

Biome Models

Wolfgang Cramer

Volume 2, **The Earth system: biological and ecological dimensions of global environmental change**, pp 166–171

Edited by

Professor Harold A Mooney and Dr Josep G Canadell

in

Encyclopedia of Global Environmental Change

(ISBN 0-471-97796-9)

Editor-in-Chief

Ted Munn

© John Wiley & Sons, Ltd, Chichester, 2002

Biome Models

Wolfgang Cramer

Potsdam Institute for Climate Impact Research, Potsdam, Germany

Biomes may be defined as "... the world's major (plant and animal) communities, classified according to the predominant vegetation and characterized by adaptations of organisms to that particular environment" (Campbell, 1996). A synonym for biome is major life zone. Typical biomes are, e.g., coniferous forest (taiga), desert, grassland, Mediterranean shrubland, rain forest, savanna, temperate forest, tundra, coastal waters, coral reef, freshwater, and open ocean; but the number of subdivisions in any biome list is arbitrary and depends on the list's specific purpose. Due to their broad geographic extent, often covering broad continent spanning zones, biomes normally consist of multiple types of ecosystems, which reflect local environmental gradients and interactions. For example, the same taiga biome contains wet oceanic cold rain forests and cold adapted continental deciduous conifer forests.

On land, biomes are usually characterized by their dominant vegetation expressed in broad categories. Just like in the more narrowly defined ecosystems, animals and soil biota are equally important elements in their function and therefore also for their structure. Biome definitions usually do not relate to the kind of human land use that takes place within their boundaries. Biomes may, however, be considered as indicators for the agricultural or forest practice that can be carried out potentially in a given region.

CLIMATIC FACTORS THAT DETERMINE BIOME DISTRIBUTIONS

Biomes are well determined by macroclimatic and soil characteristics. Indeed, before the advent of large-scale climate maps based on weather stations, both geographers and climatologists have often considered biomes as indicators for climate in areas with insufficient weather stations (Köppen, 1884; Cramer and Leemans, 1993). Climatic factors may be used to identify environmental correlates or even causes for the distributional limits of either biomes or species. Classically, the factors used were easily accessible longer-term averages of standard variables, such as annual or monthly averages of temperature and precipitation. By visual map comparison, coinciding climatic and biome limits could be used to further characterize the biome and its typical environment.

Increasingly, so-called *bioclimatic* indicators are being developed from climatic boundaries that are based on specific processes of plant growth or survival. Ultimately,

the goal of such indicators is to be able to predict the location, and the possible change, of biome distribution limits in response to past or future climate change. Examples are growing degree days or heat sums (i.e., the sum of all temperatures above a certain threshold), absolute cold tolerance limits or estimates of typical maximum drought stress based on a simple water balance calculation. The life zone classification by Holdridge (1947, 1967) was the first attempt to provide a complete biome (life zone) system defined by only two such bioclimatic variables (see **Holdridge Life Zone Classification**, Volume 2). The Holdridge system could be applied globally and thereby provided a first simple global biome model that could be used to assess the sensitivity of global vegetation distribution to climate change (Emanuel *et al.*, 1985).

BIOME MODELING APPROACHES

The arrival of digital computers with sufficient capacity to store and manipulate large global climatic databases, as well as maps of other environmental variables, triggered the development of more elaborate mathematical models of global biome distribution. Such models are global in the sense of being applicable at any (ice-free) land surface, if given a description of environmental conditions at this location. The models have no implicit spatial resolution, and there is no lateral interaction between neighboring locations.

Depending on their purpose, biome models have been developed for the characterization of biome distributions as a function of climate and soils. Some related models have also been used to assess the dynamics of carbon and water fluxes, using a map of biome types. A third, more recent group of models combines these two aspects. The most recently developed class of models adds transient dynamics of vegetation structure and carbon pools to the picture. All four classes of models are briefly discussed in the following subsections.

Equilibrium Models of Biome Distribution

For the first generation of the biome models, biome distribution is assumed to be in equilibrium with climate. Box (1981) developed such a model, combining the concepts of life form (Raunkjær, 1907) and life zone (Holdridge, 1967). To capture the essential life forms of all higher plants, Box defined 90 different plant types, as well as bioclimatic envelopes (lower and upper boundaries) for eight variables (listed in Table 1), which all could be mapped on the basis of available climatic normals. Woodward (1987) was the first to show that a more appropriate analysis of biome distribution required the representation of the physiological

Table 1 Bioclimatic indices used by the Box model

T_{\max}	Mean temperature of the warmest month ($^{\circ}\text{C}$)
T_{\min}	Mean temperature of the coldest month ($^{\circ}\text{C}$)
D_T	Range between T_{\min} and T_{\max} ($^{\circ}\text{C}$)
P	Mean total annual precipitation (mm)
MI	Moisture index, defined as the ratio between P and annual potential evapotranspiration (Thornthwaite and Mather, 1957)
P_{\max}	Mean total precipitation of the wettest month (mm)
P_{\min}	Mean total precipitation of the driest month (mm)
$P_{T_{\max}}$	Mean total precipitation of the warmest month (mm)

Source: Box, 1981.

processes that control survival and performance of plants in a given ecosystem. His analysis and the resulting model focussed primarily upon cold tolerance and the water needs of plants, both of which could not easily be derived from existing climate data sets.

The development of a biome distribution model to be applied under different climate regimes (such as those of earlier periods in geological history, or for scenarios of future developments) required the incorporation of mechanistic formulations for all critical processes that could limit plant distributions, as well as the development of suitable data sets for model application worldwide. For the parameterization of process formulations, it was found necessary to group plant species into so called functional groups. Each functional group describes plant types with similar behavior for a given process. A widely used model of this type is the BIOME model (Prentice *et al.*, 1992). It involves four major bioclimatic tolerance/requirement factors (Table 2) which are characterized independently for 13 plant functional types (PFTs). Several PFTs may co-occur

at any location (Table 3). Since precipitation provides no direct indication of moisture stress, a process-based water balance model (Cramer and Prentice, 1988; Prentice *et al.*, 1993) is used to assess regions with significant differences between actual and potential evapotranspiration. The development of BIOME was possible since the climatic limitations could be mapped more precisely than earlier using a topography-sensitive global climate data base developed for this purpose (Leemans and Cramer, 1991). A significantly updated version of this data base is available free of charge from <http://www.pik-potsdam.de/~cramer/climate.htm>.

Applications of BIOME cover a broad range of questions. Since the model gives an appropriate characterization of broad land surface types (in the absence of direct human impact), it has been found to be a suitable replacement for land cover maps that are used in atmospheric general circulation models. Asynchronously coupled to the atmosphere (i.e., with permitted change in biome distribution only every five years or so), the model has allowed one to address critical issues in atmosphere/biosphere stability on the paleoecological time scale (Claussen, 1994, 1996).

Equilibrium Models of Biogeochemical Fluxes

The necessity to better quantify the role of the land biosphere for the overall balance of carbon fluxes was recognized many years ago (Bolin, 1977). As a result of the International Biological Programme (IBP), Lieth (1975) quantified the relationship between net primary productivity (NPP) and climate (temperature, precipitation) in a regression model consisting of one globally applicable equation. The model was revolutionary for its time, but the limitations of this regression for the assessment of future fluxes are nevertheless significant. Most fundamentally, inspection of the Earth's vegetation shows that a single monotonous equation is likely to fail near the boundaries

Table 2 Derivation of bioclimatic indices from interpolated climatic data in the BIOME model

Tolerance/requirement	Ecophysiological mechanism	Bioclimatic index	Climatic variable (monthly means)
Cold tolerance	Killing temperature during coldest period of the year	T_{\min} (temperature of the coldest month, lower limit)	Temperature
Chilling requirement	Winter chilling period required for budburst of woody plants	T_{\min} (temperature of the coldest month, upper limit)	Temperature
Heat requirement	Annual growth respiration requirement	GDD (growing degree days above 0°C and 5°C)	Temperature
Moisture requirement/drought tolerance	Soil moisture availability	AET/PET (annual actual evapotranspiration/annual potential evapotranspiration)	Temperature, precipitation, cloudiness

Source: Prentice *et al.*, 1992.

Table 3 Environmental constraints for each PFT in the BIOME model

PFT		T_{\min}		GDD ₀ min	GDD ₅ min	T_{\max} min	AET/PET	
		min	max				min	max
Trees	Tropical evergreen	15.5					0.80	
	Tropical raingreen	15.5					0.45	0.95
	Warm temperate evergreen	5.0					0.65	
	Temperate summergreen	-15.0	15.5		1200		0.65	
	Cool temperate conifer	-19.0	5.0		900		0.65	
	Boreal evergreen conifer	-35.0	-2.0		350		0.75	
	Boreal summergreen		5.0		350		0.65	
	Non-trees	Sclerophyll/succulent	5.0					0.28
	Warm grass/shrub					22.0	0.18	
	Cool grass/shrub				500		0.33	
	Cold grass/shrub			100			0.33	
	Hot desert shrub					22.0		
	Cold desert shrub			100				
No plants	(Dummy type)							

Source: Prentice *et al.*, 1992.

of major biomes, such as forest–tundra boundaries, where the presence of a major life form affects both the local environment and thereby also productivity.

Moreover, the observations naturally cover only the recent range of atmospheric carbon dioxide concentrations, while it is likely that higher carbon dioxide concentrations will cause changes in plant productivity. Finally, NPP is not the variable of direct interest for assessments of global change impacts; net biome production (NBP), i.e., the remaining net flux after deducting all losses due to respiration and disturbance, is more important and only weakly related to NPP (IGBP Terrestrial Carbon Working Group, 1998).

To overcome these limitations, several groups have developed process-oriented biogeochemical models, e.g., TEM (Raich *et al.*, 1991), CARAIB (Nemry *et al.*, 1996) and FBM (Lüdeke *et al.*, 1994). A detailed review of the state of the art for these models may be found in Cramer *et al.* (1999). Most of these models share the biome concept as a central feature, which is implemented in a static way, i.e., either by using a global vegetation map or by using BIOME as input. Mechanistic formulations of photosynthesis, plant and soil respiration and other processes are parameterized for each biome, and the resulting pools and fluxes of carbon are a function of both biome distribution and climate. Biogeochemical models that make use of remote sensing data are not included here, since these models are not capable of forward-looking simulations and therefore are outside the scope of biome models *per se*.

Coupled Biome Distribution/Biogeochemistry Models

Some equilibrium biome models simulate biogeochemical processes (fluxes) and pattern (vegetation type and

structure) simultaneously. Usually, the determination of the vegetation types follows process-optimization rules, e.g., by maximization of NPP according to soils and climate, or by maximization of the leaf area index (LAI) to satisfy the annual moisture and carbon balances. Examples are DOLY (Woodward *et al.*, 1995) and BIOME3 (Haxeltine and Prentice, 1996). In both models, the distribution of PFT (Plant Functional Type), and hence the resulting biomes, is a function of climate and soils, but (different from BIOME) this function is contained in modules that describe both biogeochemical fluxes and resulting pool sizes quantitatively within the basic bioclimatic limits for PFT survival. Photosynthesis, respiration and water use are simulated depending on climate, as well as on atmospheric carbon dioxide concentration, using process descriptions from field and laboratory studies. This allows one to expect a greater degree of realism even for extrapolations into future conditions, as opposed to regression type approaches.

The most recent model of this class is BIOME4 (Kaplan, personal communication). BIOME4 was developed from BIOME3 with the aim of better covering the diversity of biome types by adding additional PFT and updating some process formulations and parameters. It is based on 13 PFTs, each of which has assigned bioclimatic limits that determine whether or not NPP is calculated for a given location. A coupled carbon and water flux scheme is used to determine the LAI that maximizes NPP for each PFT. The PFT with the highest NPP is chosen to represent vegetation for the biogeochemical fluxes and pools. For savanna vegetation, where the interaction between trees and grasses is particularly important, separate rules are defined to estimate the combined effect of co-existing PFTs.

Dynamic Global Vegetation Models

Interest in biome models comes to a large extent from the need to estimate likely changes in carbon stores in the terrestrial biosphere, as a consequence of atmospheric carbon dioxide increase and the associated changing climate. In periods with rapidly changing climate, the equilibrium assumption in classical biome models is invalid, since vegetation structure and carbon stores in above- and below-ground biomass often change only over decades to centuries, except for disturbance type events such as fires. To realistically simulate NBP, growth of PFTs needs to be considered as well as the major processes affecting soil carbon pools.

Dynamic global vegetation models (DGVMs) are specifically developed for the assessment of transient changes in vegetation structure as well as NBP, driven by climate change. Their development is based on the advances made in equilibrium biome models, as well as in forest succession models. DGVMs, such as HYBRID (Friend *et al.*, 1997) or LPJ (Sitch, 2000) contain dynamic formulations for slow and fast processes of carbon and water fluxes (Figure 1), and they maintain the principal pools of carbon over long time scales. A more detailed description of current DGVMs, and an application are to be found in Cramer *et al.* (2001).

Ultimately, the quantitative and transient analysis of biospheric structure, as made in DGVMs, abandons the biome concept for all but the diagnostic description. All PFTs have more or less smooth responses to environmental gradients and they do not usually react abruptly, except for the

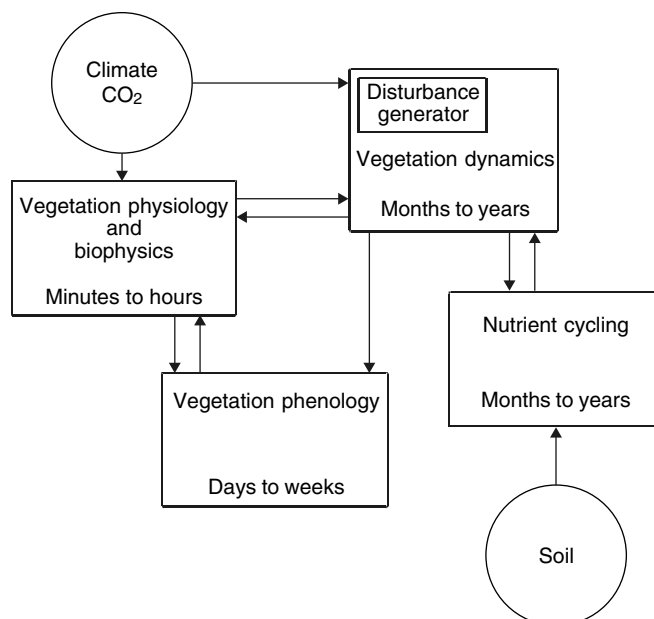


Figure 1 Basic structural elements of a DGVM and their associated time scales (Cramer *et al.*, 2001)

case of rapidly deteriorating conditions. Most biomes have broad transition zones between each other. Environmental changes, such as those that occurred after the deglaciation of Northern Europe, usually led to smooth transitions from a biome dominated by some species into one dominated by another. It is nevertheless useful for analysis and communication, if the resulting distribution of PFTs is shown as a distinct biome map. Otherwise, the reader would have difficulty grasping the distribution of multiple plant types across the globe, using a single map.

BIOMES AS PART OF THE FULL EARTH SYSTEM

Plant types, ecosystems and biomes are not only distributed as a function of climate, they also influence atmospheric processes in a way that differs between biome types. Important characteristics for this influence are the roughness of the canopy (which influences the characteristics of the surface boundary layer), its albedo (which affects the energy balance) and its LAI (which affects carbon and water fluxes). These effects have long been known at the local scale (Köppen and Geiger, 1936), but were studied at the global scale only much later (Dickinson, 1983). Now, many model experiments have shown that large-scale changes of biome distribution, e.g., due to human land use, affect atmospheric circulation (Salati, 1986). Inevitably, these effects produce feedbacks between atmosphere and biosphere which may even lead to multiple stable states of the coupled system (Claussen, 1998).

The consequence of the notion of bi-directional feedbacks between atmosphere and biosphere (expressed as biomes) is that all assessments of future conditions of the system depend on understanding all of the major elements of the Earth System, which is currently destabilized primarily by human disruption of the carbon balance. What we need to know is whether the Earth's vegetation might amplify or dampen the impacts of this disruption. Present estimates seem to indicate that physiological processes in some major biomes (e.g., the boreal forest) lead to increased uptake and storage of carbon by ecosystems, due to the increased carbon dioxide concentration in the atmosphere (Cramer *et al.*, 2001). However, the resulting changes in temperature may well lead to increased drought and fire risk in some areas, notably the drier variants of forested biomes (White *et al.*, 2000). This would in turn influence the atmosphere due to the resulting release of carbon from dying forests and mineralized soil carbon.

We cannot presently determine the exact trajectory of these changes. But model results are sufficiently plausible to raise concern over the stability of the overall system. Some biomes, such as tropical forests, have also been identified as being crucial for a sustainable Earth from other perspectives, such as the maintenance of biodiversity.

REFERENCES

- Bolin, B B (1977) Changes of Land Biota and their Importance to the Carbon Cycle, *Science*, **196**, 613–615.
- Box, E O (1981) *Macroclimate and Plant Forms: an Introduction to Predictive Modeling in Phytogeography*, Dr W Junk Publishers, The Hague.
- Campbell, N A (1996) *Biology*, 4th edition, The Benjamin/Cummings Publishing Company, Menlo Park, CA.
- Claussen, M (1994) On Coupling Global Biome Models with Climate Models, *Clim. Res.*, **4**, 203–221.
- Claussen, M (1996) Variability of Global Biome Patterns as a Function of Initial and Boundary Conditions in a Climate Model, *Clim. Dyn.*, **12**, 371–379.
- Claussen, M (1998) On Multiple Solutions of the Atmosphere–Vegetation System in Present-day Climate, *Global Change Biol.*, **4**, 549–560.
- Cramer, W, Bondeau, A, Woodward, F I, Prentice, I C, Betts, R A, Brovkin, V, Cox, P M, Fisher, V, Foley, J, Friend, A D, Kucharik, C, Lomas, M R, Ramankutty, N, Bitch, S, Smith, B, White, A, and Young-Molling, C (2001) Global Response of Terrestrial Ecosystem Structure and Function to CO₂ and Climate Change: Results from Six DGVMs, *Global Change Biol.*, in press.
- Cramer, W, Kicklighter, D W, Bondeau, A, Moore, III, B, Churkina, G, Nemry, B, Ruimy, A, Schloss, A L, and participants of the Potsdam NPP Model Intercomparison (1999) Comparing Global Models of Terrestrial Net Primary Productivity (NPP): Overview and Key Results, *Global Change Biol.*, **5**(1), 1–15.
- Cramer, W and Leemans, R (1993) Assessing Impacts of Climate Change on Vegetation using Climate Classification Systems, in *Vegetation Dynamics and Global Change*, eds A M Solomon and H H Shugart, Chapman and Hall, New York, 190–217.
- Cramer, W and Prentice, I C (1988) Simulation of Soil Moisture Deficits on a European Scale, *Norsk Geografisk Tidsskrift*, **42**, 149–151.
- Dickinson, R E (1983) Land Surface Processes and Climate, Surface Albedos and Energy Balance, *Adv. Geophys.*, **25**, 305–353.
- Emanuel, W R, Shugart, H H, and Stevenson, M P (1985) Climatic Change and the Broad-scale Distribution of Terrestrial Ecosystems Complexes, *Climatic Change*, **7**, 29–43.
- Friend, A D, Stevens, A K, Knox, R G, and Cannell, M G R (1997) A Process-based, Terrestrial Biosphere Model of Ecosystem Dynamics (Hybrid v3.0), *Ecol. Model.*, **95**, 249–287.
- Haxeltine, A and Prentice, I C (1996) BIOME3: An Equilibrium Biosphere Model Based on Ecophysiological Constraints, Resource Availability and Competition Among Plant Functional Types, *Global Biogeochem. Cycles*, **10**, 693–709.
- Holdridge, L R (1947) Determination of World Plant Formations From Simple Climatic Data, *Science*, **105**, 367–368.
- Holdridge, L R (1967) *Life Zone Ecology*, revised edition, Tropical Science Center, San José, Costa Rica.
- IGBP Terrestrial Carbon Working Group (1998) The Terrestrial Carbon Cycle: Implications for the Kyoto Protocol, *Science*, **280**, 1393–1394.
- Köppen, W, (1884) Die Wärmazonen der Erde, nach der Dauer der Heissen, Gemässigten und Kalten Zeit und nach der Wirkung der Wärme auf die Organische Welt Betrachtet, *Meteorologische Zeitschrift*, **1**, 215–226 (+map).
- Köppen, W and Geiger, R (1936) *Handbuch der Klimatologie*, Gebrüder Bornträger, Berlin.
- Leemans, R and Cramer, W (1991) *The IIASA Database for Mean Monthly Values of Temperature, Precipitation and Cloudiness of a Global Terrestrial Grid*, Research Report RR–91–18, International Institute for Applied Systems Analysis (IIASA), Laxenburg, Austria.
- Lieth, H (1975) Primary Production of the Major Vegetation Units of the World, in *Primary Productivity of the Biosphere*, eds H Lieth and R H Whittaker, Springer-Verlag, Berlin, 203–215.
- Lüdeke, M K B, Badeck, F-W, Otto, R D, Häger, C, Dünges, S, Kindermann, J, Würth, G, Lang, T, Jäkel, U, Klaudius, A, Range, P, Habermehl, S, and Kohlmaier, G H (1994) The Frankfurt Biosphere Model. A Global Process Oriented Model for the Seasonal and Long-term CO₂ Exchange Between Terrestrial Ecosystems and the Atmosphere, I: Model Description and Illustrative Results for Cold Deciduous and Boreal Forests, *Clim. Res.*, **4**, 143–166.
- Nemry, B, François, L, Warnant, P, Robinet, F, and Gérard, J-C (1996) The Seasonality of the CO₂ Exchange Between the Atmosphere and the Land Biosphere: A Study with a Global Mechanistic Vegetation Model, *J. Geophys. Res.*, **101**, 7111–7125.
- Prentice, I C, Cramer, W, Harrison, S P, Leemans, R, Monserud, R A, and Solomon, A M (1992) A Global Biome Model Based on Plant Physiology and Dominance, Soil Properties and Climate, *J. Biogeogr.*, **19**, 117–134.
- Prentice, I C, Sykes, M T, and Cramer, W (1993) A Simulation Model for the Transient Effects of Climate Change on Forest Landscapes, *Ecol. Model.*, **65**, 51–70.
- Raich, J W, Rastetter, E B, Melillo, J M, Kicklighter, D W, Steudler, P A, Peterson, B J, Grace, A L, Moore, III, B, and Vürismarty, C J (1991) Potential Net Primary Productivity in South America: Application of a Global Model, *Ecol. Appl.*, **1**, 399–429.
- Raunkiær, C (1907) *Planterigetets Livsformer*. Gyldendalske Boghandel and Nordisk Forlag, Copenhagen/Kristiania.
- Salati, E (1986) Amazon: Forest and Hydrological Cycle, in *Climate–Vegetation Interactions*, eds C Rosenzweig and R E Dickinson, UCAR-OIES, NASA/Goddard Space Flight Center, Greenbelt, MD, January 27–29, 110–112.
- Sitch, S (2000) *The Role of Vegetation Dynamics in the Control of Atmospheric CO₂ Content*, PhD Lund University, Lund, Sweden.
- Thornthwaite, C W and Mather, J R (1957) *Instructions and Tables for Computing Potential Evapotranspiration and the Water Balance*, Drexel Institute of Technology, Laboratory of Climatology.
- White, A, Cannell, M G R, and Friend, A D (2000) CO₂ Stabilization, Climate Change and the Terrestrial Carbon Sink, *Global Change Biol.*, **6**, 817–833.
- Woodward, F I (1987) *Climate and Plant Distribution*, Cambridge University Press, Cambridge.
- Woodward, F I, Smith, T M, and Emanuel, W R (1995) A Global Land Primary Productivity and Phytogeography Model, *Global Biogeochem. Cycles*, **9**, 471–490.