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A global biome model based on plant physiology and dominance, soil properties and climate

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Abstract. A model to predict global patterns in vegetation physiognomy was developed from physiological considerations influencing the distributions of different functional types of plant. Primary driving variables are mean coldest-month temperature, annual accumulated temeprature over 5°C, and a drought index incorporating the seasonality of precipitation and the available water capacity of the soil. The model predicts which plant types can occur in a given environment, and selects the potentially dominant types from among them. Biomes arise as combinations of dominant types. Global environmental data were supplied as monthly means of temperature, precipitation and sunshine (interpolated to a global 0.5° grid, with a lapse-rate correc-tion) and soil texture class. The resulting predictions of global vegetation patterns were in good agreement with the mapped distribution of actual ecosystem complexes (Olson, J.S., Watts, J.A. & Allison, L.J. (1983) *ORNL-5862*, Oak Ridge Nat. Lab., 164 pp.), except where intensive agricul-ture has obliterated the natural patterns. The model will help in assessing impacts of future climate changes on potential natural vegetation patterns, land-surface characteristics and terrestrial carbon storage, and in analysis of the effects of past climate change on these variables.

Key words. Biome, carbon cycle, climate change, map comparison, plant functional types.

INTRODUCTION

The transcontinental correspondence between geographic patterns of vegetation and climate is one of the oldest ob-servations in plant ecology, and forms the basis for several empirical classification schemes that have been used to predict the broad physiognomic vegetation types known as plant formations, or biomes (Mather & Yoshioka, 1968; Cramer & Leemans, 1992). The best-known schemes are those of Köppen (1936) and Holdridge (1947). Köppen's scheme was intended as a classification of climates, al-though its boundaries were chosen to coincide approxi-mately with vegetational boundaries and are expressed in terms of aspects of climate (particularly seasonality) that are relevant to plants. Holdridge's scheme on the other hand was meant to relate potential natural vegetation to climate, although its boundaries are merely a regular dis-section of a climate space defined by two variables, annual precipitation and growing-season temperatures. The Köppen scheme has recently been improved by Guetter & Kutzbach (1990) and the Holdridge scheme by K.C. Pren-tice (1990). Such schemes owe their present popularity to

their ease of application in assessments of the effects of climate change on potential natural vegetation at a global scale (Emanuel, Shugart & Stevenson, 1985; Shugart *et al.* 1986; Leemans, 1990; Prentice & Solomon, 1991).

The Köppen and Holdridge schemes are however not the only available tools for this purpose, and there are already models that are better in various ways. Box (1981) de-scribed a model in which almost 100 plant functional types were assigned climatic tolerances (upper and/or lower bounds) for six climate variables expressing levels and sea-sonality of temperature and precipitation, and a moisture index expressing the ratio of precipitation and potential evapotranspiration. An 'environmental sieve' based on these climatic limits determined which plant types could occur in a given climate. A dominance hierarchy was then applied to reduce the list of plant types to a set of potential dominants. Global maps based on Box's model are present-ed by Cramer & Leemans (1992).

Box's model can be considered as a 'Gleasonian' model, in contrast with the Clementsian determinism implicit in the earlier schemes. The biomes are not taken as given, but emerge through the interaction of constituent plants. The

117

Quaternary record demonstrates unequivocally that plants react to climate change as individual taxa; entire biomes can form, dissolve and re-form within a single Milankovitch cycle (Huntley & Webb, 1988; Prentice, 1992). Models to predict the response of global vegetation patterns to climate change must therefore start from the climatic tolerances of different types of plants, rather than from the apparent climatic distributions of biomes as they exist today (Davis, 1989; Prentice & Solomon, 1991). Box's model satisfies this requirement, although the basis for determining climatic limits of plant types remains essentially correlative, rather than mechanistic.

The early plant geographers were concerned with explaining the distributions of different types of plants in physiological terms, and some of the basic mechanisms involved in cold tolerance and drought resistance, for example, have been known for decades. But it is only recently that predictive models have been derived explicitly from physiological considerations (Woodward, 1987; Woodward & Williams, 1987). Woodward's models differ from their predecessors in incorporating *only* those environmental constraints that were considered to have a clear physiological basis. Woodward's models are formulated in terms of biomes, but the logic by which the biomes arise is ultimately based on the notion of physiological plant types. Woodward's models resolve only a few distinct biomes, yet they have proved remarkably successful in reproducing broad global-scale patterns. The model of Neilson *et al.* (1989, 1992) pursues a similar theme, explaining and predicting the major vegetation boundaries within the conterminous United States in terms of a set of rules derived from a consideration of the seasonal temperature and soil-moisture requirements of different plant types. It seems

likely that models thus based on mechanistic considerations will be more robust under changed climatic conditions than those based on correlations that may cease to apply (Prentice & Solomon, 1991; Woodward & Rochefort, 1991).

We present a predictive model for potential natural vegetation that builds on the various innovations of Woodward and Box. The model is based on a small number of plant functional types applied with an environmental sieve and dominance hierarchy as in Box (1981), while the environmental limits of each plant type are defined with reference to physiological constraints as in Woodward (1987). The model was exercised with climate data on a 0.5° grid, to yield high-resolution global maps. These were compared quantitatively and visually with maps derived from the data on global ecosystem complexes compiled by Olson, Watts & Allison (1983). The model can be considered as a prototype, whose structure would easily allow the incorporation of more accurate or detailed information about the environmental constraints affecting different types of plants. It has been designed in such a way as to allow immediate application to assessments of changes in global vegetation patterns and terrestrial carbon storage in response to changes in climate.

THE MODEL

Principles

We aimed for the simplest possible model—that is, the smallest number of plant functional types, constraints and driving variables—to achieve our goal of simulating the broad features of present vegetation as indicated in the data of Olson *et al.* (1983). The selection of plant functional

TABLE 1. Environmental constraints (mean temperature of the coldest month, T_c; growing degree-days on 5°C base, GDD; growing degree-days on 0°C base, GDD_0; mean temperature of the warmest month, T_w; Priestley–Taylor coefficient of annual moisture availability, (α) and dominance class (D) for each plant type in the model*

| | T_c | | GDD | GDD_0 | T_w | α | | D |
	min	max	min	min	min	min	max	
Trees								
tropical evergreen	15.5					0.80		1
tropical raingreen	15.5					0.45	0.95	1
warm-temperate evergreen	5					0.65		2
temperate summergreen	−15	15.5	1200			0.65		3
cool-temperate conifer	−19	5	900			0.65		3
boreal evergreen conifer	−35	−2	350			0.75		3
boreal summergreen		5	350			0.65		3
Non-trees								
sclerophyll/succulent	5					0.28		4
warm grass/shrub					22	0.18		5
cool grass/shrub			500			0.33		6
cold grass/shrub				100		0.33		6
hot desert shrub					22			7
cold desert shrub				100				8

*An additional 'dummy type' is defined for computational consistency. This type has dominance class 9 and no environmental limits, representing the 'plant type' that would occur under conditions unfavourable for any other type (e.g. ice caps).

types was further restricted by the need to specify a distinct set of environmental constraints for each type. Current information does not permit the construction of a physiologically-motivated model with as many plant types as that of Box (1981). The selection of driving variables was restricted by the need to derive values of these variables from climate data available at sufficient resolution for the whole globe.

These criteria led us ultimately to define just fourteen plant functional types, three primary and two subsidiary driving variables, and thirty-two constraints (Table 1). Table 1 specifies the environmental sieve used to determine which plant types can occur at a site.

Table 1 is *largely empty*, because constraints are not specified without a known or hypothesized mechanism. This conservative approach to the specification of environmental constraints is an important difference from the model of Box (1981), where most plant types were assigned empirical upper and lower limits for most of the climatic variables in the model. The difference matters, because such empirical limits can be artificial. For example, tropical rainforest trees in Box's model have an upper temperature limit because at present climates warmer than this are too dry for rainforest—an association that may not hold in a changed climate (Cramer & Leemans, 1992). By limiting the number of constraints on each plant type, we hope to minimize the risk of making spurious predictions of the effects of climate change on plants.

Where possible we assigned environmental limits based on independent physiological data from a representative selection of plant species. Otherwise we used physiological reasoning to suggest which environmental variable(s) should constrain which types of plant, then inferred numerical limiting values by comparing global maps of these variables with maps based on the data of Olson *et al.* (1983). The descriptions of the ecosystem complexes in Olson *et al.* (1983) were used to determine which plant types were present in each complex.

Cold tolerance

Sakai & Weiser (1973), Wolfe (1979), Larcher (1983), Woodward (1987, 1988) and others have emphasized the importance of *minimum* temperatures in determining the world distributions of different types of woody plants. Each value in Table 2 represents the approximate point of failure for a different cold tolerance mechanism, based on observations summarized by Woodward (1987). Most woody plants of the tropics are killed if subjected to temperatures below 0°C, and drought-deciduous taxa are sensitive to temperatures in the range 0–10°C. Broad-leaved evergreen trees and shrubs of temperate regions resist occasional frost, but generally suffer leaf damage when subjected to temperatures below *c.* −15°C; subtropical gymnosperms, such as *Agathis* and *Araucaria*, also belong to this group of plants. Broad-leaved deciduous trees of the temperate zone survive lower temperatures by shedding leaves in winter and by supercooling in the dormant buds, which however are damaged by spontaneous ice nucleation below −40°C (Sakai & Weiser, 1973). The leaves and buds of many coni-

TABLE 2. Minimum temperatures (°C) tolerated by various woody plant forms, from data summarized in Woodward (1987).

Broad-leaved raingreen	0 to 10
Broad-leaved evergreen (frost-sensitive)	0
Broad-leaved evergreen (frost-resistant)	−15
Broad-leaved summergreen	−40
Broad-leaved summergreen (e.g. *Betula, Populus* spp)	No limit
Needle-leaved evergreen (e.g. *Agathis, Araucaria*)	−15
Needle-leaved evergreen (temperate taxa)	−45
Needle-leaved evergreen (boreal taxa)	−60
Needle-leaved summergreen (e.g. *Larix*)	No limit

fers resist temperatures down to *c.* −45°C, and some species of *Abies* and *Picea* resist temperatures down to *c.* −60°C, by a freeze-drying mechanism in which water is progressively expelled from the tissues during cooling (Sakai, 1979). Some broad-leaved deciduous taxa, including species of *Betula* and *Populus*, and deciduous conifers belonging to the genus *Larix*, seem to have unlimited cold resistance due to this mechanism (Sakai, 1979; Sakai & Weiser 1973).

Woodward (1988) showed good correlations between absolute minimum temperature and the continental limits of several plant species in Europe. However, worldwide data on temperature extremes were not available at sufficient resolution for our purpose. We therefore adopted the mean temperature of the coldest month as a primary driving variable, as a surrogate for minimum temperature (Dahl, 1990; Solomon, 1986). Worldwide data from *c.* 2000 stations given by Müller (1982) yielded a regression of absolute minimum temperature (T_{mn}) on mean temperature of the coldest month (T_c), in °C:

$$T_{mn} = 0.006\,T_c^2 + 1.316\,T_c - 21.9 \qquad (1)$$

with $R^2 = 0.938$. Solution of this equation for T_c allowed us to convert the critical values from Table 2 into the model constraints of Table 1.

Chilling requirements

Woody plants of temperate regions commonly require a winter chilling period with temperatures below *c.* 5°C for rapid budburst the following spring. The length of this period influences the growing degree-days (GDD, see below) required for budburst. The relationship can be expressed as:

$$GDD_{budburst} = a + be^{-r\,CD} \qquad (2)$$

where *a*, *b* and *r* are species-specific constants and CD is the number of days with mean temperatures below 5°C during the previous winter (Murray, Cannell & Smith, 1989). The GDD requirement increases more and more steeply as CD is reduced, and becomes excessive when CD is reduced to below *c.* 1–2 months (Nelson & Lavender, 1979; Cannell & Smith, 1983, 1986). Equation (2) has been demonstrated for cool-temperate conifers such as *Picea sitchensis* and *Tsuga heterophylla*, a variety of broad-leaved summergreen trees including cold-tolerant *Betula* and *Populus* spp., and for *Larix decidua* (Cannell & Smith,

1983; Murray *et al.*, 1989). For modelling purposes we have simply assigned the corresponding plant types a minimum requirement of 1 month with mean temperatures >5°C.

Conifers with a more strictly continental distribution, including many *Picea* and *Abies* species, appear to have more stringent chilling requirements for budburst (Nienstaedt, 1967) and regeneration. We adopted a mean coldest-month temperature of −2°C as the upper limit for these taxa, based on their distributions inferred from Olson *et al.* (1983).

The observation that broad-leaved summergreen trees leaf asynchronously—and eventually die—if planted in botanical gardens in the tropics (Box, 1981) is interpreted as evidence that such plants will not survive long in frost-free climates. Using equation (1), we translate this into a requirement for mean coldest-month temperatures <15.5°C. Plants requiring mean coldest-month temperatures >5°C are assumed to have no chilling requirement.

Heat requirements

All plants require a period with temperatures sufficient for growth. The polar and alpine treelines do not correspond with winter temperatures that are too cold for trees. Instead, they can be correlated with measures of accumulated growing-season warmth, such as GDD:

$$GDD = \int (T - T_o)\,dt \qquad (3)$$

where integration is over the period with $T > T_o$ (Tuhkanen, 1980; Kauppi & Posch, 1985). T_o is the minimum temperature for growth, which is *c.* 5°C for trees of cold environments. These tree-lines are formed in the northern hemisphere by boreal evergreen conifers such as species of *Picea* and *Abies*, by cold-hardy, broad-leaved summergreen trees such as species of *Betula* and *Populus*, or by *Larix* (Hustich, 1966; Tuhkanen, 1984). Temperate broad-leaved summergreen trees also commonly show northern limits that can be correlated with higher values of GDD (Solomon, 1986; Prentice & Helmisaari, 1991).

The mechanisms responsible for these heat limits are not known with certainty, but there is some support for the hypothesis that trees have an annual *growth respiration* requirement that is not met beyond the treeline (Dahl & Mork, 1959; Penning de Vries, 1975). Many species show positive net assimilation at low, even sub-zero temperatures (Larcher, 1983), but if respiration is insufficient, cellulose synthesis is inhibited and assimilates are stored rather than used (Skre, 1990; Dahl, 1990). This hypothesis implies an Arrhenius-type response to temperature, rather than the linear response implied by equation (3). However, species adapted to different annual temperature ranges may have different Q_{10}'s for growth respiration (Skre, 1972, 1990), producing an overall treeline that correlates better with GDD than with the accumulated respiration units based on any particular Q_{10}. We have formulated plants' growing-season warmth requirements in terms of GDD, while recognizing that more mechanistic approaches may be possible.

We estimate GDD by interpolation through the mean monthly temperatures to yield quasi-daily values T_i, followed by summation of $(T_i - T_o)$ over the days with $T_i > T_o$.

For trees and for temperate grasses and shrubs, we take $T_o = 5$°C, yielding the primary driving variable called GDD in Table 1. The GDD limits for different types of trees were estimated by comparing global maps of this variable with distributions inferred from Olson *et al.* (1983). The GDD limit for temperate grasses and shrubs separates cool grasslands and shrublands *sensu* Olson *et al.* from tundra, where this plant type is assumed to be lacking. This limit is approximate because under present climatic conditions there is no major geographic transition zone between tundra and steppe. Such transitions do occur on a microscale on mountain slopes in interior Alaska (Edwards & Armbruster, 1989); these may provide a basis for more accurate calibration.

For plants of tundra and cold deserts, which can survive in climates with very short growing seasons, we take $T_o = 0$°C (e.g. Woodward, 1987) yielding the subsidiary variable called GDD_o. The GDD_o limit for tundra and cold desert plants separates tundra from older polar desert, where higher plants are essentially absent. Plant types that require coldest-month temperatures >5°C are assumed never in practice to be restricted by heat requirements. They are therefore not assigned limits in terms of GDD or GDD_o.

Different global vegetation classifications adopt different definitions of 'warm' or 'hot' versus 'cool' or 'cold' grasslands, shrublands and deserts. We have not attempted to analyse this question further in terms of different types of grasses and shrubs. The distinctions made by Olson *et al.* (1983) correspond reasonably well with a summer-month temperature distinction and do not reflect the pattern of winter temperatures or GDD. We adopted an empirical limit for another subsidiary variable, mean temperature of the warmest month (T_w), for tropical grasses and shrubs and hot desert shrubs in order to approximate the boundaries drawn by Olson *et al.* This limit might be related to the importance of C4 grasses, which perform best where summers are hot (Teeri & Stowe, 1976). In each case the 'cooler' ecosystem type is assumed to lack the 'warmer' plant type. As in the case of plants requiring warm winters, plant types requiring hot summers are assumed never in practice to be limited by heat requirements and are not assigned any limit for GDD or GDD_o.

Moisture requirements

The moisture available for plant growth is best expressed in terms of the seasonal course of soil water content. Good fits to the distribution of vegetation physiognomy in terms of available moisture have been obtained using climatic indices such as the ratio of precipitation to potential evapotranspiration (PET) as used by Box (1981), and the closely-related radiative dryness index used by Budyko (1974). Box estimated PET by the Thornthwaite (1948) method; better PET estimates can be substituted. However, plants do not experience PET as such, but respond to the interaction of seasonal PET with soil moisture (Stephenson, 1990). Soil moisture in turn responds to the seasonal course of precipitation and PET, mediated by the water-storage capacity of the soil.

The seasonal distribution of precipitation can strongly affect the severity of drought experienced by the plants, and therefore the plant forms that are adapted to the climate (Neilson *et al.*, 1989). In mediterranean climates, for example, excess precipitation during the wet (winter) season may be lost to plants through runoff despite the large moisture deficit that develops in summer. The extent of this effect is related to soil type—deep, loamy soils can carry over moisture from the wet season into the dry season more effectively than shallow, sandy soils. Soil depth and texture are therefore especially important in highly seasonal climates.

Specht (1972), Woodward (1987) and Nemani & Running (1989) have developed models that include these considerations. They predict vegetation physiognomy by convergence towards an equilibrium between foliage cover and soil moisture balance, based on prescribed relationships between foliage cover and water use. We have adopted an intermediate course between the 'climatic moisture index' approach of Box (1981) and the 'sustainable foliage estimation' approach of Woodward (1987) and others. Our model computes a scalar, α, based on the seasonal course of soil moisture with water use treated as independent of vegetation cover. α is the Priestley–Taylor coefficient, or ratio of actual evapotranspiration to equilibrium evapotranspiration, assessed over the full year (Hare, 1980). It can be considered as an integrated measure of the annual amount of growth-limiting drought stress on plants.

The soil is treated as a single moisture store whose size is a characteristic of the soil. Prentice, Sykes & Cramer (1992) give a complete specification of the algorithm. Required input data are site latitude, soil water-storage capacity, and monthly means or totals of temperature, precipitation and sunshine (as percentages of possible sunshine hours, i.e. an inverse measure of cloudiness). Monthly data are interpolated to yield quasi-daily values. Evaporative *demand* is equated with the equilibrium evapotranspiration, a function of net radiation and temperature which approximates actual evapotranspiration under conditions of adequate water supply; this measure is conveniently independent of either humidity or surface resistances to water vapour transport. The approximation is poor for small areas of forest, but improves with increasing spatial scale and is appropriate for the vegetation as a whole over areas as large as a 0.5° grid cell (Jarvis & MacNaughton, 1986). Evaporative *supply* is taken to be proportional to current soil moisture, reaching a maximum evapotranspiration rate of 1 mm h^{-1} when the soil is fully wet. Actual evapotranspiration (AET) is then taken to be the lesser of the instantaneous supply and demand (Federer, 1982) and is analytically integrated for each day based on the assumed sinusoidal time course of demand, taking the supply as a constant for the day. The soil moisture store is then increased or depleted at the end of the day, according to the balance of precipitation and AET. Excess water runs off and is lost.

If this procedure is computed for a single year, the result can depend on the soil moisture at the beginning of the year. To avoid this dependence, we find the equilibrium soil-moisture values by iteration. We begin with a soil that is saturated on 1 January, and continue using the same (mean) monthly data for a succession of years until the 1 January soil moisture converges. Convergence is immediate in humid climates, and takes 3–5 years in most semi-arid or arid climates. Larger numbers of iterations are required only in climates where precipitation is very low and PET is even lower, i.e. some polar deserts. The computed equilibrium values of α for North America show good agreement with a map by Hare (1980). Hare estimated AET as the difference between long-term areal averages of precipitation and river discharge, and equilibrium ET from similar averages of net radiation and temperature, allowing α to be assessed in a model-independent way.

We assumed that all plant types, except desert shrubs, would have minimum tolerated values of α; these values were inferred by comparing global maps of α with plant type distributions inferred from Olson *et al.* (1983). The absence of raingreen trees from the tropical rainforest was used to infer a maximum value of α for this plant type.

Dominance hierarchy

Table 1 also summarizes the rule used to select potentially dominant plant types. After applying the environmental sieve to determine which plant types can occur, the dominance class values (D) of these types are examined and only those in the highest class (lowest D) present are retained in the code indicating the biome type.

The dominance hierarchy is an admittedly artificial device, whose main purpose is to facilitate comparison with global vegetation classifications such as that of Olson *et al.* (1983). There is no global data set on the actual distributions of plant functional types, and vegetation classifications such as that of Olson *et al.* give informatin only on the plant types that give the 'character' to each class. There is no obvious way to test the model's predictions at the level of individual plant types, but comparisons are possible at the biome level if attention is confined to the landscape dominants.

DATA SETS AND MAPPING

Principles

Three kinds of data were needed: climate and soils data on a 0.5° grid to drive the model, and vegetation data on the same grid to test the model. The vegetation data were also used to infer numerical values of some climatic limits, as described above. The test then consisted of observing the extent to which (a) the small number of inferred constraints succeeded in reproducing the vegetation boundaries, and (b) boundaries were correctly placed in different continents.

The total number of land grid cells (excluding Antarctica) is >60,000. Manipulation and mapping of the large data sets required by this application was carried out on VAX workstations with a specially written GIS, using UNIRAS mapping routines.

Climate data

The climate data base is described by Leemans & Cramer (1991). Temperature data for each 0.5° cell were

obtained by reduction to sea level and interpolation fol-
lowed by extrapolation to the mean elevation of the cell, as-
suming an environmental lapse rate of 0.6°C/100 m. Mean
elevations were obtained from the FNOC topographic data
base as distributed by the US Geological Survey. The data
base has a resolution of 10'. Mean elevations for each 0.5°
cell were approximated by averaging the modal elevations
of nine 10' cells.

Precipitation and sunshine data were interpolated without
correction for elevation. Thus, the accuracy of these data
depends entirely on the density of recording stations. The
interpolation procedure probably freqently underestimates
precipitation on mountains in areas where weather station
data are sparse. Sunshine data exist for a smaller number of
stations, but the geographic patterns of cloudiness are
coarser-grained than those for temperature and precipita-
tion. The errors resulting from sparse data are therefore
likely to be less severe for sunshine than they would be for
the other variables.

Soils data

The soils data consisted of estimates of soil water-storage
capacity, based on textural information digitized by Zobler
(1986) from the FAO soils map (FAO, 1974). The textural
units distinguished for each 0.5° cell in this data base are
fine, medium and coarse and combinations of these classes
(e.g. coarse-medium), with a separate category for organic
soils.

Global maps of these data show broad-scale patterns
that are not simply a reflection of present patterns of veg-
etation or climate. For example, the areas covered by
continental ice sheets at the last glacial maximum gener-
ally have coarser-textured soils than unglaciated areas.
Some other patterns are related to bedrock differences,
such as the prevalence of fine-textured soils over the
humid regions of South America in contrast with the
generally coarser texture of soils in areas of similar
climate in Africa. Such patterns have the capacity to
modulate the control of vegetation physiognomy by
climate.

Table 3 lists values of available water capacity (AWC)
assigned to each combination of soil-texture classes. AWC
is the difference between the volumetric moisture contents
of soil at field capacity and wilting point. Mean values for
three parameters—saturation matric potential, saturated
moisture content, and the slope of the moisture retention
curve—were derived from Table 3 of Cosby *et al.* (1984)
for each soil class. Field capacity and wilting point were
assumed to correspond to matric potentials of 100 and
4500 cm respectively. Equation (1) of Cosby *et al.* (1984)
was then solved to yield values for the water content at
these two potentials. We derived values in this way for all
of the twelve USDA texture classes, except silt. We then
calculated an average AWC based on the USDA classes
that fell within each of the three FAO classes. Wherever a
USDA class overlapped two FAO classes, its contribution
to each class was weighted in proportion to the relative
extent of the two areas of overlap on the textural triangle.
AWC values for combined classes, e.g. coarse-medium,

TABLE 3. Available water capacity (%) imputed to soil texture
classes

Fine	12.4
Medium	17.1
Coarse	11.5
Fine-medium	14.8
Medium-coarse	14.3
Fine-coarse	12.0
Fine-medium-coarse	13.7
Organic	90

were obtained by averaging. Organic soils were assigned a
value of 90% AWC. Finally, AWC values were multiplied
by a nominal root-zone depth of 1 m, to yield a first ap-
proximation of the potential size of the soil-moisture store
on each grid cell.

Vegetation data

The vegetation data were obtained from the Olson *et al.*
(1983) data base as supplied by Oak Ridge National Labor-
atory, Oak Ridge, Tennessee, with the names of vegetation
units corrected to agree with the published text and map.
The GIS was used first to produce maps showing all the
units in this data base, then with the types combined in
various ways. For this paper, the majority of the Olson *et
al.* types have been assigned to one of fifteen mapping units
(Table 4) that can be unambiguously identified with combi-
nations of dominant plant types listed in Table 1. The re-
maining types recognized by Olson *et al.* are classified here
as 'other', including mangroves, paddylands, heathlands,
crops, and woods/fields complexes where the woodland
type was not specified precisely enough for our purpose
(e.g. 'warm woods/fields', which includes both tropical and
temperate woodlands).

Olson *et al.* (1983) described their mapping units as 'eco-
system complexes', emphasizing that the vegetation of a
0.5° cell is not homogeneous but is a mosaic of types in-
cluding different microhabitats, successional stages and
land-use. For many units where human impact is
significant, Olson *et al.*'s description gives enough informa-
tion to categorize the natural vegetation. As a result, only a
limited part of the land surface was classified as 'other'.

The advantage of using Olson *et al.*'s data, in preference
to any of the available mappings of potential natural vege-
tation, is that the data are based explicitly on an assessment
of *actual* vegetation present. There are no built-in assump-
tions about the natural vegetation to be expected in a given
climate; terms like 'warm' in Olson *et al.*'s classification
are labels for units that are distinguished on structural or
phenological criteria. The disadvantage of using these data
is that some discrepancies between data and model are in-
evitable, due to human impact on many vegetation types,
and that the most intensively impacted areas have to be ex-
cluded from the comparison. The model's predictions of
vegetation in heavily agricultural areas can then be regard-
ed as an independent, climatically based assessment of the
potential natural vegetation of these areas.

TABLE 4. Ecosystem complexes distinguished by Olson *et al.* (1983), and their allocation to biomes for mapping

Biome name	Ecosystem complex name(s)
Tropical rain forest	Evergreen equatorial forest
Tropical seasonal forest	Tropical seasonal forest
Tropical dry forest/savanna	Tropical dry forest and woodland
	Tropical savanna and woodland
Broad-leaved evergreen/warm mixed forest	Broad-leaved evergreen or partly deciduous forest
	Warm conifer forest
	Partly evergreen broad-leaved or subtropical conifer forest
	South-temperate broad-leaved and/or conifer forest
	Broad-leaved south-temperate forest
	Deciduous warm woods with conifers
	Tropical montane complexes
Temperate deciduous forest	Deciduous (summer green) forest
Cool mixed forest	Cool hardwood-conifer forest
Cool conifer forest	Cool conifer forest
Taiga	Main taiga
	Northern or maritime taiga
	Southern continental taiga
Xerophytic woods/scrub	Semi-arid woodland or low forest
	Mediterranean types
	Succulent and thorn woods and scrub
	Dry or highland tree or shrub
Warm grass/shrub	Warm or hot shrub/grassland
Cool grass/shrub	Cool grassland/scrub
	Siberian parklands
	Tibetan meadows
	Cool irrigated dryland
Tundra	Wooded tundra and timberline
	Tundra
	Cold irrigated dryland
Hot desert	[Warm to hot] desert and semi-desert
	Sand desert
	Warm-hot irrigated dryland
Semidesert	[Cool] semi-desert scrub
Ice/polar desert	Polar or rock desert
	Ice

MAP COMPARISON

Comparison based on individual grid cells

Global biome maps derived from the model, and from the data of Olson *et al.* (1983), were compared numerically using the kappa statistic to assess agreement (Cohen, 1960; Monserud, 1990). The kappa statistic is derived as follows.

Let p_{ij} be the proportion of the total number of grid cells assigned to category i by one map and to category j by the other map. These values form a square matrix, whose main diagonal contains proportions of grid cells on which both maps agree (p_{ii}). The sum of these proportions is the overall proportion of observed agreement $(p_o = \Sigma_i p_{ii})$. Chance alone would be expected to produce some agreement; the expected value of p_{ii} being due to chance alone is the product of the row and column sums $p_{i.}$ and $p_{.i}$ for category i. (These sums are simply the proportions of grid cells assigned to each category by each map.) The overall expected value of agreement due to chance is the sum of these row and column cross-products $(p_e = \Sigma_i p_{i.} \cdot p_{.i})$. This is subtracted from the overall proportion of observed agreement, and the

result normalized by the maximum possible value of the difference, to give the kappa statistic:

$$\kappa = (p_o - p_e)/(1 - p_e). \qquad (4)$$

κ is approximately zero when agreement is no better than random, and reaches unity when agreement is perfect.

An individual kappa statistic can also be calculated for each category i, as follows (Monserud & Leemans, 1992):

$$\kappa_i = (p_{ii} - p_{i.} \cdot p_{.i})/[(p_{i.} + p_{.i})/2 - p_{i.}p_{.i}]. \qquad (5)$$

The overall value of κ is a weighted average of these individual κ_i's.

Statistical tests with kappa are possible, but not very useful, because with so many grid cells almost any two maps will be different at a high level of significance. Values of κ_i and κ can be compared more profitably by rank ordering. For example, they may show that agreement is better for some categories than others, or they can be used to compare the predictive ability of different models. Alternatively, kappa statistics can be assessed on a subjective scale. Monserud (1990) suggested that values <0.4 be considered poor or very poor, 0.4–0.55 fair, 0.55–0.7 good,

0.7–0.85 very good and >0.85 excellent. We adhere to this convention.

Comparison at larger spatial scales

A limitation of the kappa statistic is that it treats grid cells independently. This matters for several reasons. First, the appropriate scale of comparison may be larger than a 0.5° cell, due to deficiencies in the climate data; the realism of simulated vegetation distributions is limited by the density of weather stations, which is considerably less than one per grid cell on average. Second, human impact may have created artificial patterns that would reduce agreement at 0.5° resolution, but which would become less important if the maps were compared in a more generalized way. Third, since one possible application of the model is to problems involving the land-atmosphere interface as represented in atmospheric general circulation models (GCMs), it is appropriate to ask how well the model performs in terms of patterns expressed at the relatively coarse (*c.* 2–10°) resolution of GCMs (K.C. Prentice, 1990).

These considerations suggest the definition of a generalized kappa statistic, in which overall agreement between the maps is based on the similarity between proportions within blocks of adjacent cells. Let f_{ik} be the proportion of cells in block k assigned to category i by one map, and g_{ik} the proportion of cells in block k assigned to category i by the other map. Then substitute

$$p_{ii} = \min(f_{ik}, g_{ik}) \tag{6}$$

for the p_{ii} in the preceding formulae for calculating the individual and overall kappa statistics. By this definition, p_{ii} is simply the amount in common between f_{ik} and g_{ik}. The row and column totals (p_i and p_i) have the same meaning as before.

The resulting statistics, $\kappa(x)$ and $\kappa_i(x)$, are functions of the block size x. At the finest scale ($x = 1$) they reduce to the ordinary kappa statistics. At the coarsest scale ($x = n$, where n is the total number of grid cells) they reduce to a measure of the similarity between the overall proportions of the categories on the two maps.

RESULTS

Global patterns

The model produced a total of seventeen unique combinations of dominant plant types, or biomes (Table 5). Fifteen of these can be equated directly with the aggregated units of the Olson *et al.* (1983) data. The model produced two additional biomes, occupying limited areas, 'cold mixed forest' and 'cold deciduous forest'. For numerical comparisons we lumped these with their nearest equivalents in Olson *et al.* (1983), cool mixed forest and taiga. Areas marked as 'other' in Fig. 1, and Antarctica, were excluded.

Visual comparison of predicted biome distributions with their real-world equivalents indicates fair agreement (Fig. 1). This impression is supported by the overall value of the kappa statistic for the two maps (0.49). This is larger than the value of 0.40 (Monserud, 1990) obtained in a compari-

TABLE 5. Combinations of dominant plant types that occurred in the global model application, and the names they were given for mapping

Plant types	Biome name
Tropical evergreen =	Tropical rain forest
Tropical evergreen +	
Tropical raingreen =	Tropical seasonal forest
Tropical raingreen =	Tropical dry forest/savanna
Warm-temperate evergreen =	Broad-leaved evergreen/warm mixed forest
Temperate summergreen +	
Cool-temperate conifer +	
Boreal summergreen =	Temperate deciduous forest
Temperate summergreen +	
Cool-temperate conifer +	
Boreal evergreen conifer +	
Boreal summergreen =	Cool mixed forest
Cool-temperate conifer +	
Boreal evergreen conifer +	
Boreal summergreen =	Cool conifer forest
Boreal evergreen conifer +	
Boreal summergreen =	Taiga
Cool-temperate conifer +	
Boreal summergreen =	Cold mixed forest
Boreal summergreen =	Cold deciduous forest
Sclerophyll/succulent =	Xerophytic woods/scrub
Warm grass/shrub =	Warm grass/shrub
Cool grass/shrub +	
Cold grass/shrub =	Cool grass/shrub
Cold grass/shrub =	Tundra
Hot desert shrub =	Hot desert
Cool desert shrub =	Semidesert
Dummy type =	Ice/polar desert

son of the Olson *et al.* (1983) data with the Holdridge scheme.

The generalized kappa statistic increases with increasing block size (0.53 for 2.5° blocks; 0.59 for 10° blocks). This implies that greater reliance can be placed on the model's predictions of broad-scale patterns than on its assignments of individual grid cells, and that good agreement of mapped patterns is obtained at the broader scales.

We now consider the performance of the model on a geographic, biome by biome basis. Values of the kappa statistic at the 2.5° block scale, given in parentheses after the name of each biome, indicate the relative success of the model in predicting the distribution of that biome as mapped by Olson *et al.* (1983). We draw attention both to the model's successes, and to failures that should be addressed in future developments of the model.

Tropical rain forest (0.58)

Tropical trees are predicted to occur in humid to semi-arid regions with a mean coldest-month temperature >15.5°C. Tropical rain forest is the biome dominated by tropical evergreen trees; it is predicted to occur only in the wettest regions of the tropics where rainfall meets >95% of annual evaporative demand. These criteria provide a good fit to the data and correctly predict the major distribution areas of tropical rain forest in Amazonia, West and central
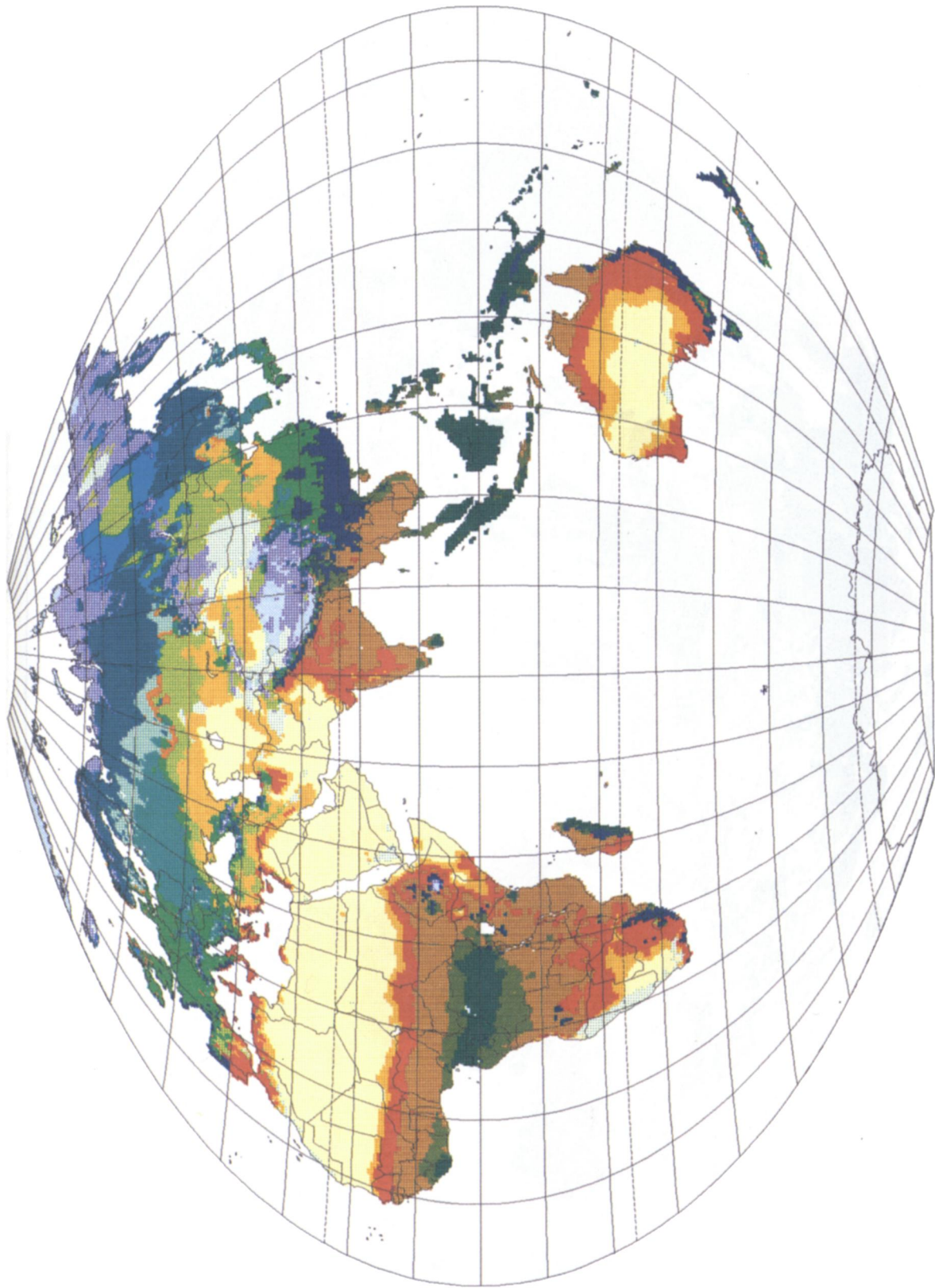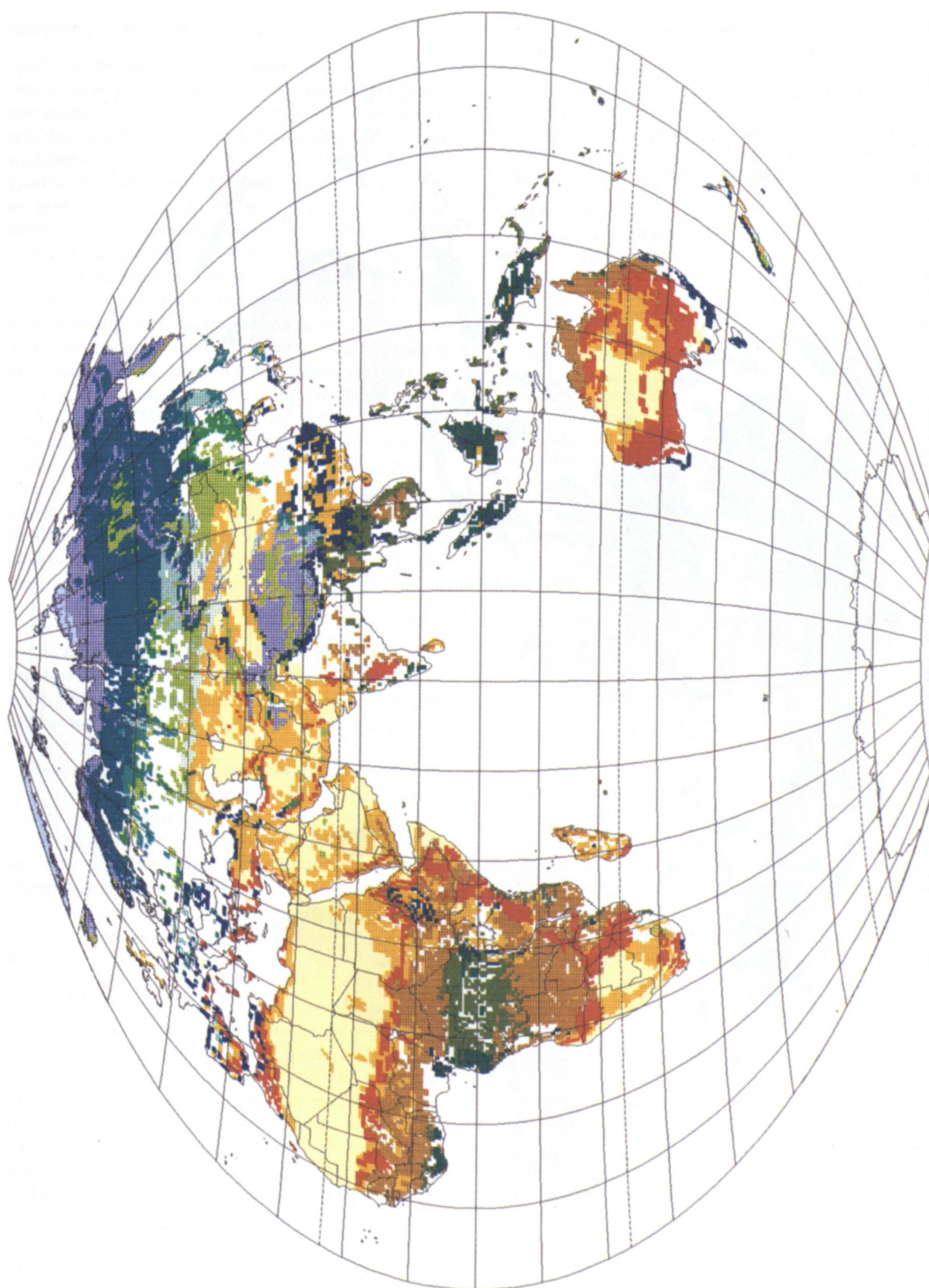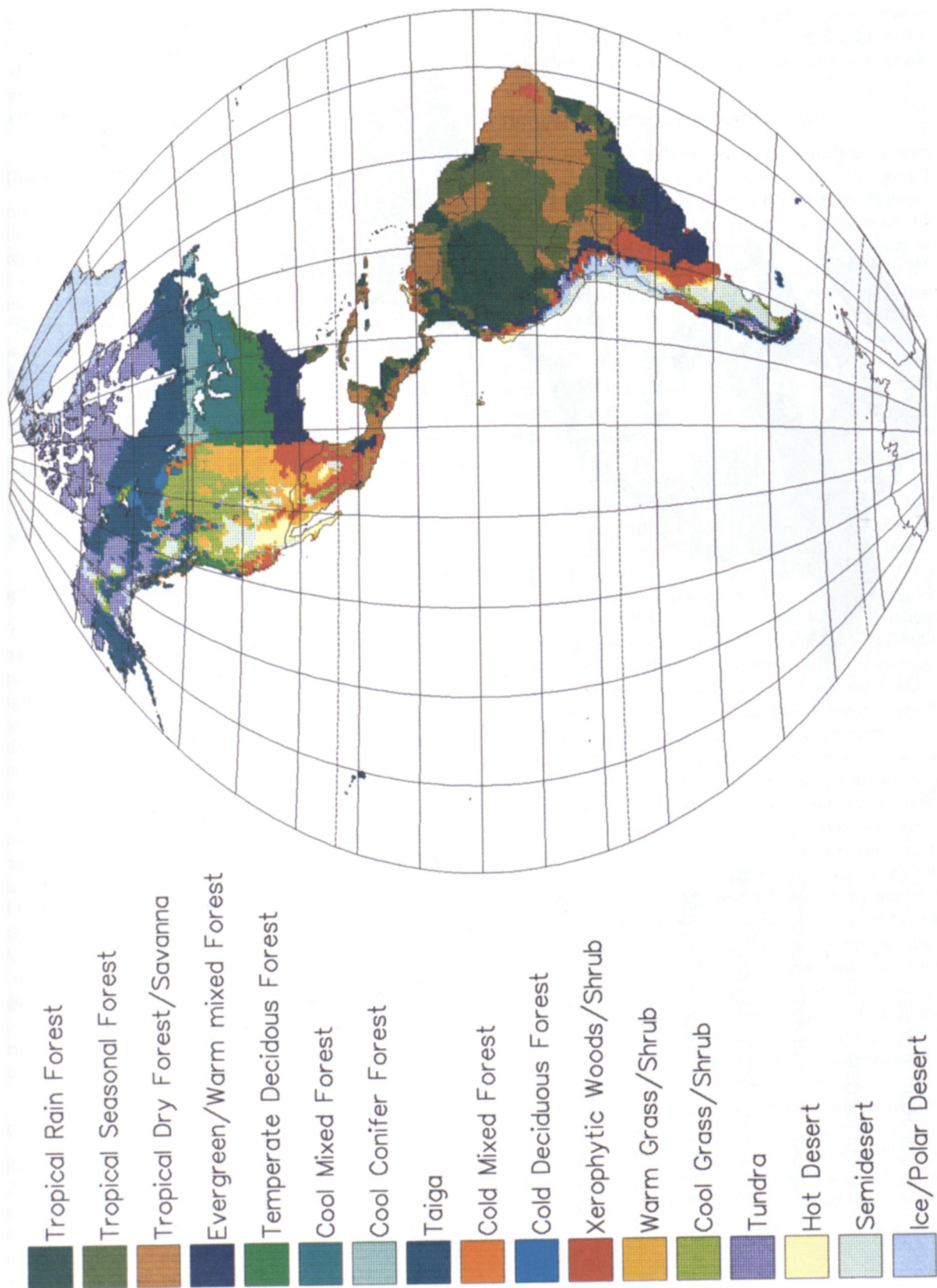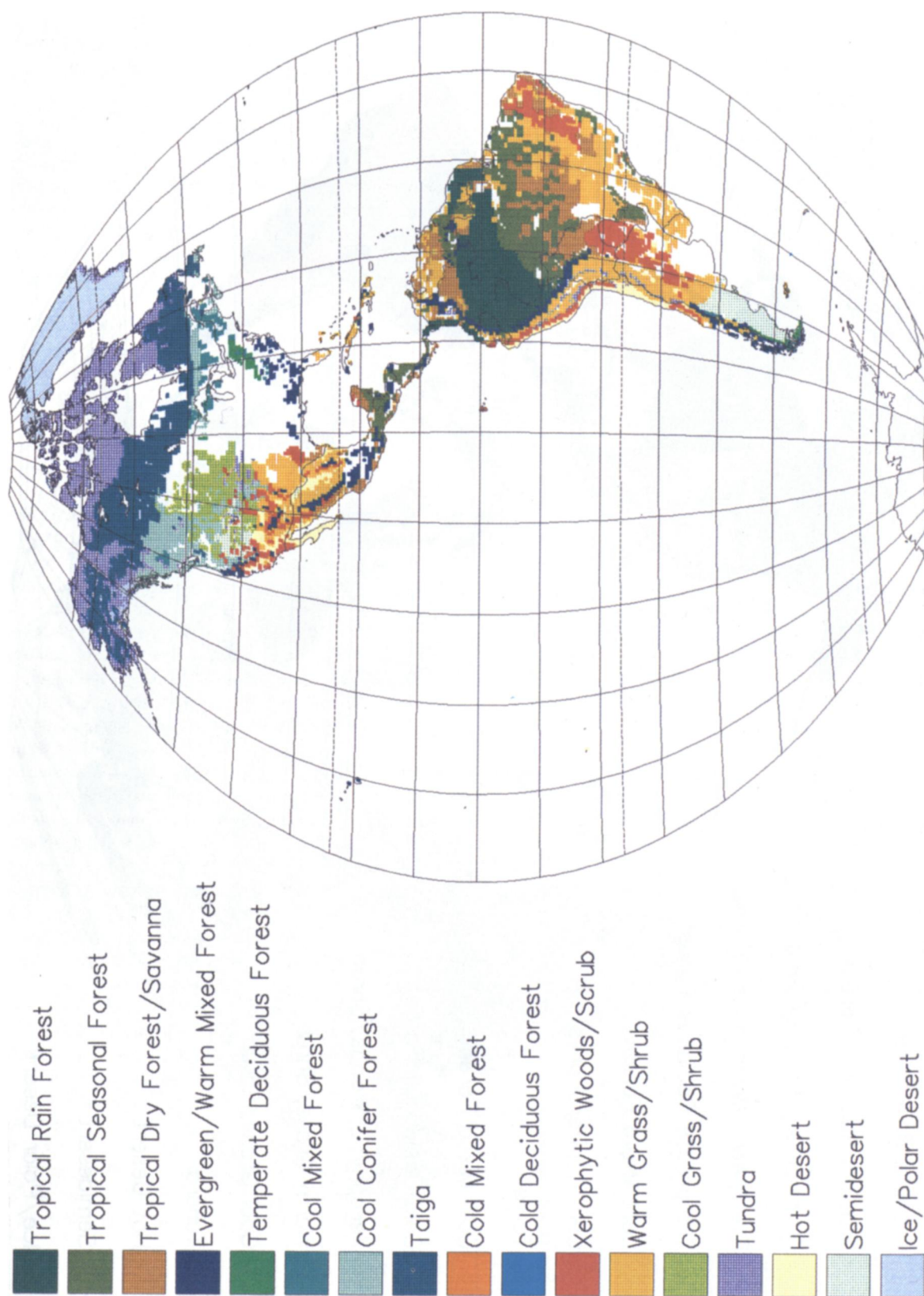
FIG. 1. Present biome distributions: model predictions, and data from Olson *et al.* (1983). (a) Old World–data; (b) Old World–model predictions; (c) New World–model predictions; (d) New World–data.
NB. Keys common to all maps (a)–(d).

Tropical Rain Forest
Tropical Seasonal Forest
Tropical Dry Forest/Savanna
Evergreen/Warm mixed Forest
Temperate Decidous Forest
Cool Mixed Forest
Cool Conifer Forest
Taiga
Cold Mixed Forest
Cold Deciduous Forest
Xerophytic Woods/Shrub
Warm Grass/Shrub
Cool Grass/Shrub
Tundra
Hot Desert
Semidesert
Ice/Polar Desert

Tropical Rain Forest
Tropical Seasonal Forest
Tropical Dry Forest/Savanna
Evergreen/Warm Mixed Forest
Temperate Deciduous Forest
Cool Mixed Forest
Cool Conifer Forest
Taiga
Cold Mixed Forest
Cold Deciduous Forest
Xerophytic Woods/Scrub
Warm Grass/Shrub
Cool Grass/Shrub
Tundra
Hot Desert
Semidesert
Ice/Polar Desert

Africa, Malaysia, Indonesia and Papua New Guinea.

Small areas of tropical rain forest are also predicted in Sri Lanka and Madagascar, where only fragments (not shown by Olson *et al.*) remain. No true rain forest is predicted for Queensland, possibly because the climate data underestimate the precipitation at higher elevations on the coastal ranges.

Tropical seasonal forest (0.42)

Tropical seasonal or semi-deciduous forests, including both evergreen and raingreen trees, are predicted for tropical regions with a dry season such that rainfall meets 80–95% of demand. The prediction is fair, comprising areas around the periphery of the rain forest centres in Central and South America, Africa and southeast Asia, coastal areas of eastern Brasil and East Africa, and a few locations in Queensland.

There are some discrepancies regarding the boundary between tropical rain forest and tropical seasonal forest. For example, seasonal forest is predicted for the Ghat, southern India, which Olson *et al.* mapped as true rain forest; rain forest is predicted for southern Paraguay and part of southeastern Brasil, where Olson *et al.* show seasonal forest.

Tropical dry forest/savanna (0.58)

Tropical climates where rainfall meets 45–80% of demand are assigned to tropical dry forest or savanna. These are vegetation types where the dominant trees are raingreen, with tree cover from continuous (in true forests) to sparse (in some savanna). The variables used in the model are not sufficient to discriminate dry forests from savannas, but the predicted distribution of the biome as a whole is good. The coastal dry forests of central America, the campos cerrados of Brasil, the miombo and mopane woodlands and savannas of subsaharan and southern Africa, much of interior India and continental southeast Asia, the driest parts of Indonesia and Papua New Guinea, and the deciduous woodlands of northern Australia are correctly assigned to this biome.

A notable discrepancy occurs in South America where the model fails to predict the extensive grasslands that exist in the high-rainfall environment of the Pampas. These areas are assigned mainly to tropical forests or savanna, or (further south) to broad-leaved evergreen/warm mixed forest.

Broad-leaved evergreen/warm mixed forest (0.38)

Regions with mean coldest-month temperatures in the 5–15.5°C range, and sufficient rainfall to meet >65% of demand, are assigned to this biome, which includes all vegetation types where warm-temperate evergreen trees, whether broad- or needle-leaved, are dominant. Such forests are correctly predicted to occur in numerous disjunct areas: the southeastern USA, at moderate elevations in Mexico and the tropical Andes, southern Chile, western coastal areas of Europe and high-rainfall areas around the Mediterranean, the highlands of tropical Africa and southeast Asia, southern China, southernmost Japan, moderate elevations on the south side of the Himalayas, small coastal areas of South Africa and southwestern Australia, the coast and uplands of southeastern Australia, and New Zealand.

Temperate deciduous forest (0.09)

This biome is defined by the dominance of temperate summergreen trees, cool-temperate conifers and boreal summergreen trees. It is predicted in areas with cool (−2 to 5°C) winters and enough precipitation to meet 65% of demand. It is also predicted in areas with colder winters (down to −15°C) where conditions are too dry (<75%) for boreal evergreen conifers. A further limitation is that temperate summergreen trees have a fairly high (>1200) GDD requirement, which indirectly excludes temperate deciduous forests from regions with a very low seasonal temperature range. On tropical mountains, for example, the model predicts that the upper elevational limit of broad-leaved evergreens (corresponding to a mean coldest-month temperature of 5°C) is above the 1200 GDD limit, so no temperate deciduous forest belt is present.

A large part of the predicted area of temperate deciduous forest is classified by Olson *et al.* (1983) as woods–fields or fields–woods complexes, units which are too broad to be assigned categorically to one biome or another. The model nevertheless shows the main areas usually considered as potential temperate deciduous forest—middle latitudes of the eastern USA, western and central Europe (excluding the Mediterranean region, eastern Europe and the central European mountains), and large parts of China and Japan.

In common with many predictive schemes (e.g. Woodward, 1987), the model also predicts temperate deciduous forest in the Pacific Northwest of the USA, where tall conifer forests predominate. The model's definition of the biome allows for dominance by cool-temperate conifers as well as temperate deciduous trees, and both are represented in the forests of the Pacific Northwest. However, the Pacific Northwest forests are mapped as 'cool conifer' by Olson *et al.* (1983), and the variables included in the model do not discriminate between these overwhelmingly coniferous forests and the largely deciduous forests of the other regions. The missing factor may be the seasonality (as opposed to annual total) of drought stress (Neilson *et al.* 1989 and submitted): conifers may be favoured by the mild winters and unusually dry summers of the Pacific Northwest, compared with areas of broadly similar climate on the other continents (Waring & Franklin, 1979).

The model also incorrectly predicts deciduous forests at the highest elevations in southeastern Australia. This may be because winter minimum temperatures in temperate latitudes of the Southern Hemisphere are somewhat higher than predicted by the global relationship expressed in equation (1).

Cool mixed forest (0.46)

This biome is defined by dominance of the same types as the previous biome, with the addition of boreal evergreen conifers. It is predicted to occur poleward of the temperate

deciduous forests, in climates with moderately cold winters (mean coldest-month temperatures from −2 to −15°C), enough GDD (>1200) for temperate summergreen trees, and enough precipitation (>75%) for boreal evergreen conifers. The GDD demand restricts the poleward extent of cool mixed forests in maritime climates.

The prediction is fair. Cool mixed forests are correctly predicted to occur in the Great Lakes/St Lawrence region, the mountains of central Europe, between *c.* 50° and 60°N in the USSR west of the Urals, along the eastern slope of the Tibetan plateau, and in the northern parts of Korea and Japan. They are absent from the Southern Hemisphere because of the absence of cold continental climates.

Cool conifer forest (0.21)

Cool conifer forests are defined in a similar way to cool mixed forests except that they lack temperate summergreen trees. Such forests are predicted for climates with mean coldest-month temperatures in a narrow band (−15 to −19°C) separating the winter-temperature tolerances of temperate summergreens and cool-temperate conifers. They can also occur in climates with milder winters (−2 to −15°C) where the growing season is not warm enough for temperate deciduous trees (GDD <1200). The poleward extent of these forests is however restricted in these more maritime climates because cool-temperate conifers demand at least 900 GDD. Thus, cool conifer forests are predicted and found (a) in northern mid-continental locations, north and west of Lake Superior and in southwestern Siberia, and (b) in more maritime climates between cool mixed forests and taiga in eastern Canada and the Soviet Far East.

A cool conifer zone is predicted around 60°N in northern Eurasia, but not distinguished as such by Olson *et al.* (1983). On the other hand, the model does not predict the extent of cool conifer forest in the Rocky Mountains and Pacific Northwest shown by Olson *et al.* (1983).

Taiga (0.65)

Taiga is the biome dominated by boreal evergreen and summergreen trees. It is predicted for climates where winters are cold (−19 to −35°C) (extending to somewhat warmer winters in maritime climates with GDD <900) and where precipitation meets >75% of demand. The poleward extent of taiga is limited by the requirement of GDD >350 for tree growth.

These criteria make a good prediction of the broad taiga zones that traverse North America and Eurasia. The model also predicts montane taiga in the Altai mountains and at high elevations in the central European mountains. In eastern Siberia taiga is predicted to give way to cold deciduous forest (dominated by boreal summergreen taxa) in areas that are either too dry, or too cold in winter, to support boreal evergreen conifers; this unit is included in the taiga by Olson *et al.* (1983).

Additional areas predicted as taiga, in central China and the Rocky Mountains, are mapped as cool conifer by Olson *et al.* (1983). The location of the polar treeline is predicted accurately for the most part, but is shown somewhat too far south in the most extreme continental areas (interior Alaska and eastern Siberia).

Cold mixed forest

Cold mixed forests are defined by the dominance of cool-temperate conifers and boreal summergreen trees. They are predicted to occur (a) in humid, maritime climates with winters too mild for boreal conifers (−2 to 5°C) and summers too cool for temperate summergreen trees (GDD <1200), and (b) in continental climates with colder winters (−15 to −19°C) but too little precipitation (<75% of demand) to support boreal conifers.

Vegetation maps confirm this prediction of disjunct areas where cool-temperate conifers (especially *Pinus* spp.) and boreal summergreen trees (*Betula* and *Populus* spp.) are the dominant trees. Thus, the model shows cold mixed forests (a) in a band along the forest-steppe transition in north-central North America and east of the Urals, where there are in fact woodlands and parklands with *Pinus* and *Populus*; and (b) on the extreme maritime fringes of Canada and north-west Europe, where there are woodlands with *Betula* and conifers. These vegetation types occupy relatively small areas and are not mapped separately by Olson *et al.* (1983).

Cold deciduous forest

Cold deciduous forests are dominated by boreal summergreen trees alone. They are predicted to occur (a) in extremely continental climates where the requirement of 350 GDD for tree growth is met despite coldest-month temperatures too cold for boreal evergreen conifers (< −35°C); (b) in extremely maritime climates where the requirement of 900 GDD for cool-temperate conifers is not met in spite of winters that are too *warm* for boreal evergreen conifers (−2 to 5°C); and (c) in continental climates with cold winters (−19 to −35°C) but insufficient precipitation to support boreal evergreen conifers.

As with the previous biome, the model's prediction of limited, disjunct areas is supported by evidence from vegetation descriptions and maps. Climate type (a) is represented by the *Larix* forests of northeastern Siberia, which Olson *et al.* (1983) include in the taiga. No such area is predicted for North America because areas in North America that have such cold winters do not have sufficient GDD to support trees. Climate type (b) is represented by the 'subarctic' *Betula* woodlands of coastal Iceland, part of Scotland, and coastal Scandinavia and Beringia including the Aleutian Islands (Hustich, 1966; Tuhkanen, 1984). Deciduous forests are also correctly predicted for this climate type at high elevations in the southern Andes, although these are mapped as temperate deciduous forest by Olson *et al.* (1983), and southern New Zealand. Climate type (c) is represented by the *Populus* parklands that occur in a belt along the southern taiga-steppe transition in North America and Eurasia, and by the *Larix* forests of southern Siberia.

Xerophytic woods/scrub (0.42)

This biome is defined by the absence of tree types and the dominance of tall xerophytic plants such as *Juniperus* spp., mediterranean sclerophyll shrubs, succulents and tropical thorns, all plants that may reach tree stature towards the margins of the forested biomes. In climates with mean coldest-month temperature >15.5°C, xerophytic woods/scrub are predicted for areas where rainfall meets 28–45% of demand—too dry for raingreen trees, but moister than the grasslands or low-stature shrublands mapped by Olson *et al.* (1983) as 'warm grass/shrub'. In climates with cooler winters (5–15.5°C), they are predicted for a broader range of moisture values (28–65%) representing climates too dry for warm-temperate evergreen trees.

According to Olson *et al.* (1983), semi-arid woods comprise primarily the quebracho woodlands of northern Argentina, and sparse *Eucalyptus* and/or *Acacia* woodlands in northern and eastern interior regions of Australia. Mediterranean vegetation types are shown in the coastal zone of California, central Chile, the circum-Mediterranean region, the Cape region of South Africa and the west-facing coastal areas of southwestern and southeastern Australia. Other dry scrub types include pine, juniper and oak scrub of the southwestern USA, the northern edge of the Sahara and mountains of western and central Asia, and mulga and mallee vegetation in the semi-arid interior of Australia. Succulent and thorn woods and scrub are shown for the western submontane belt of tropical South America, northern Argentina, the caatinga of eastern Brasil, desert marginal zones of Africa and highlands of southern and eastern Africa, southwestern Madagascar, and the Deccan of southern India. The model assigns every one of these areas correctly to this biome and makes a fair prediction overall.

Warm grass/shrub (0.25)

This biome is predicted to occur in climates with mean warmest-month temperatures >22°C and enough precipitation to meet 18–28% of demand, enough for tropical and subtropical grasses, but not enough for succulents or thorn bushes. In climates too cold for mediterranean sclerophyll plants (mean coldest-month temperatures <5°C) this biome can also occur where precipitation meets up to 65% of demand, i.e. wherever conditions are too dry for temperate summergreen trees. As a result warm grass/shrublands are predicted to occur in a thin band along the margins of hot deserts, and also in the dry interiors of the northern continents—the US Great Plains and the steppes of central Asia.

The predicted and mapped distributions of this biome show only an approximate correspondence, however. Olson *et al.* (1983) show a patchy distribution of grass and shrublands through many of the areas of hot desert, and there is also some discrepancy in the definition of cool and warm types which results in warm grasslands being predicted too far north in the USA while cool grass/shrublands are incorrectly predicted in central Turkey, for example.

Warm grass/shrublands are also mapped for many grid cells in areas where the model predicts forest. In areas where Olson *et al.* (1983) show a mosaic of grasslands and forest, e.g. south China, this discrepancy may simply reflect patchy clearance. In some other areas, particularly South America, grasslands that seem to occur in a dry forest or savanna climate may be explained by the occurrence of extensive iron pans unfavourable to tree growth (Walter, 1979).

Cool grass/shrub (0.47)

This biome is predicted for regions with summers cooler than 22°C and enough precipitation to meet 28–65% of demand. The areas involved are the prairies and sagebrush of western North America, the steppes of Russia and Mongolia and the disjunct area of 'Siberian parklands' (grasslands with scattered *Larix* trees) of Yakutia. The model makes a fair prediction and correctly assigns the interior (steppe) areas of Spain and Turkey to grass/shrubland although Olson *et al.* (1983) consider these as 'warm' whereas the model assigns some to 'cool'. Areas of northern Russia shown as cool grass/shrub may reflect human conversion of forests to grasslands.

In the Southern Hemisphere, the model correctly predicts cool grass/shrubland in Lesotho, but not in New Zealand where the grasslands are in part due to forest clearance. The vegetation that Olson *et al.* (1983) describe as 'Tibetan meadows' is mapped with cool grass/shrub in Fig. 1, but the model assigns this area to tundra.

Tundra (0.71)

Tundra is predicted for humid regions where precipitation meets >65% of demand but GDD is insufficient for tree growth (<350), and semi-arid regions where precipitation meets 28–65% of demand but GDD is insufficient for 'cool' grasses and shrubs (<500). The poleward extension of the tundra is limited by the GDD_0 requirement (>100) for the growth of higher plants. These criteria result in very good agreement with the mapped distribution of tundra, in the Arctic and at high elevations in the Andes (páramo and puna vegetation types), Tien-Shan, Altai, Himalayas and Tibet. The simulated distribution of tundra however extends a little too far equatorward in the extreme continental areas of interior Alaska and eastern Siberia.

Hot desert (0.66)

Hot deserts are predicted to occur in arid climates where precipitation meets <18% of demand and mean warmest-month temperatures are >22°C. These criteria result in a good overall prediction with correct placing of the Mojave, Sonoran, Chihuahuan, Sahara, Kalahari, Somali-Chalbi, Arabian, Irano-Turanian, Kara-Kum, Thar, central Asian and Australian deserts.

Semidesert (0.24)

Semideserts are predicted for cooler climates, where precipitation meets <28% of demand and mean warmest-month temperatures are <22°C, provided GDD_0 is sufficient (>100) for higher plants. Semideserts are correctly placed

by the model in the US Great Basin, Patagonia, and the northern fringes of the Kara-Kum and central Asian deserts.

A few areas, usually considered as hot deserts, have warmest-month temperatures less than 22°C—the Gobi desert of southern Mongolia and the southern-hemisphere coastal fog deserts (Peruvian-Chilean and Namib deserts). These are incorrectly assigned to semidesert by the model. Some mountain meadow areas in central Asia, mapped as tundra by Olson *et al.* (1983), and a few small areas within the tundra of Siberia and Alaska, are also incorrectly assigned to semidesert.

Ice/polar desert (0.78)

This 'biome' is predicted wherever growing conditions are too cold (GDD_0 <100) for higher plant growth. These conditions are shown correctly for part of the Canadian high Arctic, most of Greenland, part of Svalbard, northern Novaya Zemlya, the northern part of Taimyr and the other islands of the Soviet high Arctic. The extent of high-elevation rock desert in the Andes is overestimated, possibly because of inadequate temperature data.

DISCUSSION

The climatic control of plant distribution has not been regarded as a central research field in ecology or biogeography for fifty years or more. Crawley (1986) summarized the situation:

> 'The first generation of plant ecologists (Warming, 1909; Raunkiaer, 1934) dedicated themselves to understanding why certain structures of vegetation are restricted to certain combinations of climate and soil . . . *modern* plant community ecologists are occupied by questions involving species richness . . . , species abundance . . . , and patterns of spatial and temporal change.' (p. 1; italics mine)

'Patterns of spatial and temporal change' in vegetation are however ultimately controlled by climate and its dynamics (Huntley & Webb, 1988; Prentice, 1991), and the need to anticipate the effects of potential global warming has begun to focus the attention of ecologists on this. Grubb (1989), for example, argued that experimental ecology should proceed towards an understanding of what determines the geographic distribution (as well as the local abundance) of different kinds of plants.

Our model represents an attempt to translate experimental and observational findings on the climatic controls of plant distribution into testable predictions of large-scale vegetation patterns. The model is Gleasonian, and as mechanistic as we could achieve with limited data. These features of the model contrast with (for example) the popular Holdridge scheme, which is implicitly Clementsian and based on correlations. Our model also succeeded in predicting the present-day distribution of biomes more accurately than the Holdridge scheme and is thus to be preferred on empirical as well as theoretical grounds.

Application of the model with warm-world climate scenarios will suggest the general directions of change to be expected, including the ultimate consequences for secondary characteristics of vegetation, such as surface water and energy balances and carbon storage, as equilibrium is approached in a new climate. It will also be instructive to apply the model to past times with climate changes inferred by independent methods, and to test the model's performance under different climatic regimes with the help of data from palaeoecology. By testing the model in a variety of past climatic regimes, we hope to lerarn more about the long-term interactions of vegetation and climate that will continue to operate in the future.

The model cannot simulate the *time course* of vegetation changes during a period of rapid climate change; this is a limitation of all static (equilibrium) models when applied to situations when the rate of change in the environment exceeds the rate of vegetational response (Prentice & Solomon, 1991). Dynamic (transient) models must represent many more processes explicitly, and the development of a global vegetation dynamics model will be a major task. Nevertheless, the environmental constraints that are at the centre of our present, static model will provide a necessary framework for the modelling of dynamic vegetation processes at a global scale.

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