

# Global and regional modelling of Arctic–boreal vegetation distribution and its sensitivity to altered forcing

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## Abstract

Understanding the distribution and function of Arctic and boreal ecosystems under current conditions and their vulnerability to altered forcing is crucial to our assessment of future global environmental change. Such efforts can be facilitated by the development and application of ecological models that simulate realistic patterns of vegetation change at high latitudes. This paper reviews three classes of ecological models that have been implemented to extrapolate vegetation information in space (e.g. across the Arctic and adjacent domains) and over historical and future periods (e.g. under altered climate and other forcings). These are: (i) equilibrium biogeographical models; (ii) frame-based transient ecosystem models, and (iii) dynamic global vegetation models (DGVMs). The equilibrium response of high-latitude vegetation to scenarios of increased surface air temperatures projected by equilibrium biogeographical models is for tundra to be replaced by a northward shift of boreal woodland and forests. A frame-based model (ALFRESCO) indicates the same directional changes, but illustrates how response time depends on rate of temperature increase and concomitant changes in moisture regime and fire disturbance return period. Key disadvantages of the equilibrium models are that they do not simulate time-dependent responses of vegetation and the role of disturbance is omitted or highly generalized. Disadvantages of the frame-based models are that vegetation type is modelled as a set unit as opposed to an association of individually simulated plant functional types and that the role of ecosystem biogeochemistry in succession is not explicitly considered. DGVMs explicitly model disturbance (e.g. fire), operate on plant functional types, and incorporate constraints of nutrient availability on biomass production in the simulation of vegetation dynamics. Under changing climate, DGVMs detail conversion of tundra to tree-dominated boreal landscapes along with time-dependent responses of biomass, net primary production, and soil organic matter turnover—which all increase with warming. Key improvements to DGVMs that are needed to portray behaviour of arctic and boreal ecosystems adequately are the inclusion of anaerobic soil processes for inundated landscapes, permafrost dynamics, and moss-lichen layer biogeochemistry, as well as broader explicit accounting of disturbance regimes (including insect outbreaks and land management). Transient simulation of these landscapes can be further tailored to high-latitude processes and issues by spatially interactive, gridded application of arctic/boreal frame-based models and development of dynamic regional vegetation models (DRVMS) utilizing plant functional type schemes that capture the variety of high-latitude environments.

*Keywords:* arctic vegetation, boreal vegetation, climate impacts, DGVM, global change, vegetation modelling

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## Introduction

Terrestrial ecosystems of the Arctic and adjacent boreal regions are expected to be highly sensitive to directional climate change and to play a significant role in biospheric feedbacks to global climate (Foley *et al.* 1994; Bonan *et al.* 1995; Ciais *et al.* 1995; Betts *et al.* 1997; Cramer 1997; Claussen 1998; Ganopolski *et al.* 1998; Levis *et al.* 1999). Their sensitivity arises from complex interactions (including threshold relationships) among ecosystem structure and function, soil and permafrost processes, and regional climate. In turn, biophysical and biogeochemical dynamics of these landscapes play a strong role in the global climate system through control over surface–atmosphere exchange of energy, carbon, and radiatively active trace gases (Bonan *et al.* 1995; Barry 1967; Reeburgh & Whalen 1992; Pielke & Vidale 1995; Randerson *et al.* 1999; Eugster *et al.* 2000; McGuire *et al.* 2000; and see other papers in this issue). Biophysical feedbacks are illustrated by spring albedo differences between tundra and boreal forest which strongly influence the energy absorbed at the surface at high latitudes, which in turn affects regional and global atmospheric circulation. As a result, potential future large-scale changes in boreal forest extent are expected not only to influence regional temperatures in the Arctic, but also to have climatic effects extending to the tropics (Bonan *et al.* 1992; Thomas & Rowntree 1992). Because arctic and boreal systems are characterized by large carbon stocks, altered vegetation dynamics, including changes in disturbance rates, additionally have potentially large biogeochemical feedbacks to the climate system through loading of global atmospheric pools of biogenic radiatively active gases (e.g. CO<sub>2</sub>, CH<sub>4</sub>).

Driven by scenarios of increasing atmospheric levels of greenhouse gases (GHGs), recent transient climate experiments with atmosphere–ocean general circulation models (AOGCMs) estimate potentially large, rapid climate changes at high latitudes of the Northern Hemisphere (Mitchell *et al.* 1995; Kattenberg *et al.* 1996). For three AOGCMs, across Alaska, for example, these changes range from 1.0 to 3.5°C increases in annual mean surface air temperatures over the next 30–50 years, with larger changes in winter than in summer, and –20 to +30% changes in summer precipitation (from simulations with increases in both GHGs and sulphate aerosols; Mitchell *et al.* 1995; Boer *et al.* 2000; Dai *et al.* 2000). Changes in surface solar radiation inputs and growing season humidity accompany these simulated changes in thermal and precipitation regimes. While there is considerable uncertainty in these climate experiments associated with driving GHG and sulphate emission scenarios and model estimates of climate sensitivity, such climatic changes and concomitant changes in atmo-

spheric CO<sub>2</sub> levels have the potential to severely alter the distribution of tundra and boreal forests, the extent of permafrost and flooded landscapes, the storage of carbon in peat soils, and the emission of methane and other trace gases from these systems.

For these reasons, understanding the distribution and function of arctic and boreal ecosystems under current conditions and their vulnerability to altered forcing is crucial to global assessments of future environmental change. This can be facilitated by the development and application of ecological models that simulate realistic patterns of vegetation change at high latitudes. The primary objective of this paper is to provide an overview of such models as a means towards extrapolating high-latitude vegetation processes in space (e.g. zonally across arctic and adjacent domains) and time (over historical and future periods, e.g. under climate change and other forcings). In addition, we review results from model experiments evaluating the sensitivity of the distribution and structure of arctic and boreal vegetation to altered forcing. Finally, we discuss needed improvements to models to adapt them specifically to high-latitude domains.

## Global and regional vegetation modelling

### *Classes of vegetation models*

In the next sections, we review the capabilities of and results from three classes of models: (1) equilibrium biogeographical models, (2) frame-based transient ecosystem models, and (3) dynamic global vegetation models (DGVMs). These models (i) operate at a coarse spatial resolution (not, with some exceptions, at the resolution of individual plants), (ii) represent vegetation at the level of biome or plant functional types, rather than the species level, and (iii) have been or can readily be applied across multicontinental domains.

This is not a complete set of models that have been applied to the question of vegetation change in the high latitudes. Others include patch or gap models that simulate horizontal and vertical interactions of individual plants that give rise to succession (Shugart 1984; Shugart & Smith 1996). These models have traditionally been limited to a specific region and correspondingly restricted pool of potential species. They are often also limited to interactions among a single structural lifeform (e.g. trees) and to processes selected to represent a specific ecosystem type (rather than inclusive of mechanisms key to controlling community dynamics across multiple environments). As a result, global or zonal generalization of these models has

been hindered. Nonetheless, there has been recent progress in gap models towards (a) 'unified' patch models for boreal forests (Bonan 1992; Shugart *et al.* 1992) and temperate forests (Bugmann & Solomon 2000), where identical model structure is applied across different biogeographical regions, and (b) the use of plant functional types in place of individual species (e.g. Huston & Smith 1987; Smith & Huston 1989; Bugmann 1996). These developments have led to incorporation of patch models in some DGVMs; we revisit patch models in the discussion of DGVMs (see below).

#### *Generic approach for regional and global modelling*

In general, regional and global ecological models are developed with the intention of extrapolating site dynamics to broader scales. Site or plot process studies contribute to our understanding of which environmental variables exert primary control over processes of interest. Integration of such studies across landscapes, continents, and the globe leads to generalization of these relationships at broad spatial scales. At larger scales, some relationships tend to become dominant relative to others that are important at finer scales, resulting in a distillation of processes represented and data inputs required by global models relative to site-level models. This is often because their corresponding drivers show strong gradients at coarser scales (e.g. temperature and precipitation trends across continents).

Limited by computational demand and availability of input data, regional and global models are implemented on coarse grids, e.g. with 5–50-km grid intervals. However, to simulate continental responses to altered global forcing adequately, processes operating at finer (e.g. patch) scales such as succession and disturbance must also be incorporated. If included, these processes are commonly parameterized, such that empirical relationships between grid-scale drivers and cell-averaged dynamics are developed. An alternative method is a 'statistical dynamical' treatment of subgrid processes, where groups of similar landscape units within a cell are simulated separately and then combined using an area-weighted average to give a cell value (Avisar & Pielke 1989; Bonan 1996; Kittel *et al.* 1996). This approach yields more accurate cell estimates for highly nonlinear fine-scale processes, but it is more intensive in terms of data and computational requirements and so is not commonly implemented in large domain simulations.

The generic approach of deriving models from geographical integration of site-level process studies has led to the successful development of global and regional vegetation models. Included among these are equilibrium biogeographical models, which are implemented globally and evaluate potential natural vegeta-

tion distribution in equilibrium with a given climate (Class 1, below), and frame-based models, implemented for a given biome or selected set of biomes and focused on transition dynamics among vegetation types as governed by succession and disturbance (Class 2, below). Global dynamic vegetation models have merged consideration of biogeochemical processes limiting production and nutrient recycling into a modelling framework that determines vegetation structure derived from equilibrium biogeography models and/or models that explicitly treat succession and disturbance (e.g. patch and fire models, or potentially, frame-based models) (Class 3, below). In the next sections, we consider each of these classes of models and their application to the arctic–boreal domain. First, we discuss the use of plant functional types as an important innovation for generalizing ecosystem structure and function in global and regional models.

#### **Plant functional type approach**

Modelling the response of vegetation structure and function at regional and global scales requires strategies to deal with the complexity of nature. Clearly not every species can be modelled individually. The concept of plant functional types (PFTs) has been introduced to reduce this complexity to a manageable level (Woodward 1987) and has been strongly promoted during the past decade as a central tool in modelling global change effects on terrestrial ecosystems (Steffen *et al.* 1992; Smith *et al.* 1997; Woodward & Cramer 1997a).

The basic rationale for the PFT approach is that classifying plants functionally rather than phylogenetically is a more appropriate way to reduce nature's complexity from the perspective of modelling global change. However, the consensus from most analyses of the PFT approach is that there is no single, universal PFT scheme that can be used for all modelling applications (Woodward & Cramer 1997b). Rather, a given PFT scheme is usually defined by the issue being addressed and is cast in the framework of the modelling approach adopted.

The functional type approach is based on the assumptions that: (i) species can be readily grouped into relatively few categories according to key structural and functional characteristics, (ii) parameterizations of each functional group adequately represent those of constituent species with relatively low variance, and (iii) functional types are the same from continent-to-continent (i.e. biogeography does not matter). An implication of these assumptions is that diversity of species within functional types is not important in terms of critical aspects of ecosystem function. The validity of this assumption is now being tested through a rapidly

expanding international research effort on the functional role of biological diversity (Chapin *et al.* 1998; Sala *et al.* 1998).

Most PFT schemes used in regional and global vegetation modelling are based on a mix of structural and functional attributes of plants. Thus, most schemes begin by differentiating between woody and herbaceous plants and then classifying them further by attributes such as leaf longevity (evergreen vs. deciduous), leaf structure (broadleaf vs. needleleaf), temperature tolerance (e.g. warm evergreen, cool conifer), and photosynthetic pathway (e.g. C3 vs. C4 grasses) (e.g. Table 1). Structural and functional aspects of the classification are commonly closely linked. For example, differences in structure in terms of leaf longevity and structure are related directly to key aspects of ecosystem function, such as momentum transfer between the land surface and the atmosphere (via surface roughness), soil organic matter decomposition rates (via biochemical composition), and seasonality and rates of primary production, evapotranspiration, and soil water use.

The need to take into account both *feedback* and *response* aspects of ecosystem function with respect to climate adds another layer of complexity to the PFT approach (Walker 1997). Most PFT schemes to date focus on functional responses of vegetation to environmental change, such as response to temperature or moisture. Rather less attention has been given to the classification of vegetation based on the functional characteristics of its feedbacks to climate, such as albedo or stomatal conductance. In addition, very few PFT schemes consider the functional response of vegetation disturbance such as fire and insect infestations to climate. These are likely to be at least as important as physiological effects in determining the overall response of vegetation to global change.

Cramer *et al.* (1999) reviewed the use of the PFT approach in global vegetation modelling. While PFT schemes implemented in DGVMs have some significant differences, they uniformly consist of highly aggregated, broad functional types (Table 1a). By comparison, Chapin *et al.* (1996) and Bugmann (1996) present more detailed schemes tailored to projecting ecosystem change at high latitudes (Table 1b; see also Shaver *et al.* 1997).

### **Class 1: Equilibrium biogeographical models**

#### *Model class description*

Equilibrium biogeographical models determine the regional distribution of upland (nonwetland) vegetation types in equilibrium with a given mean seasonal climate. Examples of this class of models are BIOME3 (Haxeltine & Prentice 1996), MAPSS (Neilson 1995), and DOLY

(Woodward *et al.* 1995), which generally use a combination of mechanistic and rule-based approaches. For example, vegetation structural type (e.g. tree, shrub, grass) or a mix of types is determined numerically as that which optimizes, e.g. in MAPSS, leaf area index (LAI) or, in BIOME3, net primary production (NPP) under a given soil moisture and light regime. In some of these models, there is explicit competition among lifeforms for water and other resources. In addition, thermal and moisture thresholds (rules) govern the distribution of other plant functional type characteristics such as warm vs. cold tolerance, leaf longevity (deciduous vs. evergreen), and leaf morphology (needleleaf/microphyllous vs. broadleaf). In general, disturbance is not considered explicitly; however, in MAPSS, the effect of fire in controlling the extent of woody vegetation is accounted for as a function of mean climate and biomass.

Such models also incorporate direct, physiological effects of atmospheric CO<sub>2</sub> concentration on carbon assimilation and water-use efficiency. However, there are considerable differences among models in their treatment of CO<sub>2</sub> effects and gaps in our understanding of longer term responses, including plant- and ecosystem-level acclimation to elevated CO<sub>2</sub> (VEMAP Members 1995; Bazzaz *et al.* 1996; Neilson *et al.* 1997). Outputs from these models include potential natural vegetation type (generally defined in terms of coexisting PFTs), water budget terms, and carbon uptake by plants or some measure of biomass (e.g. LAI).

#### *Simulated response of high-latitude systems to climate change and elevated CO<sub>2</sub>*

Simulations using equilibrium biogeographical models under current climate conditions and their response to altered climate and elevated CO<sub>2</sub> have been compared globally (Neilson 1993a; Neilson *et al.* 1997) and regionally (VEMAP Members 1995; Cramer 1997; Yates *et al.* 2000). Neilson *et al.*'s (1997) results for arctic and boreal regions illustrate the simulated equilibrium sensitivity of high-latitude vegetation (Table 2). They compared responses of BIOME3 and MAPSS to a range of climate-change scenarios selected from doubled-CO<sub>2</sub> equilibrium climate model experiments (Mitchell *et al.* 1990) and transient greenhouse-gas simulations (both with and without sulphate aerosol effects; Kattenberg *et al.* 1996). In the high latitudes, these climate scenarios are characterized by large increases in surface air temperatures.

In both MAPSS and BIOME3, tundra decreased in area under all climate scenarios evaluated (Table 2). This was due largely to a poleward shift of boreal forests and woodlands with higher surface temperatures and a lack

**Table 1a** Plant functional types used in five dynamic global vegetation models: HYBRID (Friend *et al.* 1997), IBIS (Foley *et al.* 1996), LPJ DGVM (Sitch *et al.* in preparation), Sheffield DGVM (Beerling *et al.* 1997), and MCI (Lemihan *et al.* 1998; Daly *et al.* 1999, Expanded from Cramer *et al.* 2000)

Type group	HYBRID	IBIS	LPJ DGVM	Sheffield DGVM	MCI
<i>Woody vegetation (trees, shrubs)</i>					
Evergreen	Broadleaf evergreen	Tropical evergreen Warm temperature evergreen	Tropical broadleaf evergreen Temperate broadleaf evergreen	Broadleaf evergreen	Broadleaf evergreen
	Needleleaf evergreen	Cool conifer Boreal conifer	Temperate needleleaf evergreen Boreal needleleaf evergreen	Needleleaf evergreen	Needleleaf evergreen
Deciduous	Broadleaf dry deciduous Needleleaf dry deciduous	Tropical rainingreen	Tropical broadleaf rainingreen	Broadleaf deciduous	Broadleaf deciduous
	Broadleaf cold deciduous Needleleaf cold deciduous	Temperate summergreen Boreal summergreen	Temperate broadleaf summergreen Boreal summergreen	Needleleaf deciduous	Needleleaf deciduous
<i>Herbaceous vegetation (grasses, etc.)</i>					
	C3 herbs	C3 herbs	C3 perennial grasses	C3 herbs	C3 grasses
	C4 herbs	C4 herbs	C4 perennial grasses	C4 herbs	C4 grasses

**Table 1b** Plant functional types for arctic vegetation outlined in Chapin *et al.* (1996) and for boreal and northern hemisphere temperate forests in Bugmann (1996). For temperate and boreal forest types, '+' = tolerant, '~' = moderately tolerant, and '-' = intolerant. N/A = not applicable (not included in classification). See above references for ecological relationships associated with each functional type and characteristic traits or model parameter values

Type group	Boreal and temperate forests	Arctic vegetation
Trees (height > snow depth)		
Evergreen	Evergreen, cold +, drought +, shade - Evergreen, cold ~, drought -, shade +	Evergreen
Deciduous	Deciduous, cold +, drought ~, shade - (broadleaf and needleleaf spp.) Deciduous, cold -, drought ~, shade + Deciduous, cold -, drought ~, shade - Deciduous, cold -, drought +, shade +	Deciduous
Shrubs (height < snow depth)	N/A	Evergreen Deciduous
Herbaceous	N/A	Aerenchymatous: sedges Non-aerenchymatous: grasses and forbs
Non-vascular	N/A	Peat-forming: <i>Sphagnum</i> moss Non-peat forming: non- <i>Sphagnum</i> moss Lichens

**Table 2** Range of changes in global area of tundra, boreal forests and woodlands (aggregated and disaggregated), and temperate (evergreen plus mixed) forests as simulated by two equilibrium biogeographical models (BIOME3 and MAPSS) under a range of greenhouse gas-induced climate change scenarios, including scenarios with and without sulphate aerosol effects (from Neilson *et al.* 1997). Area changes are relative to simulated distributions under current conditions. Simulations are both with and without direct physiological CO<sub>2</sub> effects

Vegetation type	Change in area (%)
Tundra <sup>1</sup>	-67 to -40%
Boreal Forest and Woodland	-36 to -5%
Boreal Woodland <sup>2</sup>	-65 to -36%
Boreal Forest <sup>2</sup>	-36 to +33%
Temperate Forests	+7 to +58%

<sup>1</sup>Includes alpine tundra (most extensive in central Asia), as well as arctic tundra.

<sup>2</sup>Boreal woodlands and forests treated separately only in MAPSS.

of significant land mass north of 75°N latitude (most of Greenland is specified as an ice sheet in these simulations). That is, arctic tundra was largely 'pushed off' the northern edge of Eurasia and North America. In MAPSS, boreal woodlands also decreased in area with the northward movement of boreal forests. In spite of their poleward extension, boreal woodlands and forests together decreased in area largely due to even greater poleward expansion of temperate forests (Table 2).

The inclusion of direct CO<sub>2</sub> effects in these simulations had little influence on the patterns of change. The direct effect of CO<sub>2</sub> on water-use efficiency would not be expected to play a role in the moist Arctic, so that what little CO<sub>2</sub> effect there was likely came from the direct effect on carbon assimilation (as included in BIOME3, but not in MAPSS). Note, however, that these models include neither nutrient constraints on the response of photosynthesis and growth to elevated CO<sub>2</sub>, nor other related ecosystem and community feedbacks which likely account for the limited CO<sub>2</sub> response observed

experimentally in arctic and boreal systems (Oechel & Vourlitis 1997).

*Limitations*

Important limitations of these models with respect to arctic and boreal systems are their lack of treatment of (i) flooded landscapes (including anaerobic soil processes), (ii) permafrost and its role in controlling vegetation distribution, and (iii), for some models, the mean effects of disturbance (e.g. fire) on vegetation composition. In addition, while equilibrium models tell us something about the direction of upland vegetation change in response to climate change, they do not simulate transitions from one vegetation state to another in response to changing climate and the associated changes in disturbance regime. Simulations of such transitions are important for understanding potential near-term effects (10–100-y time horizons) of global environmental change across arctic–boreal landscapes. To simulate time-dependent responses, vegetation models must consider community and biogeochemical successional processes that control the rate and nature of transitions.

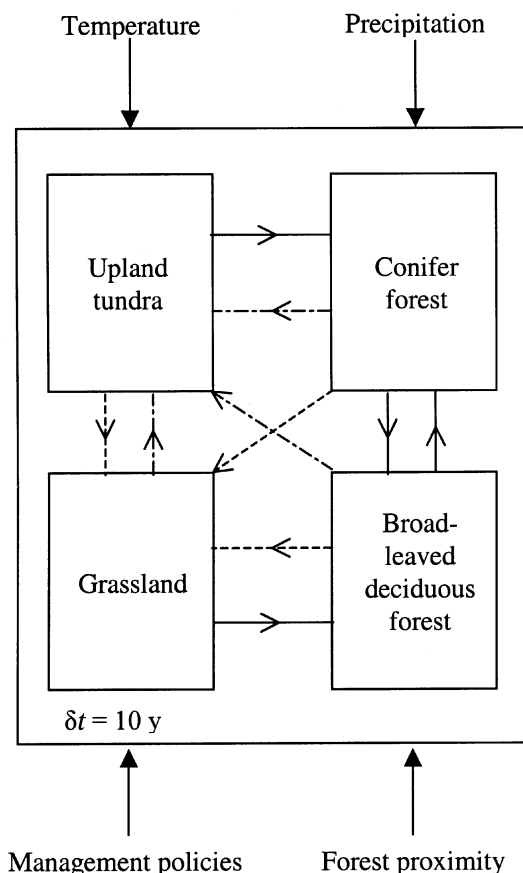
**Class 2: Frame-based transient ecosystem models**

*Description*

Frame-based transient ecosystem models focus on transient dynamics of vegetation change by modelling processes that cause vegetation to switch from one ecosystem type to another (Neilson 1993b; Noble 1993; Starfield & Chapin 1996). These models consist of a series of submodels (frames), each of which simulates transient changes for a different ecosystem type (e.g. Fig. 1). The processes modelled in each frame are those such as succession and disturbance (e.g. fire, insect attack, timber harvest) that determine the probability of switching from one ecosystem type to another. When this switch occurs, another frame (ecosystem type) is activated, which then simulates changes in factors determining a switch to yet other ecosystem types. Because each ecosystem type is modelled separately, differences among ecosystems in rates of succession, transition probabilities, and sensitivities to climate and disturbance are readily incorporated. Submodels for each frame can be kept relatively simple so that the model can be implemented on a grid and run as a regional or global model.

*Application to high-latitude systems*

Simulation of the movement of boreal forest into tundra under climate change using the model ALFRESCO is an



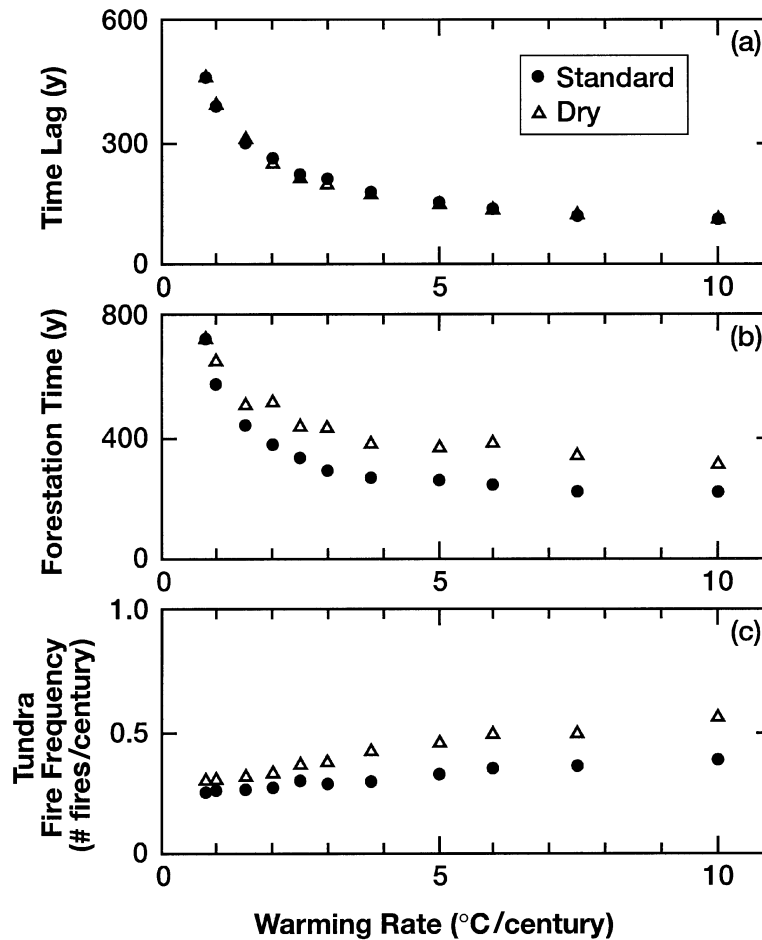
**Key to frame switches:**

- > Normal successional switch
- > Switch under hot, dry conditions
- .-.-.-> Switch under sustained cold conditions

**Fig. 1** General structure of a frame-based transient ecosystem model (ALFRESCO) for high-latitude ecosystems (modified from Starfield & Chapin 1996). Structure shows major ecosystem types (frames) and transition switches between types under normal conditions and altered forcing (see key to switches).  $\delta t$  = time step.

example of the application of frame-based transient ecosystem modelling. This model, operating with a 10-y time-step, simulates gradual tree invasion of deciduous or coniferous boreal trees into tundra as a function of climate, climatically sensitive probabilities of fire and insect outbreaks, and a prescribed rate of seed input (Fig. 2; Starfield & Chapin 1996; Rupp *et al.* 2000a,b). The probability and timing of subsequent transitions among evergreen and deciduous forests are also functions of climate and climatically sensitive disturbance, with these functions, in turn, dependent on ecosystem type.

As a transient model, ALFRESCO captures lags in vegetation change behind climate change which cannot be simulated by equilibrium biogeographical models



**Fig. 2** Time-dependent responses of tundra in transition to boreal forest as a function of rate of climate warming (increasing summer surface air temperature, °C/century) as simulated by the frame-based model in Fig. 1 (adapted from Chapin & Starfield 1997). (a) Time lag between initiation of climate change and forest initiation; (b) time required for 80% conversion to forest; and (c) tundra fire frequency. Two moisture scenarios evaluated in conjunction with temperature changes are: standard (summer precipitation increases in proportion to temperature based on current climatological relationships) and dry (no change in precipitation).

(Fig. 2a; Chapin & Starfield 1997). Applied to a tundra site, the model showed that the rate of conversion to forest depended nonlinearly on the rate of climatic warming (Fig. 2b). Conversion time ranged from over 700 y for a warming rate of 0.75 °C/century down to 250–400 y (depending on accompanying precipitation changes) for rates exceeding 5 °C/century (Fig. 2b). Above this level of forcing, the response flattened because of a diminishing response of tree growth to warming under higher temperatures, as well as a warming-induced increase in fire frequency that suppressed tree invasion (Fig. 2c). An important implication of these frame-based model results is that biome composition will not be in equilibrium with climate at the rates of climatic change suggested for high latitudes.

This class of models allows inclusion of ecosystem types that occupy a climate space which is currently rare or absent, but which might become common in the

future. For example, dry boreal grassland was common during the Pleistocene but occurs today only on dry south-facing slopes. Under scenarios of a warmer, drier climate, this grassland might become more widespread (Chapin & Starfield 1997). Frames for currently absent types can be conceived and developed based on the occurrence of these types outside the domain.

ALFRESCO has also been implemented with spatially explicit interactions among neighbouring cells. In a grid-based simulation of Alaska, probabilities of disturbance and vegetation transition were also a function of the state of neighbouring cells, allowing for spread of fire and migration of vegetation through seed dispersal in response to climate (Rupp *et al.* 2000b). Such contagion effects are limited by physiographical barriers such as large bodies of water (ocean bays, large lakes) and massive, high-elevation mountain systems that are too cold to support forests and that have too little vegetation

(a)

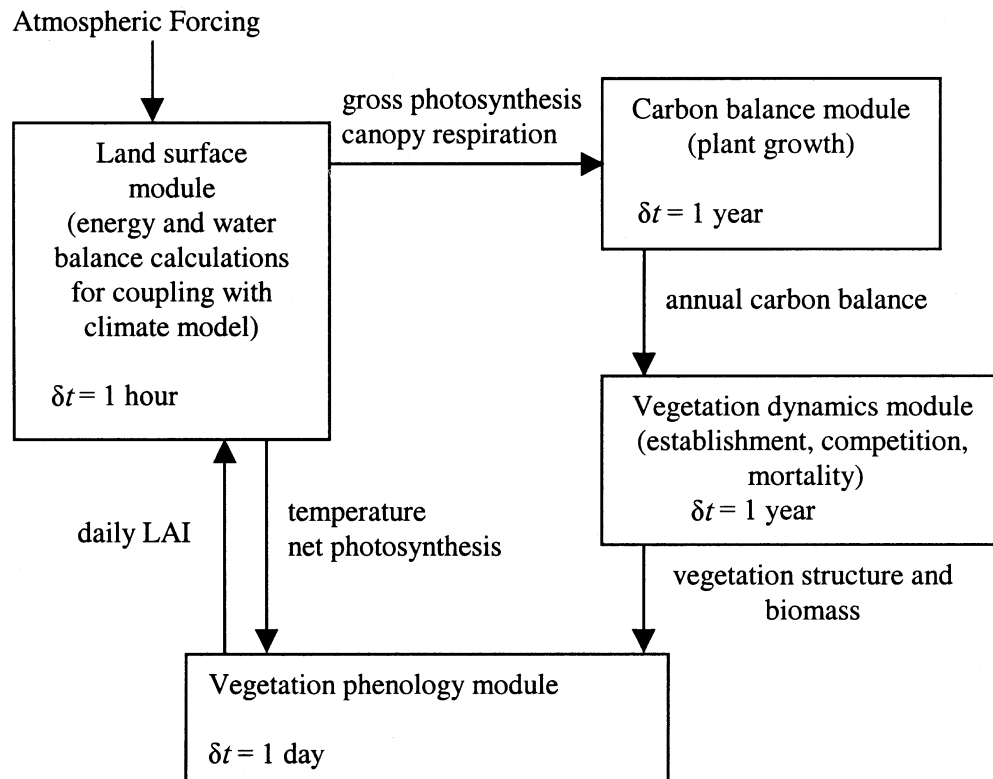


Fig. 3a (caption on next page)

to burn (Rupp *et al.* 2000a). These barriers are defined explicitly in a recently developed satellite-derived land-cover map for Alaska (S. Rupp & M. Macander, unpubl. map).

#### *Lines of model development and limitations*

Variables modelled within each frame represent ecological processes, such as biomass accumulation, which in turn influence fuel load and disturbance probability. The influences of soil fertility and permafrost depth were not included in ALFRESCO because of the limited additional explanatory power with respect to ecosystem-type switching; however, these processes may be more important for simulating within-ecosystem type dynamics (Starfield & Chapin 1996). Frame-based models can be expanded to additionally track these and other landscape properties that influence carbon exchange (e.g. soil carbon stocks) and water/energy exchange (e.g. canopy conductance and albedo). Such functions would provide additional insight into the nature of time-dependent ecosystem change and would output those land-surface properties required to link to climate system models.

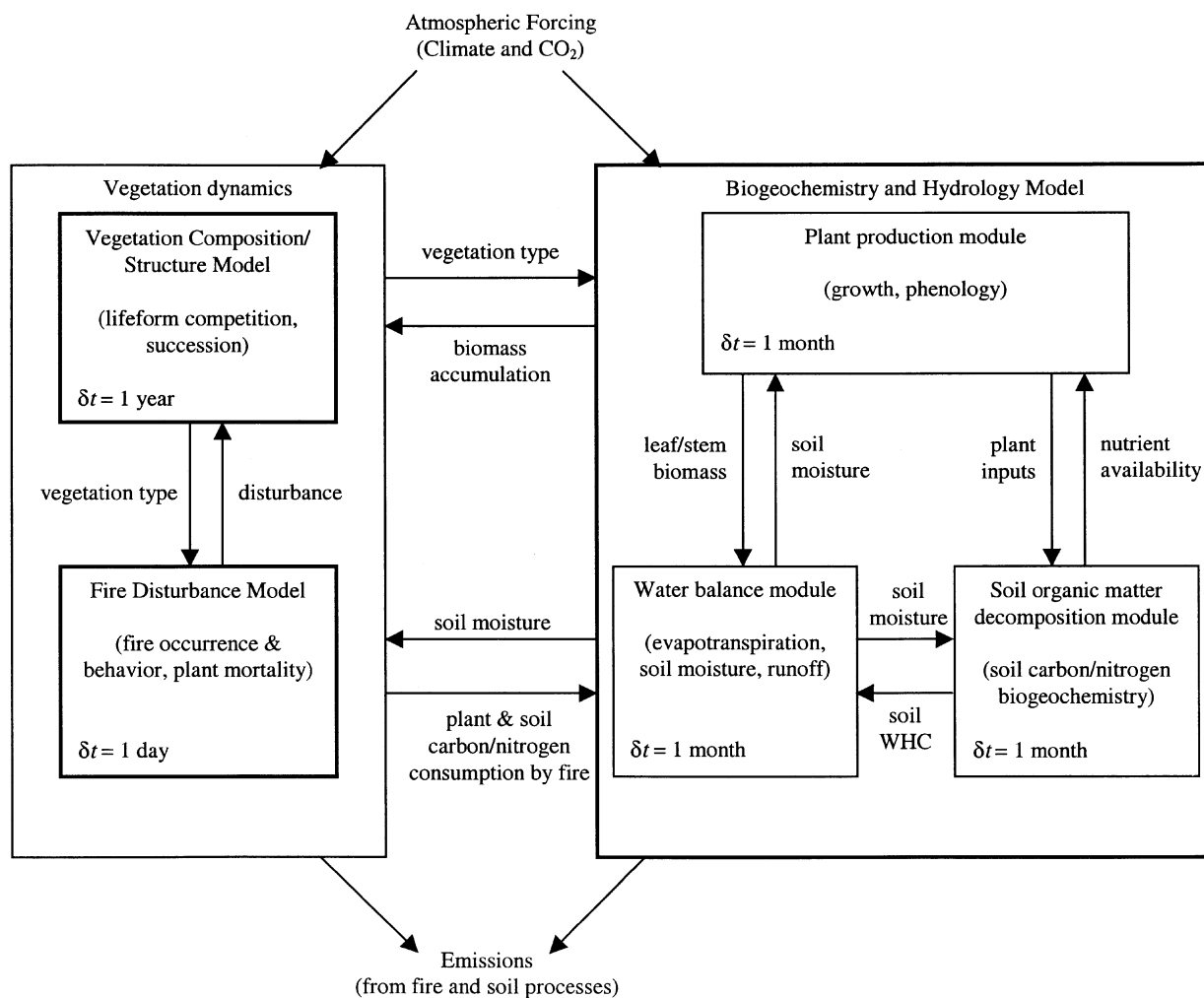
An important shortcoming of frame-based models is that ecosystem types are prescribed, so that vegetation comprising novel combinations of species cannot be simulated. The palaeorecord clearly indicates that species respond individually to climate (Davis 1981; Overpeck *et al.* 1992; Pitelka & Plant Migration Workshop Group 1997), so that rapid climate change results in new plant associations rather than the movement of existing, intact communities. Models that simulate this vegetation response to climate realistically must operate on individual species or plant functional types rather than ecosystem types or biomes.

### **Class 3: Dynamic global vegetation models**

#### *Model class description*

Timescales for changes in ecosystem structure and composition (e.g. biome shifts) are often several orders of magnitude greater than those of many physiological processes (e.g. photosynthesis). It is thus a reasonable first approximation in projecting global vegetation

(b)



**Fig. 3** Two generalized examples of DGVM structure, incorporating processes with a range of timescales through a suite of coupled modules: (a) IBIS (adapted from Foley *et al.* 1996); and (b) MC1 (Lenihan *et al.* 1998; Daly *et al.* 2000).  $\delta t$  = time step. In (b), soil WHC = soil water-holding capacity. In MC1, three models (bold boxes) are linked: a biogeochemistry/hydrology model (derived from CENTURY), a vegetation composition model (derived from MAPSS), and a fire model (MCFIRE).

response to environmental change to hold structure and composition fixed for long periods of time and simulate only the change in function (e.g. Cao & Woodward 1998). However, structure and function interact, so that simulation of the transient response of vegetation to global change on decadal to century timescales requires an integrated approach.

A new class of global biosphere models, known as DGVMs, has been developed to simulate transient changes in both ecosystem structure and function. DGVMs are a significant advance over earlier separate biogeographical and biogeochemical models in that they (i) link vegetation structure and function in an integrated

way and (ii) simulate the transient responses of both structure and function to changing conditions (Neilson & Running 1996; Goudriaan *et al.* 1999).

Two approaches have been taken to develop DGVMs. The first is to convert equilibrium biogeographical models to transient models by coupling them with models that simulate rates of disturbance (e.g. fire models) and rates of vegetation growth (e.g. biogeochemistry models, discussed below) (e.g. Figure 3b). Examples of recent DGVMs that fully couple biogeographical and biogeochemical/carbon balance models are the Sheffield DGVM (Beerling *et al.* 1997), MC1 (MAPSS-CENTURY version 1; Lenihan *et al.* 1998; Daly *et al.* 2000),

LPJ DGVM (Lund–Potsdam–Jena DGVM; Sitch *et al.* in prep.), and IBIS (Foley *et al.* 1996). The second approach is to scale up (statistically or by brute force) an individual-based patch model to the global scale and to couple this model to a biogeochemistry model. Smith & Shugart (1996) described these two DGVM approaches as top-down and bottom-up strategies, respectively. Examples of the second approach are HYBRID v3.0 (Friend *et al.* 1997) and GUESS (Smith *et al.* 2000). HYBRID v3.0 was developed by linking patch, plant physiology, and soil organic matter models, and GUESS by replacing generalized relationships among competing PFTs in the LPJ DGVM with patch-based community dynamics.

The range of dynamics and corresponding timescales included in DGVM simulations are: (i) short-term dynamics of photosynthesis and water and energy exchange (timescale of seconds to minutes), (ii) seasonal patterns of carbon assimilation (timescale of weeks), and (iii) long-term changes in vegetation composition due to competition, mortality, and disturbance (timescales of years and decades). Most DGVMs incorporate these processes with widely varying timescales through a hierarchical suite of coupled modules. However, the overall structure linking process submodels and the time-step at which these processes are estimated vary by model (Fig. 3a,b). Several of these models (e.g. Sheffield DGVM and IBIS) were developed explicitly to be linked to climate system models.

Most DGVMs simulate the growth of vegetation in a way following that of stand-alone biogeochemical models (e.g. BIOME-BGC, CENTURY, and TEM; Running & Hunt 1993; Parton *et al.* 1994; Tian *et al.* 1999). These models simulate carbon and nitrogen cycling through the plant–soil system, with carbon assimilation limited by temperature, light regime, and water and nitrogen availability and with soil organic matter decomposition controlled by soil temperature and moisture and biochemistry (C:N ratio, lignin content) of plant inputs to the soil (Fig. 3b). However, representation of nitrogen cycling varies among DGVMs, affecting the manner and degree to which nutrient availability constrains plant growth and vegetation dynamics. DGVMs also incorporate the direct effects of CO<sub>2</sub> on plant production. However, as with the biogeochemical models, DGVMs differ in their conceptualization of how biogeochemical processes control these effects (cf. Pan *et al.* 1998).

The current generation of DGVMs all adopt a plant functional type approach, usually with seven to 10 different PFTs (Table 1a), which is a smaller number of types than species used in standard patch models. The PFTs compete for basic resources under a varying climate (e.g. historical or future series) and specified or climatically determined disturbance regime (e.g. fire).

The resulting simulation gives, for each grid cell, a distribution of those PFTs that can generate significant biomass. This approach allows the simulation of new biome types, through the generation of a novel mix of PFTs, and can project structural changes within a biome, such as a changing tree:grass ratio in a semiarid tropical savanna. More well-known descriptive characterizations of biomes (e.g. ‘tropical rainforest’) can be recovered from DGVM output by overlaying the PFT mix with climatic zone. Outputs from DGVMs include dominant PFTs and their combination into vegetation type, some measure of foliar cover (e.g. LAI), net primary production (NPP), net ecosystem–atmosphere carbon exchange (NEE), water budget terms, soil and vegetation carbon stocks, and net nitrogen mineralization.

Disturbance is recognized as an important triggering phenomenon in determining change to vegetation structure in DGVMs. Disturbance mechanisms represented include age-dependent mortality and, in some models, fire is simulated explicitly. In MC1, for example, fire is a function of fuel loading (determined from biomass production) and ignition as a stochastic function of monthly climate (Lenihan *et al.* 1998). Windthrow and other disturbances are often incorporated as part of a background mortality rate.

#### *High-latitude response to altered climate and increasing CO<sub>2</sub>*

A recent intercomparison of the response of four DGVMs to transient climate and CO<sub>2</sub> change showed considerable differences among models globally in terms of both function (NPP and total vegetation biomass) and vegetation distribution (Cramer *et al.* 1999). Results for the high latitudes, however, were the most consistent of any zone, probably due to the overriding importance of temperature in influencing the response of these ecosystems. In response to warming, the models all projected (i) increasing NPP and biomass in the high latitudes (Fig. 4a) and (ii) northward movement of tundra into the arctic desert and, in turn, forests and woodlands into tundra zones (as shown for LPJ in Fig. 4b; see also Cramer *et al.* 1999; plate 6). Some models predicted that needleleaf evergreen trees would dominate these new northern forests while others indicated dominance by boreal broadleaf deciduous trees. This disagreement is probably due to differences in the sensitivity of DGVMs to climatic parameters. This result was not found in many earlier global experiments with equilibrium models because those models did not specify boreal broadleaf deciduous forest as a separate vegetation type (however, see Cramer 1997). In LPJ, the greatest change from 2000 to 2100 was for the southern limit of the boreal evergreen forest in central and western Eurasia to be replaced by

temperate deciduous forests and grasslands (Fig. 4b). Accompanying the transition from, for example, tundra to tree-dominated landscapes, the DGVMs also detailed the time sequence of responses of plant and soil processes, including carbon, water, energy, and trace gas fluxes to the atmosphere. For example, by 2100, simulated NPP in Siberia north of 65°N increased by 1.5–10 times preindustrial conditions, depending on model and location (Cramer *et al.* 1999).

### Limitations

Because they were developed for the global domain (and accompanying coarse grid implementation), DGVMs carry with them some of the same limitations specific to high-latitude environments as in the equilibrium biogeographical models. DGVMs need to incorporate processes associated with inundated landscapes and saturated, anaerobic soils and dynamic interactions among permafrost, climate, and vegetation cover. Permafrost dynamics are under development for LPJ (S. Venevski & S. Sitch, pers. comm.); IBIS includes the effect of frozen soil water on soil porosity (Foley *et al.* 1996). Because boreal and arctic landscapes are highly heterogeneous, adequate simulation of the contribution of inundated vs. upland terrain and of permafrost landforms to grid-cell carbon and vegetation dynamics requires treatment of subgrid processes in DGVMs through their parameterization or a statistical dynamical approach (see p. 3 of this paper). Inclusion of these processes will require input datasets that differ from the standard land-cover and soil texture data generally required by global models. Additional inputs include (i) those that describe subgrid topographic and depth-to-bedrock controls over drainage, and (ii) extent of and depth to permafrost (e.g. Brown 1998; Brown *et al.* 1998; Ferrians 1998; Leibman 1998).

An additional limitation with respect to treatment of high-latitude ecosystem physiology is that extant DGVMs do not consider the role of moss and lichen explicitly in tundra and boreal forest biogeochemical dynamics, including N-fixation by some lichens (Sveinbjörnsson & Sonesson 1997). In addition, with respect to all environments, DGVMs will benefit from improved understanding from laboratory and field experiments of short- and long-term effects of CO<sub>2</sub> on (i) plant physiology (especially in regard to water vs. nutrient limitation, allocation of C and N to short vs. long-lived tissues, and acclimation), (ii) N-fixation, and (iii) ecosystem C–N cycle interactions (including impacts of atmospheric N deposition) (Cole & Heil 1981; Schimel 1995; Bazzaz *et al.* 1996; Oechel & Vourlitis 1997; Pan *et al.* 1998; Mooney *et al.* 1999).

Population biology lag effects related to seed source distance and dispersal mechanisms, which would influence the northward migration of trees, were not included in the DGVMs evaluated by Cramer *et al.* (1999). Although the importance of such effects is still a matter of debate, they could be a significant factor in overall vegetation response to rapid climate change (Pitelka & Plant Migration Workshop Group 1997; see also Huntley 1997 for review of past rates of migration in arctic and boreal regions from the palaeo-record). These effects could be incorporated by using some features of frame-based spatial models.

DGVMs are designed to give broad-scale simulations of time-dependent ecosystem change that are consistent across continents. Thus, DGVMs only provide simulations of vegetation response for any particular region, such as the high latitudes, that are coarse both spatially and ecologically (in terms of plant functional types). For finer-scale simulations of vegetation change, more detailed dynamic regional vegetation models (see below), biome-specific frame-based models, or patch models are required.

### Future model improvements and adaptation for high-latitude ecosystems

#### *Disturbance ecology and land-use/cover change*

A number of important improvements to the performance of DGVMs with respect to natural disturbance and land-cover change are currently under development or planned for the near future (Woodward & Steffen 1996). Compilations of continental-scale data in the high latitudes suggest that human-induced changes in disturbance regimes already have a major impact on the terrestrial carbon cycle in this part of the globe (Kurz *et al.* 1995; Auclair & Bedford 1997). Fire is probably the most important disturbance in boreal systems. However, because of increasing human activities in these regions, fire modules in DGVMs need to incorporate the effects of changing land-use (e.g. forest harvest, fire suppression) on the probability of fire outbreak. Other disturbance factors, such as insect attack (Holling 1992), are also likely to be key determinants of the future of these systems. Patch-scale forest insect infestation models (e.g. Logan *et al.* 1995; Powell *et al.* 1996), linked to forest stand models, are being adapted for landscape- and century-scale simulations of insect–host–climate change interactions (J. Powell & J. Logan, pers. comm.). Modelling of insect outbreaks and other disturbance regimes across the boreal zone is limited by poor understanding of current disturbance frequency and extent and their response to climate variability. The development of regional databases of fire (e.g. Murphy *et al.* 1999), insect

outbreaks, windthrow, and other disturbance factors based on field and remotely sensed observations and understanding their relationships with climate, vegetation, and other drivers are crucial areas of research necessary to improve disturbance modules in DGVMs (Woodward & Steffen 1996).

All current DGVMs simulate potential vegetation only. However, the most important driver of change in vegetation structure globally over the next several decades at least will be land-use change. There are global models which project human-driven changes to land-use and cover (e.g. IMAGE; Alcamo 1994; Alcamo *et al.* 1996) but none are yet incorporated into a DGVM framework. Given current projections, accounting for land-use change is less important for the Arctic than for most other parts of the world, but still has significant consequences for the boreal zone (Chapin & Danell 2000).

#### Dynamic regional vegetation models

The generalized framework of DGVMs can be adapted to provide more detailed simulations for particular regions by (i) incorporation of processes that are specific to and important for that domain, such as, in the case of high latitude systems, permafrost dynamics and anaerobic processes for poorly drained soils, and (ii) adoption of an expanded PFT scheme tailored to the region's particular vegetation characteristics, such as in Chapin *et al.* (1996) and Bugmann (1996) for the pan-arctic/boreal domain (Table 1b). For example, a species of special interest, such as an endangered species or a valued timber species, either of which could influence the probability of logging, could be modelled as a PFT in its own right. While species-based rather than PFT-based, LINKAGES (Pastor & Post 1986) is an example of a DRVM consisting of linked patch and biogeochemistry models implemented to evaluate climate change responses of a specific region (eastern U.S.).

#### Summary

Mechanistic global and regional vegetation models provide the means for extrapolating our understanding of ecosystem processes in space and time. Both regional and global implementations of equilibrium biogeographical models have had a key role in indicating the direction of structural changes in equilibrium with altered forcing (i.e. new potential 'climax' natural vegetation). Under climate scenarios dominated by increased surface air temperatures, these models simulated replacement of arctic tundra by northward shifts of boreal woodlands and forests, whose southern reaches

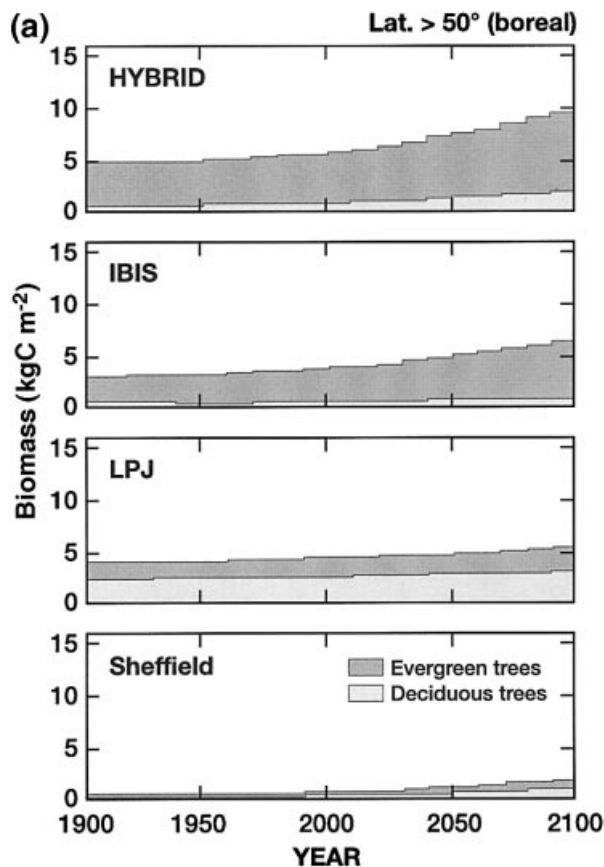


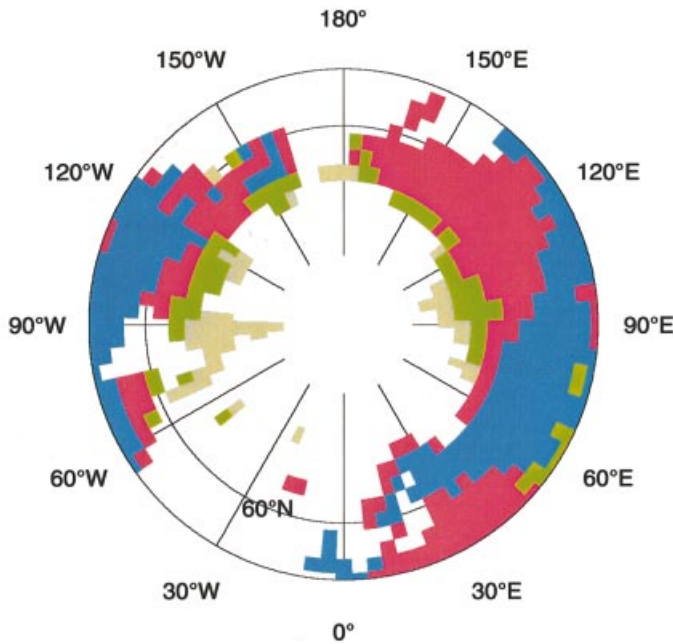
Fig. 4a (caption on next page)

were in turn replaced by temperate mixed and deciduous forests.

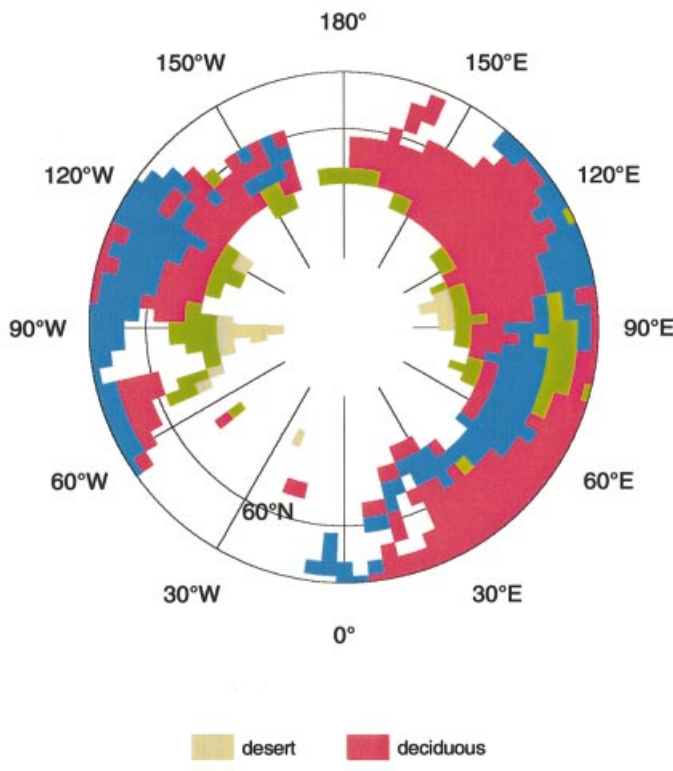
Simulation of transient vegetation dynamics is also crucial to understanding potential change because ecosystems have inherent lags and threshold responses and are expected to exhibit complex responses to multiple forcings (climate, CO<sub>2</sub>, land-use, N deposition, etc.). Recently developed DGVMs and frame-based models provide the tools for evaluating response times and transitional states. ALFRESCO, a frame-based model, indicated the same directional changes as the equilibrium models, but portrayed how response times depend on the rate of temperature increases and concomitant changes in moisture regime and fire return period.

DGVMs additionally (i) simulate time-dependent functional responses of ecosystems (e.g. nutrient and fire dynamics) and so account for their role in vegetation dynamics, and (ii) allow for shifting composition of vegetation types as PFTs remix under novel environmental conditions. Under changing climate and CO<sub>2</sub>, DGVMs have simulated the time course of high-latitude vegetation change from arctic tundra to tree-dominated

(b) LPJ-DGVM VEGETATION CLASS (YEAR 2000)



LPJ-DGVM VEGETATION CLASS (YEAR 2100)



**Fig. 4** Simulated Northern Hemisphere high-latitude (north of 50°N) vegetation responses to transient climate forcing and increasing CO<sub>2</sub> from (a) four DGVMs in terms of tree biomass changes from 1900 to 2100 (adapted from Cramer *et al.* 1999). Although small relative to tree biomass, grass/tundra biomass (not shown) was also present in the simulations. (b) Change in distribution of evergreen and deciduous-dominated forests/woodlands, grasslands/tundra, and deserts from 2000 to 2100 for the LPJ model (courtesy S. Sitch, Potsdam Institute for Climate Impact Research). Models are among those in Table 1a. Transient climate forcing was from Hadley Centre Coupled Model 2 experiments with increasing greenhouse gases and sulphate aerosols (HADCM2 SUL; Mitchell *et al.* 1995).

landscapes. This transition was both affected by and in turn influenced changes in biomass, net primary production, and soil organic matter turnover, which all increased with warming. Some DGVMs showed emergence of boreal broadleaf deciduous forest, a vegetation type not zonally dominant today.

The global implementation of DGVMs has, at least initially, forced limited representation of processes key to dynamics of specific regions, such as the high latitudes. Crucial improvements to DGVMs needed to portray the behaviour of arctic and boreal systems are the inclusion of anaerobic soil processes for inundated landscapes, permafrost dynamics, moss-lichen processes, and a broad accounting of disturbance regimes (e.g. fire, insect outbreaks, and land management). Also needed are parameterization and driving variable datasets required for modelling these processes and implementation of techniques to account for their subgrid representation. Modelling further tailored to explore the transient response of high-latitude landscapes can be accomplished by large domain (e.g. zonal) and spatially interactive gridded application of arctic/boreal frame-based models and development of DRVMs more adequately detailing key processes and plant functional types specific to the pan-arctic and boreal domain.

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