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## INCORPORATING DYNAMIC VEGETATION COVER WITHIN GLOBAL CLIMATE MODELS

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**Abstract.** Numerical models of Earth's climate system must consider the atmosphere and terrestrial biosphere as a coupled system, with biogeophysical and biogeochemical processes occurring across a range of timescales. On short timescales (i.e., seconds to hours), the coupled system is dominated by the rapid biophysical and biogeochemical processes that exchange energy, water, carbon dioxide, and momentum between the atmosphere and the land surface. Intermediate-timescale (i.e., days to months) processes include changes in the store of soil moisture, changes in carbon allocation, and vegetation phenology (e.g., budburst, leaf-out, senescence, dormancy). On longer timescales (i.e., seasons, years, and decades), there can be fundamental changes in the vegetation structure itself (disturbance, land use, stand growth). In order to consider the full range of coupled atmosphere–biosphere processes, we must extend climate models to include intermediate and long-term ecological phenomena. This paper reviews early attempts at linking climate and equilibrium vegetation models through iterative coupling techniques, and some important insights gained through this procedure. We then summarize recent developments in coupling global vegetation and climate models, and some of the applications of these tools to modeling climate change. Furthermore, we discuss more recent developments in vegetation models (including a new class of models called “dynamic global vegetation models”), and how these models are incorporated with atmospheric general circulation models. Fully coupled climate–vegetation models are still in the very early stages of development. Nevertheless, these prototype models have already indicated the importance of considering vegetation cover as an interactive part of the climate system.

**Key words:** *atmosphere-biosphere interactions; climate change; coupled models; dynamic global vegetation models; vegetation cover affects climate.*

### INTRODUCTION

During the last decade the international scientific community has become increasingly concerned with the interconnections between terrestrial ecosystems and the atmosphere. For example, there is significant interest in how climate variability and climate change affect the structure and functioning of ecosystems on regional and global scales. Furthermore, there is increasing interest in how changes in terrestrial ecosystems can, in turn, affect the atmosphere.

One of the most obvious manifestations of atmo-

sphere–ecosystem interactions is the relationship between global patterns of vegetation cover and climate. The location of deserts, tropical rainforests, and tundra ecosystems, for example, is obviously dictated by climate. In fact, the use of a few basic climate parameters (e.g., growing degree-days, minimum wintertime temperatures, soil moisture availability) allows the successful prediction of the geographic distribution of many plant functional types on continental and global scales (Box 1981, Woodward 1987). Following this logic, several models of global vegetation patterns, based on the relationships between climate and vegetation, have been developed (e.g., BIOME of Prentice et al. 1992, BIOME-3 of Haxeltine and Prentice 1996, MAPSS of Neilson 1995, DOLY of Woodward et al. 1995).

Changes in climate affect the geographic distribution of global vegetation communities in fundamental ways. For example, climatic changes during the late Quaternary and the Holocene drove large-scale changes in global biome distributions (e.g., Prentice et al. 1993,

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Foley 1994, TEMPO 1996, Claussen and Gayler 1997, Texier et al. 1997, Kutzbach et al. 1998). Moreover, projected changes in future climate associated with an increase in greenhouse gases are expected to be large enough to cause fundamental changes in global vegetation distribution (Solomon and Cramer 1993). Changes in vegetation structure may also significantly influence the climate (Pielke and Avissar 1990). The physical characteristics of vegetation and soils have a strong influence on the exchange of energy, water, and momentum between the land surface and the atmosphere. Changes in vegetation therefore imply changes of the physical properties of the land surface, including surface albedo, surface roughness, leaf-area index, rooting depth, and the availability of soil moisture.

Consequently the atmosphere and terrestrial biosphere must be considered as a coupled system, acting on a range of timescales. On short timescales (i.e., seconds to hours), the coupled system is dominated by the rapid biophysical and physiological processes that exchange energy, water, carbon dioxide, and momentum between the atmosphere and the land surface. Intermediate-timescale (i.e., days to months) processes include changes in the store of soil moisture, changes in carbon allocation, and vegetation-phenology phenomena (e.g., budburst, leaf-out, senescence, dormancy). On longer timescales (i.e., seasons, years, and decades) there can be fundamental changes in the vegetation cover itself (disturbance, land use, stand growth). Most climate models already describe the rapid biophysical processes occurring at the land-atmosphere interface, but they do not consider longer term ecological phenomena.

#### INFLUENCE OF VEGETATION COVER ON CLIMATE

Global climate models, including atmospheric general circulation models (GCMs), require some specification of the fluxes of energy (including radiative and turbulent fluxes), water vapor, and momentum between the lower atmosphere and the underlying surface. Over land these fluxes are determined generally by biophysical and physiological processes occurring between the soil, plant canopies, and the atmospheric boundary layer. Nearly all GCMs now include land-surface parameterization schemes to simulate rapid land-atmosphere exchange processes. A large number of land-surface models now exist; most of them are based at least in part on the early BATS (Dickinson et al. 1986) and SiB (Sellers et al. 1986, 1996) land-surface parameterization schemes.

GCM land-surface models typically operate by prescribing the geographic distribution of vegetation and soil characteristics across the globe. Vegetation and soil properties are taken as prescribed "boundary conditions," which are not allowed to change with the climate, and thus neglect long-term changes in vegetation cover and resultant feedbacks. In studies of short-term

climate variability, where changes in vegetation and soils are unlikely to be of major importance in most areas, this is a reasonable approach. However, in long-term, transient climate simulations, including scenarios of future global warming, where changes in climate may drive fundamental changes in vegetation distribution, this approach is no longer adequate. To demonstrate the importance of vegetation structure, a number of studies have considered the sensitivity of atmospheric processes to changing global vegetation distribution. Below, we present three examples of how changes in vegetation structure in different biomes are likely to influence broad-scale climate.

#### *Tropical deforestation*

The clearing of tropical rainforests for pasture and croplands is one of the most prominent environmental issues of our time. Many authors have discussed the possible effects of tropical deforestation on global climate processes. For example, exploratory GCM modeling studies have considered the sensitivity of the climate system to a complete conversion of Amazonian rainforests to pastures (e.g., Dickinson and Henderson-Sellers 1988, Shukla et al. 1990, Nobre et al. 1991, Henderson-Sellers et al. 1993). Table 1 compares several recent GCM simulations of Amazonian deforestation.

Replacing a tropical rainforest with a pasture typically increases the surface albedo, lowers the surface roughness, and reduces the leaf-area index (and associated canopy interception) and available soil moisture (mainly because pasture plants often have shallower roots than rainforest trees). As a consequence, tropical deforestation is expected to lower the ability of the land surface to maintain a high rate of evapotranspiration throughout the year, leading to changes in the latent heating of the atmospheric boundary layer and the strength of tropical convection. Generally speaking, this change in the surface energy and water balance (and the associated changes to the atmospheric boundary layer) leads to a significant reduction in rainfall and an increase in surface temperature.

Costa and Foley (2000) recently conducted a series of GCM sensitivity studies to compare the potential effects of large-scale deforestation and CO<sub>2</sub>-induced global warming on the climate of the Amazon basin. In these simulations deforestation caused a significant decrease in regional precipitation, in association with a general decrease in latent heating and vertical motion over the deforested area. On the other hand, the overall effects of increased CO<sub>2</sub> concentrations (including both the CO<sub>2</sub> radiative forcing and the physiological effects of increased CO<sub>2</sub> on stomatal conductance) caused an increase in precipitation. Together, the combined effects of deforestation and doubled CO<sub>2</sub>, including the interactions among the processes, caused a precipitation decrease of ~ 0.4 mm/d (Fig. 1). While the effects

TABLE 1. Tabulation of recent climate-model simulations of Amazonian deforestation, by information source (from Costa and Foley 2000).

Characteristic	Dickinson and Kennedy 1992	Henderson-Sellers et al. 1993	Lean and Rowntree 1993	Polcher and Laval 1994	Sud et al. 1996	Manzi and Planton 1996	Lean and Rowntree 1997	Costa and Foley 2000
GCM	CCM1	CCM1-OZ	UKMO	LMD	GLA	EMERAUDE	UKMO	GENESIS
Resolution	$4.5^\circ \times 7.5^\circ$	$4.5^\circ \times 7.5^\circ$	$2.5^\circ \times 3.75^\circ$	$2.0^\circ \times 5.6^\circ$	$4.0^\circ \times 5.0^\circ$	$2.8^\circ \times 2.8^\circ$	$2.5^\circ \times 3.75^\circ$	$4.5^\circ \times 7.5^\circ$
Surface model	BATS (Dickinson et al. 1986)	BATS (Dickinson et al. 1986)	Warrilow (1986)	SECHIBA (Ducroude et al. 1993)	SSiB (Xue et al. 1991)	ISBA (Noilhan and Planton 1989)	Warrilow (1986) modified	IBIS (Foley et al. 1996)
Ocean	mixed layer	mixed layer	prescribed SST	prescribed SST	prescribed SST	prescribed SST	prescribed SST	mixed layer
Simulation length (yr)	3	6	3	1.1	3	3	10	15
Roughness length <sup>†</sup>	2.00/0.05	2.00/0.20	0.80/0.04	no change	2.65/0.077	2.00/0.026	2.10/0.026	interactive
Albedo <sup>†</sup>	0.12/0.19	0.12/0.19	0.14/0.19	0.098/0.177	0.092/0.142	0.12/0.163	0.13/0.18	interactive

<sup>†</sup> Each data entry represents two values (before deforestation/after deforestation) and is dimensionless.

Notes: GCM = general circulation model; SST = sea surface temperature.

of deforestation and increasing CO<sub>2</sub> concentrations on precipitation tended to counteract each other, both processes worked to warm the Amazon basin. Deforestation caused an increase in surface temperature, largely because of decreases in evapotranspiration. In addition, the physiological effects of CO<sub>2</sub> also tended to increase the surface temperature, associated with the decrease in canopy conductance and transpiration. Finally, the radiative effect of CO<sub>2</sub> also increased the surface temperature. The combined effect of deforestation and doubling CO<sub>2</sub> concentrations, including the interactions among the processes, was a temperature increase of roughly 3.5°C.

Climate-model sensitivity studies have clearly established the importance of tropical forests in influencing Earth's climate. According to the current generation of climate models, a complete deforestation of tropical land masses could have global climatic significance. However, future studies should concentrate on more realistic scenarios of land use and deforestation, rather than conducting only total-deforestation simulations (Chu et al. 1994). Furthermore, other modes of land use (including mid-latitude deforestation and agricultural expansion) should be further evaluated for their climatic significance (e.g., Pielke et al. 1991, Chase et al. 1996, Bonan 1997).

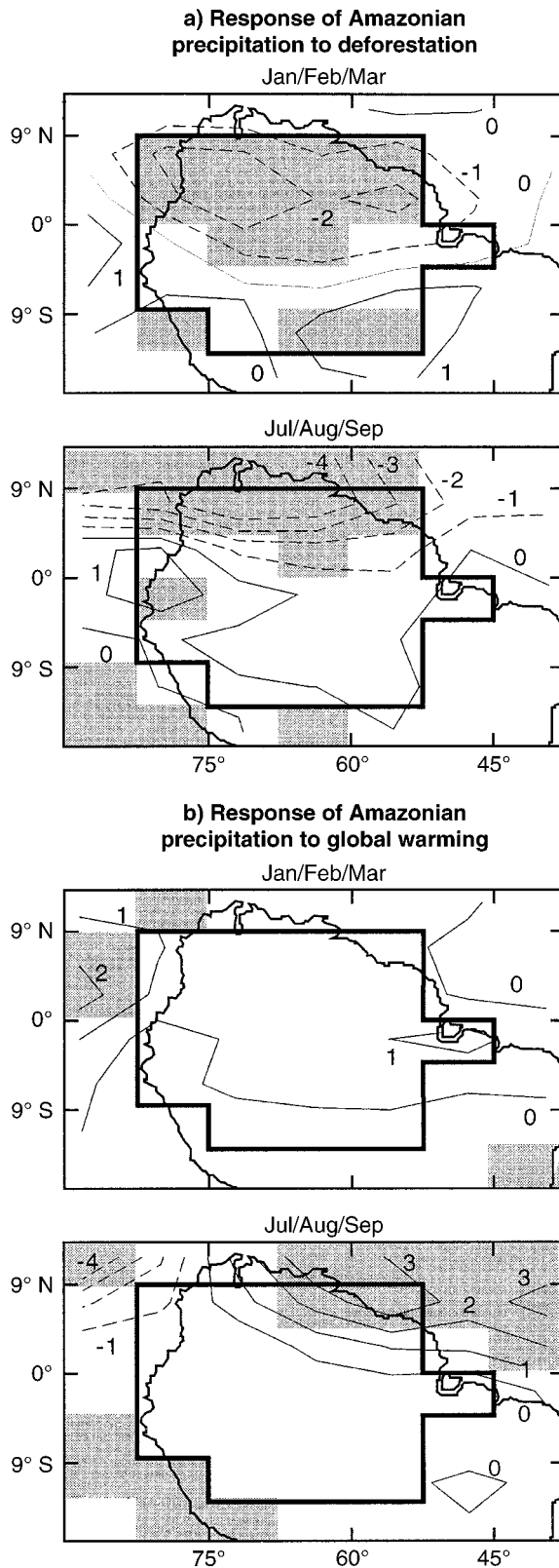
#### *Boreal forests and tundra*

The boundary between boreal forests and Arctic tundra represents a dramatic change in land-surface properties, with a known history of climate-driven fluctuations (Huntley and Cramer 1997). For example, the albedo (or reflectivity) of boreal forests and tundra is markedly different, especially in spring when the tundra is covered by snow (Robinson and Kukla 1985, Laine and Heikinheimo 1996, Sharratt 1998). Furthermore, boreal forest and tundra have significantly dif-

ferent surface roughness and surface emissivity (Bonan et al. 1995, Kurvonen et al. 1998, Levis et al. 1999a).

The differences in the physical properties of boreal forests and tundra ecosystems may have great significance to the climate system. For example, an increase in forest area (at the expense of tundra) would result in a decreased albedo, thereby warming the land surface with additional absorbed solar radiation. The reverse, caused by an expansion of tundra replacing boreal forest, would therefore act to cool the surface through albedo increases. Across the high northern latitudes the relative amount of boreal forest and tundra could therefore have a significant impact on the overall energy balance, temperature, and general circulation of the atmosphere. On smaller spatial scales, Pielke and Vidale (1995) noted that the forest-tundra boundary could have a significant impact on local atmospheric circulations, which may lead to the enhancement of frontal boundaries along the forest-tundra ecotone.

Using the GENESIS GCM (Thompson and Pollard 1995, 1997), Bonan et al. (1992) examined the potential impact of complete boreal deforestation on the climate system, finding that temperatures were dramatically cooler year-round. While this study uses an extreme and unlikely deforestation scenario, it does point to the significance of vegetation cover in affecting high-latitude climates. Foley et al. (1994) therefore considered how changes in the boreal forest-tundra boundary during the early and middle Holocene (roughly 5000–10 000 yr BP) might have affected climate. During this time, northern high-latitude regions were substantially warmer than at present (TEMPO 1996), presumably in response to increases in incoming solar radiation during summer that resulted from changes in Earth's orbital geometry (Kutzbach et al. 1998). Paleobotanical evidence indicates that the boundary between boreal forest



and tundra was, at least in some high-latitude locations, farther north than at present (TEMPO 1996). Foley et al. (1994) showed that the poleward movement of the boreal forest-tundra ecotone might have greatly amplified the orbitally induced warming of the high northern latitudes during the middle Holocene. They found that the high-latitude warming caused by orbital forcing was nearly doubled by the poleward expansion of boreal forests (Fig. 2). This vegetation feedback mechanism acted to amplify the initial warming (induced by changes in Earth's orbit) through changes in the surface albedo associated with boreal forest and tundra.

These and other studies show that changes in the boundary between boreal forests and tundra may lead to important climatic feedbacks. Considering that future warming may be strongest in the high latitudes, we need to further evaluate the possibility of high-latitude vegetation feedbacks and not neglect them in the assessment of global warming scenarios.

#### *Sahara/Sahel vegetation transition*

The regional differences in albedo, surface roughness, leaf-area index, and soil moisture-holding capacity between the Sahara and the vegetation of the Sahel zone have a significant impact on the surface energy balance, and the consequent rate of atmospheric heating. Furthermore, the shrublands and grasslands to the south can maintain a higher rate of evapotranspiration than can deserts, and therefore have a greater ability to recirculate precipitation (and, therefore, add latent heat) back into the atmosphere. Changes in the vegetation cover of northern Africa, whether due to climate change or human activity, are therefore likely to have profound impacts on the atmosphere. For example, Charney (1975) suggested that human-induced desertification in the Sahel could reduce the latent heating and moisture recirculation to the atmosphere, and partially explain increasing drought conditions occurring in the region during the 1970s. Recent studies by Zheng and Eltahir (1997, 1998) indicated that deforestation along the coastal tropical forests of West Africa might also contribute to reduced rainfall over the Sahel. However, the importance of land-surface feedbacks in changing Sahelian rainfall, relative to the possible in-

FIG. 1. Potential climatic impact of global warming and Amazonian deforestation. Costa and Foley (2000) used the GENESIS global climate model to compare the impact of tropical deforestation and global warming on the climate of Amazonia. The thick black line outlines the Amazon drainage Basin. (a) Changes in precipitation resulting from the complete deforestation of Amazonia alone. (b) Changes in precipitation resulting from a doubling of atmospheric  $\text{CO}_2$  concentrations alone. The dashed contour lines indicate decreases in precipitation. Gray shaded areas are areas of statistical significance. Units are millimeters per day. (Adapted from Costa and Foley 2000).

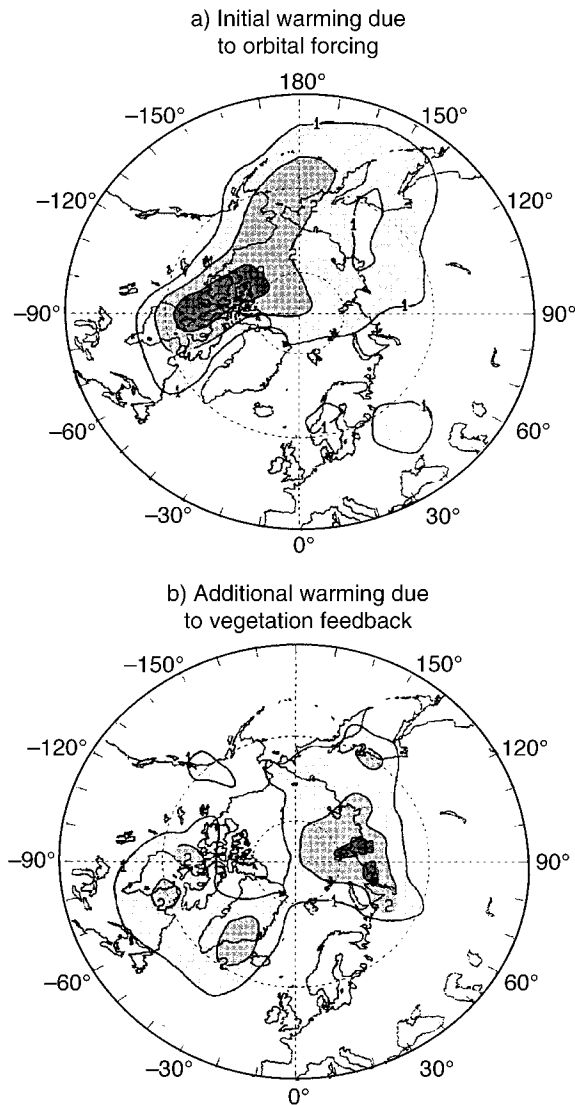


FIG. 2. Vegetation feedbacks on high-latitude warming during the Middle Holocene. Foley et al. (1994) used the GENESIS global climate model to examine how changes in the border of boreal forests and tundra may have affected the mid-Holocene climate. (a) Annually averaged simulated mid-Holocene temperature changes (compared to modern) associated with changes in Earth's orbital geometry. (b) The *additional* simulated warming associated with the northward movement of boreal forests, replacing tundra, during the middle Holocene. (Adapted from Foley et al. 1994).

fluence of changes in ocean conditions (Eltahir and Gong 1996), is still being debated.

For the recent geologic record, several authors have discussed how changes in the vegetation cover over the Sahara might have affected climate during the early to middle Holocene period (Kutzbach et al. 1996, Broström et al. 1997, Claussen and Gayler 1997, Broström et al. 1998, Pollard et al. 1998, Claussen et al. 1999). Changes in Earth's orbit during this time increased the

seasonal variation of incoming solar radiation in the northern hemisphere (compared to present day), leading to an increase in the heating (in summer) and cooling (in winter) of continental land masses. The oceans, because of their large heat capacity, show relatively little change in temperature during the seasonal cycle. As a result, increases in the seasonal cycle of land temperatures (compared to the ocean) enhanced the strength of subtropical monsoon circulations in Africa and south Asia, relative to the present day (Kutzbach et al. 1998).

Paleobotanical data from northern Africa demonstrate that much of the modern desert was covered with grasslands, savannas, and lakes until ~ 5000–6000 yr BP (e.g., Ritchie and Haynes 1987, COHMAP 1988, Lézine 1989, Hoelzmann et al. 1998, Jolly et al. 1998a,b). These large changes in vegetation structure must have dramatically altered patterns of atmospheric heating, and also led to increased recirculation of rainfall back to the atmosphere (through increases in evapotranspiration), which may have been a significant feedback on the African monsoon. Kutzbach et al. (1996) and Broström et al. (1997) conducted simple GCM sensitivity studies, showing that changing vegetation about 6000 yr BP (increasing grassland and shrubland area, at the expense of desert) led to a significant enhancement to the monsoon circulation and associated rainfall.

#### LINKING CLIMATE AND EQUILIBRIUM VEGETATION MODELS

While the influence of vegetation cover on climate can be documented on a case-by-case basis with existing general circulation models (GCMs), there is a need for a more generalized framework for exploring climate–vegetation interactions across the globe. In particular, climate models need to consider vegetation cover as an interactive surface boundary, which can change in response to changes in climate. Interactions take place regarding fluxes of energy and momentum (physical feedbacks) and of matter, mostly carbon and water (biogeochemical feedbacks).

#### *Physical feedbacks*

The first attempt to link climate and vegetation models to address physical feedbacks was made by Henderson-Sellers (1993), using the CCM1-Oz climate model together with the Holdridge (1947) bioclimatic scheme. The Holdridge scheme uses simple delineations of annual temperature and rainfall to predict the geographic distribution of vegetation types in relation to climate. In the Henderson Sellers study the Holdridge scheme is applied at the end of each year to update the geographic pattern of vegetation types within the GCM. Hence, the coupling procedure iterates between the climate and vegetation models (Fig. 3), where a single year of the climate simulation is used to predict

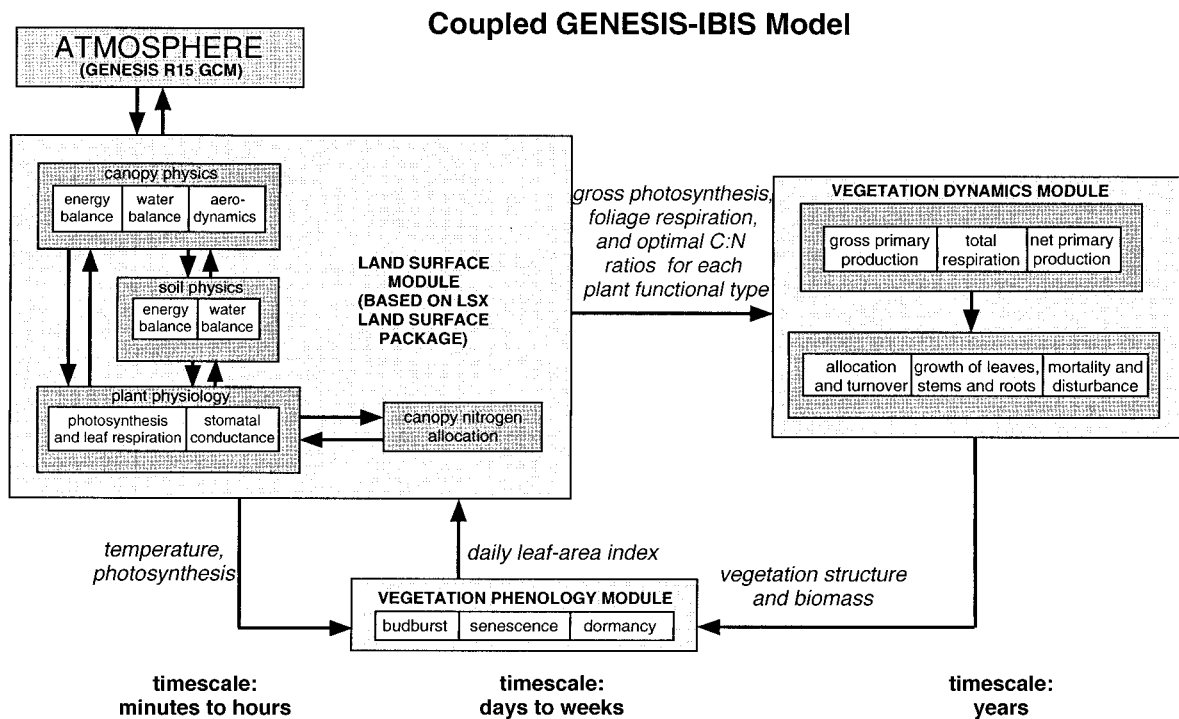


FIG. 3. Coupling of the IBIS dynamic global vegetation model to the GENESIS global climate model. (Adapted from Foley et al. 1998.)

changes in equilibrium vegetation cover. The changes in vegetation cover are, in turn, used by the GCM to simulate the next year of climate. This asynchronous coupling cycle is repeated until the results of the two models converge to equilibrium.

Since asynchronous coupling may introduce more interannual variability into the simulated vegetation structure than actual buffering of the biosphere permits, a somewhat more elaborate approach was put forth by Claussen (1994), wherein he iteratively coupled the ECHAM GCM with the BIOME equilibrium vegetation model of Prentice et al. (1992). Instead of individual years, Claussen used multi-year averages of the climate model simulation to drive changes in vegetation. This coupled model was used to study the sensitivity of climate and vegetation to the choice of initial conditions. Specifically, he examined how changes in the initial distribution of deserts and tropical forests could lead to different equilibrium states. In follow-on simulations, Claussen (1997, 1998) and Claussen and Gayler (1997) noted how the Western Sahara region could, under certain conditions, maintain two alternative stable equilibria: one as a desert, another as a grassland.

Several other investigators have employed the iterative, asynchronous coupling of GCMs and equilibrium vegetation models. For example, de Noblet et al. (1996) linked the LMD GCM to the BIOME equilibrium vegetation model to study how changes in boreal forest and tundra may have helped initiate glacial conditions

during the Quaternary. Texier et al. (1997) showed that climate-induced changes in the vegetation of northern Africa influenced the African monsoon during the middle Holocene epoch. De Conto et al. (1999) used the GENESIS GCM, linked to the EVE equilibrium vegetation model, to examine high-latitude climate-vegetation interactions of the Cretaceous (~ 80 million yr BP).

#### *Biogeochemical feedbacks*

All of the above-cited studies exclusively addressed physical feedback processes caused by changing vegetation structure. It has only recently become possible to also study the exchange of matter between atmosphere and biosphere, particularly the flux of C as plant nutrient and as powerful greenhouse gas. This development has become possible through the development of biogeochemical models of the land biosphere—these models simulate the flux of C and water through plants and soil using physiological process models (the breadth of these models was recently reviewed by Cramer et al. [1999]).

Off-line calculations have illustrated the sensitivity of biospheric C fluxes to the state of the atmosphere for some time already, the most direct factor being the reduction of stomatal conductance, which is assumed to take place in many plants at higher CO<sub>2</sub> levels. Cao and Woodward (1998) showed that terrestrial ecosystems, when influenced by both changing climate and

increased atmospheric CO<sub>2</sub>, might take up additional C for some time—an important element in the calculation of future radiative-forcing scenarios, since clearly these have to be adjusted by the (nonlinear) temporal evolution of terrestrial C uptake. Using an equilibrium vegetation model that contains physiological as well as structural responses, Betts et al. (1997) evaluated the potential for vegetation feedbacks on CO<sub>2</sub>-induced future climate change. They found that the feedbacks due to structural changes (i.e., the physical feedbacks) might be significantly affected by changes in physiology (e.g., changes in stomatal conductance), but the overall vegetation feedbacks remain considerable.

#### LINKING CLIMATE AND DYNAMIC GLOBAL VEGETATION MODELS

The exploratory modeling studies discussed above all demonstrate the need to incorporate representations of changing vegetation within global climate models. Nevertheless, the technique of iteratively coupling dynamic climate models to equilibrium vegetation models poses two fundamental problems. First, there are differences in how climate and vegetation models consider the surface energy and water balance. General circulation model (GCM) land-surface models are typically based upon more detailed biophysical parameterizations than the water-balance treatments of equilibrium vegetation models. As a result, the behavior of these linked climate–vegetation model systems is not necessarily physically consistent, and does not guarantee that water and energy are properly conserved. Second, since structural and physiological vegetation dynamics (disturbance, land use, stand growth) are not considered, the use of equilibrium vegetation models prohibits realistic considerations of long-term climate variability or transient climate change.

To overcome this limitation, a new generation of ecological models, termed “dynamic global vegetation models” (DGVMs), is under development (e.g., Steffen et al. 1992, Walker 1994, Foley et al. 1996, Beerling et al. 1997, Friend et al. 1997). Conceptually similar to earlier generations of forest-dynamics models (Shugart 1984), these models are designed to simulate *transient* changes in vegetation cover (and the associated ecosystem processes) using considerations of both physiological and plant-population processes. Plant growth, resulting from the assimilation of C through

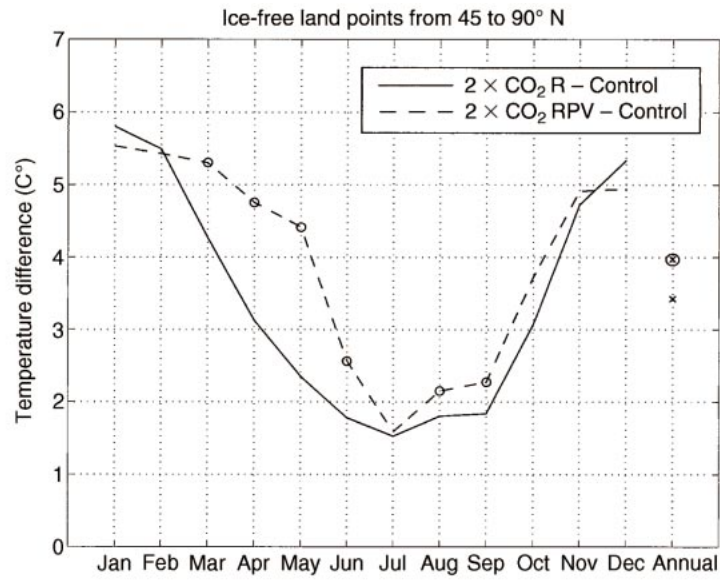
photosynthesis minus the respiration of the plants, contributes to the build-up of a canopy, which is moderated by competition-related mortality. Carbon pools in live and dead biomass, and in the soil, are continuously updated and provide the “memory” of the state of the system over a series of years to decades. In several DGVMs the canopy may be affected by disturbance such as fire or wind-throw. Implicitly, a DGVM can account for land use as an additional disturbance, although this process needs to be driven by additional forcing (such as a map of contemporary agricultural activity).

For the study of interactions between the atmosphere and biosphere, DGVMs may therefore be expected to reliably simulate transient changes in both climate and vegetation, as well as their interactions, rather than instantaneous jumps in global vegetation patterns. So far, only exploratory modeling studies have linked DGVMs directly with GCMs. For example, Foley et al. (1998) incorporated the IBIS DGVM (Foley et al. 1996) within the GENESIS atmospheric GCM of Thompson and Pollard (1997), using an R15 spectral grid (spatial resolution of approximately 4.5° latitude by 7.5° longitude). The two models exchanged information through a common land-surface model with a 45-minute interval (“synchronous coupling,” Fig. 3). For this study, the coupled model was exercised for current climate conditions, and it captured the broad, global-scale patterns of climate and vegetation fairly well. However, because of biases in the GCM climate simulation, there were a number of regional-scale errors in the simulation. For example, the coupled model correctly simulated the general placement of most biomes, but there was too little boreal forest in North America (associated with a dry bias in the climate model) and too much grassland in northern Africa (associated with a wet bias in the climate model).

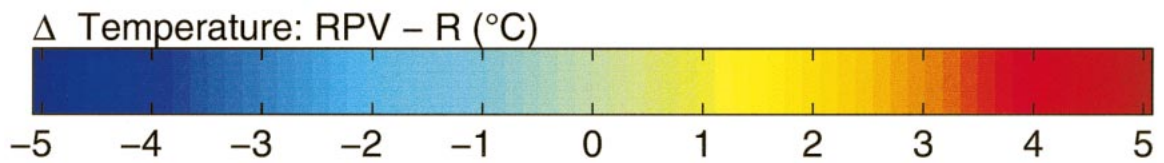
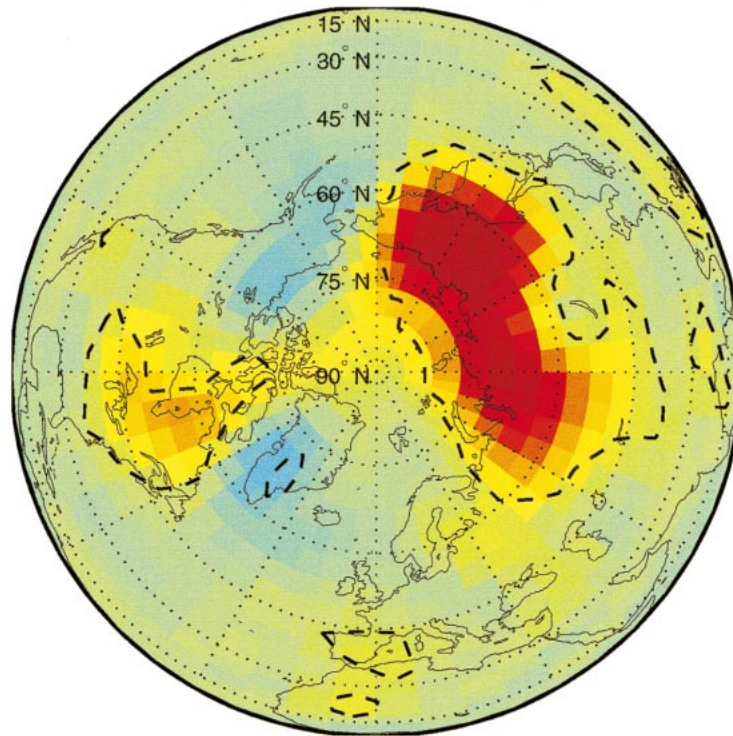
Clearly, the development of fully coupled climate–vegetation models is still in the early stages. Moreover, model testing and evaluation become a problem with new dimensions, since spatially explicit dynamics of the land biosphere have not been observed over long time scales. Below, we review two preliminary studies that have been conducted with this new generation of coupled climate–vegetation models.

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FIG. 4. Potential vegetation feedbacks on global warming. Levis et al. (1999a, 2000) simulated changes in temperature resulting from CO<sub>2</sub>-induced global warming (R – Control) and the changes in temperature resulting from global warming *and* vegetation feedbacks (RPV – Control). The results are shown in the plot at the top of the figure. Temperatures are reported over ice-free land in the northern high latitudes (between 45° and 90° N) from the lowest general-circulation-model level (~50 m above the surface). Statistically significant changes of RPV – R (at the 95% confidence level, using a Student's *t* test) are shown with open circles. Levis et al. (1999a, 2000) also simulated the *additional* warming (during the springtime months of March, April, and May) that results from vegetation feedbacks on CO<sub>2</sub>-induced global warming in the high latitudes. The results are depicted in the bottom (color) portion of the figure. Statistically significant changes of RPV – R (at the 95% confidence level, using a Student's *t* test) are surrounded by dashed lines.



March - April - May



### *High-latitude vegetation feedbacks on global warming*

Many simulations of global warming driven by fossil-fuel emissions show the greatest warming in northern high-latitude regions, where positive albedo feedbacks (resulting from large decreases in high-latitude snow and sea-ice cover) are acting to amplify the initial CO<sub>2</sub>-induced warming (Kattenberg et al. 1996).

Levis et al. (1999a, 2000) used the coupled GENESIS-IBIS model to examine the potential for climatic feedbacks resulting from changes in vegetation cover, due to both physical and biogeochemical feedbacks. By comparing “interactive-vegetation” and “fixed-vegetation” global-warming simulations, they found that there are several climatic feedbacks introduced by changes in vegetation cover in response to CO<sub>2</sub>-induced warming and CO<sub>2</sub>-induced changes in plant physiology. The most pronounced of these vegetation feedbacks resulted from the northward expansion of boreal forests into tundra. Replacing tundra with boreal forest greatly lowered the surface albedo, especially in spring when tundra becomes snow covered. This vegetation feedback mechanism therefore acted to amplify the initial CO<sub>2</sub>-induced warming, primarily in spring and summer. In particular, the northern high-latitude land surfaces are warmed between 3.5° and 5.0 °C in spring and summer by a doubling of CO<sub>2</sub> alone; the vegetation feedback produced an additional warming of ~ 1.0–2.5 °C (Fig. 4a). The additional vegetation-induced warming is concentrated over the high-latitude land masses, particularly Eurasia (Figure 4b).

These experiments corroborate the hypothesis suggested by Bonan et al. (1992) and Foley et al. (1994), where changes in the location of the boreal forest-tundra boundary were shown to have significant climate impacts, using a model with a considerably higher level of physical and biological realism.

### *Vegetation feedbacks on the climate of the last glacial maximum*

There is ample evidence showing that Earth's vegetation distribution was substantially different during the last glacial maximum (LGM), nearly 21 000 yr BP. Vegetation patterns were significantly altered not only by the presence of large continental ice sheets, but also due to changes in climate and sea level; however, the details are still debated. In particular, several modeling studies (e.g., Friedlingstein et al. 1992, Prentice et al. 1993, Crowley 1995, Jolly and Haxeltine 1997, Kutzbach and Claussen 1998) have suggested that tropical rainforests were greatly diminished during the LGM. Many field studies have also suggested that the modern tropical rainforests may have been largely replaced by drought resistant trees and grasses (van der Hammen and Absy 1994, van der Kaars and Dam 1997, Flenley 1998). Nevertheless, other field studies have confirmed

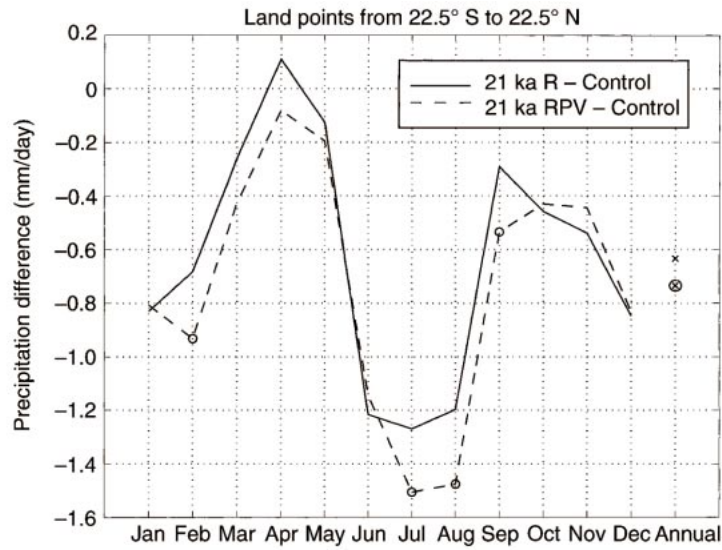
that a core of tropical rainforest remained at the LGM (Salo 1987, Colinvaux 1989, Colinvaux et al. 1996).

Crowley and Baum (1997) conducted a series of GCM sensitivity studies to determine if the climate of the LGM was sensitive to changes in tropical forest cover. They found that a reduction in tropical rainforest area had a significant impact on climate. Specifically, tropical land temperatures increased significantly (by as much as 2–4 °C) and rainfall greatly decreased (by 10–35%). Crowley and Baum pointed out that these results were somewhat analogous to simulations of modern-day tropical deforestation. Levis et al. (1999b) used the GENESIS-IBIS model to examine the potential for vegetation feedbacks on the LGM climate, including those arising from the fact that the LGM had significantly lower CO<sub>2</sub> concentrations (~200 μL/L) than present. It is likely that lowered CO<sub>2</sub> concentrations would have had a significant impact on stomatal conductance, and the relative competitive balance between C<sub>3</sub> (e.g., tropical evergreen trees) and C<sub>4</sub> (e.g., tropical grasses) plants. Levis et al. (1999b) found a dramatic reduction in rainforest area in the tropical latitudes. Sensitivity studies with the model indicated that the lowering of CO<sub>2</sub> has a more dramatic effect on tropical rainforest than the change in climate alone, a result that was suggested previously by Jolly and Haxeltine (1997). There was a 60% reduction in forest leaf-area index, with an associated increase in tropical grasslands and savannas. As suggested by Crowley and Baum (1997), Levis et al. (1999b) found that these changes in vegetation cover have a strong effect on climate, such as lowering precipitation in the tropical forests, particularly in Amazonia and Africa, by nearly an additional 3% (0.1 mm/d) (Figures 5a and b).

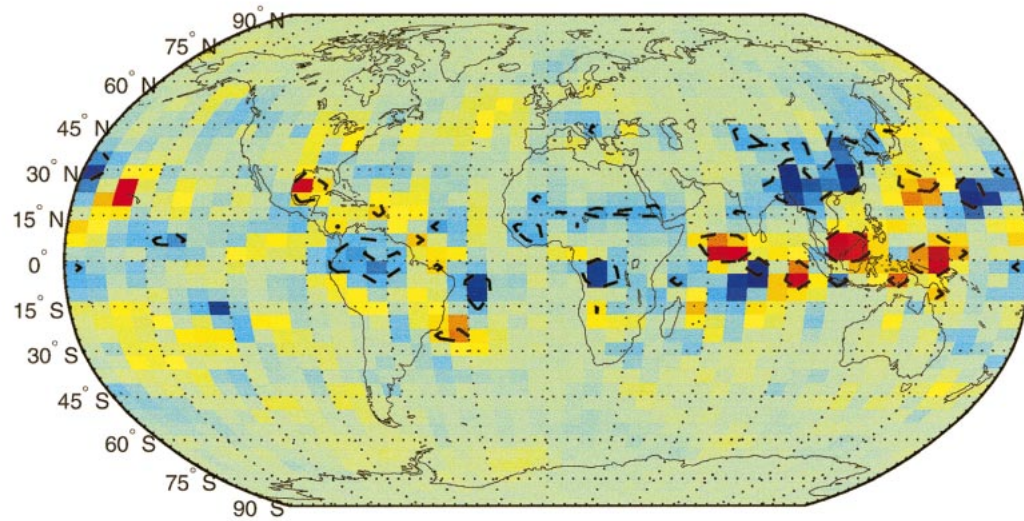
These results indicate that there may be a significant vegetation feedback on LGM climates, but that it is mainly due to the physiological effect of lowering of atmospheric CO<sub>2</sub> concentrations. However, this must still be considered preliminary as long as the fossil evidence cannot unequivocally determine the condition of tropical forests at the LGM.

### CONCLUSIONS

Our understanding of the interactions between the atmosphere and terrestrial biosphere has advanced during recent years. Modeling studies are increasingly enhanced by the availability of observations from a range of sources, and historical reconstructions with unprecedented accuracy. For example, high-resolution global land-cover maps from satellites are now available, which greatly improves our ability to characterize the nature of land surfaces across the globe. In addition, international field campaigns and observing networks of terrestrial ecosystem processes have been (e.g., ABRACOS, [Anglo-Brazilian Climate Observatory Study], FIFE [First ISLSCP (International Satellite Land Surface Climatology Project) Field Experiment],



Annual Average



$\Delta$  Precipitation (21 ka BP): RPV - R ( $\text{mm day}^{-1}$ )

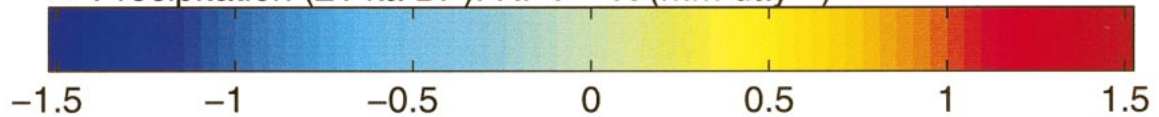


FIG. 5. Potential vegetation feedbacks on last glacial maximum (LGM) tropical precipitation. Levis et al. (1999b) simulated changes in precipitation during the LGM (R - Control), and the changes in precipitation resulting considering vegetation feedbacks (RPV - Control). The results are shown in the plot at the top of the figure. Precipitation is reported over land between 22.5° S and 22.5° N; 21 ka = 21 000 yr. Statistically significant changes of RPV - R (at the 95% confidence level, using a Student's *t* test) are shown with open circles. Levis et al. (1999b) also simulated the *additional* changes in global precipitation patterns (averaged over the entire year) resulting from vegetation feedbacks on LGM climate. The results are depicted in the bottom (color) portion of the figure. Statistically significant changes of RPV - R (at the 95% confidence level, using a Student's *t* test) are surrounded by dashed lines.

BOREAS [Boreal Ecosystem-Atmosphere Study]) or are being (e.g., LBA [Large-scale Biosphere-Atmosphere Experiment in Amazonia], AmeriFlux [the Carbon Dioxide Flux Measurement Network of North, South, and Central America], EuroFlux [the Carbon Dioxide Flux Measurement Network of Europe], FLUXNET [the Carbon Dioxide Flux Network of the globe]) formed. Large-scale ecosystem manipulation experiments, testing the response of whole-plant communities to increasing CO<sub>2</sub> concentrations and warmer temperatures, are underway across the globe. Finally, the wealth of paleoecological information is now being synthesized and organized in a manner that allows the use of such data in comprehensive broad-scale studies (e.g., BIOME 6000, Prentice and Webb 1998). Together, these developments have come in parallel with, and supported, the considerable advances in computer simulation models in ecology, particularly in examining global-scale ecological phenomena and their coupling to the atmosphere.

Here we have reported how a prototype coupled general circulation model (GCM)-dynamic global vegetation model (DGVM) has given us insight into the interactions between climate and vegetation across a wide range of climate regimes, ranging from the last glacial maximum (LGM) to a global-warming scenario.

To address feedbacks between structural change in vegetation and climate, coupled climate-vegetation models must be run for multiple decades and centuries, sometimes at high resolution, which poses limitations due to computational costs. More efficient Earth system models (EMICs = Earth system models of intermediate complexity) are now being developed that allow coupling of atmospheric, vegetation, ocean, and ice models with coarser resolution. For example, Ganopolski et al. (1998*a, b*) showed that CLIMBER-2, a synchronously coupled ocean-atmosphere-vegetation model of intermediate complexity, could successfully simulate modern, mid-Holocene, and glacial climates, as well as many of the associated features of the biosphere. Specifically, they noted that the time evolution of climate and vegetation changes from the LGM to the present (which cannot presently be simulated with any comprehensive coupled GCM-DGVM) could be simulated with many critical aspects of its nonlinear behavior. The advent of such computationally efficient climate models, as alternatives to traditional GCMs, will allow for a more even-handed treatment of the atmosphere, ocean, and terrestrial biosphere, and their respective roles in the earth system.

Future developments in atmosphere-biosphere modeling will have to consider the dynamics of the global C cycle more comprehensively than was done earlier. Global patterns of primary productivity and terrestrial C storage have been shown to be tightly linked to climate (Melillo et al. 1993, Foley 1994). Changes in climate could therefore have profound effects on the

ability of the terrestrial biosphere to store C, and to maintain the current biospheric sink of anthropogenic C. Recent modeling studies (e.g., Cao and Woodward 1998) suggest that global warming is likely to alter the C balance of the terrestrial biosphere. In order to better evaluate the potential for greenhouse warming, we must develop an Earth system model that simultaneously considers the coupled dynamics of the physical climate system and the global carbon cycle.

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