

From Static Biogeographical Model to Dynamic Global Vegetation Model: A Global Perspective on Modelling Vegetation Dynamics*

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ABSTRACT

Predicting the potential effects of future climatic change and human disturbances on natural vegetation distribution requires large-scale biogeographical models. There have been two basic approaches to modelling vegetation response to changing climates: static (time-independent) or dynamic (time-dependent) biogeographical models. This paper reviews and compares two major types of static biogeographical models, climate-vegetation classification and plant functional type models, and the first generation of Dynamic Global Vegetation Models (DGVMs). These models have been widely used to simulate the potential response of vegetation to past and future climate change. Advantage and disadvantage of each type of model are discussed. Global vegetation modelling for investigations of climate change effects has progressed from empirical modelling to process-based equilibrium modelling to the first generation of DGVMs. Some DGVMs are able to capture the responses of potential natural vegetation to climate change with a strong orientation towards population processes. Nevertheless, the uncertainty around the quantitative simulated results indicates that DGVMs are still in the early stages of development. Validating and capturing disturbance-related effects are major challenges facing the developers of the next generation of DGVMs. In future, DGVMs will become an important tool for assessing the effects of climate change on potential vegetation dynamics and terrestrial carbon storage and for managing terrestrial ecosystem sustainability.

Keywords: climate change; biogeochemistry model; climate-vegetation classification; plant functional type model; carbon storage; dynamic global vegetation model

1. INTRODUCTION

An understanding of effects of past and possible future climate change on terrestrial ecosystems and global carbon cycles will require a clear picture of how vegetation changed in the past and may change in the future (Prentice et al., 1991; Overpeck et al., 1992; Peng et al., 1995a, 1998; Cramer et al. 1999). The distribution of potential

terrestrial vegetation is determined not only by direct climatic variables (temperature, moisture, and atmospheric CO₂ concentration) and resources (nutrient availability), but also by environmental gradients (topography and geology) (Woodward, 1987, Stephenson 1990, Prentice et al., 1992). Predicting the potential impacts of climatic change on natural vegetation dynamics requires large-scale biogeographical and biogeochemical models (Overpeck et al., 1991; Smith et al., 1992; Melillo et al., 1993; VEMAP Members, 1995; Haxeltine and Prentice, 1996; Foley et al., 1996; Goudriaan et al., 1999). There have been two basic approaches to modelling the vegetation response to changing climates: static (time-independent) and dynamic (time-dependent) biogeographical models (Prentice and Solomon, 1990).

The dynamic biogeographical (patch or gap) model, which incorporates explicit representation of key ecological processes (establishment, tree growth, competition, death, nutrient cycling), was developed to capture the transient response of vegetation or simple

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biomes to a changing environment (e.g., Shugart and West, 1980, Shugart, 1984, 1990, Botkin, 1993). The first such model was JABOWA (Botkin et al., 1972), developed for forests in New England. Over the past 20 years, gap (or patch) models have been developed for a wide variety of forest ecosystems including forest-tundra transition zones (Sirois et al., 1994), boreal forest (Leemans and Prentice, 1987; Bonan, 1989; Prentice and Leemans, 1990; Kellomäki et al., 1992), temperate forest (Shugart, 1984; Martin, 1992), and tropical forest (Doyle, 1981; Shugart et al., 1981; Desanker and Prentice, 1993). The general approach has been extended to nonforested ecosystems such as grassland, shrublands and savannas (Coffin and Lauenroth, 1989, 1990, 1994, 1996). A number of different forest gap models have been used to simulate time-dependent changes in species composition and abundance under changing climate (e.g., Solomon 1986; Overpeck et al., 1990; Prentice et al., 1993b; Botkin, 1993; Bugmann and Solomon, 1995; Sykes and Prentice, 1995; Price and Apps 1996, Price et al., 1999). Several obstacles stand in the way of the extensive use of currently available dynamic vegetation models in global climate change studies. For example, it is impractical to use gap-level models to predict shifts in vegetation beyond those at the local scale because of the large number of points that would have to be simulated. Dynamics models also require much more information on the characteristics of species than is easily available or even known for some areas of the globe (Solomon, 1986). These gap models are used in predictions at the regional scale or for ecosystems, but have not yet been applied at the global scale (Smith et al., 1994; Shugart and Smith, 1996).

Static biogeographical models (SBMs) assume equilibrium conditions in both climate and terrestrial vegetation in order to predict the distribution of potential vegetation by relating the geographic distribution of climatic parameters to the vegetation. The equilibrium approach is implicitly large scale in nature as it ignores dynamic processes. It generally requires far less information than gap models and provides estimates of potential magnitude of the vegetation response at regional to global scales. Moreover, these equilibrium models are restricted to estimate steady-state conditions, but this matches that of the great majority of the doubled-CO₂ experiments conducted with general circulation models (GCMs) for climate (Houghton et al., 1990). Over the decades, several different types of static vegetation models (Köppen, 1936; Holdridge, 1947; Budyko, 1956; Box, 1981; Prentice et al., 1992; Neilson et al., 1992; Lenihan and Neilson, 1993; Tchebakova et al., 1993, 1994; Neilson, 1995) have been used to explore the role of climate in determining the distribution and structure of vegetation communities, and have been developed to simulate continental to global scale changes in potential natural vegetation.

In this paper, I focus on two major types of SBMs and

the first generation of Dynamic Global Vegetation Models (DGVMs). These models have been widely used to predict the large-scale distribution of vegetation under changing climatic conditions. A description of the major features and development of SBMs is followed by a summary of the applications of these models to simulating the potential response of vegetation to large-scale environment changes, as well as their limitations. Finally, the recent development of a new generation of biogeographical models, DGVMs, their potential applications, current limitations, and future challenges are discussed.

2. STATIC BIOGEOGRAPHICAL MODELS (SBMS)

2.1. Climate-Vegetation Classification Models

The best-known and simplest method for predicting the equilibrium response of potential vegetation to climate change is the climate-vegetation classification approach. Global bioclimate classification schemes (e.g., Köppen, 1936; Holdridge, 1947) are essentially climate classifications defined by large-scale vegetation patterns. Köppen's scheme was intended as a classification of climates, although its boundaries were chosen to coincide approximately with vegetation boundaries and were expressed in terms of aspects of climate that are related to the distribution of plants. The Köppen scheme has been improved by Guetter and Kutzbach (1990). One of the most widely used global scale bioclimate classification models is that of Holdridge (1947). Here I use the Holdridge Bioclimatic Classification (HBC) as one example of a climate-vegetation model.

The HBC is a scheme (Table 1) that uses three bioclimatic variables (biotemperature, mean annual precipitation, and a ratio of potential evapotranspiration to mean annual precipitation) derived from standard meteorological data to explicitly express the relation of climate patterns and broad-scale vegetation distribution (referred to as life zones). The Holdridge diagram (Holdridge, 1947) contains 37 named life zones. Biotemperature is defined as the mean value of all daily mean temperatures above 0°C, divided by 365. Biotemperature, which is closely related to growing degree days (Tuhkanen, 1980), gives a measure of heat during the growing season, and is likely to be more directly related to plant growth than mean annual temperature. Plant demand for moisture is expressed through the ratio of mean annual precipitation to potential evapotranspiration (PET) ratio. Note that only two primary variables (biotemperature and mean annual precipitation) are required to define a location within the life zone triangle.

The disadvantage of HBC is that the climatic variables may not be the factor to which vegetation is responding. Furthermore, a difficulty with zonal concepts like the HBC is that vegetation is defined as an aggregate vegetation type or association. The HBC assumes that the modern

vegetation biomes will remain intact and migrate as whole units with the changing patterns of climate. However, terrestrial ecosystems are composed of numerous species that can respond individually to changing environmental conditions (Davis, 1984; Webb, 1987) and whose distribution often cover more than one ecosystem or zone. Over time, the HBC has been strongly criticized for not including individual species responses and proper successional dynamics (e.g., Solomon and Leemans, 1990; Leemans et al., 1996; Davis et al., 1998; Goudriann et al., 1999).

2.2. Plant Functional Type Models

2.2.1. Box's Model

A unified global expression for the relationship between macroclimate and plant life forms was made by Box (1981). To address many of the shortcomings of previous climate-vegetation classification modelling studies and overcome the difficulty of including the large number of plant species potentially occurring in any region, Box reorganized species into characteristic species types (termed *plant life forms*) rather than the small number of vegetation biomes used in the HBC. This resulted in 90 plant functional types (PFTs) defined by eight climate parameters (Table 1).

Each PFT represents a set of plant species (e.g., tropical evergreen broad-leaf rainforest trees) characterized by their physiognomic and morphological traits and response to climate. The climatic factors used in Box's model reflect the required conditions for principal climatic constraints (warmth, frost frequency, and moisture) and include some description of seasonal cycle and the phase relationship between seasonal variations in temperature and precipitation. Moreover, Box's climatic factors differ from Holdridge's in best estimation of drought stress and are seasonally explicit (separately for warmth and moisture). Box's model describes the distribution of PFTs in a multidimensional climatic space. The climatic limits of each PFT defines "envelopes" in climate space, within which each PFT can exist. A simple height-dominance scheme is used to obtain the potential plant types.

Box's model is in contrast with the Clementsian-determinism implicit in the earlier schemes. The biomes are not taken as given, but emerge through the interaction of constituent plants. However, the complexity of this scheme has also imposed a limit on its potential to be parameterized appropriately for all plant types and climatic indices. The basis for determining climatic limits of PFTs remains essentially correlative, rather than mechanistic. Some of these problems have been overcome by dramatically reducing the number of plant types defined and the selection of climatic variables whose influence on plant distribution have a more mechanistic interpretation (e.g., BIOME1, Prentice et al., 1992; BIOME3, Haxeltine and Prentice, 1996; MAPSS, Neilson, 1995).

2.2.2. Rule-Based Biome Model (RBBM)

Rule-based modelling is an outgrowth of developments in artificial intelligence and expert systems, an area that is now being applied to ecology (Rykiel, 1989). Starfield and Bleloch (1986) first showed how rules might be used to modify conventional, quantitative models, and suggested how qualitative dynamic models could be built. Their ideas were subsequently implemented in a rule-based ecological model for the management of an estuarine lake (Starfield et al., 1989). New developments in biogeography are providing a mechanistic conceptualization of the biosphere (Neilson, 1986, 1987, Neilson et al., 1989; Woodward, 1987; Stephenson, 1990).

A rule-based biome model (RBBM) of Neilson et al. (1992) was constructed as a set of rules based on mechanistic and conceptual models of biome distribution (Neilson et al. 1989). The rules are essentially if-then-else statements similar to a general computer chart. The most unique feature of the model is the temperature-based definition of seasons (Table 1). Winter, spring, and summer are the principle seasons considered. Temperature thresholds, input as parameters, are used to define the beginning and end of the seasons. Direct effects of CO₂ on vegetation dynamics are excluded. The entire 1211 climatic station networks and their corresponding biome types, based on a map modified from Kuchler (1964) and Dice (1943), were used to calibrate the rules for the conterminous USA. This model is an early stage of MAPSS (Neilson, 1995).

Another rule-based Canadian Climate-Vegetation Model (CCVM) has been developed by Lenihan and Neilson (1993) for predicting the distribution of vegetation formation in Canada under current climatic conditions. The CCVM relies on climate parameters with an inferred mechanistic relationship to the distribution of vegetation. The climatic parameters used as model drivers (e.g., degree-days, minimum temperature, snowpack, actual evapotranspiration, soil moisture deficit) have a more direct influence on the vegetation patterns than those commonly used in equilibrium models. Splitting rules in a binary decision tree classify the potential vegetation at grid cells in a spatial distribution database. The rules are based on critical climatic thresholds that physiologically constrain the distribution of different vegetation life forms. Under current climatic conditions, CCVM predicted Canadian vegetation with more accuracy than the HBC (Holdridge, 1947) or Box's model (1981), and showed a similar level of overall predictive accuracy as the BIOME model of Prentice et al. (1992). The CCVM has been further used to predict potential vegetation patterns for Canada under two double current CO₂ climate scenarios (Lenihan and Neilson, 1995).

2.2.3. Ecophysiological-based Biome Model (BIOME)

The ecophysiological-based BIOME model (Prentice et

al., 1992) helps us understand the fundamental aspects of structure in terrestrial ecosystems. It predicts the global distribution of 14 PFTs based on a set of limiting climatic conditions (Table 1), usually with a spatial resolution of 0.5° longitude/latitude. The PFTs of the highest, pre-defined dominance values combine with each other to yield the biome type of the grid cell. The model distinguishes 17 biome types for global vegetation.

In the BIOME model (Table 1), PFTs are assigned climate tolerances in terms of amplitude and seasonality of climate variables. The cold tolerance of plant types is defined by minimum mean temperature of the coldest month (T_{\min}). Some plant types also have chilling requirements expressed in terms of a maximum mean temperature of the coldest month. The heat requirement of plant types is defined by annual accumulated temperature over 5°C (or 0°C for some PFTs). The heat requirement of some shrub types is defined by mean temperature of the warmest month (T_{\max}). Mean moisture availability is defined as the ratio of actual evapotranspiration (AET) to potential evapotranspiration (PET), which depends on net radiation.

Like Box's model, the BIOME model is based on a set of PFTs, with each type described by a set of limiting climatic conditions. However, the BIOME model differs from other bioclimatic schemes in that the climatic limits of each PFT are expressed in terms of fundamental phenomenological constraints, rather than observed correlations between vegetation and climate. Woodward's (1987) ideas about the physiological and ecological mechanisms for the climatic limitation of PFTs are represented in the BIOME model. Biomes are not taken as given, as it the case with the Holdridge classification, but emerge through the interaction of constituent plants. So the BIOME model can be applied to the assessment of changes in potential vegetation patterns in response to different climate in a equilibrium state. However, the BIOME model does not simulate the transient dynamics of vegetation. At best, it provides constraints within which plant community dynamics should operate (Claussen, 1994, Claussen and Esch 1994). A potential weakness of the BIOME model is that the direct effects of CO₂ on vegetation are not considered.

In BIOME2, developed by Haxeltine and Prentice (1997), ecophysiological constraints, which are based largely on the original BIOME model (Prentice et al., 1992), are applied to select which plant functional types can occur in a given set of climatic conditions. The model then identifies the quantitative combination of plant functional types which maximizes ecosystem net primary productivity (NPP). Gross primary production (GPP) is calculated on a monthly time step as a linear function of absorbed photosynthetically active radiation and is reduced by lack of moisture and low temperature. Plant respiration is estimated as 50% of the non-water-limited GPP. A two-layer hydrology model with a daily time step allows

simulation of the competitive balance between woody vegetation and grass. It accounts for the effects of soil texture and differences in rooting depth. The prescribed CO₂ concentration has a direct effect on GPP through the photosynthesis algorithm, and affects the competitive balance between C₃ and C₄ plants. The water balance calculation is based upon the equilibrium evapotranspiration theory (Jarvis and McNaughton, 1986). However, the direct effect of CO₂ on the water balance was not represented in the model. This has been improved in latest version – BIOME3 – developed by Haxeltine and Prentice (1996). In BIOME3, canopy conductance is calculated as a function of optimal photosynthetic rate and water stress, and regional evapotranspiration is estimated as a function of canopy conductance, equilibrium evapotranspiration rate, and soil moisture using a simple planetary boundary layer parameterization. These schemes lead to a two-way coupling of carbon and water fluxes through canopy conductance and allow the model to simulate the response of photosynthesis, stomatal conductance, and leaf area to atmospheric CO₂ and other environmental factors.

2.3. Model Applications

Static biogeographical models (SBMs) have been used to simulate the global distribution of natural vegetation under a varying climate, using both past conditions associated with the Last Glacial Maximum (LGM) (Prentice and Fung, 1990; Guetter and Kutzbach, 1990; Prentice et al., 1993a; Esser and Lautenschlager, 1993; Friedlingstein et al., 1995; Jolly and Haxeltine, 1997; Cowling, 1999) and future climate patterns under doubled-CO₂ scenarios (Emanuel et al., 1985; Prentice and Fung, 1990; Leemans, 1992; Smith et al., 1992a,b, 1993; Leemans et al., 1996). SBMs have also been combined with estimates of carbon storage in both vegetation and soil to estimate current patterns of potential carbon storage under both current and changing climate conditions (Prentice and Fung, 1990; Smith and Shugart, 1993, Peng, 1994; Peng et al., 1998). Here I concentrate on three aspects of applications: coupling SBMs with a climate model, coupling SBMs with an ecosystem model, and using them to predict palaeovegetation patterns and carbon storage.

2.3.1. Coupling SBMs with Climate Model

The climate system consists of several subsystems including the atmosphere, oceans, geosphere, and biosphere – all of which affect and are affected by the circulation and chemical composition of the atmosphere (Bolin, 1984). These systems interact in a complex, nonlinear way at a wide range of time scales. The interaction of biosphere and atmosphere has been studied intensively by coupling SBMs with General Circulation Models (GCM) (Henderson-Sellers 1991, 1993; Claussen 1994, 1997; Cirtet and Henderson-Sellers 1995; Claussen

and Gayler, 1997). The Simple Biosphere models (SiB) of Sellers et al., (1986), and the Biosphere-Atmosphere Transfer Scheme (BATS) of Dickinson et al. (1986, 1993) have been coupled with GCMs. Recently, there is increasing interest in coupling vegetation models to the simulated climate predicted by GCMs. Global vegetation classifications have been used to compute the distribution of global vegetation, and potential vegetation shifts due to greenhouse gas-induced climate warming (e.g., Emanuel et al., 1985; Prentice and Fung, 1990; Henderson-Sellers, 1991; Claussen and Esch, 1994).

The first attempt to incorporate continental vegetation as a dynamic component of global climate models was reported by Henderson-Sellers (1993). A simple Holdridge classification was used; the vegetation scheme was found to be a stable component of the global climate system, without any discernible trends over the integration period. Differences between simulations with and without interactive vegetation were small. However, Henderson-Sellers (1993) did not study the problem of coupling vegetation with climate models in great detail. More recently, Claussen (1994) coupled the BIOME model of Prentice et al. (1992) with the ECHAM climate model of the Max-Planck-institut für Meteorologie, Hamburg, Germany (Roeckner et al., 1992). He suggested that a biome model should be coupled with climate in the following ways: (1) the climate models should be integrated over several years; and (2) a biome distribution should be computed from the corresponding multi-year simulated climatology. Sensitivity analyses by Ciret and Henderson-Sellers (1995) suggest that using the correct time step is very important for coupling vegetation models with GCMs. To date, there has been little effort to compare simulated vegetation patterns with observed vegetation distribution.

2.3.2. Coupling SBMs with Ecosystem Model

A number of ecophysiological-based ecosystem process models have been developed and used to examine potential effects of both increasing atmospheric CO₂ and associated climate change on patterns of NPP and biogeochemical cycles (e.g., CENTURY, Parton et al., 1987, 1993; FOREST-BGC, Running and Coughlan, 1988; BIOME-BGC, Running and Gower, 1991; GEM, Rastetter et al., 1991, 1992; TEM, Raich et al., 1991; Melillo et al., 1993; FBM, Lüdeke et al., 1994; DEMETER, Foley, 1994a, 1995). These models simulate ecosystem processes, such as canopy photosynthesis, transpiration, litterfall, soil moisture, water use efficiency, net primary productivity, and carbon and nitrogen cycling at a variety of spatial scales. The explicit consideration of ecosystem carbon and nitrogen dynamics in these models allows them to simulate short-term net carbon flux for a given location, and to provide estimates of change in NPP under changing climatic conditions. However, they cannot be used to simulate long-term changes in the composition and

structure of vegetation in response to changing environmental conditions. Equilibrium models of biosphere structure, like the BIOME model (Prentice et al., 1992; Haxeltine and Prentice, 1996), predict the major directions in potential biome redistribution after climate change. The dynamics of ecosystems under changing boundary conditions are a function of their structure, and this structure may also change due to different biogeochemical processes. Therefore, coupling SBMs (which model ecosystem structure) with the models of biogeochemical ecosystem processes (which model ecosystem function) is the first step in the development of dynamic global vegetation models (DGVMs), which could capture the transient dynamics of the biosphere in a changing climate (Tian et al., 1998; Foley et al., 1998).

A general terrestrial biosphere model, DEMETER (Dynamic and Energetic Models of Earth's Terrestrial Ecosystem and Resources), has been developed by Foley (1994a, 1995) for this purpose. By coupling a simple biome model with ecosystem processes, DEMETER is designed to provide a comprehensive, global-scale view of the terrestrial biosphere, including both a structural (predicted potential vegetation) and functional (primary production and carbon storage) perspective. It has been used to predict potential vegetation patterns, NPP, and global carbon storage in vegetation and soil (Foley 1994a,b, 1995). Simulated results and available observations are well correlated. Plöchl and Cramer (1995) coupled an ecosystem structure model (BIOME, Prentice et al., 1992) with a biogeochemical ecosystem process model, the Frankfurt Biosphere Model (FBM) (Lüdeke et al., 1994). Using the coupled models under a GCM-based scenario of changing temperature and precipitation resulted in major changes in biome boundaries at high latitudes (e.g., arctic and boreal ecosystems).

VEMAP (Vegetation/Ecosystem Modeling and Analysis Project) (VEMAP Members, 1995) has coupled three biogeographical models (e.g., BIOME2, Haxeltine and Prentice, 1997; DOLY, Woodward et al., 1995, and MAPSS, Neilson, 1995) with three biogeochemical process models (BIOME-BGC, Running and Gower 1991; CENTURY, Parton et al., 1987, 1993; TEM, Melillo et al., 1993) and compared the simulations of these coupled models in a continental-scale study of terrestrial ecosystem response to climate change and doubled CO₂ (Pan et al., 1998). The VEMAP study was limited in that it used models that only made projections about equilibrium conditions; however, it did provide a framework for coupling large-scale biogeographic models with biogeochemical models.

2.3.3. Application of SBMs to reconstruction of palaeovegetation patterns and palaeo-carbon storage

An SBM provides a tool to translate past climate into simulated palaeovegetation patterns, allowing more detailed comparison with reconstructed past vegetation

from palaeoecological data, and further estimation of past carbon storage. The global BIOME model (Prentice et al., 1992) is now widely used for this purpose (Claussen and Esch, 1994; Prentice et al., 1993a; Esser and Lautenschlager, 1993; Solomon et al., 1993). In addition, Monserud et al. (1993) used the Siberian vegetation model of Tchepakova et al. (1994) to reconstruct Siberian palaeovegetation at mid-Holocene (4,6000 to 6,000 yr. BP) and to compare it with the predicted future Siberian vegetation under climate change scenarios. They concluded that the mid-Holocene, known as a warm period, is not a good analogy for predicting future warming resulting from CO₂ doubling, although the predicted rise in temperature with future warming is similar to mid-Holocene. However, the global BIOME model of Prentice et al. (1992) has been successfully used to reconstruct palaeovegetation from pollen data in Europe at 6000 yr. B.P. (Prentice et al., 1996; Guiot et al., 1996) and since 13, 000 yr. B.P. (Peng et al., 1995c). More recently, the process-based vegetation model BIOME3 (Haxeltine and Prentice, 1996) has been used to simulate possible effects of low atmospheric CO₂ on composition and structure of North American vegetation at the Last Glacial Maximum (Cowling, 1999). It has also been used to reconstruct a probable glacial climate from pollen data in Mediterranean region under seasonal precipitation changes and lower atmospheric CO₂ in the biosphere (Guiot et al., 2000).

Prentice et al. (1996) developed a method of "biomization" to attribute a biome to each pollen assemblage. Each pollen taxon is assigned to one of the PFTs defined in BIOME (Prentice et al., 1992). A likelihood index is calculated for each PFTs and translated in terms of biome, using the combinations defined for the model. Finally for each biome, an index is defined as the sum of the percent square roots of all the taxa potentially present in the biome. These indices are compared and the biome with the biggest index is attributed to the spectrum. The method was validated by applying it to a set of more than 2000 surface pollen spectra representing contemporary vegetation, and a set of more than 200 pollen spectra representing mid-Holocene (about 6000 yr. B.P.) vegetation.

Using the new "biomization" method of Prentice et al. (1996), Peng et al. (1995c) reconstructed the temporal and spatial shifts of terrestrial biomes from pollen data in Europe since 13, 000 yr. B.P. The distribution of biomes reconstructed from pollen agrees well with results obtained from the modern climate using BIOME (Prentice et al. 1992). These pollen-based biome reconstructions were then used to translate directly into the climate parameters needed for calculating vegetation and soil carbon storage. This approach also has been used to reconstruct global vegetation distribution from palaeoecological data at the mid-Holocene (Prentice and Webb III, 1998) and extended to simulate past climate patterns from pollen data in Europe for 18, 000 yr. B.P. (Peyron et al., 1998). However,

the accuracy of these reconstructions at global scale is currently limited by sparse or absent data in some regions such as the South American tropical rainforest area, South and Southeast Asia and Siberia (Peng et al., 1998).

Shifts in the distribution of terrestrial vegetation are accompanied by changes in carbon storage (Peng et al. 1994, 1998). Using SBMs to estimate terrestrial carbon budgets is a two-step process because models do not directly simulate carbon pools and fluxes. The models are used to define potential patterns of vegetation and associated soil properties based on simple climate indices. Traditionally, calculations of carbon pools are done by multiplying the areal extent of each cover type (e.g., vegetation type, ecosystem type, biome, or life zone) by estimates of carbon densities in vegetation and soils (Adams et al. 1990; Prentice and Fung, 1990, Smith et al., 1992b; Prentice et al., 1993a). Generally these estimates are solely dependent on the vegetation or biome type and do not vary geographically within any one type (e.g., all tropical rain forests have the same value). The results are likely a rough approximation of reality, and can be improved using process-based ecosystem models (Raich et al., 1991; Potter et al., 1993; Melillo et al., 1993; Parton et al., 1987, 1993), which simulate patterns of NPP and carbon dynamics for a given vegetation type and climate. However, these models usually need to be parameterized by a large number of environmental inputs, which are not often available from palaeoecological data (Peng et al., 1998). An alternative method is the use of an empirical biospheric model, such as the Osnabrück Biosphere Model (OBM) (Esser 1987, 1991) or CARAIB biosphere model (Warnant et al., 1994), or statistical models (Peng et al., 1994, 1995a,b). These models only need three environmental parameters as input, which are easily derivable from palaeoecological data (Peng et al., 1998) or from GCM simulations (François et al., 1998, 1999). For these reasons, biosphere models have been widely used to estimate past terrestrial carbon dynamics in response to past climatic changes (Peng et al., 1994, 1995a,b,c; Esser and Lautenschlager, 1993, François et al., 1998; Peng et al., 1998).

2.3.4. Model Limitations

No model is perfect. The understanding of each model's limitations is, however, critical for future development and useful application. Scientific questions relating to the potential response of terrestrial vegetation to global climate change has created new problems and challenges for the development and application of large-scale static biogeographical models (SBMs). The major limitations of SBMs include:

(1) SBMs cannot simulate the 'time course' of vegetation changes during a period of rapid climate change because they do not incorporate migrational or successional processes (Prentice and Solomon, 1990). However, SBMs can be used to indicate probable

trajectories of vegetation change and provide a necessary framework for modelling dynamic vegetation processes at global scales (Prentice et al. 1992, Steffen et al., 1996, Goudriaan et al. 1999).

(2) Climate-Vegetation Classification models (e.g., HVC) usually predict the distribution of physiognomic units (e.g., major vegetation formation, PFTs, or life zone) at high levels in the organization of vegetation. The use of these models in global change studies has been criticized for ignoring the individualistic response of species to climate change as observed in fossil records (Webb, 1987; Davis, 1989; Graham and Grimm, 1990; Davis et al. 1998), and for not including proper successional dynamics (Solomon and Leemans, 1990; Leemans et al., 1996; Goudriaan et al., 1999). Modelling the individualistic response of species is an important approach to understanding vegetation response to a changing climate (Lenihan and Neilson, 1993; Iverson et al., 1999). However, for purposes of linking vegetation models to climatic models such as a GCM, and coupling with biogeochemical models such as a carbon and nitrogen cycle model, it is necessary to model vegetation at the scale at which it most directly interacts with the atmosphere.

(3) Most of these models do not incorporate biogeochemical processes, especially carbon and nitrogen cycling. The quantitative feedback of biogeochemical processes on vegetation distribution is still poorly understood (Neilson and Running, 1996). Therefore, a major problem when using these models to simulate the potential response of vegetation to a doubled-CO₂ climatic scenario is their inability to address the direct effects of CO₂ on vegetation (Norby et al., 1992; Mooney et al., 1991). The more recent achievement of incorporating the effects of CO₂ on NPP, leaf-area-index (LAI), water balance, and competition between C₃ and C₄ plants (Haxeltine and Prentice, 1996, 1997; Neilson, 1995, Woodward et al., 1995) in models provide some hope. However, we remain in the early stages of developing models of global vegetation dynamics.

(4) SBMs often have been limited to potential natural vegetation. Most of them ignore or simplify the role of natural disturbances (e.g., fire, pest outbreaks, storms) and human activities (e.g., land-use) in controlling the dynamic distribution of global vegetation (VEMAP Member, 1995; Haxeltine and Prentice, 1996; McIntyre et al., 1999). Models of vegetation change in response to global warming need to incorporate the effects of disturbance at large spatial scales. More detailed discussions of these issues are given in Section 3.3.

3. DYNAMIC GLOBAL VEGETATION MODELS (DGVMs)

3.1. First Generation DGVMs

To overcome the limitations of SBMs described above, a

new generation of biogeography models, which predict the dominance of various plant life forms in different environments based on ecophysiological constraints and resource limitations (e.g., water, light), have been used. These models are being coupled with biogeochemical ecosystem models to simulate terrestrial ecosystem response to climate change and doubled-CO₂ scenarios (VEMAP Members, 1995). The major features of three new biogeography models: BIOME2 (Haxeltine and Prentice, 1997), MAPSS (Neilson, 1995) and DOLY (Woodward et al., 1995), which were used by the VEMAP study (VEMAP Members, 1995), are highlighted in Table 2. However, the simulation of structure in these models is essentially static, while the real world's terrestrial vegetation structure is changing over time, driven by changes in human activities and climate systems. The weakness of this coupling is the lack of integration of biogeochemical and biogeographic processes into a single dynamic biosphere model that is able to quantify the feedbacks of biogeochemical processes on vegetation distribution.

There is an urgent need to understand how climate change, as well as natural disturbances, affect vegetation dynamics and ecosystem processes. One of the high priority activities of the International Geosphere-Biosphere Programme (IGBP); that is, the core project of the Global Change and Terrestrial Ecosystems (GCTE) is to develop a new class of dynamic biogeography models, known as DGVMs (Steffen et al., 1992, 1996). The primary framework for a DGVM was outlined by Prentice et al. (1989) over a decade ago. Based on a linkage between an equilibrium global vegetation model and smaller scale ecosystem dynamics modules, Steffen et al. (1996) proposed the structure of a first generation DGVM that simulates transient changes in vegetation distribution over a decade time scale. There has been growing interest in developing DGVMs (e.g., IBIS, Foley et al. 1996; HYBRID v3.0, Friend et al. 1997; MAPSS-CENTURY DGVM, Lenihan et al. 1998; CASA-DGVM, Potter and Klooster 1999; TEM-DVM, Pan et al., 2000), but all are still in the preliminary development stages. Key features of DGVMs are that they are able to predict transient changes in vegetation structure and function, including changes in land use, and consequent changes in direct and indirect carbon feedbacks to the atmosphere over time and space, and they could predict the variables that link the land surface to the atmosphere while being responsive to atmospheric changes predicted by GCMs. For example, IBIS (Foley et al., 1996) identified three key processes that affect terrestrial ecosystem structure and function: (1) land surface (e.g., energy and water balance); (2) carbon balance (e.g., plant growth and carbon flux); and (3) vegetation phenology and dynamics (e.g., plant establishment, competition and mortality). Most DGVMs simulate plant growth, resulting from the assimilation of carbon through photosynthesis minus the respiration of the

plants, similar to the biogeochemistry models mentioned before (e.g., VEMAP Member, 1995). Plant succession processes, such as establishment, competition, and mortality, are included in DGVMs, using a philosophy similar to that of patch models (Shugart, 1984). Competition is considered only for the most basic resources such as light and water. Vegetation changes are traditionally classified into three biome types: grasses, deciduous and evergreen trees (Cramer et al. 1999), but they are internally divided into 7-10 plant functional types (PFTs). These plant types are expected to be able to capture the simulated feedbacks of vegetation on climate system and the projection of the general nature of vegetation change. Potential approaches for DGVM development are summarized below (also see Figure 1):

(1) **Bottom-up** The bottom-up approach involves the scaling-up of patch models using a statistical sampling procedure to provide regional and global cover. This approach would require a generalized patch model, that can simulate the dynamics of all biome types (e.g., tundra, boreal forest, temperate grassland, tropical rain forest, tropical savanna) both for current and projected future climate (e.g., Bugmann and Solomon, 1995). This generalized patch model would use a PFT, rather than addressing species composition, to provide temporal patterns of plant growth and biogeochemical cycling. A further challenge is to enhance the capability of the current generation of patch models to simulate the dynamics of forest dieback and possible conversion to grassland under an extremely arid climate (Martin, 1992; Coffin and Lauenroth, 1990, 1994, 1996).

(2) **Top-down** The top-down approach includes the use of a static (equilibrium) biogeographical model that relates the large-scale patterns of climate and vegetation (e.g., HBC, Holdridge, 1947; BIOME, Prentice et al. 1992; Haxeltin and Prentice, 1996, 1997). The top-down approach of DGVM development would modify these global vegetation models by: (1) defining PFTs that make up each of the ecosystems or biomes currently used to describe vegetation pattern/composition within global models; (2) assigning an appropriate set of environmental response functions to PFTs; and (3) developing rules to group the PFTs together to form ecosystems and biomes. These PFTs would then be assigned parameters relating to rates of growth, mortality, dispersal, and other processes, that influence the transition dynamics of vegetation in response to changing environmental conditions (Steffen et al., 1996).

(3) **Linking patch models with ecosystem models of biogeochemical processes** Most ecosystem models require information about features of the vegetation structure such as leaf area, biomass, litter input, and litter quality (e.g., C/N). These parameters can be provided by the patch

models. Following this logic, several patch models have been linked with biogeochemical models that simulate the dynamics of carbon, nitrogen, hydrologic cycles, and fire disturbance (Poster and Post, 1986; Lauenroth et al. 1993; Friend et al., 1993, 1997; Keane et al. 1996; Price et al. 1999). In return, the biogeochemical model provides a description of certain environmental conditions on the patch, such as NPP, and the availability of nitrogen, soil carbon, and moisture. For example, Hybrid v3.0 (Friend et al., 1997) is an ecosystem dynamic model that links the patch model ZELIG (Urban, 1990) with process model of FOREST-BGC (Running and Coughlan, 1988). One of biggest challenges of linking patch models with biogeochemical models is the spatial scaling issue (Lauenroth et al. 1993; Burke and Lauenroth, 1993). Our ability to scale up vegetation to the entire terrestrial biosphere is still limited by gaps in our knowledge of the relationship and interactions between individual plants and ecosystems (Jarvis, 1995) and lack of methods for extrapolating ecological effects of disturbance (e.g., fire) at large scales under a changing environment (McKenzie et al., 1996; Peterson, 1998).

3.2. Applications of DGVMs

Potential applications of DGVMs are focused on three key areas: (1) simulating the transient changes in global vegetation patterns under future climate change and human disturbance (e.g., land-use) scenarios; (2) estimating the transient behaviours of terrestrial carbon pools and fluxes, including the possible effects of CO₂ fertilization, atmospheric nitrogen deposition, climatic variability, and ecosystems disturbances; (3) and providing a fully interactive representation of biosphere ecosystems within GCMs to investigate the potential for vegetation-climate interactions and feedback mechanisms.

3.2.1. Simulating global vegetation distribution, NPP, and biomass under transient climate change scenarios

A comparison of four DGVMs: Lund-DGVM (I.C. Prentice, unpubl.), HYBRID4.0 (Friend et al., 1997), IBIS-1 (Foley et al., 1996) and SDGVM (F.I. Woodward, unpubl.) was recently undertaken by the GCTE Synthesis Project (Cramer et al. 1999). All four DGVMs were run with a transient climate change scenario generated by the Hadley Centre GCM (HadCM2), which has a spatial resolution of 2.5° by 3.75°, and explicitly accounts for the combined radiative effects of CO₂ and sulphate aerosols on future global climate. Under pre-industrial CO₂ concentrations and climatic conditions, total global NPP was estimated to be 48-76 Pg C yr⁻¹ by four DGVMs, which is similar to the range of global NPP estimated by equilibrium models (Cramer et al. 1999). Over the course of the simulation for the period 1860 to 2100, total global NPP increased 42 to 71%, compared to preindustrial levels. The largest increase in NPP occurred at high latitudes, with increasing CO₂ driving additional increases in NPP in the

semi-arid regions. Global NPP also showed significant interannual variability (greatest in HYBRIDY4.0) as a result of both climatic variability and population processes. An increased in total global vegetation biomass ranging between 1.1 and 2.0 Pg C yr⁻¹ was simulated by all four models. Significant shifts in vegetation distribution over time were simulated by all DGVMs. However, it is difficult to evaluate model results by comparing with existing global vegetation maps due to the complex changes in vegetation patterns. The considerable uncertainty of these simulated results indicates that DGVMs are still in the early stages of development. They are able to capture the responses of potential natural vegetation to climate change with a strong orientation towards population processes. However, the quantitative results are still unreliable.

3.2.2. Coupling DGVM models with process-based biogeochemical models

Many currently available biogeochemical ecosystem process models capture the essential process of trace gas fluxes (e.g., CO₂, CH₄ and N₂O) between atmosphere and ecosystems, as well as associated changes in NPP. When used in changing climate conditions, one of the most serious limitations of these models is that the structure of the ecosystem itself is prescribed from a global database. Significant shifts of major global vegetation types are likely to occur under altered climatic conditions. Hence, the assumption of stable ecosystem structure could fail. To overcome this problem, it is necessary to couple an ecosystem structure model with a biogeochemical ecosystem process model. Recent advances in this effort have been reported by Pan et al., (2000) who developed a biogeochemical-based succession model of TEM-DVM that integrates the Terrestrial Ecosystem Model (TEM) (Mellilo et al., 1993) with the plant life cycle modules derived from the Dynamic Vegetation Model (BIOME-DVM) (Sitch et al., 1999). The model is independently validated against age-dependent growth data from sites of temperate forests in North America. The results suggest that the TEM-DVM can be used for investigating transient responses of ecosystem structure and function to future climate changes, and for estimating the impacts of land-use changes, such as deforestation, on carbon and nitrogen cycles in temperate forests.

3.2.3. Coupling DGVMs with GCMs for Simulating Vegetation Feedbacks on Climate

A DGVM ultimately should be coupled with a GCM for simulating vegetation effects on climate. Previous coupling of GCMs with vegetation experiments is limited by equilibrium with climate (Henderson-Sellers, 1993, Claussen and Esch, 1994, Cirtet and Henderson-Sellers, 1995). By aggregating individual patch models to the regional level, the DGVM will link to the GCM through a nested mesoscale model and a soil-vegetation-

atmosphere-transfer (SVAT) model, which involves instantaneous fluxes of water vapour, heat, and momentum. These models are being developed to specify the broad-scale transfer characteristics of land surfaces. Sellers et al. (1992) and Bonan (1994) have made a significant step towards a more integrated GCM for biosphere modelling. They constructed an SVAT that simulates photosynthesis, respiration, and canopy conductance and coupled it to a GCM for investigating the short-term biogeochemical and biophysical interaction between the atmosphere and terrestrial biosphere. Recently, Betts et al. (1997) went one step further in coupling biospheric and atmospheric processes for quantifying the effects of both physiological and structural vegetation feedbacks on a doubled-CO₂ climate scenario. In this case, the equilibrium predecessor of the Sheffield DGVM (Woodward et al. 1995) was used as part of the land surface scheme in a simplified version of the Hadley Centre's GCM. The study qualitatively suggested a potential time lag in structural response of the biosphere, as compared to the direct response in physiology (Cramer et al., 1999). To add quantitative significance to these findings, however, it is necessary to simulate the dynamic changes in both vegetation physiology and structure under the GCM predictions of future climate change. Progress in coupling DGVM with a GCM has been made by Foley et al. (1998). They linked the dynamic global vegetation model IBIS (Foley et al., 1996) with the global climate model GENESIS (Thompson and Pollard, 1995a,b) to simulate changes in global vegetation, water balance, NPP, and potential vegetation feedback mechanisms on climate. The two models are directly coupled based on a common treatment of land surface and ecosystem processes, which are used to simulate the dynamics of energy, water, and carbon between atmosphere, vegetation, and soil. IBIS has also been used to investigate the potential impacts of increasing atmospheric CO₂ concentration on the hydrology of the Amazon basin (Costa and Foley, 1997). Moreover, the coupled IBIS/GENESIS model was also used to investigate potential vegetation feedbacks on the ice age climate (Levis et al. 2000) and global warming (Levis et al. 1999). However, because of biases in the GCM climate simulation, there were some regional-scale errors in the simulation of vegetation distribution. For example, the amount of boreal forests in North America was underestimated due to a dry bias in the GCM and the grassland in northern Africa was overestimated due to a wet bias (Foley et al. 2000). The lack of explicit disturbance mechanisms (e.g., fire, wind, land-use), and interannual climate variability added to these errors.

3.3. Current Limitations and Future Challenges

The development of the first generation of DGVMs was largely based on the assumption that climate is the predominant factor controlling vegetation composition and structure at a global scale. Although

current DGVMs are able to simulate the time-dependent changes in vegetation patterns determined by climate, there are still other constraints to the transient response of vegetation (e.g., seed dispersal, dieback of forest and grassland, soil development). The major limitations of DGVMs and the needs for future development include:

(1). Current DGVMs do not adequately simulate natural disturbances such as fire, wind storm, and insect and pest attacks. Fire is one of the most important disturbances because it often controls vegetation type (Payette, 1992; McKenzie et al. 1996; Neilson, 1995) and plays a key role in the global carbon budget (Kasischke et al. 1995; Kurz et al. 1995; Kurz and Apps, 1999). For example, fire frequency affects the competitive balance between grass and woody plant types (Daubenmire, 1978; Hopkins, 1992), and controls the regeneration and succession of boreal forests (Payette, 1992; Bergeron and Flannigan, 1995; Niemelä, 1999). Changes in seasonal fire severity rating (Flannigan and Van Wagner, 1991), length of fire season (Wotton and Flannigan, 1993), and fire frequency (Bergeron and Flannigan, 1995) resulting from global warming are expected to have a significant effect on the NPP and carbon dynamics in boreal forests as well as other ecosystem types (Kasischke et al., 1995; Zoltai et al., 1998; Jiang et al., 1999; Peng et al., 1999). Most DGVMs have a simple disturbance module, but its ability to estimate the frequency and severity of disturbances needs improving, particularly given the importance of disturbance in determining long-term terrestrial vegetation dynamics and carbon budgets. The ability to simulate vegetation changes and feedbacks to the atmosphere due to changes in fire frequency and severity is a key challenge for making DGVMs useful in global climate change studies. The first attempt to incorporate the large-scale fire severity model, MCFIRE, as component of MAPSS-CENTURY DGVM was reported by Lenihan et al. (1998) and Daly et al. (2000). The MCFIRE model simulates the occurrence, behaviour, and effects of severe fire in the DGVM. Due to lack of available data sets, the model has only been tested in a 12.5 Km² study area in the Wind Cave National Park of the Black Hills of South Dakota. Similarly, White et al. (2000) incorporated a simple stochastic fire model into DGVM-HYBRID4.1 (Friend et al., 1997) to estimate the effects of fire on carbon dynamics for 100 plots within a grid square in the boreal needle-leaved forest of southern Quebec. Unfortunately, changes in fire frequency and severity were not explicitly incorporated in the simulations.

(2). A second limitation of DGVMs is that they lack a human disturbance (e.g., land-use) component. Human interference with terrestrial vegetation and biogeochemical cycles is not explicitly included in either SBMs or DGVMs, but is important for understanding of the causes of global climate changes and determining vegetation response. Because human activities are an important

determinant of many land-cover types, they influence climate change through their effects on the distribution of ecosystems and associated energy fluxes (e.g., latent and sensible heat and radiative exchanges) and mass (e.g., water vapour and trace gases) (Leemans and Solomon, 1993; Cramer and Solomon, 1993; Henderson-Sellers, 1994; Ojima et al. 1994; Dale, 1997; Mather et al. 1998). Ecosystem structures that are affected by human activities cannot be described by biogeographical models alone; these models require the inclusion of specific land-use models, which must be derived from ecosystem processes (Tian et al., 1998) and socioeconomic variables such as population growth (Ojima et al., 1994; Alcamo et al. 1998). There is an urgent need to incorporate human-driven land-cover change into DGVMs. Linkage to the land-use change models developed under the *Land-Use and Land-Cover Change* project (Turner, 1994; Turner et al. 1995) or a dynamic land-use module such as in IMAGE2 (Alcamo et al. 1998) is vital important for the development of the next generation of DGVMs. As Dale (1997) pointed out, the big challenge for modelling interactions between the climate change and land-use is the issue of scaling. Because of the large area involved, DGVMs must rely on pixel sizes of a few kilometers or more; but land-use management frequently occurs on a much smaller scale, making the interactions among land-use drivers, topography, and climate change difficult to simulate.

(3). A third limitation of DGVMs is our inability to evaluate the 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 extremely difficult at global scales, due to the long time scale of dynamics, the lack of data at the desired time scales and the uncertainty around effects of human activities (Steffen et al. 1996). However, it is possible to validate the dynamics modules at the smaller scales for which they were designed (Lenihan et al. 1998). We can also test the models in regions where appropriate data sets exist. For example, Pan et al. (2000) reported a test of TEM-DVM against age-dependent growth data from sites of temperate ecosystems across a moisture gradient in North America. The results showed reasonable patterns of vegetation development in sites from the east coast forests to the Midwest grasslands using NPP, foliage projective cover, and vegetation and soil organic carbon. The simulated global vegetation and NPP patterns can be compared to a high resolution global data set of percentage tree cover (Defries et al. 2000) and estimated global NPP (Prince and Goward. 1995) derived from remote sensing data. In addition, palaeo-vegetation data have been used to test equilibrium global vegetation models such as BIOME 1 (Prentice et al., 1992) and may be useful for testing a DGVM because they provide records of past vegetation

change resulting from long-term climatic change at various spatial and temporal scales (Prentice et al. 1996; Guiot et al., 1996; Peng et al. 1998; Prentice and Webb, 1998).

4. SUMMARY

Efforts to develop large-scale static biogeographical models (SBMs) from a continental to a global scale have escalated in recent years. These models have proven to be useful tools in assessing the potential effects of changes in global climate patterns as predicted by general circulation models (GCM) for a doubling of CO₂ scenarios on future vegetation distribution. Moreover, SBMs, which have been used to reconstruct palaeovegetation patterns from palaeoecological data, and further estimate the carbon storage of past terrestrial ecosystems, do have an important role in the study of past global changes. However, the major limitations of SBMs are the equilibrium approach and that they often have been limited to potential natural vegetation. These models do not simulate the 'time course' of vegetation response to rapid climate change; e.g., plant succession and carbon and nitrogen cycling, or the impacts of changes in land-use and natural disturbances (e.g., fire, pest outbreaks, storms) on vegetation dynamics. New generation of SBMs – the prototype of dynamic global vegetation models (DGVMs), which are based on ecophysiological constraints and resource limitations (water and light), may overcome some of the above limitations. They are being coupled with biogeochemical ecosystem models for simulating the responses of ecosystem structure and function to climate change. This paradigm shift in developing DGVMs will rely greatly on the development of parameters for the PFTs provided by large-scale biogeographical models. Validating and capturing disturbance-related effects are major challenges faced by the developers of the next generation of DGVMs. In the coming years, DGVMs that can predict transient changes in vegetation structure and composition, land-use, and consequently direct and indirect vegetation feedbacks to the atmosphere over time and space, will become an important tool for understanding mechanisms of vegetation dynamics and for sustainable management of terrestrial ecosystems.

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Table 1. General comparison of the features for four types of static biogeographical models.

Environmental constraints	HBC	Box's Model	BIOME	RBBM
Bioclimatic Variables				
Air temperature				
Mean (T)			Require	require
Minimum (T_{\min})		require	Require	require
Maximum (T_{\max})		require	Require	require
Biotemperature ^a	require			
Precipitation				
Mean (P)	require	require	require	require
Minimum (P_{\min})		require		
Maximum (P_{\max})		require		
Warmest ($P_{T_{\max}}$)		require		
Growing degree-days				
>5°C			require	
>0°C			require	require
Moisture availability				
P/PET	require	require		
PET/AET				
WUE				require
Vegetation characteristics				
Plant life forms	37 life zones	90 PFTs	17 biomes	35 LTs
Height dominance		require	require	
Leaf area index (LAI)				require
Soil texture			require	

^aBiotemperature is defined as the mean value of all daily mean temperatures above 0°C, divided by 365; WUE is water use efficiency; PFTs are plant functional types; LTs are landcover types; $P_{T_{\max}}$ is mean total precipitation of the warmest month (mm); PET is potential evapotranspiration (mm); AET is actual evapotranspiration (mm); HBC is Holdridge Bioclimtic Classification; RBBM is Rule-Based Biome Model.

Table 2. Vegetation discrimination criteria and ecophysiological processes in the new generation of static biogeography models.

	BIOME 2	MAPSS	DOLY
	Haxeltine and Prentice (1997)	Neilson (1995)	Woodward et al. (1995)
Vegetation definition:			
Evergreen/deciduous	cold tolerance, chilling,	cold tolerance, summer	cold tolerance, low
	annual C balance, drought	drought, summer C balance	temperature limit, drought
Needleleaf/broadleaf	cold tolerance, GDD	cold tolerance, GDD, summer drought	cold tolerance, GDD
Tree/shrub	precipitation seasonality	LAI	NPP, LAI, moisture balance
Woody/non-woody	annual C balance, FPC	understory light	LAI, moisture balance, NPP
C ₃ /C ₄ plant	Temperature	soil temperature	growing season temperature
Continental/maritime	Winter temperature	winter-summer temperature difference	growing season temperature
Ecophysiological process:			
PET/ET	equilibrium	Aerodynamic (Marks 1990)	Penman-Monteith (Monteith 1981)
Stomatal conductance	Implicit via soil water content	soil water potential, VPD	soil water content, VPD, soil nitrogen, photosynthesis
Productivity index	NPP (Faruhaar-Collatz)	leaf area duration	NPP (Farquhar, N uptake) (Farquhar et al. 1980)
LAI/FPC	water balance, temperature	water balance, temperature	water balance, light, nitrogen
Soil water layers	two layers	one layer	three layers

where C is carbon; GDD is growing degree days; LAI is leaf area index; NPP is net primary productivity; FPC is foliar projected cover; PET is potential evapotranspiration; ET is evapotranspiration; VPD is vapour pressure deficit. (Modified from VEMAP Members, 1995)

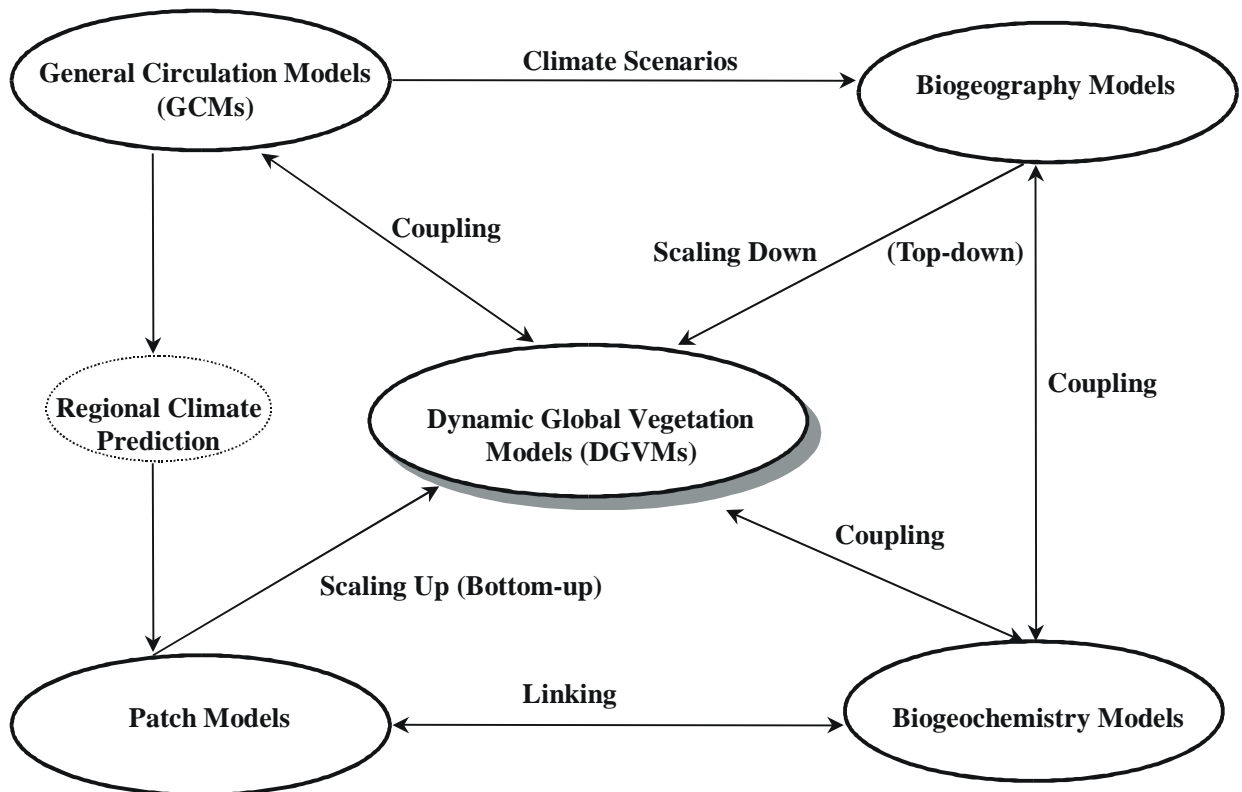


Figure 1: Schematic representation of the potential approaches of the Dynamics Global Vegetation Models (DGVMs) coupling with global circulation, biogeochemistry, biogeography, and patch models.