Toward dynamic global vegetation models for simulating vegetation–climate interactions and feedbacks: recent developments, limitations, and future challenges

Anne Quillet, Changhui Peng, and Michelle Garneau

Abstract: There is a lack in representation of biosphere–atmosphere interactions in current climate models. To fill this gap, one may introduce vegetation dynamics in surface transfer schemes or couple global climate models (GCMs) with vegetation dynamics models. As these vegetation dynamics models were not designed to be included in GCMs, how are the latest generation dynamic global vegetation models (DGVMs) suitable for use in global climate studies? This paper reviews the latest developments in DGVM modelling as well as the development of DGVM–GCM coupling in the framework of global climate studies. Limitations of DGVM and coupling are shown and the challenges of these methods are highlighted. During the last decade, DGVMs underwent major changes in the representation of physical and biogeochemical mechanisms such as photosynthesis and respiration processes as well as in the representation of regional properties of vegetation. However, several limitations such as carbon and nitrogen cycles, competition, land-use and land-use changes, and disturbances have been identified. In addition, recent advances in model coupling techniques allow the simulation of the vegetation–atmosphere interactions in GCMs with the help of DGVMs. Though DGVMs represent a good alternative to investigate vegetation–atmosphere interactions at a large scale, some weaknesses in evaluation methodology and model design need to be further investigated to improve the results.

Key words: dynamic global vegetation model (DGVM), vegetation modelling, climate change, coupling, global climate model (GCM), land surface scheme (LSS).

Résumé : Dans les modèles climatiques actuels, il y a un manque de représentation des interactions biosphère-atmosphère. Pour palier à ce manque, il est possible d'introduire la dynamique de la végétation dans les schèmas de transfert de surface ou encore coupler les modèles de climat global (« GCMs ») avec les modèles dynamiques de végétation. Puisque ces modèles dynamiques de la végétation n'ont pas été conçus pour inclure les GCMs, jusqu'à quel point les modèles de globaux dynamiques végétation (« DGVMs ») peuvent ils être utilisés dans les études climatiques globales? Les auteurs passent en revue les derniers développements dans la modélisation DGVM ainsi que le développement de couplage des DGVM–GCM dans le cadre d'études sur le climat global. On souligne les limites du DGVM et du couplage et on met en lumière les défis posés par de ces méthodes. Au cours de la dernière énnie, les DGVMs ont subi des modifications majeures dans la représentation des mécanismes biogéochimiques tels que les processus de photosynthèse et de respiration ainsi que la représentation des propriétés régionales de la végétation. Cependant, on a identifié plusieurs limitate comme les cycles du carbone et de l'azote, la compétition, l'utilisation des terres et les modifications de ces utilisations, ainsi que les perturbations. D'autre part, de récentes avancées dans les techniques de couplage permettent de simuler les interactions végétation–atmosphère dans les GCMs à l'aide des DGVMs. Bien que les DGVMs représentent une bonne alternative pour étudier les interactions végétation–atmosphère à grande échelle, il faudra examiner de plus près certaines faiblesses dans les méthodologies d'évaluation et la conception des modèles afin d'améliorer les résultats.

Mots-clés : modèles de globaux dynamiques végétation (« DGVM »), modélisation de la végétation, changement climatique, couplage, modèle global de climat (« GCM »), schéma de surface continentale (« LSS ») .

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A. Quillet.[1] Institut des Sciences de l'Environnement, GEOTOP and Chaire DÉCLIQUE–UQAM – Hydro Québec, Université du Québec à Montréal, 201 Président-Kennedy, Montréal, QC H2X 3Y7, Canada.
C. Peng. Institut des Sciences de l'Environnement, Université du Québec à Montréal, 201 Président-Kennedy, Montréal, QC H2X 3Y7, Canada.
M. Garneau. GEOTOP, Département de Géographie and Chaire DÉCLIQUE–UQAM – Hydro Québec, Université du Québec à Montréal, 201 Président-Kennedy, Montréal, QC H2X 3Y7, Canada.

[1]Corresponding author (e-mail: quillet.anne@courrier.uqam.ca).

1. Introduction

Vegetation interacts with the atmosphere in many ways including photosynthesis, productivity, competition, disturbances, etc. (Deman et al. 2007). Biophysical, ecological, and physiological processes of vegetation and soils have strong influences on the thermal and chemical composition of the atmosphere and thus on climate. The land–atmosphere exchange of turbulent fluxes of energy, water, momentum, and trace gases is primarily regulated by the state of the land surface, which is determined by a range of biological processes (Arora 2002; Pitman 2003). These biological processes, depending on the local climate, determine the type of vegetation that grows in a region and its structural attributes including albedo, roughness length, leaf area index (LAI), rooting depth, and distribution, all of which affect the regional climate by regulating turbulent fluxes (Pitman 2003). The bidirectional interactions between vegetation and climate determine the dynamic equilibrium state of the climate–vegetation system. However, most global and regional climate models represent vegetation as a static component of the climate system. In this framework, although specified vegetation structural attributes influence the state of the climate, the vegetation itself is not allowed to respond to the climate model or any climatic changes. Thus, the effect of changes in vegetation on climate via feedback processes is not represented and the land surface is treated as a specified boundary rather than as an interactive interface.

There have been efforts in the past decade to develop vegetation models and progress from static equilibrium to transient–dynamic models (Kucharik et al. 2000; Peng 2000; Cramer et al. 2001; Sitch et al. 2003; Sitch et al. 2008; Tang and Bartlein 2008). At present, only a handful of regional climate modelling groups simulate vegetation as a dynamic component (e.g., Lu et al. 2001). In addition, several assessments of vegetation–climate feedbacks lead to the conclusion that there is a regional difference in the sensitivity and response of vegetation to climate. For example, the mid- and high-latitude vegetation variability is mostly controlled by temperature, and vegetation shows a strong positive feedback on temperature. The strongest feedback occurs in the boreal regions. In the tropics and subtropics, the vegetation variability depends mainly on precipitation but vegetation exerts only a weak feedback on precipitation (Zheng et al. 1999; Wang and Eltahir 2000; Snyder et al. 2004; Liu et al. 2006; Notaro et al. 2006). However, the observation of the vegetation feedback on precipitation is quite challenging (Notaro et al. 2006). Furthermore, the consideration of a delayed response of vegetation on precipitation shows a stronger feedback (Alessandri and Navarra 2008). Sensitivity to variations in vegetation and climate vary at a regional scale; therefore, it is of great importance to investigate its significance at regional resolution to integrate this feedback into the global vegetation models.

The patch or gap models were originally developed to quantitatively represent vegetation dynamics. They are able to simulate tree establishment, growth, competition, mortality, and nutrient cycling. Although these models were originally developed for forest ecosystems, they have been adapted to other environments such as savannas or grassland (Shugart and Smith 1996; Peng 2000; Bugmann 2001). The mechanisms of these early models are still used in the current dynamical models. Moreover, biogeographical models were developed for ecological studies and are based on ecophysiological constraints and resource limitations. These models give a static representation of the vegetation distribution (based on the dominance of plant functional type (PFT)) and do not take the successional processes into account (Melillo 1995; Peng 2000). Prentice et al. (1989; 1992) developed the first global vegetation model (e.g., BIOME model). Biogeochemical models represent the ecosystem functions and are based on climate and soil characteristics. These models simulate the carbon cycle, nutrients, and water in terrestrial ecosystems. Some models, such as BIOME3 and DOLY (Woodward et al. 1995; Haxeltine and Prentice 1996) integrate both biogeochemical processes and a biogeographical description of vegetation (Cramer et al. 1999). These models are in equilibrium and are not able to simulate the vegetation dynamics. Peng's (2000) reviewgives an insight into the advantages and limitations of the static and dynamic biogeographical models. In this paper, we focus on the dynamic global vegetation models (DGVMs) that are currently the most complete representation of integrated dynamics in this domain. These models include biogeochemical and biogeographical processes as well as their dynamical links to the atmospheric system.

The DGVMs aim to represent the complexity of the vegetation dynamics in the most comprehensive way. Thus, DGVMs offer an opportunity for global climate models (GCMs) to include vegetation–atmosphere interactions in the climate simulations by the means of coupling. First, this paper intends to review the state of the art of DGVM and of DGVM–GCM couplings. Many ecological and dynamical processes are not yet well understood. This induces a lack in the representation of vegetation dynamics and some limitations in the simulation results of the models. Second, the review of these issues along with the validation issue and DGVM–GCM coupling limitations will be raised. The third goal of this paper is to identify the future challenges to improve the effectiveness of DGVMs and develop new features that could be applicable for DGVMs alone, or coupled DGVM–GCMs or even for Earth system models (ESMs) or any similar representation of vegetation dynamics at large scale.

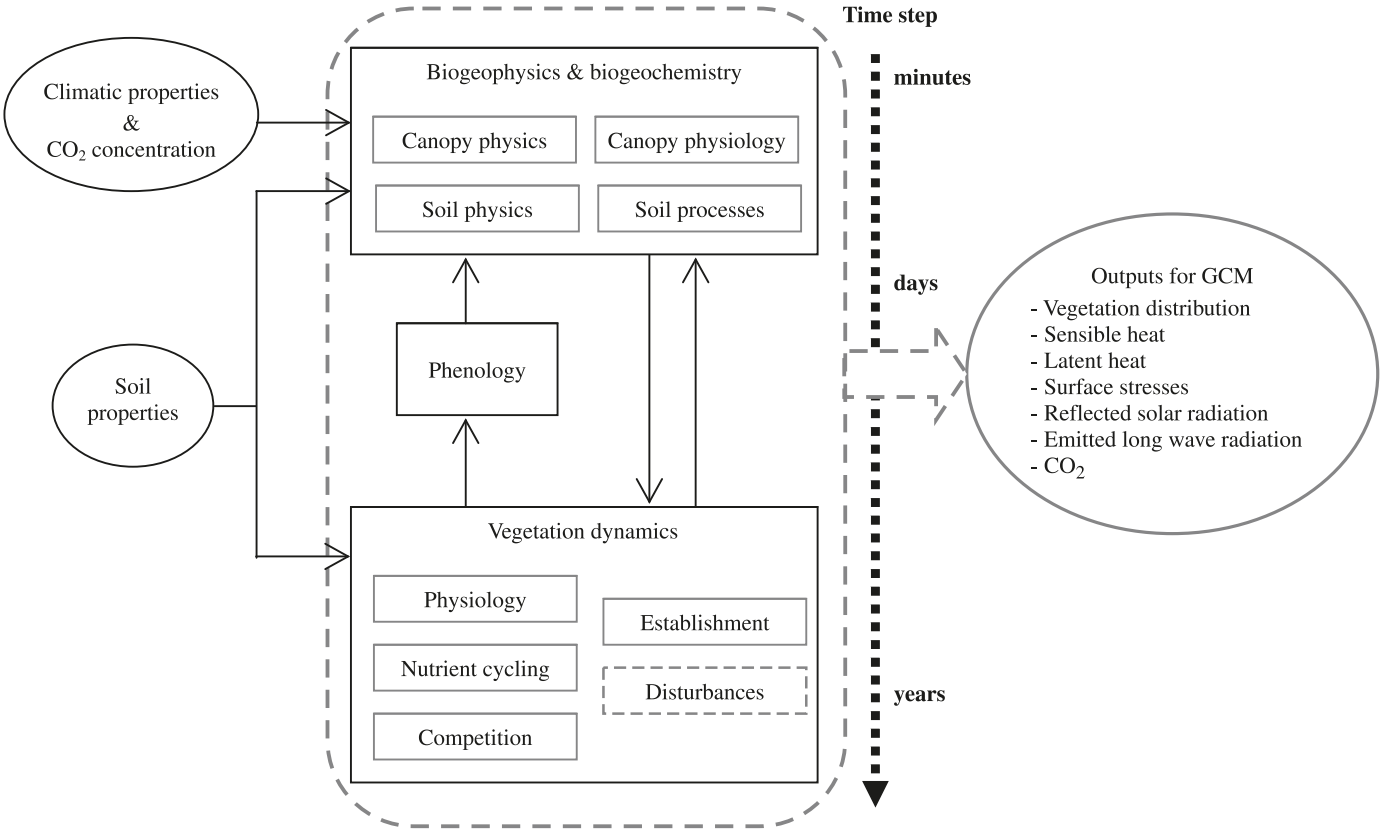
2. State of the art of vegetation modelling for global climate change studies

At present, DGMVs are the best available representation of vegetation dynamics used in global scale studies. The coupling of DGVMs and GCMs present a new approach allowing a more comprehensive inclusion of vegetation–atmosphere interactions in climate simulations. The following sections provide an insight into these topics.

2.1. Dynamic global vegetation model (DGVM)

Vegetation dynamics includes: photosynthesis, respiration, surface energy fluxes, and carbon and nutrient allocation within the plant in different modules of the model (Fig. 1). Along with successional processes, biogeochemical and biogeographical processes also provide some basic components of the current DGVMs. The DGVMs are basically designed

Fig. 1. Typical structure of a dynamic global vegetation model (DGVM).



to simultaneously track vegetation changes driven by climate variability, together with the associated energy exchange, carbon, nutrient, and water fluxes. External forcings to the DGVMs include both climate and soil characteristics. The main application of the DGVMs is to capture and simulate the transient changes in vegetation cover and carbon fluxes and to supply the GCMs with a representation of vegetation dynamics (Foley et al. 2000; Peng 2000).

The complexity and representation of processes such as nutrient cycling or canopy physics differ among models as it mainly depends on the aim of the study (Foley et al. 1998). For instance, when the purpose of the simulation is to provide data for a GCM, the outputs are commonly vegetation distribution and surface fluxes.

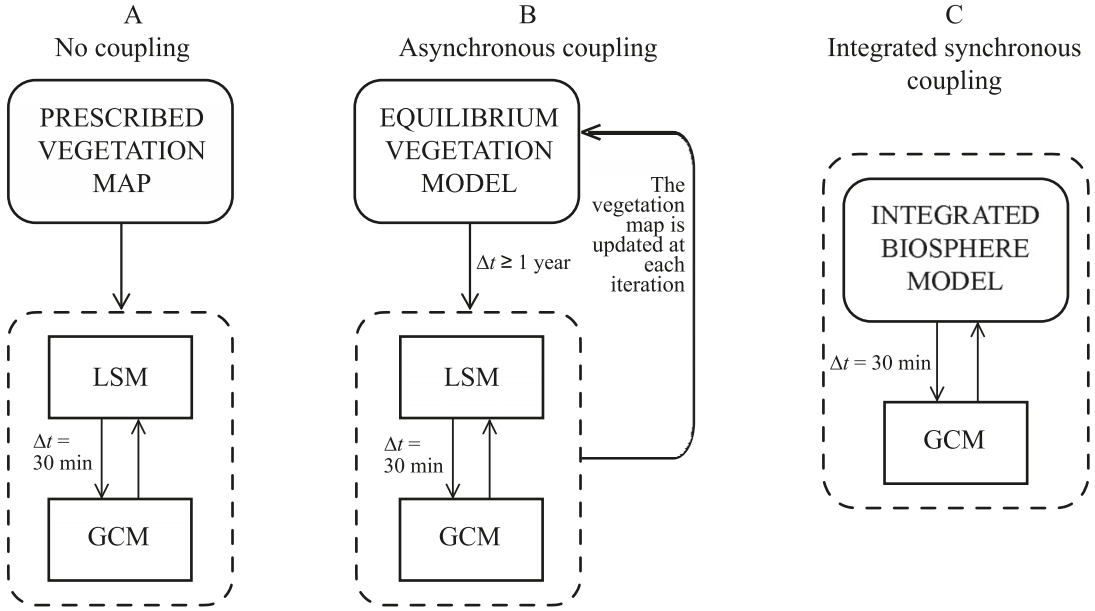
2.2. Coupling vegetation models with climate models

The DGVMs can be of great interest for climate modellers since they are able to simulate vegetation dynamics and provide some important outputs for GCMs. Model couplings have already been accomplished between DGVMs and GCMs in the past decade (Levis et al. 1999; Zeng et al. 2002; Friedlingstein et al. 2003; Delire et al. 2004; Crucifix et al. 2005; Bonan and Levis 2006; Alessandri et al. 2007; O'Ishi and Abe-Ouchi 2009). The modules representing the interactions between biosphere and climate in GCMs are called soil–vegetation–atmosphere transfer schemes (SVATs). Until the 1980s, only land surface parameterizations (LSP) estimating the simple biophysical processes were introduced in GCM computations. The first generation, characterized by the simple exchanges of energy, heat, and momentum, was followed by a second generation that handled vegetation canopy and soil independently. The third generation (by the early 1990s) brought biological and chemical processes into the models. These third generation models described specifically the photosynthesis mechanism and the light interception of leaves among other processes. However, all of these SVATs remained static and did not include the dynamical component of vegetation (Sellers et al. 1997; Arora 2002; Pitman 2003).

The vegetation models, first developed for forestry or agriculture management, were adapted and revised to allow for use in new applications. Instead of developing SVAT schemes especially designed for GCMs, one could choose to couple a vegetation model with a GCM to account for the vegetation–atmosphere interactions.

The earlier GCMs ran with LSP where the geographical distribution of vegetation was prescribed and stayed unchanged during the simulation (Fig. 2A). Several methods have been used to couple a vegetation model with a climate model. The vegetation models can be coupled with climate models in an asynchronous way; i.e., the models iterate until the equilibrium of both models is reached (Fig. 2B). This technique was first tried by Henderson-Sellers (1993) who coupled a GCM with a SVAT already combined with a simplified vegetation distribution schema. Asynchronous coupling presents little effort but has shortcomings. The calculations of the fluxes (e.g., surface energy and water balance) by the two models might be inconsistent, so that the conservation of water and energy is not guaranteed (Betts et al. 2000; Foley et al. 2000). Moreover, the method

Fig. 2. Methods of coupling climate and vegetation models (after Foley et al. 1998).



compares equilibrium states so that the simulation of long-term variations or transient changes in vegetation in response to environmental changes are excluded (Foley et al. 1998, 2000). However, this method is efficient enough to realise sensitivity studies becausethe components of the feedbacks are handled in isolation (Betts et al. 2000). Another method consists in coupling synchronously the dynamic vegetation model with the GCM (Fig. 2C, e.g., Foley et al. 1996). This approach is more complex but intrinsically allows the dynamic interaction of both models.

The coupling of a vegetation model with a climate model requires the linkage of two models that have inherent structural and process-based differences. The primary purpose of the coupling is to share the characteristics of the processes modelled in both models. To do so, vegetation models have to share variables (e.g., LAI, rooting depth, stomatal conductance, momentum, and energy fluxes) with the SVAT scheme of the GCM. In addition, the SVAT has to share variables such as soil moisture or canopy temperature with the vegetation model that allow the calculation of the stomatal conductance and the net photosynthetic rate. The SVAT then transmits the data to the module of the GCM where the information is needed. It should be noted that the time scales differ from process to process. For example, processes involved with the stomatal conductance vary on a short time scale (within minutes to hours) while processes linked with net primary productivity (NPP) or allocation vary on a long time scale (from years to centuries). Arora (2002) reviews and illustrates in detail the manner in which models can be linked.

3. Current issues

3.1. Issues in dynamical vegetation modelling

Several studies present comparisons of the principal characteristics of some of the DGVMs. For example, Cramer et al. (2001) and Sitch et al. (2008) compare the simulation results of six and five DGVMs, respectively, but do not analyse the basics of these models. Here, we focus on the critical structural aspects of the DGVMs rather than on their results, and present a synthesis of selected aspects for 11 DGVMs (Table 1). After addressing the dependence of vegetation distribution on bioclimatic constraints affecting the theoretical grounds for DGVMs, this section analyses their major issues presented in Table 1.

3.1.1 Dependence of vegetation distribution on bioclimatic constraints

The transient changes of vegetation under changing climatic conditions involve many processes (e.g., phenology, soil moisture, stomatal conductance, carbon and nitrogen allocation processes, water stress, etc.). The way these processes interact with environmental conditions (disturbances, topography, climate conditions) determines the response of vegetation to these changes. In the case of global change, the response of vegetation depends on the new climatic conditions but also on the response of ecological processes to this change.

To set up a classification for vegetation, the common approach is to separate vegetation forms into classes, biomes, or PFTs according to their physiological response to climatic conditions (e.g., GDD, chilling requirement, or any other constraint based on current observation). In DGVMs, bioclimatic constraints can also play a role in an indirect manner, for example, by applying a bioclimatic constraint like GDD on the calculation of LAI (LPJ–DGVM). Both direct and indirect uses of bioclimatic constraints are still widely used in DGVMs (e.g., HYBRID, IBIS, LPJ–DGVM, SEIB–DGVM, Table 1). However, using bioclimatic constraints in modelling ecological processes that are dynamic and evolve with vegetation change seems inappropriate. For example, if a current minimal temperature threshold is not reached in a warmer climate, the model could omit to allow for leaves falling in autumn and finally simulate a virtual (i.e., non-observable) vegetation state. Moreover, surface temperature

Table 1. Comparison of some critical aspects of 11 dynamic global vegetation models (DGVMs).

DGVM (reference)	Bioclimatic constraints	Number of plant functional types (PFTs)	Nitrogen	Soil Carbon	Competition	Disturbances			
						Nitrogen deposition and (or) nutrient stress	Fire / disease / grazing	Land-use and land-use change	Implicit*
CLM–DGVM (Zeng et al. 2002; Dai et al. 2003; Levis and Bonan 2004)	Direct and indirect	10	Based on LPJ (Sitch et al. 2003)		Light, water, space among PFTs	No	Fire	3 land-use classes	n/a
CTEM (Arora 2003; Arora and Boer 2005*b*; Arora and Boer 2006)	No	9	No nitrogen cycle	1 pool	Modified Lotka–Volterra equations (Lotka 1925; Volterra 1926)	No	Fire	2 cropland PFTs land-use change (in C emissions)	n/a
HYBRID 3.0 (Friend et al. 1997)	Indirect	8	Complete N cycle, 8 carbon pools from CENTURY (Parton 1993)		Light, water, nitrogen among individual plants	No	No	No	Random mortality only
IBIS 2.6 (Foley et al. 1998; Kucharik et al. 2000; Delire et al. 2003; Kucharik et al. 2006)	Direct and indirect	12 on 2 canopy levels	Constant C:N ratios	5 pools	Light, water among PFTs	No	Fire	No	No
LM3V (Shevliakova et al. 2009)	Direct	5	No nitrogen cycle	2 pools	Based on climatic conditions and on ED model (Moorcroft et al. 2001)	No	Fire; grazing	4 land-use classes and several land-use change possibilities	Mortality rate
LPJ–DGVM (Sitch et al. 2003)	Direct and indirect	10	Implicit	2 pools	Light, water among PFTs	No	Fire	No	n/a
MC1 (Bachelet et al. 2001, 2003)	Direct and indirect	6 combinable	N uptake and allocation	3 pools	Light, water and nutrients among PFTs	No	Fire	No	n/a
ORCHIDEE (Krinner et al. 2005)	Direct and indirect	12	Implicit	3 pools	Light among PFTs	No	Fire; grazing	2 cropland PFTs	n/a
SDGVM (Woodward et al. 1998; Woodward and Lomas 2004)	Direct and indirect	7	Based on CENTURY model (Parton et al.1993)		Light, water among PFTs	N deposition	Fire	No	n/a
SEIB–DGVM (Sato et al. 2007)	Direct	10	N contents estimated for each PFT	2 pools	Light, space among individual plants	No	Fire	No	n/a
TRIFFID (Cox 2001; Hughes et al. 2006)	Indirect	5	Fixed contents for each PFT	1 pool	Lotka–Volterra adapted to PFTs† (Lotka 1925; Volterra 1926)	N deposition	No	No	Fraction of the PFT reduces the area

Note: n/a, not available

*Some disturbances are implicitly included in the calculation of the models (e.g., a fractional loss representing undifferentiated disturbances).

†i.e., horizontal competition (herbs replace grasses and trees have the advantage on herbs) and carbon density competition.

has to be used with caution because it is partly determined by the partitioning of energy by vegetation. Thus, determining the influence of vegetation in the vegetation–climate interactions is complex. Empirical rules based on physiological processes, as suggested by Arora and Boer (2005*b*), should then be preferred to bioclimatic constraints.

3.1.2. Limitations due to the plant functional type method

The classification of the vegetation distribution into PFT also implies other shortcomings as shown in this section.

The PFT approach is designed for large spatial and temporal scales and does not take into account the behaviour of individual species. This is especially true when the number of PFTs is small (Table 1). Individual species have an impact on ecology at a regional scale. Locally driven factors accounting for changes in vegetation composition (e.g., competition, mortality, recruitment and also land use changes) are not well considered in the PFT approach and certainly have an impact on long-term analyses involving biosphere–atmosphere dynamics (Moorcroft 2006). Moreover, Kucharik et al. (2006) point out that the PFT parameterizations affect the results of the simulation at regional scale because they are originally generalized to run at a global scale. This drawback worsens at higher resolutions.

However, this issue can be improved by coupling the DGVM with an ecosystem demographic model (Bond et al. 2003; Woodward and Lomas 2004). Such a model represents vegetation by modelling individuals explicitly as in the gap models approach, e.g., the ecosystem demography model (Moorcroft et al. 2001). Alternatives to the PFT approach are presented in the Section 4.1.

3.1.3 Weaknesses in competition and nutrient cycling modelling

Weaknesses in competition and nutrient cycling modelling are related to the representation of competition in the DGVMs and to the representation of the plants as individuals. Some DGVMs represent the competition among PFT (e.g., TRFFID, IBIS, and SDGVM in Table 1). These competition models present several limitations. They simulate competition between average individuals, but the actual competition occurs at a local scale and between heterogeneous individuals, because nutrient, water, light, and space are locally distributed (Sato et al. 2007). Competition among PFTs leads to broad results, with particular difficulties in the representation of the wood–grasses competition. For example, two averaged PFT compete for water, whereas single individual species included in theses PFTs have different behaviour and sensitivity to the water resource. The competition of these averaged PFTs does not represent a competition occurring in nature. Consequently, the competition among PFT leads to additional errors in the model simulations (Smith et al. 2001). Moreover, this competition model favours a dominant PFT and excludes the subdominants, leading to a poor representation of species coexistence (Arora and Boer 2006). In addition, Purves and Pacala (2008) argue that competition processes are highly nonlinear. It is to be expected that the errors in the simulations will increase with the errors in the definition of the competition processes. Therefore, natural ecosystem heterogeneity is poorly represented.

However, representing heterogeneity in DGVMs is challenging when passing from local scale to mesoscale and global scale (Gusev and Nasonova 2004). Nevertheless, it is worth noting that heterogeneity may be an important factor that affects the resilience of an ecosystem to disturbances (Loreau 2000; Loreau et al. 2001).

In addition to competition, migration processes are another weakness observed in many DGVMs. Paleo-ecological studies show that a combination of competition and migration has been the response of vegetation to changes in climate in the past (Midgley et al. 2007; Thuiller et al. 2008). Also, physiological tolerances and migration properties of species, along with growth and competition processes, lead to a time lag between changes in climatic conditions and vegetation response. For example, replacement of an extinct PFT by a new PFT (excluding dispersal effect) may cause a lag (50–150 years) in the response of vegetation to changes in climate (Arora and Boer 2006). However, dispersal capabilities might be particularly critical for the migration of certain species. This could imply a drastic change in communities of species if species cannot migrate fast enough. (Davis 1989; Pitelka 1997; Neilson et al. 2005; Midgley et al. 2007). Dispersal and associated migration processes are considered as a significant source of uncertainty in the simulation of climate change impacts on vegetation (Thuiller et al. 2008). The six models studied by Cramer et al. (2001), five of which are presented in Table 1, consider the stand development of the species but not dispersal.

Another critical aspect that is not fully integrated in DGVMs concerns the representation of nutrient cycles. Determining soil carbon pools can be an issue. The amount of carbon stored has an influence on the biogeochemical CO_2 feedback from climate change and should be adequately modelled. Schröter et al. (2004) argued that carbon pools should be treated separately depending on the turnover rate (Table 1). For example, partitioning of the soil organic carbon (SOC) into an three-pool (minimum) model gave consistent results for the feedback of the SOC decay on global warming (Knorr et al. 2005). Nitrogen cycle is not always taken into account in DGVMs (Hungate et al. 2003; Zaehle et al. 2010*b*). However, nitrogen limits the capacity of plants to grow and is tightly coupled with the carbon cycle, therefore, it is of great importance when working with future CO_2 scenarios (Luo et al. 2004; Luo et al. 2006). Some components of the nutrient cycles are compared in Table 1 in terms of carbon and nitrogen availability and nitrogen deposition. It is remarkable that only two out of the eleven models (SDGVM, TRIFFID) take the nitrogen deposition into account. New developments on carbon and nitrogen models simulating dynamic nitrogen cycle and taking carbon–nitrogen interactions into account are presented in Section 4.4.

Aboveground and belowground processes are also an important aspect that is not taken into account in DGVMs (Schröter et al. 2004). These processes have an impact on vegetation productivity and decomposition and on estimates of carbon and nitrogen fluxes in DGVMs (Dufresne et al. 2002). Moreover, these processes are also affected by changes in climatic conditions and by species migration processes and their feedback on the ecosystem is uncertain (van der Putten et al. 2009).

Indeed, representation of respiration is also a critical as-

pect in DGVMs. In many models, plant respiration is defined as a fixed fraction of photosynthesis (e.g., IBIS, LPJ, HYBRID). Other models assume that plant respiration increases exponentially with an increase in temperature (Q_{10} function, e.g., TRIFFID, CTEM). Both methods have major drawbacks since the NPP to GPP ratio and the response of plant respiration to temperature cannot be considered constant (Atkin and Tjoelker 2003; Wythers et al. 2005; De Lucia et al. 2007). Indeed, the calculation of gross primary production (GPP) is often derived from NPP and plant respiration. This method leads to near constant values of the NPP to GPP ratio, suggesting artificially that this ratio remains constant among vegetation types (De Lucia et al. 2007). However, NPP to GPP ratio shows large spatial variations associated with ecosystem types, even though the global average remains around 0.52 (Zhang et al. 2009). In the case of the Q_{10} function, it appears that plant respiration reacts differently to changes in temperature depending on maximum enzyme activity (at low temperatures) and substrate limitations (at higher temperatures) (Atkin and Tjoelker 2003).

The major criticism regarding these methods concerns the lacking representation of acclimation of the base rate to temperature (Wythers et al. 2005; King et al. 2006; Atkin et al. 2008; Piao et al. 2010). Acclimation of respiration to changes in temperatures is twofold: short-term acclimation (seconds to hours) and long-term acclimation (days to months). The Q_{10} function describes the short-term acclimation but is poorly validated against empirical data (Wythers et al. 2005). Ignoring acclimation in respiration modelling has an important impact on the calculation of aboveground NPP (Wythers et al. 2005) and the calculation of the feedback between vegetation and climate at global scale. King et al. (2006) found that accounting for acclimation induces a reduction of the global leaf respiration by the year 2100, reducing the strength of the vegetation–climate feedback. On the other hand, Atkin et al. (2008) obtained results that emphasize the importance of acclimation when studying different biomes but negligible impact was found on global scale results.

Since the calculation of plant respiration also relies on C:N ratios, nitrogen effect on plant respiration should be taken into account (Reich et al. 2006, 2008; Piao et al. 2010). Reich et al. (2008) show that the relationship between plant respiration and nitrogen differs depending on the different plant parts. A unique relationship is inappropriate for the calculation of respiration of different plant parts.

Soil respiration is also identified as a poor process in the TRIFFID model (Cox et al. 2000; Cox 2001) as well as in the DGVMs studied by Sitch et al. (2008). Soil respiration represent a major terrestrial carbon flux but is still poorly understood (Bond-Lamberty and Thomson 2010). Soil respiration increases with temperature and this relationship is also defined by a Q_{10} function in DGVMs. However, estimates of acclimation of soil respiration to increase in temperature seem to become more accurate. Bond-Lamberty and Thomson (2010) could quantify the response of soil respiration to changes in air temperature between 1989 and 2008 and thus refine the Q_{10} value.

Nevertheless, to improve simulations, Davidson et al. (2006) recommend the modelling of direct effects of temperature separately from the indirect effects of temperature and soil water content. Additionally, Kucharik et al. (2006) suggest that the effects of soil moisture and seasonal ecosystem changes may be as important as temperature in the simulation.

3.1.4. Issue in disturbances modelling and geographical specificities modelling

Disturbances represent an important issue because they have a significant effect on the modelling of the vegetation response to climate change (Shellito and Sloan 2006). For the purpose of this review, we consider disturbances as processes inducing dynamic changes in vegetation through natural hazards or anthropogenic influence (e.g., fire, insects, diseases, land use change). On the other hand, "geographical specificities" can be defined as timeless (i.e., static events), acting as perturbations in the vegetation cover (e.g., topographical barriers, elevated environments, lakes, wetlands, and land use).

One dynamic disturbance, fire, is considered as the most important disturbance in vegetation modelling (Thonicke et al. 2001) though it has only recently been introduced in DGVMs (10 out of 11 DGVMs reviewed, see Table 1). Some DGVMs only account for fire as an estimate of burned area or as a fractional loss of biomass (e.g., IBIS, BIOME–BGC). However, there have been some attempts to model fire in a more realistic manner. Arora and Boer (2005*a*), Krinner et al. (2005), and Thonicke et al. (2001) chose to model fire as a probability function depending, among other things, on the moisture content of the soil and on the burning properties of the different PFTs. The simulation also takes the resulting CO_2 emissions into consideration and in some cases includes the impact of aerosols emissions on the atmosphere. Recently, Kloster et al. (2010) included a new representation of fire, based on Arora and Boer (2005*a*) and Thonicke et al.'s (2001) work, in the CLM–CN model. Additionally, this fire model accounts alsofor land-use changes, deforestation, and influence of human activities on fire ignitions and suppressions to best estimate burned areas and associated carbon emissions.

Often linked with fire or storms, insect outbreaks have been much less investigated than fire. Insects are absent in DGVM modelling, however they can strongly influence vegetation (Schelhaas et al. 2003; Kurz et al. 2008). Insects are completely ignored in vegetation dynamics modelling at present and therefore, their impact needs to be further investigated.

The anthropogenic disturbances, such as land-cover conversions into cropland or grazing land, water withdrawals, or impoundment strongly affect the energy fluxes, the carbon storage, the nitrogen cycle, and the water cycle (Gerten et al. 2004; Ellis and Ramankutty 2008; Gruber and Galloway 2008). Moreover, changes in land cover greatly affect the simulations of respiration, net ecosystem production (NEP) and GPP in the SDGVM, when they are imposed in the model (Woodward and Lomas 2004). However, the only occurrences of these anthropogenic disturbances are grazing, that is included in the ORCHIDEE DGVM, land-use change driven by GCM data in the CTEM model and a more complete representation of land-use and land-use changes implemented in the LM3V model (Table 1). It is obvious that

dynamic disturbances have an impact on simulation results and some of them are progressively integrated in DGVMs. Recently, great efforts have been made to understand and model dynamic disturbances, mostly in the forestry sector (e.g., Kurz et al. 2009). Progress in modelling these factors will help reduce the errors in the simulation in DGVMs.

Among geographical specificities, there is no topographical effect included in the DGVMs yet. However, in the case of the BIOME–BGC model (Schmid et al. 2006), the lacking description of processes related to topography render a poor simulation of the high-altitude ecosystems carbon dynamics.

Wetlands can also be considered a geographical specificity in the vegetation cover because their behaviour is very different from a forested area or a cropland. The carbon fluxes in wetlands are particularly significant when modelling global carbon fluxes: wetlands are an important sink of carbon under the current climatic conditions but they also represent a very large source of methane (Prentice et al. 2007; Lafleur 2009). However, wetlands are only represented in the CLM–DGVM, which uses the IGBP DISCover dataset (Loveland et al. 2000), and in the LPJ–DGVM complemented with a permafrost and peatland model (LPJ–WHy) developed by Wania et al. (2009*a*, 2009*b*).

Additionally, land-use classes such as cropland or urban areas are rarely taken into account (by only three out of eleven DGVMs in Table 1). These classes represent an important part of the global land cover and should not be disregarded. Urban areas and croplands differ from natural vegetation in several ways. For example, croplands have different bioclimatic constraints and competition rules are altered.

Until now, modelling vegetation dynamics has been approached from the atmospheric modelling side, which only leads to a partial consideration of the biosphere dynamics. Some efforts have to be made to get a better representation of vegetation dynamics. For example, according to Loreau et al. (2001) a major issue is to understand how biodiversity dynamics, ecosystem processes, and abiotic factors interact.

3.2. Issues in DGVM–GCM coupling

Modelling interaction processes between atmosphere and biosphere still remains imprecise. For example, Friedlingstein et al. (2003) compared the simulations of two coupled models under current and increased CO_2 climate conditions. The first experiment coupled TRIFFID to an OAGCM and the second one used the IPSL coupled climate–carbon cycle model (without coupled vegetation dynamics, Dufresne et al. 2002). The results show large biases between the two simulations, so that the positive feedback resulting from the coupled simulations vary by a factor of two between the simulations. A 10% to 30% enhanced warming due to the inclusion of vegetation dynamics was observed by O'Ishi and Abe-Ouchi (2009) after coupling the LPJ–DGVM with the MIROC GCM (Hasumi and Emori 2004). A similar behaviour was observed by Bonan and Levis (2006) while coupling the CLM–DGVM with the GCM CAM3 (Collins et al. 2006). Vegetation dynamics has an indubitable impact on the GCM simulations. However, the interactions between vegetation dynamics, soil processes and atmosphere should be further explored to get more realistic simulations under climate change scenarios.

Several studies show that coupling a DGVM with a GCM significantly affects simulations (Delire et al. 2002; Zeng et al. 2002; Delire et al. 2003, 2004; Crucifix et al. 2005; Alessandri et al. 2007). It is noticed that such coupled models might show results unexpectedly different from GCM results. Occasionally, negative (positive) biases, compared with observations, become positive (negative) after coupling. Coupled DGVM–GCMs and GCMs then show opposing results, as in the simulated temperature field in Delire et al. (2002). The coupled simulation shows positive temperature bias where the GCM simulation shows a negative one. This is due to lack of representation of water bodies, wetland, and cropland in the vegetation cover in IBIS compared with the SVAT included in the GCM (Delire et al. 2002). The CLM model used by Zeng et al. (2002) presented an improved fractional vegetation cover (including developed areas, water bodies and wetlands) and snow cover. Zeng et al. (2002) argued that this factor improves simulations. Crucifix et al. (2005) and Delire et al. (2004) also underlined the role of vegetation cover representation in the simulations. Moreover, two simulations (IBIS–CCM3) of Delire et al. (2004) with fixed and dynamic vegetation representations highlight the significant influence of vegetation dynamics on long-term climate variability. It appears that both vegetation dynamics and vegetation cover representation have an impact on the coupled DGVM–GCM simulation results. In particular, land-cover classes should be carefully defined to limit biases in simulations.

The impact of the DGVM on a coupled DGVM–GCM simulation also depends on the strength of the land–atmosphere coupling. The GLACE experiment (Guo et al. 2006; Koster et al. 2006) aims to quantify the coupling strength in 12 AGCMs. Results of the experiment showed that coupling strength can vary widely between models. However, some "hot spots" (e.g., Sahel, Great Plains) show a similar behaviour in different models. Soil moisture appears to be a key process leading to great differences in temperature and precipitation variability. Soil moisture, evaporation, and precipitation interact differently depending on the region and on model parameterization (Guo et al. 2006; Seneviratne et al. 2006*a*). These results highlight the importance of the land–atmosphere interactions under a changing climate and its variability (Seneviratne et al. 2006*b*).

3.3. Evaluation of DGVMs and coupled DGVMs–GCMs

The assessment of the performance of a model includes several steps. One important issue is the development of data sets reliable at large scale and suitable for evaluation of these models.

3.3.1. Evaluation methods

One of the currently identified limitations of global models of vegetation dynamics concerns the evaluation of simulations at regional or global scales. More rigorous tests at various spatial and temporal scales will hopefully reduce the uncertainty due to differences among models. Validation of DGVMs as a whole is not straightforward at global scales, due to a long time scale of dynamics, lack of data at the desired time scales, and uncertainty around effects of hu-

man activities (Steffen et al. 1996). However, it is possible to validate dynamic modules at the scale of their design, which is usually smaller (Lenihan et al. 1998). Models can also be tested in regions where appropriate datasets exist.

Validation through replication of global vegetation patterns is a simple method, previously used to validate biogeographical models (e.g., Haxeltine and Prentice 1996). This method is still widely used in DGVM validation processes (Cosgrove et al. 2002; Gerber et al. 2004; Woodward and Lomas 2004; Hickler et al. 2006; Sato et al. 2007). It allows to validate processes controlling vegetation distribution (i.e., ecophysiological constraints in most cases), but it may not be the best to validate DGVMs (Moorcroft 2006). In fact, the reproduction of vegetation distribution does not give information about the behaviour of the DGVM. The dynamical processes cannot be validated in this manner. Thus, the validation of the model outputs should be favoured.

Since the DGVMs simulate transient changes in vegetation, validation with a time series of observations appears to be straightforward. Long time-series measurements regarding ecosystem processes are scarce and often locally constrained. To bypass this limitation, validation with single point data is possible when considering a certain point in time and space, which is assumed to be in equilibrium with the current climate (or with palaeoclimate for palaeological studies), i.e., after spin-up (Bugmann 2001).

The validation of coupled DGVM–GCMs undergoes same limitations, even though a time series of climate measurements are more accessible. However, simulation results of both DGVM and GCM might show biases in comparison with observations. After coupling, these biases might be enhanced or reduced, but they have to be carefully investigated because their origin is hard to determine (Delire et al. 2003).

To assess the validation possibilities, established and more recent observation methods are reviewed below.

3.3.2. Datasets

Direct and indirect observation methods are reviewed in this section. Firstly, different direct field measurement methods are described. Secondly, the use of FluxNet data is presented followed by the potential of using of remote sensing data.

Field measurements

Field measurements comprise numerous methods. Measurements are continuous or discrete on diverse time scales. For example, for validation of long time scale variations, pollen or tree ring data can be useful. Tree ring data have been used to assess results of the fully coupled LPJ–FOAM (fast ocean atmosphere model) against the increasing atmospheric CO_2 concentration over the last century (Notaro et al. 2005). Moorcroft (2006) mentions that forest inventories can also be used for validation. A 140-years chronosequence of relative cover has been used by Smith et al. (2001) to compare the results of two models: LPJ and GUESS. On a much longer time scale, other studies compare simulations (LPJ–DGVM and Bern CC) with vegetation reconstruction based on proxy data from the Holocene and the last glacial maximum periods (Joos et al. 2004; Ni et al. 2006). Sensitivity studies performed on the LSM–DGVM with Eocene geography and era-specific climate conditions (specifically for CO_2 concentration) highlight uncertainties in using DGVMs for palaeobotanical studies. For example, the use of modern PFTs is not suitable for the study of the Eocene epoch, (Shellito and Sloan 2006) as these former conditions do not correspond to observed environmental conditions.

Several point measurement techniques such as aircraft measurements, CO_2 flask monitoring, and towers can be taken into account for validation (Moorcroft 2006). The measuring towers are brought together in the FluxNet network and discussed in the following section.

FluxNet network

The aim of the FluxNet network is to provide long-term continuous eddy-covariance tower measurements of the hourly to yearly soil–plant–atmosphere CO_2, water, and energy exchanges for different vegetation cover types (e.g., tropical, temperate, boreal) (Baldocchi et al. 2001). Eddy-covariance towers usually measure the net ecosystem exchange (NEE) at rather small scales (a few hectares) and CO_2 flux measurements from the eddy-covariance towers have been tested against aircraft measurements at several continental sites in the northern hemisphere (Bakwin et al. 2004). This study concludes that eddy-covariance towers capture adequately seasonal and regional variations of CO_2 fluxes, although it is known that measurements include systematic and random errors. Thus, eddy-covariance tower measurements are suitable for use in regional carbon balance model validation, and numerous modelling studies have already used FluxNet data to evaluate model results (e.g., Woodward and Lomas 2004; Krinner et al. 2005; Morales et al. 2005; Hickler et al. 2006; Kucharik et al. 2006; Mao et al. 2007). A new methodology of validation taking the errors into account has been developed by Williams et al. (2009) and this approach represents a step forward in the systematisation of validation with eddy-covariance tower data.

Atmospheric transport modelling

Although observation of trends and interannual variations of atmospheric CO_2 concentrations are now possible thanks to highly precise measurements, responses of land and ocean carbon sinks to increased CO_2 concentrations and their impact on future atmospheric CO_2 concentrations remain a large source of uncertainty (Le Quéré et al. 2009). The atmospheric transport modelling (top-down approach) is used to obtain the best possible estimation for the CO_2 source area, i.e., to identify an area as the release area that would best match the CO_2 observations. Early studies about inversions techniques for atmospheric transport modelling were reviewed by Enting (2002) and several studies, focusing on the analysis of surface carbon sources and sinks based on the variations in atmospheric CO_2 concentration measurements, have been undertaken within the TransCom Intercomparison Project (e.g., Baker et al. 2006; Gurney et al. 2003). Therefore, spatial distributions of atmospheric CO_2 concentration measurements can be used as a powerful test to confront the bottom-up models. Indeed, CO_2 concentration measurements have been used to evaluate seasonal and interannual variations of the carbon balance simulated by DGVMs (Heimann et al. 1998; Nemry et al. 1999; Prentice et al. 2000; Fujita et al. 2003; Friend et al. 2007; Weber et al. 2008; Randerson et al. 2009). Historical trends of the car-

bon balance have also been investigated with this method (Bousquet et al. 2000; McGuire et al. 2001; Rivier et al. 2010; Rödenbeck et al. 2003). Instead of CO_2 concentration measurements, one can choose a similar method based on other atmospheric constituents such as $\delta^{13}CO_2$ or O_2/N_2 (e.g., Rayner et al. 1999; Prentice et al. 2000). Moreover, chemical transport models can also be useful to evaluate other components of the DGVMs with tracers such as nitrogen or NO_x (Arneth et al. 2010; Chen et al. 2010). Another approach is the combination of several methods as suggested by Randerson et al. (2009). The authors present a framework to evaluate terrestrial biogeochemistry models based on a comparison of model results with several datasets including data from the TransCom Project and remote sensing datasets.

Remote sensing

Satellite observations are useful in vegetation dynamics validation because they capture the natural vegetation distinctions such as deciduous–evergreen, perennial–annual, or broadleaf–needle leaf (Bonan et al. 2003; Moorcroft 2006). Such information permits the calculation of stomatal conductance or photosynthesis rates. Liu et al. (2006) quantify the vegetation–atmosphere interactions on a global scale from remote sensing data. Despite uncertainty and limitations of their dataset and method, their results remain useful for the evaluation of climate–vegetation feedbacks in GCMs. Limitations of the method based on satellite data have also been raised by Notaro et al. (2006). For example, FPAR (fraction of photosynthetically active radiation) data shows some biases, especially in the snow cover signal. Moreover, intense cloudiness in equatorial regions makes the capture of continuous satellite data almost impossible (Botta et al. 2000). Satellite observation is a relatively new method and therefore only 20 years of data are available. One other limitation is related to the methodology. The method applied in these studies (Liu et al. 2006; Notaro et al. 2006) is based on linear statistics which do not adequately represent the natural nonlinear feedback processes (Rial et al. 2004). Nonetheless, new global land-cover products have recently been developed for use in vegetation modelling (e.g., DeFries et al. 2000; Jung et al. 2006). These datasets, based on remote sensing observation, provide more accurate and more reliable data for the vegetation cover components.

4. Future challenges

4.1. Concrete alternatives for DGVM improvement

A discrete global vegetation distribution based on PFTs presents weaknesses since it simulates abrupt changes in vegetation where gradients can be observed in nature. Aware of this issue, Bonan et al. (2002*a*, 2002*b*) develop a new way to distribute PFTs for the NCAR LSM (National Centre for Atmospheric Research Land Surface Model). They use unique compositions of PFTs for each grid cell. This method allows the formation of vegetation gradients and thus uniform treatment of vegetation in the model. Despite the fact that it has been developed for an LSM, the method could also be implemented in a DGVM.

Hickler et al. (2006) implemented a plant hydraulic architecture in the LPJ–DGVM, initially developed by Sitch et al. (2003). This increases the functional diversity of the combinations of PFT that favours the ecosystem response to perturbations. An improvement of the PFT combinations is also proposed by Schröter et al. (2004). Their approach includes the aboveground–belowground interactions into local to global models. Each PFT is associated with functional groups of belowground organisms to build new aboveground and belowground functional types (ABFTs).

Instead of multiplying the number of PFTs or reducing the size of the grid cells, Sato et al. (2007) choose to develop an individual-based model (SEIB–DGVM, Table 1) to avoid the discrete representation of the vegetation. This technique has the advantage to simulate a spatially explicit vegetation distribution. Both the SEIB–DGVM and the ecosystem demography (ED) model (Moorcroft et al. 2001) explicitly represent the height of the canopy at regional scale (Hurtt et al. 2004) and enable individual-based competition. The ED model cannot be used at global scale yet, and is therefore not included in Table 1.

Another way to avoid the discrete PFT approach is chosen for the equilibrium vegetation model (EVE) (Bergengren et al. 2001). Instead of a small number of PFTs, the authors use 110 "life forms" defined with ecoclimatic predictors to build the global vegetation cover. This approach allows a more realistic representation of the continuous gradients of vegetation across the major ecotones and also permits the comparison with long-term palaeological data. As EVE model is static, it is not comparable to DGVMs. Thus, EVE is not presented in Table 1.

Plant functional traits can also be used as a baseline for the study of vegetation dynamics. Reich et al. (1997) associate PFTs of different species to find different axes of plant behaviour at a global scale. This approach leads to a new species and plant types classification method according to their physiological, morphological traits, or climatic preferences. A combination of theses traits may be useful to define plant types for modelling applications (Bonan et al. 2002*b*). As leaf traits relationships show modest response to climate and can be continuously quantified, this method is of great interest for understanding of key ecosystem processes such as carbon and nitrogen allocation, nutrient fluxes, or the response of vegetation migration to environmental changes (Wright et al. 2004). Moreover, this approach may help in understanding the consequences of land-use change on ecosystem processes (Díaz et al. 2007; McIntyre and Lavorel 2007). Actually, some plant traits can be associated with grazing or land use and, if included in PFTs, they can help improving DGVM results.

A review of articles on this subject suggests that the effectiveness of current DGVMs would be enhanced by using several technical and design improvements. For example, a dynamic model of leaf canopy based on light distribution and nitrogen presents a new way to simulate the canopy photosynthesis rate (Hikosaka 2003, 2004). The author argues that the leaf turnover processes allow the determination of canopy photosynthesis. Arora and Boer (2006) recommend to "generalize" the Lotka–Volterra model in modelling the competition module in the Canadian terrestrial ecosystem model (CTEM, Arora 2003; Arora and Boer 2005*b*), which is specifically designed to run with the CCM3 GCM. This new formulation of the competition

model yields reasonable agreement with observations. Another proposition is made by Botta et al. (2000), who explore the possibility of using local leaf onset date models at a global scale. A satellite dataset (NDVI data from NOAA/AVHRR) is combined to a land-cover map to identify the patterns.

The nitrogen cycle has recently been the subject of new advances in DGVM development. Several studies focus on the integration of nitrogen interactions with vegetation, soil, and the carbon cycle in DGVMs (Thornton and Zimmermann 2007; Thornton et al. 2007, 2009; Xu-Ri and Prentice 2008; Ostle et al. 2009; Fisher et al. 2010; Gerber et al. 2010; Zaehle and Friend 2010; Zaehle et al. 2010*b*). For example, Xu-Ri and Prentice (2008) implement a global scale dynamic nitrogen scheme (DyN) in the LPJ–DGVM including the interactions with carbon, water cycle, and with vegetation dynamics. The results include global pattern of nitrogen stores and fluxes and also improve carbon stores and fluxes due to the integration of the nitrogen productivity feedback. A better simulation of NPP in cold ecosystems in also achieved. Gerber et al. (2010) made a similar experiment by introducing a complete nitrogen cycle in the LM3V model. Here, spatial and temporal variations in carbon and nitrogen dynamics are reproduced and the response of NPP to changes in CO_2 is improved. Moreover, the influence of the integration of the nitrogen cycle in the models is most visible when dynamic coupled simulations are performed. For example, Thornton and Zimmermann (2007) add coupled carbon–nitrogen cycles dynamics and leaf C:N properties in the CLM. Similarly, Zaehle and Friend (2010) and Zaehle et al. (2010*b*) developed a new model based on ORCHIDEE that accounts for the nitrogen cycle. In both studies, the implementation of nitrogen cycle in a coupled climate system model significantly affects the results and lead to the conclusion that models ignoring nitrogen–carbon interactions might overestimate the reaction of the biosphere to changes in atmospheric CO_2 concentration (Thornton et al. 2007; Zaehle et al. 2010*a*, see also Section 4.4).

The nitrogen cycle also impacts atmospheric chemistry through emissions of trace gas from the land surface (e.g., NO, NO_2, NO_x). Other trace gas emissions are related to the carbon cycle (e.g CH_4, CO) or are caused by other natural and anthropogenic processes (e.g., fire, fertilization, and fossil fuel combustion). They have an impact on the atmospheric chemistry, cloud formation, and climate and should be taken into account when land–atmosphere interactions are studied (Pielke et al. 1998; Prentice et al. 2007). Some attempts have been made to include specific trace gas emissions in the DGVMs. For example, Wania et al. (2010) recently developed a new process-based CH_4 emissions model from wetlands coupled directly with the LPJ–DGVM (namely LPJ–WHyMe) to simulate the interactions between vegetation composition, water table position, and soil temperature. Thonicke et al. (2010) aim to explore the impact of fire on the carbon cycle and on the related trace gas emissions. A comprehensive review of this issue including a comprehensive description of the non-CO_2 trace gases exchange between the land surface and the atmosphere is presented by Arneth et al. (2010). The magnitude of future feedbacks and the representation of these trace gases in current vegetation models are also discussed in this review. To date, no single DGVM, as mentioned previously, is capable of exhaustively simulating trace gas emissions. Further incorporation of a main trace-gas emission scheme into the DGVMs will be necessary.

One of the main challenges in Earth system science is the integration of our growing knowledge from observations and experimental results into a coherent modelling framework that leads to the development of Earth system models (ESMs). Within the last decade, a different modelling approach that integrates the main components of the Earth's system has been developed: the Earth's system model of intermediate complexity (EMIC). An EMIC is a model based on the interactions between ocean, atmosphere, and biosphere and is not specifically based on climate as is the GCMs model. The modelling of processes is simplified compared to a GCM, but it still takes into account all possible feedbacks (Claussen et al. 2002; Claussen 2005).

4.2. Improving the evaluation methodologies

The evaluation of DGVMs and coupled DGVM–GCMs requires global datasets or at least well-distributed data. Furthermore, validation of transient change simulations necessitates long-term datasets. These two constraints greatly limit validation possibilities. The field measurements mentioned previously are not well distributed in space and extrapolation is needed to obtain a global dataset, which diminishes data quality. On the other hand, remote sensing datasets are available at a global scale but not for long-term data comparison. Furthermore, datasets on measurements or observations of specific processes such as carbon accumulation rates and turnover time of soil organic matter are very poor (Zaehle et al. 2005). In conclusion, there is an obvious need to build new datasets in a broad range of domains and scales to improve the validation of models.

The validation methodology of coupling studies should also be improved; a lack of testingan inadequate validation methodology can produce misleading results. For example, the coupling of two nonlinear models, which were only tested uncoupled, induces complications (e.g., processes show different behaviours when used in a coupled versus uncoupled model) (Bonan and Levis 2006). To avoid misinterpretation of results, Delire et al. (2003) recommend to validate the results of the coupled model with both observations and the individual components of the two coupled models.

A useful way to assess the validity of models would be to homogenize the validation methodology. For this purpose, Moorcroft (2006) suggests an approach based on the weather-forecast-model technique using "skill-scores" to assess the performance and the specific abilities of the models. Gulden et al. (2008) suggest a similar approach based on three metrics to get "fitness scores". The proposed methodology is specifically designed for LSM but could be applicable for DGVMs too.

4.3. Incorporating human activities (land-use and land-cover changes)

Land-cover changes are gaining increasing importance as a factor in atmosphere–biosphere interaction studies. There have been a lot of changes in the distribution of the land use since the Industrial Revolution (e.g., deforestation, graz-

ing, and conversion of forest to cropland). The Earth's land surface consists of vegetation covered areas, snow and ice areas, desert, bare soil, and also croplands, grazing lands, and urban areas. At least 34% of these terrestrial surfaces are currently dedicated to some anthropogenic activity (Betts et al. 2007) and 42%–75% of the ice-free land surface has been affected by anthropogenic land use in the past (Hurtt et al. 2006; Ellis and Ramankutty 2008). An increasing amount of studies are investigating past, present and future effects of land-cover changes on vegetation dynamics and related climate equilibrium (Huntly 1991; Claussen et al. 2001; Goldewijk 2001; Betts 2006; Brovkin et al. 2006; Betts et al. 2007; Díaz et al. 2007; McIntyre and Lavorel 2007; Pielke et al. 1998; Tett et al. 2007). As highlighted by Foley et al. (2003), land-cover change is a very important factor that affects climate over a large region with a greater magnitude than global warming. They suggest that assessments on future climate change should take into account land-cover changes at local, regional, and global scales. Land use has already been included in some DGVMs through the addition of specific modules or through the coupling of existing cropland models (e.g., McGuire et al. 2001; Kucharik and Brye 2003; De Noblet-Ducoudré et al. 2004; Bondeau et al. 2007). An important step has recently been achieved by Shevliakova et al. (2009): the new LM3V model is the first DGVM, to our knowledge, to include land use in the representation of the Earth's surface and to take into account land-use changes and their interactions with the biogeochemical cycles at a global scale.

However, land-use changes induced by anthropogenic activities are not represented in coupled biosphere–atmosphere models yet. To fill this gap, new datasets based on remote sensing data and data from previous studies on historical land-use changes were created (Ramankutty and Foley 1998; Hurtt et al. 2006; Wang et al. 2006). Wang's et al. (2006); Ito et al. 2008; Ramankutty et al. 2008; Sterling and Duchame 2008; and Sterling and Duchame (2008) datasets, representing land-cover changes based on remote sensing data and surveys, are designed for coupled atmosphere–biosphere models and are expected to enhance the Earth's surface representation. A similar approach has been used by Ito et al. (2008) to consolidate the estimates in carbon fluxes from vegetation including the influence of land-cover change. Hurtt et al. (2006) produced a global gridded database including areas impacted by human activities and secondary land areas. Land-use transition estimates are provided for the period from 1700 to2000. A new classification of the areas affected by anthropogenic activities is proposed by Ellis and Ramankutty (2008). These authors built up 18 anthropogenic biomes to help capture ecological changes within and across anthropogenic biomes. Recent advances in this domain are very promising, and land-cover changes will most likely be taken into account in coupled global models soon.

4.4. Nonlinearity, multiple-steady states and vegetation–climate feedbacks

The relationship between components of the Earth's system is complex and nonlinear. While some natural events may appear episodically, other natural behaviour may show abrupt changes. The capacity of models to simulate the response to these abrupt changes (leading to multiple equilibriums) remains uncertain. This is uncertain since the role played by biogeochemical processes, such as terrestrial carbon processes, are rarely taken into account (Pitman and Stouffer 2006). Natural or anthropogenic perturbations as well as initial vegetation cover conditions have an impact on equilibrium solutions (Wang and Eltahir 2000; Wang 2004) and may lead to transitions or to distinct equilibrium states (Claussen 1998). That is to say that the same climatic conditions could yield multiple possible global vegetation distributions.

Nonlinearity is also observed in various scale phenomena such as soil organic matter processes (Rial et al. 2004) and equilibrium storage capacity of the terrestrial biosphere (Gerber et al. 2004), which impact on both global carbon cycle and climate. It should be taken into account that nonlinear behaviours occur at different time and spatial scales, from global to micro scale (Scheffer et al. 2005). Kleidon et al. (2007) investigate the emergence of multiple steady states in a coupled atmosphere–biosphere system and particularly analyses the representation of vegetation in models. Their results emphasize the use of discrete vegetation classes in a model to take into account a sufficient number of classes since a small number can lead to an artificial emergence of multiple steady states. In their case study, Kleidon et al. (2007) have to use at least eight vegetation classes to avoid this problem.

Analyses of carbon cycle – climate feedback indeed show multiple responses. Whether the influence of an increasing CO_2 or of a change in climate on vegetation will induce a positive or a negative feedback remains unclear. Under current conditions, a greater availability of CO_2 in the atmosphere for plants increases photosynthesis and (or) decreases transpiration. Nutrient availability and soil moisture conditions play an important role in the response of vegetation to increased CO_2 (Chapin et al. 2008; Körner et al. 2007) but this response might not be straightforward. Species compositions might change under different environmental conditions, acting as sources or sinks of carbon depending on the alteration experienced by the species (Luo 2007). Luo et al. (2004) expected that, under higher atmospheric CO_2 concentration, nitrogen availability would limit the increase in NPP. However, this hypothesis was not corroborated by field observations encompassing 8 years (free-air CO_2 enrichment experiment FACE, Moore et al. 2006).

Two recent studies aim to explore the carbon cycle – climate feedback by comparing the results of different models under projected future conditions. In the framework of the Coupled Climate – Carbon Cycle Model Intercomparison Project (C^4MIP), Friedlingstein et al. (2006) used a common protocol to study 11 coupled climate–carbon cycle models. The A2 scenario was used for the study. Land uptake shows a negative sensitivity to changes in climate for all models, even though results show a large variation among the models. Unlike the other models, it is noticeable that two models (HadCM3LC and UMD) show a carbon release from the land after the year 2050. Moreover, the authors state that it remains unclear whether the sensitivity of land to climate is attributable to respiration or NPP. Sitch et al. (2008) compared five DGVMs forced with climatic and CO_2 data and coupled with HadCM3LC. Four SRES (special report emis-

sion scenarios) are tested. With a large variability in the results, increase in temperature resulted in a release of carbon from the land surface for all DGVMs with higher values in tropical regions than in extra-tropical regions. Nevertheless, when applying the A1F1 scenario, three DGVMs (TRIFFID, LPJ, and HYLAND) simulate an important decrease in carbon uptake from the land toward the end of the 21th century (relative to the period 1980–1999). In general, the results do not show a clear agreement among models on the reaction of DGVMs under climate-change conditions. The NPP (for the tropics) and soil respiration (for the extra-tropics) responses to climate change are identified as the major uncertainties. It is to be noticed that there is a significant influence of the GCM chosen to drive the DGVM (Berthelot et al. 2005). For example, LPJ simulated either a large land-carbon uptake or a source of carbon by the year 2100 when driven by results from different GCMs. (Schaphoff et al. 2006).

Including the nitrogen cycle and its interactions with carbon in the analyses of the carbon cycle – climate feedback strongly affects the model simulation results. Thornton et al. (2009) and Sokolov et al. (2008) implemented nitrogen cycle and nitrogen–carbon interactions in a fully coupled OAGCM and in a model of intermediate complexity, respectively. As a result, the carbon uptake linked to an increase in CO_2 decreases, whereas the carbon uptake linked to climate warming increases. Overall, carbon uptake by land decreases but an increase in decomposition caused by climate warming induces an increase in nutrient availability and thus an increase in plant growth. The influence of the nitrogen cycle is so important that a negative feedback occurs in certain model simulations. Nevertheless, Zaehle et al. (2010*a*) made a similar experiment with the O–CN land-surface model and found that nitrogen dynamics accelerates CO_2 increase in the atmosphere overall. In conclusion, large uncertainties remain in the analysis of the carbon cycle – climate feedbacks but modelling coupled nitrogen–carbon cycles (Thornton et al. 2009) and species adaptation within PFTs to new climatic conditions (Sitch et al. 2008) is crucial.

Whether working on model development or on atmosphere–biosphere system description, the importance of the use of multiple time scales in the dynamical vegetation system functions is highlighted by many authors (Betts et al. 1997; Foley et al. 2000; Moorcroft 2003; Sitch et al. 2003; Delire et al. 2004; Knorr et al. 2005). However, less attention is granted to the influence of the different spatial scales on these functions. Hu et al. (2006) and Scheffer et al. (2005) argue that micro-scale (1–100 m) to global scale (1000 km) should be investigated to improve the understanding of the climate change effects.

5. Summary and conclusion

The complexity of vegetation dynamics makes it difficult to determine the influence of vegetation on climate and some processes of interaction such as respiration, soil carbon behaviour, and competition are still poorly understood and need to be further analyzed. The last generation of DGVMs presents the most complete representation of the systemsince they include regional variations and their interactions with the atmosphere and the different components of the system. However, these models have limitations and it is important to keep in mind that the use of bioclimatic constraints in DGVMs might cause difficulties, particularly when climatic changes are studied. The use of PFTs in the description of vegetation dynamics might also lead to limitations in the interpretation of the simulation results. Therefore, the model should be carefully chosen before starting any study.

Several important issues about DGVMs have been addressed in this paper. One important issue concerns the explicit representation of carbon and nitrogen cycles as well as soil processes in the DGVMs. Some very encouraging work has already been achieved on this issue. Also, there have been great efforts to consider the issue of competition in the models by using different approaches that seem to give valuable results. However, some key processes need to be further improved because they represent important functions of the vegetation dynamics (i.e., competition, nutrient cycling, and aboveground and belowground processes).

Another major issue in vegetation dynamics modelling is the incorporation of disturbances. They have been progressively introduced in DGVMs (i.e., fire, better description of the land cover: land use and nonvegetative surfaces, e.g., lakes). However, many DGVMs do not include any disturbance at all even when fire, land use and (or) management, and grazing have been shown to have marked effects in model simulations. A better definition of the Earth surface at a fine scale (including large lakes, snow-covered areas, wetlands, cropland, grazed areas, and urbanized areas) will be of great importance to assess the role of vegetation on the atmosphere at a global scale. Some developments (CLM–DGVM, ORCHIDEE, LM3V) show an improvement of the land-cover representation but a systematisation of these processes should be achieved in model development. Including disturbances in the models is expected to improve simulation resultsthereby bringing DGVMs simulations closer to the observations in the fields.

Besides modelling of natural and anthropogenic perturbations, two other important issues still need to be overcome: (1) the modelling of previously mentioned poorly understood processes, (2) the modelling of processes following diverse spatial and temporal scales. The second issue is more challenging and modellers have the tendency to chose different approaches to avoid the "scale problem" (e.g., individual-based models, PFT models). The assumption of an artificial vegetation hierarchy inherent to these techniques, along with weakly represented disturbance factors (e.g., land use, land-use change, and topography) and rough modelling of some ecological processes, lead to reduced quality of simulation results. The results of dynamic vegetation models would be improved if these aspects could be better represented.

Regarding the recent developments in coupling, there have been great efforts to integrate the vegetation dynamics by means of DGVMs into global climate models. Though in its early stages, this approach seems promising. The use of DGVMs to replace the original SVAT, designed for the GCM, greatly affects simulation results of the GCM. Though, the simulation results reproduce fairly the global trends (e.g., energy fluxes, carbon, and water cycles), the representation of the interactions between vegetation dynamics, soil processes, and atmosphere is a major weak point in

DGVM–GCM coupling. There is a need to further improve the coupling processes and the vegetation cover representation. The constraints of the GCM should be taken into account in the DGVM development itself, in the case of a DGVM specifically developed for GCM applications. The association of DGVMs with GCMs will be particularly important for improving the accuracy of calculations of carbon fluxes calculations at a global scale.

The validation method is also a key issue when dealing with DGVMs or coupled DGVMs–GCMs. Many obstacles remain in achieving accurate and homogeneous datasets needed for the evaluation of models. Until this goal has been met, methodologies chosen to evaluate a model should be systematized to help in model comparison and identification of model weakness.

In conclusion, DGVMs integrate regional variations in their representation of the vegetation cover. They are efficient and powerful tools for studying global climate change. They are relevant when studying processes and interactions between vegetation and atmosphere. Some mechanisms require improvement (e.g., competition, land-cover representation, disturbances etc.). However, DGVMs are effective when coupled with GCMs and we argue that they are the best alternative that includes vegetation dynamics in the global climate simulations.

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