2016), it appears that rising [CO₂] may have contributed considerably to the terrestrial C sink during the past decades.

However, even at continental scales, the attribution of the terrestrial C sink to specific regions remains challenging. Based on models, semiarid ecosystems have been identified as the largest

contributor to the positive trend of the C sink, with the mean C sink dominated by highly productive areas in the tropics (Ahlström *et al.*, 2015). Atmospheric inversion studies generally attribute most of the sink to the northern extratropics (Tans *et al.*, 1990; Peylin *et al.*, 2013) and are supported by regional aircraft measurements (Graven *et al.*, 2013); however, this interpretation has been challenged (Stephens *et al.*, 2007), and recent evidence seems to support a larger tropical sink (Schimel *et al.*, 2015). These findings are partially different to bottom-up estimates largely based on forest inventory data, which attribute the terrestrial C sink to tropical forests (Pan *et al.*, 2011; Espírito-Santo *et al.*, 2014), though more recent estimates suggest that, in particular, the sink capacity of the Amazon is declining (Brienen *et al.*, 2015), partly due to the occurrence of two important droughts in 2005 and 2010 (Lewis *et al.*, 2011). This is in contrast to a recent study based on aboveground C stock measurements suggesting that tropical forests may be a net C source (Baccini *et al.*, 2017). Overall, the use of ground-based measurements to locate the terrestrial C sink is still very limited (Zscheischler *et al.*, 2017), and these complementary but also contrasting findings suggest that representativeness of single studies must be interpreted with care.

Generally, a substantial terrestrial C sink is rather surprising from experimental studies and theoretical considerations, because biogeochemical effects such as stoichiometric limitation should potentially constrain GPP, and even more so plant growth (Hungate *et al.*, 2003; Norby *et al.*, 2010; Reich *et al.*, 2014; Ellsworth *et al.*, 2017). Climate trends may also act unfavourably given the tendency toward prolonged dry seasons in the tropics (Fu *et al.*, 2013). Nutrient and water availability should limit the plant C sink from a theoretical and physiological point of view (e.g. Millard *et al.*, 2007; Fatichi *et al.*, 2014; Körner, 2015; Campany *et al.*, 2017 – also, see Fig. 1 and discussion in Section IV). Arguments based on plant physiological response suggest that plant C sink limitation occurs earlier than source limitation for low temperatures and water stress (Hsiao, 1973; Parent *et al.*, 2010; Muller *et al.*, 2011). This also agrees with forest stand observations showing that fertile forests produce biomass more efficiently with a larger carbon use efficiency (CUE, the ratio between NPP and GPP; Vicca *et al.*, 2012; Fernández-Martínez *et al.*, 2014) and with nitrogen (N)-addition experiments demonstrating widespread signs of nutrient limitation (e.g. Le Bauer & Treseder, 2008). While indirect effects through water savings (due to reduced stomatal conductance under increasing [CO₂]) could contribute to increased NPP (Donohue *et al.*, 2013; Fatichi *et al.*, 2016a), the C sink of intact vegetation must show a progressive attenuation in the long term according to results of TBMs that account for N and phosphorus cycles (Zaehle *et al.*, 2010; Wieder *et al.*, 2015b).

Concurrently, analyses of tree rings suggest a [CO₂] stimulation of tree water-use efficiency but not of aboveground tree growth. This is the case for tropical trees (van der Sleen *et al.*, 2014; Groenendijk *et al.*, 2015), but similar patterns have been found in temperate forests (Peñuelas *et al.*, 2011; Lévesque *et al.*, 2014; Frank *et al.*, 2015). Similarly, Clark *et al.* (2013), using a unique long-term record of annual field measurements, show that increasing minimum temperatures and greater dry-season water

stress control annual aboveground NPP more than increased [CO₂] in a tropical forest stand.

These discrepancies between global- and stand- or tree-scale data demand for more scrutiny in the uncertainty and representativeness of the different observations. This will allow not only for a better identification of the underlying patterns and mechanisms, but also for a holistic model–data integration. For instance, change in wood density in different tree rings can affect their interpretation for intra- and interannual tree growth (e.g. Björklund *et al.*, 2017); also, tree demography can affect the interpretation of stand growth (Brienen *et al.*, 2017). Ecological processes such as changes in species composition, age distribution or stem density can affect trends in C stocks without affecting tree rings (e.g. Bunker *et al.*, 2005). Additionally, single forest stands may not be representative of the overall forest or biome behaviour (Körner, 2006), as often assumed, and global-scale estimates may be affected by much larger uncertainties than currently thought (e.g. Zscheischler *et al.*, 2017). Reconciliation of all this diverging observational evidence should also pass through the development of models of plant C sinks and sources based on better-resolved mechanisms, as discussed in the following sections.

III. Carbon and nutrient storage in plants and its modelling

From simple mass-budget considerations, and assuming typical values of leaf mass per area (50 g C m⁻²), peak LAI (4.5 m² m⁻²) and leaf N content (0.015 g N g⁻¹ DM) for a broadleaf deciduous forest in Europe or North America (e.g. Reich *et al.*, 1998a; Asner *et al.*, 2003), a full canopy costs around 225 g C m⁻² and 6.7 g N m⁻², which is roughly one-third of the annual NPP (Saugier *et al.*, 2001) and more than half of the annual N uptake (Reich *et al.*, 1997) for such a forest. Since full leaf cover is attained in roughly 1 month in spring (1/5th or 1/6th of the growing season), it is clear that, at least for deciduous forests, leaf flushing must rely on translocation of stored C and N. Short payback times of leaves could potentially explain such a rapid growth, but they refer to mature, top of the canopy sunlit-exposed leaves (Poorter *et al.*, 2006) and are not representative of the full canopy or forest scale. This trivial mass-budget consideration suggests that storage of C and other nutrients is fundamental for plant functioning. Storage happens at multiple temporal scales. There is a day/night leaf-level conversion of sucrose to starch and back to ensure a nearly constant flux of C from the leaves (Smith & Stitt, 2007). There are daily to seasonal storage dynamics at plant level in the form of NSCs across various compartments to buffer C uptake and C demands (Klein & Hoch, 2015; Hartmann & Trumbore, 2016). Similarly, nutrient reserves are used to buffer nutrient uptake and investment into tissue formation dictated by stoichiometric constraints (Ågren, 2008).

Several reviews have provided syntheses on the role of NSCs and the difficulty of their measurement (Dietze *et al.*, 2014; Martínez-Vilalta *et al.*, 2016). Unfortunately, owing to financial and time constraints, many observations of NSCs are not representative of the entire plant because some tissues are not sampled and because quantities are rarely scaled up to the tree level (but see Richardson

et al., 2013). Another problem is that what we can measure (i.e. the concentration of NSCs) does not provide causal evidence of what we would like to know (i.e. the regulation of NSCs according to environmental, phenological and ontogenetic changes in the plant; Hartmann & Trumbore, 2016). Some of the stored C is recent, reflecting that there is a continuous allocation to storage of fresh C assimilates. However, plants can mobilize old storage in specific situations, such as resprouting after disturbance (Keel *et al.*, 2007; Carbone *et al.*, 2013; Richardson *et al.*, 2015; Muhr *et al.*, 2016). Recent evidence also suggests that new roots can be formed with C that has been taken up years earlier (Vargas *et al.*, 2009; Solly *et al.*, 2018).

Despite some information on C residence times in plants, we know very little on how and when storage is regulated, what rules it follows and whether it is prioritized over allocation to growth and/or defence mechanisms. Note that a change in C allocation priorities may modify how a plant grows regardless of C source or sink limitation as defined in Box 1. Recent findings support that storage is not a passive compartment (Sala *et al.*, 2012), and allocation to storage can occur even during periods of C shortage (Palacio *et al.*, 2014). It is still unclear whether NSCs can be fully depleted when transport is not impaired (Hartmann *et al.*, 2013; Piper & Fajardo, 2016; Wiley *et al.*, 2017). In any case, daily and sub-seasonal dynamics are poorly characterized, and we often lack the means to upscale C storage and its changes from the individual plant to the ecosystem (e.g. g C m⁻²; but see Klein & Hoch, 2015). Such quantities will not only facilitate a better representation of NSC dynamics in TBMs but will also allow for an improved understanding of the underlying processes. Hoch *et al.* (2003) show that, in deciduous trees, NSC stores are high enough to provide three to five times the C required for a full canopy cover, but similar estimates are scarce for other ecosystems. Concurrently, some models use two-thirds of the living sapwood C-mass as a maximum threshold for C storage (Friend *et al.*, 1997; Fatichi *et al.*, 2012), corresponding to mean C reserves slightly below annual NPP, but from one to six times that of annual leaf-fall (Fig. 2). Unfortunately, empirical support for the plausibility of these assumptions and quantities is limited.

Modelling of C storage has been neglected for a long time in TBMs (e.g. Smith *et al.*, 2001; Peng *et al.*, 2002; Sitch *et al.*, 2003; Levis *et al.*, 2004) with rare exceptions (Friend *et al.*, 1997), and has only been introduced in the more recent models (Krinner *et al.*, 2005; Oleson *et al.*, 2013; Fatichi *et al.*, 2016b – but not always, e.g. Clark *et al.*, 2011). This was largely due to a poor understanding and quantification of how C is stored and allocated in plants, as discussed earlier. More recently, including C reserves was found to be pivotal not only for reproducing the seasonality of LAI (leaf phenology), but also to correctly represent the temporal C dynamics in all plant tissues (e.g. Delpierre *et al.*, 2016a). Moreover, simulating C reserves allows us to better represent plant resilience to disturbance, since, for instance, maintenance respiration during a drought that severely limits photosynthesis must rely on C storage (McDowell, 2011). Without C reserves, LAI seasonality is mostly empirically parameterized (e.g. Sitch *et al.*, 2003), rather than an emerging property based on vegetation C source–sink dynamics and environmental controls. Some TBMs

activate the NSC component only to drive leaf expansion at the onset of the growing season, whereas in others carbohydrates can be allocated to reserves throughout the growing season and can subsequently be translocated to leaves and fine roots in periods of low photosynthesis or after a severe disturbance (Medvigy *et al.*, 2009; Oleson *et al.*, 2013; Fatichi *et al.*, 2016a). While this structure better represents our conceptual understanding of the process, even these models lack a thorough evaluation of how C from storage pools is allocated and utilized (Mahmud *et al.*, 2018). Modelling of nutrient reserves is even rarer, with very few current attempts (e.g. Zaehle & Friend, 2010; Meyerholt & Zaehle, 2015). Despite these uncertainties, possible steps forward based on current knowledge are discussed in the following sections.

IV. Modelling the source and the sink: a plant perspective

1. Photosynthesis and stomatal conductance

Modelling of photosynthesis at the leaf scale is well established, since Farquhar *et al.* (1980) developed a physiologically based and mathematically tractable framework that allows for simulation of leaf-level C assimilation in response to radiation, temperature and leaf interior CO₂ concentration (Bernacchi *et al.*, 2013). The model requires biochemical parameters – the most important ones being maximum Rubisco capacity ($V_{c,\max}$), maximum electron transport capacity ($J_{c,\max}$) and intrinsic quantum use efficiency (ϕ). In its essence, the model simulates gross C assimilation (net assimilation plus leaf maintenance respiration) as a minimum or smoothed minimum between the velocity of the carboxylating enzyme Rubisco, a light-limited rate and, in certain model versions, the export-limited rate of carboxylation (for C₃ plants) and the phosphoenolpyruvate-carboxylase-limited rate of carboxylation (for C₄ plants). In order to obtain a value for the leaf-interior CO₂, the biochemical photosynthesis model must be combined with a stomatal model, which links net assimilation and stomatal conductance. Empirical models or models based on optimality principles are typically used in TBMs to compute stomatal conductance (Damour *et al.*, 2010; Fatichi *et al.*, 2016b; Buckley, 2017; Franks *et al.*, 2017). The biochemical model of photosynthesis can be upscaled from the leaf to the ecosystem scale accounting for the photosynthetic capacity and radiation profiles through the canopy (Niinemets *et al.*, 2015). Different levels of complexity in upscaling from the leaf to the canopy can be adopted and are indicated as ‘big-leaf’, ‘two-big-leaves’ or multilayer approaches (e.g. de Pury & Farquhar, 1997; Wang & Leuning, 1998; Bonan *et al.*, 2014). They mostly differ in their way of considering sunlit and shaded canopy fractions and in how different canopy fractions are averaged. Several refinements of the original Farquhar model have been presented in literature (e.g. Collatz *et al.*, 1991; Bonan *et al.*, 2011), and criticism has been also raised (Rogers *et al.*, 2017). However, this framework for modelling photosynthesis is used in almost all TBMs (but see recent developments by Wang *et al.*, 2017). This represents one of the most robust solutions adopted in vegetation modelling that passed multiple tests and the proof of time. There is more concern

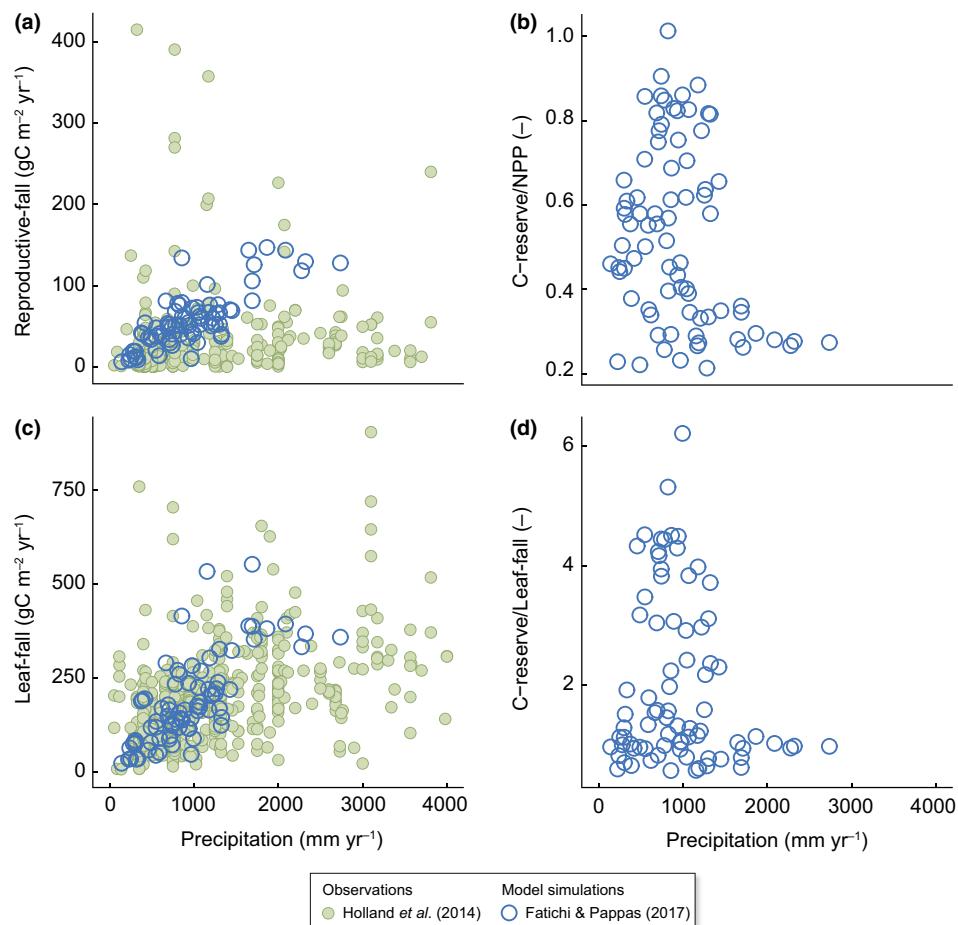


Fig. 2 Average annual values of litter production in terms of (a) reproductive-fall (fruits and flowers) and (c) leaf-fall as function of precipitation as derived from the global database of litterfall mass and litter pool carbon (C) and nutrients (Holland *et al.*, 2014). Superimposed onto observations are the simulations with the Tethys–Chloris model at the ecosystem scale for 79 sites world-wide characterized by different biomes and climates (Fatichi & Pappas, 2017). Simulated ratios between C reserve, annual net primary productivity (NPP) and annual leaf-fall (subplots (b) and (d), respectively) are also shown as a function of mean annual precipitation. The lack of observations of these quantities hampers model testing and development.

regarding the choice of the stomatal conductance models, which are still largely empirical. Mechanistic attempts to model stomatal dynamics exist (e.g. Buckley & Mott, 2013; Buckley, 2017), but their use in TBMs would require more extensive testing and knowledge of parameter distributions for various plant species. Despite similar performance under current climate, stomatal models may respond differently to climate change, especially to eCO₂ (Paschalidis *et al.*, 2017). In summary, we argue that we can model photosynthesis relatively well compared with other plant processes. This unbalanced complexity between the many simulated processes of TBMs leads also to unrealistic model sensitivities characterized by high sensitivity of ecosystem responses merely to photosynthesis parameters (Bonan *et al.*, 2012; Pappas *et al.*, 2013). Furthermore, the accuracy of the modelled photosynthesis can typically be tested at various scales, since good observation-driven estimates of C assimilation exist from the leaf to global scale (e.g. Wullschleger, 1993; Zhang *et al.*, 2016). However, issues related to scaling photosynthesis from chloroplast to leaf, and from leaf to forest, as well as parameter identification, and a lack of understanding of specific processes, such as acclimation of

photosynthetic capacity, downregulation of photosynthesis due to sugar accumulation or environmental responses of mesophyll conductance, still pose important challenges (e.g. Tholen *et al.*, 2012; Nikinmaa *et al.*, 2013; Smith & Dukes, 2013).

2. Autotrophic respiration

Contrary to photosynthesis, respiration is represented in a very simplistic way in all models. Only a few studies attempted a mechanistic approach to model respiration; that is, assigning respiration costs to tissue growth, nitrate reduction, symbiotic N₂ fixation, ion uptake, phloem loading, protein turnover and other maintenance operations (Amthor, 2000; Cannell & Thornley, 2000). However, mechanistic approaches are not implemented in TBMs to date.

Growth respiration in TBMs is a fixed fraction of NPP, and maintenance respiration is just a function of temperature (typically a modified Arrhenius equation), and often a linear function of N content in the different tissues (e.g. Sitch *et al.*, 2003; Clark *et al.*, 2011; Fatichi *et al.*, 2012; Oleson *et al.*, 2013; Pavlick *et al.*, 2013;

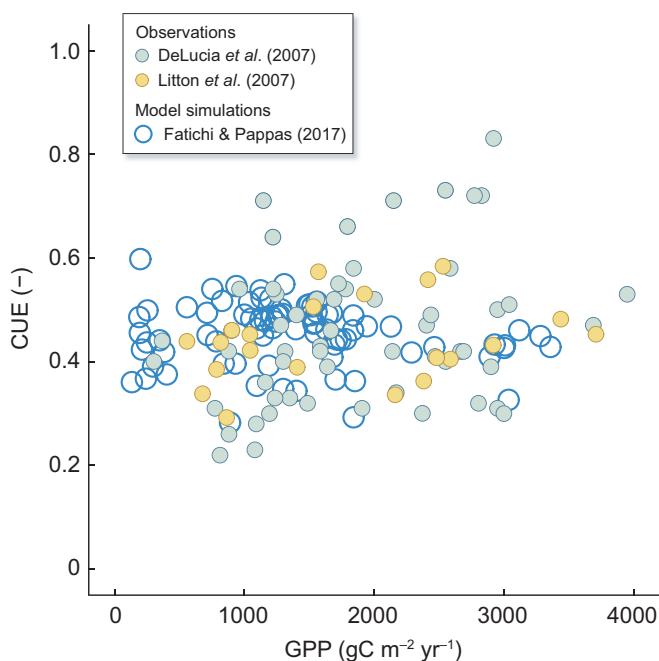


Fig. 3 Observed values of forest carbon use efficiency (CUE) as a function of gross primary production (GPP; data from Litton *et al.*, 2007; DeLucia *et al.*, 2007) compared with simulated values of CUE with the Tethys-Chloris model at ecosystem scale for 79 sites world-wide characterized by different biomes and climates (Fatichi & Pappas, 2017). The lack of correlation between CUE and GPP and the spread of observations are comparable for both model results and observations.

Huntingford *et al.*, 2017). The main parameters (growth respiration fraction (ω_g) and specific respiration coefficient (r_N in $\text{g C g}^{-1} \text{N d}^{-1}$) are typically assumed to be the same regardless of the vegetation type or plant tissue. Some models do not separate between the entire stem and its living part (e.g. Sitch *et al.*, 2003), making this parameter essentially an adjustment factor. Such a modelling solution is relatively simple and mostly follows Ryan (1991), who inspired almost all subsequent model implementations. A linear relation between respiration and N content is in contradiction with the multiple evidence for an exponential dependence of respiration on plant tissue N content (e.g. Reich *et al.*, 1998b, 2008). Additionally, the values of the parameters used in models (Sitch *et al.*, 2003; Levis *et al.*, 2004; Fatichi *et al.*, 2012) are at least one order of magnitude different from values reported in observational studies (Reich *et al.*, 2008; Atkin *et al.*, 2015). However, these values of model parameters are needed to obtain realistic ecosystem-scale CUE (Fig. 3), which challenges both the overly simple representation of autotrophic respiration in TBMs and the representativeness of observations. Additionally, night-time and daytime respiration of leaves are modelled equivalently in all models despite evidence that this is not the case either at the leaf scale (Heskel *et al.*, 2013) or at the ecosystem scale (Wehr *et al.*, 2016), with respiration being lower during daytime than during night-time (i.e. Kok effect).

Despite the aforementioned difficulties, total respiration should be relatively well captured by current models if we assume that

observed CUE ranges between 0.4 and 0.6 (unitless; Litton *et al.*, 2007) even though a wider range (0.2–0.8) has also been reported (DeLucia *et al.*, 2007). Models provide similar estimates and support the lack of correlation between CUE and GPP (e.g. El-Masri *et al.*, 2013; Fig. 3). A possible justification for the use of very simple methods to model respiration is that respiration is less temporally dynamic than photosynthesis, which could also explain why TBM comparisons with eddy covariance flux tower observations of C fluxes are often satisfactory (e.g. Krinner *et al.*, 2005; Blyth *et al.*, 2011; but see also Schwalm *et al.*, 2010). However, ecosystem respiration observations are very uncertain, and model–data agreement could be the result of tuning the empirical parameters to match observed data or simply of capturing the major patterns of summer/winter or day/night. In summary, even if some of the modelled C respiration matches observations, owing to the lack of a mechanistic basis in the modelling of respiration we cannot be confident we are getting the right answer for the right reason.

3. Direct controls of nutrients, water and temperature on sinks

In TBMs that consider only the C cycle there is no direct sink strength modelling; that is, all the C gained through NPP must be used for growth regardless of other environmental conditions. In some TBMs that include N and/or phosphorus cycles there is a sink control related to nutrient stoichiometry (Zaehle & Friend, 2010), even though sometimes nutrient limitation is only used to downregulate photosynthetic capacity (e.g. Bonan *et al.*, 2011). If nutrient uptake or supply from reserves does not keep pace with nutrient requirement for construction of new plant tissues, plant growth is sink limited (see right side of Fig. 1). Most models have static stoichiometry or very limited flexibility (e.g. Yang *et al.*, 2009). Therefore, there typically is an abrupt transition between a condition when nutrient uptake is sufficient with respect to the prescribed stoichiometry vs when this is no longer the case and sink limitation occurs, halting growth and reducing NPP. This limited flexibility has been recognized as a potential model shortcoming (Zaehle & Dalmonech, 2011). Some TBMs have started to introduce flexible stoichiometry (Meyerholt & Zaehle, 2015), which allows for a more nuanced response to nutrient limitation. However, TBMs are still far from capturing the reality of nutrient limitation in complex settings such as the response to eCO₂ in Free-Air CO₂ Enrichment experiments (Zaehle *et al.*, 2014). Furthermore, implementation of nutrient controls in models is tightly linked to the representation of soil biogeochemistry, and it is questionable whether nutrient limitation could be realistically implemented without an accurate description of soil C, N and phosphorus cycles, the modelling of which is currently one of the main challenges for TBMs (Wieder *et al.*, 2015a).

Only a few studies have introduced modules that account for sink limitation related to plant water stress and temperature controls. These reflect the idea of introducing controls on tissue growth or capability to allocate C from reserves unrelated to the quantity of assimilated C. Tissue growth activity depends on environmental controls, such as water potential, which controls turgor and therefore cell expansion (Hsiao, 1973; Muller *et al.*,

2011), or temperature, which controls enzymatic activity related to growth (e.g. Parent *et al.*, 2010). These environmental limitations on growth typically occur earlier (at less unfavourable conditions) than limitations on photosynthesis (Fatichi *et al.*, 2014). However, plants likely fine-tune the balance between assimilated C (the source) and utilized C (the sink) in the medium to long term, which makes it difficult to disentangle the cause from the effect in these two processes. For instance, inhibition of C sink activity at the leaf scale leads to an accumulation of sugars, which has been observed to downregulate photosynthesis, providing a direct negative feedback of sink controls on C uptake (Goldschmidt & Huber, 1992; Paul & Foyer, 2001; Mahmud *et al.*, 2018), to a point that the causality between photosynthesis and growth is reversed (Körner, 2015).

Attempts to introduce sink controls first originated from specialized models in agronomy, where sink limitation was implemented to better reproduce fruit growth and quality (e.g. Genard *et al.*, 2008). For natural ecosystems, Leuzinger *et al.* (2013) introduced a very simple function that accounts for temperature limitation of growth and showed that this considerably improved the representation of tree biomass with elevation and the location of the treeline at high latitudes. This approach, however, did not preserve the C mass budget, since the fate of the photosynthesized C not allocated to growth was simply discarded. Fatichi *et al.* (2014) presented a proof of concept using the Tethys-Chloris model to limit C allocation to growth when temperature and plant water potential were suboptimal, showing that this might have important consequences for forest response to eCO₂. More recently, Guillemot *et al.* (2017) introduced a new C allocation scheme using the CASTANEA model that accounts for lagged and direct environmental controls of C allocation. The explicit modelling of environmental controls of C allocation improved the ability to predict the spatial and interannual variability of aboveground forest growth with a significant effect of lagged water stress on the C allocation to leaves and wood. A formulation to introduce intrinsic limits of meristem and cellular growth rates related to temperature and water potential, as well as control mechanisms within the tree that influence its diameter and height growth, has recently been implemented at the individual tree scale with a number of simplifying assumptions (Hayat *et al.*, 2017). Such a model allows for identifying conditions of source or sink limitation related to tree height and photosynthetic capacity.

Despite these appreciable efforts to introduce sink limitations, a systematic implementation of sink control in TBMs has not yet occurred because of the scarcity of measurements to parameterize sink functions across different biomes and climates and because of the photosynthesis-centred perspective discussed previously (see also Fatichi *et al.*, 2014). A sink-limited growth module poses a series of additional challenges on the use of the ‘noninvested’ C, which implies modifications of the C reserves and allocation module and potentially also of respiration leading to a significant overhaul of the existing model formulations. However, the ongoing inclusion of N and phosphorus cycles in TBMs (Goll *et al.*, 2012; Yang *et al.*, 2014), which requires stoichiometric constraints, should facilitate the implementation of environmental sink limitation as well. Having this functionality in models is important for testing the model sensitivity to this component, which may

affect ecosystem responses to eCO₂ and, therefore, the uncertainty of climate change projections.

4. C allocation

C allocation remains the Achilles’ heel of TBMs, although this deficiency and theoretical alternatives were identified more than a decade ago (Cannell & Dewar, 1994; Le Roux *et al.*, 2001). All models use allocation strategies that are fundamentally empirical (Franklin *et al.*, 2012) and related to the number of C pools that are used to describe vegetation structure. This also allows for the inclusion of a C reserve pool (Section III). The simplest solution is to use static allocation coefficients that can be derived, for instance, from forest stand observations of NPP subcomponents (Wolf *et al.*, 2011). An alternative solution is to use functional rules based on the current understanding of the main controls over C allocation as light, water and nutrient availability (e.g. Friedlingstein *et al.*, 1998) or based upon ecological optimality principles (e.g. Farrior *et al.*, 2013). These functional rules are used to compute allocation coefficients based on temporally dynamic resource availability. Note that flexible allocation coefficients can also accommodate the capability of the plant to prioritize certain sinks over others; for example, shifting from stem to root growth in response to external stimuli, modifying the overall plant growth dynamics even in the absence of direct sink limitation. Regardless of the exact formulation of the allocation coefficients to the various C pools, allocation patterns are far from being mechanistically modelled, and current data availability prevents a thorough testing of existing alternative formulations with few exceptions (Mahmud *et al.*, 2018). Thus, in order to obtain realistic simulations, TBMs are often imposing allometric constraints; for example, a fixed or a maximum ratio between leaf and fine-root biomass or between leaf and living-stem biomass (e.g. Sitch *et al.*, 2003; Deckmyn *et al.*, 2006; Fatichi *et al.*, 2012). Although they allow for realistic representations of current conditions, results of TBMs are sensitive to the parameterization of such allometric constraints (e.g. Pappas *et al.*, 2013), which may drastically reduce the range of potential responses of vegetation C pools to environmental changes.

A step toward a mechanistic representation of C allocation in TBMs likely requires a more detailed modelling of this process at the plant scale, where water and C fluxes can be explicitly solved, as discussed in Section V, and integrated at the stand or ecosystem scale where species demography, diversity and competition also contribute to the overall forest response.

V. Plant-scale water and C flux models

A number of pioneering studies proposed models that include interactions between C, nutrient acquisition and transport within plants and subsequent C and nutrient allocation to plant structural components (Thornley, 1972, 1991, 1998; Dewar, 1993, 2000). These models are often termed transport-resistance models because their structure is centred on C transport and allocation rather than acquisition. They allocate C to different plant compartments (e.g. roots and shoots) according to a resistance network and C availability. The growth processes can be mediated

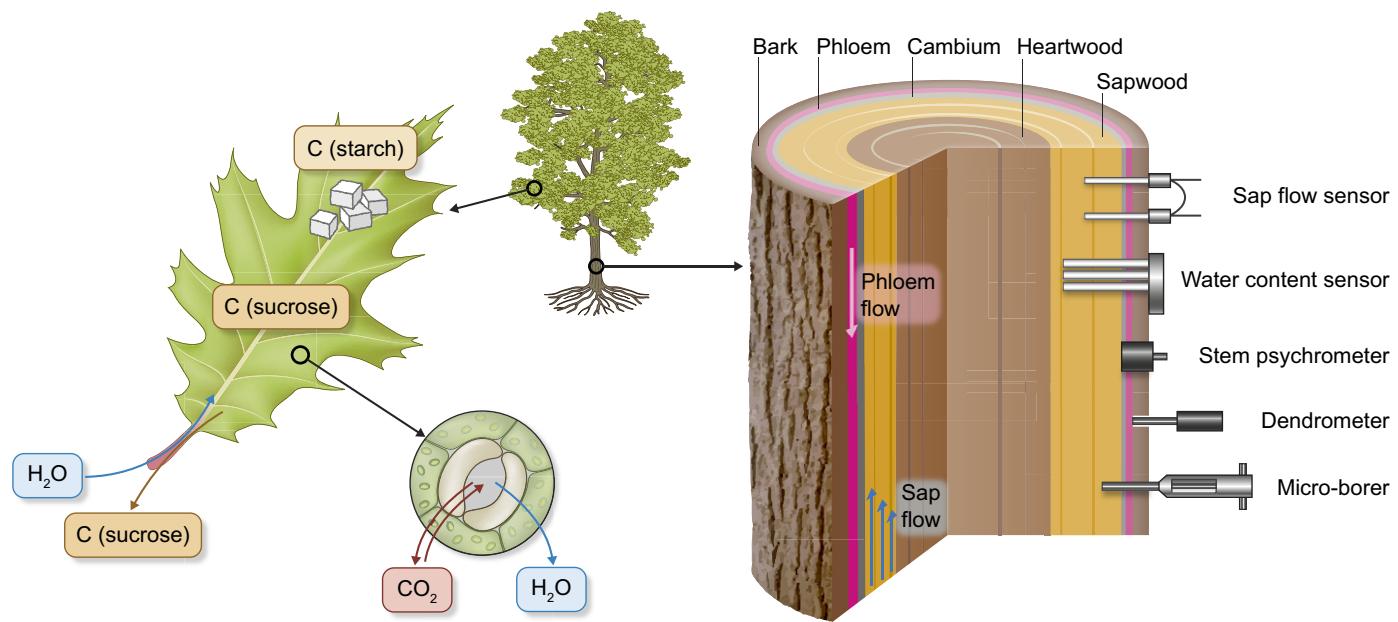


Fig. 4 An overview of the major plant processes affecting carbon (C) and water (H_2O) dynamics in the leaf and stem. CO_2 entering through stomata is assimilated by the plant (photosynthesis) and released to the atmosphere (respiration) and subsequently converted to sucrose (transportable C) and starch (stored C). The sucrose is transported to different plant tissues through phloem flow, while water absorbed from the soil, reaches the leaves passing through the conductive xylem in the sapwood. Commonly used instruments to quantify stem C and H_2O fluxes and storage are also depicted. The figure is inspired from Fig. 1 in Steppe *et al.* (2015).

by environmental conditions (e.g. Dewar, 1993), indeed making them the first plant C source–sink models. Unfortunately, these models were mostly used in idealized contexts. Therefore, parameter identification and testing for various plant species was never attempted, which can explain why their features were not incorporated in TBMs. However, similar concepts in a simplified (Gent & Seginer, 2012) or more detailed way representing phloem transport, turgor and sink controls were used by models designed for agronomic purposes (e.g. Fishman & Genard, 1998; Genard *et al.*, 2008; Jullien *et al.*, 2011; Martre *et al.*, 2011). Sink limitation is indeed fundamental for capturing the seasonal crop or fruit growth and quality and has received more attention in these settings than in forested ecosystems. More recently, several models have been developed to represent detailed plant hydraulics from root water uptake to leaf transpiration, including internal transport of water through the xylem, variations in root, stem and leaf water potential and loss of hydraulic conductivity (e.g. Hölterä *et al.*, 2006; Steppe *et al.*, 2006; Mirfenderesgi *et al.*, 2016). While important to understand plant vascular transport and the links between C and water flow, these plant hydraulic models were mostly developed to analyse plant water use and drought resilience strategies. They neglect C transport, which did not allow for modelling C dynamics and plant growth. Only a few attempts have been made to explicitly include phloem flow, tissue growth and diameter variations in realistic contexts (Hölterä *et al.*, 2006; De Schepper & Steppe, 2010; Nikinmaa *et al.*, 2014; Schiestl-Aalto *et al.*, 2015), following the initial work carried out for orchard crops (e.g. Daudet *et al.*, 2002). These models have different degrees of complexity, from a simple schematization

where various plant compartments are connected through a resistance network and capacitance functions (De Schepper & Steppe, 2010), to models discretizing the plant-transporting elements in the vertical and horizontal directions using finite volumes (Hölterä *et al.*, 2006). Regardless of their exact formulation, these works include most of the variables that are needed to simulate C transport and potentially sink controls on plant growth (Fig. 4). For instance, these models can link hydraulic transport and water potential to turgor pressure, and therefore modulate cambial growth, which reflects in changes in stem diameter and respiration (De Schepper & Steppe, 2010; Coussement *et al.*, 2018). Measurements of stem variations with high-frequency dendrometers, combined with a detailed monitoring of water and C fluxes and states (e.g. sap flow, stem water potential and content, stem CO₂ content), do in fact represent a way of testing and calibrating these plant-scale models of C and water dynamics (Steppe *et al.*, 2015; Zweifel, 2016; Salomón *et al.*, 2018). These measurements can offer fundamental observational support for mechanistic C source/sink modelling. Up to now, detailed tree-scale analyses have been mostly conducted with static vegetation parameters (e.g. fixed LAI, prescribed soil water potentials) and for a few days or only one growing season. Therefore, there is still a considerable disconnection between these models and the requirements of TBMs. However, their formulation represents an appealing scheme for introducing C allocation and sink controls in TBMs designed for larger scales in a systematic and mechanistic way. This scale gap, however, will require estimation of a considerable number of parameters and an adequate characterization of their species-specific variability, uncertainty ranges and

tools for upscaling these values at the ecosystem scale. Connecting the two approaches (plant and ecosystem scales) represents an important challenge for TBMs but holds the potential to considerably ameliorate the modelling framework of plant growth and better understand long-term C and water dynamics.

VI. Challenges for the future

1. Uncertainty on terrestrial C sink drivers

The issues discussed, particularly around sink- and source-limited vegetation modelling, should by no means overshadow the fact that TBMs have been extremely valuable in addressing a number of scientific questions related to global environmental change (e.g. Ahlström *et al.*, 2015; Forkel *et al.*, 2016). They have also been shown to reproduce the magnitude and historical trends in the terrestrial land C sink (e.g. Friedlingstein *et al.*, 2014; Keenan *et al.*, 2016), even though with remarkable uncertainties on the sensitivity to environmental variables and on the primary drivers of the cumulative C sink (Huntzinger *et al.*, 2017). For instance, TBMs completely miss the relevance of terrestrial water storage for C cycle variability (Humphrey *et al.*, 2018). Although this is likely an indication that certain components (e.g. photosynthesis) are modelled correctly, it is also partially the result of model tuning, and the huge variability in model sensitivities to environmental controls does not convey the desired confidence in future scenarios of the C budget (Huntzinger *et al.*, 2017). Increasing the reliability of long-term C-sink projections is indeed very challenging and requires representing the right causality in vegetation processes and dynamics (e.g. Zaehle *et al.*, 2014; Mastrotheodoros *et al.*, 2017). As a matter of fact, a mechanistic representation of how short-term plant physiological processes affect vegetation functioning at longer time scales is still lacking in state-of-the-art TBMs (Pappas *et al.*, 2017).

2. Observing C storage directly and mostly indirectly

A more detailed description of C allocation and remobilization processes is expected to shed light on the interplay of various plant physiological processes across time scales. There is a clear and urgent need for more information on C storage and its temporal dynamics. While we recognize the importance of NSC observations themselves (Martínez-Vilalta *et al.*, 2016), we need quantities that are more useful for models; for example, standardized and upscaled values of C pools per unit of ground area. Ideally, we should be able to understand the physiological and biochemical basis of C allocation and C storage before translating them into models (Hartmann & Trumbore, 2016). However, even in their absence, systematic data about C storage and growth in different plant compartments at relatively high temporal resolution (monthly, daily, sub-daily) can support semi-mechanistic models where C storage variability or simply C pools are modelled to change over time according to plant phenology and in response to environmental conditions (Mahmud *et al.*, 2018). As a more basic requirement, having relatively constrained estimates of C pools in g C m^{-2} for different plant compartments (e.g. Fig. 2) and

multiple species would be a great improvement in comparison with the current information used to develop C allocation schemes in several models. For instance, rather than considerably increasing time- and cost-intensive NSC observations, an easier way forward may be to estimate C budgets and seasonal NSC storage dynamics at the forest stand scale mostly indirectly as the residual of other observed C pools and C fluxes (Gough *et al.*, 2009; Klein & Hoch, 2015). Another promising avenue is represented by remote-sensing observations of forest biomass stands that can track the amount of leaves and stems in a distributed way (e.g. LiDAR; Mascaro *et al.*, 2011), yet below-ground C pools remain unquantified. Existing forest inventories could be very important for testing long-term dynamics, but they typically have too coarse temporal resolution to constrain model at sub-annual or annual time scales. Since C storage is so important for models and considering that direct observations of storage will remain challenging at the ecosystem scale, we encourage experimentalists to approximate NSCs indirectly from mass-budget analyses of other pools. For instance, defoliation as a treatment is not widespread among manipulation experiments but could provide quantitative and very useful information on the amount of C available to recover from disturbances or stress periods (e.g. Galiano *et al.*, 2011; Landhäusser & Lieffers, 2012). In summary, there is a mismatch between NSC observations and what is really needed to advance C allocation in TBMs; hopefully, a tighter collaboration between modellers and experimentalists will bridge this gap. Global repositories of C pool data, as they already exist for other plant traits (e.g. TRY database; Kattge *et al.*, 2011), could also help in achieving this task.

3. Evaluating models of plant vascular transport

A larger number of studies simulating water and C dynamics at the plant scale are also welcome, since current approaches are quite seldom compared to the number of applications with TBMs. However, these models need more thorough testing with plant-scale observations (e.g. sap flow, stem and leaf water potential, stem diameter changes, leaf growth, respiration; Steppe *et al.*, 2015) and the capability to include plant growth controls. Knowledge and parameterizations gained from the tree-scale models can then be used as the basis for conceptual implementations of C allocation and sink controls in TBMs, where we will unlikely solve xylem and phloem flow in detail globally – but see Bonan *et al.* (2014) and Xu *et al.* (2016) for recent implementations of plant hydraulic schemes in TBMs. Such a new direction does not require unconventional observations and, if supported with appropriate data, may provide the first basis for a mechanistic representation of plant C allocation.

4. Exploratory studies to quantify large-scale consequences of sink limitation

Currently, even without a precise mechanistic knowledge of sink relations, we can still use functions for limiting plant growth related to temperature and water availability in order to analyse their effects on vegetation response, similar to the proof of concept of Faticchi *et al.* (2014), or the model of forest growth of Guillemot *et al.*

(2017). As an additional motivation, given the fundamental role of sink limitation for crop modelling, we argue that forest dynamics are unlikely to be properly captured without such a component. Studying sensitivities to environmental sink limitation has the same value as explorative studies carried out to highlight the potential importance of N and phosphorus limitations on terrestrial productivity (e.g. Wieder *et al.*, 2015b) and will boost the debate about the fate of C storage in vegetation under changing climate.

5. Reconciling terrestrial C sink contradictions across scales

The new model concepts and modules presented could help to reconcile important contradictions such as the limited growth stimulation revealed by tree rings but the presence of a terrestrial C sink, and the difference in respiration coefficients between modelled quantities and observations. They can also suggest that the available observations may be less representative or more uncertain than previously thought (e.g. the terrestrial land sink, Zscheischler *et al.*, 2017; or tree ring data, Brienen *et al.*, 2017) and may help in revising upscaling methodologies or to better define representativeness of specific observations (e.g. CO₂ inversion method, forest plot inventories or tree-ring data). TBMs, because of their closure of the energy and mass budgets, may be useful for constraining the plausibility of some of the observed quantities and help resolving current controversies (e.g. Fatici & Leuzinger, 2013; Mastrotheodoros *et al.*, 2017). From tree-scale observations (Peñuelas *et al.*, 2011) and plant physiological considerations (Parent *et al.*, 2010; Muller *et al.*, 2011), expectations are that sink controls should emerge more prominently with eCO₂, and drier and warmer conditions (see also Peñuelas *et al.*, 2017). The fact that, currently, there are no signals for the occurrence of these limitations at larger scales is baffling and remains unresolved, but this could be the result of regrowing forests biased toward young ages, uncertain global estimates of C budgets or nonrepresentative local-scale observations. More mechanistic TBMs that have a balanced representation of source and sink controls on plant growth could help in solving the puzzle.

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Authors contributions

SF, CP, SL and JZ designed the structure and content of the review; SF wrote the paper and selected the references with contributions and comments from the other authors.

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