Chapter 15

Dynamic Global Vegetation Modeling: Quantifying Terrestrial Ecosystem Responses to Large-Scale Environmental Change

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15.1 Introduction

The annual exchange of carbon between the atmosphere and the land biota amounts to one-sixth of the atmospheric content of carbon dioxide (CO_2), and the average turnover time of terrestrial organic carbon (including the biota and soils, but excluding geological storages) is only about 20 years. The land biosphere therefore plays a dynamic role in the global carbon cycle on time scales relevant to human activities (Prentice et al. 2001; Schimel et al. 2001; Field et al. 2004). The land biosphere's variations in space and time also influence the fluxes of energy, momentum, water vapor, and many climatically important or reactive trace gases and aerosol precursors across the lower boundary of the troposphere. The land biota respond individualistically to local environmental factors such as photosynthetically active radiation (PAR), temperature, atmospheric humidity, soil moisture, CO_2 concentration and land management. These responses of organisms to their environment are fundamental for the continuing provision of ecosystem goods and services on which all human activities ultimately depend (MA 2003).

Among the many methods for observing the dynamics of terrestrial ecosystems, each method has a restricted window of applicability in space and time. Ground-based measurements (biomass inventories, community descriptions, productivity measurements, flux measurements) are made at single sites or across networks, but are not readily scaled up. Satellite-based measurements provide up to 20 years of global coverage with spatial resolution on the order of a few kilometres, and temporal sampling intervals of days to weeks. Satellite observations have special importance for understanding large-scale processes because they can provide comprehensive coverage, averaged over landscapes. New sensors and satellites are expanding the scope of such observations. But there are limitations on what can be observed from space, particularly with regard to biodiversity and belowground processes. For the foreseeable future, it will be important to use multiple sources of information on terrestrial ecosystem structure and dynamics, and to use modeling techniques to link them.

The identification of mechanisms in the functioning of the land biosphere has meanwhile become a high scientific priority. On a fundamental level, many nonlinearities and feedbacks in the Earth System, including processes determining changes in atmospheric composition on glacial-interglacial and longer time scales and rapid changes in ecosystems and the atmosphere during the recent geological past, originate in the incompletely understood coupling between global biogoechemical cycles and the physical climate (Prentice and Raynaud 2001; Overpeck et al. 2003). On a more practical level, anthropogenic alterations of the global environment have accelerated massively, through land-use change (Foley et al. 2005) as well as changes in atmospheric composition and climate (Houghton et al. 2001); this situation has created an urgent demand by society for tools to predict the risks of continued environmental changes for ecosystem services, and indeed for the future of climate and sustainable land management. The development of Dynamic Global Vegetation Models (DGVMs) by several research groups during the past 10–15 years has been largely a response to these dual "drivers" of interdisciplinary Earth System science.

15.2 Historical Antecedents and Development of DGVMs

The conceptual development of a DGVM dominated the activities of the Biosphere Dynamics Project, led by Allen M. Solomon, at the International Institute for Applied Systems Analysis (IIASA) during 1988–1990. GCTE subsequently adopted DGVM development as a near-term goal, and provided an umbrella for further work by several groups. DGVMs fuse research on four broad groups of processes: *plant geography*, *plant physiology and biogeochemistry*, *vegetation dynamics*, and *biophysics*, each historically pursued by a separate research community (Fig. 15.1). The early development of DGVMs concentrated on representing these processes and their interactions as they would have occurred without human influence. Lately DGVM development has expanded to include the representation of *human intervention* (agriculture, urbanization and forest management).

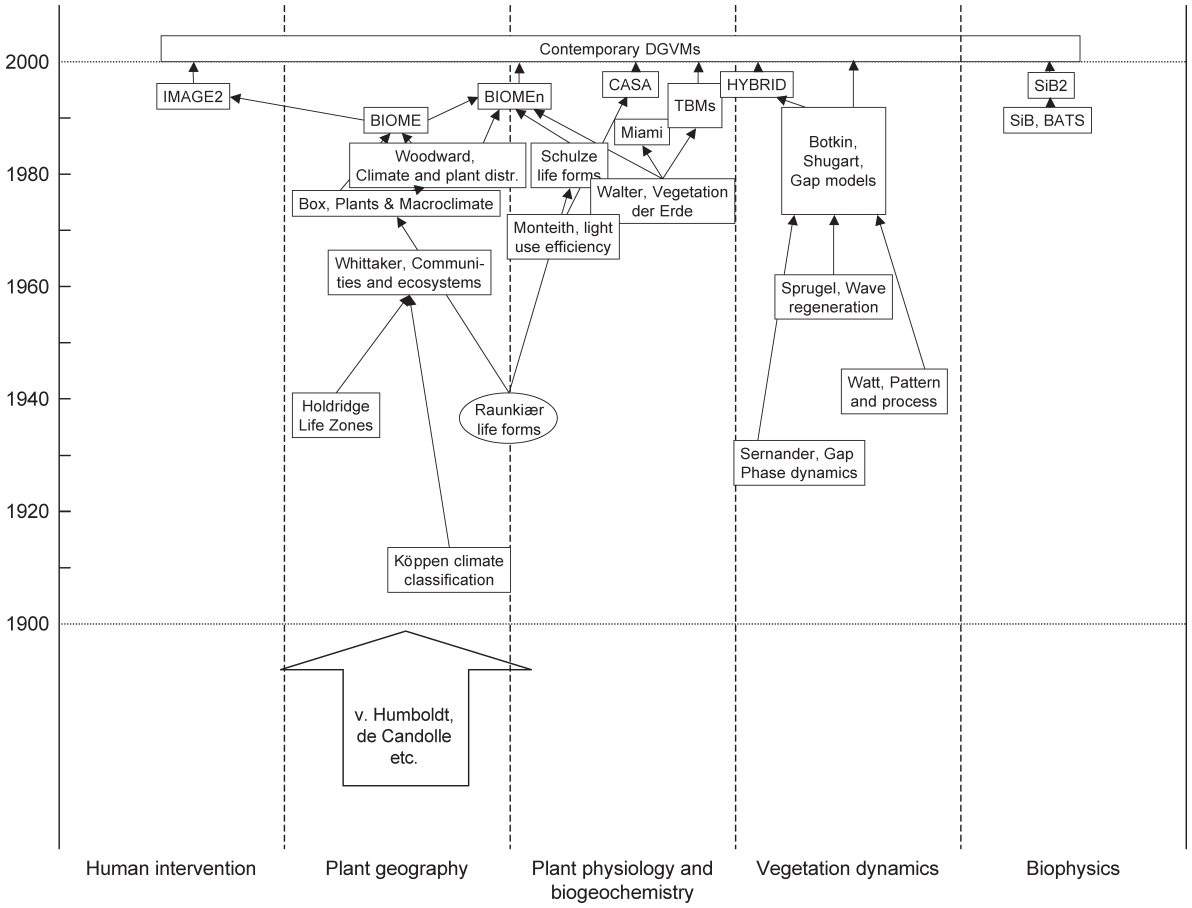

Fig. 15.1. A summary of the historical antecedents and recent development of DGVMs

15.2.1 Plant Geography

The beginnings of predictive modeling in plant geography can be traced to Köppen's (1931) world climate zones. Köppen tried to match the distribution of biomes, and included relevant seasonal aspects of climate in his classification scheme. A later (but more artificial) classification scheme based on annual climate statistics by Holdridge (1947) was used by Emanuel et al. (1985) to produce the first climate-derived map of global potential natural vegetation, and the first global projection of vegetation for a "greenhouse world" as simulated by a general circulation model (GCM). Further climate classifications designed to match biome distributions have been proposed by Whittaker (1975) and several others.

None of these schemes was based explicitly on an underlying theory of the controls on vegetation distribution, although the rudiments of a theory had been put forward by Raunkiær (1909, 1913, 1934). Raunkiær emphasized the role of mechanisms for surviving the unfavourable season in determining the distribution of different types of plants, which we would now call "plant functional types" (PFTs). Building on Raunkiær's ideas, Box (1981) created the first numerical model of global PFT distributions driven by climate. Woodward (1987) created the first explicitly process-based model of global biome distribution. The model included limits to woody PFT survival associated with cold tolerance, based on a review of experimental data. It included the dependence of leaf area index (LAI) on water availability, using an optimization principle introduced by Specht (1972). Woodward's approach was further developed in the "equilibrium biogeography models" BIOME (Prentice et al. 1992) and MAPSS (Neilson et al. 1992; Neilson and Marks 1994; Neilson 1995).

15.2.2 Plant Physiology and Biogeochemistry

General quantitative relationships between plant growth and resource availability became available during the 1960s through the International Biological Programme (IBP). Walter's *Vegetation der Erde* (Walter 1962, 1968) combined the older principles of plant geography with the new understanding of plant production. Lieth (1975) analysed IBP data statistically to create the so-called Miami model for net primary production (NPP) as a

function of climate. Schulze (1982) reviewed the role of carbon, water and nutrient constraints in determining the distribution of PFTs, emphasizing the importance of competitive success as well as survival limits.

"Terrestrial biogeochemistry models" (TBMs), as they are now known, were originally developed with the main goal of simulating NPP. The first to be applied globally was the Terrestrial Ecosystem Model (TEM) (Melillo et al. 1993). Other TBMs include Century (Parton et al. 1993), Forest-BGC (Running and Gower 1991: later BIOME-BGC; Running and Hunt 1993), CASA (Field et al. 1995), G'DAY (Comins and McMurtrie 1993), CARAIB (Warnant et al. 1994), DOLY (Woodward et al. 1995) and BETHY (Knorr 2000; Knorr and Heimann 2001). The more recent TBMs use the biochemical model of Farquhar et al. (1980) for the dependence of photosythesis on external variables. This model makes explicit the dependence of photosynthesis on the leaf-internal partial pressure of CO_2, providing a key component for process-based simulation of CO_2 effects.

Several of the original TBMs are still used widely. In addition, the BIOME*n* models (Haxeltine and Prentice 1996a,b; Kaplan et al. 2003) are a hybrid of the equilibrium biogeography and TBM approaches. They predict geographic distributions of biomes by comparing the modeled NPP of different PFTs within each PFT's survival limits. They can therefore make competition-based distinctions among biomes that the earlier equilibrium biogeography models could not, and they can incorporate CO_2 effects mechanistically (Cowling 1999; Harrison and Prentice 2003).

15.2.3 Vegetation Dynamics

All of the models discussed above are restricted in their application because they cannot represent dynamic transitions between biomes (Prentice and Solomon 1991; VEMAP Members 1995; Neilson and Running 1996; Woodward and Lomas 2004). To provide this capability, DGVMs have drawn on a very different scientific tradition. Classic ecological studies of vegetation dynamics, including Sernander (1936), Watt (1947) and Sprugel (1976), laid the foundations for the modern understanding of vegetation dynamics and prepared the way for the formal description of forest dynamics in terms of individual tree establishment, growth and mortality in JABOWA (Botkin et al. 1972), FORET (Shugart and West 1977), LINKAGES (Pastor and Post 1985) and a host of descendants (Shugart 1984), including extensions to non-forest vegetation types (e.g., Prentice et al. 1987). Newer incarnations of this "gap model" concept include FORSKA (Prentice and Leemans 1990; Prentice et al. 1993) and SORTIE (Pacala et al. 1993, 1996). These models typically are applied in a small region with parameter sets based on observations for individual species. They are computationally intensive because they simulate the stochastic behavior of many individual plants on multiple replicate plots.

DGVMs struggle to represent vegetation dynamics in a computationally efficient way without losing essential features that depend on interactions between plant individuals. Friend et al. (1997) used a simplified gap model approach, representing grid cell dynamics by a sample of patches. More efficient layer- (Fulton and Prentice 1997) and cohort-based (Bugmann 1996; Bugmann and Solomon 2000) approximations for vegetation dynamics exist, but have not been widely adopted. Most DGVMs rely instead on various *ad hoc* large-area parameterizations. Smith et al. (2001) however showed that the gap model formalism continues to give more realistic estimates of PFT dynamics, at least when compared to the large-area parameterization in the Lund-Potsdam-Jena (LPJ) DGVM (Sitch et al. 2003; see also Hickler et al. 2004a). A possible route to a more rigorously "traceable" representation of individual-based processes over large areas is suggested by the work of Moorcroft et al. (2001).

15.2.4 Biophysics

GCMs include representations of the controls on the exchange of energy, water vapor and momentum between the atmosphere and the land surface. Biophysical models developed for this purpose are called "land surface schemes" or "soil-vegetation atmosphere transfer models" (SVATs). Vegetation properties needed by the GCM include rooting depth, soil porosity, surface albedo, surface roughness, fractional vegetation cover, and surface conductance. Surface albedo depends on leaf reflectance, canopy structure and vegetation structural properties (including height) that determine the "masking" of snow. Changes in vegetation that affect surface albedo can profoundly affect climate (Bonan et al. 1992). Surface conductance depends on leaf area index and stomatal conductance, and is one of the controls on evapotranspiration. Accurate simulation of exchanges between the land and the free troposphere also depends on having an adequate representation of the planetary boundary layer (PBL). PBL dynamics depend on properties of the land surface, including the latent heat flux from the canopy (Finnegan and Raupach 1987; Monteith 1995; Prentice et al. 2004).

The first GCM land-surface schemes to represent vegetation explicitly were SiB (Sellers et al. 1986) and BATS (Dickinson et al. 1993). These models represented variations in stomatal conductance by empirical functions of PAR, temperature, humidity and soil moisture (Jarvis 1976). Later models have exploited the tight coupling of CO_2 and water exchange through stomatal conductance (Collatz et al. 1991). The current trend is to replace GCM land-surface schemes with full DGVMs. For this purpose, exchanges of energy, water vapor and momentum must be modeled at a time step similar to the shortest atmo-

spheric time step of the GCM (typically about 30 minutes). The DGVMs IBIS (Foley et al. 1996) and TRIFFID (Cox 2001) were developed for GCM coupling. Full coupling to an atmospheric GCM was first achieved by Foley et al. (1998) and Delire et al. (2002). Full physical coupling to an ocean-atmosphere GCM has been achieved by Robert J. Gallimore and others (e.g., Notaro et al. 2004) using LPJ (Sitch et al. 2003). LPJ also provided the basis for a generic vegetation dynamics component in Orchidée (Krinner et al. 2005) and several other DGVMs that are being developed for GCM coupling. All of the major climate modeling groups are now working towards full physical and carbon-cycle coupling of atmosphere, ocean and land, as first implemented by Cox et al. (2000).

15.2.5 Human Intervention

A final strand of model development addresses the changing suitability of the land for human land use and the reciprocal influence of human land use on the state of the biosphere. The most widely known example, and the most explicit in terms of representing land cover, is IMAGE2 (Alcamo 1994). IMAGE2 is widely cited and used for integrated assessment and scenario development. The land surface component of IMAGE2 was derived from BIOME (Prentice et al. 1992). However, several groups are now developing more advanced large-area representations of managed ecosystems, including explicit simulations of agricultural and forest management, as components of DGVMs (Bondeau et al. in press).

15.3 Principles and Construction of DGVMs

15.3.1 Model Architecture

The modular organization of DGVMs is rather uniform (Cramer et al. 2001; Sykes et al. 2001; Beerling and Woodward 2001; Woodward and Lomas 2004; Fig. 15.2). The design and process formulations of DGVMs are not fundamentally different from those in TBMs, which have been used to investigate some of the same questions (Heimann et al. 1998; McGuire et al. 2001). The most important unique feature of DGVMs is their ability to simulate vegetation dynamics. Within a grid cell, vegetation may be represented by fractions or strata occupied by different PFTs. Age or size classes may be distinguished, but more typically the modeled properties represent averages among the entire grid cell population of a given PFT (e.g., Sitch et al. 2003; Fig. 15.3). PFT-specific state variables, i.e., physical properties that change dynamically in the course of the model simulation, may include a description of the average geometry of individual plants, the carbon content of one or more plant biomass compartments (leaves, roots, wood), nitrogen (N) status, factors affecting resource uptake capacity (leaf area index, root density) and population density.

DGVMs implement two or three nested timing loops, calling different processes on different operational time steps (Fig. 15.2) corresponding loosely to the fastest characteristic time scale of the process. "Fast" processes varying on a diurnal cycle include energy and gas exchange

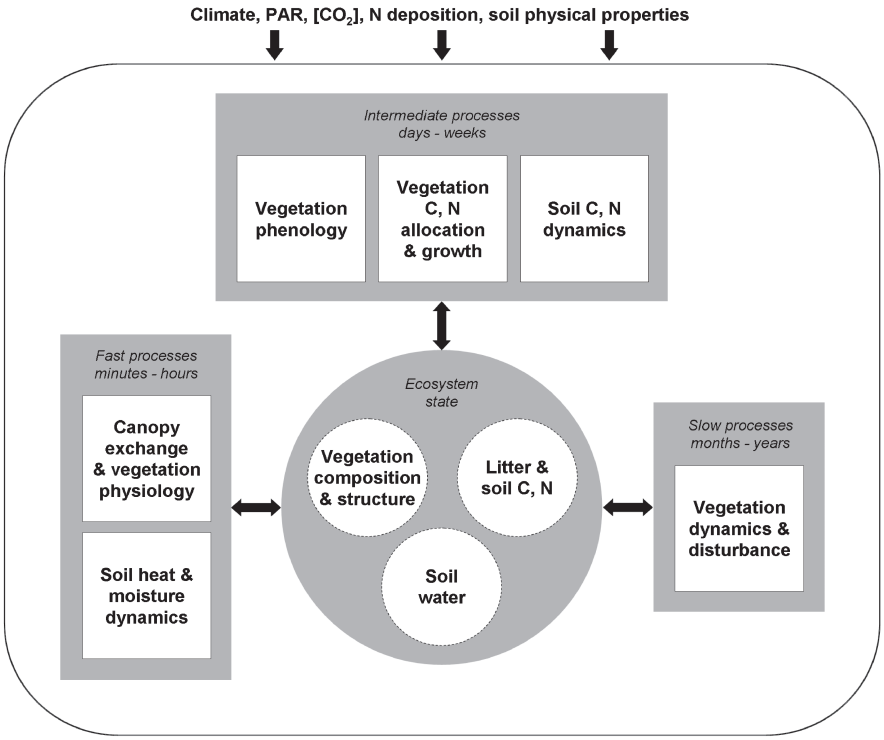

Fig. 15.2. DGVMs are structurally rather similar. This figure illustrates a typical structure, showing driving variables, main process modules (organized by operational timestep) and state variables

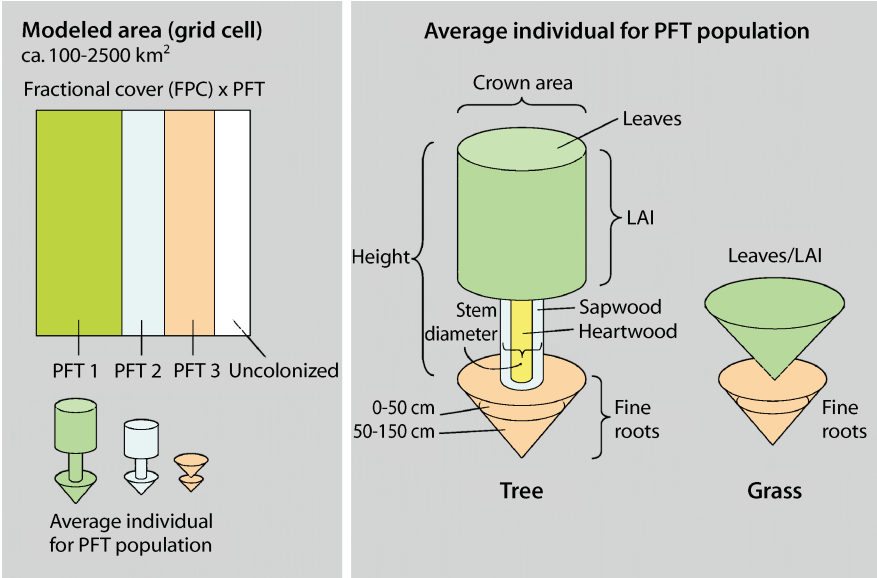

Fig. 15.3.
Each DGVM has adopted a different large-area parameterization for vegetation dynamics. This figure depicts one example (Sitch et al. 2003). Here, each PFT occupies a fraction of the modeled area (grid cell). Structural properties for one *average individual* for each PFT vary dynamically depending on carbon allocation, tissue turnover and allometric relationships. Population density scales PFT properties from the average individual to the grid cell

at the canopy-atmosphere interface, photosynthesis and plant-soil water exchange. These processes are invoked either on a time step of one day, using daily integrals of driving variables such as PAR, or (more accurately, in principle) at shorter time steps of one hour or less, in models that explicitly simulate the diurnal cycle. Processes with seasonal dynamics include plant phenology, growth and soil organic matter dynamics; the typical time step used for these processes is one month. Vegetation dynamics are generally the slowest process modeled, and are typically represented with a time step of one year.

15.3.2 Net Primary Production

The currency of growth in DGVMs is NPP, the balance of carbon uptake by photosynthesis and release by autotrophic respiration. Most DGVMs use the Farquhar et al. (1980) model, or derivatives thereof (Collatz et al. 1991, 1992; Haxeltine and Prentice 1996a,b), to model photosynthesis at the leaf level. Environmental and leaf parameters are either available from the input data (e.g., air temperature and CO_2 concentration), calculated based on the current vegetation or system state (stomatal conductance, leaf nitrogen content), or prescribed (specific leaf area). DGVMs explicitly or implicitly take into account shading of leaves at lower levels in the vegetation canopy by the levels above. Nitrogen invested in leaf functional proteins is commonly assumed to distribute among canopy layers in a fashion that maximises net assimilation, i.e., photosynthesis minus leaf respiration (Haxeltine and Prentice 1996a,b; Foley et al. 1996; Friend et al. 1997; Sitch et al. 2003), at each canopy level (see Dewar 1996 and Prentice 2001 for further discussion of this hypothesis and its variants).

The rate of diffusion of CO_2 from the ambient air via the boundary layer adjacent to leaf surfaces and the stomata is controlled by aggregate stomatal conductance, and limits photosynthesis. Plants are considered to regulate stomatal conductance, within limits, to optimise CO_2 uptake in relation to water loss through transpiration (Cowan 1977; Collatz et al. 1991). Thus, DGVMs typically couple photosynthesis, canopy biophysics and soil hydrology submodels via canopy conductance, although the detailed formulations vary.

Respiration is usually separated into maintenance and growth components. Maintenance respiration is sensitive to temperature and differs among tissues (Ryan 1991). Models may adopt a tissue-specific scaling factor combined with a common temperature response function, generally a Q_{10} or Arrhenius relationship. Alternatively, a function based on tissue C/N ratio may replace the tissue-specific multiplier. Growth respiration is usually defined as a fixed fraction of NPP. Some DGVMs alternatively use more empirical approaches to estimate NPP, with a potential rate moderated by scalars standing for environmental stresses (e.g., soil water, low temperatures, shading of grasses by trees: Daly et al. 2000) and/or resource availability and uptake capacity (Pan et al. 2002; Potter and Klooster 1999).

15.3.3 Plant Growth and Vegetation Dynamics

In all DGVMs, multiple PFTs are allowed to co-occur and compete. Tolerance limits for bioclimatic variables, such as coldest-month mean temperatures and growing-season heat sums, define the climatic space each PFT can occupy (Woodward 1987; Harrison et al. submitted). PFTs may be switched "on" or "off" in a particular grid cell, through PFT-specific establishment and mortality func-

tions, as the favourability of the climate varies. The driving force for vegetation dynamics is then the NPP of competing PFTs. In the simplest formulations of vegetation dynamics (e.g., Foley et al. 1996; Potter and Klooster 1999), individual and population growth are combined in an overall parameterization of the effects of resource competition on PFT abundances. Carbon assimilated by each PFT is partitioned among its biomass compartments (leaves, roots, stems) according to fixed allocation coefficients. Each compartment has a residence time, which determines the rate of transfer of carbon to litter pool due to tissue turnover and mortality. More mechanistic approaches distinguish individual- and population-level growth. In the LPJ implementation, the NPP accumulated by a tree PFT population during a year is first partitioned among "average individuals" based on the current population density (Sitch et al. 2003). Allocation and tissue turnover are calculated for the average individual, and are constrained to satisfy allometric relationships (Fig. 15.3). Population growth is the balance of an annual rate of establishment of new saplings, influenced by current density, and mortality, which may increase under conditions of resource limitation, crowding or disturbance.

The ability to adjust allocation patterns to maintain a balance between resource uptake and utilization is a key feature of plant competitive strategies (Field et al. 1992). Modeled allocation patterns in DGVMs can therefore be influenced by the relative supply of above- and below-ground resources. Soil water deficits in the current growing season, for example, may lead to increased investment in roots at the expense of leaves the following growing season.

15.3.4 Hydrology

DGVMs typically include some multi-layer scheme for soil water, with percolation and/or saturated flow between layers. Evaporation from the upper soil layer and the vegetation canopy (i.e., interception loss) may supplement plant transpiration. Water content in excess of field capacity is lost as runoff. Some models take account of the effects of snow and ground frost on seasonal water cycles. DGVMs have also been coupled to large-scale models for lateral water transport, in order to examine e.g., impacts of land-use change on river flow.

15.3.5 Soil Organic Matter Transformations

Carbon enters the soil as litter associated with tissue turnover and mortality. Litter and soil carbon provide the substrate for soil heterotrophs, whose respiration releases CO_2. "Pools" with different degrees of decomposability are usually distinguished. As the labile fractions are consumed, residues are transferred to pools with longer average residence times. The number of pools represented ranges from two or three to eight or more in models that implement the soil module from Century. Decomposition rates for a given pool are influenced by temperature, soil moisture status and, in some models, properties such as the C/N ratio of the decomposing material, soil texture and clay content.

15.3.6 Nitrogen (N) Cycling

After light and water availability, plant-available N is the most important limiting factor in many terrestrial ecosystems (e.g., Townsend et al. 1996). Nevertheless, only some of the current DGVMs include a full interactive terrestrial N cycle, taking into account below-ground controls on N mineralization as well as N limitations on NPP. DGVMs that incorporate the Century approach to soil processes inherit its coupled soil C and N scheme (Friend et al. 1997; Potter and Klooster 1999; Daly et al. 2000; Woodward et al. 2001; Bachelet et al. 2001). Here litter quality influences net N mineralization and decomposition rates; labile "metabolic" inputs, such as litter derived from leaves and fine roots, tend to increase net N mineralization, whereas lignin-rich "structural" material causes N immobilization and may limit N availability to plants. N limitation of production may be modeled by scaling net assimilation to plant uptake of N from the soil mineral N pool. In the Hybrid DGVM, N limitation implicitly reduces investment in Rubisco and chlorophyll, resulting in a lower maximum carboxylation rate and reduced photosynthesis (Friend et al. 1997).

15.3.7 Disturbance

The term "disturbance" is widely used to refer to processes such as fires, windstorms and floods, which rapidly destroy biomass, alter vegetation structure and alter the conditions for the growth of remaining plants and/or the establishment of new plants. This usage is illogical because "disturbances" by this definition are intrinsic to ecosystems and part of the mechanism that maintains their typical composition and character (Allen and Hoekstra 1990); however, it is entrenched in the literature. The stochastic nature of disturbance regimes makes them difficult to represent in models. Some DGVMs do not explicitly model disturbances; instead, they incorporate their effects implicitly in turnover constants for vegetation carbon (Foley et al. 1996; Friend et al. 1997).

Fire is the most important type of natural disturbance type worldwide, affecting all biomes except rainforests and deserts, at frequencies ranging from every year to once every few centuries. The most important controls on fire regimes are the frequency of ignition (whether natural or human-caused) and the amount, moisture content and flammability of biomass fuels. These controls depend on both climate and vegetation state, allowing for a variety of feedbacks in vegetation dynamics in-

volving fire. Thonicke et al. (2001) introduced a semi-empirical fire module for use in DGVMs (Pan et al. 2002; Sitch et al. 2003). The modeled area (grid cell) is considered to be large enough that ignition sources are available, and that the *fraction* of the grid cell affected by fire in a given year is equal to the *probability* of fire affecting a randomly chosen point. This probability is estimated using empirical equations based on fuel load and moisture content (estimated from the moisture of the top soil layer). PFTs differ in their resistance to fire, so that the degree of damage caused to standing biomass depends on the vegetation composition. Fires result in vegetation mortality and volatilization of a fraction of litter and biomass over the affected area.

A more advanced approach to modeling fire dynamics has been adopted in the MC1 DGVM. This model distinguishes surface and crown fires, and fire effects are sensitive to stand structure as well as fuel load (Lenihan et al. 1998; Daly et al. 2000; Bachelet et al. 2001, 2003). Venevsky et al. (2002) and Arora and Boer (in press) have developed fire models of intermediate complexity that allow for variations in ignition rates associated with human activities.

15.4 Evaluating DGVMS

DGVMs simulate processes at a wide range of space and time scales and, accordingly, many different types of contemporary observations can be used to test their performance. The following is a non-exhaustive summary of observational "benchmarks" for DGVMs. For further examples see e.g., Kucharik et al. (2000), Beerling and Woodward (2001) and Woodward and Lomas (2004).

15.4.1 Net Primary Production

Following the Potsdam NPP Intercomparison Project (Cramer et al. 1999), which engaged mainly TBMs in a first large-scale comparison of terrestrial models driven by a common set of input variables, the Ecosystem Model-Data Intercomparison project (http://gaim.unh.edu/Structure/Intercomparison/EMDI/) ran site-specific simulations of NPP and compared them to measurements of NPP from sites in each of the major biomes. A large data synthesis effort yielded NPP values at 162 Class A sites ("well documented and intensively studied") and 2 363 Class B sites ("globally extensive but less well documented and with less site-specific information"). A tendency was found for models to over-estimate low- to mid-range production at boreal and temperate sites, and to underestimate NPP in highly productive tropical sites. Modeled NPP tended towards an asymptote ~1 000 g C m^{-2} while measurements showed some higher values. The reasons for these discrepancies remain to be established.

15.4.2 Remotely Sensed "Greenness" and Vegetation Composition

The fraction of Absorbed Photosynthetically Active Radiation (fAPAR) is the ratio of vegetation-absorbed to incident PAR. It can derived from satellite spectral reflectance data and is a measure of vegetation "greenness". The seasonal course of fAPAR provides a way to test modeled phenology (Bondeau et al. 1999). Some TBMs, known as light-use efficiency models, use remotely sensed fAPAR as input (e.g., Potter et al. 1993; Knorr and Heimann 1995; Ruimy et al. 1996). Alternatively, fAPAR observations can also be used to calibrate phenology in models (Kaduk and Heimann 1996; Botta and Foley 2002; Arora and Boer 2005). Seasonal cycles of fAPAR have also been used together with ancillary information to construct global maps of vegetation composition in terms of a few broadly defined PFTs. For example, Sitch et al. (2003) used the DeFries et al. (2000) global data set of estimated fractional PFT cover as a benchmark for vegetation composition, while Woodward and Lomas (2004) used the HYDE land-cover type data set of Klein Goldewijk (2001).

15.4.3 Atmospheric CO_2 Concentration

A different approach to large-scale evaluation of terrestrial models (Prentice et al. 2000) makes use of high-precision atmospheric measurements of CO_2 concentration (http://www.cmdl.noaa.gov/ccgg/globalview/co2/). Both the amplitude and the timing of the seasonal cycle of CO_2 vary geographically, reflecting different seasonal patterns of biospheric activity. The amplitude is greatest in northern high latitudes because of the large vegetated area in the north and the large offset in the timing of NPP and heterotrophic respiration maxima in high latitudes. Heimann et al. (1998) ran the TM2 atmospheric transport model with monthly fields of net ecosystem exchange (heterotrophic respiration and combustion minus NPP) from four terrestrial models. The output was sampled at the locations of CO_2 monitoring stations. Knorr and Heimann (1995, 2001), Dargaville et al. (2002) and Sitch et al. (2003) continued this approach. The main caveat for such comparisons is that they rely on the realism of the transport model; this is an active research area (Denning et al. 1999; Gurney et al. 2003; Law et al. 2003; Gurney et al. 2004). Inversion of tracer transport models has also been used to infer regional sources and sinks of CO_2 directly from the CO_2 concentration network (Fan et al. 1998; Bousquet et al. 2000; Kaminski and Heimann 2001; Rödenbeck et al. 2003). Peylin et al. (2005) showed good agreement between interannual carbon exchanges over broad regions as calculated by inverse models and as simulated with a DGVM and a TBM. Most of the observed interannual variability in the atmospheric CO_2 growth rate was shown to be explained by the differential responses of NPP and heterotrophic respiration to climate.

15.4.4 Runoff

As all terrestrial biosphere models simulate the interaction of the carbon and water cycles, the models can be evaluated in terms of their performance in simulating measured water fluxes (Gordon and Famiglietti 2004; Gordon et al. 2004). Over multi-annual time scales, runoff – which is measured at gauging stations on rivers – is equivalent to the difference between precipitation and evapotranspiration, averaged over the catchment upstream of the station. Gerten et al. (2004) demonstrated that LPJ showed comparable skill to existing global hydrology models in predicting global runoff patterns. They went on to model the additional effect of changing CO_2 concentration (via changes in stomatal conductance) on runoff.

15.4.5 CO_2 and Water Flux Measurements

Measurements of CO_2 and water flux from towers by the eddy covariance technique provide a temporally highly resolved record, and a powerful new tool for model evaluation (Falge et al. 2002; Baldocchi 2003). The FLUXNET global network of flux measurement stations gathers data from as many as 200 sites, although these are still very unevenly distributed across the globe (Baldocchi and Gu 2002; http://www.daac.ornl.gov/FLUXNET/fluxnet.html/). The data record diurnal, seasonal and interannual variability. CO_2, water and energy fluxes are measured simultaneously and concurrently with meteorological measurements that can be used directly to drive the models. There are two main limitations: the data are typically incomplete (for reasons discussed by Dolman et al. 2003), and the results (in common with conventional NPP measurements) are site-specific so that accurate specification of local soil conditions and disturbance history may be important. The experience obtained so far (e.g., Amthor et al. 2001; Potter et al. 2001; Gerten et al. 2004; Krinner et al. 2005; Morales et al. submitted) suggests that TBMs and DGVMs can perform well in simulating seasonal cycles and interannual variability of measured CO_2 and water exchange, but that the annually integrated carbon balance may depend on site-specific and generally unknown historical management factors.

15.5 Examples of Applications of DGVMS

DGVMs can be used alone or coupled to other types of models as tools to understand changes in the Earth System. Here we summarize a selection of DGVM studies that have helped either to explain observed phenomena, or to predict the consequences of human activities in the future.

15.5.1 Holocene Changes in Atmospheric CO_2

The causes of changes in the atmospheric concentration of CO_2 since the end of the last glacial period, about 12 ka before present (BP), are controversial. Ice-core analyses show a drop of 7 ppm from 11 to 8 ka BP, followed by a gradual rise of 20 ppm towards the pre-industrial 280 ppm (Indermühle et al. 1999; Flückiger et al. 2002). Indermühle et al. (1999) attributed both the initial drop and subsequent rise primarily to changes in terrestrial carbon storage. Broecker et al. (2001) questioned this explanation for the rise, suggesting instead that CO_2 removed from the atmosphere and surface ocean water by terrestrial carbon uptake after the glacial maximum was slowly replaced due to the precipitation of $CaCO_3$ at depth ("calcite compensation"). Ruddiman (2003) on the other hand has ascribed the CO_2 rise to deforestation. This problem has been studied with DGVMs by Brovkin et al. (2002) and by Joos et al. (2004). Joos et al. (2004) forced the Bern-CC coupled carbon cycle model (which includes the LPJ DGVM for terrestrial carbon dynamics) with palaeoclimate model simulations (Kaplan 2002). The coupled model reproduced the observed CO_2 trajectory since 11 ka BP to within a few ppm. The initial drop was explained by vegetation regrowth. The subsequent increase in CO_2 concentration was mainly due to *(a)* rising sea surface temperature, and *(b)* calcite compensation, as Broecker et al. (2001) proposed. The ice-core record of $\delta^{13}C$ (Indermühle et al. 1999) rules out any large contribution from deforestation. This model version also simulates the terrestrial $\delta^{13}C$ budget, based on Kaplan et al. (2002) and Scholze et al. (2003). The modeled $\delta^{13}C$ history was consistent with the ice-core data.

15.5.2 Boreal "Greening" and the Contemporary Carbon Balance

Spectral reflectance observations have shown a persistent greening trend in northern high latitudes through the 1980s and 1990s (Myneni et al. 1997; Zhou et al. 2001). Maximum summer LAI in the boreal zone, estimated from these observations, increased by 0.19 between 1982 and 1998. Potential explanations include vegetation response to high-latitude warming, forest regrowth due to changed management, vegetation recovery from disturbance by fire or insect attacks, CO_2 fertilization, or (just possibly) incomplete correction for drifts in the response of the sensor. Lucht et al. (2002) investigated whether the greening trend could be explained by vegetation responses to climate. Simulations driven by monthly climate data (New et al. 2000) showed that the trend, its seasonal cycles and interannual variability could all be reproduced. The simulations were entirely independent of the satellite observations. Thus, it is most likely that

the observed greening trend is real and was caused by the changing climate. Further simulations showed that virtually all of the effect has been due to warming. These findings are consistent with the over-riding control of temperature on vegetation growth in high latitudes. The controls are more complex in warmer climates. Figure 15.4 shows the simulated land-atmosphere flux averaged over the whole period, compared with climate anomalies. Some regions showed a large reduction in precipitation (e.g., the Sahel), others a large increase in temperature (e.g., southern Africa), both leading to a release of carbon because of reduced NPP and/or increased heterotrophic respiration. Some regions, such as the southeastern USA, experienced increased precipitation and decreased temperatures, leading to increased carbon uptake (cf. Nemani et al. 2002; Hicke et al. 2002; Rödenbeck et al. 2003).

15.5.3 The Pinatubo Effect

Atmospheric CO_2 concentration temporarily slowed its increase after the eruption of Mount Pinatubo in 1991. Aerosols from this eruption cooled the globe by around 0.5 °C (more in northern latitudes). DGVM simulations over this period have reproduced both a temporary drop in boreal LAI (also shown by the satellite data) and an enhanced high-latitude terrestrial carbon sink (Lucht et al. 2002). Although NPP and heterotrophic respiration were both reduced, the modeled effect on respiration was stronger, producing an enhanced carbon sink. But these changes at high latitudes were not large enough to provide the full explanation. The simulated *global* patterns of simulated NPP and heterotrophic respiration anomalies are more complex, and controversial. Roderick et al. (2001) and Gu et al. (2002) have argued that an increase in the fraction of diffuse vs. direct radiation caused large-scale enhancement of NPP during the post-Pinatubo period. In other words, an enhanced sink was produced by increased NPP. But Angert et al. (2004) have shown that this hypothesis is inconsistent with observed seasonal cycles of CO_2 during these years. Jones and Cox (2001) used GCM simulations incorporating the TRIFFID DGVM to suggest that post-Pinatubo climatic anomalies overall produced enhanced NPP in the tropics, while respiration globally was reduced.

15.5.4 Future Carbon Balance Projections

Schaphoff et al. (2006) predicted the response to climate and CO_2 changes during the 21st century, as simulated by five ocean-atmosphere GCMs, all driven by a standard "business as usual" CO_2 emissions scenario. The simulated change in terrestrial carbon storage ranged from a loss of 106 Pg C to a gain of 201 Pg C (neglecting land-use changes). This finding complements Cramer et al. (2001), who found large uncertainty *within* one climate change scenario, due to differences among six DGVMs. The spatial patterns of changes in carbon content found by Schaphoff et al. were more robust than the global total. Carbon storage was enhanced due to warming in the Arctic and at high elevations, but reduced over the temperate and boreal zones. Carbon storage was also increased in many semi-arid regions due to increased vegetation water-use efficiency and woody encroachment at high CO_2, with soil carbon loss inhibited due to drought. Tropical vegetation response varied due to precipitation differences among GCMs.

15.5.5 Carbon-Cycle Feedbacks to Future Climate Change

DGVM simulations based on climate projections of the 21st century have indicated that the time course of carbon storage depends on a balance of CO_2 fertilization and the positive effect on NPP of longer and warmer growing seasons in cold climates, vs. the general increase in heterotrophic respiration rates and the negative effect of high temperatures on NPP in warm climates (Cao and Woodward 1998; Kicklighter et al. 1999; Cramer et al. 2001; Schaphoff et al. 2006). CO_2 fertilization is expected to show a "diminishing return" while the effect of warming on respiration will continue (Jones et al. 2003). As a result, future projections of terrestrial carbon storage have often shown an initial increase in terrestrial carbon storage followed by a decline. Cox et al. (2000) used a fully coupled GCM, including the Hadley Centre (HADCM3) ocean-atmosphere model and the TRIFFID DGVM, to perform a comprehensive analysis based on a "business as usual" CO_2 emissions scenario. They found that the carbon-climate feedback had generated an additional 1.5 K global warming by 2100, mostly due to increased heterotrophic respiration. A similar analysis using the IPSL ocean-atmosphere model and the SLAVE TBM (Dufresne et al. 2002) also found a positive feedback, but the change was less, and was mostly due to reduced NPP in the tropics. Reasons for the difference include stronger vertical mixing in the IPSL ocean model, and greater initial soil carbon storage in the Hadley Centre model (Friedlingstein et al. 2003). Yet despite uncertainty about the size of carbon cycle feedbacks, the largest uncertainty in the future CO_2 concentration is still the unknown future of CO_2 emissions from fossil fuels. Joos et al. (2001) used the Bern-CC model to examine the consequences of six different emissions scenarios. A positive carbon-cycle feedback to climate change was found in all cases and atmospheric CO_2 rose to between 540 and 960 ppm, depending on the scenario and on assumptions about climate sensitivity, by 2100.

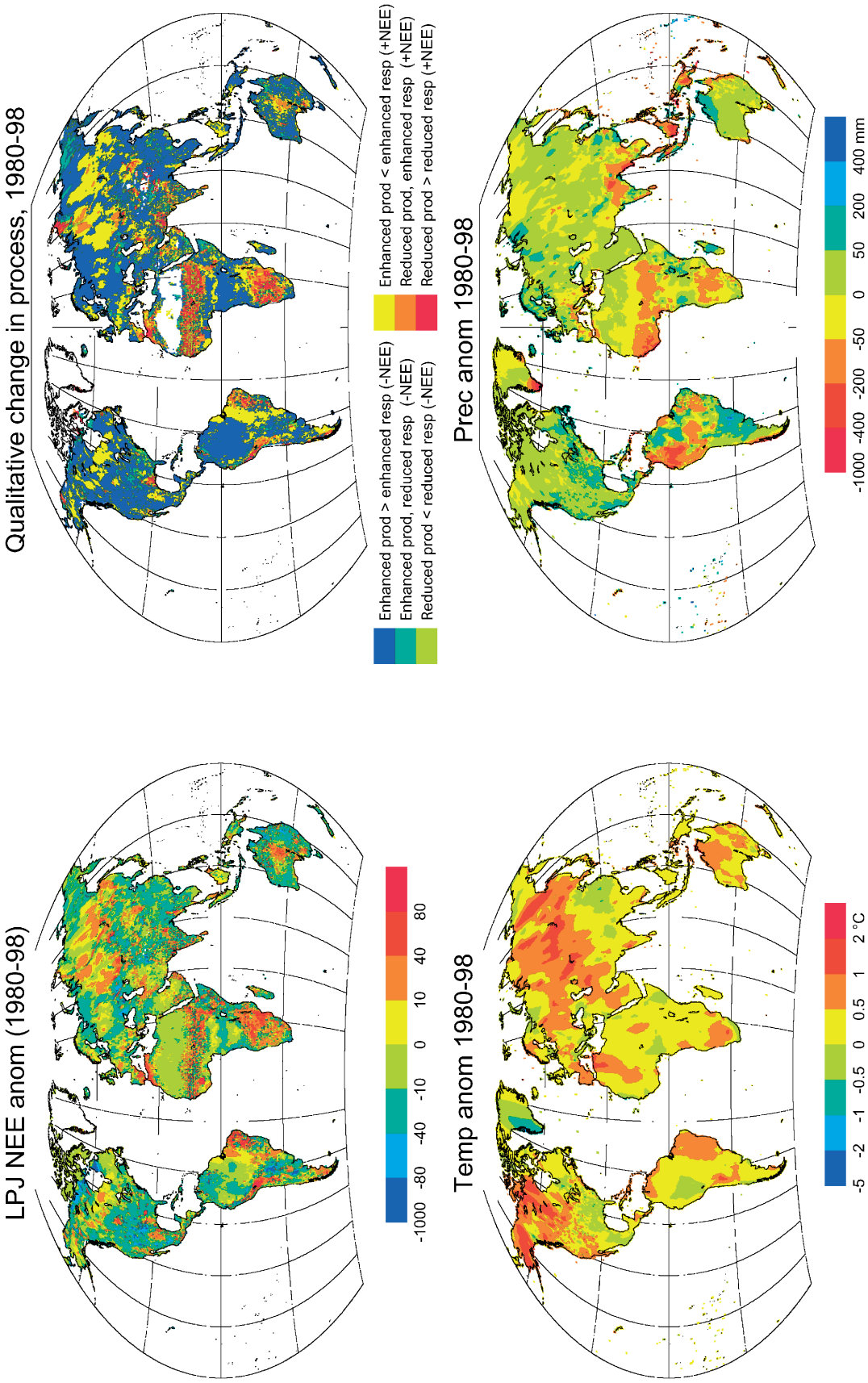

Fig. 15.4. Global patterns of the modeled terrestrial carbon balance during 1980–1998, simulated with the LPJ DGVM. The *top left panel* shows anomalies of net ecosystem exchange (*NEE* = heterotrophic respiration + combustion – *NPP*), i.e., mean *NEE* during 1980–1998 minus *NEE* for the standard climatological period (1931–1960). The *top right panel* shows the origin of the anomalies in terms of increases or decreases in "respiration" (strictly, heterotrophic respiration + combustion) and "production" (*NPP*). The corresponding annual mean anomalies of temperature and precipitation are shown in the *bottom panels*

15.5.6 Effects of Land-Use Change on the Carbon Cycle

Land-use change was the main cause of increasing atmospheric CO_2 in the early industrial period, and is still a substantial contributor. McGuire et al. (2001) used four terrestrial models to assess the relative roles of CO_2 fertilization, climate variation and land-use change through the industrial era. The simulated cumulative effect of cropland establishment and abandonment from 1920 to 1992 was a release of 56–91 Pg C. The concurrent simulated uptake, due mainly to CO_2 fertilization, was 54–105 Pg C. The modeled net terrestrial carbon budget proved broadly consistent with independent estimates from atmospheric measurements (Prentice et al. 2001; House et al. 2003). This global analysis has not yet been extended beyond 1992, nor carried into the future. Some possible consequences of future land-use change have been analysed, however. Cramer et al. (2004) used LPJ to estimate past and potential future losses of carbon from wet tropical ecosystems, which are the main site of deforestation today. During the 20th century, deforestation was estimated to have released 39–49 Pg C. Extrapolating a range of estimates for current rates of deforestation into the future yielded a projected additional loss of 158–243 Pg C by 2100. By comparison, CO_2 fertilization and climate change produced a response ranging from a gain of 80 Pg C to a loss of 50 Pg C. Direct human intervention, therefore, is likely to be the most important determinant of the fate of carbon in tropical forests.

15.6 Some Perspectives and Research Needs

The following discussion is by no means a complete overview of the aspects of DGVMs that are in need of further testing and development. However, it points to some key areas where an international collaborative effort, building on the achievements of GCTE, would very likely lead to more rapid progress than could be achieved by individual groups working alone.

15.6.1 Comparison with Field Experiments

Experimental studies of the response of terrestrial ecosystems to environmental changes has been a major focus for GCTE. For example, experimental evidence from studies with small trees in open-top chambers has shown an average stimulation of photosynthesis by ≈60% for a 300 ppmv increase in CO_2, while the annual increment in wood mass per unit leaf area increased by ≈27% (Norby et al. 1999). The Free-air CO_2 enrichment (FACE) methodology was introduced so that experiments on the effects of raised CO_2 concentrations could be conducted on intact ecosystems (Hendry et al. 1999; Nowak et al. 2004; Long et al. 2004). The first FACE study in an intact forest ecosystem was set up in a *Pinus taeda* plantation in the southeastern USA (DeLucia et al. 1999). Ambient CO_2 concentrations were increased to 560 ppmv in the replicated plots from autumn 1996. From 1997 to 2000, annual NPP was on average 23% higher in plots with elevated CO_2 than in the control plots (Delucia et al. 1999; Hamilton et al. 2002; Schäfer et al. 2003). F. I. Woodward and M. Lomas (personal communication 2004) used the SDGVM to simulate this experiment. They obtained a realistic 20% enhancement in net primary production after four years. Hickler et al. (2004b) obtained a range from 15 to 33% increase over the same period. There is considerable scope for rigorous testing of different process formulations in DGVMs using the data now available from experiments involving artificial warming, drought and N fertilization as well as an increasing range of FACE studies.

15.6.2 Plant Functional Types

PFT schemes in current DGVMs are simplistic, and the values of most PFT-specific parameters are neither agreed nor well founded. GCTE has stimulated new interest in PFT classification (Díaz and Cabido 1997; Díaz et al. 1999a; Gitay and Noble 1997; Lavorel et al. 1997; Lavorel and Cramer 1999; Lavorel and Garnier 2002; Lavorel et al. 2007, Chap. 13 of this volume), but this has not yet filtered through to influence DGVM design. Current approaches to PFT classification emphasize readily observable plant traits that confer characteristic responses to factors of the environment and disturbance or management regime (e.g., Díaz et al. 1999b; Díaz et al. 2002; Gurvich et al. 2002; Barboni et al. 2004; Díaz et al. 2004; Wright et al. 2004). This is precisely the kind of information that is needed for the more rational representation of PFTs in DGVMs. The development of an internally-consistent, global vegetation map explicitly based on PFTs and based on high-resolution multispectral reflectance data is a related but distinct goal, proposed by Nemani and Running (1996). Such a map would be extremely useful for testing DGVMs. Various satellite-based global land-cover maps are now available, but there are still considerable differences among them, and the procedures used to generate them are not entirely transparent.

15.6.3 The Nitrogen Cycle

Hungate et al. (2003) suggested that scenario analyses with current DGVMs (Cramer et al. 2001; Prentice et al. 2001) exaggerate the amount of carbon the biosphere could take up in response to a continued increase in atmospheric CO_2. In fact, the two DGVMs in Cramer et al. (2001) that explicitly allow for N cycle constraints on NPP produce lower estimates of future carbon storage than those that do not. But these estimates still fall above the

range postulated by Hungate et al. (2003). Recent simulations with the LPJ model (Schaphoff et al. 2006) produce estimates within this range, even though this model does not yet include N cycle constraints on NPP. Whatever the correct view on future CO_2 uptake, improving the representation of N cycling within DGVMs is a research priority. This work is hampered by inadequate quantification of gain and loss terms in the N cycle at regional and global scales (e.g., amount of N in precipitation, controls of N_2 fixation and dissolved organic N losses, and the release and fate of N-containing trace gases). Incorporation of a realistic N cycle is also important for prediction of the influence of soil nutrient status controls on PFT distributions, and to assess the impacts of anthropogenic N deposition on the carbon cycle and ecosystems.

15.6.4 Plant Dispersal and Migration

Current DGVMs assume that the rate of plant dispersal and migration does not limit the response of vegetation to climate change. This assumption is called into question by the fact that large changes in climate could occur rapidly (i.e., over a few decades) in some regions, and by the potential barriers to plant migration caused by landscape fragmentation. The issue is hard to address observationally because of the difficulty in quantifying rare long-distance dispersal events, which are believed on theoretical grounds to be crucial to explaining how rapid, continent-wide plant migrations occurred in response to climate changes in the Quaternary (Pitelka and Plant Migration Working Group 1997; Clark et al. 1998). Model formalisms to represent plant dispersal (e.g., Higgins et al. 2003) have been devised, but not implemented in DGVMs.

15.6.5 Wetlands

Wetlands are a major carbon store and are sources of the greenhouse gases methane (CH_4) and nitrous oxide (N_2O). The lateral transport of water is generally less important as a determinant of terrestrial vegetation than the *in situ* water balance, but this is not so for wetlands. DGVMs to date treat only dryland ecosystems. Extension to wetlands will require DGVMs to be coupled to water routing models with high spatial resolution. It will also be important to account for specific wetland PFTs, and the controls on nutrient supply to different types of wetland.

15.6.6 Multiple Nutrient Limitations

Realistic simulation of nutrient constraints on vegetation productivity will require not only the incorporation of lateral transport of nutrients by water, but also lateral transport in the atmosphere. For example, on geological time scales, aeolian transport of dust is a major control on phosphorus supply to terrestrial ecosystems (Chadwick et al. 1999). Transport of sulfate-containing aerosols derived from the production of dimethylsulphide by phytoplankton is a unique natural route for the redistribution of sulfur to the land surface. Precipitation is a significant source of N even in remote, unpolluted regions. Models of plant growth have scarcely begun to address the way in which different nutrient limitations interact. Marine ecosystems are already beginning to incorporate the interactions of the cycles of nitrogen, phosphorus, iron and silicon and their consequences for competition among phytoplankton PFTs (Aumont et al. 2003; Blackford and Burkill 2002; Blackford et al. 2004; Le Quéré et al. in press) and may inspire further DGVM development in this field.

15.6.7 Agriculture and Forestry

Efforts are already underway to simulate crop productivity and yield generically using DGVMs (e.g., Kucharik and Brye 2003). One objective of this work is to predict the consequences of climate change for agriculture. Such predictions will also have to consider climatically induced changes in the suitability of different crops, and non-climatic as well as climatic drivers of changes in land use – requiring that DGVMs be embedded in an integrated assessment framework. Forest management likewise has been only partially treated in DGVMs. Global carbon cycle studies have taken into account the consequences of deforestation and reforestation (Houghton 2003; McGuire et al. 2001), but not changes in logging intensity although these are thought to have had a major role in creating a present-day carbon sink in northern temperate forests (Nabuurs et al. 2003). The representation of forest management places new demands on DGVMs to show the correct response of forest NPP to stand age and density. Progress in modeling economically important ecosystems must be matched by progress in the collection and standardization of statistical data on crop distribution, yields and farming practices, and past and present forest management regimes. Adequate representation of management is important for the assessment of practices designed to increase carbon storage in ecosystems, which the present generation of DGVMs is not well adapted to address (Bondeau et al. in press).

15.6.8 Grazers and Pests

The eventual expansion of DGVMs to cover components of the ecosystem other than autotrophic plants and heterotrophic soil organisms (bacteria and fungi) is unavoidable. The abundances of grazing animals, and of pests such as leaf- and bark-eating insects, exert an important control on vegetation productivity and disturbance in several biomes. It should be possible to simulate the impact of changes in

both natural and managed grazing regimes by introducing a small number of animal functional types (AFTs). Models of marine ecosystems, where the ratio of secondary to primary production is much higher, already incorporate functional types of zooplankton grazers with different feeding preferences and population growth rates (Bopp et al. 2002; Aumont et al. 2003; Le Quéré et al. in press).

15.6.9 Biogenic Emissions of Trace Gases and Aerosol Precursors

Through various processes, the terrestrial biosphere emits the greenhouse gas N_2O, reactive gases that have a major influence on atmospheric chemistry including the greenhouse gas CH_4, carbon monoxide (CO), nitrogen oxides (NO_x), volatile organic compounds (VOCs) such as isoprene, and aerosol precursors in the form of dust, black carbon and VOCs. The extension of DGVMs to model sources and sinks of trace gases and aerosol components is a natural development. DGVMs will be called on to model CH_4 production in wetlands and oxidation in drylands (Kaplan 2002; Ridgwell et al. 1999), VOC production (e.g., Guenther et al. 1995), the N cycle including controls on the relative production of N_2, N_2O and NO in soils (Potter and Klooster 1999), ozone (O_3) uptake by vegetation, the relationships among dust emission, vegetation density and height (Tegen et al. 2002), the occurrence and intensity of fires, and the emissions of CO, CH_4, NO_x and black carbon associated with fires (Andreae and Merlet 2001; Thonicke et al. 2005). Progress has been made in most of these areas individually, but further efforts will be required to develop a comprehensive emissions model that can be coupled to an atmospheric chemistry and transport model (CTM) and ultimately to a GCM, in order to better understand the role of the biosphere in determining the atmosphere's changing chemical composition and, through this, the Earth's climate.

15.7 Summary and Conclusions

DGVMs exploit the power of modern computers and computational methods to yield a predictive description of land ecosystem processes that takes account of knowledge previously developed through long histories of separate disciplinary approaches to the study of the biosphere. The degree of interaction between the different scientific approaches still falls far short of optimal; thus, DGVM developers have a responsibility to be aware of progress in several disciplines in order to ensure that their models remain state-of-the-art. We have presented a series of case studies of the evaluation of DGVMs that demonstrate the predictive capability that current models have achieved. Nevertheless, there are plenty of unresolved issues – differences among models that are not well understood, important processes that are omitted or treated simplistically by some or all models, and sets of observations that are not satisfactorily reproduced by current models. More comprehensive "benchmarking" of DGVMs against multiple data sets is required and would be most effectively carried out through an international consortium, so as to avoid duplicating the large amount of work involved in selecting and processing data sets and model experiments. We have also presented a series of case studies that illustrate the power of DGVMs, even with their known limitations, in explaining a remarkable variety of Earth System phenomena and in addressing contemporary issues related to climate and land-use change. These case studies encourage us to believe that the continued development of DGVMs is a worthwhile enterprise. Finally, new directions in Earth System Science point to a range of aspects in which DGVMs could be improved so as to take account of recently acquired knowledge, such as experimental work on whole-ecosystem responses to environmental modification and new understanding of the functional basis of plant traits; complemented by an effort to represent semi-natural and agricultural ecosystems and the impacts of different management practices on these ecosystems; and extended to include processes such as trace-gas emissions, which are important in order to understand the functional role of the terrestrial biosphere in the Earth System. Together, these potential developments add up to an ambitious research program, requiring the economies of scale that only an international collaborative effort can provide.

References

Alcamo J (1994) IMAGE 2.0: Integrated Modeling of Global Climate Change. Kluwer Academic Press, Dordrecht, Boston, pp 314

Allen TFH, Hoekstra TW (1990) The confusion between scale-defined levels and conventional levels of organization in ecology. Journal of Vegetation Science 1:5–12

Amthor JS, Chen JM, Clein JS, Frolking SE, Goulden ML, Grant RF, Kimball A, King W, McGuire AD, Nikolov NT, Potter CS, Wang S, Wofsy SC, (2001) Boreal forest CO_2 exchange and evapotranspiration predicted by nine ecosystem process models: Inter-model comparisons and relations to field measurements. Journal of Geophysical Research, 106: D24 33623–33648

Andreae MO, Merlet P (2001) Emission of trace gases and aerosols from biomass burning. Global Biochemical Cycles 15:955–966

Angert A, Biraud S, Bonfils C, Buermann W, Fung I (2004) CO_2 seasonality indicates origins of post-Pinatubo sink. Geophysical Research Letters 31: L11103, doi:10.1029/2004GL019760

Arora VK, Boer GJ (2005) A parameterization of leaf phenology for the terrestrial ecosystem component of climate models. Global Change Biology 11:39–5

Arora VK, Boer GJ (in press) Fire as an interactive component of dynamic vegetation models. Journal of Geophysical Research – Biogeosciences

Aumont O, Maier-Reimer E, Blain S, Pondaven P (2003) An ecosystem model of the global ocean including Fe, Si, P co-limitations. Global Biochemical Cycles 17: doi:10.1029/2001GB001745

Bachelet D, Lenihan JM, Daly C, Neilson RP, Ojima DS, Parton WJ (2001) MC1: A dynamic vegetation model for estimating the distribution of vegetation and associated ecosystem fluxes of carbon, nutrients and water. USDA Forest Service General Technical Report, PNW-GTR-508:1–95

Bachelet D, Neilson RP, Hickler T, Drapek RJ, Lenihan JM, Sykes MT, Smith B, Sitch S, Thonicke K (2003) Simulating past and future dynamics of natural ecosystems in the United States. Global Biochemical Cycles 17: 1045 doi:1010.1029/2001GB001508
Baldocchi D (2003). Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. Global Change Biology 9:479–492
Baldocchi D, Gu LH (2002) Fluxnet 2000 synthesis – Foreword. Agricultural and Forest Meteorology 113:1–2
Barboni D, Harrison SP, Bartlein PJ, Jalut G, New M, Prentice IC, Sanchez-Goñi M-F, Spessa A, Davis B, Stevenson AC (2004) Relationships between plant traits and climate in the Mediterranean region: A pollen data analysis. J Vegetat Sci 15:635–646
Beerling DJ, Woodward FI (2001) Vegetation and the Terrestrial Carbon Cycle: Modelling the first 400 Million Years. Cambridge University Press
Blackford JC, Burkill PH (2002) Planktonic community structure and carbon cycling in the Arabian Sea as a result of monsoonal forcing: the application of a generic model. Journal of Marine Systems 36:239–267
Blackford JC, Allen JI, Gilbert FJ (2004) Ecosystem dynamics at six contrasting sites: a generic modeling study. Journal of Marine Systems 52:191–215
Bonan GB, Pollard D, Thompson SL (1992) Effects of boreal forest vegetation on global climate. Nature 359:716–718
Bondeau A, Kicklighter DW, Kaduk J (1999) Comparing global models of terrestrial net primary productivity (NPP): importance of vegetation structure on seasonal NPP estimates. Global Change Biology 5:35–45
Bondeau A, Smith PC, Zaehle S, Schaphoff S, Lucht W, Cramer W, Gerten D, Lotze-Campen H, Müller C, Reichstein M, Smith B (in press) Modelling the role of agriculture for the 20th century global terrestrial carbon balance. Global Change Biology
Bopp L, Le Quéré C, Heimann M, Manning AC, Monfray P (2002) Climate-induced oceanic oxygen fluxes: Implications for the contemporary carbon budget. Global Biogeochemical Cycles 16: doi:10.1029/2001GB001445
Botkin DB, Janak JF, Wallis JR (1972) Some ecological consequences of a computer model of forest growth. J Ecol 60:849–872
Botta A, Foley JA (2002) Effects of climate variability and disturbances on the Amazonian terrestrial ecosystems dynamics. Global Biogeochemical Cycles 16(4): doi:10.1029/2000GB001338
Bousquet P, Peylin P, Ciais P, Le Quéré C, Friedlingstein P, Tans P (2000) Regional changes in carbon dioxide fluxes of land and oceans since 1980. Science 290:1342–1346
Box EO (1981) Predicting physiognomic vegetation types with climate variables. Vegetatio 45:127–139
Broecker WS, Lynch-Stieglitz J, Clark E, Hadjas I, Bonani G (2001) What caused the atmosphere's CO_2 content to rise during the last 8 000 years? Geochem. Geosyst. 2: doi:2001GC00177
Brovkin V, Bendtsen J, Claussen M, Ganopolski A, Kubatzki A, Petoukhov V, Andreev A (2002) Carbon cycle, vegetation, and climate dynamics in the Holocene: Experiments with the CLIMBER-2 model Global Biogeochemical Cycles 16: 1139; doi:10.1029/2001GB001662
Bugmann H (1996) A simplified forest model to study species composition along climate gradients. Ecology 77:2055–2074
Bugmann H, Solomon AM (2000) Explaining forest composition and biomass across multiple biogeographical regions. Ecological Applications 10:95–114
Cao M, Woodward FI (1998) Dynamic responses of terrestrial ecosystem carbon cycling to global climate change. Nature 393:249–252
Chadwick OA, Derry LA, Vitousek PM, Huebert BJ, Hedin LO (1999) Changing sources of nutrient during four million years of ecosystem development. Nature 397:491–497
Clark JS, Fastie C, Hurtt G, Jackson ST, Johnson C, King GA, Lewis M, Lynch J, Pacala S, Prentice C, Schupp EW, Webb T, Wyckoff (1998) Reid's paradox of rapid plant migration – Dispersal theory and interpretation of paleoecological records. Bioscience 48:13–24
Collatz GJ, Ball JT, Grivet C, Berry JA (1991) Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. Agricultural and Forest Meteorology 54:107–136
Collatz GJ, Ribas-Carbo M, Berry JA (1992) Coupled photosynthesis stomatal conductance model for leaves of C_4 plants. Australian Journal of Plant Physiology 19:519–538
Comins HN, McMurtrie RE (1993) Long-term response of nutrient-limited forests to CO_2-enrichment; equilibrium behaviour of plant-soil models. Ecological Applications 3:666–681
Cowan IR (1977) Stomatal behaviour and environment. Advances in Botanical Research 4:117–228
Cowling SA (1999) Simulated effects of low atmospheric CO_2 on structure and composition of North American vegetation at the Last Glacial Maximum. Global Ecology and Biogeography 8:81–93
Cox PM (2001) Description of the TRIFFID dynamic global vegetation model, Tech. Note 24, Hadley Centre, Bracknell, UK, pp 16
Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408:184–187
Cramer W, Kicklighter DW, Bondeau A, Moore B, Churkina C, Nemry B, Ruimy A, AL S (1999) Comparing global models of terrestrial net primary productivity (NPP): overview and key results. Global Change Biology 5:1–15
Cramer W, Bondeau A, Woodward FI, Prentice C, Betts RA, Brovkin V, Cox PM, Fisher V, Foley JA, Friend AD, Kucharik C, Lomas MR, Ramankutty N, Sitch S, Smith B, White A, Young-Molling C (2001) Global response of terrestrial ecosystem structure and function to CO_2 and climate change: results from six dynamic global vegetation models. Global Change Biology 7:357–374
Cramer W, Bondeau A, Schaphoff S, Lucht W, Smith B, Sitch S (2004) Tropical forests and the global carbon cycle: impacts of atmospheric carbon dioxide, climate change and rate of deforestation. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 359:331–343
Daly C, Bachelet D, Lenihan JM, Neilson RP, Parton W, Ojima D (2000) Dynamic simulation of tree-grass interactions for global change studies. Ecological Applications 10:449–469
Dargaville RJ, Heimann M, McGuire AD, Prentice IC, Kicklighter DW, Joos F, Clein JS, Esser G, Foley J, Kaplan J, Meier RA, Melillo JM, Moore III B, Ramankutty N, Reichenau T, Schloss A, Sitch S, Tian H, Williams LJ, Wittenberg U (2002) Evaluation of terrestrial carbon cycle models with atmospheric CO_2 measurements: Results from transient simulations considering increasing CO_2, climate, and land-use effects. Global Biogeochemical Cycles 16: 1092, doi:1010.1029/2001GB001426
DeFries RS, Hansen MC, Townsend JRG, Janetos AC, Loveland TR (2000) A new global 1-km dataset of percentage tree cover derived from remote sensing. Global Change Biology 6:247–254
Delire C, Levis S, Bonan G, Foley JA, Coe M, Vavrus S (2002) Comparison of the climate simulated by the CCM3 coupled to two different land-surface models Climate Dynamics 19:657–669
DeLucia EH, Hamilton JG, Naidu SL, Thomas RB, Andrews JA, Finzi A, Lavine M, Matamala R, Mohan JE, Hendrey GR, Schlesinger WH (1999) Net primary production of a forest ecosystem with experimental CO_2 enrichment. Science 284:1177–1179
Denning AS, Holzer M, Gurney KR, Heimann M, Law RM, Rayner PJ, Fung IY, Fan S, Taguchi S, Friedlingstein P, Balkanski Y, Maiss M, Levin I (1999) Three-dimensional transport and concentration of SF6: A model intercomparison study (Transcom 2). Tellus 51B: 266–297
Dewar RC (1996) The correlation between plant growth and intercepted radiation: an interpretation in terms of optimal plant nitrogen content. Annuals of Botany 78:125–136
Díaz S, Cabido M (1997) Plant functional types and ecosystem function in relation to global change. J Vegetat Sci 8:463–474
Díaz S, Cabido M, Casanoves F (1999a) Functional implications of trait-environment linkages in plant communities. In: Weiher E, Keddy P (eds) Ecological assembly rules – Perspectives, advances, retreats. Cambridge University Press, Cambridge, pp 338–362
Díaz S, Cabido M, Zak M, Martínez Carretero E, Araníbar J (1999b) Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. Journal of Vegetation Science 10:651–660
Díaz S, McIntyre S, Lavorel S, Pausas JG (2002) Does hairiness matter in Harare? Resolving controversy in global comparisons of plant trait responses to ecosystem disturbance. New Phytologist 154:7–9

Díaz S, Hodgson JG, Thompson K, Cabido M, Cornelissen JHC, Jalili A, Montserrat-Marti G, Grime JP, Zarrinkamar F, Asri Y, Band SR, Basconcelo S, Castro-Diez P, Funes G, Hamzehee B, Khoshnevi M, Perez-Harguindeguy N, Perez-Rontome MC, Shirvany FA, Vendramini F, Yazdani S, Abbas-Azimi R, Bogaard A, Boustani S, Charles M, Dehghan M, de Torres-Espuny L, Falczuk V, Guerrero-Campo J, Hynd A, Jones G, Kowsary E, Kazemi-Saeed F, Maestro-Martinez M, Romo-Diez A, Shaw S, Siavash B, Villar-Salvador P, Zak MR (2004) The plant traits that drive ecosystems: Evidence from three continents. Journal of Vegetation Science 15:295–304

Dickinson RE, Henderson-Sellers A, Kennedy PJ (1993) Biosphere-Atmosphere Transfer Scheme (BATS) Version 1E as coupled to the NCAR Community Climate Model, Tech. Note NCAR/TN-383+STR, Natl. Cent. For Atmos. Res., Boulder, Colorado, pp 72

Dolman AJ, Schulze ED, Valentini R (2003) Analyzing carbon flux measurements. Science 301 (5635):916–916

Dufresne JL, Friedlingstein P, Berthelot M, Bopp L, Ciais P, Fairhead L, Le Treut H, Monfray P (2002) On the magnitude of positive feedback between future climate change and the carbon cycle. Geophysical Research Letters 29:43.41–43.44

Emanuel WR, Shugart HH, Stevenson MP(1985). Climatic change and the broad-scale distribution of terrestrial ecosystem complexes. Climatic Change 7:29–43

Falge E, Baldocchi D, Tenhunen J, Aubinet M, Bakwin P, Berbigier P, Bernhofer C, Burba G, Clement R, Davis KJ, Elbers JA, Goldstein AH, Grelle A, Granier A, Gudmundsson J, Hollinger D, Kowalski AS, Katul G, Law BE, Malhi Y, Meyers T, Monson RK, Munger JW, Oechel W, Paw UKT, Pilegaard K, Rannik U, Rebmann C, Suyker A, Valentini R, Wilson K, Wofsy S (2002) Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. Agricultural and Forest Meteorology 113:53–74

Fan S, Gloor M, Mahlman J, Pacala S, Sarmiento J, Takahashi T, Tans P (1998) A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models. Science 282:442–446

Farquhar GD, van Caemmerer S, Berry JA (1980) A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. Planta 149:78–90

Field CB, Chapin FS, Matson PA, Mooney HA (1992) Responses of terrestrial ecosystems to the changing atmosphere: a resource based approach. Annual Review of Ecology and Systematics 23:201–235

Field CB, Randerson JT, Malmström CM (1995) Global net primary production: combining ecology and remote sensing. Remote Sensing of Environment 51:74–88

Field CB, Raupach MR, Victoria R (2004) The Global Carbon Cycle: Integrating Humans, Climate, and the Natural World. In: Field CB, Raupach MR (eds) The Global Carbon Cycle: Integrating Humans, Climate, and the Natural World. Island Press, Washington, D.C., pp 1–13

Finnegan JJ, Raupach MR (1987) Transfer processes in plant canopies in relation to stomatal characteristics. In: Zeiger, E. Farquhar GD, Cowan IR (eds) Stomatal Function, Stanford University Press, Stanford, pp 385–429

Flückiger J, Monnin E, Stauffer B, Schwander J, Stocker TF, Chappellaz J, Raynaud D, Barnola J-M (2002) High-resolution Holocene N_2O ice core record and its relationship with CH_4 and CO_2. Global Biogeochemical Cycles 16: doi:10.1029/2001GB001417

Foley JA, Prentice IC, Ramankutty N, Levis S, Pollard D, Sitch S, Haxeltine A (1996) An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics. Global Biogeochemical Cycles 10:603–628

Foley JA, Levis S, Prentice IC, Pollard D, Thompson SL (1998) Coupling dynamic models of climate and vegetation. Global Change Biology 4:561–579

Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH, Holloway T, Howard EA, Kucharik CJ, Monfreda C, Patz CJ, Prentice IC, Ramankutty N, Snyder PK (2005) Global consequences of land use. Science 309: 570–574

Friedlingstein P, Dufresne J-L, Cox PM, Rayner P (2003)How positive is the feedback between climate change and the carbon cycle? Tellus B55 692–700

Friend AD, Stevens AK, Knox RG, Cannell MGR (1997) A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3.0). Ecological Modelling 95:249–287

Fulton MR, Prentice IC (1997) Edaphic controls on the boreonemoral forest mosaic. Oikos 78:291–298

Gerten D, Schaphoff S, Haberlandt U, Lucht W, Sitch S (2004) Terrestrial vegetation and water balance – hydrological evaluation of a dynamic global vegetation model. J Hydrol 286:249–270

Gitay H, Noble IR (1997) What are functional types and how should we seek them? In: Smith TM, Shugart HH, Woodward FI (eds) Plant functional types: their relevance to ecosystem properties and global change. Cambridge University Press, Cambridge, pp 3–19

Gordon WS, Famiglietti JS (2004) Response of the water balance to climate change in the United States over the 20th and 21st centuries: Results from the VEMAP Phase 2 model intercomparisons, Global Biogeochemical Cycles 18: GB1030, doi:10.1029/2003GB002098

Gordon WS, Famiglietti JS, Fowler NA, Kittel TGF, Hibbard KA (2004) Validation of simulated runoff from six terrestrial ecosystem models: Results from VEMAP. Ecological Applications 14:527–545

Gu LH, Baldocchi D, Verma SB, Black TA, Vesala T, Falge EM, Dowty PR (2002) Advantages of diffuse radiation for terrestrial ecosystem productivity. Journal of Geophysical Research-Atmospheres 107: ACL 2.1–2.23

Guenther A, Hewitt CN, Erickson D, Fall R, Geron C, Graedel T, Harley P, Klinger L, Lerdau M, McKay WA, Pierce T, Scholes B, Seinbrecher R, Tallamraju R, Taylor J, Zimmerman P (1995) A global model of natural volatile organic compound emissions. Journal of Geophysical Research 100:8873–8892

Gurney KR, Law RM, Denning AS, Rayner PJ, Baker D, Bousquet P, Bruhwiler L, Chen YH, Ciais P, Fan S, Fung IY, Gloor M, Heimann M, Higuchi K, John J, Kowalczyki E, Maki T, Maksyutov S, Peylin P, Prather M, Pak BC, Sarmiento J, Taguchi S, Takahashi T, Yuen CW (2003) Transcom 3 CO_2 Inversion Intercomparison: 1. Annual mean control results and sensitivity to transport and prior flux information. Tellus 55B: 555–579

Gurney KR, Law RM, Denning AS, Rayner PJ, Pak B, TransCom3 L2 modelers (2004) TransCom3 Inversion Intercomparison: Control results for the estimation of seasonal carbon sources and sinks. Global Biogeochemical Cycles 18: GB1010, doi:10.1029/2003GB002111

Gurvich DE, Díaz S, Falczuk V, Perez-Harguindeguy N, Cabido M, Thorpe PC (2002) Foliar resistance to simulated extreme temperature events in contrasting plant functional and chorological types. Global Change Biology 8:1139–1145

Hamilton JG, George K, DeLucia EH, Naidu SL, Finzi AC, Schlesinger WH (2002) Forest carbon balance under elevated CO_2. Oecologia 131:250–260

Harrison SP, Prentice IC (2003) Climate and CO_2 controls on global vegetation distribution at the last glacial maximum: analysis based on palaeovegetation data, biome modelling and palaeoclimate simulations. Global Change Biology 9:983–1004

Harrison SP, Prentice IC, Barboni D, Kohfeld KE, Ni J, Sutra J-P (submitted) Towards a global plant functional type classification for ecosystem modelling, palaeoecology and climate impacts research. Journal of Vegetation Science

Haxeltine A, Prentice IC (1996a) BIOME3: an equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types. Global Biogeochemical Cycles 10:693–709

Haxeltine A, Prentice IC (1996b) A general model for the light-use efficiency of primary production. Functional Ecology 10: 551–561

Haxeltine A, Prentice IC, Creswell ID (1996) A coupled carbon and water flux model to predict vegetation structure. Journal of Vegetation Science 7:651–666

Heimann M, Esser G, Haxeltine A, Kaduk J, Kicklighter DW, Knorr W, Kohlmaier GH, McGuire AD, Melillo J, III BM, Otto RD, Prentice IC, Sauf W, Schloss A, Sitch S, Wittenberg U, Würth G (1998) Evaluation of terrestrial carbon cycle models through simulations of the seasonal cycle of atmospheric CO_2: first results of a model intercomparison study. Global Biogeochemical Cycles 12: 1–24

Hendry GR, Ellsworth DS, Lewin KF, Nagy J (1999) A free-air enrichment system for exposing tall forest vegetation to elevated atmospheric CO_2. Global Change Biology 5: doi: 10.1046/j.1365–2486.1999.00228.x
Hicke JA, Asner GP, Randerson JT, Tucker C, Los S, Birdsey R, Jenkins JC, Field C (2002) Trends in North American net primary productivity derived from satellite observations, 1982–1998. Global Biogeochemical Cycles 16: doi:10.1029/2001GB001550
Hickler T, Prentice IC, Smith B, Sykes MT (2004a) Simulating the effects of elevated CO_2 on productivity at the Duke Forest FACE experiment: a test of the dynamic global vegetation model LPJ. In: Hickler T, Towards an integrated ecology through mechanistic modelling of ecosystem structure and functioning. Meddelanden från Lunds Universitets Geografiska Institution. Avhandlingar: 153
Hickler T, Smith B, Sykes MT, Davis M, Sugita S, Walker K (2004b) Using a generalized vegetation model to simulate vegetation dynamics in northeastern USA. Ecology 85:519–530
Higgins SI, Clark JS, Nathan R, Hovestadt T, Schurr F, Fragoso JMV, Aguiar MR, Ribbens E, Lavorel S (2003) Forecasting plant migration rates: managing uncertainty for risk assessment. Journal of Ecology 91:341–347
Holdridge LR (1947) Determination of world plant formations from simple climatic data. Science 105:367–368
Houghton RA (2003) Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850–2000. Tellus 55B: 378–390
Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Xiaosu D (Eds.) (2001) Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC). Cambridge University Press, UK
House JI, Prentice IC, Ramankutty N, Houghton RA, Heimann M (2003) Reconciling apparent inconsistencies in estimates of terrestrial CO_2 sources and sinks. Tellus 55:345–363
Hungate BA, Dukes JS, Shaw MB, Luo Y, Field CB (2003) Nitrogen and Climate Change. Science 302:1512–1513
Indermühle A, Stocker TF, Joos F, Fischer H, Smith HJ, Wahlen M, Deck B, Mastroianni D, Tschumi J, Blunier T, Meyer R, Stauffer B (1999) Holocene carbon-cycle dynamics based on CO_2 trapped in ice at Taylor Dome, Antarctica. Nature 398: 121–126
Jarvis PG (1976) The interpretation of the variances in leaf water potential and stomatal conductance found in canopies in the field. Phil. Trans. Roy. Soc. Lond. B273:593–610
Jones CD, Cox PM (2001) Modeling the volcanic signal in the atmospheric CO_2 record. Global Biogeochemical Cycles 15: 453–465
Jones CD, Cox PM, Essery RLH, Roberts DL, Woodage MJ (2003) Strong carbon cycle feedbacks in a climate model with interactive CO_2 and sulphate aerosols. Geophysical Research Letters 30: 1479, doi:1410.1029/2003GL016867
Joos F, Prentice IC, Sitch S, Meyer R, Hooss G, Plattner G-K, Gerber S, Hasselmann K (2001) Global warming feedbacks on terrestrial carbon uptake under the Intergovernmental Panel on Climate Change (IPCC) emission scenarios. Global Biogeochemical Cycles 15:891–907
Joos F, Gerber S, Prentice IC, Otto-Bliesner BL, Valdes PJ (2004) Transient simulations of Holocene atmospheric carbon dioxide and terrestrial carbon since the Last Glacial Maximum. Global Biogeochemical Cycles 18: GB2002, doi: 2010.1029/2003GB002156
Kaduk J, Heimann M (1996) A prognostic phenology model for global terrestrial carbon cycle models, Climate Research 6:1–19
Kaminski T, Heimann M (2001) Inverse modeling of atmospheric carbon dioxide fluxes. Science 294: 259a
Kaplan JO (2002) Wetlands at the Last Glacial Maximum: Distribution and methane emissions. Geophysical Research Letters 29: doi: 10.1029/2001GL013366
Kaplan JO, Prentice IC, Knorr W, Valdes PJ (2002) Modeling the dynamics of terrestrial carbon storage since the Last Glacial Maximum. Geophysical Research Letters 29: 2074, DOI: 2010.1029/2002GL015230
Kaplan JO, Bigelow NH, Prentice IC, Harrison SP, Bartlein PJ, Christensen TR, Cramer W, Matveyeva NV, McGuire AD, Murray DF, Razzhivin VY, Smith B, Walker DA, Anderson PM, Andreev AA, Brubaker LB, Edwards ME, Lozhkin AV (2003) Climate change and arctic ecosystems II: Modeling, paleodata-model comparisons, and future projections. Journal of Geophysical Research 108: 8171, doi: 8110.1029/2002JD002559
Kicklighter DW, Bruno M, Donges S, Esser G, Heimann M, Helfrich J, Ift F, Joos F, Kaduk J, Kohlmaier GH, McGuire AD, Melillo JM, Meyer R, Moore B, Nadler A, Prentice IC, Sauf W, Schloss AL, Sitch S, Wittenberg U, Wurth G (1999) A first-order analysis of the potential role of CO_2 fertilization to affect the global carbon budget: a comparison of four terrestrial biosphere models. Tellus Series B-Chemical and Physical Meteorology 51:343–366
Klein Goldewijk K (2001) Estimating global land use change over the past 300 years: the HYDE database. Global Biogeochemical Cycles 15:417–433
Knorr W (2000) Annual and interannual CO_2 exchanges of the terrestrial biosphere: process-based simulations and uncertainties. Global Ecology and Biogeography 9:225–252
Knorr W, Heimann M (1995) Impact of drought stress and other factors on seasonal land biosphere CO_2 exchange studied through an atmospheric tracer transport model. Tellus Series B-Chemical and Physical Meteorology 47:471–489
Knorr W, Heimann M (2001) Uncertainties in global terrestrial biosphere modeling. Part II: global constraints for a process-based vegetation model. Global Biogeochemical Cycles 15:227–246
Köppen W (1931) *Grundriss der Klimakunde*. Walter de Gruyter, Berlin
Krinner G, Viovy N, de Noblet-Ducoudré N, Ogée J, Polcher J, Friedlingstein P, Ciais P, Sitch S, Prentice IC (2005) A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system. Global Biogeochemical Cycles 19: GB1015, doi:10.1029/2003GB002199
Kucharik CJ, Brye KR (2003) Integrated BIosphere Simulator (IBIS) yield and nitrate loss predictions for Wisconsin maize receiving varied amounts of nitrogen fertilizer. J Environ Qual 32:247–268
Kucharik CJ, Foley JA, Delire C, Fisher VA, Coe MT, Lenters JD, Young-Molling C, Ramankutty N, Norman JM, Gower ST (2000) Testing the performance of a Dynamic Global Ecosystem Model: Water balance, carbon balance, and vegetation structure. Global Biogeochemical Cycles 14:795–825
Lavorel S, Cramer W (1999) Plant functional response to land use and natural disturbance. Journal of Vegetation Science 10:604–732
Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16:545–556
Lavorel S, McIntyre S, Landsberg J, Forbes TDA (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. Tree 12:474–478
Lavorel S, Díaz S, Cornelissen H, Garnier E, Harrison SP, McIntyre S, Pausas JG, Pérez-Harguindeguy N, Urcelay C (2007) Plant functional types: are we getting any closer to the Holy Grail? In: Canadell J, Pataki D, Pitelka L (eds) Terrestrial ecosystems in a changing world. IGBP Series, Springer-Verlag, Heidelberg, this volume
Law R, Chen YH, Gurney KR, Rayner P, Denning AS, TransCom3 modelers (2003) TransCom3 CO_2 inversion intercomparison: 2. Sensitivity of annual mean results to data choices. Tellus 55B: 512–521
Le Quéré C, Harrison SP, Prentice IC, Buitenhuis ET, Aumont O, Bopp L, Claustre H, Cotrim da Cunha L, Geider R, Giraud X, Klaas C, Kohfeld KE, Legendre L, Manizza M, Platt T, Rivkin R, Sathyendranath S, Uitz J, Watson AJ, Wolf-Gladrow D (in press) Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models. Global Change Biology
Lenihan JM, Daly C, Bachelet D, Neilson RP (1998) Simulating broad-scale fire severity in a dynamic global vegetation model. Northwest Science 72:91–103
Lieth H (1975) Modeling the Primary Productivity of the World. In: Lieth H, Whittaker RH (eds) Primary Productivity of the Biosphere, Springer-Verlag, Berlin, pp 237–263
Long SP, Ainsworth EA, Rogers A, Ort DR (2004) Rising atmospheric carbon dioxide. Annual Review of Plant Biology 55:591–628
Lucht W, Prentice IC, Myneni RB, Sitch S, Friedlingstein P, Cramer W, Bousquet P, Buermann W, Smith B (2002) Climatic control of the high-latitude vegetation greening trend and Pinatubo effect. Science 296:1687–1689

MA (Millenium Ecosystem Assessment) (2003) Ecosystems and Human Well-being: A Framework for Assessment. Island Press, Washington DC

McGuire AD, Sitch S, Clein JS, Dargaville R, Esser G, Foley J, Heimann M, Joos F, Kaplan J, Kicklighter DW, Meier RA, Melillo JM, Moore III B, Prentice IC, Ramankutty N, Reichenau T, Schloss A, Tian H, Williams LJ, Wittenberg U (2001) Carbon balance of the terrestrial biosphere in the twentieth century: Analyses of CO_2, climate and land use effects with four process-based ecosystem models. Global Biogeochemical Cycles 15:183–206

Melillo JM, McGuire AD, Kicklighter DW, Moore B, Vorosmarty CJ, Schloss AL (1993) Global climate change and terrestrial net primary production. Nature 363:234–240

Monteith JL (1995) Accommodation between transpiring vegetation and the convective boundary layer. J Hydrol 166:251–263

Moorcroft PR, Hurtt GC, Pacala. SW (2001) A method for scaling vegetation dynamics: the ecosystem demography model (ED). Ecological Monographs 71:557–585

Morales P, Sykes MT, Prentice IC, Smith P, Smith B, Bugmann H, Zierl B, Friedlingstein P, Viovy N, Sabate S, Sanchez A, Pla E, Gracia CA, Sitch S, Arneth A, Ogee J (submitted) Comparing and evaluating process-baserd ecosystem model predictions of carbon and water fluxes in major European forest biomes. Global Change Biology

Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. Nature 386:698–702

Nabuurs GJ, Schelhas MJ, Mohren GMJ, Field CB (2003) Temporal evolution of the European Forest sector carbon sink 1950–1999. Global Change Biology 9:152–160

Neilson RP (1995) A model for predicting continental scale vegetation distribution and water balance. Ecological Applications 5:362–385

Neilson RP, Marks D (1994) A global perspective of regional vegetation and hydrologic sensitivities and risks from climatic change. Journal of Vegetation Science 5:715–730

Neilson RP, Running SW (1996) Global dynamic vegetation modellingg: coupling biogeochemistry and biogeography models. pp 451–465 in Walker B, Steffen W, (eds.) Global Change and Terrestrial Ecosystems. Cambridge University Press, Cambridge

Neilson RP, King GA, Koerper G (1992) Toward a rule based biome model. Landscape Ecology 7:27–43

Nemani R, Running SW (1996) Implementation of a hierarchical global vegetation classification in ecosystem function models. Journal of Vegetation Science 7:337–346

Nemani R, White M, Thornton P, Nishida K, Reddy S, Jenkins J, Running S (2002) Recent trends in hydrologic balance have enhanced the terrestrial carbon sink in the United States. Geophysical Research Letters 29: Art. No. 1468

New M, Hulme M, Jones P (2000) Representing twentieth-century space-time climate variability. Part II: Development of 1901–96 monthly grids of terrestrial surface climate. Journal of Climate 13:2217–2238

Norby RJ, Wullschleger SD, Gunderson CA, Johnson DW, Ceulemans R (1999) Tree responses to rising CO_2 in field experiments: implications for the future forest. Plant Cell and Environment 22:683–714

Notaro M, Liu Z, Gallimore R, Vavrus SJ, Kutzbach JE, Prentice IC, Jacob RL (2004) Simulated and observed pre-Industrial to modern vegetation and climate changes. Journal of Climate 18:3650–3671

Nowak RS, Ellsworth DS, Smith SD (2004) Functional responses of plants to elevated atmospheric CO_2 – do photosynthetic and productivity data from FACE experiments support early predictions? New Phytologist 162:253–280

Overpeck JT, Whitlock C, Huntley B (2003) Terrestrial biosphere dynamics in the climate system: past and future. In: Alverson K, Bradley R, Pedersen T (eds) Paleoclimate, Global Change and the Future (IGBP Synthesis Volume), Springer-Verlag, Berlin, pp 81–111

Pacala SW, Canham CD, Saponara J, Silander Jr. JA (1993) Forest models defined by field measurements: I. The design of a northeastern forest simulator. Canadian Journal of Forest Research 23:1980–1998

Pacala SW, Canham CD, Saponara J, Silander Jr. JA, Kobe RK, Ribens E (1996) Forest models defined by field measurements: estimation, error analysis and dynamics. Ecological Monographs 66:1–43

Pan Y, McGuire AD, Melillo JM, Kicklighter DW, Sitch S, Prentice IC (2002) A biogeochemistry-based dynamic vegetation model and its application along a moisture gradient in the continental United States. Journal of Vegetation Science 13:369–382

Parton WJ, Scurlock JMO, Ojima DS, Gilmanov TG, Scholes RJ, Schimel DS, Kirchner T, Menaut J-C, Seastedt T, Garcia Moya E, Apinan Kamnalrut, Kinyamario JI (1993) Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. Global Biogeochemical Cycles 7:785–809

Pastor J, Post WM (1985) Development of a linked forest productivity-soil process model. ORNL/TM-9519. Oak Ridge, Tennessee

Peylin P, Bousquet P, Le Quéré C, Sitch S, Friedlingstein P, McKinley G, Gruber N, Rayner P, Ciais P, (2005) Multiple constraints on regional CO_2 flux variations over land and oceans. Global Biogeochemical Cycles 19: GB1011, doi:10.1029/2003GB002214

Pitelka LF, Plant Migration Workshop Group (1997) Plant migration and climate change. American Scientist 85:464–473

Potter CS, Klooster SA (1999) Dynamic global vegetation modelling for prediction of plant functional types and biogenic trace gas fluxes. Global Ecology and Biogeography 8:473–488

Potter CS, Randerson JT, Field CB, Matson PA, Vitousek PM, Mooney HA, Klooster S (1993) Terrestrial Ecosystem Production – A Process Model-Based On Global Satellite And Surface Data Global Biogeochemical Cycles 7:811–841

Potter CS, Wang S, Nikolov NT, McGuire AD, Liu J, King AW, Kimball JS, Grant RF, Frolking SE, Clein JS, Chen JM, Amthor JS (2001) Comparison of boreal ecosystem model sensitivity to variability in climate and forest site parameters. Journal of Geophysical Research 106: D24, 33, 671 (2000JD000224)

Prentice IC (2001) Controls on the primary productivity of terrestrial ecosystems. In: Geider RJ, DeLucia EH, Falkowski PG, Finzi A, Grime JP, Grace J, Kana TM, LaRoche J, Long SP, Osborne BA, Platt T, Prentice IC, Raven JA, Schlesinger WH, Smetacek V, Stuart V, Sathyendranath S, Thomas RB, Vogelmann TC, Williams P, Woodward FI (2001) Primary productivity of planet Earth: biological determinants and physical constraints in terrestrial and aquatic habitats. Global Change Biology 7:849–882

Prentice IC, Leemans R (1990) Pattern and process and the dynamics of forest structure: a simulation approach. Journal of Ecology 78:340–355

Prentice IC, Raynaud D (2001) Paleogeochemistry, in Global Biogeochemiscal Cycles in the Climate System (eds. Schulze ED, Heinmann M, Holland E. et al.), San Diego: Academic Press, 2001, 87–94

Prentice IC, Solomon AM (1991) Vegetation models and global change. In: Bradley RS (ed.) Global changes of the past: Papers arising from the 1989 OIES Global Change Institute; Snowmass, Colorado, 24. July–4. August 1989. UCAR, Office for Interdisciplinary Earth Studies, Boulder, Colorado. 365–384

Prentice IC, van Tongeren O, de Smidt JT (1987) Simulation of heathland vegetation dynamics. Journal of Ecology 75:203–219

Prentice IC, Cramer W, Harrison SP, Leemans R, Monserud RA, Solomon AM (1992) A global biome model based on plant physiology and dominance, soil properties and climate. Journal of Biogeography 19:117–134

Prentice IC, Sykes MT, Cramer W (1993). A simulation model for the transient effects of climate change on forest landscapes. Ecological Modelling 65:51–70

Prentice IC, Heimann M, Sitch S (2000) The carbon balance of the terrestrial biosphere: Ecosystem models and atmospheric observations Ecological Applications 10 (6):1553–1573

Prentice IC, Farquhar GD, Fasham MJR, Goulden ML, Heimann M, Jaramillo VJ, Kheshgi HS, Le Quéré C, Scholes RJ, Wallace DWR (2001) The carbon cycle and atmospheric carbon dioxide. In: Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA (eds.) Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, 185–225

Prentice IC, Le Quéré C, Buitenhuis ET, House JI, Klaas C, Knorr W (2004) Biosphere dynamics: questions for Earth System modellingg. In: Hawkesworth CJ, Sparks RSJ (eds) The State of the Planet: Frontiers and Challenges. AGU Monograph

Raunkiær C (1909) Formationsundersøgelse og formationstatistik. Bot. Tidsskr. 30:20–80

Raunkiær C (1913) Formationsstatistike Undersøgelser paa Skagens Odde. Botanisk Tidsskrift. Dansk Botanisk Forening 33:197–243

Raunkiær C (1934) The life-forms of plants and statistical plant geography. Clarendon Press, Oxford

Ridgwell A, Marshall S, Gregson K (1999) Consumption of atmospheric methane by soils: a process-based model. Global Biogeochemical Cycles 13:59–70

Rödenbeck C, Houweling S, Gloor M, Heimann M (2003) CO_2 flux history 1982–2001 inferred from atmospheric data using a global inversion of atmospheric transport. Atmos. Chem. Phys. 3:1919–1964

Roderick ML, Farquhar GD, Berry SL, Noble IR (2001) On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation. Oecologia 129:213–232

Ruddiman WF (2003). The Anthropogenic Greenhouse Era Began Thousands of Years Ago. Climatic Change, 61:261–293

Ruimy A, Dedieu G, Saugier B (1996) TURC: A diagnostic model of continental gross primary productivity and net primary productivity Global Biogeochemical Cycles 10:269–285

Running SW, Gower ST (1991) FOREST-BGC, a general model of forest ecosystem processes for regional applications. 2. Dynamic carbon allocation and nitrogen budgets. Tree Physiology 9:147–160

Running SW, Hunt ER (1993) Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global-scale models. Scaling processes between leaf and landscape levels. In: Ehleringer JR, Field CB (eds) Scaling Physiological Processes: Leaf to Globe. Academic Press, San Diego, 141–158

Ryan MG (1991) Effects of climate change on plant respiration. Ecological Applications 1:157–167

Schäfer KVR, Oren R, Ellsworth DS, Lai CT, Herrick JD, Finzi AC, Richter DD, Katul GG (2003) Exposure to an enriched CO_2 atmosphere alters carbon assimilation and allocation in a pine forest ecosystem. Global Change Biology 9: 10, 1378–1400

Schaphoff S, Lucht W, Gerten D, Sitch S, Cramer W, Prentice IC (2006) Terrestrial biosphere carbon storage under alternative climate projections. Climatic Change 74:97–122, doi: 10.1007/s10584-005-9002-5

Schimel DS, House JI, Hibbard KA, Bousquet P, Ciais P, Peylin P, Braswell BH, Apps MJ, Baker D, Bondeau A, Canadell J, Churkina G, Cramer W, Denning AS, Field CB, Friedlingstein P, Goodale C, Heimann M, Houghton RA, Melillo JM, Moore III B, Murdiyarso D, Noble I, Pacala SW, Prentice IC, Raupach MR, Rayner PJ, Scholes RJ, Steffen WL, Wirth C (2001) Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. Nature 414:169–172

Scholze M, Kaplan JO, Knorr W, Heimann M (2003) Climate and interannual variability of the atmosphere-biosphere $^{13}CO_2$ flux. Geophysical Research Letters 30: 1097, doi:10.1029/2002GL015631

Schulze E-D (1982) Plant life forms and their carbon, water and nutrient relations Encyclopedia of Plant Physiology. Springer-Verlag, Berlin, Heidelberg, 615–676

Sellers PJ, Mintz Y, Sud YC, Dalcher A (1986) A simple biosphere model (SiB) for use within general circulation models. Journal of the Atmospheric Sciences 43:505–531

Sernander R (1936) The primitive forest of Granskär and Fiby. Acta Phytogeogr. Suec. 8

Shugart HH (1984) A Theory of Forest Dynamics. Springer-Verlag, New York

Shugart HH, West DC (1977) Development of an Appalachian deciduous forest succession model and its application to assessment of impact of chestnut blight. Journal of Environmental Management 5:161–179

Sitch S, Smith B, Prentice IC, Arneth A, Bondeau A, Cramer W, Kaplan JO, Levis S, Lucht W, Sykes MT, Thonicke K, Venevsky S (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. Global Change Biology 9:161–185

Smith B, Prentice IC, Sykes MT (2001) Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. Global Ecology and Biogeography 10:621–637

Specht RL (1972) Water use by perennial evergreen plant communities in Australia and Papua New Guinea. Australian Journal of Botany 20:273–299

Sprugel DG (1976) Dynamic structure of wave-generated *Abies balsamea* forests in the northeastern United States. Journal of Ecology 64:889–911

Sykes MT, Prentice IC, Smith B, Cramer W, Venevsky S (2001) An introduction to the European Terrestrial Ecosystem Modelling Activity. Global Ecology and Biogeography 10:581–593

Tegen I, Harrison SP, Kohfeld KE, Prentice IC, Coe MT, Heimann M (2002) Impact of vegetation and preferential source areas on global dust aerosol: Results from a model study. Journal of Geophysical Research-Atmospheres 107: 4576, doi:4510.1029/2001JD000963

Thonicke K, Venevsky S, Sitch S, Cramer W (2001) The role of fire disturbance for global vegetation dynamics: coupling fire into a Dynamic Global Vegetation Model. Global Ecology and Biogeography 10:661–677

Thonicke K, Prentice IC, Hewitt C (2005) Modelling glacial-interglacial changes in global fire regimes and trace gas emissions. Global Biogeochemical Cycles 19, GB3008, doi:10.1029/2004GB002278

Townsend AR, Braswell BH, Holland EA, Penner JE (1996) Spatial and temporal patterns in terrestrial carbon storage due to deposition of fossil fuel nitrogen. Ecological Applications 6:806–814

VEMAP Members (1995) Vegetation/ecosystem modeling and analysis project: Comparing biogeography and biogeochemistry models in a continental-scale study of terresttrial ecosystem responses to climate change and CO_2 doubling. Global Biogeochemical Cycles 9:407–437

Venevsky S, Thonicke K, Sitch S, Cramer W (2002) Simulating fire regimes in human-dominated ecosystems: Iberian Peninsula case study. Global Change Biology 8:984–998

Walter H (1962) Die Vegetation der Erde in ökophysiologischer Betrachtung – Die tropischen und subtropischen Zonen, Band 1. VEB Gustav Fischer Verlag, Jena

Walter H (1968) Die Vegetation der Erde in ökophysiologischer Betrachtung – Die gemässigten und arktischen Zonen, Band 2. VEB Gustav Fischer Verlag, Jena

Warnant P, François L, Strivay D, Gérard J-C (1994) CARAIB: a global model of terrestrial biological productivity. Global Biogeochemical Cycles 8:255–270

Watt AS (1947) Pattern and process in the plant community. Journal of Ecology 1/2:1–22

Whittaker RH (1975) Communities and ecosystems, 2nd edition. Macmillan, New York

Woodward FI (1987) Climate and Plant Distribution. Cambridge University Press, Cambridge, pp 174

Woodward FI, Lomas ML (2004) Vegetation dynamics – simulating responses to climatic change, Biological Reviews 79, 1–28; DOI: 10.1017/S1464793103006419

Woodward FI, Smith TM, Emanuel WR (1995) A global land primary productivity and phytogeography model. Global Biogeochemical Cycles 9:471–490

Woodward FI, Lomas MR, Lee SE (2001) Predicting the future productivity and distribution of global terrestrial vegetation. In: Roy J, Mooney HA, Saugier B (eds) Terrestrial Global Productivity, Academic Press, San Diego, pp 521–541

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets U, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004) The worldwide leaf economics spectrum. Nature 428:821–827

Zhou LM, Tucker CJ, Kaufmann RK, Slayback D, Shabanov NV, Myneni RB (2001) Variations in northern vegetation activity inferred from satellite data of vegetation index during 1981 to 1999. Journal of Geophysical Research-Atmospheres 106: 20069–20083