生物地理模型及其在全球气候变化研究中的应用

BIOGEOGRAPHICAL MODELS AND THEIR APPLICATION TO THE GLOBAL CLIMATE CHANGE STUDIES: A REVIEW *

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摘 要　预测未来的气候变化对自然植被系统的潜在影响需要大尺度的生物地理模型。这些模型常被归纳为两大类:静态和动态模型。本文概述和比较了四种主要类型的静态生物地理模型:(1)气候——植被分类模型;(2)Box 模型;(3)规则基础上(Rule-based)的植被模型;(4)生理生态基础上的生物群区(biome)模型。这 4 种类型的模型已被广泛地用来模拟自然植被生态系统对过去和未来气候变化的可能影响。我们还扼要地讨论了上述模型的适用范围及局限性,并简要介绍了新一代静态生物地理模型的最新发展动态。最后,本文对即将成为未来研究重点的全球动态植被模型的发展进行了讨论。动态植被模型将成为一个评估全球气候变暖对植被动态影响及实现生态系统持续发展的重要工具。

关键词　气候变化,生物地理模型,气候——植被分类模型,Box 模型,生物群区模型,模拟,净初量

ABSTRACT　Predicting the potential impact of future climatic change on natural vegetation requires large—scale biogeographical models. There have been two basic approaches to modelling the vegetation response to changing climates: static (time—independent) or dynamic (time—dependent) biogeographical models. This paper attempts to review and compare four major types of static biogeographical models: (1) climate—vegetation classification model, (2) Box's model, (3) rule—based vegetation model, and (4) ecophysilogical—based biome model. , These models which have been widely used to simulate the potential response of vegetation to past and future climate change. The advantage and disadvantage of these different models approach are discussed.　The recent development of a new generation of

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static biogeographical models is summarized. The potential approaches for global models of vegetation dynamics which will become an important tool for assessing impacts of future climate changes on potential vegetation dynamics and terrestrial carbon storage and for managing terrestrial ecosystem sustainably is outlined.

1　INTRODUCTION

An understanding of past and possible future climate changes will require a clear picture of how vegetation changes in the past and may change in the future (Prentice et al. 1991, Overpeck et al. 1992, Peng et al. 1995a). The distribution of potential terrestrial vegetation is determined not only by direct climatic variables (temperature, moisture, and atmospheric CO_2 concentration), and resources (nutrient availability), but also by environmental gradient (topography and geology) (Woodward 1987, Stephenson 1990, Prentice et al. 1992) (Figure 1). Predicting the potential impacts of future or past climatic change on natural vegetation requires large — scale biogeographical and biogeochemical models (Overpeck et al. 1991, Smith et al. 1992, VEMAP Members 1995). There have been two basic approaches to modelling the vegetation response to changing climates: static (time — independent) or dynamic (time — dependent) biogeographical models (Prentice and Solomon 1990).

The dynamic biogeographical (or gapvegetation) model, which incorporates explicit representation of key ecological process (establishment, tree growth, competition, death, nutrient cycling), has been developed to capture the transient response of vegetation or simple biome to changing climate (Shugart and West 1980, Shugart 1984, Shugart 1990). The first such model was the JABOWA model (Botkin et al. 1972), developed for forests in New England. Over the past twenty years, gap (or path) models have been developed for a wide variety of forest ecosystems including forest — tundra transition zone (Sirois et al. 1994), boreal forest (Leemans and Prentice 1987, Bonan 1989, Prentice and Leemans 1990), temperate forest (Shugart 1984), and tropical forest (Doyle 1981, Shugrat et al. 1981). The general approach has been extended to nonforested ecosystems such as grassland, shrublands and savannas (Coffin and Lauenroth 1989, 1990, 1991). A number of different forest gap models have been used to simulate time — dependent changes in species composition and abundance under changing climate (Solomon 1986, Overpeck et al. 1990, Prentice et al. 1993b, Botkin 1993, Bugmann and Solomon 1995, Sykes and Prentice 1995, Price and Apps 1996, in press). Several obstacles stand in the way of the extensive use of currently available dynamics vegetation models in global change study. 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 silivical characteristics of species than is easily available or even known for some areas of the

globe (Solomon 1986). These ecosystem models are resulted in predictions for region scale or ecosystem, but have not yet been applied at the global scale (Smith *et al* . 1994).

Static biogeographical model assumes equilibrium conditions in both the climate and the terrestrial vegetation and it predicts the distribution of potential vegetation by relation the geographic distribution of climatic parameters to the vegetation. The equilibrium approach is implicitly large scale in nature as it ignore any dynamic processes. It generally requires far less information and provides estimates of potential magnitude of the vegetation response at regional to global scales. Moreover, the restriction of equilibrium models to estimating steady—state conditions matches that of the great majority of the doubled—CO_2 experiment conducted with general circulation model (GCM) (Houghton *et al* . 1990). Over the decadesyears, several different types of static vegetation models (K"ppen 1936, Holdridge 1947, Box 1981, Prentice *et al* . 1992, Neilson *et al* . 1992, Neilson 1995) have been used to explore the role of climate in determining the distribution and structure of vegetation communities, and developed to simulation continental to global scale changes in potential nature vegetation.

In this paper, we focus on the four major types of static biogeographical models which have been widely used to predict the large—scale distribution of vegetation under changing climate conditions. First, we describe the major features and development of biogeographical models. We then summarize the applications of these models to simulatinge the potential response of vegetation to large—scale environment changes and their current limitations. Finally, the recent development of new generation of static biogeographical models and potential approaches for global models of vegetation dynamics are discussed.

2 MODELS

Climate—Vegetation Classification Model

The best—known and simplest method for predicting the equilibrium response of potential vegetation to climate change is the approach of climate—vegetation classification. Global bioclimate classification schemes (Köppen 1936, Holdridge 1947) are essentially climate classification defined by the large—scale pattern of vegetation. Köppen's scheme was intended as a classification of climates, although its boundaries were chosen to coincide approximately with vegetation boundaries and wereare expressed in terms of aspects of climate that are related to plants. The Köppen scheme has recently been improved by Guetter and Kutzbach (1990). One of the most widely used of the bioclimate classification model at a global scale is the model of Holdridge (1947). Here we only take the Holdridge Bioclimatic Classification (HBC) as one example (Fig. 1).

The HBC is a scheme (Table 1) that uses three bioclimatic variables (biotemperature, mean annual precipitations and a ratio of potential evapotranspiration to mean annual precipitation) derived from standard meteorological data to express explicitly the relation of climate patterns and broad—scale vegetation distribution (referred to as life zone). Figure 2 illus-
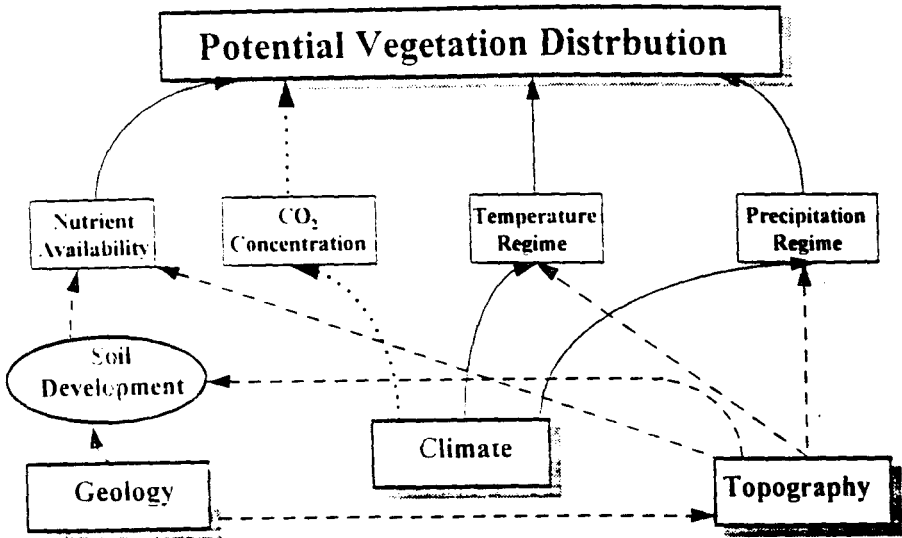
Figure 1: Relationship between climatic variables (temperature, moisture, CO_2 concentration), resource (nutrient availability), environmental gradient (topography and geology), and potential nature vegetation.

trates the Holdridge diagram (Holdridge 1947), which contains 37 named life zones.

The disadvantage of HBC is that the climatic variables may not be the factor to which vegetation is actually responding. Furthermore, a difficulty with zonal concepts like the HBC is that vegetation is defined as an aggregate vegetation type or association. The HBC assume: that the modern vegetation biomes will remain intact and migrate as whole units with th changing patterns of climate. However, terrestrial ecosystems are composed of numerou species which can respond individualistically to changing environmental conditions (Davi 1984, Webb 1987) and whose distribution often cover more then one ecosystem or zone.

The biotemperature is defined as the mean value of all daily mean temperatures abov $0°C$. Biotemperature, which is closely related to the growing degree days (Tuhkanen 1980) gives a measure of heat during the growing season that is likely to be more directly related plant growth than simply mean temperature. The demand of plants for moisture is express through the mean annual precipitation and potential evapotranspiration (PET) ratio. Note th only two primary variables, e. g. , biotemperature and mean annual precipitation are requir to define a location within the life zone triangle.

Figure 2: The Holdridge life zones.

Table 1   General comparison of the features for four types 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[*]	require			
Precipitation				
Mean (P)	require	require	require	require
Minimum (P$_{min}$)		require		
Maximum (P$_{max}$)		require		
Warmest (P$_{Tmax}$)		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			rerequire	

[*] biotemperature defined as the mean value of all daily mean temperature above 0 C. WUE, water use efficiency. PFTs is plant functional types; LTs is landcover types; P$_{Tmax}$ 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.

Box's Model

A unified global expression for the relationship between macroclimte and plant life fo:
was made by Box (1981). To address   many of the shortcoming of the previous Climat
Vegetation Classification modelling studies and overcome the difficulty of exceeding a l
number of plant species potentially occurring in any region, Box defined a number of p
species types (termed *plant life forms*) rather than the small number of vegetation biome
the HBC and lumped all higher plant species into 90 functional plant types as defined by e
climate parameters (Table 1).

Each functional plant type represents a set of plant species (e. g. , tropical evergreen b
—leaf rainforest trees) and is characterized by physiognomic and morphological traits and
response to climate. The climatic factors used in Box's model reflect the plants required co
tions for principal climatic constraints (warmth, frost frequency, and moisture) and inc
some description of seasonal cycle and the phase relationship between seasonal variatior
temperature and precipitation. Moreover, Box's climatic factors differ from Holdridge's in

estimation of drought stress and address seasonally explicit (separately for warmth and moisture). The Box's model describes the distribution of functional plant types in a multi—dimensional climatic space. The defined climatic limits of each functional plant type defines "envelopes" in climate space, within which each functional plant type 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 functional plant types remains essentially correlative, rather than mechanistic. Some of these problems have been overcomed 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 (BIOME, Prentice et al. 1992, MAPSS, Neilson 1995).

Recently, the Equilibrium Vegetation Ecology Model (EVE) of Bergengren and Thompson (1995), which is partially based on the Box scheme, has added a very sophisticated method for determining the relative abundance of functional types in the vegetation communities. The EVE simulates the distribution of plant communities based on the relative adaptiveness and competitive ability of the 110 plant life forms under a given climatic regime. Plant life forms represent aggregations of plant species with similar morphology and growth patterns. In addition, a disturbance algorithm is used to incorporate the dynamic effects of fire on plant communities.

However, the EVE classification still possesses the fundamental flaws of Box's scheme: (1) one cannot identify the real plant species that   belong to each functional type, and hence, cannot determineing if their geography is correct or not. (2) all modelled plant functional types respondse to the same eight environmental variables in the same manner (Solomon, personal, communication).

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 Bbleloch (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 described by Neilson et al. (1989). The rules are essentially if—then—else statements similar to the general comput-

er chart. The most unique feature of the model is the temperature—based definition of season (Table 1). Winter, spring and summer are the principle seasons considered. Temperatur thresholds, input as parameters, were used to define the beginning and ending of the seasons The entire 1211 climatic station networks and their corresponding biome types based on a ma modified from Küchler (1964) and Dice (1943) was used to calibrate the rules for the conte: minous USA. This model is in an early stage of development   model of MAPSS (Neilsc 1995).

Another rule—based Canadian Climate—Vegetation Model (CCVM) has been recent developed by Lenihan and Neilson (1993) for predicting the distribution of vegetation form tion in Canada under current climatic conditions. The CCVM relies on climate parameters wi an inferred mechanistic relationship to the distribution of vegetation. The climatic paramete used as models drivers (e. g. , degree—days, minimum temperature, snowpack, actual evap transpiration and soil moisture deficit) have a more direct influences on the vegetation patter than those commonly used in equilibrium models. Splitting rules in a binary decision tree clas fy the potential vegetation at grid cells in a spatial   distribution database. The rules are criti climatic threshold which physiological constrain the distribution of different vegetation life form. Under current climatic conditions, CCVM predicted the Canadian vegetation with m accuracy than the HBC (Holdridge 1947) and Box's model (1981), and showed a similar le of overall predictive accuracy with the BIOME model of Prentice *et al*. (1992). The CC\ has been further used to predict the potential vegetation patterns of Canada under the two d bled $-CO_2$ climatic scenarios (Lenihan and Neilson 1995).

Ecophysiological—based Biome Model (BIOME)

The BIOME model (Prentice *et al*. 1992) is a ecophysiological—based model for the f damental aspects of structure in terrestrial ecosystem. It predicts the global distribution o: plant functional types based on a set of limiting climatic conditions (Table 1), usually wi spatial resolution of 0. 5 C longitude/latitude. The plant functional types of the highest, p defined dominance values combine with each other to yield the biome type of the grid cell. model distinguishes 17 biome types for global vegetation.

In the BIOME model (Table 1), the plant functional types are assigned climate tolera in terms of amplitude and seasonality of climate variables. The cold tolerance of plant typ given in terms of minimum mean temperature of the coldest month (T_{min}). Some plant t also have chilling requirements expressed in terms of a maximum mean temperature of coldest month. The heart requirement of plant types is given in terms of annual accumu temperature over 5 C (a threshold of 0 C used for some plant functional types). The hea quirement of some shrub types is presented by mean temperature of the warmest m (T_{max}). The mean moisture availability is defined as a ratio of actual evapotranspir (AET), and potential evapotranspiration (PET) which basically depends on net—radiati Like the Box's model, the BIOME model (Table 1) is based on a set of plant funct

types, with each plant 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 plant functional type are expressed in terms of fundamental phenomenological constraints, rather than observed correlations between vegetation and climate. Some ideals of Woodward (1987) about the physiological and ecological mechanisms for the climatic limitation of plant functional types are presented by the BIOME model. Biomes are not taken as given as, for instance, in 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 CO_2 direct effects on vegetation are not considered.

3˙ MODEL APPLICATIONS

Application of Biogeographical Model to Global Change Studies:

The biogeographical models (BM) have a history of application in simulating the global distribution of natural vegetation under altered climate condition, both past climatic conditions associated with the Last Glacial Maximum (LGM) (Hansen *et al*. 1984, Prentice and Fung 1990, Guetter and Kutzbach 1990, Prentice *et al*. 1993a, Esser and Lautenschlager 1993, Friedlingstein *et al*. 1995) and predictions of future climate patterns under doubled—CO_2 scenarios (Emanuel *et al*. 1985, Prentice and Fung 1990, Leemans 1992, Smith *et al*. 1992, 1993). The BM model has 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 changed climate condition (Prentice and Fung 1990, Smith *et al*. 1993). Here we concentrate on the following three aspects of applications.

(1) Coupling BM 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), which interact in a complex nonlinear way at a wide rage—of—time scale. The interaction integration of biosphere and atmosphere has been studied intensively by coupling the BM with General Circulation Model (GCM) (Henderson—Sellers 1991, 1993, Claussen 1994, Ciret and Henderson—Sellers 1995). There are the Simple Biosphere models (SiB) of Sellers *et al*. (1986), and the Biosphere—Atmosphere Transfer Scheme (BATS) of Dickinson *et al*. (1986, 1993) which have been incorporated into the GCM. Recently, there is an increasing interest in coupling of so—called vegetation models to the simulated climate predicted by GCM. The global vegetation classification have been used to compute distribution of global vegetation, and potential vegetation shift due to a possible greenhouse gas induceds climate warming from climate simulation in a diagnostic model (E

mauel et al. 1985, Prentice and Fung 1990, Henderson—Sellers 1991, Claussen and Eschand Esch 1994).

Perhaps the first attempt to incorporate continental vegetation as a dynamics component of global climate models was reported by Henderson—Sellers (1993). In this study, a simple Holdridge classification was used and the results indicated that the vegetation scheme was to be a stable component of the global climate system without any discernible trends being observed over the integration period. Differences between simulation with and without interactive vegetation turned out to be rather small. However, Henderson—Sellers (1993) did not study the problem of coupling vegetation with climate models in great detail. More recently, Claussen (1994) has coupled the BIOME model of Prentice et al. (1992) with the ECHAM climate model of the Max—Planck—institut fur Meterologie, Hamburg, Germany. He suggested that a biome model should be coupled with a climate in the following two ways: (1) the climate models should be integrated over several years: (2) a biome distribution should be computed from the corresponding multi—year simulated climatology. Similarly, the results of sensitivity analysis by Ciret and Henderson—Sellers (1995) suggested that the correct time step and time scale to employ is very important for coupling of vegetation models into GCM. To date there has been little attempt to compare the vegetation simulated by GCM with the nature vegetation distribution based on observation.

(2) Coupling BM with Ecosystem Model

Several ecophysiological—based ecosystem process models have been developed and are being used to examine potential effects of both increasing atmospheric CO_2 and the associated prediction of climate change on patterns of net primary productivity and biogeochemical cycles (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, Leke et al. 1994, DEMETER, Foley 1994a, 1995). These models simulate some of the ecosystem processes including 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 C and N dynamics in these models allows them to simulate the short—term changes in net C flux for a given location, providing estimates of change in net primary productivity (NPP) under changing climate conditions. However, they are unable 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) predict the major directions in potential biome redistribution after climate change. The dynamics of ecosystem under changing boundary conditions are a function of their structure, and this structure may also change due to differentce biogeochemical processes. Therefore, coupling the BM model (model of ecosystem structure) with the biogeochemical ecosystem processes (model of ecosystem function) is the first step of the development towards dynamics global vegetation models, which could capture the transient dynamics of biosphere in a changing climate.

Recently, a general terrestrial biosphere model named DEMETER (Dynamic and Ener-

getic Models of Earth's Terrestrial Ecosystem and Resources) has been developed by Foley (1994a, 1995) for this purpose. (Fig. 2). On coupling a simple biome model with biogeochemical ecosystem processes, DEMETER is designed to provide a comprehensive, global — scale view of the terrestrial biosphere, including both a structure (predicted potential vegetation) and functional (primary production and carbon storage) perspective. It has been used to predict the potential vegetation patterns, NPP and global carbon storage in vegetation and soil (Foley 1994a,b, 1995). The results show a good agreement between the simulation and the available observations. Plöchl et al. (1995) have coupled an ecosystem structure model (BIOME, Prentice et al. 1992) with a biogeochemical ecosystem process model of the Fankfurt Biosphere Model (FBM) (Lüdeke et ai. 1994). The application of the coupled models under a GCM based scenario of changing temperature and precipitation results in major changes of the biome boundaries at these high latitudes (such as arctic and boreal ecosystems).

More recently, the VEMAP (Vegetation Ecosystem Modeling and Analysis Project) (VEMAP Members 1995) has coupled the three biogeographical models (BIOME2, Haxeltine and Prentice 1995, DOLY, Woodward et al. 1995, and MAPSS, Neilson 1995) with three biogeochemical ecosystem process models (BIOME — BGC, Running and Gower 1991, CENTURY, Parton et al. 1987, 1993, and 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 — CO_2. The VEMAP study is limited by the models that only made projection about equilibrium conditions; however, it provides a first necessary framework for coupling the large — scale biogeograpogic models with biogeochemical models.

(3)   Application of BM to reconstruction of paleovegetation patterns and paleo — carbon storage

On the one hand, the BM model (such as BIOME model) provides the tool required to translate past climate simulation into simulated paleovegetation patterns, allowing more detailed comparison with reconstructed past vegetation from paleodata, and further estimation of carbon storage of the past terrestrial. 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).

On the other hand, the global BIOME model of Prentice et al. (1992) has been successfully used to reconstruct the paleovegetation from the pollen data in Europe at 6000 yr BP (Prentice et al. 1996, Guiot et ai. 1996) and since last 13,000 yr BP (Peng et ai. 1995a).

Prentice et al. (1996) have developed a method of 'biomization' to attribute a biome to each pollen assemblage. Each pollen taxon is assigned to one of the plant functional types such as defined in the BIOME model (Prentice et al. 1992). A likelihood index is calculated for each plant functional type and translated in terms of biome according to the combinations defined for the BIOME model. Finally for each biome, we obtain an index defined as the sum of percentage square root of all the taxa potentially present in the biome. These indices are compared and the biome for which the index is maximum is attributed to the spectrum. The method was validated by application to a set of more 2000 surface pollen spectra (representing

contemporary vegetation), then applied to a set of more 200 pollen spectra representing mid-Holocene (about 6000 yr BP).

Using the new 'biomization' method of Prentice *et al* . (1996), Peng *et al* . (1995a) hav reconstructed the temporal and spatial shifts of terrestrial biomes from the pollen data in Et rope since last 13,000 yr BP. The distribution of biomes reconstructed from pollen   agree well   with results obtained from the modern climate using the BIOME model Prentice *et al* . (1992). These pollen—based biome reconstructions then were used to transla directly into the climate parameters needed for calculating the vegetation and the soil carb storage considering a good correspondence between climate and biome.

Shifts in the distribution of terrestrial vegetation are accompanied by changes in the rel tive carbon storage on land. Usually, the use of BM to estimate terrestrial carbon budget is two step process, because   the models do not directly simulate carbon pools and fluxe The models are used to define potential patterns of vegetation and associated soil propert based on simple climate indices. Traditionally, the calculation of carbon pools are done by m tiplying the area extent of each cover type (e. g. , vegetation type, ecosystem type, biome, life zone) by estimates of carbon densities in vegetation and soils (Adams *et al* . 1990, Prent and Fung 1990, Smith *et al* . 1992, Prentice *et al* . 1993a). Generally these estimate are sc ly dependent on the vegetation or biome type and do not vary geographically within any (type (e. g. all tropical rain forests have the same value). The results are likely a rough appr imation of reality, and can be improved by the use of process—based ecosystem models (Ra *et al* . 1991, Potter *et al* . 1993, Melillo *et al* . 1993, Parton *et al* . 1987, 1993), which s ulate patterns of net primary productivity and carbon dynamics for a given vegetation and mate. However, these models usually need to be parameterized by a large number of envir mental inputs, which are not often available from paleodata. An alternative method is the of an empirical biospheric model, such as the Osnabrück Biosphere Model (OBM) (E 1987, 1991) and statistic models (Peng *et al* . 1995a,b).   These models which need as ir only three environmental parameters, which are easily derivable from paleodata or from G simulations. Moreover, it improves estimations of carbon density of the various ecosyste For these reasons, it has been widely used to estimate past terrestrial carbon dynamics ir sponse to past climatic changes (Peng *et al* . 1994, Peng *et al* . 1995a,b,c, Esser and Lau schlager 1993)

4 Current MODEL LIMITATIONS

The scientific questions relating to the potential response of terrestrial vegetation to g climate change create arise new problems for the development and application of large— biogeographical models (BM). The following points reflect the major current limitations c model and need to further overcome them.

(1) The static biogeography model cannot simulate the 'time course' of veget changes during a period of rapid climate change. This is a limitation of all static biogeogra

models when applied to conditions when the rate of change vegetation response. Because they do not incorporate migrational or successional processes (Prentice and Solomon 1990). Dynamic (transient) vegetation models must represent many more processes explicitly. and development of global vegetation dynamics models will be a new challenge. However, the static biogeography model can be used to indicate probable trajectories of vegetation change and provide a necessary framework for modelling of dynamic vegetation process at a global scale (Prentice *et al*. 1992).

(2) Climate — Vegetation Classification models (e. g. , HBC) usually predict the distribution of physiognomic units (e. g. , major vegetation formation. plant functional type. or life zone) at high — levels in the organization of vegetation. The use of these models in global change studies has been criticized by Davis (1989) and Graham and Grimm (1990) for ignoring the individualistic response of species to climate change observed in the fossil records (Webb 1987). Modelling the individualistic response of species is an important approach to understanding the vegetation response to changing climate (Lenihan and Neilson 1993). However. for purposes of linking the vegetation models to climatic models such as GCM, and of coupling it 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 interactions with the atmosphere.

(3) The BM often have been limited to potential natural vegetation. Land use changes modify ecosystem properties more rapidly than would naturally occur (Ojima *et al*. 1994). There is a convincing body of data about the potential distribution of anthropogenically derived ecosystems. such as agronomic and forest crops. as a function of bioclimatic constraints. This type of information can be embedded into a predictive models of potential natural vegetation. thereby giving the potential for land use as well (Leemans and Solomon 1993. Cramer and Solomon 1993). Although Eecosystems structures   which are affected by human effects cannot be described by biogeographical models alone.   these models require the inclusion of a specific land — use models. which must be derived from. socioeconomic variables such as population growth (Ojima *et al*. 1994).

(4) Another current limitation for most of these models is that they do not incorporate biogeochemical processes, especially carbon and nitrogen cycling. Therefore. one major problem in application of these models to simulating the potential response of vegetation to a doubled — CO_2 climatic change is their inability to address the direct response of CO_2 on vegetation (Norby *et al*. 1992. Mooney *et al*. 1991). The more recent achievement of incorporating the effects of CO_2 on the NPP. the leaf — area — index (LAI). the water balance. and competitive between C_3 and C_4 plants (Haxeltine and Prentice 1995. Neilson 1995. Woodward *et al*. 1995) seems to provide a promising direction.

5   **RECENT DEVELOPMENT**

To overcome the limitation of BM described above. the new generation of biogeograph y models. which predict the dominance of various plant life forms in different environments.

used, and these models are being to couple with biogeochemical ecosystem models for simulat
ing the terrestrial ecosystem response to climate change and doubled—CO_2 (VEMAP Member
1995). We highlight here the major features of three new biogergraphy models: BIOME
(Haxeltine and Prentice 1995), MAPSS (Neilson 1995) and DOLY (Woodward et al
1995), which were used by VEMAP study (VEMAP Members 1995). The vegetation di:
crimination criteria and ecophysiological process for these models are showed in Table 2.

Table 2 Vegetation discrimination criteria and ecophysiological
process in the new generation of static biogeogahy models

	BIOM 2	MAPSS	DOLY
	Haxeltine and Prentice (1995)	Neilson (1995)	Woodward et al . (1995)
Vegetation Definition:			
Evergreen/deciduous	cold tolerance, chilling, annual C balance, drought	cold tolerance, summer drought, summer C balance	cold tolerance, low temperature limit, drought
Needleal/broadleaf	cold tolerance, GDD	cold tolerance, GDD, summer drought	cold tolerance, GDD
Tree/shrub	precipitation seasonality	LAI	NPP, LAI, moisture balance
Wood/non—woody	annual C balance, FPC	understory light	LAI, moisture balance, NPF
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)	Peman—Montieth (Monteith 1981)
Stomatal conductance	implicit via soil water content	soil water potential, VPD	soil water content, VPD, sc nitrogen, photosynthesis
Productivity index	NPP (Faruhar—Collatz)	leaf area duration	NPP (Farquhar, N uptake
LAI/FPC	water balance, temperature	water balance, temperature	water balance, light, nitrog
Soil water layers	two layers	one layer	three layers

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 vapor pressure deficit. (source: modified fron
VEMAP Members 1995)

BIOME2: BIOME2 (a new version of the BIOME model) has been developed by Ha
tine and Prentice (1995). In BIOME2, ecophysilogical constraints, which are based largel:
the BIOME model of Prentice et al . (1992), are applied first to select which plant functi
types can occur in a given set of climatic conditions. The model then identifies the quantit:
combination of plant functional types that maximizes whole ecosystem NPP. Gross Prir
Production (GPP) is calculated on a monthly times step as a linear function of absorbed ph
synthetically active radiation and is reduced by limitation of moisture and low temperat
Plant respiration is simply estimated as 50% of the non—water—limited GPP. A two—l
hydrology model with a daily time step allows simulation of the competitive balance bet
woody vegetation and grass, including the effects of soil texture, based on the differen
rooting depth. The prescribed CO_2 concentration has a direct effects on GPP through the
tosynthesis algorithm, and affects the competitive balance between C_3 and C_4 plants.

MAPSS: A new biogeographical model. Mapped Atmosphere — Plant — Soil System (MAPSS), has been recently developed by Neilson (1995) to predict changes in vegetation LAI, site water balance and runoff, as well as changes in biome boundaries. The MAPSS combines a process — based water balance model with a physiologically conceived rule — based model of Neilson *et al*. (1992) to simulate both water and thermal balance constraints on vegetation life — form (e. g., tree, shrub, or grass: evergreen or deciduous: broadleaf or needlleaf) and biome physiognomy (e. g., forest, savanna, or shrub—steppe).

A two—layer hydrology module with a monthly time step then allows simulation of leaf phenology, LAI and the competitive balance between grass and woody vegetation. A productivity index, derived frc m leaf area duration and AET, is used to assist in the determination of leaf form, phonology, and vegetation type. Stomatal conductance is explicitly included in the water balance calculation and water competition occurs between the woody and grass life—forms through different canopy conductance characteristics as well as rooting depths. The direct effect of CO_2 on the water balance is simulated by reducing maximum stomatal conductance. Presently, only a simple fire model has been incorporated in shrub and tree savanna systems. Biotic interactions, such as grass—tree competition, can alter the state of the ecosystem and have also been incorporated in the MAPSS. However, there is no representation of effects CO_2 on the competition of C_3 and C_4 plant.

DOLY: Based on the Farquhar *et al*. (1980) and Penman—Monteith (Montheith 1981) models, the Dynamic Global Phytogeography Model (DOLY) (Woodward *et al*. 1995) simulates photosynthesis and AET at a daily time step. Maximum assimilation and respiration rates are calculated as a function of temperature and nitrogen. The effects of CO_2 concentration on NPP and AET are modelled explicitly. The maximum sustainable LAI for a location is estimated from long — term average annual carbon and hydrologic budgets, as the highest LAI that is consistent with maintaining the soil water balance. DOLY used an empirical statistical procedure, implemented after the biogeochemical process calculations, to derive the vegetation. This procedure takes account of both ecophysiological constraints and resource limitation effects, based on their observed outcome ,in a range of present climate.   Estimates of NPP, LAI, AET, and PET are combined with bioclimatic variables (absolute minimum temperature, growing degree days, annual precipitation) and a previously defined vegetation classification to develop a biogeographhy model using multiple discriminate function analysis, as in work by Rizzo and Wiken (1992). Increasing CO_2 reduces stomatal conductance and increases NPP, but does not affect the competition of C_3 and C_4 plant.

6 FUTURE RESEARCH

One of the high priority activities of the International Geosphere — Biosphere Programme

features of the DGVM are that (1) it is able to predict the transient changes in the vegetation
structure and function, changes in land use, and consequent changes in direct and indirect
feedbacks to the atmosphere over time and space, and (2) it could provide predictions of
variable   which link the land surface to the atmosphere while being responsive to the atmospheric changes predicted by the GCM.

Currently, there are no global—scale biogeography models available that simulate both the
distribution of plant life form and biogeochemical cycle (e. g. carbon and nitrogen) in response
to changing environmental conditions. Large—scale simulations of vegetation dynamics could be
generated by deriving very large sets of patch models solution. The primary framework for
DGVM has been outlined by Prentice et al. (1989). The potential approaches for DGVM
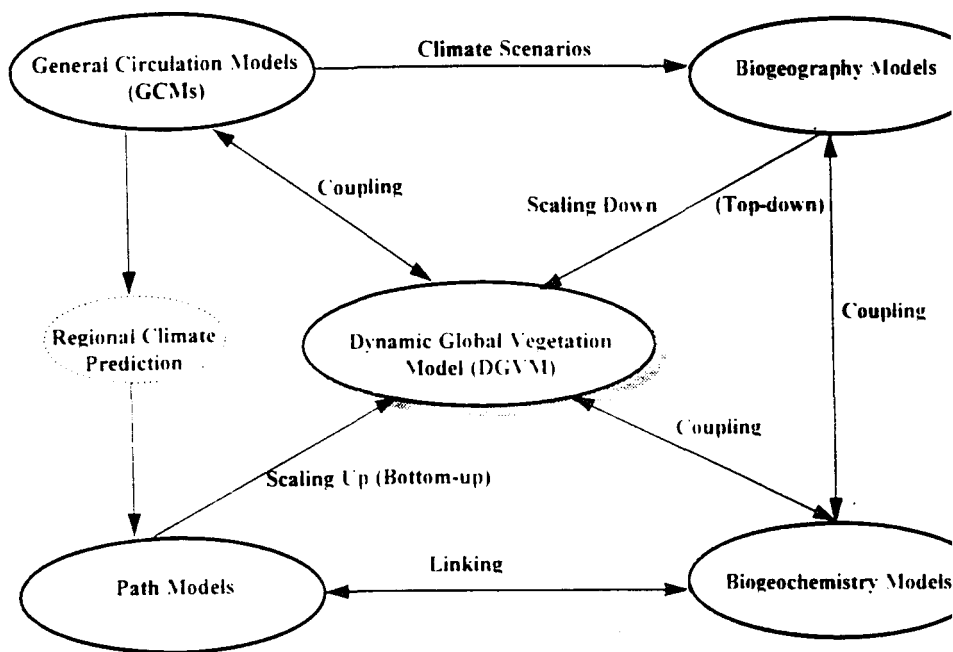model development are summarized in Figure 3.

Figure 3: Schematic representation of the potential approaches
of the Dynamics Models of Global Vegetation (DGVM) coupling with GCMs,
biogeochemistry, biogeography, and patch models.

(1) Bottom—up: The approach involves the scaling—up of path models using a statistical
sampling procedure to provide regional and global cover. This approach would require a generalized path model, which is able to simulate the dynamics of all biome types (e. g. tundra, boreal forest, temperature grassland, tropical rain forest, tropical savanna). This general

path model would use a plant functional types rather than addressing species composition. to provide temporal patterns of plant growth and biogeochemical cycling.

(2) Top—down: The second approach is to use the current static (equilibrium) biogeographical models which relates the large—scale patterns of climate and vegetation (HBC, Holdridge 1947. BIOME, Prentice *et al*. 1992). The top—down approach of DGVM development would modify these global vegetation models by defining the plant functional types which make up each of the ecosystem or biome currently used to describe vegetation pattern/composition within global models. These plant functional types would then be assigned parameters relating to rates of growth. mortality. dispersal and other process, which influence the transition dynamics of vegetation in response to changing environmental conditions.

(3) Linking path models with ecosystem models of biogeochemical processes: pPath models have been linked with biogeochemical models that simulate the dynamics of carbon. nitrogen, hydrologic cycles and fire disturbance (Price *et al*. 1996). The ecosystem models require information on 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 path model. In return, the biogeochemical model provides a description of certain environmental conditions on the path, such as NPP, the availability of nitrogen, soil carbon and moisture.

(4) Coupling BM and DGVM models with process — based biogeochemical models: mMany currently available biogeochemical ecosystem process models are able to capture the essential process of trace gas fluxes between atmosphere and ecosystems, as well as the associated changes in net primary productivity. When used in changing climate conditions. one of the most serious limitations of these models is due to the fact that the structure of the ecosystem itself is prescribed from a global database. Significant shifts of the major global vegetation types of global 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. A continental—scale coupling of three biogeographical models (e. g. , BIOME2, MAPSS, and DOLY) with the three biogeochemical models (e. g. BIOME—BGC, CENTURY, and TEM) has been recently carried out by VEMAP study. However, an important limitation of the VEMAP analysis is that the models only make projections about equilibrium conditions (VEMAP Member 1995).

(5) Coupling DGVM with GCM: The DGVM ultimately should be able to be coupled to the GCM. Since no DGVM exist at the present, consequently, the previous coupling of the GCM with vegetation experiments is limited by equilibrium with climate (Henderson—Sellers 1993. Claussen and Esch 1994. Ciret and Henderson—Sellers *et al*. 1995). By aggregating the individual path models to the regional level, the DGVM will link to the GCM made through a nested mesoscale model and a soil — vegetation — atmosphere — transfer (SVAT) model, which involves instantaneous fluxes of water vapor, heat and momentum. These models are being developed in response to needs by specifying 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 to biosphere modelling. They have constructed the SVAT that

simulated photosynthesis, respiration and canopy conductance and have coupled it to the GCM for investigating the short—term biogeochemical and biophysical interaction between the atmosphere and terrestrial biosphere. We expect a model of SVAT on time scales of 10—1000 years that includes all the critical ecosystem processes—physical, chemical and biological operating on this time scale

7 SUMMARY

Many efforts have made to develop the large—scale static biogeographical model (BM) in recent years. Generally speaking, there are four classes of static biogeographical models which have been developed to simulate the distribution of potential vegetation f. rom a continental to global scale. The simplest model is the Climate—Vegetation Classification Model (Köppe 1936, Holdridge 1947) based on correlations between potential vegetation distribution and climate. The second type of static biogeographical model is the Box's Model (Box 1981), based on correlations between the distribution of plant life forms and climate variables that describe the seasonality of climate. The Equilibrium Vegetation Ecology Model (EVE) of Bergengre and Thompson (1995) has revised the Box's Model to include the competition and fire disturbance between life forms. A third class of models is a rule—based biome model (RBBM that was constructed as a set of rules—based on mechanistic and conceptual models of biome distribution described by Neilson *et al* . (1992) and developed recently by MAPSS model (Neilson 1995). The fourth class of models is an ecophysilogical—based BIOME model (Prentice *et al* . 1992) which is being developed by incorporating the ecophysiological mechanisms that control the distribution of plant functional types (BIOME 2, Haxeltine and Prent 1995, DOLY, Woodward *et al* . 1995).

These biogeographical models (BM) have proven useful tools in assessing the potential impacts on future vegetation distribution resulting from changes in global climate patterns as predicted by general circulation models (GCM) for a doubling of CO_2. Moreover, BM, which been used to reconstruct the paleovegetation patterns from paleodata and further estimate carbon storage of *past* terrestrial, do have an important role in the study of the past global changes.

However, the major limitations of BM are equilibrium approached and often have b limited to potential natural vegetation. The model does not simulate the 'time course' of vetation response to a rapid climate change, including plant succession and carbon and nitro cycling. The new generation of BM, based on ecophysiological constrains and resource limitation (water and light), may overcome part of the above limitations, and are being to cou with biogeochemical ecosystem models for simulating the responses of ecosystem structure function to climate change.

The future development of DGVM will rely greatly not only on path dynamics model but also on the development of parameters for the plant functional types provided by the large—scale biogeographical models. It is expected that during the coming years the DGVM, wi

can predict   transient changes in vegetation structure and composition, in land — use, and consequently in direct and indirect feedbacks to the atmosphere over time and space, will become an important tool for understanding mechanisms of vegetation dynamics and for sustainably managing terrestrial ecosystem.

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LITERATURE CITED

Adams, j. M., Faure, H., Faure — Denard, L., McGlade, J. M. and F. I. Woodward. (1990). Increases in terrestrial carbon storage from the Last Glacial Maximum to the present. Nature 348: 711 — 714.

Bergengren, J. and S. L. Thomposon. 1995. EVE: An equilibrium vegetation ecology model. (in preparation)

Bonan, G. 1989. A computer model of the solar radiation, soil moisture, and soil thermal regimes in boreal forest. Ecological Modelling 45: 275 — 306.

Bonan, G. 1994. Comparisons of two land surface processes models using prescribed forcing. J. Geophys. Res. 99: 25803 — 25818.

Botkin, D. B., Janak, J. S. and J. R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. Journal Ecology 60: 849 — 872.

Botkin, D. B. 1993. Forest Dynamics: An ecological model. Oxford University Press, Oxford, U. K.

Bolin, B. 1984. Biogeochemical processes and climate modelling. Pages 213 — 223 in J. T. Houghton, editor. The Global Climate. Cambridge University Press, Cambridge, UK.

Box, E. O. 1981. Macroclimate and plant forms: an introduction to predictive modelling in phytogeography. Junk. The Hague.

Bugmann, H. K. M. and A. M. Solomon. 1995. The use of a European forest model in North America: a study of ecosystem response to climate gradients. Journal Biogeography 22: 477 — 484.

Ciret, C. and A. Henderson — Sellers. 1995. Static vegetation and dynamic globe climate: preliminary analysis of the issues time steppes and time scales. Journal Biogeography 22: 843 — 856.

Claussen, M. 1994. On coupling global biome models with climate models. Climate Research 4: 203 — 221.

Claussen, M. and M. Esch. 1994. Biomes computed form simulated climatologies. Climate Dynamics 9: 235 — 213.

Coffin, D. P. and W. K. Lauenroth. 1989. Disturbances size and gap dynamics in a semiarid grassland: A landscape—level approach. Landscape Ecology 3: 19—27.

Coffin, D. P. and W. K. Lauenroth. 1990. A gap dynamics simulation models of succession in the shortgrass steppe. Ecological Modelling 49: 229—266.

Coffin, D. P. and W. K. Lauenroth. 1994. Successional dynamics of a semiarid grassland: Effects of soil texture and disturbance size. Vegetatio 110: 67—82.

Cramer, W. and A. M. Solomon. 1993. Climate classification and future distribution of global agriculture land. Climate Research 3: 97—110.

Davis, M. B. 1984. Climatic instability, time lags, and community disequilibrium. Pages 269 —284 in I. Diamond and T. J. Case, editors. Community Ecology. Harper and Row, New York, USA.

Davis, M. B. 1989. Insights from paleoecology on global change. Bull. Ecol. SoC. Am. 70: 222—228.

Dice, L. R. 1943. The biotic provinces of North America. University of Michigan Press, Ann Arbor, MI, USA, 1—79.

Dickinson, R. E., A. Henderson—Sellers, P. J. Kennedy and M. F. Wilson. 1986. Biosphere—Atmosphere Transfer Scheme (BATS) for NCAR community climate model. NCAR Technical Note, NCAR—TN—275, Boulder, ColoradoUSA.

Dickinson, R. E., A. Henderson—Sellers, P. J. Kennedy and F. Giorgi. 1993. Biosphere—atmosphere Transfer Scheme (BATS) version 1. 0 as coupled to the NCAR community climate model. NCAR Technical Note, NCAR—TN—387, Boulder, USA.

Doyle, T. W. 1981. The role of disturbance in the gap dynamics of a mountain rain forest: An application of tropical forest succession model. Pages 56—73 in D. C. West, H. H. Shugart, and D. B. Botkin, editors. Forest Succession: Concepts and Application. Springer, New York, USA.

Emanuel, W. R., Shugart, H. H. and M. P. Stevenson. 1985. Climate change and the broad —scale distribution of terrestrial ecosystem complexes. Climatic Change 7: 29—43.

Esser, G. 1987. Sensitivity of global carbon pools and fluxes to human and potential climatic impacts. Tellus 39B: 245—260.

Esser, G. 1991. Osnabrück Biosphere Model: structure, construction, results. Pages 679—709 in G. Esser and D. Overdick, editors. Modern Ecology: Basic and Applied Aspects. Elsevier Amsterdam, Lodon, New York, Tokyo.

Esser, G., and M. Lautenschlager. 1993. Estimating the change of carbon in the terrestrial biosphere from 18,000 BP to present using a carbon cycle model. Environmental Pollution 83: 45—53.

Farquhar, G. D., S. Von Caemmerer and J. A. Berry 1980. A biogoechemical model of photosynthetic CO_2 assimilation in leaves of C3 species. Planta 149: 78—90.

Foley, J. A. 1994a. Net primary productivity in the terrestrial biosphere: The application of a global model. J. Geophys. Res., 99, 20773—20783.

Foley, J. A. 1994b. The sensitivity of ecosystems to climatic change: A simulating the terres-

trial biosphere of the mid—Holocene. Global Biogeochemical Cycles 8: 505—525.

Foley, J. A. 1995. An equilibrium model of the terrestrial carbon budget. Tellus 47: 310—319.

Friedlingstein, C. Prentice, K. C. Fung, I. Y., John, J. G. and G. P. Brasseur. 1995. Carbon—biosphere—climate interaction in the last glacial maximum climate. J. Geophys. Res. 100: 7203—7221.

Graham, R. W and E. C. Grimm. 1990. Effects of global climate change on thepatters of terrestrial biological communities. Trends in Ecol. Evol. 5: 289—292.

Guetter, P. J. and J. E. Kutzbach. 1990. A modified Köppen classification applied to model simulations of glacial and interglacial climate. Climatic Change 16: 193—215.

Guiot, J. R. Cheddadi, I. C. Prentice and D. Jolly. 1996. A method of biome and land surface mapping from pollen data: Application to Europe 6000 years ago. Palaeoclimates 1: 311—324.

Hansen, J., A. Lacis, D. Rind, G. Russell, P. Stone, I. Fung, R. Ruedy, and J. Lerner. 1984. Climate sensitivity: analysis of feedback mechanisms. Pages 130—163 in J. Hamsen and T. Takahashi, editors. Climate Sensitivity. American Goephysical Union, Washington, D. C. USA.

Haxeltine, A. and I. C. Prentice 1995. A general models for the light—use efficiency of primary prediction. Funct. Ecol. (in press).

Haxeltine, A., I. C. Prentice and I. D. Cresswell. 1995. A coupled carbon and water flux model to predict vegetation structure. J. Veg. Sci. (in press).

Henderson—Sellers, A. 1990. Predicting generalized ecosystem group with the NCAR CCM: first steps towards an interactive biosphere. Journal of Climate 3: 917—940.

Henderson—Sellers, A. 1991. Developing an interactive biosphere for global climate models. Vegetatio 91: 149—166.

Henderson—Sellers, A. 1993. Continental vegetation as a dynamic component of a global climate models: a preliminary assessment. Climatic Change 23: 337—377.

Henderson—Sellers, A. and K. McGuffie. 1994. Landsurface characterization in greenhouse climate simulations. International Journal of Climatology (in press) Holdridge, L. R. 1947. Determination of world plant formations from simple climate data. Science 105: 367—368.

Houghton, J. T., Jenkins G. and J. J. Epharams. 1990. Climate Change: IPCC Scientific Assessment. Cambridge University Press, New York.

Javis, P. G. and K. G. McNaughton. 1986. Stomatal control of transpiration: Scaling up from leaf to region. Adv. Ecol. Res. 15: 1—49.

Köppen, W. 1936. Das geographisches system der klimate, in W. Köppen W. and R. Geiger R, editors. Handbuch der Klimatologie, Gerbruder Borntraeger, Berlin.

Küchler, A. W. 1964. The potential nature vegetation of the conterminous United States. Am. Geo. Soc. Special Publication No. 36.

Leemans, R. and I. C. Prentice 1987. Description and simulation of tree—layer composition

and size distribution in a primaeval Picea—Pinus forest. Vegetatio 69: 147—156

Leemans, R. 1992. Modelling ecological and agricultural impacts of global changes on a : scale. Journal of Scientific and Industrial Research 51: 709—724.

Leemans, R. and A. M Solomon, 1993. The potential change in yield and distribution (earth's crops under a warmed climate. Climate Research 3: 79—96.

Lenihan, J. M. and R. P. Neilson. 1993. A rule—based formation model for Canada. Jc of Biogeography. 20: 615—628.

Lenihan, J. M. and R. P. Neilson. 1995. Canadian vegetation sensitivity to projected cli change at three organizational levels. Climatic Change 30: 27—56.

Lüdeke, M. K. B. , F. W. Badeck, R. D. Otto, C. Häger, S. Döngers, J. Kindermann Würth, T. Lang, U. Jäkel, A. Klaudius, P. Ramge, A. Habermehl, and (Kohlmaier. 1994. The Frankurt Biosphere Model: A global process oriented mod the seasonal and long—term CO_2 exchange between terrestrial ecosystems and the : sphere. Climate Research 4: 143—166.

Marks, D. 1990. The sensitivity of potential evapotraspiration to climate change over the tinental United State. Page 20—31 in H. Gucinski, D. Marks and D. P. Turner tors. Biospheric Feedbacks to Climate Change: The Sensitivity of regional trace gas sions, evapotraspiration, and energy balance to vegetation redistribution. EPA/60(90/078, Corvaillis, USA.

Melillo, J. M. , A. D. McGuire, D. W. Kicklighter, B. Moore III, C. J. Vorosmarty A. L. Schloss. 1993. Global climate change and terrestrial net primary production. ture 363: 234—240.

Mooney, H. A. , B. G. Drake, R. L. Luxmoore, W. C. Oechel, and L. F. Pitelka. Predicting Ecosystem Response to Elevated CO_2 Concentrations. BioScience 41: 104.

Monteith, J. L. 1981. Evaporation and surface temperature. Q. J. R. Meteorol. Soc. 1C 27.

Neilson, R. P. 1986. High—resolution climatic analysis and southwest biogeography. S 232: 27—34.

Monteith, J. L. 1987. Biotic regionalization and climatic controls in west North Am Vegetatio 70: 135—147.

Monteith, J. L. 1993. Vegetation redistribution: A possible biosphere source of CO_2 c climatic change. Water, Air, Soil Pollution 70: 659—673.

Monteith, J. L. 1995. A model for predicting continental—scale vegetation distributio water balance. Ecology Application 5: 362—385.

Neilson, R. P. , G. A. King, R. L. DeVelice, J. Lenihan, D. Marks, J. Dolph, B. Ca and G. Dlick. 1989. Sensitivity of ecological landscapes and regions to global cl change. U. S. Environmental Protection Agency, Environmental Research Labora EPA 600/3—89—073, Corvallis, USA.

Neilson, R. P. , G. A. King and G. Koerper. 1992. Toward a rule—based biome m

Landscape Ecology 7: 27 – 43.

Norby, R. J., C. A. Gunderson, S. D. Wullschleger, E. G. O'Neill, M. K. McCracken. 1992. Productivity and compensatory response of yellow – poplar trees in elevated CO_2. Nature 357: 322 – 324.

Ojima, D. S., K. A. Galvin and B. L. Turner, II. 1994. The global impact of land – use change. BioScience. 44: 300 – 304.

Overpeck, J. T., D. Rind and R. Goldberg. 1990. Climate – induced changes in forest disturbance and vegetation. Nature 343: 51 – 53.

Overpeck, J. T., P. J. Bartlein and T. Webb III. 1991. Potential magnitude of future vegetation change in Eastern North America: comparisons with the past. Science 254: 692 – 695.

Overpeck, J. T., R. S. Webb, and T. Webb III. 1992. Mapping eastern North American vegetation change of the past 18 Ka: No – analogs and the future. Geology 20: 1071 – 1074.

Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Sci. Soc. Am. 51: 1173 – 1179

Parton, W. J., J. M. O. Scurlock, D. S. Ojima, T. G. Gilmanov, R. J. Scholes, D. S. Schimel, T. Kirchner, J – C. Menaut, T. Seastedt, E. Garcia Moya, A. Kamnalrut and J. L. Kinyamario. 1993. Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. Global Biogeochemical Cycles 4: 785 – 809.

Peng, C. H., J. Guiot, E. Van Campo and R. Cheddadi. 1994. The vegetation carbon storage variation in Europe since 6000 BP: reconstruction from pollen. Journal of Biogeography 21: 19 – 31.

Peng, C. H., J. Guiot, and E. Van Campo. 1995c. Reconstruction of the past terrestrial carbon storage of the Northern Hemisphere from the Osnabrück Biosphere Model and palaeodata. Climate Research 5: 107 – 118.

Peng, C. H., J. Guiot, E. Van Campo and R. Cheddadi. 1995b. The variation of terrestrial carbon storage at 6000 yr BP in Europe: reconstruction from pollen data using two empirical biosphere models. Journal of Biogeography. 22: 581 – 59.

Peng, C. H., J. Guiot, E. Van Campo and R. Cheddadi. 1995a. Temporal and spatial variations of terrestrial biomes and carbon storage since 13000 yr BP in Europe: reconstruction from pollen data and statistical models. Water, Air and Soil Pollution 82: 375 – 391.

Plöchl, M. and W. Cramer 1995. Coupling global models of vegetation structure and ecosystem processes. Tellus 47B: 240 – 250.

Prentice, I. C. and GVDM Members. 1989. Developing a global vegetation dynamics model: Results of an IIASA summer workshop. International Institute for Applied Systems Analysis (IIASA). RR – 89 – 7. Laxenburg, Austria.

Prentice, I. C. and R. Leemans 1990. Pattern and process and the dynamics of forest structure: a simulation approach. Journal of Ecology 78: 340—355.

Prentice, I. C. and A. M. Solomon. 1990. Vegetation models and global change. Pages 365 —383 in R. S. Bradley, editor. Global changes of the past, UCAR/Office for Interdisciplinary Earth Studies, Boulder, Colorado, USA.

Prentice, I. C. P. J. Bartlein and T. Webb III. 1991. Vegetation and climate change in eastern north America since the last glacial maximum. Ecology 72: 2038—2056

Prentice, I. C. , W. Cramer, S. P. Harrison, R. Leemans, R. A. Monserud and A. M. Solomon. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. Journal of Biogeography 19: 117—134.

Prentice, I. C. , M. T. Sykes, M. Lautenschlager, S. P. Harrison, O. Denissenko and P. J. Bartlein. 1993a. Modelling the increase in terrestrial carbon storage after the last glacial maximum. Global. Ecol. Biogeogr. Lett. 3: 67—76.

Prentice, I. C. , M. T. Sykes and W. Cramer. 1993b. A simulation model for the transient effects of climate change on forest landscapes. Ecological Modelling 65: 51—70.

Prentice, I. C. , J. Guiot, D. Jolly, B. Huntley and R. Cheddadi. 1996. Reconstructing biomes from palaeoecological data: a general method and its application to European pollen data at 0 and 6 ka. Climate Dynamics 12: 185—194.

Prentice, K. C. and I. Y. Fung. 1990. The sensitivity of terrestrial carbon storage to climate change. Nature 346: 48—51.

Price, D. T. and M. J. Apps. 1996. Boreal forest response to climate change scenarios along an ecoclimatic transect in central Canada. Climatic Change (in press). Price, D. T. , C. H. Peng, M. J. Apps and D. H. Halliwell. 1996. Simulated effects of climate change on boreal ecosystem and carbon dynamics along a central Canadian transect. (in preparation)

Potter, C. S. , J. T. Randerson, C. B. Field, P. A. Matson, P. M. Vitousek, H. A. Mooney and S. A. Klooster. 1993. Terrestrial ecosystem production: a process model based on global satellite and surface data. Global Biogeochemical Cycles 4: 811—841.

Raich, J. W. , E. B. Rastetter, J. M. Melillo, D. W. Kicklighter, P. A. Steudler, B. J. Peterson,. A. L. Grace, B. Moore III and C. J. Vorosmarty. 1991. Potential net primary productivity in South America: Application of a global model. Ecol. Appl. 1: 399—429.

Rastetter, E. B. , M. G. Ryan, G. R. Shver, J. M. Melillo, K. J. Nadelhoffer, J. E. Hobbie and J. D. Aber. 1991. A general model describing the response of the C and N cycles in terrestrial ecosystems to changes in CO2, climate and N deposition. Tree Physiology 9: 101—126.

Rastetter, E. B. , R. B. McKane, G. R. Shaver, and J. M. Melillo. 1992. Changes in C storage by terrestrial ecosystems: How $C-N$ interactions restrict response to CO_2 and temperature. Water, Air, Soil Pollution 64: 327—344.

Rizzo, B. and E. D. Wiken. 1992. : Assessing the sensitivity of Canada's ecosystems to climatic change. Climatic Change 21: 37—55.

Running, S. W. and J. C. Coughlan 1988. A general model of forest ecosystem processes for

regional applications. 1. Hydrologic balance, canopy gas exchange and primary production processes. Ecological Modelling 42: 125—154.

Running, S. W. and S. T. Gower 1991. FOREST—BGC: a general model of forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets. Tree Physiol. 9: 147—160.

Rykiel, E. J. Jr. 1989. Artificial intelligence and expert systems in ecology and natural resource management. Ecological Modelling 46: 1—2.

Sirois, L. , Bonan, G. B. and H. H. Shugart. 1994. development of a simulation model of the forest—tundra transition zone of northeastern Canada. Can. J. For. Res. 24: 697—706.

Starfield, A. M. and A. L. Bleloch 1986. Building Models for Conservation and Wildlofe Management. Macmillan, New York, USA.

Starfield, A. M. Farm, B. P. and R. H. Taylor 1989. A rule—based ecological models for the management of an estuarine lake. Ecological Modelling 46: 107—119. Sellers, P. J. Y. Mintz, Y. C. Sud and A. Dalcher 1986. A Simple Biosphere Models (SiB) for use within general circulation models. Journal of the Atmospheric Sciences 43: 505—531.

Sellers, P. J. J. A. Berry, G. J. Collatz, C. B. Field and F. G. Hall. 1992. Canopy reflectance, photosynthesis, and transpiration. III. A reanalysis using improved leaf models and a new canopy integration scheme. Remote Sens. Environ. 42: 187—216.

Steffen, W. L, B. H. Walker, J. S. I. Ingram, and G. W. Koch. 1992. Global change and terrestrial ecosystems: the operational plan, IGBP Report No. 21, The Royal Swedish Academy of Sciences, Stockholm, Sweden.

Steffen, W. L. Cramer, W. Pl(chl, M. and H. Bugmann. 1996. Global vegetation models: incorporating transient changes to structure and composition. Journal of Vegetation Science 7: 321—328.

Stephenson, N. L. 1990. Climatic control of vegetation distribution: The role of the water balance. Am. Nat. 135: 649—670.

Shugart, H. H. and D. C. West 1980. Forest succession models. BioScience 30: 308—313.

Shugart, H. H. , Hopkins, M. S. Burgess, P. and A. T. Mortlock. 1981. The development of a succession model for subtropical rain forest and its application to assess the effects of timber harvest at Wiangaree State Forest, New South Wales. J. Environ. Manage. 11: 243—265

Shugart, H. H. 1984. A theory of forest dynamics: The ecological implication of forest succession models. Spring, New York, USA.

Shugart, H. H. 1990. Using ecosystem models to assess potential consequences of global climatic change. Tree 5: 303—307.

Smith, T. M. , Shugart, H. H. , Bonan, G. B. and J. B. Smith. 1992. Modelling the potential response of vegetation to global climate change. Advances in Ecological Research 22: 93—116.

Smith, T. M. and Shugart. H. H. 1993. The transient response of terrestrial carbon storage to a perturbed climate. Nature 361: 523—526.

Smith, T. M., R. Leemans and H. H. Shugart. 1992. Sensitivity of terrestrial carbon storage to CO_2—induced climate change; comparison of four scenarios based on general circulation models. Climatic Change 21: 367—384.

Smith, T. M., R. Leemans and H. H. Shugart. editors. 1994. The application of patch models of vegetation dynamics to global change issues. GCTE Workshop summary. Kluwer Academic Publishers, the Netherlands.

Solomon, A. M. 1986. Transient response of forests to CO_2—induced climate change; Simulation modeling experiments in eastern North America. Oecologia 68: 567—579.

Solomon, A. M., I. C. Prentice, R. Leemans and W. P. Cramer. 1993. The interaction of climate and land use in future terrestrial carbon storage and release. Water, Air and Soil Pollution 70: 595—614.

Sykes, M. T. and I. C. Prentice. 1995. Boreal forest futures; modelling the controls on tree species range limits and transient responses to climate change. Water, Air and Soil Pollution 82: 415—428.

Tuhkanen, S. 1980. Climatic parameters and indices in plant geography. Acta Phytogeographica Suecica 67: 28—35.

VEMAP Members. 1995. Vegetation/ecosystem modeling and analysis project; Comparing biogeography and biogeochemistry models in a continent—sacle study of terrestrial ecosystem response to climate change and CO_2 doubling. Global Biogeochemical Cycles 9: 407—437.

Webb, T. III. 1987. The appearance and disappearance of major vegetation assemblages; long—term vegetation dynamics in eastern North America. Vegetatio 69: 177—187.

Woodward, F. I. 1987. Climate and Plant distribution. Cambridge Univ. Press, Cambridge.

Woodward, F. I., T. M. Smith and W. R. Emanuel. 1995. A global land primary productivity and phytogeography model. Global Biogeochemical Cycles 9: 471—490.

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