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Review

Key knowledge and data gaps in modelling the influence of CO_2 concentration on the terrestrial carbon sink☆

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ABSTRACT

Primary productivity of terrestrial vegetation is expected to increase under the influence of increasing atmospheric carbon dioxide concentrations ([CO_2]). Depending on the fate of such additionally fixed carbon, this could lead to an increase in terrestrial carbon storage, and thus a net terrestrial sink of atmospheric carbon. Such a mechanism is generally believed to be the primary global driver behind the observed large net uptake of anthropogenic CO_2 emissions by the biosphere. Mechanisms driving CO_2 uptake in the Terrestrial Biosphere Models (TBMs) used to attribute and project terrestrial carbon sinks, including that from increased [CO_2], remain in large parts unchanged since those models were conceived two decades ago. However, there exists a large body of new data and understanding providing an opportunity to update these models, and directing towards important topics for further research. In this review we highlight recent developments in understanding of the effects of elevated [CO_2] on photosynthesis, and in particular on the fate of additionally fixed carbon within the plant with its implications for carbon turnover rates, on the regulation of photosynthesis in response to environmental limitations on in-plant carbon sinks, and on emergent ecosystem responses. We recommend possible avenues for model improvement and identify requirements for better data on core processes relevant to the understanding and modelling of the effect of increasing [CO_2] on the global terrestrial carbon sink.

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1. Introduction

The capacity of terrestrial ecosystems to act as a net source or sink of carbon over decadal or centennial timescales is one of the largest uncertainties in estimates of the present and future global carbon budget, and its role in the radiative forcing of climate (Le Quéré et al., 2014, 2009; Friedlingstein et al., 2014). It is by now without dispute that a substantial amount of anthropogenic CO_2 emissions are removed from the atmosphere annually due to a net global CO_2 uptake by terrestrial ecosystems. A combination of global constraints based on mass balance (Le Quéré et al., 2014), atmospheric CO_2 inversions (Stephens et al., 2007), forest inventories (Pan et al., 2011) and process-based terrestrial carbon cycle models (Sitch et al., 2015) suggests that increases in terrestrial carbon storage resulting from the effects of CO_2 fertilisation, here defined as enhancements in photosynthesis under elevated atmospheric CO_2 concentration ([CO_2]), may explain as much as 60% of the contemporary terrestrial carbon sink (Schimel et al., 2015). However, the contributions of different regional ecosystems to the global sink (Ahlström et al., 2015), and the relative importance of different mechanisms and historical factors in driving it, are still being debated; particularly the roles of CO_2 fertilisation, high-latitude climate warming and secondary forest regrowth (e.g. Smith et al., 2016). Estimates may be confounded by uncertainties in land-use change emissions (Pugh et al., 2015). In the absence of consensus on the origins and behaviour of the present-day carbon sink, future projections remain highly tenuous, often showing striking divergence among alternative models (Friedlingstein et al., 2006; Friedlingstein et al., 2014; Sitch et al., 2008; Friend et al., 2014; Jones et al., 2013). The simulated increases in vegetation biomass over the 21st century may be high, typically amounting to 100–400 Pg C for scenarios with strong [CO_2] (and therefore warming) increases (Friend et al., 2014), in the mean equivalent to about a 50% increase in global vegetation carbon pools relative to the present day. However, there has been a great deal of discussion over whether such projections are realistic, or whether the models used miss critical plant and ecosystem processes (e.g. Hungate et al., 2003; Körner, 2009; Fatichi et al., 2014; Hickler et al., 2015; Bugmann and Bigler 2011).

Calculations of the current terrestrial carbon sink, including the effects of elevated [CO_2], along with projections of the carbon cycle in the late 21st century and beyond, are available from a variety of bottom-up modelling approaches that we here collectively term Terrestrial Biosphere Models (TBMs). These models include biogeochemical Land Surface Models (LSMs) and Dynamic Global Vegetation Models (DGVMs) configured for 'off-line' simulations, as well as interactive versions of the same models coupled to the physical climate component of Earth System Models (ESMs). The models rely on bottom-up principles whereby component processes affecting carbon fluxes into, out of, and between ecosystem compartments are represented explicitly and linked via dependencies on external drivers and evolving system state. This bottom-up approach is argued to be necessary because carbon cycle dynamics emerge from the joint behaviour of a multitude of processes linked across widely-ranging time (and space) scales, leading to legacy effects with time-signatures from seasons to centuries. There is thus a strong imperative to ensure these models build on process representations that reflect observational constraints, and formalise biological and ecological understanding.

The expectation of the existence of a CO_2 fertilisation effect stems from a mechanistic understanding of photosynthesis, whereby elevated [CO_2] leads to increased concentrations of CO_2 within the leaf, thereby enhancing the carboxylation rate of Rubisco and reducing photorespiration, and thus increasing gross primary production (Drake et al., 1997). An indirect effect of [CO_2] on photosynthesis is also widely observed, whereby stomatal conductance is reduced, reducing water loss for a given assimilation rate (Ainsworth and Rogers 2007). The resulting reduction in water stress may be particularly important in dry-climate ecosystems. These direct and indirect responses of photosynthesis have been well established in laboratory and open-top chamber experiments, where they have also been found to translate into enhanced plant growth (e.g. Drake et al., 1997; Norby et al., 1999). This increase in growth provides the basis for hypothesising the potential existence of an on-going net flux, or "sink", of carbon to the terrestrial biosphere resulting from CO_2 fertilisation, contingent on the assumption that downstream plant and ecosystem processes also affected indirectly by elevated [CO_2] do not result in a compensating increased flux of carbon *out* of the system, for example due to increased plant mortality, soil respiration or carbon leaching. This sink would continue to exist until carbon outputs through vegetation and soil turnover came into balance with the increased inputs, a process that, even if changes in environmental conditions are halted, could take many decades or even centuries (Port et al., 2012).

The existence and strength of a "CO_2-caused" sink depends on a number of key factors. Firstly, are large enhancements of photosynthesis seen in early experiments in laboratories or open-top chambers realised in real world ecosystems across the globe? Second, to what processes or pools do plants allocate any additional carbon resulting from CO_2 fertilisation? Third, how long does carbon remain in those pools before they are turned over, either through tissue death or whole-plant mortality? Finally, what is the emergent ecosystem response arising as a sum of these effects, including the fate of turned over carbon? Whether or not CO_2 fertilisation results in a net terrestrial carbon sink therefore goes well beyond the question of whether or not primary production increases.

In this article, we assess the potential to improve TBM-based simulations of the contemporary and future terrestrial biospheric carbon cycle by reviewing how processes relating to vegetation growth and turnover under increasing [CO_2] are represented in these models in comparison to current knowledge. We restrict our scope to plant and vegetation processes, while recognising that soil carbon turnover is also critically important for biosphere carbon balance. Much of the focus is upon trees, as these reflect the major stores of vegetation biomass. In contrast to other reviews which have focused on synthesising results of ecosystem experiments (Norby et al., 1999; Ainsworth and Long 2005; Ainsworth and Rogers 2007; Leakey et al., 2009; Norby and Zak 2011), on comparisons of models to particular ecosystem experiments (Medlyn et al., 2015), or on modelling forest productivity (Hickler et al., 2015), we focus on the model development and data requirements in order to improve understanding and projections of the effect of increasing [CO_2] on the terrestrial vegetation carbon sink in TBMs.

We begin with an overview of relevant process representations in current TBMs (§2). We then discuss opportunities to improve TBM representations of processes related to the effects of elevated [CO_2] on photosynthesis (§3), allocation and turnover (§4), feedbacks of in-plant sink limitations on photosynthesis (§5), and direct effects of [CO_2] on turnover (§6), as well as indirect [CO_2]-induced feedbacks which influence the terrestrial carbon sink (§7). The core of the review focuses on processes relating to plant allocation of photosynthate, and its resultant effects on carbon turnover, which we contend to be the key area of uncertainty in understanding the effect of elevated [CO_2] on the terrestrial carbon sink. We define allocation here in its broadest sense, to encompass the division of carbon to all processes downstream of photosynthesis, including respiration and symbiotic associations, as well as the plant structural growth and allocation to non-structural carbohydrates. We limit the scope of our review to the effects of [CO_2] on the net flux of carbon to vegetation (the vegetation carbon sink) and resultant changes in vegetation carbon storage.

2. State of the art in global terrestrial biosphere modelling

Fig. 1 shows an overview of carbon stocks and flows, and the governing processes, within a typical state-of-the-art TBM. Representations of photosynthesis in TBMs are rooted in data from controlled leaf-level experiments, often embodied in the Farquhar model (Farquhar et al., 1980). Initial enhancements in net primary productivity (NPP) in these models for a step-change increase in [CO_2] have been found to be broadly consistent with those observed in stand-scale Free-Air CO_2 Enrichment (FACE) experiments (Hickler et al., 2008; Piao et al., 2013; Zaehle et al., 2014), although these observed enhancements were not always maintained over multiple years, as we discuss further in §4. Fixed carbon not used for respiration (i.e. NPP) is assumed to be used for plant growth, and allocated to carbon compartments of the plant, typically fine roots, wood or leaves. Depending on the TBM, this allocation usually follows either fixed empirical coefficients, or functional balance rules whereby resource shortages (light, water, nutrients) lead to allocation shifts in an attempt to alleviate that shortage. Of these parsimonious approaches, allocation by functional balance has proven successful in capturing the nature of allocation shifts under elevated [CO_2] (De Kauwe et al., 2014). Photosynthesis is closely coupled to the water cycle through stomatal conductance and resultant effects on the leaf-internal CO_2 concentration (C_i), allowing indirect effects of elevated [CO_2] through increased water use efficiency to be simulated. Increasingly, TBMs are also explicitly representing nitrogen (N) dynamics in vegetation and soil, with photosynthesis being limited when nitrogen is in short supply, for instance through a limitation of the carboxylation capacity of Rubisco (V_{max}) (Yang et al., 2009; Zaehle and Friend 2010; Wang et al., 2010; Smith et al., 2014). Turnover of carbon and nitrogen stocks within vegetation is represented by a variety of processes relating to phenology and mortality, with the turned-over material being transferred to litter and soil stocks, from where they are eventually transferred to the atmosphere in the case of carbon, or partially leached or recycled into vegetation in the case of nitrogen. The rates and outcomes of these various processes relating to carbon and nitrogen uptake, allocation and turnover are closely intertwined with properties relating to ecosystem composition and canopy structure. The DGVM sub-group of TBMs also explicitly represent competition between different plant types, allowing them to emulate the functional consequences of changes in species composition brought about by changing environmental drivers.

TBMs have proved successful in capturing important aspects of the global carbon cycle: modelled distributions and magnitudes of gross primary productivity (GPP) and NPP correspond with those derived from satellites and flux-tower observations (e.g. Piao et al., 2013; Anav et al., 2013), and models have been able to recreate the season cycle of [CO_2] in both hemispheres (Sitch et al., 2003; Forkel et al., 2016) as well as important aspects of the pattern of inter-annual variability in [CO_2] (Sitch et al., 2008). Nonetheless, the nature of the terrestrial carbon flux, as a relatively small residual of two very large fluxes (GPP and ecosystem respiration), means that even relatively small inaccuracies in these larger fluxes will cause very large uncertainties in the net terrestrial flux of carbon. This is reflected in the divergent trajectories of terrestrial carbon balance simulated by different models (Ciais et al., 2013; Sitch et al., 2015; Le Quéré et al., 2014).

3. Advances in understanding of photosynthesis

Some recent empirical evidence has suggested that the effect of elevated [CO_2] on photosynthesis could be underestimated by current modelling approaches. Sun et al. (2014) suggest that C_3 plants are currently much more strongly CO_2-limited than assumed in the photosynthesis algorithms used by TBMs, since these algorithms do not include the leaf mesophyll resistance, associated with diffusion of CO_2 from the sub-stomatal cavity to sites of carboxylation. As a consequence, the CO_2 concentration in the models that is "seen" by the carbon-fixing enzymes under current atmospheric CO_2 levels is overestimated. As pointed out by Sun et al. (2014), this overestimation of CO_2 concentration in the chloroplast translates into an underestimation of the sensitivity of Rubisco to increasing [CO_2] since, at the same levels of stomatal conductance, temperature and photosynthetically active radiation, the carboxylation reaction by Rubisco is more sensitive to changes in CO_2 at low CO_2 concentrations. When accounting for mesophyll resistance in an empirical approach within the TBM CLM4.5, Sun et al. simulated an enhanced effect of [CO_2] on global GPP of 0.05 Pg C a^{-1} $ppmv^{-1}$, compared to the standard formulation. This amounted to an additional 16% increase in global GPP over the period 1901–2010 in their simulations.

A second line of evidence also appearing to suggest a steeper response of GPP to [CO_2] than commonly assumed by models stems from the analysis of isotopomers (i.e. differences in stable isotope abundance at specific positions within a molecule) of deuterium in glucose and sucrose, which give an indication of the ratio of photorespiration (i.e. linked to the oxygenation reaction catalyzed by Rubisco) to carboxylation under different levels of [CO_2]. Such data assembled by Ehlers et al. (2015) from herbarium samples of different plant types collected between the late 19th and early 21st century indicate that this ratio decreased by ca. 25% since the late 19th century, demonstrating increased carboxylation over oxygenation in response to increasing [CO_2]. Using a simple model Ehlers et al. showed that this would result in a 35% increase in GPP, with all else being constant. This is substantially more than the 6–20% increases calculated by an ensemble of DGVMs over a similar period (Piao et al., 2013), or the 18% enhancement calculated for the TBM LPJ-GUESS following the same protocol but without changes in climate (authors, unpublished). Although the TBM simulations also integrate over other factors such as changes in temperature and leaf area index, these measurements appear to show some consistency with the results of Sun et al. (2014) and taken together appear to indicate an underestimation of GPP enhancements over the last century by global models. However, it should be cautioned that the herbarium samples used by Ehlers et al. (2015) are leaf, rather than canopy-scale, measurements and, further, are not necessarily representative of natural ecosystems globally, whilst Sun et al. (2014) rely on TBMs for upscaling the effects of their findings, meaning that the proposed effects on global GPP are therefore subject to the limitations in other aspects of these models discussed below. As we

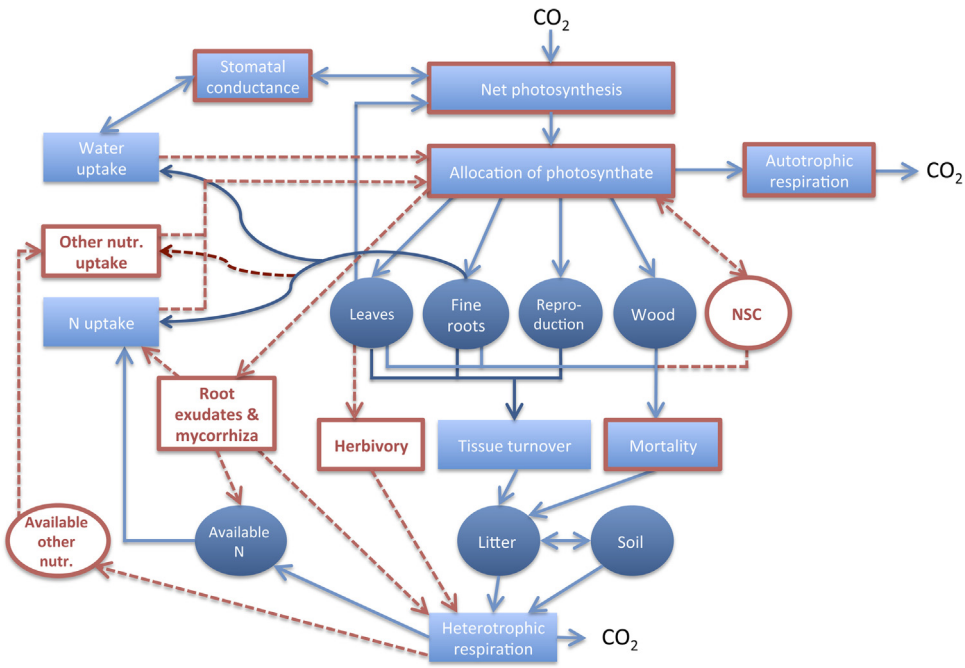

Fig. 1. Schematic of stocks (ellipses) of carbon and nutrients in a typical TBM, and the processes which link them (rectangles). Blue shading indicates processes and pools typically represented, red borders those we argue are in need of update for the consideration of the effects of elevated [CO_2] on carbon cycling, and red borders and red text those we believe should be included but are generally missing currently. Shades of blue and red are only for clarity. Note that processes are shown from a TBM structural perspective, as opposed to an ecological perspective. Diagram is only indicative; process representations vary substantially between TBMs, and for clarity not all processes can be shown (for instance, vegetation dynamics are encapsulated within mortality, nutrient sources are excluded).

expand on in the following sections, such effects on GPP may only be realised in a small subset of plants or ecosystems.

4. Are effects on growth and carbon storage overestimated?

Whilst understanding the presence (or absence), magnitude and continuity of the response of photosynthesis in (C_3) vegetation to [CO_2] is an important first step, from the perspective of ecosystem-level carbon balance a more fundamental question is whether enhanced leaf-level photosynthesis translates into enhanced growth, and whether this enhanced growth results in a net increase in carbon storage within the ecosystem. Correct allocation of plant carbon to different vegetation compartments and losses in the form of, e.g., respiration, exudates or volatile organic compounds (VOCs) represents a fundamental challenge for modellers. A wide range of empirical, allometric or evolution-based formulations exists (see Franklin et al., 2012 for a review), although these are usually applied only for allocation between plant compartments. Evolution-based approaches, which typically allocate carbon to maximise a fitness proxy, are shown to give realistic relative responses to environmental variability and climate change, but are included only to a limited extent in some large-scale models (e.g. Haverd et al., 2016). Empirical and allometric alternatives are the common choice in many models (§2). Likewise, allocation of carbon to purposes other than autotrophic respiration and growth, such as exudates or biogenic VOC emissions, are neglected in most TBMs. In this section we discuss allocation of carbon to growth (§4.1), then partitioning of that carbon within different growth components (§4.2) and then other carbon losses (§4.3).

4.1. Growth limitations

As noted above, most TBMs assume that, after subtraction of respiration costs from GPP, all remaining carbon is used for growth. This means that increases in GPP automatically translate into increases in growth unless compensated by a corresponding increase in respiration. Some authors argue that direct environmental limitations on growth may be more important than the availability of carbon substrate from photosynthesis, i.e. the strength of in-plant carbon sinks exerts a dominant control on carbon allocation and plant growth (e.g. Körner, 2003; Fatichi et al., 2014; Körner, 2015; Tardieu et al., 2011). These authors argue that, because environmental limitations typically affect growth processes before photosynthesis, TBMs currently overestimate increases in plant growth under elevated [CO_2]. Three sources of environmental limitation on growth have been debated most widely: water stress, low temperatures, and nutrient limitation.

Considerable evidence exists that low water potentials inhibit cell division due to low cell turgor (Muller et al., 2011; Tardieu et al., 2011) and, importantly, that the shape of this response differs from that for reduction of photosynthesis under low water potentials, such that growth in leaves and shoots typically becomes limited at higher water potentials than photosynthesis. There is also evidence of a decoupling between carbon availability and root growth under water stress (Muller et al., 2011; Fatichi et al., 2014). Furthermore, the capability of the plant to transport sugars may be reduced (Sevanto 2014), starving parts of the plant distal to the leaves of substrate for growth, although such responses are equivocal (Hartmann et al., 2015). Such a disconnect between growth and photosynthesis has been demonstrated for Mediterranean forests (Gea-Izquierdo et al., 2015), and is consistent with build-up of leaf sugars observed under water stress (Körner, 2003; Muller et al., 2011). It may help explain the relatively poor performance of ecosystems models at simulating net carbon exchange at water-limited sites (Morales et al., 2005). Fatichi et al. (2014) used a model analysis to demonstrate that implementing water limitations on growth might reduce accumulation of biomass under elevated [CO_2] by ca. 75% in a Swiss deciduous forest, although it remains to be proven whether this approach improves model performance in comparison to independent, e.g. experimental,

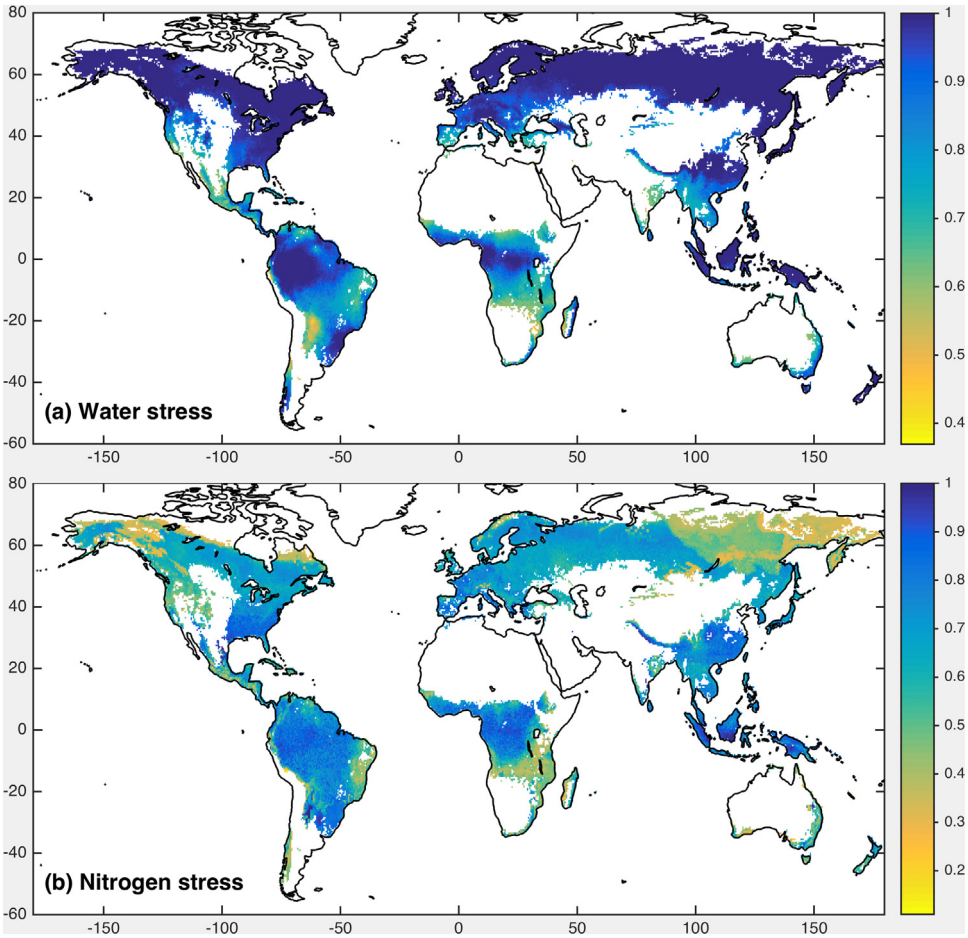

Fig. 2. Estimated geographical distributions of limitations on growth in forested areas. (a) Fraction of time period 2001–2010 during which terrestrial vegetation is under water stress, as identified by a water scaling factor which varies between 0 and 1 according to the ratio of available water supply versus atmospheric demand, as modulated by plant stomata. A value of 1 indicates no water stress and all areas with a value of 0.95 or less are assumed to be substantially affected by water stress for at least part of the year. Output is from a simulation with the LPJ-GUESS dynamic global vegetation model carried out by Ahlström et al. (2012) using potential natural vegetation and forced using bias-corrected historical climate from the CCSM4 simulation carried out for the CMIP5 model intercomparison (Ciais et al., 2013). (b) Scaling factor from LPJ-GUESS for canopy carboxylation capacity (V_{max}) below its maximum rates (as determined by available light, temperature and leaf-internal CO_2 concentration) when available nitrogen is not sufficient to meet the V_{max} demand. A value of 1 indicates no nitrogen stress; lower values increasing nitrogen stress. Simulation as described in Smith et al. (2014) and results are shown for 1996–2005.

observations of cause and effect. Using output from the TBM LPJ-GUESS, we find that a large fraction of global forests are located in areas that spend a substantial portion of the average year in water stress (Fig. 2). Based on output from this model, we therefore calculate that water limitations have the potential to influence growth conditions across a forested area which corresponds to 37% of the simulated global annual terrestrial C sink. Therefore if such limitations on growth are substantial and sustained, they could markedly reduce modelled estimates of the global C sink resulting from elevated [CO_2]. This effect may, however, be offset by reductions in water stress resulting from increased water use efficiency under elevated [CO_2] (Ainsworth and Rogers 2007; Leakey et al., 2009), although this is complicated by the unknown size of hydrological feedbacks with the atmosphere (Leuzinger et al., 2015). TBMs generally capture observed increases in water use efficiency under elevated [CO_2] (although see §5) (e.g. Medlyn et al., 2015); however, when it comes to growth limitations, data on tissue growth rates as a function of water stress are only available for a small selection of plants, but show substantial variation between species (Muller et al., 2011). Many more observations would be required to parameterise a model for the major global biomes. Therefore, the gathering of appropriate observations, and the testing of models including water-based growth limitations against ecosystem experiments under elevated [CO_2], is a pre-requisite for model advancement.

The rate of cell division is also a function of temperature, which can effectively halt growth both at very high and very low temperatures (Körner, 2003). Leuzinger et al. (2013) have shown that a sink-limited implementation of plant growth improves modelled biomass estimates for near-treeline boreal and alpine areas. However, sink limitations due to temperature are most likely to occur at the extremities of the growing season, when assimilation is in any case relatively low, and along biome boundaries determined by high and low temperature limits. Consideration of direct temperature limitation on growth may, for example, prove useful in projecting the advance of treelines under climate change, but is probably of limited relevance with regard to the effect of [CO_2] on the terrestrial carbon sink at the global scale.

Nutrient constraints under elevated [CO_2], underpinned by clear stoichiometric requirements for tissue formation (Elser et al., 2010), have been much discussed, with several notable reviews (Hungate et al., 2003; De Graaff et al., 2006; Reich et al., 2006a; Arneth et al., 2010a; Zaehle and Dalmonech 2011; Lenka and Lal 2012; Ciais et al., 2013; Medlyn et al., 2015). Although there can be some limited flexibility of carbon to nutrient ratios within plants (e.g. Leakey et al., 2009), plant growth requires sufficient nutri-

ent supply to sustain these ratios; Hungate et al. (2003) showed that some early TBM projections of terrestrial carbon uptake under elevated [CO_2] would require matching amounts of N far beyond reasonable projections of N availability. Experiments have shown that plants which were artificially fertilised with N showed much greater responses of plant biomass to elevated [CO_2] than those growing under native conditions (Oren et al., 2001; De Graaff et al., 2006; Reich et al., 2006a; McCarthy et al., 2010; Norby et al., 2010; Reich and Hobbie 2013), indicating a clear N limitation effect.

Diagnostic modelling of the assumed process by which elevated [CO_2] leads to a decline in the N concentration of plant litter, causing the microbial decomposers to immobilise nitrogen, and thereby reducing availability to the plants, suggests a limitation effect which progressively develops following an initial GPP and growth enhancement (Luo et al., 2004). The progressive nitrogen limitation hypothesis is supported by observations in FACE experiments in grassland (Reich et al., 2006b) and in an 11 year long FACE experiment in a plantation forest (ORNL; Norby et al., 2010). Initial but unsustained increases in annual biomass increment were also observed in a Swiss FACE experiment in mature trees (Körner et al., 2005), but in the only other closed-canopy forest FACE experiment (Duke) biomass increment remained elevated throughout the experiment (McCarthy et al., 2010). It is not clear whether the biomass increment at Duke would have persisted if the experiment had continued beyond the 10 years of elevated [CO_2] treatment (Norby and Zak 2011). We emphasise here the results for closed-canopy forests as the availability of nutrients can be strongly affected by the structure of the ecosystem (Körner, 2006; Norby and Zak 2011). In young ecosystems where canopy closure has not been achieved, individual plants have room to expand and access new resources. This is not the case in more mature ecosystems where canopy closure has been attained (Norby and Zak 2011). Large biomass increments in young trees (Norby et al., 1999) have relevance only for re-growing forests before they reach canopy closure (Körner, 2006), and do not give a clear picture of nutrient limitations likely to be present across wider ecosystems. Such differences in plant response clearly emphasise the importance, when parameterising models based on experimental findings, of considering ecosystem-level, rather than plant-level, responses.

Several TBMs have incorporated nitrogen limitation of productivity (and thus in these models, at least implicitly of growth), and results generally show N limitation, and a resultant decreased effect of elevated [CO_2] on modelled carbon sequestration, especially in the temperate and boreal zones (Fig. 2b; Zaehle and Friend 2010; Smith et al., 2014). Comparison of N-enabled TBMs against detailed ecosystem N measurements from two elevated CO_2 experiments in temperate forests suggested deficiencies in model ability to capture underlying processes at the stand scale (Zaehle et al., 2014). While Zaehle et al. (2014) were able to refute a number of common model assumptions, such as a high degree of stoichiometric flexibility in the allocation of C and N to new tissue, the experimental data were insufficient to constrain some assumptions, such as turnover rates of woody tissue and N losses through exudation (Medlyn et al., 2015). Further, TBMs lack constraint of the future ecosystem N supply (Smith et al., 2014), which requires mechanistic formulations of biological nitrogen fixation that can be applied at the global scale, as e.g. proposed by Fisher et al. (2010b). Also lacking are realistic large-scale parameterisations of N losses through leaching and gaseous emissions, which in forest ecosystems are strongly dependent on variations in soil water status, pH, texture and freeze-thaw processes, as well as microbial properties (Wu et al., 2010; Arneth et al., 2010b). So whilst progress has been made in modelling N limitations in TBMs in recent years, much work remains to be done to ensure that the models correctly simulate emergent ecosystem responses to [CO_2] and climate change.

Beyond nitrogen, other nutrients such as phosphorus and potassium may be very important in tropical regions (e.g. Lloyd et al., 2015; Sardans and Peñuelas 2015), where the relative effects of [CO_2] on photosynthesis are expected to be largest (Hickler et al., 2008), but phosphorus is considered in only a handful of TBMs (Wang et al., 2010; Goll et al., 2012; Yang et al., 2014), whilst to our knowledge potassium is explicitly considered in none. A recent study applying observed stoichiometric constraints to ESM simulations used in the IPCC 5th Assessment Report (Ciais et al., 2013) suggested that consideration of N and P availability would reduce global NPP by ca. 25% in 2100 (Wieder et al., 2015). In contrast to changes in nitrogen, for which limitation at ecosystem level is ultimately determined by the fixation rate of an abundantly available element, the finite plant-availability of other nutrients such as phosphorus imposes fundamental limitations on growth in ecosystems where they are in short supply. There is also evidence that limitations in non-nitrogen nutrients such as phosphorus and molybdenum may prevent enhancements of biological N fixation (van Groenigen et al., 2006). In contrast to water and temperature limitations, it is not yet clear whether GPP and growth are differentially affected by nutrient constraints, although stoichiometric arguments and observations of photosynthetic down-regulation mechanisms imply that growth is the controlling factor (§5).

Larger-scale support for strong limitations on stem growth comes from dendrological datasets which suggest that there has been no overall increase in stem growth in trees across many major biomes over the last century, despite a ca. 100 ppmv increase in atmospheric CO_2 mixing ratio (Penuelas et al., 2011; Battipaglia et al., 2013; van der Sleen et al., 2015). However, these results stand in contrast to those of Cole et al. (2010) and McMahon et al. (2010) who found, based on forest inventory data, that forest growth rates in parts of the United States are increasing in excess of rates predicted from stand-age effects alone. The discrepancies between these two sources of data cannot easily be reconciled by the successional stage of the forest; McMahon et al. (2010) used a dataset with tree ages from 5 to 250 years. Additionally, Los (2013) attributed 40% of the global greening trend to the influence of increasing [CO_2] based upon satellite observations (although we note that greening differs from stem growth increment). While these growth increments cannot be definitively attributed to any one environmental driver, it nonetheless appears evident that forests differ greatly in their degree of stem growth limitation.

As discussed above, young forests without canopy closure are likely to respond very differently to elevated [CO_2] compared with mature forests, with arguments for little or no additional growth response in mature ecosystems focusing on the idea that these ecosystems are often making the maximum use of their available nutrient resources, i.e. they are nutrient-limited (see above), or upon arguments relating to ecosystem dynamics (e.g. Körner, 2009; Bugmann and Bigler 2011; see §6). A key objective of the next generation of forest FACE experiments is to evaluate whether the growth enhancements that were achieved in young forests or plantations in previous FACE experiments (even those with closed canopies) hold for mature old-growth ecosystems (Norby et al., 2016). However, the extent to which CO_2 enhancements of growth are limited by environmental conditions at the global scale remains an open question, which will require results from FACE, process-based ecosystem modelling, inventory and dendrological methods to be combined and reconciled.

Although the magnitude of sink-related growth limitations may be uncertain, their existence clearly is not. So does accounting for this require a paradigm shift in TBMs? This seems unlikely; the structure of TBMs allows for demand-side limitations to be included in the algorithms governing C allocation, as initial attempts have demonstrated (Leuzinger et al., 2013). The key aspect of the problem then becomes balancing supply and demand of

C within the plant in order to retain mass balance. Short-term imbalances can be accounted for by the representation in TBMs of non-structural carbohydrates (NSC), and several TBMs include this pool of carbon in some form (e.g. Fisher et al., 2010a; Zaehle and Friend, 2010). The challenge here may be to correctly characterise the capacity and response rate of the NSC pool, as well as the strategy of the plant for allocating to NSC, and this is likely to differ greatly across species. The problem of parameterisation at the large scale is increased by difficulties in defining a baseline for absolute measurements of NSC (Quentin et al., 2015). Alternatively, NSC dynamics may be informed not by observations of NSC per se, but by leaf- and root-phenology, which emerge from lags between growth and assimilation, buffered by NSC (Haverd et al., 2016). Longer-term imbalances can be resolved by characterising other plant C losses (§4.3) and by capturing individual-plant and whole-ecosystem responses to limitations on ecosystem water and nutrient resources (§5). Here, again, TBMs are well placed to adapt to better represent these processes, though data limitations remain an issue.

4.2. Allocation to different components of growth

Changes in allocation ratios, i.e. relative growth rates, between wood, leaves and fine roots are also of potentially critical importance for the terrestrial CO_2 sink. Assuming no change in turnover rates of individual tissues (see §6), then increases in allocation of carbon to a particular pool within the plant will lead to an increase in the standing biomass of that pool. The longer the residence time of carbon within that particular pool, the greater influence a given additional carbon input flux will have on pool size. Thus, if trees invest disproportionately in wood, which has a long carbon residence time (low turnover rate), a given increase in whole-plant growth will result in a greater increase in standing biomass than if allocation favours fast-turnover pools such as leaves or fine roots. Likewise the relative allocation between roots and leaves is important for determining inputs into soil carbon pools.

In a study of allocation responses to elevated [CO_2], De Kauwe et al. (2014) found increased allocation towards fine roots at the expense of wood and leaves at one forested FACE site (ORNL), but a small increase in wood allocation at the expense of leaves at another forested FACE site (Duke). These differences in allocation ratios had a profound influence on carbon storage; at Duke 88% of additional NPP generated by elevated [CO_2] remained at the end of the experiment, whereas at ORNL none of the additional NPP was reflected in the measured biomass at the end of the experiment, as it had been allocated to parts of the plant with rapid turnover rates. In comparing these results with predictions of ecosystem models including TBMs, De Kauwe et al. (2014) found that models with functional-balance approaches to allocation caught the general character of the observations, providing encouragement that such approaches may be suitable for modelling responses to elevated [CO_2]. Similarly, results from another forested FACE experiment found increases in photosynthesis, but no overall increase in stand biomass, indicating a shift in typical allocation patterns away from wood, although it was not clear where this carbon was allocated (Bader et al., 2010).

As well as changes at the plant scale, elevated [CO_2] can also modify allocation, and thus turnover of carbon at the ecosystem scale, if preferentially advantaged species have different allocation patterns compared to disadvantaged species. For instance, leguminous plants have been observed to be advantaged in some ecosystems under increased [CO_2] (Reich et al., 2006a). At its most extreme, such change can manifest as biome shifts. One of the most reported examples is the shrub encroachment and woody thickening observed in many semi-arid ecosystems around the world over recent decades (Liu et al., 2013; Mitchard and Flintrop 2013), along with a general increase in observations of vegetation cover (Donohue et al., 2013), which has been linked to CO_2-induced enhancement of photosynthesis and water-use efficiency. In another example, whilst many N-enabled TBMs also predict a decline in biospheric carbon storage when the interactive effects of climate change are considered (e.g. Zaehle et al., 2010; Fisher et al., 2010b), a study based on the LPJ-GUESS DGVM found that the combination of elevated [CO_2] with increasing N mineralisation rates in warming high-latitude soils leads to forest advance and increase in woody biomass (Wårlind et al., 2014). In the latter study, this provides a new transient sink for carbon in growing trees over the 21st century. This contrasts with the general expectation that N limitation will decrease growth and therefore carbon storage (§4.1). To understand the effect of elevated [CO_2] on the terrestrial C sink we therefore need to understand not only effects on carbon allocation and turnover at the plant scale, but also effects on vegetation dynamics at the ecosystem scale. Such understanding for forested ecosystems will not be obtained from ecosystem manipulation experiments, meaning that we must be confident in the ability of our models to correctly capture competitive dynamics between species with different functional traits, as well as having access to on-going monitoring data from unmanaged ecosystems to evaluate such predictions from models.

4.3. Additional losses

Root exudates and export to symbionts are prime candidates for additional plant carbon losses, not represented in most models. These processes are difficult to quantify experimentally. In total, as much as 60–70% of GPP has been observed to be transferred to the soil in studies of *Pinus sylvestris* and *Pseudotsuga menziesii* trees (Grayston et al., 1996), the vast majority of which is likely to be rapidly returned to the atmosphere through heterotrophic respiration. Separating the portion of the total plant-soil flux attributable to root exudates from that due to processes such as fine root turnover and growth respiration (which are often explicitly represented in TBMs) is challenging. Estimates of root exudate amount range from 1 to 10% of GPP under ambient conditions (Grayston et al., 1996). Experiments on trees under elevated [CO_2] have shown exudation to be enhanced by ca. 50% during the main growing season for a 200 ppmv increase in atmospheric CO_2 mixing ratio (Phillips et al., 2009; Phillips et al., 2011). One interpretation of this additional C exudation would be a simple overflow response to excessive carbon. Alternatively, plants may produce exudates to alleviate nutrient limitations, for instance through priming (§7). TBM estimates of plant N uptake may potentially be improved by accounting for such a response (Medlyn et al., 2015). The relation of exudate rate to [CO_2| is equivocal, however; Uselman et al. (2000) saw no such [CO_2]-mediated enhancement in an experiment in *Robinia pseudoacacia* grown in an artificial medium. Observations are required from a range of biomes, and particularly in real soils, both to assess the present-day carbon balance, and to understand the response of assimilate export to [CO_2].

A further possible carbon loss pathway is the synthesis of VOCs. Emissions of isoprene, the most globally emitted biogenic VOC, have been observed to constitute up to 10% of leaf GPP in some instances (Sharkey and Yeh 2001), although 1–2% might be a more common value globally (Guenther et al., 2012). There is evidence that emission rates of many VOCs are suppressed by elevated [CO_2] (Possell et al., 2004; Arneth et al., 2007), suggesting that VOCs are unlikely to be fundamental in balancing the global plant carbon budget.

It is questionable whether the carbon demands of the myriad processes that contribute to autotrophic respiration are adequately captured by the simple temperature or fixed-fraction functions currently employed in most TBMs. For instance, there is evidence that leaf respiration initially increases under water stress, possibly to

repair damage inflicted by water deficit, a feature not captured by TBMs (Powell et al., 2013), and which might partially balance growth reductions under water stress. Evidence that plants are able to acclimate their respiration levels to temperature (see Smith and Dukes 2013 for an overview) is increasingly recognised and may be a standard feature in the next generations of TBMs. Evidence for a direct response of autotrophic respiration to elevated [CO_2] is, however, mixed (e.g. Ryan 1991; Bunce 2004), with strong increases observed for soybeans, but not in many other species examined (Leakey et al., 2009).

5. Multi-scale feedbacks on photosynthesis

Overwhelmingly the consensus from the last two decades of large-scale ecosystem manipulation experiments is that enhancements in assimilation are seen, but often to a lesser extent than in earlier, more artificial, experiments, and they were not always maintained over many years (Norby et al., 2010; Norby and Zak 2011), indicating feedbacks on assimilation rates. Reductions of photosynthesis to balance sources with sinks within plants may take many forms. Photosynthesis in trees and grasses is typically limited by carboxylation capacity at atmospheric CO_2 mixing ratios up to ca. 500 ppmv (Ainsworth and Rogers 2007). Both laboratory and field studies under elevated [CO_2] have shown that if source processes outstrip sinks, or transport of photosynthate away from the leaves is limited, then the build-up of leaf sugars leads to a direct down-regulation of photosynthesis (reviewed in Paul and Foyer 2001; Ainsworth and Long 2005; Ainsworth and Rogers 2007; Leakey et al., 2009). Such down-regulation reduces leaf-level photosynthetic capacity, either by reducing leaf Rubisco content and therefore carboxylation capacity (generally reflected by a reduction in leaf C:N ratio, although Rubisco activity has also been observed to be modified; Cen and Sage 2005), or by decreasing the maximum rate of electron transport. This is exemplified in observations that reductions in carboxylation capacity under elevated [CO_2] appear to be much greater under conditions of low N availability (Ainsworth and Rogers 2007; Leakey et al., 2009). Such reductions are not uniformly present across all species however. For instance, *Populus* trees have been observed to avoid down-regulation of leaf photosynthesis by transporting sugars away from leaves, combined with a large capacity to store non-structural carbohydrates (NSC), thereby maintaining the capacity of in-plant C sinks (Karnosky et al., 2003; Davey et al., 2006). Bader et al. (2010) also reported no down-regulation of photosynthesis under elevated [CO_2] in a FACE experiment in a mature forest stand in Switzerland.

The observations above demonstrate a close linkage between photosynthesis and the capacity of the plant to transport and utilise photosynthate. TBMs incorporating C–N interactions commonly parameterise a direct reduction in photosynthesis when N becomes limiting, in some cases by directly modelling leaf C:N ratios, which then results in less growth compared to a model with no N limitations, since less C is assimilated (e.g. Zaehle and Friend 2010; Smith et al., 2014). This assumes that plants allocate N such that photosynthesis is maximised within the constraints of the N limitation on structural growth. This parsimonious approach avoids the need to model leaf sugar concentration, which, given its strong coupling with phloem transport, presents huge data limitations (Fatichi et al., 2014) and currently seems an unrealistic target for global scale models. Effects of limitations in other resources needed for growth (water, nutrients other than N) could be parameterised in a similar manner. An alternative approach is to adopt a representation in which photosynthesis is regulated as a net result of the whole-plant carbon balance, i.e. down-regulation occurs when C assimilation exceeds the sum of all sinks and losses, including maximum allocation to NSC, and when there is nothing the plant can do with the extra C to attempt to alleviate any sink constraints. This alternative approach has the advantage that it accommodates a range of plant response strategies to changes in resource supply/demand arising under elevated [CO_2]. A disadvantage is that model accuracy in capturing photosynthetic down-regulation is then contingent on the currently limited observational basis on which to characterise the response of various sinks and losses of carbon within the plant (§4).

Another possible route to reducing photosynthesis is to reduce stomatal conductance, thereby reducing the leaf intercellular CO_2 concentration (C_i). Laboratory and ecosystem experiments often show that stomatal conductance is regulated such that C_i changes proportionally to [CO_2] (Drake et al., 1997; Ainsworth and Rogers 2007). This results in an increase of water use efficiency (WUE) under elevated [CO_2], as a given C_i can be maintained for less water loss. This increase in WUE has been widely observed (Leakey et al., 2009; Penuelas et al., 2011; De Kauwe et al., 2013; van der Sleen et al., 2015). Using a network of temperate and boreal forest sites where above-canopy fluxes for both CO_2 and water were both measured, Keenan et al. (2013) found a large increase in WUE over recent decades which they attributed to plant responses to increasing [CO_2]. The increase in WUE was so large, however, that their results suggested that trees must be closing their stomata to hold C_i relatively constant, i.e. they were prioritising limiting water loss over increasing GPP. The contrast to the previous studies finding proportionality of [CO_2] and C_i has sparked debate (e.g. Medlyn and De Kauwe, 2013). Nonetheless, if borne out by future research, one possible interpretation of the results of Keenan et al. (2013) would be that plants may be actively down-regulating photosynthesis in favour of maintaining turgor for growth. As TBMs currently assume proportionality of [CO_2] and C_i, large reductions in stomatal conductance as suggested by Keenan et al. (2013) could have profound implications for TBM simulations of terrestrial carbon cycling, affecting not only productivity, but many other processes through the resultant modification of soil water content. A decrease in C_i:[CO_2] ratio under elevated [CO_2] was also seen in tree ring data at three FACE sites (Battipaglia et al., 2013), whilst other studies of tree rings have revealed evidence of large increases in WUE as a result of rising [CO_2], without corresponding increases in growth, across a wide range of global ecosystems (Penuelas et al., 2011; van der Sleen et al., 2015). In contrast, syntheses of FACE experiments have found no such strong effect of increased [CO_2] on stomatal conductance at either leaf or stand scale (Leakey et al., 2009; Norby and Zak 2011). Possibly the discrepancy between results from FACE sites stems from the different sampling periods of the techniques involved (Leuzinger and Hättenschwiler, 2013). In comparing their historical samples to results from controlled [CO_2] experiments, Ehlers et al. (2015) found evidence that there have been no adjustments of properties such as stomatal function or photosynthetic regulation in sugar beet in response to increased [CO_2], but as these results come from managed ecosystems, comparisons with natural ecosystems are non-trivial.

On longer time-scales there are other ways for plants to redistribute resources to balance supply and demand. Environmental limits may induce plants to reduce photosynthesis by reducing total leaf area, either through reduced leaf growth (§4.1), by investing in thicker leaves (Ainsworth and Long 2005), or by active changes in allocation patterns through changes in growth hormones (e.g. Ribeiro et al., 2012). As discussed in §4.2, changes in allocation patterns can have profound effects on vegetation carbon storage, and therefore the terrestrial C sink. Whilst some TBMs are able to capture allocation changes under increased [CO_2], changes in leaf mass per unit area (LMA) were recently highlighted as being a critical point for model development, with most TBMs treating LMA as a constant and none of those considered capturing the observed

increase (Medlyn et al., 2015). Effective changes in leaf area at the ecosystem level may also accompany biome shifts (§4.2).

Overall, whilst none of the mechanisms moderating photosynthesis discussed above are clear-cut with respect to whether, how often, and in what species they occur, there is overwhelming evidence at the plant and ecosystem scales that plants and ecosystems regulate photosynthesis under increased [CO_2].

6. Turnover

Differences in the treatment of vegetation carbon turnover have been highlighted as the primary source of variation in TBM projections of vegetation C stocks for the 21st century (Friend et al., 2014), illustrating the huge uncertainty in our understanding of this process. Myriad factors influence ecosystem carbon turnover rates, including changes in drought-induced mortality, ecosystem disturbances, insect and pathogen outbreaks, and biome shifts. Changes in turnover will fundamentally impact upon the size of any CO_2-induced vegetation carbon sink (Müller et al., 2016). This topic is, however, worthy of multiple reviews by itself, and is a topic of increasing focus for the terrestrial modelling community (Running 2008; McDowell et al., 2011; Friend et al., 2014; Seidl et al., 2011; Johnson et al., 2016). Further, as discussed in §4.2, CO_2-induced shifts in allocation between leaves, stems and roots can alter turnover. In this section we restrict our focus to plant turnover processes which may be directly affected by increased [CO_2].

Bugmann and Bigler (2011) hypothesised that tree life cycles could be accelerated under elevated [CO_2], citing evidence that (i) trees in several elevated [CO_2] experiments invested little of the extra carbon gained in defence, thus making them more vulnerable to early mortality, (ii) earlier cone production was observed in trees subject to elevated [CO_2] at the Duke forest FACE experiment (Ladeau and Clark 2006), (iii) crops mature and die younger under elevated [CO_2] than under ambient conditions (Kimball et al., 1995), and (iv) growth increment in tree rings was negatively correlated with longevity in a study of three conifer species (Bigler and Veblen 2009). By parameterising tree longevity in a forest model based on observed correlation to growth rate in temperate tree species across multiple continents, they re-parameterised tree longevity in a forest model and showed that the simulated decrease in longevity tended to offset the increased growth. Furthermore, even without changes in longevity, individual tree growth enhancements of up to 30% could lead to a very small overall increase in stand biomass, mainly due to increased competition for light in the mature stand. These results again emphasise the dangers of assuming that observed tree-level relationships will hold true at the ecosystem scale, and if they turn out to be generally applicable for global forests, they would have profound effects for the size of any CO_2-driven terrestrial sink.

Lianas present an example of a community-level effect on vegetation turnover rates. Several studies now point towards increased growth of lianas in tropical forests under elevated [CO_2] (Körner, 2004; Phillips et al., 2002; Schnitzer and Bongers 2011). Lianas appear to be advantaged because they grow under light-limited rather than nutrient-limited conditions in the forest understorey, and light-limited plants benefit more than light-saturated plants from increased [CO_2] (Körner, 2009). Forest plots with lianas have been found to exhibit higher mortality of trees and branches compared to plots in which the lianas were cleared (van der Heijden et al., 2015). As with biome-type shifts, an increased portion of the canopy occupied by lianas also modifies the ratio of leaves to wood, in this case increasing it, resulting in a higher proportion of forest NPP being invested in short-lived tissues compared to stands in which lianas are not present.

Insect herbivory may be increased under elevated [CO_2]. This may occur through a reduction in investment in defence, as argued by Bugmann and Bigler (2011), and observed in soybean plants (Zavala et al., 2008). It may also occur through a reduction in leaf nutritional quality as a result of reduced nitrogen content, leading to herbivores increasing their leaf consumption to compensate. Evidence for the latter comes both from field studies (Stiling and Cornelissen 2007) and from palaeo-evidence showing that insect herbivory tends to be higher during periods of relatively high [CO_2] and temperature (Currano et al., 2008). However, field observations under elevated [CO_2] have also reported a reduction in insect herbivory, apparently driven by lower densities of herbivores (Stiling et al., 2003; Hamilton et al., 2004; Knepp et al., 2005; Stiling and Cornelissen 2007). The reasons for these lower insect densities are not clear, but may relate to poorer nutrition slowing insect development, and therefore increasing their vulnerability to predators, or to insects preferentially choosing to feed on plants outside the experimental plots (Knepp et al., 2005). Elevated [CO_2] may also change the emission of defensive compounds such as VOCs, although the effects are difficult to generalise (Zavala et al., 2013), whilst decreased stomatal conductance can lead to a rise in leaf temperature which can increase insect metabolism and feeding rates (Zavala et al., 2013). Our limited understanding of such responses at the ecosystem scale makes including insect herbivory in TBMs a challenge, but given the large fraction of NPP consumed by herbivores, particularly in nutrient-rich ecosystems (Cebrian et al., 1998), their impacts could be of substantial importance for vegetation turnover rates, and thus for the terrestrial carbon sink (Metcalfe et al., 2014).

Interactions with pathogens have also been observed, but the responses are mixed, with susceptibility to some pathogens increased under increased [CO_2], but the effects of other pathogens being lower than under ambient [CO_2] (summarised in Reich et al., 2006a). Whilst, in theory, change in susceptibility to pathogens could profoundly affect vegetation carbon cycling, the variety of responses and the often close coupling of plant and pathogen species make ecosystem responses very difficult to predict; likely long-term impacts on the carbon cycle would be indirect through a change in the balance of ecosystem composition.

7. Complex impacts of elevated atmospheric [CO_2] on the terrestrial carbon cycle

7.1. Interactions with land-use change

Elevated [CO_2] also affects the terrestrial carbon sink through indirect feedback mechanisms other than climate change and the effects on photosynthesis and plant growth and turnover as discussed above. Land-use dynamics are important to consider, as the effect of increased [CO_2] on projections of crop (Rosenzweig et al., 2014; Challinor et al., 2014) and timber (Kirilenko and Sedjo 2007) yields, as well as water availability (Elliott et al., 2014), are likely to affect future land-use patterns (Schmitz et al., 2014; Nelson et al., 2014) and thus modify land-use emissions, which currently offset the effects of elevated [CO_2] on terrestrial carbon storage (Le Quéré et al., 2014). Reductions in rotation period of forest plantations in response to accelerated growth under elevated [CO_2] stands to reduce the mean standing biomass at such managed sites (Körner 2006). The uncertainty in crop yield response to elevated [CO_2] has been identified as a major scientific challenge in crop modelling (Rosenzweig et al., 2014; Müller et al., 2016) but here additional experimental evidence is also needed to enhance process understanding. Most crops use the C_3 photosynthetic pathways and are essentially subject to the same mechanisms as described above in sections 3–5, while C_4 crops such as maize (*Zea maize* L.),

sorghum, sugar cane and millet species may be expected to show smaller, or different, responses to [CO_2]. Crop-specific allocation to yield organs represents an additional complication. There is evidence that stimulated photosynthesis under elevated [CO_2] does not increase crop yields proportionally, especially if nutrients are limiting (Leakey et al., 2009). However, Kimball (2016) argues that FACE experiments indeed show substantial increases in crop yields, especially when considering that the unsteady CO_2 concentrations in FACE experiments may reduce the effect (Bunce 2013). Also in crop production, elevated [CO_2] can lead to reduced consumptive water use in crop fields. This leads, especially in combination with enhanced crop yields, to higher crop water productivity and thus to a more efficient use of water resources (Deryng et al., 2016), although as in natural systems, hydrological feedbacks may prove important (Leuzinger et al., 2015).

7.2. Interactions with soil processes

The majority of carbon in the terrestrial biosphere is stored in the soils, where biomass from litterfall is converted to various forms of soil organic matter and eventually returned to the atmosphere as respired CO_2. This conversion of organic matter to carbon dioxide is driven by microorganisms that respond to temperature and moisture regimes, and to the chemical and structural composition of the mineral and organic soil compartments. The effect of elevated [CO_2] on soils was reviewed in Reich et al. (2006a) and De Graaff et al. (2006), who found that soil C content typically increased under elevated [CO_2] when additional N was added to the system, but not in ecosystems with low N availability, although measurement of effects on soil was confounded by long response times relative to experimental duration. Elevated [CO_2] can change the stoichiometry of the organic matter from litter by e.g. leading to lower nitrogen content of leaves and roots (Yang et al., 2011). This in turn changes the decomposition rate of organic matter (Zhang et al., 2008). It can also lead to a priming effect, i.e. the enhanced decomposition of soil organic matter by supplying easily degradable material in the form of root exudates under elevated CO_2 (Carney et al., 2007; Phillips et al., 2011), resulting in the break down of organic-mineral compounds that otherwise prevent mineralization of the associated organic matter (Keiluweit et al., 2015). Such priming effects can both reduce soil C content and liberate N, although Reich et al. (2006a) point out that any additional N made available by priming is likely to be negated in the longer-term by increased N immobilisation resulting from higher C inputs to the soil under increased [CO_2].

8. The road ahead: closer integration between measurements and modelling

What recommendations may be made for the improvement of TBMs when applied to modelling the effect of increasing [CO_2] on the terrestrial carbon sink? Advances in knowledge are sufficient for some of the processes discussed above to be implemented and tested in TBMs. For some processes and observed phenomena more consistent or comprehensive observations will be required in order to provide enough information to design robust parameterisations for implementation in models. A model is by definition a simplified representation of the real system it stands for, and TBM modelling generally strives for a reductionist approach, representing the biosphere and its component ecosystems in the least amount of detail necessary to reproduce salient features and dynamics. A model with high process complexity will only become more accurate if the functional forms, scaling and linkages among processes, drivers and descriptors of system state can be unequivocally constrained by observations, and this is rarely the case, even for empirically well-studied processes such as photosynthesis or transpiration. Overall the aim for global modellers must be to maintain model parsimony: only include new processes when they are well constrained and make a substantial difference to the output metric of interest. TBMs that are solely tuned to emerging properties such as net ecosystem exchange, rather than observations of individual processes, can be expected to fail in this context. Further, it will be important to ensure that when new process mechanisms are included, related parameterisations within the model are reassessed to ensure that any implicit "double counting" is avoided. We summarise recommendations below.

1) Within-plant carbon allocation, and its resultant effects on plant carbon turnover, is a key step governing any changes in the size of the vegetation carbon pool, and thus in the terrestrial C sink. Allocation responses may confound any direct association between primary productivity and the net terrestrial carbon flux. Inclusion of in-plant C sink constraints (beyond N availability, which is already included in some models), and their feedbacks to photosynthesis, is highly feasible within current TBM structure, but will require further work to parameterise typical growth responses to resource stress for different species globally, as well as refining N and P models and developing new parameterisations to test the importance of other nutrients. Inclusion of an NSC pool will likely be necessary to balance sources and sinks in the short term, as will the effects of photosynthetic down-regulation in the long-term. The HAVANA approach (Haverd et al., 2016) in which growth and NPP have separate time courses, but balance in the long term, provides a useful modelling framework.
2) It is not enough to understand response to [CO_2] at the single tree level; rather, whole ecosystem response, including effects of inter-plant and inter-species competition for resources, as well as large-scale plant-atmosphere interactions, must be considered. Some TBMs already aim to capture such effects. The challenge is to better evaluate and parameterise this aspect of the models, allowing confidence in the resultant emerging ecosystem responses.
3) Effects of [CO_2] on turnover rates at the tissue, plant and ecosystem scales have only been lightly investigated. Those changes relating to the partitioning of carbon among different pools within the plant are tightly tied to plant allocation strategies, and uncertainty should be reduced as our confidence in modelling plant allocation in TBMs increases. The veracity of possible acceleration of tree life cycles, and thus decreased tree longevity, must be a priority for future research.
4) Evidence suggests that plants may invest a large fraction of carbon through root exports to soil, and that these exports are likely to increase under nutrient deficiency induced by elevated [CO_2]. Below-ground dynamics, including root growth, exudates, symbioses and plant-soil interactions are not well observed in most empirical studies. Better quantification of this carbon export is crucial to understanding the whole-plant carbon balance, and effectively modelling plant allocation strategies.
5) The effect of mesophyll conductance on GPP is sufficiently constrained to be implemented in global models. Although we expect that it will be much more limited in its global influence than suggested by Sun et al. (2014), it is favourable nonetheless to incorporate the best knowledge if it does not substantially degrade model parsimony.
6) A large proportion of natural ecosystems has been cleared by man for use in agriculture, or appropriated for other uses such as forestry. Effects of elevated [CO_2] on the productivity of these managed ecosystems can feed back directly on the amount of land occupied by unmanaged vegetation, providing an indirect, but potentially very important, driver for the size of the terres-

trial carbon sink. Enhanced TBMs which can also capture effects in managed ecosystems will be better able to feed into land-use assessments and provide overarching assessments of the effect of increased [CO_2] on the terrestrial C sink.

7) Although not reviewed in depth here, soil processes are key to the supply of nutrients and water, as well as representing the largest store of ecosystem carbon, and are often represented with very simple functions in TBMs. Further attention must be, and is being, paid to soil processes. The reader is directed to reviews by De Graaff et al. (2006) and Reich et al. (2006a), as well as recent modelling advances by e.g. Koven et al. (2013) and Todd-Brown et al. (2012).

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