



# AMAZALERT Delivery Report

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## Modelling Amazonian carbon budgets and vegetation dynamics

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### Executive Summary

Modelling the Amazon terrestrial carbon budget and vegetation dynamics is, despite the large amount of research on dynamic vegetation models and land-atmosphere exchange, still at an early stage in comparison to the development of global climate models, to which DGVMs are ultimately coupled to generate Earth system simulations. The principal uncertainties deriving from model analyses have focussed on a lack of knowledge on the response of tropical vegetation to increases in temperature and atmospheric CO<sub>2</sub> concentrations, and to a lesser extent, upon reduced water availability. The extent to which water availability is important is also model dependent (Rammig et al. 2010, Galbraith et al. 2010, Huntingford et al. 2013). The size of the predicted effect of moisture stress on Amazon vegetation is dependent on both the forest response and the future risk of drought, which varies among climate models (Meir and Woodward 2010). However, if the risk of drought is kept constant, DGVM sensitivity to moisture stress appears frequently to be smaller than, for example, sensitivity to warming (Galbraith et al. 2010), even though recent empirical evidence demonstrates that drought can have large impacts on the forest carbon cycle (Phillips et al. 2009; da Costa et al. 2010); hence this area may need revisiting in the future. These environmental factors directly affect primary productivity and respiration, the main components of the carbon budget of a forest ecosystem.. At longer time scales, the indirect effects of carbon allocation (eg root-shoot –leaf partitioning) and demography (recruitment, longevity, mortality) might be of equal importance to determine vegetation biomass and carbon storage. Again however, there is limited information specific to the Amazon, especially upon how forests vary with climate and soils, although this picture is likely to change as present day allocation patterns are investigated in more detail (e.g. Malhi et al. 2009).

The uncertainty on moisture dependence partly stems from lack of spatial information on water supply parameters: soil hydraulic properties, including hydraulic lift; rooting depth and root dynamics. Apart from that, knowledge is only now being expanded on the variability in water stress response among species and groups of species. The latter affects, apart from ecosystem water use, the demography within ecosystems: drought-limited establishment and drought-induced mortality differ among these groups and vulnerability to increased mortality during drought has been shown to be size (or perhaps age) dependent (Engelbrecht et al. 2007; da Costa et al. 2010; Phillips et al. 2010). The effects of water stress on plant respiration are still poorly understood. Although the majority of evidence from non-tropical studies indicates a decline in plant respiration following short term reductions in moisture availability (Atkin and Macherel 2009), there are indications that it is enhanced under long term water stress (Metcalf et al. 2010, da Costa et al. in press), and following seasonal drought in Amazonian rain forest (Miranda et al. 2005).

To better represent water stress, systematic efforts are needed to map soil hydraulic properties and root distribution across the Amazon (Fisher et al. 2008). Plant response to soil water and atmospheric demand need to be inventoried for a range of ecological groups, and if the data support categorisation, for example of the sort observed in mortality trends (da Costa et al. 2010), distinct response modes need to be parameterised, informed by data obtained at canopy, tree and leaf scales. Models need to be made suitable to simulate water supply, root dynamics, allocation and use of carbon resources, and stomatal response by a focal set of ecological groups; data-model comparison should then be used to parsimoniously identify the most important processes.

The uncertainties in the temperature response of photosynthesis and respiration mainly stem from lack of information on the shape this response, specific of the Amazon (or indeed, any tropical forest region), in particular with respect to minimum, optimum and maximum temperatures (Atkin et al. 2008 GCB, Smith and Dukes 2013). It is largely unknown how these response curves in turn are likely to acclimate, , to long-term changes in average temperatures or moisture availability. Most models, in their current form, rely on parameterisations from earlier work in temperate zone vegetation. There is some concern that they combine sets of parameters from different experimental data sets, where different model formulations were used, potentially leading to erroneously simulated temperature response irrespective of climate zone. Temperature also affects stomatal conductance and VPD, which interact to affect net photosynthesis (Lloyd and Farquhar 2008), so care must be taken to distinguish temperature response of overall leaf or canopy productivity from temperature response of individual model parameters.

To reduce uncertainty in the temperature response of Amazon vegetation productivity, in-situ temperature responses of the model parameters involved in simulating photosynthetic capacity and respiration need to be determined. Canopy-scale data, such as from eddy correlation can be used but especially here it should be taken into account that these show overall response, including stomatal response and soil respiration. At the leaf scale, detailed response properties of photosynthesis and respiration parameters can be determined, as can the impacts on gas exchange capacity of long-term experimental manipulation of leaf temperature. Here, of course, there are important issues relating to the need to represent diversity across the whole ecosystem and indeed the wider Amazon basin. Linking warming responses in vegetation to those below ground presents a bigger experimental challenge, although translocation studies within rainforests at different elevations provide some insight (Zimmermann et al. 2010), as may future ecosystem-scale warming experiments (Wood et al. 2012) The main modelling issue here is that models should be equipped to allow acclimation of temperature optima.

Uncertainty in CO<sub>2</sub> response is strongly linked to our understanding of its dependence on nutrient availability, and over time, nutrient dynamics. As photosynthesis and water use become more efficient under higher CO<sub>2</sub>, the rate of increase in productivity depends on nutrient availability and the allocation of carbon to long and short-term residence pools. Given the relative abundance of nitrogen in Amazonian soils, this question primarily concerns phosphorus availability (refs) which is limited and dynamically dependent on soil properties and vegetation activity The challenge is to introduce a dynamic model for phosphorus availability in Amazon soils. Apart from the need for comprehensive mapping of nutrient availability across the Amazon (Quesada et al. 2010), , specific investigations into soil nutrient dynamics and plant-soil interactions are required to parameterise such model improvements.

As much of the issues in modelling the Amazon carbon cycle and vegetation functioning revolves around the question whether or not important shifts in vegetation type, or degradation can be expected, it is important that simulation models can represent such transitions, either through soil and vegetation processes alone, or the interaction of fire and ecological process. In their current state, most models only represent two or three tropical vegetation types (Plant Functional Types, or PFTs), and consequently there is a risk that rapid and substantial shifts from, e.g. evergreen to seasonal forests or savannas are simulated prematurely, partly because of a lack of intermediate functional types which exist in the real world. Solutions to this that modelling efforts should aim at, include the introduction of

more types or statistical approaches with more types co-existing in the same model grid points, but perhaps more fruitfully models could represent the abundance and range of plant traits, or ranges of species groups, rather than discrete PFTs.

The carbon storage capacity of an ecosystem depends both on the short-term budget of carbon, as discussed above, and on the subsequent fate of sequestered carbon (or: NPP). Carbon that is allocated to short-lived or easily decomposable tissues will disappear from the ecosystem much more rapidly than long-lived carbon components. Therefore, understanding allocation is equally important as photosynthesis and respiration. Allocation is, however, much less well-understood than the primary production processes. Several approaches exist to model it, varying from fixed partitioning, via resource limitation dependency, to finding evolutionary optimality. If compared to data sets from the Amazon, which are very scarce, these models usually show poor agreement, although the evolutionary class seems to perform best. Data show that the strongest trade-off in allocation seems to be between aboveground wood and (fine) roots. What is needed for modelling response to climate change, is models in which allocation can also dynamically change and adjust (or adapt) to changed climate. Such change will affect the carbon retained in the ecosystem.

Plant mortality and recruitment can be seen as ultimate allocation (to litter and to next generations, respectively), however, the factors driving these processes are very different from those affecting allocation in live plants. Mortality may be associated with (or negatively correlated with) the investment of carbon into wood and roots, i.e. in resilience to enhance longevity at minimum 'cost'. Partly this is related to the same environmental factors, such as drought, but for mortality also windthrow is important. Being rather random and indiscriminate, wind can have strong disturbing effects. These demographic processes are among the least well represented in DGVMs, even though their effect on ecosystem carbon is of the same magnitude as primary production and allocation. One of the problems for models is that they work with groups of plants or whole ecosystems, and at best deal with separate groups or cohort within vegetation patches. More individual-oriented models would offer advances in demographic effect.

Fire, in turn is an ultimate form of disturbance, and can act as the defining switch for vegetation change from closed forest to degraded vegetation. The occurrence of fires can be self-reinforcing, as initial understory fires and localised lead to dry-down, opening up and increase of edge length. All these enhance the probability of ignition of fire. Observation techniques from remote sensing to detect, for example, understory fire are improving, and several fairly detailed models exist for fire susceptibility. However coupling these new techniques to DGVMs or global climate models still proves a challenge, and modelling the spread of fire is also still an important issue to resolve. A promising way ahead is, apart from coupling fire models to DGVMs and coupled earth system models (including climate), is to link fire models to land-use change models.

The capacity to reliably represent Amazon forest biomass and vegetation in models has definitely improved greatly over the last decade. Also, our insight into which factors are most important to sensitively evaluate climate change impact has improved, and it can be expected that these insights will soon lead to much more reliable DGVMs. Lack of data, both process-oriented experiments and ecosystem-scale validation data, are still sparse, however, so that uncertainties will remain substantial in the foreseeable future. Nevertheless, we are confident that given experimental effort and model development, within a few years we will be able to assess the effects of climate change on the Amazon for the upcoming century with reasonable confidence.

## Introduction

The forests of the Amazon region are under threat of both climate change and land-use change, with risks of accelerated degradation involving positive feedbacks through moisture, CO<sub>2</sub> and temperature (Davidson, 2012). The notion of accelerated degradation under 21<sup>st</sup> century climate change was brought into focus first by White et al. (1999) and Cox et al (2000), followed by a series of studies showing inter-model variability in this climate sensitivity (e.g., Friedlingstein, 2006, Nobre and Borma, 2009, Sampaio et al, 2007). Simulated changes in biomass depend on a number of factors. First, the emissions scenario behind the simulation, second the climate model, third, the vegetation model used and finally the inclusion of land-surface feedbacks. The early studies relied on one single climate model (HADCM3), which was severe in its forecasts and one surface model (MOSES-TRIFFID) which was very sensitive (Huntingford et al, 2008, Galbraith et al, 2010). The Recent studies appear to indicate a more modest sensitivity (Good et al, 2013; Cox et al, 2013; Huntingford et al, 2013). In this review we focus on the vegetation component, which is substantial. Some recent studies have highlighted the strong sensitivity to CO<sub>2</sub> and temperature in vegetation models used to make these predictions (e.g. Lapola et al. 2009, Galbraith et al. 2010, Huntingford et al. 2013). The degree of sensitivity, especially with respect to temperature, differs among models, in particular the Dynamic Global Vegetation models (DGVMs), and the way different processes are represented in them. Moreover, although a subject of discussion (Poulter et al. 2010), recent work suggests that the uncertainty associated with the physiologically-driven ecosystem-scale responses in the models is higher than the uncertainty associated with future climate projections (Huntingford et al. 2013). Increased atmospheric CO<sub>2</sub> concentration potentially reduces water stress, but also may lead to changes in vegetation structure and competition. The effects of CO<sub>2</sub> on tropical vegetation, however, remain largely unmeasured, especially because limitations by nutrients and temperature are poorly understood and also because little is known about how enhanced productivity might affect growth patterns and demography (allocation, recruitment, ageing and mortality). The effects of changing temperature on the balance of primary productivity (photosynthesis), respiration and decomposition are poorly understood for the tropics, with most available information coming from temperate vegetation and agricultural crops.

Several efforts have been made to develop and compare appropriate models to simulate the carbon budgets, seasonal variability, and climate sensitivity of the region. A recent effort coming into publication soon, within the scope of the Large-Scale Biosphere-Atmosphere experiment in Amazonia (LBA) is the LBA-MIP (Model Intercomparison Project, Gonçalves et al., 2013, Von Randow et al, 2013, submitted). Other studies include a World Bank funded initiative (Vergara and Sholz, 2010), the Moore foundation funded Amazon-Andes Initiative (Moorcroft et al in prep.), and AMAZALERT (Kruijt et al, in progress). A recent collection of studies on the climate sensitivity of the Amazon can be found in New Phytologist journal (Meir et al, 2010). The publications in this special issue focused on drought sensitivity, but also pointed out other, sometimes larger sensitivities in the relevant models, such as the simulated responses to CO<sub>2</sub> and temperature (Rammig et al, 2010, Jupp et al, 2010, Galbraith et al, 2010, also see Poulter et al, 2010). Recent reviews covering the importance of a better understanding of dynamics dependence of ecosystem productivity on environmental factors and climate change include Booth et al. (2012) and Smith and Dukes (2013).

Dufresne et al (2002) noted that the Cox et al (2000) predictions of amazon dieback depend strongly on allocation of the extra carbon gained by increasing CO<sub>2</sub> to vegetation versus soil pools, affecting respiration rates, explaining some of the differences between the HADCM3 simulations (Cox et al, 2000) and IPSL simulations (Friedlingstein, 2006). In general, DGVMs are to date not very successful in reproducing the observed spatial variability and biomass over the Amazon basin (see AMAZALERT Mid-term report and Delbart et al, 2011, Castanho et al, 2013). A more detailed representation of the vegetation dynamics might enable us to simulate processes as mortality, disturbance and recruitment in a more realistic way. This could possibly lead to better simulations of spatial variability in biomass.

This review aims to give an overview of the most important issues concerning the modelling of carbon budgets and vegetation dynamics of the Amazon forests, and tropical forests in general. Subsequently, we briefly cover water relations, temperature dependence, CO<sub>2</sub> and nutrient dependence and patterns in growth and mortality. The review should also assist to set the agenda for model improvement and data needs, to adequately equip global and regional dynamics vegetation models in assessing climate sensitivity of the region's vegetation.

## Key issues in DGVMs for the Amazon

### *Soil-plant water relations*

In the Amazon, flux tower data, data from manipulative experiments and remote sensing indices show unexpected responses of vegetation properties and carbon fluxes to dry periods. Where soils are deep and the dry season moderate, productivity appears to be hardly affected by drought, and even to peak during the dry season (Saleska et al, 2003; Fisher. 2006. Originally considered largely a-seasonal in terms of productivity, Malhi et al, (1998) showed seasonality in NEE at a Central Amazon site near Manaus. This variability in apparent carbon uptake was correlated with soil moisture, especially where during the dry season where uptake was reduced; the moisture constraint at this site imposed by the specific soil characteristics was considered further by Fisher et al. (2008) and shown to be related to soil properties as well as climate. Malhi's (1998) results, however, appear to be somewhat anomalous, as for example Araujo et al (2002) found little seasonal variation in CO<sub>2</sub> fluxes. Following the early measurements near Manaus it was suggested that Amazon rain forest carbon uptake tends to be higher rather than reduced and vegetation tends to 'green-up' during the dry season or late dry season. This was supported by eddy correlation flux measurements (higher NEE) and by the analysis of satellite reflectance data (MODIS EVI) (Saleska et al. 2003, Saleska et al, 2007, Huete et al, 2006). The latter large scale analysis, however, was later criticised because EVI values can be affected by changes in (dry season) canopy structure (Anderson et al, 2010) and by imperfect correction for clouds and aerosols (Samanta et al., 2010, 2012). The phenomenon, where observed at individual flux sites, has been explained by vegetation being relatively tolerant of normal dry season conditions because of deep root soil water access and soil moisture storage combined with higher insolation and reduced litter decomposition and respiration during the dry season (Fisher et al. 2008, Saleska et al. 2003, Bonal et al, 2008). These studies demonstrate variability in the responses by GPP and respiration processes to seasonal rainfall that is not represented in large-scale and global models. In recent years several large scale models have been altered to improve the simulated seasonality of carbon fluxes for flux tower sites by introducing improved equations (e.g. Baker et al. 2008) or by optimising model parameters (e.g. Verbeeck et al. 2011).

The response to severe or extended drought has been studied further, using two rainfall exclusion experiments in Amazonia (Brando et al, 2008; Davidson et al, 2008; Da Costa et al, 2010), and also observations of natural forest growth and mortality following the extreme natural drought of 2005 in the region (Marengo et al. 2008, Phillips et al. 2009). Under two multi-year, large scale experimental drought treatments, photosynthesis, transpiration and/or biomass increment responded sharply to the onset of artificial soil moisture reduction, while tree mortality increased substantially only after about three years of the drought treatment (Fisher et al. 2006 Brando et al. 2008, da Costa et al, 2010). The severe natural drought of 2005 in Amazonia included atmospheric as well as a soil drought effect; it also impacted mortality substantially, but over a shorter timescale of one year, causing an estimated overturn of the preceding regional carbon sink, as calculated using data from the region-wide inventory plot network, Rainfor (Phillips et al. 2009). In both types of studies (experimental and observational), bigger trees were affected disproportionately (da Costa et al. 2010, Phillips et al, 2010). Hence, current understanding suggests that the response by rainforest ecosystem productivity to seasonal drought varies over time and space, dependent partly on soil conditions, time scale and drought severity, as well as upon differences among species in vulnerability to drought (Van der Molen et al, 2011, Fisher et al.

2006, da Costa et al. 2010). The impacts of drought on tree mortality are treated in a subsequent section; here we address the direct effects of water stress on GPP and transpiration.

Reduced water availability affects photosynthesis through its effect on stomatal aperture, which modulates not only water loss but also CO<sub>2</sub> uptake. At longer (leaf ontogeny) time scales, water stress can also affect leaf structure and, for example, mesophyll conductance, directly affecting photosynthetic capacity (Egea et al, 2012). In simulation models, the effects of water stress can be approached from two sides: from the demand imposed by the atmosphere and the leaves on the plant's hydraulic systems and the soil, and from the supply of water from the soil through the rooting system to the leaves and atmosphere. In models, demand and supply have to be matched somehow. The atmospheric demand is can be represented as a radiation-dependent potential evapotranspiration with implicit boundary-layer (Priestly-Taylor or equivalent, Monteith, 1995) or by only considering exchange with the lowermost layer of the atmosphere (through a Penman-Monteith equation or explicit vapour gradient-diffusion). In both cases, the demand is modulated by the surface (or stomatal) conductance, through which (water and CO<sub>2</sub>) demand is made to match the supply. Most modelling effort in the past has gone into finding efficient representations of stomatal response to water stress and CO<sub>2</sub> demand. Broadly speaking, the approaches have been to: (i) consider stomata to respond in a linear multiplicative model to a range of independent environmental factors, where each response is determined by a set of parameters (eg Jarvis 1976; Stewart 1988); (ii) to maintain a fixed ratio of conductance to photosynthesis and humidity (or internal to atmospheric [CO<sub>2</sub>], Ball et al. 1987; Leuning, 1995); (iii) to maintain a fixed, or optimal ratio of CO<sub>2</sub> uptake to water loss (water use efficiency, Cowan (1977); Medlyn et al., 2011), or to leaf water potential (the SPA model, Williams et al, 1998).

The issues at the demand side are mainly related to the behaviour of the stomata. Different species or groups of species take different strategies in economising the rate of water loss per unit of CO<sub>2</sub> gained. This distinction is recently made between 'isohydric' and 'anisohydric' strategies, referring to those that tend to conserve water potential vs those that do not (and tend to conserve labile carbon), respectively (Fisher, 2006; van der Molen, 2012). To assess the productivity and survival of these different groups the surface conductance submodels of these need to be parameterised. It can be expected that more 'conservative' species tend to reduce conductance more quickly in the face of drought stress.

These kind of necessary improvements in models are often parameter intensive. As DGVMs are typically run for many grid points, the number of site-specific parameters needs to be minimised. For this reason it is attractive to explore model formulations that rely on few parameters and, instead, assume interdependency or optimisation of photosynthesis and transpiration. A promising candidate is the class of models that optimise marginal carbon gain per unit water lost (Cowan, 1977, Groenendijk, 2011, Medlyn, 2011). The LPJ class of DGVMs already applies this approach in a simplified way. In this algorithm, stomatal conductance is reduced iteratively from an unstressed maximum, until water demand matches the supply from the soil. One of the major uncertainties is, however, how stomata respond to limited water supply, usually quantified as relative soil moisture availability or as water tension. Many models impose an empirical reduction function of soil moisture on surface conductance (e.g. ORCHIDEE, Verbeeck et al. 2011). Usually this function is highly non-linear, leading to reductions only at low values of soil water content. Other models explicitly model the hydraulic resistances of the plant and the soil matrix as an intermediate, affecting the stomata through the leaf water potential (SPA, Williams et al. 1998; Fisher et al. 2006, Medvigy et al. 2009, Christoffersen et al. in prep). These different approaches mainly affect the rate of soil drying and the reduction of transpiration as drought progresses. Whichever way, with extended drought periods soil moisture eventually gets depleted and then the critical issue is how roots access and potentially expanding the supply of available water. Adequate understanding and representation of root growth strategies is essential, especially specifying the maximum soil volume and depth that roots can access (Nepstad et al. 1994) and whether they can cope with low-oxygen groundwater conditions. What appears to be important here is information on soil hydraulic properties such as the pressure-volume relationship and hydraulic conductivity; such datasets are scarce for Amazonia. Belk et al. (2007) and Fisher et al (2008) illustrated the importance of how these parameters cause differences in the rate at which hydraulic resistance declines with soil moisture

content, comparing sites that differed in dry season soil moisture stress. Although specific mechanisms such as hydraulic lift have been investigated in some modelling analyses (Baker et al. 2008), soil depth, the presence of ground water and potential for capillary rise are likely to be important integrating parameters for large-scale models (Christofferson et al. in prep). These aspects are poorly represented in most larger-scale models such as DGVMs, and they can also cause systematic biases in simulations.

In terms of experimental work, to advance the issue of drought sensitivity in the Amazon, there is a need for more comprehensive basin-wide information on soil hydraulic properties, measured for a sufficient number of soil types. This would enable modellers to consistently project simulation across the basin. The strategies that roots of different ecological groups take to explore and enhance the supply of water are also important, though challenging to study. The latter could, however, be interpreted as part of the whole plant response to water stress, leading to different rates of stomatal response to drought in different ecological groups. Thus, stomatal response curves as a function of the soil water balance and atmospheric demand (e.g. VPD) for these groups could provide the empirical parameters that in fact are needed by most models. Such responses can be studied the leaf scale (using porometers or chambers), tree scale (using sap flow sensors) or whole-ecosystem scale (using eddy covariance data, with the provision that soil evaporation needs to be eliminated first). Creating and studying artificial drought, such as in the 'Esecaflor' plots of the Caxiua reserve (Fisher et al. 2007, Meir and Woodward 2010, da Costa et al, 2010) and 'Secaflor' in the Tapajos area (Nepstad et al, 2002, Brando et al. 2008, Markewitz et al. 2010) greatly helps such analysis.

#### *Temperature dependence of GPP.*

The temperature dependence of photosynthesis in dynamic global vegetation models typically takes the shape of an optimum function, bell-shaped or composed of two exponential functions. Sensitive parameters typically include a minimum temperature, a maximum, an activation energy and an optimum temperature. Some models assume a wide, flat optimum range, others assume sharp optima. A range of typical temperature functions is shown by Galbraith (2010), who also shows that in many cases, model results on 21<sup>st</sup> century changes in productivity with climate depend more strongly on temperature than on moisture. Several studies have highlighted the strong sensitivity of DGVM-simulated GPP (and NEP) under climate change to assumed shapes of temperature dependence (Booth et al, 2012; Huntingford et al, 2013; Vermeulen, submitted)

The temperature responses as represented in most current DGVMs are based on fixed parameter settings, determined about two decades ago in laboratory experiments on a few species only (eg Von Caemmerer et al. 1994, Bernacchi et al. 2001, Medlyn et al. 2002). Alternatively, optima have been tuned such that they represent average growing-season temperatures of temperate ecosystems, and have remained fixed or even hard-coded in the photosynthesis modules of models. An important question here, of course, is how plastic are such optima, and the associated second-order parameters such as minimum and maximum temperatures of the temperature response (Smith and Dukes, 2013)? In theory, as Lloyd and Farquhar (2008) argue, enzyme kinetics speed up exponentially with rising temperatures until a high-temperature cell lysis or enzyme denaturation point is reached. So, for enzyme-dominated processes such as carboxylation by RuBisCo it is unlikely to expect a temperature optimum in ambient conditions. The net effect of several complex processes interacting together, however, such as those involving membrane transport (photon absorption, electron transport, osmosis and active uptake) is more likely optimised to ambient temperatures and to be plastic (Lloyd and Farquhar, 2008) resulting in temperature-related plasticity for the overall process of photosynthesis

The temperature response of photosynthesis depends on several parameters, all of which are temperature-dependent, both in reality and in most vegetation models. The much-used Farquhar equations depend on a maximum carboxylation rate,  $V_{cmax}$  and a maximum electron transport rate,  $J_{max}$ , both of which can vary strongly within and between ecosystems. There are also more intrinsic temperature-dependent parameters, such as the CO<sub>2</sub>-compensation point in the absence of



mitochondrial respiration,  $\Gamma^*$ , and the Michealis-Menten constants for carboxylation and oxidation,  $k_c$  and  $k_o$ . The strong temperature dependence of these intrinsic parameters is hard to quantify independently, and thus they are usually assumed and invariable with respect to other variation than temperature, with values taken from the literature (e.g. Bernacchi et al. 2001, Sharkey and Schrader, 2006). The formulations differ between sources, however, and affect the shape of the temperature dependencies of  $V_{cmax}$  and  $J_{max}$  as well, when these are fitted to data using the Farquhar equations. Although this may seem a technical issue, the consequence of this is also that it is important to distinguish in model-data evaluations whether the temperature dependence of maximum photosynthetic rate ( $A_{max}$ ) is considered or that of the underlying  $V_{cmax}$  and  $J_{max}$  parameters. Where the latter may show sharp, peaked responses, the effective  $A_{max}$  might be rather insensitive to temperature as the variation with temperature of the underlying parameters compensate. Also, it is essential that parameter sets are consistent in models, i.e., all should refer to the same set of pre-assumed model parameters. These issues of relatedness of parameters are often overlooked (e.g. in Smith and Dukes, 2013).

As a consequence of the assumed optimum functions, temperature dependence can be strong in DGVMs, and therefore it is very important that the associated parameters of temperature response curves are made realistic. Also, apart from any immediate temperature responses, it is important to assess how fast, if at all, these optima acclimate to changing ambient temperatures. Even then, we could distinguish acclimation of existing leaves and ontogenetic acclimation, i.e. where acclimation can only occur during the formation of new leaves (Smith and Dukes, 2013). At the time scale of interest in climate impacts on vegetation, genetic adaptation is not likely to be relevant, but competition between species or groups with different temperature responses is.

To achieve such improvement in parameterisation of temperature responses, experimental data are needed. Long-term ecosystem flux data, with naturally co-varying temperatures and GPP estimates can be used to some extent, but the lack of distinction in these data between species or species groups, between respiration and photosynthesis, and the inevitable covariance between temperature and other environmental variables, limit their application. There is a need for photosynthetic temperature parameters determined at leaf-level, both for the immediate response and the long-term response. In a vast tropical rain forest domain like the Amazon it seems almost impossible to achieve any meaningful and representative quantification of this, but with limited work at a few sites it should at least be possible to test the implicit assumption that temperature responses and optima are fairly conserved across species and regions given similar climate. If variability within ecosystems in this is high about a mean value of limited change, then overall temperature sensitivity of ecosystem productivity will be limited, but in the long run, species composition may change as a consequence of different temperature dependences.

Some work at plant and leaf scale is already under way. Along the Peruvian slopes of the Andes into Amazonia, gradient studies shed light on the plasticity of plant- and ecosystem GPP under different ambient temperature regimes (e.g. van de Weg et al. 2012, Girardin et al. 2010 Malhi et al. in review and unpublished). In central Amazonia Doughty et al (2008, 2010) has studied both immediate temperature responses and acclimation to elevated temperatures. It is, however, possible that in some of this analysis temperature response and response to correlated VPD change were hard to distinguish. It should be noted, that in analysing temperature or moisture response in models, correlated temperature and VPD also present a challenge.

Concluding, more leaf-scale data of photosynthetic temperature response are needed. Studies should quantify the response of photosynthetic capacity ( $V_{cmax}$ ,  $J_{max}$ ) and stomatal conductance rather than (maximum) net photosynthesis. Longer-term warming (or cooling) experiments should shed light on acclimation to extended periods of temperature change. Care should be taken that several species groups are considered. To capture the main ecosystem response, emphasis should be on leaves in the upper canopy of ecosystems or those exposed to direct radiation.

### *Temperature dependence of respiration*

Although it is an integral part of ecosystem carbon budgets, in this section we offer only a brief outline of the issues concerning respiration in ecosystems. More elaborate analyses of the issues can be found elsewhere (e.g. Atkin et al. (2003, 2008), Meir et al. 2008, Chambers et al. 2004 and Smith and Dukes (2013)).

With 'respiration' here we refer to all biological processes in ecosystems that lead to production of CO<sub>2</sub> derived through the oxidative reduction of organic material. The two distinct respiration pathways, autotrophic (plant) respiration and heterotrophic respiration (by consumers and decomposers of all kinds) are best modelled separately as environmental responses can be quite distinct. Few to no process-based models, for application at large scale, have been used to comprehensively represent respiration in forest ecosystems (though see Atkin et al. 2008). Although several DGVMs distinguish autotrophic and heterotrophic respiration, in general a few parameters are used to determine environmental response: a base respiration rate, roughly related to the amount of substrate or respiring organisms, whichever is limiting; and parameters describing dependence on temperature (exponential) or moisture (an optimum curve or linear function).

DGVMs often couple the (base) rate of plant respiration to productivity (photosynthesis capacity, net primary productivity, or root activity), on the grounds that the necessary enzymes in these processes turn over and need re-synthesising quickly. This coupling of parameters in models typically operates at longer time scales (months-years), but sometimes also at daily time scales, where photosynthetic capacity also acclimates at these rates to the environment (LPJ, Sitch et al, 2003).

Respiration of all types (autotrophic as well as heterotrophic) in models typically responds to temperature in an exponential way, with no optimum. The fact that respiration was formulated this way did to a large extent contribute to the predicted Amazon die-back in the HADCM3 simulations of Cox et al, (2000). The physiological basis of such exponential relationships is fairly weak. In reality, there is good reason to assume that, in the absence of other limitations such as those imposed by moisture, respiration, like most enzymatic processes, will increase with temperature monotonously up to cellular dysfunction (eg lysis) or potentially enzymatic denaturation. The empirical basis for specifying this kind of relationship has hitherto been limited, though this is beginning to change with new empirical datasets testing temperature responses over large temperature ranges (O'Sullivan et al. 2013 PCE in press). The main uncertainties here concern the exponential coefficients and how they might alter over large temperature ranges, the maximum and/or critical point beyond which respiration declines, and base respiration values. For autotrophic respiration the base respiration mainly depends on growth, transport and maintenance requirements, and in the absence of stress responses (eg drought) will be generally correlated with productivity and productive capacity. Whether and why the temperature coefficient of autotrophic respiration varies much from the  $Q_{10}=2$  standard value (Atkin and Tjoelker 2003, Davidson et al. 2006) is actively debated. There are also indications that moisture stress (i.e., plant water potential) has the potential to affect either base respiration or temperature coefficients ((Atkin and Macherel 2009, Metcalfe et al. 2010)).

For respiration in soil, the processes are more diverse and less well-understood partly because of the complexity of soil composition and structure. First of all, while models usually split autotrophic (root-derived) respiration from heterotrophic respiration, most available data refer to bulk soil respiration, although there is an increasing amount of information on root exclusion experiments (Subke et al. 2006). While root respiration and its exponential coefficients are closely linked with productivity, heterotrophic soil respiration is related to the activity of a multitude of soil organisms, and depends on accessible and decomposable soil organic matter, soil moisture, oxygen and nutrients, as well as temperature. Traditionally, decomposition is modelled for a few 'fractions' of soil carbon, defined by their readiness to decompose, while this description sometimes relates poorly to observable organic matter fractions (Buurman and Roscoe, 2011). The dynamics of SOM breakdown are complicated at short and longer time scales by feed-backs such as occlusion of SOM in aggregates (eg. Zimmermann et al. 2012; Stockmann et al, 2013) and this may be affected by the activity and diversity of soil

organisms themselves, and at short time scales by root activity stimulating exudation and mycorrhizal activity.

Thus, respiration, in spite of the fact that it represents 30-50% of ecosystem carbon dynamics (Loveys et al. 2003), is still poorly understood and represented in models, and there is no general model for respiration, as is available for photosynthesis (Farquhar et al. 1980). This implies that models have to rely largely on empirical data for parameterisation: respiration rates of a few main ecosystem components across a range of environmental conditions. When combined with GPP, a full suite of respiration estimates enables the calculation of forest ecosystem-scale carbon use efficiency, CUE ( $CUE = GPP/R$ ). Empirical estimates of CUE for tropical rain forests appear to be substantially lower than the 50% originally estimated for temperate forest ecosystems, at around 30% (Waring et al. 1998, Chambers et al. 2004, Malhi et al. 2009), and CUE is incorporated as a fixed value in some models, usually with a temperate value. Notwithstanding limitations in our understanding of the multiple ecosystem components contributing to net respiratory effluxes (Meir et al. 2008), the modelling community is in urgent need of a simple well-substantiated concept, beyond the exponential response, to model the relationship between vegetation productivity and respiration, the growth rate of soil organisms in response to the environment and substrate, and the mobilisation of substrate.

#### *CO<sub>2</sub> and nutrient sensitivity*

Several recent studies have pointed out the strong sensitivity of DGVM predictions to atmospheric CO<sub>2</sub> concentrations (Rammig et al. 2010, Jupp et al. 2010, Lapola et al. 2009, Booth et al. 2012, Huntingford et al. 2013), a key area of uncertainty that was identified by plant physiologists some 20 years ago (eg. Long et al. 1991). In most simulations for the 21<sup>st</sup> century, if atmospheric CO<sub>2</sub> concentration is assumed to increase, Amazonian forest biomass will increase despite increased temperature and drought severity, whereas if the CO<sub>2</sub> concentration is kept constant, biomass is forecast to decrease (Galbraith, 2010, Huntingford et al. 2013). In the absence of other constraints (eg. by nutrient availability) the effects of high CO<sub>2</sub> concentrations on GPP are potentially particularly strong at tropical temperatures (Hickler et al. 2008). Despite this modelled sensitivity, there is very little empirical information on the CO<sub>2</sub> response of tropical forest trees and forest ecosystems (Franks et al. 2013, Cernusak et al. 2013, Smith and Dukes, 2013), mainly because of the practical difficulty of obtaining such information. As CO<sub>2</sub> is the primary resource for photosynthetic productivity, the immediate response to elevated CO<sub>2</sub> is the production of more carbohydrates in leaves. The efficiency of this production depends on the usual photosynthesis parameters, including maximum carboxylation and electron transport, as well as the affinity of the photosynthetic enzyme Rubisco to CO<sub>2</sub> and O<sub>2</sub>. All these parameters are temperature dependent and therefore the sensitivity of carbohydrate production to CO<sub>2</sub> also depends on temperature. To what extent plants and ecosystems utilise the additional carbohydrate supply, however, to increase biomass and, ultimately, to alter the total amount of carbon stored in the ecosystem, depends on a suite of co-limiting factors, such as nutrient availability (to maintain the photosynthetic apparatus and other essential biomass components), ecological strategies of species present (determining their longevity, carbon turnover, carbon allocation and mortality), soil biochemistry and disturbance regime. Where carbohydrates are not used for growth or storage, respiration will potentially increase. Therefore, to understand CO<sub>2</sub> sensitivity, these secondary processes, including their dependence on the environment, need to be understood as well.

The supply and usage of nutrients appears to be particularly tightly coupled to plant and ecosystem responses to elevated CO<sub>2</sub>. Until recently most DGVMs lacked proper representation of nutrient dynamics, let alone their impact on NPP (some newer developments mentioned below). Based on field scale FACE experiments in temperate forests, if CO<sub>2</sub> concentrations increase, nutrients are likely to limit the response to CO<sub>2</sub> (Norby et al. 2010). Nutrient availability may first affect photosynthetic capacity and respiration, but not necessarily with the same proportionality, and with differing impacts on the allocation of newly fixed carbon to above and belowground components. As many models rely on fixed parameters for photosynthetic capacity ( $V_{cmax}$ ) and respiration, nutrient availability is only implicitly accounted for through these parameters, and not dynamically. This has as a consequence, for example, that the modelled response in productivity to elevated atmospheric CO<sub>2</sub> is only limited by radiation

under well-watered conditions. Photosynthetic capacity of plant canopies is often simulated as an optimised response to available light and water and assuming an overall fixed nitrogen availability, with respiration changing in concert. Several studies show that such optimisation is likely to be an oversimplification (Meir et al, 2002; Kull and Kruijt, 2002, Lloyd et al, 2010) but the concept leads to very powerful simplified model characteristics. For example, Haxeltine and Prentice (1996) even show that this type of model can predict canopy nitrogen quite well from absorbed radiation. In nutrient-stressed environments, or where phosphate is more limiting, such as in vegetation growing on old highly-weathered soils, such as across large parts of Amazonia, this predicted capacity is likely to lead to overestimation of productivity. Also, just as with models using fixed photosynthetic capacity, the response to CO<sub>2</sub> is not limited, and does not yet incorporate processes that might simulate alterations in the availability of the relevant limiting nutrient.

Two different approaches to modelling nutrient dependence in DGVMs can be envisaged. One approach is to link soil nutrient availability directly to concentrations in the leaves and photosynthetic capacity (Mercado et al, 2009, 2011), an approach that at minimum requires a soil nutrients map (such as in Quesada et al, 2011, , Castanho et al 2013), but is not dynamic in its treatment of nutrient use or availability. The other approach is to simulate plant nutrient concentrations as the balance between demand from the plant and photosynthesis system and supply by soil and deposition; this dynamic approach is favourable, but is a bigger challenge.

A substantial part of the demand for nutrients is determined by photosynthetic capacity, growth and metabolism (turnover) of the leaves. Nitrogen is mainly used for the enzymes of photosynthesis and respiration, and phosphorus is required for enzyme manufacture, energy transfer and nucleic acids. Depending on the plant's strategy for defence and drought resistance, nutrients are also involved in formation of additional cell wall material and to a lesser extent, secondary compounds that are not directly affecting productivity. The optimality assumption (Haxeltine and Prentice, 1996), however, implies that where absorbed light is high, the demand for nutrients to build up and maintain photosynthetic capacity will also be high. In the systematics of, for example, the LPJ model for photosynthesis, this demand varies with water stress, CO<sub>2</sub> concentration and temperature as well. If leaf area is high as a consequence of high productivity, then absorbed light is high and consequently the demand for nutrients is high. This approach does not fully recognise the effects of different plant strategies in the allocation of carbon to plant organs and on the proportion of nutrients directly used for photosynthesis. In DGVMs, either plant traits need to be specified more explicitly for different plant functional types, or these traits need to be modelled as parameters that respond to the climate and environment.

The supply of nutrients is more complex and less well-understood. Primary factors are available nutrients and rooting depth. Available N depends on N fixing, deposition and denitrification. Phosphorus exists in a number of different pools in soils not all of which are available to vegetation. Available P depends on the balance of chemically bound or sorbed P and labile P. This balance depends on several factors, such as Ph, actively secreted root enzymes, occlusion by soil aggregates, the sorption capacity of the soil and soil organisms (Turner and Blackwell 2013, Turner and Engelbrecht 2011, Lloyd et al, 2001). All these processes are generally poorly represented in DGVMs, although some first attempts, mainly on the N supply side, are being tested now (Zaehle And Friend 2010, Zaehle et al. 2010; Fisher et al, 2010) This dynamic approach of modelling nutrient availabilities has been attempted in some land surface carbon cycle models. Wang et. al., (2010) have developed a coupled P and N model for use in the CASA global carbon cycle model. Under steady-state, present day conditions, the model estimates that P limitation reduces NPP by approximately 20% in tropical evergreen broadleaf forests and tropical savannas. A phosphorus and nitrogen sub model has also been developed for use in the land surface model JSBACH (Goll et. al., 2012). Parameters affecting the partitioning of phosphorus between pools are assigned by soil order in both of these models. The majority of the Amazon basin is represented by only two soil types in these models, thus the spatial variation observed across the Amazon in soil P fractions (Quesada et. al., 2010) will not be represented by these models. The processes and parameters in these existing nutrient cycle models need to be adapted to the Amazon basin soils and incorporated into DGVMs.

Modelling the cycling of phosphorus between different pools is limited by the lack of data from tropical ecosystems with which to both validate and parameterise such models. The most comprehensive dataset to date for the Amazon is from Quesada, et. al., (2010). Experimental work that is needed to advance the representation of nutrient cycling in DGVMs is manifold. There is a straightforward need for detailed soil maps containing data on available nutrients (such as in Quesada et al, 2010). For P availability, this is not immediately obvious. To inventory leaf N/P concentrations as a function of soils, absorbed light, water stress, leaf trait or strategy and CO<sub>2</sub> concentration is another big, but fairly straightforward and prerequisite task (Malhi et al, 2002). But such data will not provide the definitive material to dynamically model the interaction of productivity, nutrients and CO<sub>2</sub>. For that, nitrogen fixation, denitrification as well as phosphate mobilisation/immobilisation need to be quantified and parameterised. Particularly, more information is needed on the mechanisms and rates of P transfer between pools. For example an improved quantification of the rates of biochemical mineralization and the investment by vegetation to nutrient acquisition strategies such as phosphatase enzyme production and mycorrhizal associations under different levels of soil phosphorus and moisture availability is required (Cernusak et al. 2011, Liu et al. 2013, in press). This is a field of research that still has to mature and, where already existing, it needs to be linked much more closely with DGVM development.

#### *Functional types versus continuous traits*

Most state-of-the-art DGVMs treat vegetation at a grid cell as belonging to one of a range of 'Plant Functional Types' (PFTs). A PFT represents a broad group of ecological vegetation types by a set of model parameters determining, for example, bioclimatic limits, deciduousness, water stress sensitivity, photosynthetic capacity, specific leaf area. Typically these PFTs have been poorly parameterised for tropical vegetation but recent work by (Fyllas *et al.* 2012) has suggested a proposed classification for Amazon forests that is much more in line with the main ecological axes of variation in plant traits: relative investment into leaf and stem longevity and nutrient contents. However, simply modifying the definition of PFTs is unlikely to be sufficient, as the discussion above shows that variability in such plant traits can be large and more continuous than assumed in such simplified and discrete PFTs. Although this approach allows relatively efficient global coverage, a disadvantage may be that process representation is too coarse and modelled transitions between vegetation types in space and time (such as forecasts of 'savannisation' and multiple stable states in Amazonian vegetation) become unnecessarily sharp and unrealistic. For example, a study of the impact of a prolonged drought in Ghanaian forests (Fauset *et al.* 2012) demonstrated that intact forests could continue to maintain high carbon stocks and increase in biomass despite an average reduction in annual rainfall of 165 mm yr<sup>-1</sup>. This was associated with a shift in the composition of the forest towards more drought tolerant species, suggesting that the resistance of the tropical forests to drought over long timescales may be increased with subtle shifts in the characteristics of the species that are present. There are two challenges to capturing more effectively these kinds of interactions within DGVMs. Firstly, one key problem is that changes to different vegetation types in reality occur at the level of the individual, but DGVMs currently operate at a patch scale. So if the processes represented at patch scale cannot be made to reflect individual-scale processes (and for some it's almost impossible), then it is inevitable that DGVMs cannot represent this change appropriately, as they are currently structured. A second problem is to recognise the range of life-history strategies that exist both within individuals of a species, and among species. Therefore several attempts are being made to develop models with continuous plant traits rather than discrete ones (e.g. Scheiter *et al.* 2013).

Some DGVMs, especially those that aim to simulate vegetation dynamics at patch scale, do allow several PFTs to co-exist and compete for coverage within one grid cell (ED, Moorcroft et al. 2001, Medvigy et al. 2009, LPJguess, Smith et al, 2001 ). In such models, individual plants or 'cohorts' of individuals compete for resources within one patch. Also, some DGVMs either allow a range of plant traits within each PFT, represented by statistical distributions (Moorcroft et al. 2001), or make several traits, such as photosynthetic capacity, an internally calculated variable rather than being externally given. The latter situation occurs with the LPJ class of models, already discussed before.

Especially for the Amazon it may be important to study the effect of discreteness in PFT formulations, and compare models with single, multiple, or plastic PFT's, as well as models that approach vegetation parameters as a continuum. It should be interesting to evaluate whether the degree of continuity in plant traits represented by each model is related to the occurrence of discrete or abrupt transitions in vegetation types, either in time or in space.

One particularly relevant option is to at least allow variation in, and competition between, plant traits that relate to drought tolerance. As described in the section on water stress, trees appear to exhibit at least two different strategies along a likely natural continuum, usually referred to as 'isohydric' and 'non-isohydric' (Tardieu and Simmoneau 1998), distinguishing species that tend to avoid water stress by reducing transpiration but then also reduce carbon uptake, and those that avoid carbon limitations by maintaining stomatal aperture, but then risk irreversible damage from water stress. In terms of existing models, such variation between stomatal traits could be expressed by varying the sensitivity of stomata to soil/plant water potential and atmospheric VPD, as explored in the previous section on water relations. However, the trait space needed to simulate water stress tolerance is likely to be broader than this, incorporating vulnerability to embolism in xylem, and potentially the capacity to use carbohydrate supply to ameliorate conductivity losses in xylem (Plaut et al. 2012).

The implications for experimental work of implementing more explicit plant trait diversity in models are first to quantify and better understand the key trait spectra, as described in previous sections, but also to understand the mechanisms that determine these differences, so that trait variation can be modelled rather than parameterised.

#### *Allocation of primary productivity over vegetation components*

The simulation of aboveground biomass depends not only on mortality processes and net primary productivity (NPP) but also on the allocation of NPP into different plant tissues. Typically, models consider three vegetation carbon pools to which NPP is allocated: wood, leaves and fine roots (Galbraith *et al.* 2013). The commonly used approaches to simulate NPP allocation in global vegetation models include: 1) constant allocation patterns, where the relative fractions of NPP allocated to each plant carbon pool are determined by fixed coefficients (e.g. IBIS and Hyland), 2) allocation driven by allometric constraints – the size of different plant pools are related to each other by allometric relationships that must be satisfied when NPP is allocated (e.g. JULES or LPJ) or 3) allocation based on the resource limitation hypothesis where NPP allocation is governed by the availability of light, water and nutrients (e.g. ORCHIDEE). Malhi *et al.* (2011) reviewed allocation patterns in tropical rainforests based on field measurements and compared these to the allocation patterns simulated by a number of ecosystem models. Mean NPP allocation fractions across tropical forests were found to be 34 +/- 6% for canopy, 39 +/- 10% for wood and 27 +/- 11% for fine roots. Furthermore, canopy NPP was found to be a relatively invariant component of total NPP with the main trade-off believed to be between fine roots and wood, rather than leaves. Mean values for global vegetation models were close to the mean of the data, but varied considerably across models. For example, allocation to wood across the models reviewed ranged from 16% to 77% of total NPP. Models whose allocation schemes were based on the resource limitation hypothesis simulated particularly high allocation to wood in Amazonian rainforests, suggesting that this model requires refinement for use in tropical forests.

A number of alternative, evolution-based models of allocation have recently been developed, although these have yet to be widely applied in global vegetation models. These recent developments in allocation modelling were recently reviewed by Franklin *et al.* (2012) and include optimal response (OR) models, game-theoretic optimisation (GTO) models and adaptive dynamics (AD) models. In OR models, such as the models of McMurtrie *et al.* (2008) or Franklin *et al.* (2009), allocation is optimised so as to maximise a fitness proxy such as canopy photosynthesis or net growth. GTO models such as that of King *et al.* (1993) are designed around the concept of an evolutionary stable strategy (ESS) which is a strategy that cannot be invaded by a different strategy when it is in equilibrium with its environment. GTO models differ fundamentally from OR models in that they explicitly include the effect of competition with other plants. Both OR and GTO models assume some *a priori* fitness proxy. In AD models, on the

other hand, the fittest strategy is an emergent feature of the model. Furthermore, AD models allow for co-existence of different evolutionary stable strategies. Dybzinski *et al.* (2011) recently developed the first allocation model based on AD. One of the predictions of this model is indeed the fine root/wood trade-off observed in the review of Malhi *et al.* (2011) across tropical forests.

NPP allocation has to date been a remarkably understudied ecosystem process. The most comprehensive published field study to date on carbon allocation to date is that of Aragão *et al.* (2009) who studied how aboveground and belowground productivity varied across 10 Amazonian sites. The study identified a strong negative correlation between the fraction of NPP allocated belowground and the soil clay content. The higher belowground allocation to NPP in sandier soils was suggested to be related to the poorer water holding capacity of those soils as greater root productivity was necessary for access to soil moisture reserves. Our understanding of NPP allocation in tropical forests should be greatly boosted by the establishment of a network of intensive carbon cycle measurements across Amazonia (<http://gem.tropicalforests.ox.ac.uk/>) allowing the seasonal and interannual dynamics of carbon allocation in Amazonian rainforests to be studied for the first time. This data provides a much-needed testing ground for competing models of carbon allocation in tropical forests.

How will increasing atmospheric CO<sub>2</sub> affect allocation processes in tropical forests? This question is very important for simulation of future biomass stocks in tropical forests, but we have insufficient knowledge at present to answer it with any confidence. While no FACE experiments exist for tropical regions, FACE experiments from temperate zones point to very different patterns in the response of carbon allocation to high CO<sub>2</sub>. DeLucia *et al.* (2005) provide a fascinating description of carbon cycling consequences of high CO<sub>2</sub> in two FACE experiments, one being a loblolly pine site in North Carolina (Duke) and the other a sweetgum tree forest in Tennessee (ORNL). Although the stimulation of GPP and NPP in both sites was of a similar magnitude (18-22% for GPP, 18%-24% for NPP), the impacts on carbon allocation were very different. At the pine site, >50% of the additional NPP due to CO<sub>2</sub> fertilisation was allocated to long-lived woody tissues while at the sweetgum site, the majority of the additional NPP was allocated to short-lived roots rather than longer-lived woody biomass. The knock-on consequences for biomass storage resulting from such different responses of carbon allocation to high CO<sub>2</sub> could be considerable.

#### *Modelling biomass: demography of vegetation carbon, mortality, disturbance, dispersal and recruitment*

Changes in primary productivity and soil respiration are important for the ecosystem carbon content, but to understand its long-term behaviour it is equally important to understand the dynamics of mortality and disturbance. Currently DGVM's do not adequately represent these population dynamics. This exclusion of dynamics can introduce a large source of uncertainty in model estimations of biomass; conversely including better representation of dynamics can radically modify the response of the modelled forest to a changing climate (Fisher *et al.* 2010). Simple or poor representation of these processes in DGVMs is not a trivial problem for the Amazon where we know there are large spatial gradients in tree mortality ((Phillips *et al.* 2004)) and biomass ((Baker *et al.* 2004)). As discussed above for modelling nutrient availability, one approach might be to simply introduce observed spatial variation in biomass losses from mortality directly into the model framework (e.g (Castanho *et al.* 2013, Galbraith *et al.* 2013). Studies where this type of approach has been attempted have demonstrated the sensitivity of modelled biomass to these parameters (e.g. (Delbart *et al.* 2010; Castanho *et al.* 2013). However, a more fundamental challenge is to relate forest dynamics to the underlying mechanistic drivers, related to soil and climatic drivers (Quesada *et al.* 2012). The lack of any mechanistic relationship between forest dynamics and environmental conditions, maybe the reason why some DGVMs do not capture the approximate 20% and 25% losses of biomass following 2 multi-year throughfall exclusion experiments, but instead remain largely insensitive to the 50% reduction in precipitation (Galbraith *et al.* 2010). These experiments showed that mainly large trees died in the third year after the treatment ((Nepstad *et al.* 2007). If the models cannot reproduce these mortality events then we may hugely overestimate future biomass stocks after expected reductions of rainfall in the dry season (Malhi *et al.* 2009).

One of the reasons that mortality is still a rudimentary process in models is because tree mortality is complex and we do not fully understand the physiological reasons of why some trees die and some survive, particularly in response to drought (McDowell et. al., 2008). However physiological response to environmental stress is only one cause of mortality, other potential causes of tree death include those arising from disturbance, eg. windthrow, or death due to senescence. It is evident that multiple factors play a role in the Amazon so all must be considered when including dynamic processes into these models. For example, there are differences in the mode and cause of death in different sites in the Amazon (Chao et al. 2008). In a site in NW Amazonia there is evidence of higher frequency, small mortality events compared to low frequency, large tree death in a site in the NE Amazon. In the NW mechanical tree breakage is the dominant cause which we may attribute to external forces, whereas in the NE the majority of trees die standing perhaps a result of senescence or drought

Currently mortality schemes in DGVMs range in complexity from having no explicit formulation, , to having a constant rate - which can vary greatly (0.5%-5%) across DGVMs (Galbraith et al. 2013) -and therefore no interaction with climate, or a carbon balance scheme where mortality results from negative NPP (LPJ, ED) (McDowell et. al. 2011). Complexity in ED is increased as mortality also increases with decreasing wood density to reflect the higher likelihood of mortality of low wood density PFTs (Moorcroft et al. 2001). More realistic or mechanistic ways of modelling mortality based on the physiological processes discussed in earlier sections are limited by the PFT approach. However, individual-based models will allow us to explore some of these avenues. Or for example, predictive methods could be used to estimate individual mortality risk based on plant characteristics (e.g, productivity, size or plant traits) which have been developed from empirical observations (e.g. Lines et. al., 2010; Chao et. al., 2008).

Recruitment is another component of forest dynamics where there is a lack of process-based understanding, particularly understanding the feedbacks with climate change. For example, Kursar et al. (2009) showed that performance of seedlings during drought may be a major determinant of species distribution patterns in tropical forests, and shifts in species composition due to drought have been observed in African forests (Fauset et al. 2012). For modelling such dynamic vegetation processes, models would, besides including the above described physiological processes, need to consider for example age-structure of forest stands, competition between plants/species, establishment patterns (e.g. shade-tolerance/-intolerance of seedlings) and seed dispersal as some models do (e.g. ED: Moorcroft et al. 2001, Kim et al. 2012; LPJ-GUESS: Smith et al. 2001).

#### *The role of fire in natural forests*

While natural fires in Amazon rainforests play a minor role, the impacts of human-caused fires in tropical rainforests are substantial today (Uhl and Kauffman 1990). Therefore, fire is an important driver for future dynamics of remaining tropical rainforest "fragments" and may in some circumstances act as the causative switch in vegetation change. Deforestation in any form creates large forest edges that are more susceptible to fire (Cochrane & Laurance 2002, Numata et al. 2010). Fires in natural tropical rainforests lead to forest degradation, such as biomass loss and changes in vegetation composition and dynamics (e.g. Cochrane 2003, Barlow & Peres 2008, Cochrane et al. 1999). Occurrence of fire also potentially leads to changes in the composition of species/plant traits, as some traits are more fire-resistant than others. Biophysical and socioeconomic feedbacks from fire may also create a feedback with regional climate (Davidson et al. , 2012). Shifts in temperature and precipitation patterns, altering vegetation structure, can in turn change fire probability and fire behaviour (e.g. Golding & Betts 2008). To estimate the extent of understorey fires and related ecosystem degradation, remote sensing products are currently being developed (e.g. Nepstad et al. 1999, Morton et al. 2011). Including the role of fires in current models is crucial for understanding potential future dynamics of Amazon rainforests. Current models include the calculation of potential human ignitions, fire probability and fire danger index (e.g. Golding & Betts 2008, Silvestrini 2011), but are yet to have the capacity to be fully coupled with global climate models. More process-understanding of interaction of fire and vegetation dynamics is needed to improve simulation of fire spread and fire behaviour in different ecosystems. Only a few approaches include process-based interaction of fire and vegetation (e.g.



potential fuel load and flammability of the forest) at the ecosystems scale (e.g. Thonicke 2010). For a better understanding of the occurrence of human-caused fires, changes in current and future land-use patterns need to be evaluated (e.g. Aguiar 2012). It is crucial to include the spread of fires from deforested areas in natural forest fragments in models, edge effects, behaviour and spread of understorey fires and the effects on ecosystems.

## Conclusion

In conclusion, we have identified the most important issues that should be addressed in upcoming research into the climate sensitivity of Amazonian vegetation. Concrete data collection and model priorities have been indicated. These include systematic inventories of driver data, experimental investigations into specific processes, as well as adapting vegetation models to better represent and accept these processes and their driver data. Focus should be on moisture, temperature, nutrients and ecosystem demography. These are issues not only of importance to the Amazon, but relevant at the global scale, too, and thus consist of an exciting field of study promising important improvements in the near future.

The capacity to reliably represent Amazon forest biomass and vegetation in models has definitely improved greatly over the last decade. Also, our insight into which factors are most important to sensitively evaluate climate change impact has improved, and it can be expected that these insights will soon lead to much more reliable DGVMs. Lack of data, both process-oriented experiments and ecosystem-scale validation data, are still sparse, however, so that uncertainties will remain substantial in the foreseeable future. Nevertheless, we are confident that given experimental effort and model development, within a few years we will be able to assess the effects of climate change on the Amazon for the upcoming century with reasonable confidence.

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