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Simulating Biome Distribution on the Tibetan Plateau Using a Modified Global Vegetation Model

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Abstract

We used a regionally modified global vegetation model (BIOME4-Tibet) to simulate biome distribution on the Tibetan Plateau under current climate conditions derived from regional meteorological observations. The bioclimatic limits (mean temperatures of the coldest and warmest months, minimum temperature, growing degree-days on 5 °C and 0 °C bases) for some key alpine plant functional types (temperate deciduous and conifer trees, boreal deciduous and conifer trees, desert woody plants, tundra shrubs, cold herbaceous plants, and lichens/forbs) were redefined based on regional vegetation-climate relationships. Modern vegetation maps confirmed that the BIOME4-Tibet model does a better job of simulating biome patterns on the plateau (gridcell agreement 52%) than the original BIOME4 model (35%). This improved model enhanced our ability to simulate temperate conifer forest, cool conifer and mixed forest, evergreen taiga, temperate xerophytic shrubland, temperate grassland and desert, and steppe and shrub tundra biomes, but made a negligible or reduced difference to the prediction of temperate deciduous forest, warm-temperate mixed forest, and three tundra biomes (erect dwarf-shrub tundra, prostrate dwarf-shrub tundra, and cushion forb, lichen, and moss tundra). Future modification of the vegetation model, by increasing the number of shrub and herb plant functional types, re-parameterization of more precise bioclimatic constraints, and improved representation of soil, permafrost, and snow processes, will be needed to better characterize the distribution of alpine vegetation on the Tibetan Plateau.

Introduction

The Tibetan Plateau, with an average elevation of ca. 4000 m and often described as a third pole, is a unique region for climate and vegetation studies. High altitude and seasonal monsoonal circulation systems control the regional climate and land surface properties on the Tibetan Plateau (Chang, 1983; Lau and Li, 1984). The Neogene-Quaternary uplift of the plateau has significantly affected the vegetation distribution patterns in East Asia (Chang, 1983; Chen et al., 2005). In turn, the land surface, particularly the vegetation, affects regional atmospheric circulation and monsoonal systems (Liu et al., 2003; Yasunari, 2006). The species composition and diversity of Tibetan vegetation is highly sensitive to warming and grazing (Klein et al., 2004). Large-scale vegetation distribution is also vulnerable to climatic warming and enhanced atmospheric CO_2 concentrations (Ni, 2000, 2011). Despite its potential significance for environmental studies, the impacts of climate change on Tibetan vegetation still are not sufficiently explored.

In order to quantify the impacts of global change on terrestrial ecosystems, a modeling approach is necessary. This is because ecosystem models, both statistically and mechanically, simplify yet synthesize the ecological processes, patterns, and structures of the biosphere at the appropriate temporal and spatial scales for simulating interactions with atmosphere and anthropogenic disturbances. Dynamic and equilibrium global vegetation modeling leads to a better understanding of vegetation distribution and feedbacks under changed land cover, climate, and atmospheric compositions in the past and future. It provides a useful tool for predicting vegetation distribution and carbon and water processes at regional to global scales and for various time periods in response to large-scale environmental changes (Peng, 2000; Prentice and Raynaud, 2001; Prentice et al., 2007).

The modeling of global vegetation has been conducted from simulations by equilibrium biogeographical (e.g. BIOME1: Prentice et al., 1992) or biogeochemical models (e.g. TEM: Melillo et al., 1993; CENTURY: Parton et al., 1993), coupled biogeography and biogeochemistry models (e.g. MAPSS: Neilson and Marks, 1994; BIOME3: Haxeltine and Prentice, 1996; BIOME4: Kaplan et al., 2003), and dynamic models of ecosystem processes (e.g. IBIS: Foley et al., 1996; LPJ: Sitch et al., 2003; five dynamic global vegetation models: Sitch et al., 2008; LPJ-Why: Wania et al., 2009a, 2009b). With an aim of working towards Earth System modeling, dynamic global vegetation models have been coupled with atmosphere-ocean dynamic models (Prentice and Raynaud, 2001; Prentice et al., 2007; Smith et al., 2011). However, equilibrium models are still useful for simulating past vegetation change and future vegetation development under particular simulated climate conditions (Prentice and Raynaud, 2001).

Focusing on Tibetan biome simulation, Ni (2000) improved the biome classification of the BIOME3 equilibrium global vegetation model (Haxeltine and Prentice, 1996) in terms of alpine vegetation, and updated climatic parameters, yielding a good agreement between modern and predicted vegetation on the Tibetan Plateau. However, the modified model only used very simple climate factors such as growing degree days on the 0 °C

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base and annual mean precipitation (Ni, 2000). The successor to BIOME3, the BIOME4 model (Kaplan et al., 2003) has been modified to simulate both modern and mid-Holocene Tibetan vegetation (Song et al., 2005). Biomes and their plant functional types (PFTs) have been re-classified (Song et al., 2005) according to an old Chinese vegetation classification at 1:4 million scale (Hou et al., 1982), but regional biome classification and bioclimatic parameters are not comparable with global biome and bioclimate systems.

In this paper, we modify the BIOME4 model by redefining the bioclimatic parameters of key PFTs on the Tibetan Plateau. The modified BIOME4-Tibet model is applied to simulate modern biome distribution on the Tibetan Plateau driven by local climatic observations. The aims of this study are (1) to test the performance of the original global vegetation model in simulating high-altitude biome distribution and to improve the global vegetation model to better predict regional biomes, particularly tundra; (2) to conduct a detailed assignment of regional vegetation types to biomes; and (3) to compare potential and simulated biomes. Reasons for incorrect simulations and potential improvements that could be made to the model will be further discussed.

Study Area

The Tibetan Plateau defined here (27°–40°N, 73°–105°E) includes the Karakorum and Kunlun Mountains in the southern Xinjiang Autonomous Region, the Qaidam Basin and surrounding mountains in Qinghai Province, the whole Xizang Autonomous Region, and the western mountainous areas of Yunnan and Sichuan Provinces. The high elevation and associated upper atmospheric circulation has resulted in the development of a series of so-called 'high-cold' vegetation types on the Tibetan Plateau (Chang, 1983). The western part of the plateau receives very little precipitation (ca. 50 mm y^{-1}) and is therefore dominated by semi-shrubby desert and steppe desert vegetation, especially *Ceratoides latens*. In the northwest, the climate is very dry and cold due to the high altitude and higher northern latitude. A sparse high-cold desert of low semi-shrubby and cushion-like shrub (*Ceratoides compacta*) occurs there. Annual precipitation increases to ca. 200 mm in the center of the plateau where high-cold steppe vegetation (*Stipa purpurea*) occupies large, flat areas. In the east, where cold and wet climates dominate (annual precipitation reaches 600 mm), there is a high-cold meadow, dominated by several *Kobresia* species mixed in with low scrubs comprised of *Potentilla* and *Caragana* (Chang, 1983; ECVC, 1980). Temperate desert and steppe vegetation are also distributed on the northern margin of the plateau and around the Qaidam Basin in the northeast where elevations are lower and the climate is relatively dry. Subalpine coniferous (*Abies* and *Picea*) and mixed forests as well as *Rhododendron* shrublands are found on the southeastern and eastern margins. Therefore, the vegetation of the plateau follows a transitional gradient from the southeast to the northwest, graduating from subalpine forests, high-cold meadow and scrub, through high-cold steppe and desert to high-cold desert (ECVC, 1980).

Methods

BIOME4 AND THE REGIONAL MODIFICATION

The BIOME4 model (Kaplan, 2001; Kaplan et al., 2003) is a global vegetation model with coupled biogeographical and biogeochemical processes to predict steady-state vegetation distribution, structure, and carbon and water fluxes, and interactions among these processes. The primary simulated unit is the plant functional type (PFT), which represents broad, physiognomically and physiologically distinct plant groups, ranging from cushion forb to tropical rainforest tree. The computational core of BIOME4 is a coupled carbon and water flux scheme (Haxeltine and Prentice, 1996), which determines the seasonal maximum leaf area index (LAI) that maximizes net primary productivity (NPP) for any given PFT, based on a daily time step simulation of soil water balance and monthly process-based calculations of canopy conductance, photosynthesis, respiration, and phenology. The model is sensitive to changes in atmospheric CO_2 concentration because of the responses of NPP and stomatal conductance to CO_2 and the differential effects of CO_2 on the NPP of C_3 and C_4 plants (Kaplan, 2001).

Thirteen PFTs were used to assign 28 biomes throughout the world (Kaplan, 2001). Three PFTs (cold shrub, cold graminoid/forb, and cushion forb) were used to distinguish among five tundra biomes. Six non-tundra PFTs (cold deciduous tree, cold evergreen tree, temperate broadleaf deciduous tree, temperate needleleaf evergreen tree, xerophytic shrub, and temperate grass) were used to simulate high-latitude vegetation types including four boreal forests, three temperate forests, temperate grassland, and xerophytic shrubland. Other PFTs including tropical/warm-temperate grass and desert woody C_3 and C_4 plant types were also used (Kaplan, 2001).

The BIOME4 model uses widely accepted bioclimatic and ecophysiological parameters to define PFTs and for the assignment of biomes (Woodward, 1987; Prentice et al., 1992; Kaplan, 2001; Kaplan et al., 2003). However, some of these parameters are not suitable for PFTs on the Tibetan Plateau. In this study we did not modify the rules for assigning Tibetan biomes, but instead re-calibrated some of the parameters for key PFTs. The phenological type of C_3/C_4 temperate grass has been defined as 'raingreen' in the global vegetation classification (Kaplan, 2001), but is 'summergreen' in the temperate regions of China (ECVC, 1980; EBVAC, 2001). The phenology of tundra shrub and lichen/forb on the plateau is 'summergreen' in most cases rather than 'evergreen.' On the basis of Chinese vegetation, the expected leaf longevity was modified from 8 to 6 months in the case of cold herbaceous plants, from 12 to 10 months for C_4 tropical grass and from 8 to 7 months in the case of C_3/C_4 temperate grass plants (ECVC, 1980). The limits of some climatic indices, such as the mean coldest month temperature and the growing-degree days on 5 °C base, were redefined (Table 1) based on established Tibetan vegetation-climate relationships and published literature (ECVC, 1980; Ni, 2000; EBVAC, 2001; Song et al., 2005). The basic structure and subroutines remained the same (Kaplan, 2001; Kaplan et al., 2003).

INPUT DATA OF BIOME4-TIBET

The regional climate data set consisted of four variables (monthly temperature, precipitation and cloudiness, and minimum temperature) that were averaged from long-term records at 1814 meteorological stations across China (China Meteorological Administration, unpublished data in 2003). Climate data obtained from 703 standard stations were averaged between 1971 and 2000, and from 1111 local stations were averaged between 1981 and 1990. These data were interpolated into 10 km × 10 km gridcells using a thin plate smoothing spline surface-fitting technique (Hutchinson, 2006; ANUSPLIN version 4.36) that takes the impact of elevation into account on the basis of the STRM digital elevation model (Farr et al., 2007). An atmospheric CO_2

TABLE 1

Bioclimatic parameters in BIOME4-Tibet. T_{cm} and T_{wm} are the mean temperatures of the coldest month and the warmest month, respectively. T_{min} is the minimum temperature, and GDD_5 and GDD_0 are the growing degree days on the basis of 5 °C and 0 °C, respectively. * indicates that the original parameters have been changed. Numbers in parentheses are the original parameters from Kaplan (2001).

	T_{cm} (°C)		T_{min} (°C)		GDD_5 (°C)	GDD_0 (°C)	T_{wm} (°C)	
Plant functional types (PFTs)	Min	Max	Min	Max	Min	Min	Min	Max
Tropical evergreen	16*(no limit)		0				10	
Tropical raingreen	12*(no limit)		0				10	
Temperate broadleaved evergreen	7*(2)		-8	5	1500*(1200)		10	
Temperate summergreen	3*(−15)			−8	1200			
Temperate evergreen conifer	−3*(−2)			10	900			
Boreal evergreen	−8*(−32.5)	0*(−2)						21
Boreal deciduous	−10*(no limit)	5		−10	900*(no limit)			21
Temperate grass		1*(no limit)		0	550			
Tropical/warm-temperate grass			−3					
Desert woody C_3/C_4 plant		2*(no limit)			500			
Tundra shrub		−1*(no limit)				50		15
Cold herbaceous		−13*(no limit)				50		12*(no limit)
Lichen/forb								10*(15)

concentration of 360 ppmv was used for the modern baseline simulation. In addition, BIOME4 utilizes soil properties of the water-holding capacity and percolation rate of two layers (top: 0–30 cm; bottom: >30 cm). Data regarding these two soil properties are not available in regional resource, although there is a soil database of China at 1:1 million scale (Shi et al., 2004). The soil data used in this paper was read from a global digital soil map at a 0.5° resolution (FAO, 1995; Kaplan, 2001).

VEGETATION AND BIOMES

The Tibetan vegetation map, derived from the Vegetation Atlas of China at a scale of 1:1 million, was originally comprised of 269 vegetation formations and sub-formations which belong to 37 vegetation types and 10 non-vegetation categories (EBVAC, 2001). The most common Tibetan vegetation are alpine steppe (grass and *Carex* high-cold steppe), alpine meadow (*Kobresia* and forb high-cold meadow), and alpine sparse vegetation. They are distributed on flat areas and account for 60% of the total area of the whole plateau. Montane conifer forest, subalpine evergreen broadleaved shrubland, and subalpine deciduous broadleaved shrubland occupy ca. 14% of the total area and are distributed mainly in southeastern and eastern Tibet. Subalpine dwarf-shrub desert, alpine cushion dwarf-shrub desert, and areas with no vegetation account for an additional 14% of the plateau and are distributed in the north and northwest, and in the Qaidam Basin. Other vegetation types account for the remaining 12% of the plateau.

Observed vegetation patterns are needed to evaluate the model simulation. Vegetation classification based on observations must be translated into the biomes used in the vegetation model. This is always a complicated task because of the difficulty in matching observed vegetation with modeled biomes and where some vegetation definitions and biome classifications are ambiguous. Previous assignments of vegetation to biomes in China (e.g. Ni et al., 2000) and on the Tibetan Plateau (e.g. Ni, 2000; Song et al., 2005) were based on bioclimatic features and spatial distributions of observed vegetation from published maps. A particular vegetation type (a named category of plant community or vegetation in vegetation science, including one to several vegetation formations or sub-formations) was assigned to one biome, although some vegetation types span very broad horizontal and/or vertical ranges. However the practice of assigning a vegetation type to only one biome on the Tibetan Plateau is questionable because vegetation distribution is largely controlled by the altitudinal gradient. The Tibetan vegetation types often span a large elevational range where bioclimates are different and various biomes are likely to occur. Therefore in this study we attempted to assign vegetation types which span large elevation ranges to different biomes. Based on information of vegetation regionalization (division) of the Tibetan Plateau (ECVC, 1980; CITTP, 1988), for example, *Abies* forests (*A. faxoniana*, *A. squamata*, *A. georgei*, *A. georgei* var. *smithii*, *A. delavayi*, *A. delavayi* var. *motuoensis*, and *A. densa*) and *Picea* forests (*P. likiangensis* var. *balfouriana*, *P. likiangensis* var. *linzhiensis*, and *P. spinulosa*) were assigned to evergreen taiga if elevation was >3000–4000 m (varied depending on latitude), and to cool conifer forest if elevation was ≤3000–4000 m. *Pinus* forests (*P. densata* and *P. yunnanensis*) were assigned to cool mixed forest or cool conifer forest or cold mixed forest if elevation was >2000–3000 m, and to temperate conifer forest or warm mixed forest if elevation was ≤2000–3000 m. *Rhododendron* scrubs (*R. fastigiatum*, *R. heiliolepis*, *R. adenogynum*, *R. racemosum*, *R. nivale*, and *R. thymifolium*) and other alpine and subalpine evergreen or deciduous scrubs were assigned to shrub tundra if elevation was >3500–4000 m, and to cool/cold mixed forests and shrubland if elevation was ≤3500–4000 m. *Kobresia* meadows (*K. pygmaea*, *K. humilis*, and *K. capillifolia*) and *Stipa* steppes (*S. purpurea*) were assigned to shrub tundra if they are in mosaics distributed with shrubs and otherwise to graminoid and forb tundra (ECVC, 1980; CITTP, 1988).

Biomes simulated by the vegetation model represent potential natural vegetation, so cultivated vegetation types must be assigned to a potential biome in the same bioclimatic zone. Additionally some vegetation types, particularly azonal (local habitat-controlled) shrublands and coniferous forests, need to be assigned to zonal (broad bioclimate-controlled) biomes (Table 2).

We used the original biome classification of the BIOME4 model for simulation and mapping rather than combined vegetation and mega-vegetation types as per Song et al. (2005), meaning that the biomes are comparable with the global biome scheme. All of the vegetation formations and sub-formations were assigned to 18 biomes (Table 2; Fig. 1, a) used in the BIOME4 simulation. The most widely distributed biomes are steppe tundra and shrub tundra (Fig. 1, a) which occupy ca. 73% of the total area of the Tibetan Plateau. Steppe tundra (38%) is distributed across the whole plateau but mainly in central, northwestern, and

TABLE 2

Assignment of vegetation types (EBVAC, 2001) to biomes on the Tibetan Plateau.

Biomes	Vegetation formation and sub-formation (code in Vegetation Atlas of China, EBVAC, 2001)
Tropical evergreen forest	*Dipterocarpus pilosus*, *Artocarpus chaplasha*, *Dysaxylum binectariferum* forest (148); *Terminalia myriocarpa*, *Pometia tomentosa* forest (154); *Dysaxylum gobara*, *Terminalia myriocarpa*, *Altingia excelsa* forest (156)
Warm-temperate mixed forest	*Tsuga dumosa* forest (39); *Abies georgei* forest (53); *Cyclobalanopsis multinervis*, *Fagus longipetiolata* forest (109); *Castanopsis indica*, *C. hystrix*, *Schima wallichii* forest (123); *Lithocarpus variolosus*, *Schima argentea* forest (134); *Rose sericea*, *Cotoneaster adpressus* scrub (237); *Rhododendron fastigiatum* scrub (250); *Rhdodendron heiliolepis* scrub (252); Summer rice, winter wheat, corn, rape, tobacco field; apple, walnut orchard (566)
Temperate deciduous forest	*Pinus yunnanensis* forest, with shrub layer dominated by *Ternstroemia gymnanthera*, *Illicium yunnanense* (24a); *Quecrus liaotungensis* forest (70a); *Quercrs variabilis* forest (75); *Weigela japonica* var. *sinica*, *Hydrangea paniculata* scrub (204); *Lyonia ovalifolia*, *Myrica nana* scrub (206); *Phyllanthus emblica* scrub (222); *Rhododendron adenogynum* scrub (255); *Quercus monimotricha* scrub (258)
Temperate conifer forest	*Tsuga dumosa* forest (39); *Pinus densata* forest (40); *Abies georgei* var. *smithii* forest (54); *Abies delavayi* forest (55); *Abies delavayi* var. *motuoensis* forest (56); *Abies densa*, *Picea spinulosa* forest (57)
Cool-temperate conifer forest	*Pinus armandii* forest (28a); *Tsuga dumosa* forest (39); *Pinus densata* forest (40); *Picea likiangensis* var. *balfouriana* forest (45); *Picea likiangensis* var. *linzhiensis* forest (46); *Abies faxoniana* forest (50); *Abies squamata* forest (52); *Abies georgei* forest (53); *Abies georgei* var. *smithii* forest (54); *Abies delavayi* forest (55); *Abies delavayi* var. *motuoensis* forest (56)
Cold-temperate mixed forest	*Pinus yunnanensis* forest, with shrub layer dominated by *Ternstroemia gymnanthera*, *Illicium yunnanense* (24a); *Pinus yunnanensis* forest, with shrub layer dominated by *Lyonia ovalifolia*, *Rhododendron spiciferum* (24b); *Pinus yunnanensis* forest, with shrub layer dominated by *Quercus monimotricha*, *Rhododendron siderophyllum* (24d); *Pinus yunnanensis* forest, with shrub layer dominated by *Rubus ellipticus* (24e); *Tsuga chinensis*, *Acer* spp., *Betula* spp. forest (65a); *Tsuga dumosa*, *Quercus semicarpifolia* forest (66c); *Populus nigra* forest (81); *Populus davidiana* forest (83); *Populus tremula* forest (84); *Betula platyphylla* forest (87a); *Betula albo-sinensis* forest (89); *Castanopsis indica*, *C. hystrix*, *Schima wallichii* forest (123); *Lithocarpus variolosus*, *Schima argentea* forest (134); *Quercus aquifolioides* forest (136); *Quercus pannosa* forest (137); *Quercus guyavaefolia* and *Q. longispica* forest (138); *Quercus rehderiana*, *Q. senescens* forest (140); *Sinarundinaria* spp. scrub (175); *Corylus heterophylla* scrub (178); *Cotinus coggygria* var. *cinerea* scrub (183); *Berberis circumserrata* scrub (184); *Rosa* spp., *Cotoneaster* spp. scrub (192); *Sophora viciifolia, Bauhinia faberi* var. *microphylla* scrub (224); *Sophora moorcroftiana* scrub (225); *Rhododendron adenogynum* scrub (255); *Rhododendron racemosum* scrub (256); *Rhododendron nivale*, *Rh. thymifolium* scrub (257); *Quercus monimotricha* scrub (258); *Miscanthus sinensis*, *Arundinella hirta*, *Eulalia speciosa* grassland (421a); *Arundinella steosa* grassland (424a); *Arundinella setosa*, *Schizachyrium delavayi* grassland (424b); *Arundinella chenii* grassland (425); *Heteropogon contortus*, *Bothriochloa pertuosa*, *Cymbopogon* spp. grassland (427b); *Neyraudia reynaudiana*, *Thysanolaena maxima*, *Saccharum arundinaceum* grassland (430); *Sanguisorba parviflora*, *Trollius* spp., grass meadow (454); *Ligularia jamesi*, *Trollius chinensis*, grass meadow (456)
Evegreen taiga/montane forest	*Picea wilsonii* forest (11); *Picea crassifolia* forest (13); *Picea schrenkiana* forest (14); *Sabina przewalskii* forest (15); *Sabina komarovii* forest (16); *Pinus tabulaeformis* forest (17); *Pinus yunnanensis* forest (24); *Pinus griffithii* forest (34); *Larix potaninii* forest (36); *Larix potaninii* var. *macrocarpa* forest (37); *Tsuga dumosa* forest (39); *Pinus densata* forest (40); *Picea asperata* forest (41); *Picea purpurea* forest (42); *Picea brachytyla* forest (43); *Picea likiangensis* forest (44); *Picea likiangensis* var. *balfouriana* forest (45); *Picea likiangensis* var. *linzhiensis* forest (46); *Abies fargesii* forest (48); *Abies fabri* forest (49); *Abies faxoniana* forest (50); *Abies forrestii* forest (51); *Abies squamata* forest (52); *Abies georgei* forest (53); *Abies georgei* var. *smithii* forest (54); *Abies delavayi* forest (55); *Abies delavayi* var. *motuoensis* forest (56); *Abies densa*, *Picea spinulosa* forest (57); *Abies spectabilis* forest (58); *Saina tibetica* forest (60); *Sabina saltuaria* forest (61); *Sabina convallium* forest (62); *Rhododendron adenogynum* scrub (255); *Rhododendron racemosum* scrub (256); Spring barley, spring wheat, navew, rape field (548); Spring wheat, pea, rape field; apple orchard (554)
Deciduous taiga/montane forest	*Populus davidiana*, *Betula platyphylla* var. *szechuanica* forest (104); *Populus davidiana* forest (104a); *Betula utilis* forest (105)
Tropical xerophytic shrubland	*Opuntia dillenii*, *Acacia farnesiana* scrub (229)
Temperate xerophytic shrubland	*Sabina vulgaris* scrub (263); *Haloxylon ammodendron* desert (265); *Haloxylon ammodendron* sandy desert (265a); *Haloxylon ammodendron* gravel desert (265b); *Haloxylon ammodendron* loamy desert (265c); *Haloxylon ammodendron* saline desert (265d)
Temperate grassland	*Caragana tibetica*, low grass desert (290); *Stipa krylovii* steppe (359); *Stipa bungeana* steppe (360a); *Stipa bungeana*, *Aneurolepidium dasytachys*, *Artemisia* spp. steppe (360b); *Achnatherum splendens* steppe (366); *Achnatherum splendens* steppe (366a); *Achnatherum splendens*, *Stipa breviflora* steppe (366b); *Bromus inermis* meadow (437); *Festuca ovina*, *Deyeuxia arundinacea*, forb meadow (446); *Achnatherum splendens* meadow (473); *Iris lactea* var. *chinensis*, grass, forb meadow (477); *Sophora alopecuroides*, *Poacynum hendersonii*, *Glycyrrhiza inflata*, *Alhagi pseudoalhagi*, *Karelinia caspica* meadow (478); Spring wheat, rice, sugar beet, sunflower, chinese wolfberry field; pear orchard (555)
Temperate desert	*Populus diversifolia* woodland (92); *Hippophae rhamnoides* scrub (189); *Caragana tibetica* scrub (191d); *Cotoneaster multiflorus* scrub (194); *Myricaria squamosa* scrub (195); *Tamarix chinensis* scrub (196); *Ephedra przewalskii* desert (267); *Calligonum mongolicum* desert (276); *Tamarix ramosissima* desert (277); *Tamarix hohenackeri* desert (278); *Tamarix hispida* desert (279); *Nitraria sibirica* desert (281); *Nitraria roborowskii* desert (282); *Reaumuria soongorica* desert (293); *Reaumuria soongorica* desert (293b); *Reaumuria soongorica* loamy desert (293c); *Reaumuria kaschgarica* desert (294); *Reaumuria trigyna* desert (295); *Ceratoides latens* desert (296); *Ceratoides latens* gravel desert (296b); *Salsola abrotanoides* desert (299); *Salsola abrotanoides* gravel desert (299a); *Salsola abrotanoides* rocky desert (299b); *Sympegma regelii* desert (303); *Sympegma regelii* sandy desert (303b); *Sympegma regelii* rocky desert (303c); *Iljinia regelii* desert (306); *Anabasis brevifolia* sandy desert (307a); *Seriphidium santolinum* desert (316); *Artemisia rhodantha* desert (317); *Artemisia rhodantha* sandy desert (317a); *Artemisia rhodantha* gravel desert (317b); *Atemisia rhodantha* loamy desert (317c); *Artemisia parvula* desert (318); *Artemisia arenaria* desert (319); *Ajania fruticulosa* desert (324); *Brachanthemum pulvinatum* desert (326); *Hedysarum mongolicum*, *Artemisia salsoloides*, *Psammochloa mongolica* desert (328); *Kalidium cuspidatum* desert (331); *Kalidium gracile* desert (332); *Kalidium foliatum* desert (333); *Halostachys belangeriana* saline desert (336); *Stipa roborowskii* steppe

TABLE 2

Continued.

Biomes	Vegetation formation and sub-formation (code in Vegetation Atlas of China, EBVAC, 2001)
	(362); *Stipa penicillata* steppe (364); *Stipa breviflora*, *Stipa bungeana* steppe (365); *Stipa glareosa* steppe (384); *Stipa breviflora* steppe (385); *Stipa capillata*, nano-semi-shrub steppe (386); *Stipa caucasica* steppe (388); *Stipa roborowskii*, *Artemisia rhodantha* steppe (390); *Achnatherum splendens*, *Ceratoides latens* steppe (391); *Agropyron cristatum*, *Stipa glareose* steppe (395); *Festuca ovina* subsp. *sphagnicola* steppe (396); *Caragana tibetica*, low grass steppe (400); *Artemisia dalailamae*, low grass steppe (402); *Seriphidium borotalense*, *Festuca ovina* steppe (403); *Phragmites communis* meadow (469); *Phragmites communis*, *Poacynum hendersonii* meadow with *Nitraria* spp., *Tamarix* spp. (472); *Aneurolepidium dasystachys* meadow (474); Spring barley, spring wheat, navew, rape field (548); Sandy desert (Sa); Gravel desert (Gr); Rocky desert or alpine rock debris (R); Saline soil (Ss); Salt marsh (Sm); Takir (T); Rocky mountain (Rm); Marsh (M); Yardan (W)
Low- and high-shrub tundra	*Salix gilashania* scrub (231); *Salix sclerophylla* scrub (232); *Salix oritrepha* scrub (233); *Salix oritrepha*, *Dasiphona fruticosa*, *Caragana jubata* scrub (233a); *Salix oritrepha* var. *amnematchinensis* scrub (234); *Salix vaccinioides* scrub (235); *Sibiraea angustata* scrub (236); *Rose sericea*, *Cotoneaster adpressus* scrub (237); *Dasiphora fruticosa* scrub (238); *Dasiphora parvifolia* scrub (239); *Dasiphora glabra* var. *veitchii* scrub (240); *Myricaria prostrata* scrub (241); *Spiraea myrtilloides, S. alpina* scrub (242); *Caragana jubata* scrub (243); *Caragana tibetica* scrub (244); *Caragana versicolor* scrub (245); *Rhododendron rufum*, *Rh. przewalskii* scrub (248); *Rhododendron capitatum*, *Rh. thymifolium* scrub (249); *Rhododendron fastigiatum* scrub (250); *Rhododendron flavidum* scrub (251); *Rhododendron heiliolepis* scrub (252); *Rhododendron telmateium* scrub (253); *Rhododendron nivale*, *Rh. thymifolium* scrub (257); *Sabina pingii* var. *wilsonii*, *S. squamata*, *S. wallichiana* scrub (262); *Dasiphora parvifolia* desert (272); *Caragana korshinskii*, *Calligonum mongolicum*, *Zygophyllum xanthoxylon*, low grass desert (288); *Artemisia salsoloides* var. *wellbyi*, *Stipa* spp. steppe (417); *Artemisia younghusbandii*, *Orinus thoroldii* steppe (418); *Sanguisorba officinalis*, *Artemisia laciniata*, *Carex pediformis*, grass meadow (455); *Kobresia pygmaea* meadow (486); *Kobresia pygmaea* meadow (486a); *Kobresia pygmaea*, *Stipa purpurea* meadow (486b); *Kobresia pygmaea*, *Stipa aliena* meadow (486c); *Kobresia pygmaea*, *Polygomum sphaerostachyum* meadow (486d); *Kobresia humilis* meadow (487); *Kobresia capillifolia* meadow (488); *Kobresia capillifolia* meadow (488a); *Kobresia capillifolia*, *Stipa purpurea* meadow (488b); *Kobresia capilifolia*, *Polugonum viviparum* meadow (488c); *Kobresia setchwanensis* meadow (489); *Kobresia vidua*, forb meadow (490); *Kobresia bellardii* meadow (491); *Kobresia* spp. meadow (492); *Kobresia smirnovii* meadow (492a); *Kobresia filifolia* meadow (492b); *Kobresia myosuroides* meadow (492c); *Kobresia stenocarpa* meadow (492d); *Kobresia* spp., *Carex* spp. meadow (493); *Kobresia schoenoides*, *Carex* spp. meadow (493a); *Kobresia littledalei* meadow (493b); *Kobresia deasyi* meadow (493c); *Korbresia stenocarpa*, *Calamagrostis macrolepis* meadow (494); *Elymus nutans*, *Reogneria nutans* meadow (495); *Poa* spp. meadow (497); *Poa rossbergiana*, *Littledalea racemosa* meadow (497a); *Carex scabrirostris* meadow (500a); *Carex atrofusca* meadow (500b); *Carex* spp. meadow and *Myricaria prostrate* scrub (501); *Polygonum sphaerostachyum*, *P. viviparum* meadow (502); *Ligularia virgaurea*, *Anemone* spp. meadow (503); *Anaphalis flavescens*, *Leontopodium longifolium*, *Spenceria ramalana* meadow (504); *Saussurea arenaria*, *S. humilis* meadow (505a); *Saussurea alpine* meadow (505b); *Phragmites communis* marsh with *Typha angustifolia*, *Hippuris vulgaris* (507a); *Carex vesicaria*, *Puccinellia hauptiana* marsh (513); *Halerpestes tricuspis*, *Batrachium tricophullum*, *Potamogeton pectinatus* marsh (518); *Carex muliensis* marsh (528); *Carex* spp., *Deschampsia caespitosa* marsh (529); *Carex* spp., *Blysmus sinocompressus* marsh (530); Snow capped (Sc)
Graminoid and forb tundra	*Rhododendron nivale*, *Rh. thymifolium* scrub (257); *Filifolium sibiricum*, grass, forb steppe (356); *Festuca ovina* steppe (368); *Agropyron cristatum* steppe (370); *Poa litwinowiana*, *Festuca olgae* steppe (371); *Stipa glareosa* steppe (384); *Stipa breviflora* steppe (385); *Stipa capillata*, nano-semi-shrub steppe (386); *Stipa caucasica* steppe (388); *Stipa sareptata* steppe (389); *Stipa roborowskii*, *Artemisia rhodantha* steppe (390); *Agropyron cristatum*, *Stipa glareose* steppe (395); *Caragana tibetica*, low grass steppe (400); *Seriphidium borotalense*, *Festuca ovina* steppe (403); *Stipa purpurea* steppe (405a); *Stipa purpurea*, *Ceratoides compacta* steppe (405b); *Stipa purpurea*, *Carex ivanoviae* steppe (405c); *Stipa purpurea*, *Carex montis-everestii* steppe (405d); *Stipa purpurea*, *Cerex moorcroftii* steppe (405e); *Stipa subsessiliflora* var. *basiplumosa* steppe (406a); *Stipa subsessiliflora* steppe (407); *Stipa roborowskii* steppe (408); *Stipa aliena* steppe (409); *Festuca pseudovinas* steppe (410); *Festuca olgae* steppe (412); *Poa litwinowiana*, *Androsace squarrosula* steppe (413); *Orinus thoroldii* steppe (414); *Orinus kokonorica* steppe (415); *Carex moorcroftii* steppe (416); *Carex moorcroftii* steppe (416a); *Carex moorcroftii*, *Stipa purpurea* steppe (416b); *Carex moorcroftii*, *Ceratoides compacta* steppe (416c); *Dactylis glomerata* meadow (438); *Festuca ovina*, *Deyeuxia arundinacea*, forb meadow (446); *Phragmites communis* meadow (469); *Aneurolepidium dasystachys* meadow (474); *Arenaria pulvinata* cushion vegetation (534); *Arenaria musciformis*, *Androsace tapete* cushion vegetation (536); *Androsace squarrosula* cushion vegetation (537); *Sibbaldia tetrandra*, *Anthoxanthum alpinum* cushion vegetation (538); *Oxytropis chionobia*, *Poa festucacens* cushion vegetation (540); *Ajania tibetica* cushion vegetation (541); *Saussurea medusa*, *Saussurea* spp. sparse vegetation (543); *Saussurea* spp., *Rhodiola rosea*, *Cremanthodium* spp. sparse vegetation (544); *Saussurea tridactyla*, *Waldheimia glabra* sparse vegetation (545); Sandy desert (Sa); Gravel desert (Gr); Rocky desert or alpine rock debris (R); Bare ground (B); Bare salt lick (Bs); Rocky mountain (Rm); Snow capped (Sc)
Erect dwarf-shrub tundra	*Artemisia rhodantha* desert (338); *Ajania tibetica* desert (340); *Blysmus sinocompressus*, *Carex* spp. meadow (493d)
Prostrate dwarf-shrub tundra	*Ceratoides compacta* desert (341); *Rhodiola algida* var. *tangutica* desert (342); Snow capped (Sc)
Cushion forb, lichen, and moss tundra	*Saussurea medusa*, *Saussurea* spp. sparse vegetation (543); *Saussurea tridactyla*, *Waldheimia glabra* sparse vegetation (545); Snow capped (Sc)
Barren/Land ice	Snow capped (Sc)

northern Tibet. Shrub tundra (35%) is concentrated in southern, southeastern, and eastern Tibet (Fig. 1, a). Temperate desert (9.5%, in the northern margin and the Qaidam Basin), evergreen taiga/montane forest (4.5%, in southeastern Tibet) and prostrate shrub tundra (4%, in northwestern Tibet) biomes account for ca. 18% of the entire plateau. The erect dwarf-shrub tundra and cushion forb, lichen, and moss tundra only occupy a small area of the plateau (Fig. 1, a).

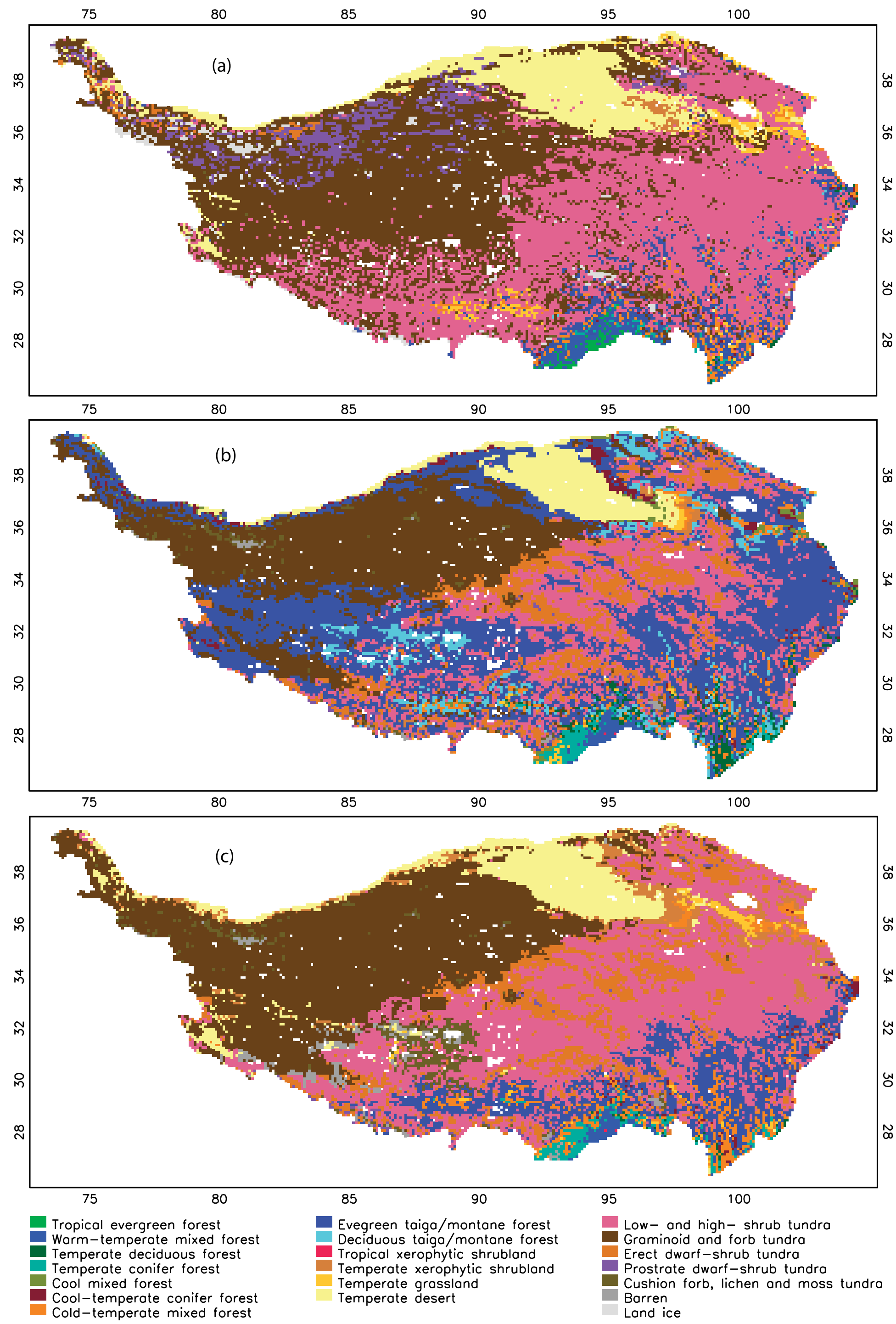

FIGURE 1. Biomes on the Tibetan Plateau (a) derived from the Vegetation Atlas of China, (b) simulated by the original BIOME4 model without redefined parameters, and (c) simulated by the improved BIOME4 model where parameters have been redefined.

Results

OVERALL BIOME SIMULATIONS

The original BIOME4 simulation produced 18 biomes (Fig. 1, b). The model failed to simulate tropical evergreen forest and land ice. Instead it predicted cool mixed forest and barren areas, which do not exist in the observational data (Fig. 1, a). The model over-predicted three biomes: evergreen taiga/montane forest in large areas of northeastern, eastern, central western, and northern Tibet; erect dwarf-shrub tundra in the central plateau; and deciduous taiga/montane forest in northeastern and southern plateau. Temperate desert, steppe tundra, and shrub tundra biomes were under-estimated in ca. 40–50% (based on the number of gridcells) of instances (Fig. 2, a and b; Table 3). Agreement between observed and simulated biomes was only 35.1% (Fig. 1, a and b), with particularly large disagreement in the central, southern, and eastern areas of the plateau (Fig. 2, a and b).

The improved model with re-parameterized PFTs predicted a better biome distribution on the Tibetan Plateau (Fig. 1, c) with an overall match rate to observational data (Fig. 1, a) of 52.4%. The extent of evergreen taiga/montane forest (Fig. 1, c) was significantly reduced compared to the original simulation and there was no simulation of deciduous taiga/montane forest (Fig. 1, b), although the amount of evergreen taiga vegetation was still over-predicted (Fig. 2, c and d). The accuracy of correct

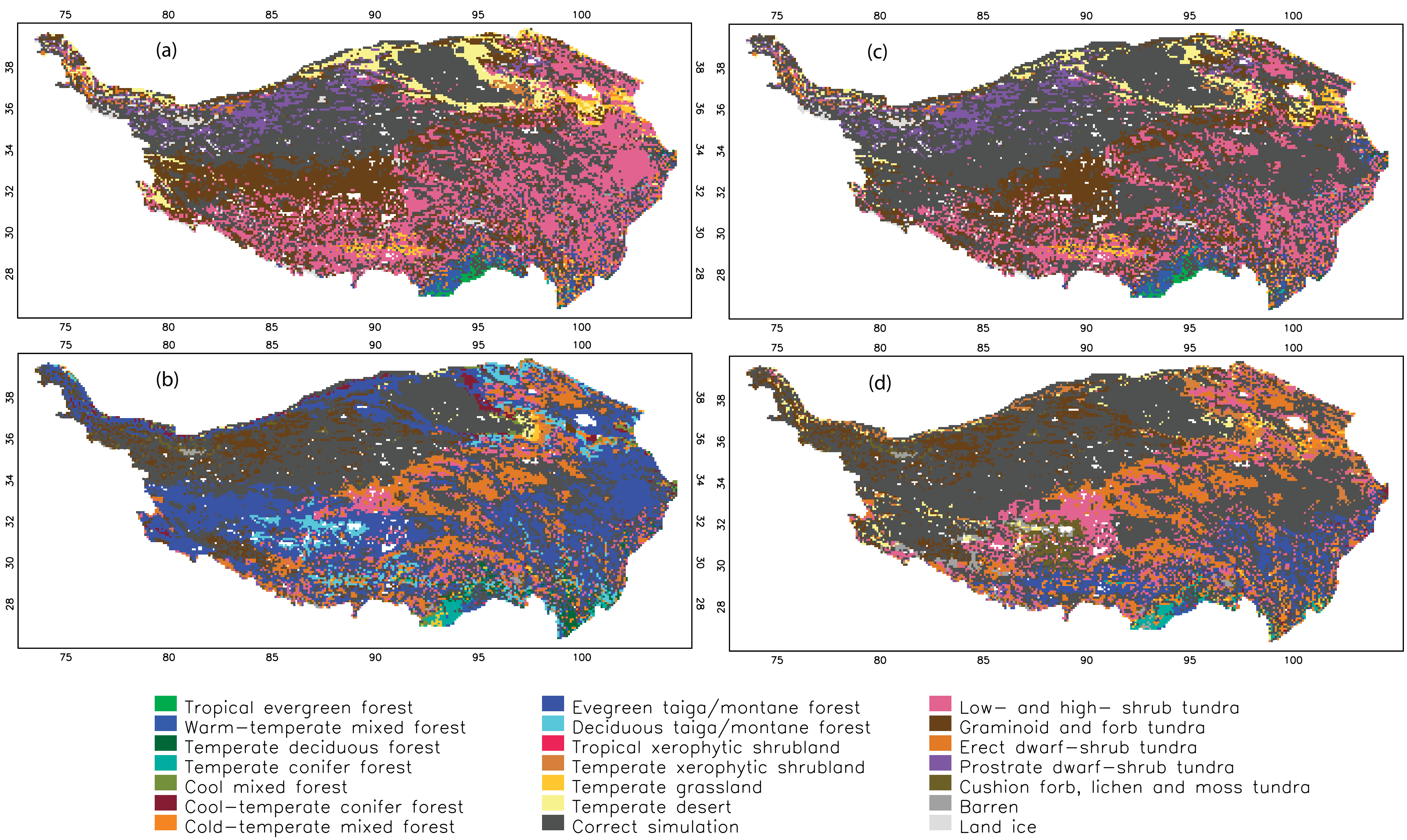

FIGURE 2. Differences between (a) observed and (b) original BIOME4 simulated biomes, and between (c) observed and (d) modified BIOME4 simulated biomes. Correct matches are shown in gray.

TABLE 3

Comparison between observed and original BIOME4 simulated biomes (gridcell number) on the Tibetan Plateau.

Biomes	TREF	WTMF	TEDF	TECF	COMF	CTCF	CTMF	ETMF	DTMF	TRSH	TESH	TEGR	TEDE	SHTU	GFTU	ESTU	PSTU	CUTU	BARN	LICE	Observed	Sim. /Obs. (%)
TREF	0	54	1	28	1		2		1	2		11									100	0.0
WTMF		80	38	108	9	1	12	3	4			10									265	21.9
TEDF		2	12	2	4	2	5	3	3						1						34	35.3
TECF		18	14	24	1		6					3									66	36.3
COMF					0																0	—
CTCF			8	4	5	14	15	4	1			1									52	27.0
CTMF		8	71	19	21	7	66	156	60		4	11	3	7	38	5	2				478	13.8
ETMF		1	104	17	10	10	76	589	83		12	4		7	150	42	3	2	6		1116	52.8
DTMF			3		1	1	1	16	0						7						29	0.0
TRSH			2							0				1							3	0.0
TESH					22	18	4	4			6	7	39								100	6.0
TEGR		1	7	4	28	17	54	138	88		14	4		22	24	5					406	1.0
TEDE			2		68	205	55	644	105		35	22	1144	60	17	2					2359	48.5
SHTU		3	8		9	30	22	2875	301		23	3	29	4075	1031	787	34	84	16		9330	43.5
GFTU		4	65	8	10	28	125	3834	273		51	7	9	344	2666	1271	38	15	5		8753	30.5
ESTU					2	7		41						71		0		5			126	0.0
PSTU					1	2		131	1				4	805	28	15	0	4			991	0.0
CUTU							1	16						17	18	11	7	6			76	7.9
BARN																			0		0	—
LICE						1		24						192	33	65	17	67	32	0	431	0.0
Simulated	0	171	335	214	192	343	444	8478	920	2	145	83	1228	5601	4013	2203	101	183	59	0	24,715	35.1

TREF (Tropical evergreen forest), WTMF (Warm-temperate mixed forest), TEDF (Temperate deciduous forest), TECF (Temperate conifer forest), COMF (Cool mixed forest), CTCF (Cool-temperate conifer forest), CTMF (Cold-temperate mixed forest), ETMF (Evegreen taiga/montane forest), DTMF (Deciduous taiga/montane forest), TRSH (Tropical xerophytic shrubland), TESH (Temperate xerophytic shrubland), TEGR (Temperate grassland), TEDE (Temperate desert), SHTU (Low- and high-shrub tundra), GFTU (Graminoid and forb tundra), ESTU (Erect dwarf-shrub tundra), PSTU (Prostrate dwarf-shrub tundra), CUTU (Cushion forb, lichen and moss tundra), BARN (Barren), and LICE (Land ice).

predictions for desert, shrub tundra, and steppe tundra increased (Fig. 1, c) but the prediction of erect dwarf-shrub tundra was still poor, and cold mixed forest, temperate xerophytic shrubland, and cushion forb, lichen, and moss tundra were all over-predicted (Fig. 2, c and d; Table 4).

DETAILED COMPARISON OF BIOME PREDICTIONS

Although an agreement of 52.4% between observed and modified model simulated biomes is still not high, the difference of 17% in the number of accurate predictions compared to the original model is a substantial improvement. Under closer examination (Tables 3 and 4), biomes were often mismatched to others with similar bioclimatic characteristics (Fig. 2).

Tundra is the most extensive biome on the Tibetan Plateau. Low- and high-shrub tundra (hereinafter shrub tundra) and graminoid and forb tundra (steppe tundra) were both correctly simulated in 58% of instances (Fig. 1, a and c; Table 4), which is better than the original model simulation of 43.7% and 30.4%, respectively (Fig. 1, a and b; Table 3). However, they were also wrongly simulated as each other in many cases, and also as three other tundra biomes (erect dwarf-shrub tundra, prostrate dwarf-shrub tundra, and cushion forb, lichen, and moss tundra—hereinafter cushion forb tundra), barren areas, temperate xerophytic shrubland, temperate grassland, temperate desert and cool- and cold-temperate, and boreal forests (Fig. 2, c and d; Table 4). Other tundra biomes, especially erect dwarf-shrub tundra, prostrate dwarf-shrub tundra and steppe tundra, and temperate desert and land ice were incorrectly predicted to be shrub tundra. The shrub tundra, temperate grassland and desert, and two forest biomes (evergreen taiga/montane forest and cold-temperate mixed forest) were also incorrectly predicted to be steppe tundra in many sites (Fig. 2, c and d; Table 4). Both the original and modified models could not accurately predict erect and prostrate dwarf-shrub tundra, and only predicted cushion forb tundra correctly in a few cases. Barren areas and land ice were also not simulated well (Tables 3 and 4).

Temperate shrubland was correctly predicted in 56% of cases and was wrongly simulated as temperate desert and cold-temperate mixed forest. Temperate grassland was wrongly simulated as temperate shrubland, steppe tundra, evergreen taiga/montane forest, and cold-temperate mixed forest, and was only correctly predicted in 16% of instances. Temperate desert was largely correctly simulated (65%) and the wrong predictions came mainly from shrub tundra and steppe tundra (Table 4). These temperate shrubland, grassland, and desert biomes were all better predicted than the original model (Tables 3 and 4).

Cool-temperate conifer forest was correctly simulated by the modified model in 56% of cases and was mainly wrongly assigned to cold-temperate mixed forest. Cold-temperate mixed forest was correctly predicted in only 33% of cases and was largely incorrectly predicted to be evergreen taiga/montane forest (39%). It was also wrongly assigned to steppe tundra, temperate grassland, and shrubland (in total ca. 19%). In addition to this, many other forest sites (73%) of evergreen taiga/montane forest and temperate conifer forest, grassland, desert, and tundra (steppe and shrub tundra) were incorrectly predicted to be cold-temperate mixed forest (Table 4). All these cold- and cool-temperate forests were better simulated than the original model (Table 3). Evergreen taiga/montane forest was correctly simulated by the modified model in 46% of cases (Table 4) which is slightly worse than the original model prediction (Table 3), but the modified simulation reduced the number of sites from steppe tundra, shrub tundra, temperate grassland, and cold-temperate mixed forest which were wrongly predicted as evergreen taiga/montane forest (Tables 3 and 4). Non-deciduous taiga/montane forest was largely correctly simulated by both models. Temperate deciduous forest and temperate conifer forest were slightly better predicted, but warm-temperate mixed forest was more poorly simulated by the modified model (Tables 3 and 4).

Discussion and Conclusions

REASONS FOR INCORRECT SIMULATIONS

The modified BIOME4-Tibet yielded a 17% improvement in the correct simulation of Tibetan biomes compared to the original BIOME4 model. The simulation of two tundra biomes (steppe tundra and shrub tundra), temperate grassland, desert, and several forest biomes such as cool conifer forest and evergreen taiga was improved (Fig. 1; Tables 3 and 4). The model benefited from restrictions to the bioclimatic limits of key PFTs (Table 1) compared to the original model setup (Kaplan, 2001; Kaplan et al., 2003). The narrowed bioclimatic range ensured that the biome boundaries were more accurate at regional scales, although these parameters may not be accurate at global and continental scales.

No model is perfect, and the global vegetation model BIOME4 has its limitations. The BIOME4 model uses 13 PFTs to characterize 28 biomes throughout the world (Kaplan, 2001), but this number of PFTs is insufficient to properly characterize non-forest biomes. Several key shrub types on the Tibetan Plateau exist: subalpine evergreen/deciduous broadleaved and coniferous shrubs, semi-tree shrub, semi-shrub, dwarf shrub, and cushion dwarf shrub in subalpine and alpine environments (ECVC, 1980; EBVAC, 2001) (Table 2). Conversely, the BIOME4 model only has one tundra shrub PFT and one woody desert PFT, which do not sufficiently separate different shrub vegetation on the Tibetan Plateau. Different herbaceous plant types also occur on the plateau, such as the dominant species of *Stipa*, *Festuca*, *Carex*, *Kobresia* and cushion forbs from various steppe, meadow, and sparse vegetation (Table 2). Three herbaceous PFTs (temperate grass, cold herbaceous, and lichen/forb type) were used in BIOME4, but the limited numbers of herb PFTs did not accurately characterize the key bioclimatic features of different herb types (e.g. precipitation limits of graminoids mentioned above), and so they could not successfully separate different herb types-based biomes.

Sharing key PFTs among biomes is a key reason for mismatches among certain biomes, for example among the five tundra biomes. This is mainly due to the mixture of shrub, grass, and forb PFTs among these tundra biomes, and the model could not differentiate between them under similar bioclimatic conditions. Desert and tundra biomes contain similar grass and shrub PFTs (temperate grass, desert woody shrub, tundra shrub, and cold herb). They were also wrongly simulated to each other in some places. Several conifer and mixed forests had the same situation because they share conifer PFTs and they are also distributed in a transitional zone between forest and grassland at high altitudes. Incorrect simulations of temperate, cool-, cold-, and warm-temperate forests are mainly due to the shared deciduous and conifer PFTs.

The BIOME4 model uses broad climate constraints to differentiate between biomes (Kaplan, 2001). Previous work on arctic biomes resulted in incorrect predictions of forest and dwarf-shrub tundra biomes due to problems with regional climate data and bioclimatic constraints (Kaplan et al., 2003). We improved the climate parameters of some key PFTs in BIOME4-Tibet, but the

TABLE 4

Comparison between observed and regional-improved BIOME4 simulated biomes (gridcell number) on the Tibetan Plateau.

Biomes	TREF	WTMF	TEDF	TECF	COMF	CTCF	CTMF	ETMF	DTMF	TRSH	TESH	TEGR	TEDE	SHTU	GFTU	ESTU	PSTU	CUTU	BARN	LICE	Observed	Sim. /Obs. (%)
TREF	0		34	50		1	6			2		1							6		100	0.0
WTMF		5	3	1		6	11	2			1	3			2						34	14.7
TEDF		12	44	1		6	3														66	66.7
TECF		11	128	63		5	47	5				1	1						4		265	23.8
COMF					0																0	—
CTCF		1	4			29	11				1	3			3						52	55.8
CTMF		2	16			14	159	185			13	16	5		61	5	2				478	33.3
ETMF		3	11			12	193	514			34	9	8		277	42	3	3	7		1116	46.1
DTMF						1	4	14	0		1	1			8						29	0.0
TRSH							3			0											3	0.0
TESH							9				56	2	33								100	56.0
TEGR			6			1	66	68			92	65	13	4	84	5		2			406	16.0
TEDE						3	49	6			369	39	1536	288	66	2			1		2359	65.1
SHTU			4			6	32	197			172	24	239	5419	1925	787	34	317	174		9330	58.1
GFTU		3	11	1		33	176	1292			186	24	54	397	5048	1271	38	147	72		8753	57.7
ESTU											8		15	98		0		5			126	0.0
PSTU											4		16	909	43	15	0	4			991	0.0
CUTU						1		8			1			21	20	11	7	6	1		76	7.9
BARN																			0		0	—
LICE								3					2	195	45	65	17	68	36	0	431	0.0
Simulated	0	37	261	116	0	118	769	2294	0	2	938	188	1922	7331	7582	2203	101	552	301	0	24715	52.4

The biome codes are the same as in Table 3.

rules for assigning biomes based on their differences in bioclimate and optimal PFT-based LAI and NPP (Kaplan, 2001; Kaplan et al., 2003) were not changed. This may have resulted in some of the incorrect simulations.

Permafrost and snow cover set important limits on vegetation distribution, especially in arctic and alpine regions (Vaganov et al., 1999; Wang et al., 2006). The BIOME4 model has built-in mechanisms for simulating permafrost and snow processes, but improvements to these modules are needed to more precisely characterize the permafrost and snow–vegetation relationships in Tibet. In addition, soil properties derived from the global data set at 0.5 degree resolution are relatively coarse. Song et al. (2005) used a digitized soil texture data set from an old version of Soil of China (Xiong and Li, 1987), but estimations of soil texture-based water-holding capacity and percolation rate are not available. More detailed and accurate data from regional resources, for example the new Chinese soil database (Shi et al., 2004), are required for future study.

We used regional climate data to drive the model, but gaps in the distribution of weather stations in central and western Tibet may be responsible for some incorrect simulations. There are 207 weather stations in the study area, but almost all of them are distributed in central, eastern, and the northern margins of Tibet and are mainly below 4500 m. In the central and western areas there are only three stations, and the sparsity of weather stations might lead to the incorrect interpolation of climate data. From a similar example, winter temperature was not accurately represented in Alaskan arctic climate interpolation in large valleys and basins with a sparse density of climate data, but the interpolated maps were still consistent with regional climatology (Fleming et al., 2000). We used the same interpolation method as Fleming et al. (2000), so the climate data should be sufficiently precise for regional vegetation modeling.

The BIOME4 model uses global definitions for five arctic tundra biomes (Kaplan et al., 2003). Tibetan vegetation was assigned to tundra biomes based on the global classification of tundra (Kaplan et al., 2003; Walker et al., 2005). However, there is some debate among most of ecologists in China who do not agree that tundra biomes are widely distributed on the Tibetan Plateau. The Tibetan vegetation was called "alpine" or "high-cold" vegetation (mainly alpine meadow, shrubland, steppe, and desert) rather than "tundra" (ECVC, 1980; EBVAC, 2001). There are three types of tundra vegetation in China: small shrub and moss tundra (*Dryas octopetala*, *Phyllodoce caerulea*, and *Rhacomitrium canescens*) and forb and moss tundra (*Papaver pseudo-radicatum*, *Oxytropis anertii*, and *Polyprachasrum alpinum*) which occur in the Changbai Mountains in northeastern China, and moss and lichen tundra (*Cetraria nivalis*) situated in the Altay Mountains in northwestern China (ECVC, 1980). They grow in cold and wet high mountains and are thought to be connected to tundra biomes that occur in boreal and arctic zones in Siberia and the Far East (ECVC, 1980). High-cold alpine vegetation on the Tibetan Plateau grows in very cold yet dry conditions except in the southeastern subalpine region, which is different from boreal and arctic habitats. However, based on the global definitions of tundra biomes (Walker et al., 2005), high-cold vegetation on the Tibetan Plateau should be assigned to tundra biomes.

The eco-physiognomy of high-cold vegetation is similar to that of tundra biomes, but their composition and structure are different. For example, the continuous, 50-cm- to 2-m-tall low- and high-shrub tundra in circumpolar regions consists of deciduous shrubs (*Alnus*, *Betula*, and *Salix*), evergreen pine (*Pinus pumila* in eastern Siberia), and *Eriophorum* and *Sphagnum*, sometimes with tussock-forming graminoids (Kaplan et al., 2003; Walker et al., 2005). However, in the eastern and southern areas of the Tibetan Plateau, this biome is mainly composed of evergreen shrubs (*Rhododendron*, *Juniperus*, and *Sabina*) and moss, with some deciduous shrubs (*Salix*, *Dasiphora*, *Rose*, *Cotoneaster*, and *Spiraea*). These are mostly 25–50 cm to 1–1.5 m tall, with very few herbs (ECVC, 1980). Steppe tundra, dominated by forbs and graminoids, includes typical taxa such as *Artemisia*, *Kobresia*, Brassicaceae, Asteraceae, Caryophyllaceae, Gramineae, and true mosses in arctic regions (Kaplan et al., 2003; Walker et al., 2005). This graminoid and forb tundra has a similar species composition on the Tibetan Plateau (*Stipa*, *Festuca*, *Poa*, *Carex*, *Artemisia*, and *Polygonum*), although there remain issues with the assignment of *Kobresia* meadows. *Kobresia* meadow, which could be assigned to graminoid and forb tundra, is normally distributed on the southern slopes between 3200 and 5200 m (ECVC, 1980). However, *Kobresia* meadow also occurs in conjunction with *Rhododendron* shrub tundra on the northern slopes at altitudes of 4200–4800 m, such as the *K. pygmaea* meadow which occupies the largest area on the plateau (ECVC, 1980). This area is described as a shrub-meadow complex in Chinese vegetation (ECVC, 1980). The simulated biome for this area consists mostly of shrub tundra rather than steppe tundra. The erect dwarf-shrub tundra (consisting of *Betula*, *Cassiope*, *Empetrum*, *Salix*, *Vaccinium*, Gramineae, and Cyperaceae in circumpolar regions, and *Artemisia* and *Ajania* on the Tibetan Plateau) and prostrate dwarf-shrub tundra (consisting of *Salix*, *Dryas*, *Pedicularis*, Asteraceae, Caryophyllaceae, Gramineae, and true mosses in circumpolar regions, and *Ceratoides* and *Rhodiola* in Tibet) biomes are very different, and belong to alpine desert vegetation on the Tibetan Plateau (ECVC, 1980; EBVAC, 2001). Cushion forb, lichen, and moss tundra on the plateau (*Saussurea* and *Waldheimia*) have a different composition than the same tundra in the Arctic (*Papaver*, *Draba*, Saxifragaceae, and Caryophyllaceae) and is often found alongside *Kobresia* meadow (ECVC, 1980). These issues made the assignment of high-cold vegetation to tundra biomes difficult and in some cases incorrect, and have affected the model-data comparison.

COMPARISONS WITH PREVIOUS SIMULATIONS

Two previous simulations of Tibetan biomes (Ni, 2000; Song et al., 2005) have three features in common: they all adopted the Chinese classification of Tibetan vegetation rather than the global biome scheme; simulated modern biomes were compared to a vegetation map of China at a scale of 1:4 million published 30 years ago; and the baseline atmospheric CO_2 concentration was set at 340 ppmv. Ni (2000) used the BIOME3 model and by improving the climatic constraints (GDD_5 and annual precipitation) of seven alpine and subalpine biomes, was able to simulate 11 biomes on the Tibetan Plateau. PFT parameters were not changed. The climate data (1951–1980) and soil data at 10′ resolution came from regional observations in China (Ni, 2000). The BIOME3 model did not include any alpine PFTs such as cold herbaceous and lichen/forb types and, therefore, although there was a good agreement (ca. 62%) between the simulated and observed biomes (Ni, 2000), the simulation was less precise than the present simulations. The BIOME4 model, improved by changing the bioclimatic limits for each PFT (T_{cm}, T_{wm}, GDD_5, GDD_0, annual moisture availability α, and dominance class D) and by using a new ranking of PFTs for biome assignment, was able to simulate nine biomes in Tibet (Song et al., 2005). The improved model was driven by PRISM long-term mean climatological data (1961–1990) at 3′ resolution. The soil data used referred to soil texture properties rather than the water holding capacity and percolation index used in the BIOME4 simulations. The two dominant biomes, alpine meadow and alpine steppe, showed reasonable agreement with vegetation maps, while there was good agreement for the alpine desert biome (Song et al., 2005).

The different models, biome classifications, and climate and soil data used in previous studies make it difficult to compare the results with our model, but the simulation using the improved BIOME4 model (Song et al., 2005) produced a general trend in biome change from subalpine conifer forest in southeastern Tibet, alpine meadow and montane shrub steppe and steppe in the eastern central region, alpine steppe in the central of the plateau, to alpine desert and montane desert in the northwest. This pattern is more similar to our simulation than the BIOME3 prediction (Ni, 2000).

CONCLUSIONS

The well-tested equilibrium global vegetation model (BIOME4) was modified by redefining the regional bioclimatic limits of key PFTs in order to simulate biome distribution on the Tibetan Plateau. A detailed comparison between the simulated biomes and vegetation map showed that the improved model (BIOME4-Tibet) did a better job of simulating several alpine biomes such as steppe tundra, shrub tundra, and evergreen taiga. The agreement between modeled and observed biome data increased by 17%, which indicates that the global model has potential for regional vegetation modeling. The modified model can be further used to illustrate the impacts of past and future climate change on alpine vegetation and to asses the role of vegetation in atmosphere–biosphere interactions, including changes in carbon and water cycles.

The large proportion of incorrect simulations mean that further improvements to the model are necessary, in addition to obtaining more accurate regional climate, soil, and vegetation data. Extra shrub and herbaceous PFTs also need to be added to BIOME4-Tibet, and more precise bioclimatic and ecophysiological parameters are required in order to constrain the distribution of PFTs and biomes. Further modification of permafrost, snow, and soil modules is also required.

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References Cited

Chang, D. H. S., 1983: The Tibetan Plateau in relation to the vegetation of China. *Annals of Missouri Botanical Garden*, 70: 564–570.

Chen, X. W., Zhang, X. S., and Li, B. L., 2005: Influence of Tibetan Plateau on vegetation distributions in East Asia: a modeling perspective. *Ecological Modelling*, 181: 79–86.

CITTP [The Comprehensive Investigation Team of Tibetan Plateau, Chinese Academy of Sciences], 1988: *Vegetation of Xizang*. Beijing: Science Press.

EBVAC [Editorial Board of Vegetation Atlas of China, Chinese Academy of Sciences], 2001: *Vegetation Atlas of China (1:1 000 000)*. Beijing: Science Press, 280 pp.

ECVC [Editorial Committee of Vegetation of China], 1980: *Vegetation of China*. Beijing: Science Press, 1382 pp.

FAO [Food and Agriculture Organization], 1995: *Digital Soil Map of the World and Derived Soil Properties*. Rome: Food and Agriculture Organization.

Farr, T. G., Rosen, P. A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin, M., Burbank, D., and Alsdorf, D., 2007: The shuttle radar topography mission. *Reviews of Geophysics*, 45(2): article RG2004, doi:10.1029/2005RG000183.

Fleming, M. D., Chapin, F. S., Cramer, W., Hufford, G. L., and Serreze, M. C., 2000: Geographic patterns and dynamics of Alaskan climate interpolated from a parse station record. *Global Change Biology*, 6(suppl. 1): 49–58.

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

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

Hou, X. Y., Sun, S. Z., Zhang, J. W., He, M. G., Wang, Y. F., Kong, D. Z., and Wang, S. Q., 1982: *Vegetation Map of the People's Republic of China*. Beijing: Map Press of China.

Hutchinson, M. F., 2006: *ANUSPLIN Version 4.36 User Guide*. Canberra: Centre for Resource and Environmental Studies, Australian National University, 54 pp.

Kaplan, J. O., 2001: *Geophysical Applications of Vegetation Modeling*. Ph.D. dissertation, Lund University, Lund, Sweden, 36 pp.

Kaplan, J. O., Bigelow, N. H., Prentice, I. C., Harrison, S. P., Bartlein, P. J., Christensen, T. R., Cramer, W., Matveyeve, N. V., McGuire, A. D., Murray, D. F., Razzhivin, V. Y., Smith, B., Walker, D. A., Anderson, P. M., Andreev, A. A., Brubaker, L. B., Edwards, M. E., and Lozhkin, A. V., 2003: Climate change and arctic ecosystems: 2. Modeling, paleodata-model comparisons, and future projections. *Journal of Geophysical Research*, 108: 8171, doi:10.1029/2002JD002559.

Klein, J. A., Harte, J., and Zhao, X. Q., 2004: Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. *Ecology Letters*, 7: 1170–1179.

Lau, K. M., and Li, M. T., 1984: The monsoon of East Asia and its global associations—A survey. *Bulletin of the American Meteorological Society*, 65: 114–125.

Liu, X. D., Kutzbach, J. E., Liu, Z. Y., An, Z. S., and Li, L., 2003: Tibetan Plateau as amplifier of orbital-scale variability of the East Asian monsoon. *Geophysical Research Letters*, 30: article 1839, doi:10.1029/2003GL017510.

Melillo, J. M., McGuire, A. D., Kicklighter, D. W., Moore, B., Vorosmarty, C. J., and Schloss, A. L., 1993: Global climate change and terrestrial net primary production. *Nature*, 363: 234–240.

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

Ni, J., 2000: A simulation of biomes on the Tibetan Plateau and their responses to global climate change. *Mountain Research and Development*, 20: 80–89.

Ni, J., 2011: Impacts of climate change on Chinese ecosystems: key vulnerable regions and potential thresholds. *Regional Environmental Change*, 11(suppl. 1): S49–S64.

Ni, J., Sykes, M. T., Prentice, I. C., and Cramer, W., 2000: Modeling the vegetation of China using the process-based equilibrium terrestrial biosphere model BIOME3. *Global Ecology and Biogeography*, 9: 463–479.

Parton, W. J., Scurlock, J. M. O., Ojima, D. S., Gilmanov, T. G., Scholes, R. J., Schimel, D. S., Kirchner, T., Menaut, J.-C., Seastedt, T., Moya, E. G., Kamnalrut, A., and Kinyamario, J. I., 1993: Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochemical Cycles*, 7: 785–809.

Peng, C. H., 2000: From static biogeographical model to dynamic global vegetation model: a global perspective on modelling vegetation dynamics. *Ecological Modelling*, 135: 33–54.

Prentice, I. C., and Raynaud, D., 2001: Interactions of climate change and the terrestrial biosphere. *In* Schulze, E. D., Heimann, M., Harrison, S., Holland, E., Lloyd, J., Prentice, I. C., and Schimel, D. (eds.), *Global Biogeochemical Cycles in the Climate System*. San Diego: Academic Press, 176–195.

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. *Journal of Biogeography*, 19: 117–134.

Prentice, I. C., Bondeau, A., Cramer, W., Harrison, S. P., Hickler, T., Lucht, W., Sitch, S., Smith, B., and Sykes, M. T., 2007: Dynamic global vegetation modeling: quantifying terrestrial ecosystem responses to large-scale environmental change. *In* Canadell, J., Pitelka, L. F., and Pataki, D. (eds.), *Terrestrial Ecosystems in a Changing World*. Berlin, Heidelberg: Springer-Verlag, 175–192.

Shi, X. Z., Yu, D. S., Warner, E. D., Pan, X. Z., Petersen, G. W., Gong, Z. G., and Weindorf, D. C., 2004: Soil database of 1:1,000,000 digital soil survey and reference system of the Chinese genetic soil classification system. *Soil Survey Horizons*, 45: 129–136.

Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J. O., Levis, S., Lucht, W., Sykes, M. T., Thonicke, K., and Venevsky, S., 2003: Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, 9: 161–185.

Sitch, S., Huntingford, C., Gedney, N., Levy, P. E., Lomas, M., Piao, S. L., Betts, R., Ciais, P., Cox, P., Friedlingstein, P., Jones, C. D., Prentice, I. C., and Woodward, F. I., 2008: Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). *Global Change Biology*, 14: 2015–2039.

Smith, B., Samuelsson, P., Wramneby, A., and Rummukainen, M., 2011: A model of the coupled dynamics of climate, vegetation and terrestrial ecosystem biogeochemistry for regional applications. *Tellus*, 63A: 87–106.

Song, M. H., Zhou, C. P., and Ouyang, H., 2005: Simulated distribution of vegetation types in response to climate change on the Tibetan Plateau. *Journal of Vegetation Science*, 16: 341–350.

Vaganov, E. A., Hughes, M. K., Kirdyanov, A. V., Schweingruber, F. H., and Silkin, P. P., 1999: Influence of snowfall and melt timing on tree growth in subarctic Eurasia. *Nature*, 400: 149–151.

Walker, D. A., Raynolds, M. K., Daniels, F. J. A., Einarsson, E., Elvebakk, A., Gould, W. A., Katenin, A. E., Kholod, S. S., Markon, C. J., Melnikov, E. S., Moskalenko, N. G., Talbot, S. S., Yurtsev, B. A., the other members of the CAVM Team, 2005: The Circumpolar Arctic Vegetation Map. *Journal of Vegetation Science*, 16: 267–282.

Wang, G. X., Li, Y. S., Wu, Q. B., and Wang, Y. B., 2006: Impacts of permafrost changes on alpine ecosystem in Qinghai-Tibet Plateau. *Science in China Series D–Earth Sciences*, 49: 1156–1169.

Wania, R., Ross, I., and Prentice, I. C., 2009a: Integrating peatlands and permafrost into a dynamic global vegetation model: 1. Evaluation and sensitivity of physical land surface processes. *Global Biogeochemical Cycles*, 23: GB3014, doi:10.1029/2008GB003412.

Wania, R., Ross, I., and Prentice, I. C., 2009b: Integrating peatlands and permafrost into a dynamic global vegetation model: 2. Evaluation and sensitivity of vegetation and carbon cycle processes *Global Biogeochemical Cycles*, 23: GB3015, doi:10.1029/2008GB003413.

Woodward, F. I., 1987: *Climate and Plant Distribution*. New York: Cambridge University Press, 174 pp.

Xiong, Y., and Li, Q. K., 1987: *Soil of China*. Beijing: Science Press.

Yasunari, T., 2006: Land-atmosphere interaction. *In* Wang, B. (ed.), *The Asian Monsoon*. Berlin, Heidelberg: Springer-Verlag, 459–478.

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