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Evolution and challenges of dynamic global vegetation models for some aspects of plant physiology and elevated atmospheric CO_2

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Abstract Dynamic global vegetation models (DGVMs) simulate surface processes such as the transfer of energy, water, CO_2, and momentum between the terrestrial surface and the atmosphere, biogeochemical cycles, carbon assimilation by vegetation, phenology, and land use change in scenarios of varying atmospheric CO_2 concentrations. DGVMs increase the complexity and the Earth system representation when they are coupled with atmospheric global circulation models (AGCMs) or climate models. However, plant physiological processes are still a major source of uncertainty in DGVMs. The maximum velocity of carboxylation (Vc_{max}), for example, has a direct impact over productivity in the models. This parameter is often underestimated or imprecisely defined for the various plant functional types (PFTs) and ecosystems. Vc_{max} is directly related to photosynthesis acclimation (loss of response to elevated CO_2), a widely known phenomenon that usually occurs when plants are subjected to elevated atmospheric CO_2 and might affect productivity estimation in DGVMs. Despite this, current models have improved substantially, compared to earlier models which had a rudimentary and very simple representation of vegetation–atmosphere interactions. In this paper, we describe this evolution through generations of models and the main events that contributed to their improvements until the current state-of-the-art class of models. Also, we describe some main challenges for further improvements to DGVMs.

Keywords Global changes · DGVMs · Maximum velocity of carboxylation · Acclimation

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Introduction

The first terrestrial system designs were made by Alexander Humboldt, in 1849 and August Grisebach in 1872, which sought to associate climate and vegetation. In 1884, Wladimir Koppen produced a classification system of vegetation, temperature, and precipitation that was the start of predictive modeling for plant geography (Fisher et al. 2014). In the twentieth century, the late 1960s, the atmospheric global circulation models (ACGMs) used for simulating the interaction between the atmosphere and the land surface did not take into account vegetation as a key component. When vegetation

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models emerged, they incorporated the mathematical representation of photosynthesis developed in the early 1980s (Farquhar et al. 1980) (FvCB). The concept of dynamic global vegetation models (DGVMs) was developed at the International Institute for Applied Systems Analysis (IIASA) during 1988–1990. DGVMs combined four areas of research in a single framework: plant geography, plant physiology and biogeochemistry, vegetation dynamics, and biophysics (Prentice et al. 2007). One basic requirement for a dynamic vegetation model is that it must simulate plant growth, mortality, and competition (Arora and Boer 2006; Prentice et al. 2007).

When coupled with AGCMs, vegetation models should have the capacity to link plant physiology with ecosystem processes and provide a higher resolution than classifying vegetation by biomes alone, when a sufficient number of PFTs is used (Rogers 2014). DGVMs have the potential to exploit computing resources and processing speed to simulate vegetation responses under different climate change scenarios.

Specialists discussed the weak points in DGVMs in relation to plant physiology representation (New Phytologist Workshop, Montauk, New York, USA, April 2014, Rogers et al. 2014). Some points raised in the discussion were as follows: (1) Parameterization—model parameters are obtained by fitting equations to gas exchange data; if these parameters are then used with different equations without consideration of the assumptions underlying the original data, photosynthesis will be incorrectly estimated; (2) Photosynthesis acclimation to temperature; (3) Maximum velocity of carboxylation (Vc_{max}) is estimated at a canopy level and not leaf level; therefore, a discrepancy would be underestimated in the models. These issues are appointed as weakness in the models.

In this paper, we discuss some aspects of plant physiology in vegetation models, such as maximum velocity of carboxylation (Vc_{max}) and its relationship with acclimation to temperature and elevated CO_2. Others aspects such as stomatal modeling, fire, phenology, carbon distribution (allocation), carbon loss (senescence, exudation, fructification), and competition between species and air pollution (i.e., interactions between trace gases—except CO_2, climate change, and vegetation) (Arneth et al. 2012) were not included in this work. We also describe the evolution of vegetation–atmosphere interactions representation in ACGMs up to the actual state-of-the-art DGVMs.

Evolution of the models

AGCMs

The AGCMs that were developed in the late 1960s were created for the purpose of estimating the atmospheric global circulation and exchange of latent and sensible heat between the surface and the atmosphere. Early AGCMs incorporated very simple land surface parameterizations (LSPs) (Sellers et al. 1997). The LSPs are based on some surface parameters such as albedo, aerodynamic roughness, and soil moisture along the continents. The computational performance of numerical weather prediction (NWP) models was also critical to the AGCM representation. NWPs algorithms are based on mathematical and physical principles beyond datasets, allowing higher spatial resolution and hence a greater refining of results when compared with previous AGCMs. In AGCMs, the movement of the atmosphere is defined by fluid dynamics equations incorporating the mechanical forces of gravity, the rotation of the Earth, temperature, and pressure gradients caused by friction and drag forces as the wind in the lower atmosphere (Sellers et al. 1997).

First generation of vegetation models

The first-generation vegetation models, in the early 1980s, were designed to integrate climate-surface representation, explicitly recognizing the influence of vegetation on the calculation of the surface energy balance (Dickinson et al. 1984; Sellers et al. 1986) (Fig. 1). While in the AGCMs, the vegetation was seen only as a permeable sheet between the soil and atmosphere, without any interaction, the first generation of vegetation models sought to model the soil-vegetation system and how the surface interacts with the atmosphere. Basically, biophysical models considered the following interactions:

- Absorption of radiation: the spectral properties of the leaves and the multiple reflections between them (canopies are highly absorbent of photosynthetically active radiation (PAR) and moderately reflective in the infrared spectra);
- Transfer of momentum: in general, canopies have a rough and porous surface. Turbulence contributes to increased transport of latent heat and sensible heat from the surface to the atmosphere;
- Functioning of stomata: the importance of stomata for water vapor fluxes to the external environment was first considered. According to Sellers et al. (1997), the response of the stomata on the environment can be parameterized by the equation:

$$g_s = g_s(PAR)[f(\delta_e)f(T)f(\psi)] \tag{1}$$

where: g_s is the stomatal conductance; $g_s(PAR)$ is the PAR-regulated (unstressed) value of leaf conductance; $f(\delta_e)$, $f(T)$
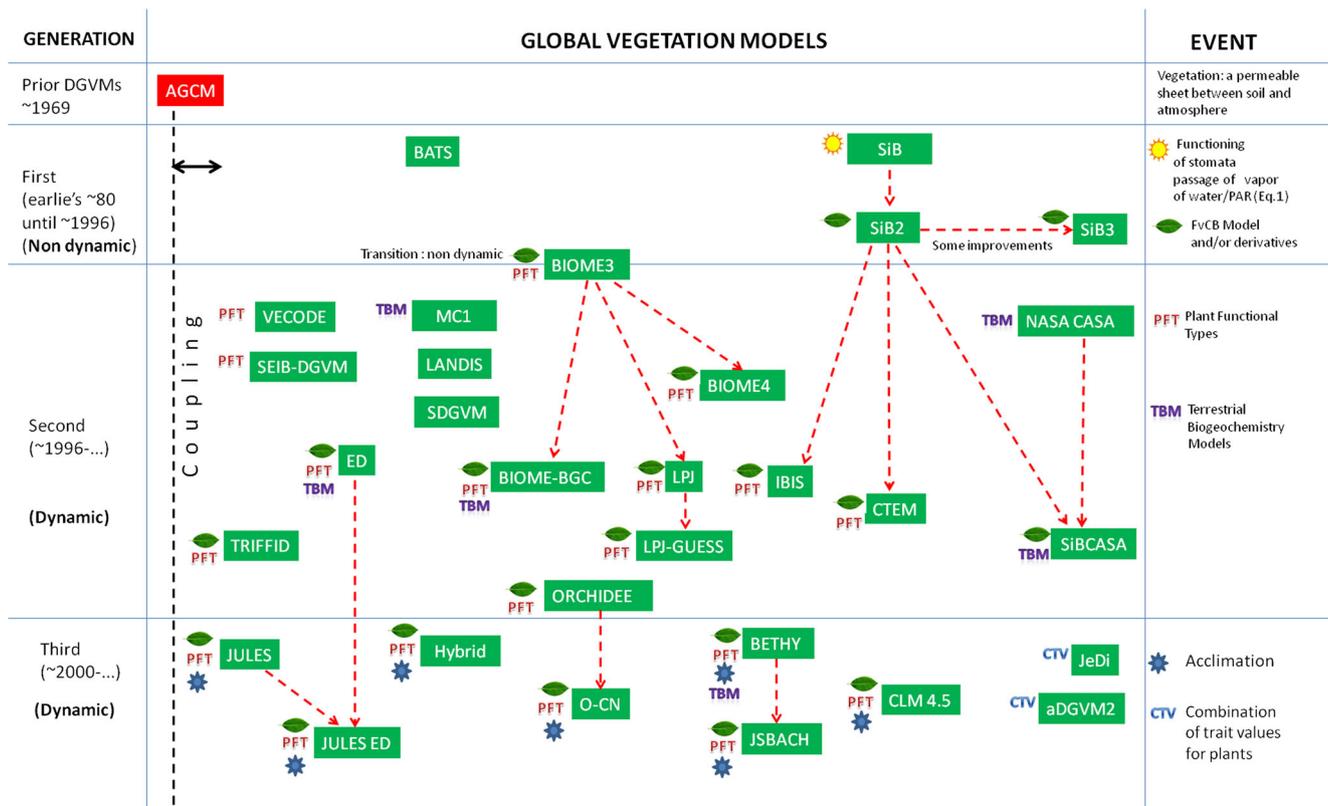
Fig. 1 Evolution of DGVMs for plant physiology processes

and $f(\psi)$ are the environmental stress factors that account for the effects of controls of vapor pressure (δ_e), air temperature (T), and leaf water potential (ψ).

In the 1980s, there were important advances in plant physiology and biochemistry with models by Farquhar et al. (1980) (FvCB), Collatz et al. (1991), and Collatz et al. (1992) for C4 plants. This knowledge was incorporated in some models of this generation (Fig. 1 and Table 1).

Farquhar, von Caemmerer, and Berry (FvCB) photosynthesis model

The calculation of carbon assimilation is given by gross production of photosynthesis for C3 plants and it is expressed as a minimum of three main limitations in the plant capacity to fix carbon (Farquhar et al. 1980; Farquhar and Sharkey 1982; Collatz et al. 1991). The gross photosynthesis rate per leaf area, Ag (CO$_2$ mol m^{-2} s^{-1}), is given by

$$A_g \approx \min(J_e, J_c, J_s) \tag{2}$$

where J_e is the light-limited rate of photosynthesis, J_c is the Rubisco-limited rate for photosynthesis, and J_s is the triose phosphate limitation for photosynthesis. In the DGVMs, the

gross primary productivity (GPP) is calculated over time for each plant functional type (i) as such:

$$GPP = \int A_{g,i} dt \tag{3}$$

The net primary productivity (NPP) over time for each plant functional type is given by the sum of carbon assimilation (Eq. 4). The equation below also includes carbon loss from the respiration processes:

$$NPP = (1-\eta) \int \left(A_{g,i} - R_{leaf,i} - R_{stem,i} - R_{root,i} \right) dt \tag{4}$$

where $R_{leaf,i}$ is the leaf respiration, $R_{stem,i}$ is the stem respiration, $R_{root,i}$ is the root respiration, and η (~0.33) is a fraction of carbon lost in building the structure of the plant due to respiration during growth (Foley et al. 1996).

Despite the advances in plant physiology, the first-generation models did not incorporate concepts of dynamic vegetation.

Second generation of vegetation models

In the second generation, models were implemented with considerations for growth, mortality, and competition of plants,

Table 1 DGVMs and main processes of plant physiology of these models

Model	Photosynthesis	Stomatal conductance	Vc$_{max}$-related leaf nitrogen content	PFTs	Acclimation	Observation
aDGVM (adaptive dynamic global vegetation model) (Scheiter and Higgins 2009)[a]	FvCB Collatz et al. (1991) Collatz et al. (1992)	Ball et al. (1987) Collatz et al. (1991) Collatz et al. (1992)	No	Modeled variables	No	
BATS (Biosphere-atmosphere Transfer Scheme) (Dickinson et al. 1984)	No	Jarvis (1976)	No	–		
BETHY (Biosphere Energy Transfer Hydrology Scheme) (Knorr 2000; Ziehn et al. 2011)[a]	FvCB and Bayesian approach	Ball et al. (1987)	Photosynthetic capacity is related to leaf nitrogen content	12	Yes	Sub-grid cells with different PFTs
BIOME3 (Haxeltine and Prentice 1996b)	FvCB Haxeltine and Prentice (1996a)	Jarvis and McNaughton (1986)	No	13	No	
BIOME4 (Kaplan et al. 2003)[a]	FvCB Haxeltine and Prentice (1996a)	Haxeltine and Prentice (1996a)	No	13	No	
BIOME-BGC 4.2 (Running et al. 2010)[a]	FvCB	Körner (1995).	Consider leaf C:N ratio	3	No	
CLM 4.5 (Community Land Model) (Oleson et al. 2013)[a]	FvCB Collatz et al. (1991) Collatz et al. (1992)	Collatz et al. (1991) Collatz et al. (1992) Sellers et al. (1996b)	Vc$_{max}$ varies with foliage nitrogen concentration and specific leaf area	17	No	
CTEM (Canadian Terrestrial Ecosystem Model) (Arora 2003; Arora and Boer 2010)[a]	FvCB Collatz et al. (1991) Collatz et al. (1992)	Collatz et al. (1991) Collatz et al. (1992)	Vc$_{max}$ were derived from unspecified sources and then tuned to reproduce observed global spatial patterns in GPP	6	No	
ED (Ecosystem Demography) (Medvigy et al. 2009)[a]	FvCB	Leuning (1995)	No. Vc$_{max}$ fixed values for each PFT	5	No	
Hybrid 6.5 (Friend 2010)[a]	Kull and Kruijt (1998)	Jarvis (1976); Stewart (1988)	Photosynthetic capacity is related to leaf nitrogen content	8	Yes	
IBIS (Integrator Biosphere Simulator) (Foley et al. 1996; Kucharik et al. 2000)[a]	FvCB	Collatz et al. (1991); Collatz et al. (1992); Leuning (1995)	No. Parameterized value of Vc$_{max}$ related to soil moisture	12	No	
JeDi (Jena Diversity-Dynamic Global Vegetation Model) (Pavlick et al. 2013)[a]	No	No	Leaf nitrogen concentration, which determines the balance between photosynthesis and respiration	–	No	Large number of randomly-generated plant growth strategies
JSBACH (Joint Scheme for Biosphere Atmosphere Couplingin Hamburg)[a]	FvCB	Collatz et al. (1992)	Yes	13	Yes	
JULES (The Joint UK Land Environment Simulator) (Mercado et al. 2007; Best et al. 2011; Clark et al. 2011)[a]	FvCB	Collatz et al. (1991) Collatz et al. (1992) Jacobs (1994)	Linearly related to leaf nitrogen	5	Support to decreasing of nitrogen	Four non-vegetation types: urban, inland water, bare soil and land ice
JULES ED (Fisher et al. 2010)[a]	FvCB	Collatz et al. (1991) Collatz et al. (1992) Jacobs (1994)	Linearly related to leaf nitrogen	7	Support to decreasing of nitrogen	
LANDIS (Spatially explicit model of forest landscape disturbance, management, and succession) (He et al. 2012)[a]	No	No	–	–	No	It simulates the dynamics of forest succession, seed dispersal, wind, fire, biological disturbance (insects and diseases), harvesting and decomposition

Table 1 (continued)

Model	Photosynthesis	Stomatal conductance	V_{cmax}-related leaf nitrogen content	PFTs	Acclimation	Observation
LPI (Lund–Potsdam–Jena DGVM) (Sitch et al. 2003)[a]	FvCB Collatz et al. (1992)	Haxeltine and Prentice (1996a)	V_{cmax} varies with foliage nitrogen concentration and specific leaf area	10	No	
LPJ-GUESS (Smith et al. 2001; Sitch et al. 2003; Gerten et al. 2004; Hickler et al. 2012)[a]	FvCB Collatz et al. (1992)	Haxeltine and Prentice (1996a)	V_{cmax} varies with foliage nitrogen concentration and specific leaf area	13	No	Source: LPJ. LPJ-GUESS updated PFT parameters and includes an interactive nitrogen cycle
MC1 (Mapping Century) (Bachelet et al. 2001)[a]	No	Neilson (1995)	No	–	No	
NASA-CASA (Carnegie Ames Stanford Approach) (Potter and Klooster 1999)[a]	No	No	No	10	Biogeochemical responses to climate and PFTs over relatively long time intervals (decades to centuries)	Plant competition for resources (water and light)—nitrogen cycle.
O-CN (Zaehle and Friend 2010)[a]	FvCB Collatz et al. (1992)	Ball et al. (1987)	Leaf N content for a given canopy layer is used to estimate the V_{cmax} in that layer	12	Long-term acclimation mainly controlled by changing investment in tissue N	
ORCHIDEE (Organizing Carbon and Hydrology in Dynamic Ecosystems) (Krinner et al. 2005)[a]	FvCB Collatz et al. (1992)	Ball et al. (1987)	It has an optimum photosynthesis temperature, leaf age and canopy position. Photosynthetic capacity is conditioned by leaf nitrogen content		No	
SDGVM (Sheffield-DGVM) (Woodward et al. 1995; Woodward and Lomas 2004)[a]	Productivity estimated through isotopic analysis and maximum photosynthesis is constrained by nitrogen uptake	No	No	–	No	Nitrogen cycle
SEIB-DGVM (Sato et al. 2007)[a]	Single leaf photosynthetic rate is formulated as a simple Michaelis type function of PAR intensity	Ball et al. (1987) Leuning (1995)	No	10	No	Model was formulated to biologists to carry out field measurements and data comparisons when data are relatively simple
SiB (Simple Biosphere Model) (Sellers et al. 1986)	No	No	No	-	No	
SiB2 (Sellers et al. 1996b; Denning 1996; Randall et al. 1996)	FvCB Collatz et al. (1991) Collatz et al. (1992)	Collatz et al.(1991) Collatz et al. (1992) Sellers et al. (1996a); Randall et al.(1996)	No. Parameterized value of V_{cmax} related to soil moisture	–	No	Source: SiB. Incorporation of FvCB and conductance
SiB3 (Simple Biosphere Model 3) (Baker 2008)	FvCB	Collatz et al.(1991) Collatz et al. (1992) Sellers et al. (1996a); Randall et al. (1996)	No. Parameterized value of V_{cmax} related to soil moisture	–	No	
SiBCASA (Schaefer et al. 2008)[a]	FvCB Collatz et al. (1991) Collatz et al. (1992)	Collatz et al. (1991) Collatz et al. (1992) Ball et al. (1987)	No. Parameterized value of V_{cmax} related to soil moisture	–	No	
TRIFFID (Top-down Representation of Interactive Foliage and Flora Including Dynamics) (Cox 2001)[a]	Collatz et al. (1991) Collatz et al. (1992)	Cox et al. (1998)	Linearly dependent on the leaf nitrogen concentration	5	No	Non-vegetation types: bare soil, inland water, urban areas and land ice

Table 1 (continued)

Model	Photosynthesis	Stomatal conductance	Vc_{max}-related leaf nitrogen content	PFTs	Acclimation	Observation
VECODE (VEgetation COntinuous DEscription) (Brovkin et al. 1997)[a]	No	No	No	3 (trees, shrubs, grasses)	No	

[a] Dynamic

featuring the concept of dynamic vegetation (Prentice et al. 2007). Another concept introduced was that of PFTs to represent the main types of plants on the planet (Box 1981, 1996). Biome3 (Haxeltine and Prentice 1996b) is partly a second-generation model, because it used PFTs but not dynamic vegetation (Fig. 1). During the second-generation period, emerged the terrestrial biogeochemistry models (TBMs) that are described in "Terrestrial biogeochemistry models".

Plant functional types

The use of plant functional types (PFTs) has become an important component in DGVMs to simulate vegetation responses to environmental changes at a regional or global scale. PFTs represent the world's most important plant types, characterize them through their functional behavior, and provide complete, geographically representative coverage of the world's land areas (Box 1996). Box (1996) observed three main approaches to PFTs that have been applied in the models: (i) a physiological focus on plant's internal function, especially at the level of basic metabolism; (ii) an ecological focus on function in relation to plant form and environmental conditions; and (iii) a geophysical representation of how plant functions affect the adjacent atmosphere. Generally, DGVMs contain a number of PFTs that vary from 5 to 19 (Scheitter and Higgins 2009; Rogers 2014). However, Lavorel et al. (2007) observed that DGVM using a low number of PFTs (less than 13) might produce coarse results, simulating abrupt changes in vegetation instead of smooth gradients that are more commonly found in nature (Quillet et al. 2010). As well, Körner (1993) argued that boundaries between functional groups are often missing and discretization becomes harder.

Terrestrial biogeochemistry models

Terrestrial biogeochemistry models (TBMs) are a subset of DGVMs (e.g., BETHY, ED, MC1, NASA-CASA) that were originally developed with the main goal of simulating NPP, using simpler parameterizations than the FvCB model (Prentice et al. 2007). For example, MC1 (Neilson 1995) limits the representation of plant physiology with stomatal conductance parameters and a combination of rules. These rules generally seek for a solution through leaf area index (LAI), biologically consistent with evapotranspiration and the rainfall of the season (Neilson 1995). To avoid exceptions which can lead to absurd results, the model uses ecophysiological rules. For example, when air and soil are very dry, stomatal conductance is reduced to a value close to zero in the model. Another model of this generation, the Carnegie Ames Stanford Approach (NASA-CASA) (Potter and Klooster 1999) is based in the resource-ratio succession hypothesis (Tilman 1985), which applies to species that are dominant during succession, considering two main elements: (i)

plant competition for resources (water and light) over relatively short periods (months and seasons); and (ii) the long-term pattern in the supply of resources, such as water and nutrients. Based on plant production as the primary carbon and nitrogen cycling source, the NASA-CASA model is designed to couple daily and seasonal patterns in soil nutrient mineralization and soil heterotropic respiration (Potter and Klooster 1999). The more recent TBMs use FvCB model for the calculation of photosynthesis for external variables (Prentice et al. 2007; Fisher et al. 2014), such as BETHY and JSBACH models (Knorr 2000; Ziehn et al. 2011).

Third generation of DGVMs

In the third generation, some models were merged to create new ones. Some incorporate acclimation to elevated CO_2 or FvCB models, such as O-CN and SibCASA, respectively. The main innovation was the implementation of some processes of acclimation, treated in "Challenges of DGVMs". Another innovation is the use of a novel approach to better represent plants traits (described in "Plant traits"), with the purpose of eliminating the limitation of low number of PFTs (more details on the next section).

Plant traits

Despite the fact that DGVMs allowed vegetation ecologists and meteorologists to address important questions in Earth System Sciences, the PFT approach still poses limitations in the representation of competition and responses of plant traits to environmental conditions. Plant traits can be related to plant function in relation to main environmental constraints, and these same traits are relevant to the distribution of species along gradients of climate, nutrient availability, and disturbance (Lavorel et al. 2007). Most DGVMs simulate plant functional responses that are based on observed correlations among their morphological, physiological, biochemical, reproductive, or demographic characteristics. However, this approach is not sufficient to predict changes in ecosystem processes directly from projected changes in plant species composition in response to global change (Lavorel et al. 2007; Pavlick et al. 2013; Fisher et al. 2014). A more realistic approach is important, in order to associate functional groups (species with a similar effect on one or several ecosystem functions, primary productivity, nutrient cycling) with groups of species with a similar response to a particular environmental factor; e.g., resource availability, disturbance, or CO_2 concentrations. Some models such as JeDi DGVM (Pavlick et al. 2013) and aDGVM or aDGVM2 (Scheitter and Higgins 2009, 2013) emerged after with this purpose. Both models use computational algorithms and use a combination of traits of plants that allow multiple possibilities to characterize plant communities, growth, and competition (Fig. 1 and Table 1). JeDi, for

example, generates a large number of hypothetical plant growth strategies, each defined by 15 functional trait parameters that characterize plant behavior with regard to carbon allocation, phenology, and ecophysiology. The trait parameter values are randomly sampled from their full observed or theoretical ranges. The plant growth module simulates the development of the plant growth strategies based on fundamental ecophysiological processes (e.g., photosynthesis, respiration, allocation, phenology, and turnover). The environmental conditions of each strategy are provided by the land surface module, which simulates canopy, interception, evaporation, root water uptake, and runoff using daily meteorological forcing as shortwave and longwave radiation, air temperature, and precipitation (Pavlick et al. 2013).

Challenges of DGVMs

The greater uncertainties of DGVMs has its origin in the physiological processes (Huntingford et al. 2013; Fisher et al. 2014; Walker et al. 2015; Belinda et al. 2015; Lin et al. 2015). We discuss some of these physiological processes below.

Acclimation to temperature and CO₂

A challenging issue for models is to represent plant acclimation. The responses of plants to increasing temperature and CO_2 concentration in the atmosphere are still poorly understood at scales relevant for models (Smith and Dukes 2012; Belinda et al. 2015). However, most DGVMs assume that plant respiration (CO_2 release) increases exponentially with temperature, regardless of acclimation (Atkins et al. 2008; Smith and Dukes 2012). The use of static parameters causes DGVMs to respond without adjusting to environmental changes (Belinda et al. 2015). Smith and Dukes (2012) surveyed 17 DGVMs under three points of view of processes of acclimation: (1) photosynthesis in relation to temperature, (2) autotrophic respiration in relation to temperature, and (3) photosynthesis in relation to elevated CO_2. Some models incorporate acclimation to some extent in their simulations (Belinda et al. 2015), but none of these analyzed by Smith and Dukes (2012) contemplates the three main aspects of acclimation cited above.

Acclimation to temperature and CO_2 concentration occurs in many species of different functional groups (Tjoelker et al. 1999). Temperature acclimation can occur in a few days and it results from an adjustment of metabolism of respiration to compensate for changes in temperature (Atkin and Tjoelker 2003). There are many uncertainties concerning temperature acclimation. Many plants adjust the temperature sensitivity of photosynthesis to the temperatures they experience in the preceding days and weeks (Rogers et al. 2014; Way and Yamori

2014). However, few DGVMs include this process of acclimation (Smith and Dukes 2012; Rogers et al. 2014).

In relation to CO_2, direct effects occur because rising CO_2 increases the activity of Rubisco and the inhibition of RuBP oxygenation, reduction of stomatal aperture affecting mitochondrial respiration and others (Sage 2002). Because of these direct effects, the carbon and water balance in plants is altered leading to secondary effects on growth, resource partitioning, and defense compounds synthesis. According to Sage (2002), the photosynthetic stimulation that initially follows an exposure to elevated CO_2 generally leads to a significant enhancement of leaf carbohydrate levels and a burst of growth. However, with a few days to weeks of exposure to CO_2 in high levels, leaf protein levels may begin to decline, decreasing Rubisco content and consequently the photosynthetic capacity and thus reducing growth enhancement. Also, positive responses of photosynthesis to elevated CO_2 concentrations may decrease over time in longer term studies due to limitation by nutrients (nitrogen uptake) needed to sustain the short-term response, a phenomenon known as progressive nutrient limitation (PNL) (Norby and Zak 2011; Smith and Dukes 2012; Rogers et al. 2014; Belinda et al. 2015).

DGVMs must reproduce these primary and secondary effects. Despite uncertainties observed in the models, physiologists that were present in the Montauk, New York, meeting suggested that the representation of CO_2 acclimation in the O-CN model is quite close to their understanding of this process (Rogers et al. 2014).

According to Berry et al. (2010) climate simulations are sensitive to small changes in stomatal conductance. However, still it is not known whether all plants in the terrestrial biosphere are responding to the CO_2 concentration growing by decreasing conductance, as represented in the simulations (Leakey et al. 2009; Berry et al. 2010). Under conditions of high atmospheric CO_2 concentrations, a decrease in stomata density in plants was observed (Beerling and Royer 2002). Long-term and paleoecological studies with plant material showed an inverse relationship between the variations of CO_2 and the number of stomata, that is, the higher the concentration of CO_2 in the atmosphere, the lower the stomata density (Beerling and Royer 2002). Berry et al. (2010) raised the question: are the DGVM simulations adequate representations of how stomata are responding to global changes?

Studies of stomata functioning are also considered a difficult and challenging area (Berry et al. 2010). Berry and colleagues commented that experiments with Free Air CO_2 Enrichment (FACE) (Ainsworth and Long 2005), using elevated atmospheric CO_2, has showed a decrease of stomatal conductance. Guard cells control the exchange of gases from inside the leaf and the atmosphere, they also acclimate to atmospheric concentrations of CO_2 (Hetherington and Woodward 2003). In the Montauk, New York, meeting, some specialists showed the importance of incorporating genetic variation in stomatal sensitivity to photosynthesis, relative humidity, and CO_2 into model parameterizations (Rogers et al. 2014).

Another issue is the estimation of Vc_{max} when acclimation occurs. Generally, a reduction of the Vc_{max} rate is observed in plants growing in elevated CO_2 in FACE experiments (Long et al. 2004; Ainsworth and Rogers 2007). This reduction varies with PFT. Legumes and trees showed a reduction of 8 and 6 %, respectively; otherwise, shrubs and grass had a reduction of 18 and 16 %, respectively (Ainsworth and Long 2005; Ainsworth and Rogers 2007). A challenge for the refinement of Vc_{max} estimation in DGVMs would be to represent this reduction of Vc_{max} rate for each PFT. A further issue is how to implement nutrient limitation (nitrogen and phosphorus) in photosynthesis within the models. Generally, DGVMs adopt an approach in the estimation of Vc_{max} considering a relationship between Vc_{max} and leaf N content (Kattge 2009; Smith and Dukes 2012; Rogers 2014). Carbon assimilation may be limited by nitrogen leaf content (Kattge 2009; Walker et al. 2015) (Fig. 2). However, models do not yet represent the decline of carbon assimilation due to progressive nitrogen limitation (PNL) observed in plants grown in a

Fig. 2 Classification of DGVMs as to FvCB model and Vc_{max} related to the nitrogen content in the leaf
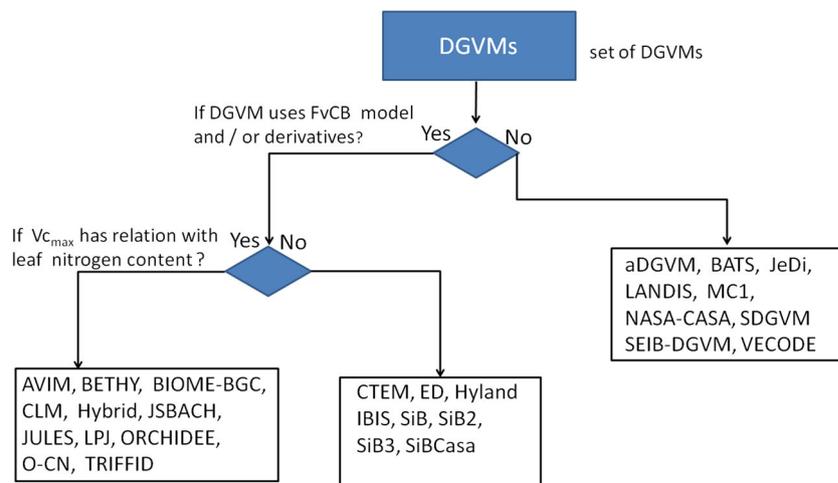
atmosphere with elevated CO_2, such as in the FACE experiments (Leakey et al. 2009; Smith and Dukes 2012; Fisher et al. 2014; Walker et al. 2015).

Maximum velocity of carboxylation

Maximum velocity of carboxylation (Vc_{max}) is considered one of the most critical parameters for modeling vegetation in face of global changes (LeBauer et al. 2013; Rogers 2014; Dietze 2014) and has a direct impact on gross primary productivity (GPP) (Bonan et al. 2012; LeBauer et al. 2013; Rogers 2014; Dietze 2014). In the calculation of GPP, several environmental parameters are needed: light, temperature, atmospheric CO_2, nitrogen, and water (McGuire et al. 1992; Fisher et al. 2014). Because of the critical dependency on empirical parameters and because those parameters are not well characterized globally over space and time, DGVMs that rely on carbon assimilation approaches may suffer from large uncertainties associated to these parameters (Arora 2002; Fisher et al. 2014).

Another uncertainty observed in simulations of DGVMs is that they tend to underestimate GPP (Bonan et al. 2011; 2012; Dietze 2014). This can be attributed to the lack of data used for proper Vc_{max} calibration and the fact that canopy-level Vc_{max} values are used, which are lower than those observed at the leaf level (Schaefer et al. 2012; Bonan et al. 2012; Dietze 2014). This difference is in the measurement of canopy-level nitrogen that is more imprecise than leaf-level nitrogen content measurement (Schaefer et al. 2012). Bonan et al. (2011) show the need to properly represent nitrogen effects on Vc_{max} when they compare output of Vc_{max} from models versus global values of Vc_{max} compiled by Katge et al. (2009). Using a nitrogen function to estimate Vc_{max} gives more accurate results (Bonan et al. 2011). Another methodology for Vc_{max} estimation is to derive parameter values from canopy scale eddy covariance flux measurements (Misson et al. 2006; Santarem et al. 2007; Ziehn et al. 2011; Bonan et al. 2012). Using high-frequency eddy covariance flux measurements, net exchange ecosystem (NEE), latent heat, sensible heat, and net radiation, Santarem et al. (2007) demonstrated skill in estimating carboxilation rates (Vc_{max}). However, this approach explicitly recognizes the difficulty in applying parameter values obtained at the leaf-level to larger scales (Bonan et al. 2012). Yet another issue, Rogers (2014) noted a wide variation in Vc_{max} used in models that had identical PFTs and which sought to represent the CO_2 uptake of the same biomes, which is critical due to the role of Vc_{max} in the carbon cycle.

The task of estimating GPP of a biome is not trivial. Calculations for monocultures are relatively easier in comparison with natural biomes which show enormous variety of life forms or PFTs (Bonan et al. 2002). When $Vc_{max}$is not well calibrated, errors and uncertainties can be added to productivity calculation.

Final remarks

Physiological processes play a critical role in DGVMs, and additional field data for Vc_{max} calibration is of particular interest. Acclimation to temperature and CO_2 is an emerging issue as a strategy to improve DGVMs. However, there is an unrealistic representation of acclimation in most of the models. Taking into account an atmosphere with elevated CO_2 concentrations, the nutrient limitation in photosynthesis and reduction of Vc_{max} rate are not well represented in DGVMs, which in our opinion are great challenges for improving the models. Furthermore, current DGVMs continue to incorporate new knowledge from experimental studies on the ecophysiological responses to environmental changes and observations from the functional structure of plants. Models are important tools that can help understand the relations in the Earth system, as well as to support policy decisions, by drawing different climatic scenarios of the planet's future.

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