Moving beyond photosynthesis: from carbon source to sink-driven vegetation modeling

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Letters

Moving beyond photosynthesis: from carbon source to sink-driven vegetation modeling

Introduction

Knowledge of future terrestrial carbon (C) pools and fluxes is based on simulations by Dynamic Global Vegetation Models (DGVMs; Cox *et al.*, 2000; Sitch *et al.*, 2008). For simplicity we used the DGVMs acronym to include all of the models able to simulate C and vegetation dynamics at large spatial scales, which are sometimes referred to as Terrestrial Biosphere Models, Terrestrial Ecosystem Models, vegetation components of Earth System Models, and Land Ecosystem Models. DGVMs are now typically coupled to climate models to account for biophysical and biogeochemical feedback caused by vegetation (Bonan, 2008; Chapin *et al.*, 2008; Anderson *et al.*, 2011). The ultimate aim is to simulate climate–vegetation dynamics that explicitly account for mutual interactions and thus provide us with a better spatiotemporal description of water fluxes together with the most realistic scenarios for the future climate and C cycle (Friedlingstein *et al.*, 2006; Thornton *et al.*, 2007; Bonan *et al.*, 2011).

Current DGVMs are simulating long-term tree and forest stand growth as a consequence of the amount of assimilated C, triggering an inevitable positive feedback between C assimilation and growth. The key factors affecting stomatal aperture and C assimilation are atmospheric CO_2 concentration, water availability, light, vapor pressure deficit and temperature (Sellers *et al.*, 1997; Lawson *et al.*, 2011). However, direct control of C sinks (defined as growth in the sense of C investment on plant tissue expansion) via environmental factors has been shown to be more important than indirect control via photosynthesis (the C source, see Fig. 1). For example, water- or temperature-limited plants tend to reduce growth but increase C storage (Körner, 2003; Sala & Hoch, 2009; Woodruff & Meinzer, 2011; Sala *et al.*, 2012), which suggests that environmental controls act first on sink activity rather than source activity (Körner, 2013). Nevertheless, in all existing DGVMs, plant growth is driven by photosynthesis directly without considering water and thermal limitations via metabolic, cambial and meristematic activity (blue arrows in Fig. 1; Bonan *et al.*, 2003; Sitch *et al.*, 2003; Krinner *et al.*, 2005). The entire photosynthesized net C (the source) is then partitioned among different C pools, mostly based on allometric rules derived from observations (Poorter *et al.*, 2012) or using simplified functional allocation schemes (Friedlingstein *et al.*, 1998; Franklin *et al.*, 2012). Allocation to carbohydrate reserves, root exudates and export to symbionts are mostly missing. This

opens up a huge discrepancy between the way plant growth is modeled today (blue arrows in Fig. 1) and the way it is understood based on experimental evidence (red arrows in Fig. 1). In this article, we suggest a revised hierarchy of plant growth control by removing the causal link from C assimilation to plant growth and by providing a description of the mechanistic connections among processes.

The hierarchy of plant growth control

Available soil water, temperature, nutrients, light, and CO_2 are indisputably the key drivers of plant growth (Boisvenue & Running, 2006; McMurtrie *et al.*, 2008; Ågren *et al.*, 2012; Fig. 1). The former three (water, temperature, and nutrients) are fundamentally different from the latter two (light and CO_2) because they can affect both sink and source activities, while light and CO_2 only affect the source activity (C assimilation, Fig. 1). In this section, we compare the hierarchy of such limitations based on experimental evidence, which will lead into the discussion of strategies for modeling plant growth.

Water

When water limitations occur, there is evidence that cambial and leaf growth are inhibited at much lower levels of water stress (higher water potentials) than photosynthesis (Fig. 2; Boyer, 1970; Hsiao, 1973; Hsiao *et al.*, 1976; Muller *et al.*, 2011; Tardieu *et al.*, 2011). Because organ expansion is affected earlier and more intensively than photosynthesis, plants experiencing soil water deficit often accumulate nonstructural carbohydrates (NSC) and reduce growth (Würth *et al.*, 2005; Woodruff & Meinzer, 2011). Drought stressed or more apical parts of trees show lower xylem- or leaf-water potential than well-watered or more basal parts. This decrease in xylem- or leaf-water potential implies a reduction in cell turgor and in the capacity to transport sugars (Woodruff *et al.*, 2004; Sala *et al.*, 2011; Woodruff & Meinzer, 2011). Specifically, lower cell turgor has the potential to limit cell wall expansion, cell wall synthesis and protein synthesis (Lockhart, 1965; Hsiao, 1973; Sala *et al.*, 2011). This means that C assimilation continues while sink activity (tissue growth) is inhibited, which most likely explains the accumulation of NSC in stressed plants (Körner, 2003). For example, Sala & Hoch (2009) showed that in *Pinus ponderosa*, mobile C compounds increase with increasing tree height. The possibility of plants actively prioritizing storage over growth allows additional interpretations of the role of accumulating NSC, for example, to maintain the integrity of the hydraulic system (Sala *et al.*, 2012) or for signaling purposes (Rolland *et al.*, 2006). However, recent evidence seems to support that when hydraulic transport is not affected, NSC is significantly depleted as a consequence of C demand (Hartmann *et al.*, 2013;
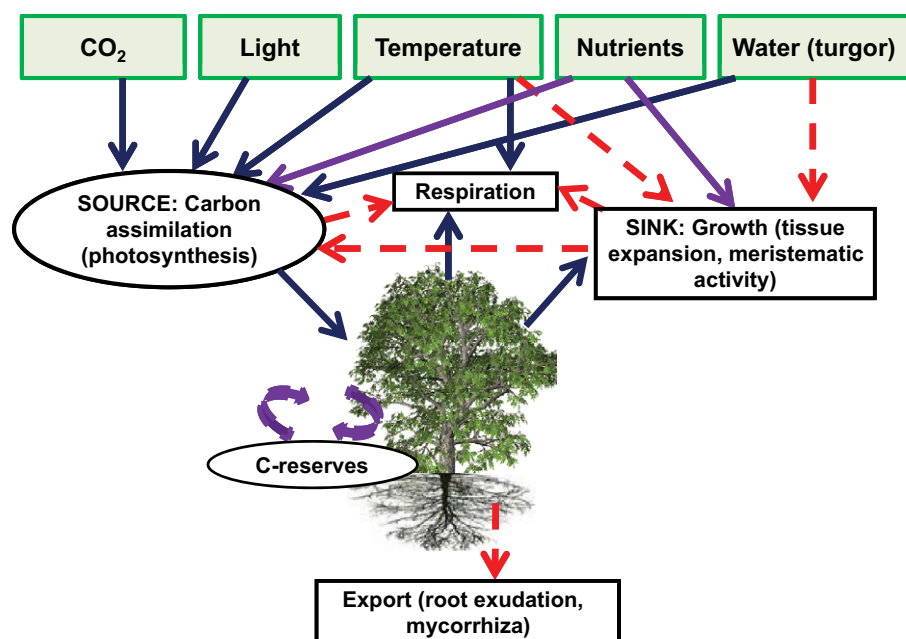
Fig. 1 Plant growth as modeled in current Dynamic Global Vegetation Models (DGVMs; blue arrows) and based on empirical evidence (additional red dashed arrows), nutrient controls on growth and carbon (C) reserves are included in a subset of models (violet arrows). The difference between the two conceptual models is fundamental, but because many processes are correlated, plausible results can be obtained in the short term, even with a mechanistically wrong approach.
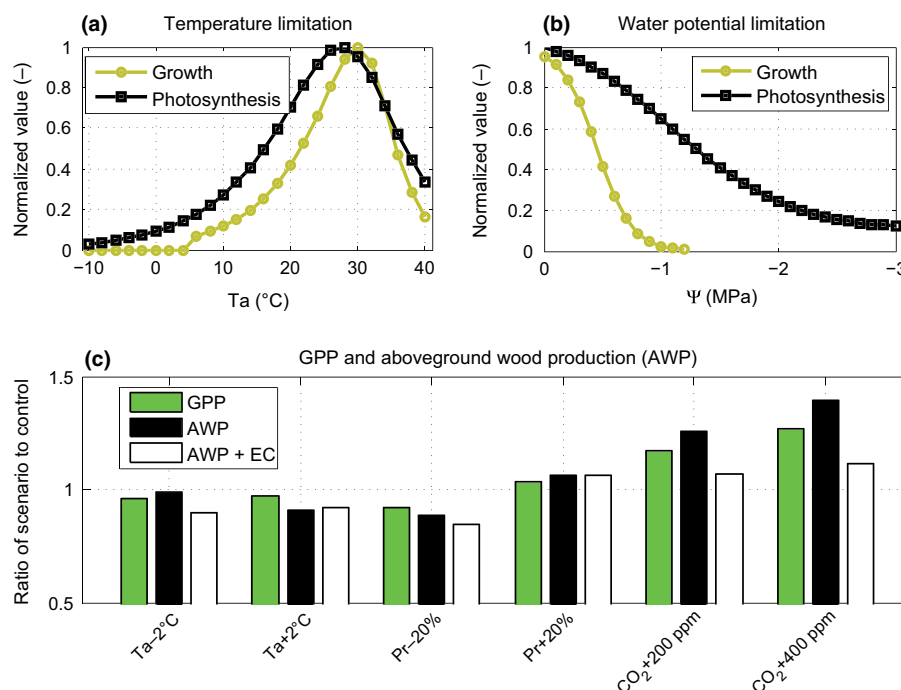

Fig. 2 Difference between normalized photosynthesis and structural growth (fractions of maximum value) as a function of temperature (a) and soil water deficit (b). The y-axis refers to both photosynthesis (squares) and organ growth (circles). Sub-plot (c) shows a proof-of-concept using a model where direct temperature and water (turgor) controls for growth were simply implemented for this analysis. The model T&C (Fatichi *et al.*, 2012) was used to simulate carbon (C) assimilation and plant growth for a 30-yr period (1980–2010), with parameters and boundary conditions characteristic of a Swiss deciduous forest and the climate of Zurich (Switzerland). The shape of the temperature and water limitation controls (a, b) was adapted from the literature (Parent *et al.*, 2010 for temperature; Muller *et al.*, 2011 for water deficit) and the actual values were derived assuming that all the C that is allocated in the original model to structural growth can be allocated in the present climate also in the model with environmental controls for growth (EC). This hypothesis implies that photosynthesis and growth are coordinated in the present climate. Imposing the same environmental controls on growth, six hypothetical scenarios were simulated: plus and minus 2°C air temperature (Ta), plus and minus 20% precipitation (Pr), and plus 200 and 400 ppm of atmospheric CO_2. The scenario to control ratios of GPP (Gross Primary Productivity), AWP (Aboveground structural Wood Production, original model) and AWP + EC (AWP + environmental controls) with respect to the present climate are shown. Differences between AWP and AWP + EC are present for Ta-2°C and Pr-20% and are striking for the CO_2 enrichment scenarios. Note that the proof-of-concept is likely to underestimate the difference because nutrient limitations and feedbacks of growth limitations on photosynthesis are not accounted for. Also, we assumed that C available at any time can be stored and successively allocated to structural growth if favorable conditions occur (i.e. infinite size of C reserve pool and no respiration or exudation from reserves).

Sevanto *et al.*, 2013). Exacerbation of these mechanisms (low turgor and incapability to transport sugars) also seems to play an important role in tree mortality and therefore long-term forest dynamics (McDowell, 2011; McDowell *et al.*, 2011).

Inhibition of sink activity via low water potentials and the resulting accumulation of photo-assimilates in leaves can also lead to direct feedback, that is downregulating photosynthesis (Paul & Foyer, 2001; Nikinmaa *et al.*, 2013), which demonstrates a direct control of photosynthesis via growth (red horizontal arrow in Fig. 1).

Temperature

Similarly to water stressed plants, temperature-limited plants such as trees at the treeline and winter crops are typically limited by sink activity (tissue expansion) earlier than by source activity (C assimilation; Fig. 1; Körner, 2012). Consequently, cold-limited plants show an increase rather than a decrease in NSC with colder temperatures (Körner, 2008; Fajardo *et al.*, 2012; Hoch & Körner, 2012).

Temperature influences several metabolic processes (e.g. cell doubling time), determining the potential growth rate of organs in the absence of other growth limiting factors (Pantin *et al.*, 2012). Most temperature-controlled processes of plant growth have been summarized by Boltzmann–Arrhenius type equations, which describe a decrease in growth rates at sub-optimal and supra-optimal temperatures (Parent *et al.*, 2010). Furthermore, a 5–6°C threshold has often been identified to limit growth in cold adapted species, irrespective of photosynthetic activity which typically ceases only at freezing point (Körner, 2008).

Nutrients

Nutrient limitation is well known to exert a negative feedback on photosynthesis via the amount of fundamental enzymes needed for C assimilation that can be produced. The amount of synthesized Rubisco, for example, is strongly controlled by nitrogen availability (Kattge *et al.*, 2009). However, nutrients also act as direct plant growth control due to the relatively constant stoichiometry of plant tissue composition (Sterner *et al.*, 2002; Leuzinger & Hättenschwiler, 2013). This has emerged clearly from FACE experiments where progressive nitrogen limitation (Luo *et al.*, 2004) has been demonstrated to limit plant growth (Norby *et al.*, 2010). While plants have the capacity to recruit additional nutrients by expanding their root system and via mycorrhizal symbioses, nutrient limitations are likely to progressively emerge at the landscape scale. Importantly, no study has been able to clearly quantify nutrient limitation acting on sink (tissue growth) vs source activity (C assimilation).

Light and CO_2

Light as well as atmospheric CO_2 clearly limit photosynthesis (the source), and unlike the previous factors discussed, they do not affect the C sinks directly. Therefore, the question here is whether (and if yes, when) the effect of CO_2 and light is limiting sink activity

(growth) via source activity (blue arrows from source to sink activity via the tree in Fig. 1). In other words, is plant growth C limited and under what conditions? Arguments in favor of C limitation of plant growth are either based on young seedlings and saplings in the forest understory or on individual leaves in dense canopies that are almost always operating below light saturation (Turner, 2001; Lloyd & Farquhar, 2008). Accordingly, CO_2 was found to have a stimulatory effect on growth of plants in the understory (Würth *et al.*, 1998; Hättenschwiler & Körner, 2000). Lloyd & Farquhar (2008) inferred that growth of tropical forests is C limited using the relationship between growth and photosynthesis: $N_p = G_p[1 - \phi]$ where N_p is net primary production (new growth), G_p is the average rate of photosynthesis, and ϕ is the proportion of assimilated C lost via total respiration plus volatile organic C emissions and root C exudation. They argue that higher G_p as a consequence of increasing CO_2 concentration or incoming light necessarily leads to enhanced growth. However, we propose that this equation should generally read $N_p = G_p(N_p)[1 - \phi(G_p(N_p))]$, thus not be interpreted as a direct causal link between photosynthesis and growth, because ϕ is a function of G_p, and N_p can feedback on photosynthesis, that is, $G_p = f(N_p)$. Rewritten in these terms the equation is highly nonlinear and an increase in G_p does not imply a proportional increase in growth.

Leaf level light responses of seedling and single leaves are difficult to extrapolate to the forest level, because this would imply that a forest stand behaves like a single leaf or shadowed tree. Light and consequently CO_2 limitations of individual leaves, saplings or trees are not a demonstration that the entire forest community operates below its CO_2 uptake capacity and even less that C acquisition is limiting forest growth (Körner, 2009; Clark *et al.*, 2013). The Leaf Area Index (LAI) in several ecosystems (e.g. tropical forest, alpine grassland) may be higher than needed to sustain maximal productivity (Amiro *et al.*, 2010; Gough *et al.*, 2013; S. Fatichi, M. J. Zeeman, J. Fuhrer & P. Burlando, unpublished). Many studies suggest that partial (moderate) defoliation hardly affects tree growth or forest productivity (Ericsson *et al.*, 1985; Hoogesteger & Karlsson, 1992; Reich *et al.*, 1993; Kaitaniemi *et al.*, 1999; Volin *et al.*, 2002). A larger than necessary LAI typically has evolutionary rather than physiological reasons: to shade competing neighbors and thus limit their performance; as insurance against herbivory and storm damage; and as an additional option to store nutrients (especially in evergreen trees). Therefore, while light and CO_2 may limit growth at the leaf or plant level, they unlikely do so at the landscape (whole forest) level and in the longer term (Leuzinger & Hättenschwiler, 2013). Short-term benefits of extra light (Graham *et al.*, 2003) or elevated CO_2 (Norby & Zak, 2011) can only be sustained to the extent a higher growth rate is supported by higher nutrient availability.

Current atmospheric CO_2 concentration (close to 400 ppm) additionally represents a rather exceptional forcing in the evolutionary context, with the current species having evolved in CO_2 concentrations between 180 and 290 ppm (Siegenthaler *et al.*, 2005; Lüthi *et al.*, 2008). This suggests that C availability is at least less limiting nowadays (Körner, 2006). Accordingly, CO_2 enrichment experiments with closed forest canopies did not show a sustained stimulation of growth by elevated CO_2, except under

high nutrient availability (Finzi *et al.*, 2007; Norby *et al.*, 2010; Bader *et al.*, 2013; Sigurdsson *et al.*, 2013).

The carbon source–sink balance

The differential sensitivity of C source and sink activities to water, temperature, and nutrient controls could lead to an imbalance between C supplied by photosynthesis and C used for tissue growth and respiratory costs. A mismatch between these two quantities would be sub-optimal and create a long-term surplus of assimilated C. In normal conditions, this situation is avoided through at least three mechanisms. First, in the short term, acclimation of photosynthesis occurs through negative feedback given by accumulation of starch or higher concentration of sucrose at the leaf level (Paul & Foyer, 2001). However, such a strategy would not be very effective to counteract mid/long-term source–sink imbalance. Second, therefore, in the mid-term, plants use sophisticated mechanisms of C storage at the leaf and whole plant level through accumulation and depletion of NSC (Kozlowski, 1992; Hoch *et al.*, 2003; Gough *et al.*, 2009; Richardson *et al.*, 2013). Fluctuations of NSC are expected to buffer the difference between C supply and demand for timescales from hours to a few years. NSC dynamics are likely to be actively controlled by plants rather than a pure passive deposit of C (Sala *et al.*, 2012). Third, in the long-term, evolutionary processes likely fine-tuned the photosynthesis apparatus (C source) to match long-term investment capacity (C sinks), which is the first to be controlled by environmental limitations. This process of internal source–sink regulation can be summarized as 'growth controls photosynthesis' (Körner, 2013) and forms the strong correlation between sinks and sources which is likely responsible for the wrong established hierarchy of controls in the literature.

Manipulating the carbon source–sink balance

Carbon dioxide enrichment experiments as well as prolonged conditions of water or temperature limitations have the possibility to break the balance between C sources and sinks. For instance, an increase of NSC is typically found in CO_2 enrichment experiments. Furthermore, increased atmospheric CO_2 almost always causes enhanced photosynthesis with little or no downregulation (Zotz *et al.*, 2005; Bader *et al.*, 2010). However, this typically does not translate into enhanced growth, especially in the long term and for mature forests (Leuzinger *et al.*, 2011; Norby & Zak, 2011; Bader *et al.*, 2013). Because the C mass has to be conserved, this imbalance has posed several questions about the fate of the 'extra-carbon' (Fatichi & Leuzinger, 2013). Tracing the extra C experimentally is extremely difficult, particularly quantitatively and belowground (Palmroth *et al.*, 2006). Therefore, the fate of the extra C in CO_2 manipulation experiments is largely unknown to date. Possible pathways are: increased respiration; root exudates and export to mycorrhiza (Phillips *et al.*, 2011, 2012). Larger C assimilation enhances maintenance respiration because of the larger substrate available, and enhances sugar loading and thus transport respiration costs (Cannell & Thornley, 2000). Additionally, if root exudation is assumed as a (passive) diffusion process (Farrar *et al.*,

2003), a larger sugar concentration in roots would produce more exudates simply due to the steeper concentration gradient, causing the frequently observed nutrient limitation through microbial competition under elevated CO_2 (Diaz *et al.*, 1993; Hättenschwiler & Körner, 1998).

The use of manipulative experiments (e.g. with elevated CO_2) is crucial to understand the C source–sink balance and therefore the true drivers of plant growth, under different environmental conditions. Taken together, there is substantial evidence that tissue growth is mostly under direct control of environmental variables rather than via the flux of assimilated C (Fig. 2, and red arrows in Fig. 1), which demands for a revision of the hierarchy of plant growth control in DGVMs. This implies a step forward from the current C source driven structure to one where C sinks are the central driving process.

Getting the right answers for the wrong reason

Because many processes shown in Fig. 1 are strongly correlated and optimized by evolution, it is possible to get similar results with either model structure in the short term. For example, biomass production will inevitably decrease with elevation, whether the model structure is sink-driven (temperature acts on growth directly), or whether temperature reduces assimilation and thus growth. However, the underlying processes are fundamentally different. We argue that if these processes and particularly the causalities are not reflected correctly, it is unlikely DGVMs will accurately simulate future C storage except under near-optimal conditions when photosynthesis may become limiting, as shown in a simple proof-of-concept in Fig. 2. Furthermore, since forest structure and composition themselves are likely to feedback on C assimilation, they will also fail in predicting long-term C fluxes.

Despite the paramount role of temperature and plant water status in controlling growth, none of the existing DGVMs we are aware of include such a model component, even in a simplified or empirical manner (Foley *et al.*, 1996; Friend *et al.*, 1997; Smith *et al.*, 2001; Bonan *et al.*, 2003; Sitch *et al.*, 2003; Krinner *et al.*, 2005; Sato *et al.*, 2007; Medvigy *et al.*, 2009; Clark *et al.*, 2011; Pavlick *et al.*, 2013; Scheiter *et al.*, 2013). After the general recognition of the potential role of nutrients in limiting C sequestration from land ecosystems (Hungate *et al.*, 2003), nitrogen and more recently phosphorous cycles have been implemented in some DGVMs (Arain *et al.*, 2006; Xu-Ri & Prentice, 2008; Zaehle & Friend, 2010; Goll *et al.*, 2012). However, all these models still consider thermal and water limitations only in relation to C assimilation but not in relation to cambial or generic meristematic activity.

The source-focused design of today's DGVMs also reflects the fact that C source-related processes such as photosynthesis (e.g. leaf gas exchange) are easily measurable, while processes of plant growth such as the rate of cell proliferation, cell expansion, phloem transport or cambial growth (C sink activity) are much harder to quantify at high temporal resolution (Körner, 2013), even though last generation dendrometers and magnetic resonance imaging seem to represent a viable source of information (Zweifel *et al.*, 2006; Mencuccini *et al.*, 2013; Van As & van Duynhoven, 2013).

The parameterization of C fluxes and especially the coupling between C and water through stomatal conductance were mostly conceived to serve the purpose of land surface models and improving estimates of transpiration and photosynthesis fluxes (Sellers *et al.*, 1996) rather than plant growth. Still, biochemical models that were presented decades ago (Farquhar *et al.*, 1980) continue to make up the core of DGVMs, and while they convincingly model C assimilation, they implicitly introduce causality in plant growth control that is based on observations in controlled glasshouse environments, but rarely supported by observations in natural systems. As a consequence, the key output parameters of DGVMs (Net Primary Productivity (NPP) and stored C) are almost exclusively sensitive to parameters of the photosynthesis process as evidenced for LPJ-GUESS by Pappas *et al.* (2013; Fig. 3; see also Bonan *et al.*, 2012). Over short periods (a few years), output from such DGVMs are typically confirmed by observed C fluxes derived from eddy covariance towers (Kucharik *et al.*, 2006; Jung *et al.*, 2007). However, such short-term comparisons only reflect C flux and not plant growth dynamics, that is they at best show a noncausal correlation over a given time period. If DGVMs are used to project future (30–100 yr from now) C pools and fluxes, wrong causalities in models may lead us to obtain a wrong answer because of the wrong underlying reason (see Fig. 2).

We recognize that in many models allocation patterns can be controlled to some extent by nutrients and environmental conditions. For instance, water and light availability can control the differential C allocation to leaf, stem and fine roots (Friedlingstein *et al.*, 1998; Krinner *et al.*, 2005). However, this is rather different from having environmental parameters directly control growth because the assimilated C is necessarily allocated to structural tissue: C export to symbionts are mostly missing and mobile C stores are implemented only in a subset of models in a simplified manner (Krinner *et al.*, 2005; Deckmym *et al.*, 2008; Zaehle & Friend, 2010; Fatichi *et al.*, 2012; Goll *et al.*, 2012;

Pavlick *et al.*, 2013). Therefore, short-term C assimilation is typically linked to growth, which contradicts evidence that shows significant temporal lags between assimilation and leaf/stem growth (Zweifel *et al.*, 2006; Gough *et al.*, 2009; Richardson *et al.*, 2013). This also implies that if more C is assimilated in a model (for instance under conditions of elevated atmospheric CO_2) the simulated vegetation will grow more with positive feedback to C assimilation through increased LAI, which again provides us with the wrong answer for the wrong reasons.

Ways forward

One way forward is to add to the existing structure of DGVMs by implementing direct growth control based on environmental drivers (Leuzinger *et al.*, 2013; see also Fig. 2). If we understand how tissue formation is controlled by environmental parameters, the amount of C to be allocated to growth at a given time step should be independent of the amount of assimilated C. Thus, growth is constrained by the limiting factor following the principle of Liebig's law. Only once all other factors (temperature, water, and nutrient availability) are nonlimiting, this coincides with the classic model formulation, that is the C source becomes limiting. However, we argue that this case is rare and only common under optimal conditions such as in a fertilized glasshouse environment. Such a modeling approach merely requires the definition of look-up tables or multidimensional response surfaces of species or plant functional type specific growth responses to environmental controls (water, temperature, nutrients). This solution does not require major amendments to the current structure of DGVMs; the gas exchange routines could be maintained but no longer determine the amount of C used for growth. The parameterization needed for such response functions however will require a large suite of experimental data.

A more distant goal to improve DGVMs relies on a more realistic representation of C allocation. We need models that simulate C and water fluxes within the plant, including nutrient transport, allocation to and translocation from nonstructural C storage and exports to mycorrhizae and root exudation (Fig. 4). This model philosophy, in its basic essence, was already outlined in pioneering studies (Thornley, 1972, 1991; Dewar, 1993, 2000) and more recently advances have been made in models that solve plant-internal hydraulics (Bohrer *et al.*, 2005; Janott *et al.*, 2010; Bittner *et al.*, 2012) and/or simulate xylem transport (Daudet *et al.*, 2002; Hölttä *et al.*, 2009) as well as phloem fluxes and cell growth activities (De Schepper & Steppe, 2010; Hölttä *et al.*, 2010). This model approach requires, in the most general case, nine components where C and water fluxes and states are simulated within the plant continuum including anatomical differentiation between xylem, phloem, and cambium in the stem (Fig. 4). Mechanistic modeling of C assimilation and transpiration (component 1) is currently implemented in most DGVMs (Bonan *et al.*, 2011). However, in the proposed model, transpired water and assimilated C are mediated by leaf water and C budgets (components 2 and 3). Leaves are capable to buffer the variability of C assimilation, exporting an almost constant flux of sucrose to the vascular phloem at the daily scale (Smith & Stitt, 2007). Structural growth (components 3 and 9) can be explicitly modeled as a function of cell
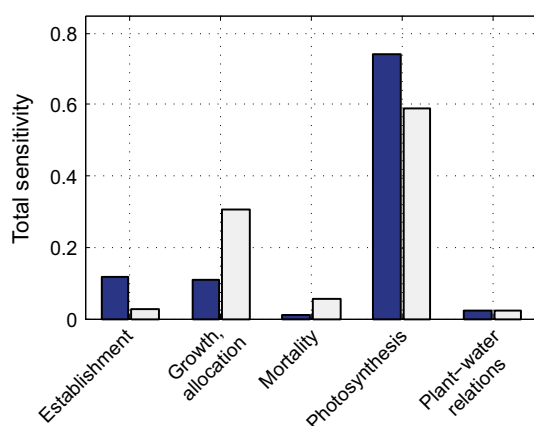

Fig. 3 Total sensitivity of the realizations of the Dynamic Global Vegetation Models (DGVM) LPJ-GUESS to its parameters grouped according to the main modeled processes. Sensitivity of vegetation carbon (C) pools (sum of the C allocated in leaves, sapwood, heartwood, and fine roots) (light bars) and of vegetation Net Primary Productivity (dark bars). Results are obtained using different climate forcings and combined together (adapted from Pappas *et al.*, 2013).
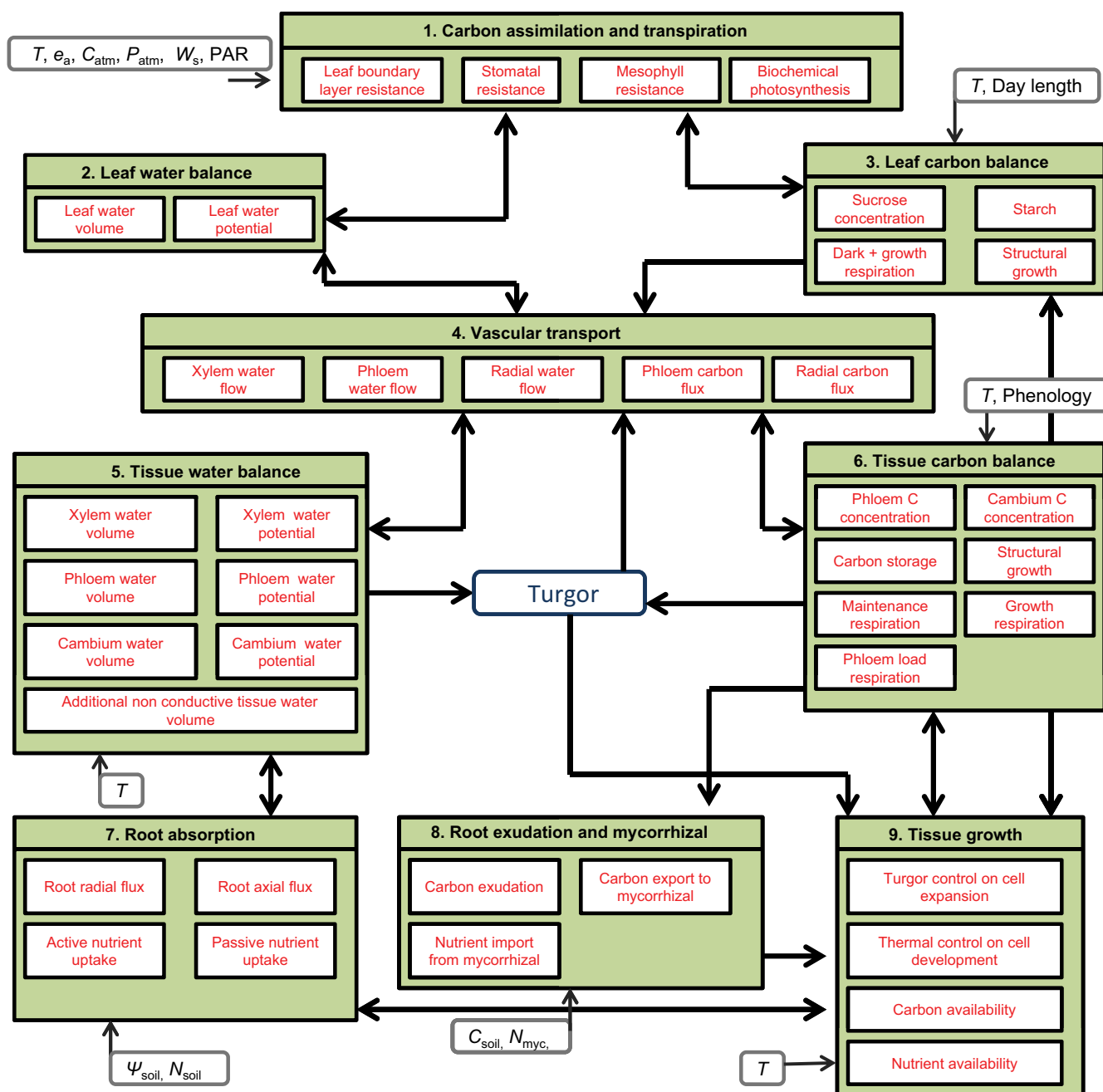
Fig. 4 Synoptic view of the main processes involved in carbon (C) and water transport within the plant. A mechanistic simulation of these processes is required for an explicit modeling of tissue growth. Environmental controls are identified through temperature (T), light (PAR), atmospheric CO_2 concentration (C_{atm}), vapor and atmospheric pressure (e_{atm}, P_{atm}), wind speed (W_s), soil water potential (ψ_{soil}), day length, and C and nutrient concentration in the soil (C_{soil}, N_{soil}, respectively) and nutrient status of the mycorrhizal symbionts (N_{myc}). Transpiration and xylem flux control the leaf water balance, which in turn determines the leaf water potential that triggers hydraulic and chemical mechanisms affecting stomatal aperture. Photosynthesis is the source of leaf C. Leaves buffer the incoming sucrose that is successively released through the phloem. Axial water flow in xylem obeys the cohesion–tension theory and is driven by a gradient of water potentials. Radial water flux between xylem, cambium and phloem is also governed by their respective water potentials. Phloem is driven by the gradient of turgor (Münch flow). Turgor is a central quantity given by the sum of water potential (ψ) and osmotic pressure (π), the latter depends on osmotic concentration. Carbon in the phloem is advected axially by the flow. Sucrose in the phloem can be exchanged laterally and converted to or withdrawn from storage reserves (nonstructural carbohydrates, NSC). Stored C can be mobilized to be used for structural growth and tissue maintenance. The C storage follows temporal dynamics function of plant age, environmental stresses, and phenology. Water flux from soil to roots is governed by the water potential gradient between the soil (ψ_{soil}) and the root xylem. Root are also responsible for soil nutrient (N_{soil}) absorption that can occur passively through water flow or actively through osmotic pumping. Root C exudation and export to mycorrhiza can be included as a function of C concentration gradients. Nutrient import from mycorrhiza depends on plant nitrogen status and nutrient content in the symbiont (N_{myc}). Finally, structural growth can be modeled as a function of cell elongation (that includes wall and protein synthesis), and cell development (division), provided that nutrients and C are sufficiently available. According to the Lockhart model (Lockhart, 1965), cell elongation is a function of turgor above a minimum threshold (water limitation to growth). Potential cell development typically follows a Boltzmann–Arrhenius function of temperature with a 5°C base temperature most commonly applied for zero growth (thermal limitation to growth).

elongation (which includes wall and protein synthesis) and cell development (division), provided the fact that nutrients and C are sufficiently available. Cell elongation is driven by cell turgor above a minimum threshold (Lockhart, 1965), which accounts for water limitation to growth. Potential cell development typically follows a Boltzmann–Arrhenius function of temperature (Parent *et al.*, 2010), with a 5°C base temperature most commonly applied for zero growth, which represents the thermal limitation to growth. When these two controls are implemented plant growth can be considered mechanistically modeled.

A central quantity given by the sum of water potential (ψ) and osmotic pressure (π), that in turn also depends on sucrose concentration, is turgor (P). In order to solve for turgor, cohesion–tension theory and Münch flow (Hölttä *et al.*, 2006) can be used for xylem and phloem transport (components 4 and 5). This will create a fully coupled system where axial and radial flow in xylem, phloem and radial flow in cambium and nontransporting tissue (e.g. outer parenchyma, inner bark) are solved together. The available C is modeled as the sum of carbohydrates in the phloem and by the active regulation of storage compartments (component 6). This C is then available for respiration, structural growth, and for root exudation and export to mycorrhiza (component 8). Direct growth control by nutrients can also be accommodated in such a framework because nutrient import through root uptake or mycorrhiza can be simulated explicitly (components 7 and 8). Nutrients are taken up both passively via transpiration and actively through the creation of concentration gradients (Porporato *et al.*, 2003; Runyan & D'Odorico, 2012). Root C exudation can be modeled as a diffusive process (Farrar *et al.*, 2003), while modeling C/nutrient exchange with mychorriza is more complicated and far from being fully understood (Allen, 2009), which pose a serious challenge in providing suitable mathematical expressions (but see Grant, 1998).

While the mechanistic understanding of certain components, for example, the leaf water and C budget or vascular transport is relatively advanced and can easily be included into models, a gap of empirical knowledge remains for characterizing the regulatory mechanism of C storage and sink priorities as well as interaction with mycorrhiza. Carbon allocated to storage is a function of plant age, environmental stress, and phenology. For instance, at temperate and boreal latitudes, C is withdrawn from storage at the beginning of the growing season to support cambial activity and shoot growth. Plants also prioritize C sinks, ranking their importance, for example, seeds > leaves > cambium > roots > storage (Minchin, 2007), although the ranking is not static and likely to change with phenology, plant age and plant stress (e.g. drought, defoliation). If such priorities of C allocation are not understood and implemented, the model of Fig. 4 will simply reflect a spatial prioritization of C allocation with the more distal parts receiving less C. Unfortunately, a full characterization of the C sink strengths is still elusive and might represent the key for successfully implementing such a model.

We acknowledge that a full implementation of the model depicted in Fig. 4 is still not possible given the limited knowledge about certain processes, however, we argue that our current understanding is sufficient for modeling most of the components. We also acknowledge that such detailed model components may

seem too complex to be included in DGVMs and would require a large number of parameters. However, its implementation can represent the basis for simpler parameterizations of environmental control of growth and of mechanistic C allocation schemes that could be transferred into global scale models. A framework where plant C/water transport and tissue expansion are represented using well defined mathematical equations and relationships among components, as was done for photosynthesis 30 yr ago, is likely to transform our way of modeling plant growth. Such a framework can also guide the collection of data on plant C storage regulation and sink functioning, which is fundamental for increasing our understanding and enable long-term scenarios for the global C cycle.

Conclusions

The relative ease of measuring photosynthetic parameters and the construction of mechanistic models of C assimilation that convincingly simulate flux tower observations have promoted the present structure of DGVMs, which have undergone few changes over the past 20 yr. Although knowledge gaps were identified previously (Moorcroft, 2006; Fisher *et al.*, 2010), the 'source-driven' structure of models remained mostly unquestioned. However, our current physiological understanding of tissue growth and expansion is in stark contrast to how it is represented in state-of-the-art DGVMs. Current scenarios describing the interaction between climate and vegetation are likely affected by a wrong representation of plant growth and are therefore questionable. We argue that direct environmental controls (temperature, water and nutrient availability) on tissue expansion and meristematic activity (sink capacity) are fundamental (more than previously thought on the basis of C flux data) because they mostly become limiting to plant growth before photosynthesis (source capacity) does. Because C can only be invested to the extent other nutrients as well as water availability and temperature permit, these non-C related drivers of growth will ultimately be prioritized over C assimilation dynamics. This reversal in our understanding of plant growth drivers has serious implications for the prediction of terrestrial C fluxes and storage in the long term. The implementation of the right causalities in DGVMs will be extremely challenging but fundamental for making future predictions of the C cycle. In our vision to achieve this goal, we proposed two approaches of different complexities: (1) to introduce growth constraints in current DGVMs according to growth limiting factors; (2) to implement mechanistic relationships of plant C/water transport and tissue expansion as was done for photosynthesis 30 yr ago. While additional empirical knowledge may be required to fully characterize some of the suggested amendments, we argue that there is enough observational evidence to tackle the challenge of revising the core structure of current DGVMs, leading from source-driven to a combined source–sink-driven plant growth.

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