大气 CO₂ 升高及气候变化对中国陆地生态系统结构与功能的制约和影响

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摘 要  在本项研究中，我们探讨了大气 CO₂ 加倍和气候变化条件下，中国陆地生态系统的结构与功能的变化。与多数研究不同的是，我们耦合了两个以地理空间为参照的生态系统模型，即生物地理模型（KBIOME）和生物地球化学模型（TEM），用此研究现状和未来的环境下，中国的植被分布和净初级生产力（NPP）的状况。我们采用 3 个大气环流模型，（GFDL-Q, GISS 和 OSU）预测的结果代表未来潜在气候变化，3 个气候模型的预测都表明未来的中国将变得更温暖并总体上更湿润。耦合的模型预测中国陆地生态系统的结构与功能都将产生十分显著的变化。植被的变化表现为：1）中国东部森林带北移，温带常绿阔叶林面积扩大，较南的森林类型取代较北的类型；2）森林和草地的总面积增加，这是为取代干旱灌木、沙漠和高山苔原的结果。净初级生产力在大气 CO₂ 加倍和气候变化条件下，增加 30％左右。与其它研究不同的另一点是，我们可以进一步区分生产力变化的原因。在所增加的生产力中，12％～21％是源于生态系统的功能变化，即 CO₂ 加倍和气候条件改变的直接影响；而 11％～17％是源于生态系统的结构变化，即由较高产的生态系统取代较低产的生态系统的结果。这项研究预测了未来中国植被和生产力潜在的变化并给出了变化的范围，为同类的研究以及有关的政策评估提供了有用的参考信息。

关键词 生态系统模型 生态系统结构与功能 气候变化 生物地球化学与生物地理学

MODELING STRUCTURAL AND FUNCTIONAL RESPONSES OF TERRESTRIAL ECOSYSTEMS IN CHINA TO CHANGES IN CLIMATE AND ATMOSPHERIC CO₂

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Abstract  China, a country with large landmass and one-fifth of the global human-population, is an important location for scientific assessment of vulnerability to climate change. In this study, we explored both structural and functional responses of terrestrial ecosystems in China to changes in climate and atmospheric CO₂. We coupled two geographically referenced ecosystem models, a biogeography model, KBIOME, and a biogeochemistry model, TEM, to investigate vegetation distribution and annual NPP under contemporary and altered environmental conditions. We used three GCM projected climate scenarios (GFDL-Q, GISS and OSU) as future conditions for the model simulations. The three GCM scenarios all suggest a warmer and generally wetter climate in China’s future. The coupled models predict significant responses of terrestrial ecosystem structure and function. The vege-

Received on June 28th, 2000  Accepted on Sep. 28th, 2000

The senior author acknowledges specially to the US Forest Service Northern Global Change program for the support that enables the author to finish the manuscript relating to the previous work in the Marine Biological Laboratory, Woods Hole.

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tation transition is shown as: 1) a northward shift of the forest zone in eastern China, with an expansion in temperate broadleaf evergreen forests, and the replacement of northern forests by more southerly types; and 2) increases in the total forested areas and grasslands at the expense of arid shrublands, desert and tundra. The annual net primary production of all terrestrial ecosystems will increase around 30% with the new climate equilibria and doubled atmospheric CO₂. We calculate that the increase in NPP is partially due to the positive functional response of NPP (12%—21%) resulting from changed climate and doubled CO₂, and partially due to the positive structure response of NPP (11%—17%) associated with the vegetation transition from less productive ecosystems to more productive ecosystems. This study presents the estimates of a range of vegetation changes and NPP responses and provides useful information that depicts potential changes in China’s future.

**Key words** Ecosystem models, Ecosystem structure and function, Climate change, Biogeochemistry and biogeography

The atmospheric concentrations of greenhouse gases (e.g. CO₂, CH₄, N₂O) have grown significantly since preindustrial times as a result of human’s activities. The increase in these gases causes a positive radiative forcing of climate that tends to warm up the surface of the earth and to produce other changes such as altering precipitation and cloud patterns (IPCC WG1, 1996). The changes in climate and atmospheric CO₂ are expected to affect both the function and structure of terrestrial ecosystems. Functional responses include changes in the cycling of carbon, nutrients and water within ecosystems and changes in the fluxes of carbon, nutrients and water between terrestrial ecosystems and aquatic ecosystems or the atmosphere. Structural responses include changes in species composition and a variety of vegetation characteristics such as canopy height and rooting depth (VEMAP Members, 1995). The responses of terrestrial ecosystems would likely have considerable spatial variations in corresponding to complicated spatial patterns of future climate scenarios. To investigate regional responses and a range of changes becomes an important approach for gaining insight into climate change effects.

China as a country with large landmass and one-fifth of the human-population in the world is an important region for conducting a scientific assessment of the vulnerability to climate change. Because major food resources and raw materials for human’s life can be greatly affected by changes in ecosystem structure and function, China, which has limited natural resources, could be fundamentally affected by the potential climate change when the situation on feeding such a huge population becomes crucial (Brown, 1995). So, from both scientific and practical perspectives, it is important to carry out a regional study in China on exploring both structural and functional responses of terrestrial ecosystems to changes in climate and atmospheric CO₂.

Few studies have been done to assess potential effects of climate change on terrestrial ecosystems in China. A study using Terrestrial Ecosystem Model (TEM) focused on functional responses of terrestrial ecosystems associated with the potential vegetation distribution (Xiao et al., 1998) and examined individual and joint effects of altered climate and doubled atmospheric CO₂ on annual net primary production (NPP). The results indicated a substantial increase of NPP in China under the altered climate and doubled atmospheric CO₂. Wang and Zhao (1995) studied only structural responses of terrestrial ecosystems in China. They used the Chinese Vegetation-Climate model (CVC), a rule-based biogeographical model, to predict dominance of plant functional types under altered climate. The future equilibrium climate scenario was based on the average of 7 General Circulation Model (GCM) scenarios. Under the scenario in the year of 2050, the CVC predicted reductions in the area extent of the northwest deserts and the Tibetan tundra, and a northward shift of the eastern forest zones by 2°-5° of latitude.
Zhang studied both structural and functional responses of terrestrial ecosystems to altered climates (Zhang, 1993). Zhang used the Holdridge Life-Zone Classification to determine distribution of vegetation types under contemporary and altered climates. Altered climates were generated by applying uniform increases of temperature (2 °C or 4 °C) and precipitation (20%) to current climate conditions. Then, the Chikugo model (Uchijima & Seino, 1985) was used to estimate NPP for vegetation types under the alternative conditions. Zhang concluded that the forest zones in the eastern China generally shift northward by 2.5° to 4.5° of latitude, which is quite consistent to the result from Wang and Zhao (1995). The NPP increases for most ecosystems in China. The study is limited by lack of geographical variations in climate change. The Holdridge vegetation model and Chikugo NPP model are all based on correlations with a few environmental constraints rather than mechanisms. The extrapolation of statistically based Chikugo NPP model could be questionable under new climate conditions.

In this study, we improved model predictions from the previous assessments. We used mechanism-based ecosystem models and three GCM projected climate scenarios for simulations of both structural and functional responses of terrestrial ecosystems in China. Besides altered climate, we also considered direct effect of doubled atmospheric CO₂ on terrestrial ecosystems. We coupled two geographically-referenced models, a biogeography model KBIOME, which is based on the model BIOME (Prentice et al., 1992), and a biogeochemistry model, the Terrestrial Ecosystem Model or TEM, to investigate vegetation distribution and annual NPP under contemporary and altered environmental conditions in China. The application of the both biogeography and biogeochemistry models allows us to examine changes in ecosystem structure and function under changed climate and atmospheric CO₂; and gain a further knowledge by identifying NPP responses due to either the change in ecosystem structure or direct effect from altered environmental conditions (VEMAP Members, 1995). The two models were coupled by using vegetation distributions simulated by KBIOME as inputs into the TEM, which estimates NPP based on vegetation-specific parameters. We used three GCM projections (OSU, GFDL-Q, and GISS) for future climate scenarios in order to examine how both spatial variations and magnitude variations among the GCM projections will affect the responses of terrestrial ecosystems to climate change. We chose to evaluate the sensitivity of terrestrial NPP because it is an important integrative ecological measure.

1.1 KBIOME

The KBIOME, which is a biogeography model that predicts dominance of various plant life forms in different environments, is based on the BIOME model developed by Prentice et al. (1992). The KBIOME is a “rule-based” model and uses a series of ecophysiological constraints and resource limitations as threshold rules to determine distribution of vegetation functional types such as forests, grasslands and deserts (Prentice et al., 1992; 1993). It was applied to predict global pattern of vegetation physiognomy. In comparison to the Holdridge Life-Zone classification that determines vegetation types based on three climatic variables, the KBIOME is able to engage more climatic variables and physiological constraints for vegetation classification. Thus, the KBIOME approach with more consideration of plant physiology mechanisms is robust for studying vegetation distribution under the novel climatic conditions (Prentice et al., 1992; Woodward & McKee, 1991).

The major ecophysiological and environmental constraints used in the KBIOME classification include mean temperature of the coldest month, growing degree-days on 5 °C base (GDD), growing degree-days on 0 °C base (GDD₀), mean temperature of the warmest month, and Prestley-Taylor coefficient of annual moisture availability (Prentice et al., 1992). Model inputs include
monthly temperature, precipitation, solar radiation, and soil water capacity data at the same spatial resolution to incorporate soil moisture variables in vegetation classification.

1.2 Terrestrial Ecosystem Model (TEM)

The Terrestrial Ecosystem Model (TEM) is a process-based ecosystem model that uses spatially referenced information on monthly temperature, precipitation, solar radiation (or cloudiness) and water availability, and elevation, soil texture, vegetation (Fig. 1) to make monthly estimates of important carbon and nitrogen fluxes and pool sizes (Raich et al., 1991; McGuire et al., 1993; 1997; Melillo et al., 1993). In this study, we used TEM version 4.0 (McGuire et al., 1993) to examine the sensitivity of terrestrial net primary productivity (NPP) in China to changes in climate, atmospheric CO₂, and vegetation distribution. Version 4.0 of TEM has been used to study responses of terrestrial ecosystems in the conterminous United States to climate change and doubled CO₂ (VEMAP Members., 1995; Schimel et al., 1997; Pan et al., 1998), high latitude ecosystems (McGuire & Hobie, 1997), and global terrestrial ecosystems (Xiao et al., 1997; McGuire et al., 1997).

In TEM, carbon enters the vegetation pool as gross primary production through the process of photosynthesis, some of this carbon transfers back to the atmosphere as plant respiration. Net primary productivity (NPP) is calculated as the difference between gross primary productivity (GPP) and plant respiration (Rₐ). Changes in temperature, moisture, radiation and atmospheric CO₂ will directly affect gross primary productivity and will indirectly affect GPP by altering several nitrogen cycling processes such as mineralization, and plant N uptake. The flux GPP is calculated at each time step as follows:

\[
GPP = C_{\text{max}} f(PAR) f(LEAF) f(T) f(C_a, G_o) f(N_a)
\]

where \(C_{\text{max}}\) is the maximum rate of C assimilation, PAR is photosynthetically active radiation, LEAF is leaf area relative to maximum annual leaf area, \(T\) is monthly air temperature, \(C_a\) is atmospheric concentration of carbon dioxide, \(G_o\) is relative canopy conductance, and \(N_a\) is nitrogen availability. The calculation of \(R_a\) considers both maintenance respiration and construction respiration. The functions in the GPP and \(R_a\) equations have been described in detail in previous work (Raich et al., 1991; McGuire et al., 1992; 1993; 1997).

The parameters in TEM are vegetation-specific, soil-specific, or constant. The model is parameterized for 18 vegetation types globally. Many of the vegetation-specific parameters are defined from published information; some are determined by calibrating the model to the annual fluxes and mean annual pool sizes of an intensively studied field site.

2 Input data

2.1 Contemporary climate, CO₂ and vegetation

All data sets of China used to drive KBIOME
and TEM are gridded at a resolution of 0.5° latitude by 0.5° longitude. There are 3852 grid-cells in China. Contemporary climate data sets (Monthly air temperature, precipitation and cloudiness/solar radiation) (Plate I) were derived from the Cramer and Leemans global data sets and represented long-term averages (Cramer, personal communication). The elevation data set was derived from the NCAR/Navy global 10-minute elevation data set (NCAR/Navy, 1984). The soil texture (or soil water capacity) data set was derived from the global soil texture database digitized at 0.5° resolution from UNESCO/FAO World Soil Map (FAO-UNESCO, 1971). Hydrological inputs for TEM were determined with a water balance model (WBM) (Vörösmary et al., 1989) that uses the same temperature, precipitation, solar radiation, soils and vegetation data as TEM.

Potential vegetation of China was simulated by KBIOME (Plate I a) and includes 14 vegetation types. For coupling KBIOME and TEM, sixteen plant functional types in TEM category were lumped into fourteen vegetation types in KBIOME classes. The temperate savanna in TEM is lumped into grasslands in KBIOME, and desert and arid shrublands in TEM are grouped together in KBIOME. The contemporary level of atmospheric CO₂ concentration was 312.5 ppmv, which is the baseline concentration for the GCM-defined climate change (Melillo et al., 1993).

2.2 Changed climate, CO₂ and vegetation

Future climate change scenarios were represented by changes in temperature, precipitation and cloudiness based on equilibrium projections of three atmospheric general circulation models (GCMs) under doubled atmospheric CO₂ (Xiao et al., 1998). The GCMs include the Geophysical Fluid Dynamics Laboratory (GFDL–Q) (Manabe & Wetherald, 1987); the Goddard Institute for Space Science (GISS) (Hansen et al., 1983; 1984); and Oregon State University (OSU) (Schlesinger & Zhao, 1989). These GCMs represent oceans as a simple “mixed-layer” that includes heat storage and vertical exchange of heat and moisture with the atmosphere.

To develop the future climate change scenarios of China for input into TEM changes in monthly mean temperature were represented as differences, and those for monthly precipitation and cloudiness as change ratios. The GCMs grid point change values were interpolated to the 0.5° grid and then applied to the Cramer and Leemans contemporary data sets to generate the altered climate scenarios in China. The level of doubled atmospheric CO₂ concentration was 625 ppmv. In this study, we developed future scenarios in which changes in climate and atmospheric CO₂ were combined. We did not specifically examine the effect of elevated atmospheric CO₂ on ecosystem processes. The vegetation redistributions under the climate change scenarios predicted by KBIOME were used as inputs in TEM runs.

3 Experimental design

We designed two sets of the model experiments to examine the effect of climate change and doubled atmospheric CO₂ concentration on ecosystem structure and function. In the first set of simulations, we examine structural responses to climate change by evaluating changes in vegetation distribution under doubled CO₂ and altered climate. First, we run the biogeography model KBIOME under the control conditions, i.e. the contemporary CO₂ concentration and climate. Then, we run KBIOME for the altered climates projected by the three GCM scenarios and doubled CO₂ and examine how representations of potential vegetation distribution change under altered conditions.

In the second set of experiments, we examine structural and functional responses to climate change by evaluating NPP estimates under doubled CO₂ and altered climate with vegetation distribution. First, we run TEM under control conditions, i.e. the contemporary climate and CO₂, and the contemporary vegetation distribution simulated by KBIOME. Then, we run TEM for the altered climates projected by the three GCM scenarios and
doubled CO₂, and the redistributed vegetation predicted by KBIOME under the same altered conditions.

In regard to the NPP resulting from the control run, NPP changes for ecosystems under altered conditions can be partitioned into two components: 1) a structural response which is caused by change in the area of ecosystem; and 2) a functional response which is caused by change of the mean NPP for an ecosystem type (VEMAP Members, 1995). The equation used to calculate the structural and functional responses of NPP is:

\[ \Delta NPP_i = NPP_{i2} - NPP_{i1} = R_{NPPi2} \times AREA_{i2} - R_{NPPi1} \times AREA_{i1} \]

\[ = (R_{NPPi1} + \Delta R_{NPPi}) \times (AREA_{i1} + \Delta AREA_i) - R_{NPPi1} \times AREA_{i1} \]

\[ = R_{NPPi1} \times \Delta AREA_i + \Delta R_{NPPi} \times AREA_{i1} + \Delta R_{NPPi} \times \Delta AREA_i \]

where, \( \Delta NPP_i \) is the NPP change in biome \( i \), caused by effects of altered conditions including changes in climate, \( CO₂ \) and vegetation; \( NPP_{i1} \) and \( NPP_{i2} \) represent NPP of biome \( i \) under control and altered conditions respectively; \( R_{NPPi1} \) and \( R_{NPPi2} \) represent the mean NPP (gC.m⁻².a⁻¹) of biome \( i \) under control and altered conditions; \( AREA_{i1} \) and \( AREA_{i2} \) are the areas occupied by biome \( i \) under control and altered conditions; \( \Delta AREA_i \) is the change in area for biome \( i \); and \( \Delta R_{NPPi} \) is the change in mean NPP for biome \( i \) resulting from altered conditions. In the equation, the term, \( R_{NPPi1} \times \Delta AREA_i \), represents the structural response of NPP whereas the term, \( \Delta R_{NPPi} \times AREA_{i1} \), represents the functional response of NPP.

4 Results

4.1 Characteristics of contemporary climate in China

The climate pattern in China is greatly influenced by the Mongolia-Siberia anticyclone and polar cold currents in winter, and the southeast warm and moist monsoon from the ocean in summer. Generally, weather is warm and moist in the southeast regions, and gradually becomes cold and dry towards the northwest inland. Annual mean temperature for China is about 5.8 °C, and annual precipitation is about 661 mm (Plate I). The Tibet-Plateau forms a special climate region because of its high elevation. The elevation of the Plateau is higher in the northwest and becomes lower down to the southeast. The weather is cold and dry in the north side of the Plateau, and cold and wet in the south side with moist air from the India Ocean. The southeast China is cloudier than the north and northwest China (Plate I).

4.2 Contemporary distribution of plant functional types

The vegetation simulated by KBIOME with contemporary conditions generally captured the pattern of vegetation distribution in China. The simulated vegetation distribution (Plate Ia) shows two gradients. One of them reflects a moisture gradient from east to west. Along this gradient, geographical zones gradually change from moist areas dominated by forests in the east, into semi-arid steppes of grasslands, and then to a large dry inland occupied by arid shrublands and desert in the west. The second gradient represents a temperature gradient from north to south. Along this gradient, vegetation changes from the boreal forests which dominate the northern region, to temperate conifer forests, temperate mixed forests, temperate deciduous forests in the middle latitude regions; to the temperate evergreen broadleaf forests further south; and finally to the tropical evergreen forests of South Island. The combination of the two gradients causes the actual distribution of vegetation belts to be more along a direction from the southeast to the northwest (Plate Ia). The Tibet-Plateau located in the southwestern region is dominated by tundra vegetation, typical of such alpine environments.

A model-induced misclassification of temperate broadleaf evergreen forests in southeast China (25-30° N of latitude) as the temperate deciduous forests (Plate Ia) is similar to that caused by using Holdridge system for classification (Zhang,
Southeast China, with a mean annual temperature of 14.7 °C and total annual precipitation from 1000-1800 mm, is relatively cold and dry in winter because of influences of the Mongolia-Siberia anticyclone and polar cold currents, and is very wet and hot in summer because of the influences of summer monsoons with no obvious drought season. As a result, evergreen woody plants in temperate climate are favored over deciduous woody plants whenever carbon and nutrient costs of replacing leaves annual exceed the costs of maintaining leaves during winter (Chapin et al., 1990). However, the climatic constraints in this region can only allow to grow temperate deciduous trees in KBIOME model. Another bias shown in the model prediction is that the forest zones in the eastern China are located more south than the observed. The summer monsoons have a large influence on the climate in eastern China. Summers are warm and moist with precipitation concentrated in growing season. The difference in temperatures between south and north is not significant. This climatic pattern benefits development of different forests and may move the boundaries of the forests more north than defined by the averaged climate.

4.3 NPP estimates under contemporary climate and CO2

TEM predicted that total annual net primary productivity (NPP) of terrestrial ecosystems of China is $3.83 \times 10^{18}$ g(Pg)C • a⁻¹ for contemporary environmental conditions with simulated vegetation types (Table 1). The potential NPP of the terrestrial ecosystems of China is about 7.6% of total global productivity of terrestrial ecosystems. Southeast China is the most productive region in the country (Plate II b). Temperate deciduous forests, temperate broadleaf evergreen forests and tropical evergreen forests combined have a potential NPP capacity of $2.53 \times 10^{18}$ gC • a⁻¹, which is about 67% of the total NPP while covering only about 30% of the total land area of China (Table 1, 2). In contrast, arid shrublands/desert and tundra in the northwest and southwest China cover 38% of the total land area, but only contribute 8% of the potential NPP of China.

4.4 Characteristics of climate change scenarios in China

Great variations in the changes in temperature, precipitation and cloudiness projected by the GCMs occur within the spatial domain of China (Xiao et al., 1998). For example, GISS predicted about 6.0 °C increase of temperature in the southeast, and about 3.0 °C in the southwest. In addition, precipitation increased more than 100% in the southwest, but decreased by 10% decrease in the southeast under the GISS scenario. Cloudiness also increased by 20% in the southwest, but decreased by 10% in the southeast. The spatial patterns also vary substantially among the GCMs scenarios (Xiao et al., 1998). The spatial patterns of the changes in the OSU scenario are less dramatic than in the other two scenarios. At the country level, the OSU scenario represents the lowest change in annual temperature (+2.9 °C), whereas GFDL-Q and GISS scenarios have larger increases (+4.1 °C and +4.2 °C). The three GCMs have similar increases in precipitation which are 16.3%, 15.5%, and 17.6% respectively for OSU, GFDL-Q and GISS, and have slight cloudiness decreases which are 0.2%, 1.0% and 1.2% for OSU, GFDL-Q and GISS (Xiao et al., 1998). The results projected from three GCMs indicate that CO2-induced climate change will generally lead to a warmer and moister China.

4.5 Vegetation redistribution with changed climate and CO2

In response to altered climate with doubled CO2, plant functional types will change their distributions (Plate II, Table 1). Indicated by the kappa statistic index, i.e. a larger value means a better agreement between the maps (Monserud, 1990), the OSU scenario has the smallest effect on vegetation change ($\kappa = 0.623$), whereas the GISS and GFDL-Q scenarios have a larger effect ($\kappa = 0.453$ and $\kappa = 0.487$, respectively) on vegetation redistribution.
Table 1  Biome areas under contemporary and altered climate and CO₂

<table>
<thead>
<tr>
<th>Biomes</th>
<th>Areas Contemporary (10⁵km²)</th>
<th>GFDL-Q (10⁵km²)</th>
<th>GISS (10⁵km²)</th>
<th>OSU (10⁵km²)</th>
<th>Area change</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>(%)</td>
<td>(%)</td>
<td>(%)</td>
<td>(%)</td>
</tr>
<tr>
<td>Alpine tundra</td>
<td>63.58</td>
<td>58.16</td>
<td>91.5</td>
<td>52.73</td>
<td>82.9</td>
</tr>
<tr>
<td>Moist tundra</td>
<td>1761.52</td>
<td>1788.24</td>
<td>44.7</td>
<td>493.52</td>
<td>28.0</td>
</tr>
<tr>
<td>Boreal forest</td>
<td>1063.48</td>
<td>1211.34</td>
<td>-19.8</td>
<td>17.67</td>
<td>-1.6</td>
</tr>
<tr>
<td>Temperate mixed forest</td>
<td>413.15</td>
<td>257.78</td>
<td>6.2</td>
<td>112.94</td>
<td>27.2</td>
</tr>
<tr>
<td>Temperate conifer forest</td>
<td>205.82</td>
<td>92.14</td>
<td>44.8</td>
<td>85.47</td>
<td>26.9</td>
</tr>
<tr>
<td>Temperate deciduous forest</td>
<td>1865.06</td>
<td>-892.73</td>
<td>47.9</td>
<td>-669.32</td>
<td>35.8</td>
</tr>
<tr>
<td>Tall grasslands</td>
<td>537.18</td>
<td>918.49</td>
<td>170.9</td>
<td>696.63</td>
<td>129.6</td>
</tr>
<tr>
<td>Short grasslands</td>
<td>778.36</td>
<td>-500.20</td>
<td>64.3</td>
<td>-342.23</td>
<td>-43.9</td>
</tr>
<tr>
<td>Tropic savanna</td>
<td>2.85</td>
<td>11.28</td>
<td>395.8</td>
<td>68.36</td>
<td>2398.5</td>
</tr>
<tr>
<td>Tropic evergreen forest</td>
<td>43.61</td>
<td>189.50</td>
<td>434.5</td>
<td>142.07</td>
<td>325.7</td>
</tr>
<tr>
<td>Tropic deciduous forest</td>
<td>22.84</td>
<td>80.46</td>
<td>352.2</td>
<td>11.51</td>
<td>50.3</td>
</tr>
<tr>
<td>Temp bl evergreen forest</td>
<td>975.62</td>
<td>995.92</td>
<td>102.1</td>
<td>-941.88</td>
<td>96.5</td>
</tr>
<tr>
<td>Total</td>
<td>9494.74</td>
<td>0.00</td>
<td>0.0</td>
<td>0.00</td>
<td>0.0</td>
</tr>
</tbody>
</table>

As predicted by the KBIOME model, total forested area increased by 8.4%, 8.7%, and 10.1% respectively for GISS, OSU and GFDL-Q scenarios. The model predicts the greatest gain in broadleaf forests with the loss in conifer forests under GISS scenario. However, the areas of both conifer and broadleaf forests increase under the OSU and GFDL-Q scenarios. Actually, the area of conifer forests in the northern area decreases in all scenarios as the result of the warming; however, the losses are balanced by gains of conifer forests in the Tibet Plateau for the OSU and GFDL-Q scenarios.

The simulations show major northward shifts of the eastern forest zones (Plate I a, Plate I b). The temperate broadleaf evergreen forests expand northward into the temperate deciduous forest region and partly or wholly replace the temperate deciduous forests while the deciduous forests replace most of the temperate mixed forests. The model predicts that the losses of the temperate deciduous forests are 12%, 36%, and 48%, and the gains of the temperate broadleaf evergreen forests are 46%, 97%, and 102% respectively under OSU, GIIS and GFDL-Q scenarios (Table 1). The losses in the temperate deciduous forests and the gains in the temperate broadleaf evergreen forests correspond to the temperature increase in the southeastern region. Tropical forests also extend their range from South Island to the southern border of the mainland under all GCM scenarios because of warming.

The model predicts that the area of grasslands also increases for all climate change scenarios with doubled CO₂. The grasslands increase by 25%, 27%, and 32% respectively under OSU, GISS and GFDL-Q climates by invading the western shrublands/desert (Plate I a, Plate I b). Increased grasslands also occur along the boundaries between the biomes of the northwestern shrublands/desert and the southwestern tundra under all GCM scenarios. The expansion of grasslands is primarily caused by the increase in precipitation. With the GFDL-Q scenario, the grasslands even expand northward into the boreal forests because of higher temperatures. Within grasslands, short grasslands tend to be converted to tall grasslands (Table 1) because warming favors tall grasslands.

The model predicts negative changes in the area extent of shrublands with all climate change scenarios and doubled CO₂. Shrublands decrease by 3%, 8%, and 15% respectively under the GFDL-Q, OSU and GIIS climates (Table 1). As mentioned earlier, the shrublands are replaced by
grasslands because grasses are more competitive than shrubs under improved moisture conditions. The area extent of the tundra biomes in the Tibet Plateau is also diminished, as predicted, by 30%, 32%, and 46% under the GISS, OSU and GFDL-Q scenarios, respectively (Table 1). On the eastern edge of the Plateau, some tundra vegetation is converted to conifer forests and temperate mixed forests. Tundra is also replaced by conifer forests in the interior areas of the Plateau. These changes are primarily caused by increased temperatures in the Plateau.

4.6 NPP response to climate change and doubled CO₂

4.6.1 Response at country scale

The total response of NPP at the country-scale is calculated by subtracting the NPP estimate for contemporary climate at 312.5 ppmv CO₂, from that for the future climate (GCM scenarios) at doubled CO₂. The TEM simulations were all based on the vegetation distribution simulated by the KBIOME under different conditions. The total NPP response to changed climate and doubled CO₂ is positive for all GCM scenarios. The total NPP increases 1.114 PgC · a⁻¹ for GISS, 1.214 PgC · a⁻¹ for OSU and 1.281 PgC · a⁻¹ for GFDL-Q scenario (Table 2); i.e. +29%, +32% and +33%, respectively.

Changes in climate and atmospheric CO₂ concentration affect both function and structure of ecosystems. The functional change is direct and rapid and has an influence on structural change. The latter, in turn, further alters the functional response to changed climate and CO₂ (Melillo et al., 1996). As described earlier, the NPP response can be partitioned into a structural response and a functional response depending on changes in area extent of ecosystems and changes in mean NPP for an ecosystem type (VEMAP Members, 1995). At the country-scale, TEM predicted that NPP has the smallest structural response (+11%) and the largest functional response (+21%) under the OSU scenario. In contrast, NPP has the largest structural responses (+17%) and the smallest functional response (+12%) under the GISS scenario. Both the NPP structural response (+15%) and functional responses (+19%) are moderate under the GFDL-Q scenario (Table 2). The positive functional responses of NPP at the country-level indicate that changed climate and CO₂ generally are beneficial to NPP of terrestrial ecosystems in China. The positive structural responses of NPP at country-level indicate that higher NPP ecosystems have expanded at the expense of low NPP ecosystems (VEMAP Members, 1995).

<table>
<thead>
<tr>
<th>Biomes</th>
<th>Control</th>
<th>GFDL-Q</th>
<th>GISS</th>
<th>OSU</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Annual NPP (Tg C · a⁻¹)</td>
<td>Total (Tg C · a⁻¹)</td>
<td>Function Structure (%)</td>
<td>Total (Tg C · a⁻¹)</td>
</tr>
<tr>
<td>Alpine tundra</td>
<td>1.9</td>
<td>-1.5</td>
<td>+7.3</td>
<td>-91.4</td>
</tr>
<tr>
<td>Moist tundra</td>
<td>180.7</td>
<td>-42.8</td>
<td>+21.1</td>
<td>-44.8</td>
</tr>
<tr>
<td>Boreal forest</td>
<td>288.3</td>
<td>+23.7</td>
<td>+5.8</td>
<td>+2.5</td>
</tr>
<tr>
<td>Temperate mixed forest</td>
<td>275.1</td>
<td>+9.2</td>
<td>+9.6</td>
<td>-6.2</td>
</tr>
<tr>
<td>Temperate conifer forest</td>
<td>91.5</td>
<td>+60.5</td>
<td>+21.4</td>
<td>+44.8</td>
</tr>
<tr>
<td>Temperate deciduous forest</td>
<td>1528.1</td>
<td>-595.8</td>
<td>+8.9</td>
<td>-47.9</td>
</tr>
<tr>
<td>Tall grasslands</td>
<td>122.3</td>
<td>+290.5</td>
<td>+64.5</td>
<td>+173.0</td>
</tr>
<tr>
<td>Short grasslands</td>
<td>158.5</td>
<td>-101.5</td>
<td>+0.2</td>
<td>-64.3</td>
</tr>
<tr>
<td>Tropic savanna</td>
<td>1.6</td>
<td>+7.9</td>
<td>+92.2</td>
<td>+395.7</td>
</tr>
<tr>
<td>Arid shrublands</td>
<td>128.7</td>
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<td>+41.2</td>
<td>-3.3</td>
</tr>
<tr>
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<td>+125.3</td>
<td>+434.6</td>
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<td>+352.2</td>
</tr>
<tr>
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<td>+1296.2</td>
<td>+27.2</td>
<td>+102.1</td>
</tr>
<tr>
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<td>+1281.3</td>
<td>+18.6</td>
<td>+14.8</td>
</tr>
</tbody>
</table>
4.6.2 Response at biome scale

At the biome scale, large NPP increases occur in temperate broadleaf evergreen forest (674 to 1296 Tg C \( \text{a}^{-1} \)), tall grasslands (207 to 290 Tg C \( \text{a}^{-1} \)) and tropical evergreen forests (139 to 200 Tg C \( \text{a}^{-1} \)) under all three GCM scenarios. The NPP increases in these biomes are primarily caused by area expansion (Table 1, 2). The temperate broadleaf evergreen forests, which are currently the most productive ecosystems with a modeled annual mean NPP of 1027 gC \( \text{m}^{-2} \cdot \text{a}^{-1} \), have a dominant influence on the NPP response at the country-level. The substantial NPP increases in this biome are attributed to the large expansions of the biome area under all GCM scenarios and are reflected by great positive structural responses of NPP (Table 1). The expansion of this biome is smallest under OSU scenario and therefore causes the smallest structural response of NPP, i.e., less than half of the structural responses in comparison to the other two scenarios. As a result, the OSU scenario also has the smallest structural responses of NPP at the country-level.

The biomes with decrease in NPP include tundra and short grasslands under all GCM scenarios (Table 1, 2). These decreases are caused primarily by the losses of area extent as indicated by the negative structural responses. The temperate deciduous forests decrease substantially in NPP under the GISS and GFDL-Q scenarios, but increase in NPP under the OSU. The KBIOME predicts area losses of temperate deciduous forests for all GCM scenarios. But, changes in climate and CO\(_2\) still benefit NPP for the remaining forests and cause the positive functional responses of NPP.

The positive functional NPP response for the temperate deciduous forests is not entirely compensated by the negative structural response to the OSU climate (+357 TgC \( \text{a}^{-1} \) vs. -163 TgC \( \text{a}^{-1} \)) in contrast to the other two scenarios (Table 2). In addition, the functional and structural responses of NPP in different biomes may enhance or offset each other, as a result of the spatial variations of the GCM scenarios. Generally, most biomes have a positive functional response for all climate change scenarios (Table 2). This indicates that future climate change and doubled CO\(_2\) generally favor C uptake for all biomes although some biomes may decrease their area extent under the new equilibria of environmental conditions. Structural responses generally overwhelm the functional responses for most biomes (Table 1). This shows that changes in regional NPP are generally more influenced by changes in the area extents of biomes than by the direct effects of climate change and doubled CO\(_2\).

4.6.3 Response at grid-cell scale

At the grid-cell scale, NPP responses are positive in most regions of China under all three GCM scenarios (Plate IV, Plate V). The NPP responses at a grid-cell level reflect the direct effects from climate change and doubled CO\(_2\) if vegetation types remain the same; otherwise, the responses reflect effects from changes in climate, CO\(_2\) and vegetation types. Relative NPP responses are generally greater in cold and dry biomes (tundra, arid shrublands) with very low (about 70-100 gC \( \text{m}^{-2} \cdot \text{a}^{-1} \)) primary production. The warmer and wetter climates under the three GCM scenarios directly enhance growth and soil decomposition. As a result, NPP in tundra biomes increases because of more favorable climate conditions elevated CO\(_2\) and improved nitrogen supply (Melillo et al., 1993). In the northwestern arid shrublands, the increase in relative NPP is more likely caused by the effect of elevated CO\(_2\). Although precipitation increases to different extents under the GCM scenarios in most of the northwestern dry region, some of this area suffers a severe drought under the GFDL-Q climate due to a precipitation decrease. The increased temperature in this region under all scenarios may also exacerbate the drought in the region. However, because elevated CO\(_2\) increases water use efficiency of plants in areas experiencing water stress (Mooney et al., 1993), the NPP is increased in the arid northwest.

Although relative increases of NPP are generally greater in the western China (Plate V), abso-
lute increases of NPP are greater in the eastern China (Plate N). The TEM estimates that the NPP increases are most substantial (200 to 600 g C·m⁻²·a⁻¹) in the forests of southeast China, which are currently the most productive ecosystems. However, spatial patterns of enhanced NPP vary among GCM scenarios. The smallest increase of NPP in this region occurs for the GISS climate because it is relatively the hottest and driest scenario in the southern China, which is less favorable to enhancing NPP. In general, the large NPP increases in this region are due to several possible factors: 1) more favorable conditions predicted by the GCMs; 2) elevated CO₂; and 3) the transition of less productive vegetation types to more productive ones.

5 Discussion
5.1 NPP and vegetation responses to changed conditions

The three GCM scenarios considered in this study all suggest a warmer and generally wetter climate in China’s future. The coupled models predicted significant responses of terrestrial ecosystem structure and function. The vegetation transition is shown as: 1) a northward shift of the forest zones in eastern China, with an expansion in the temperate broadleaf evergreen forests, and the replacement of northern forests by more south types; and 2) increases in the total forested areas and grasslands at the expense of arid shrublands, desert and tundra. The redistribution of plant functional types under changes in climate and CO₂ predicted in this study are generally consistent with similar studies for China (Zhang, 1993; Wang & Zhao, 1995).

The coupled models estimate that net primary productivity of all terrestrial ecosystems will increase around 30% with the new climate equilibria and doubled atmospheric CO₂. We are able to partition NPP responses into functional and structural components. We can figure out that the increase in NPP is partially due to the positive functional response of NPP (12%-21%) resulting from changed climate and doubled CO₂, and partially due to the positive structural response of NPP (11%-17%) associated with the vegetation transition from less productive ecosystems to more productive ecosystems.

5.2 Comparisons with other studies

The results from this study indicate that both structural and functional changes of terrestrial ecosystems significantly affect NPP in terrestrial ecosystems. Therefore, two types of models (i.e. biogeography models and biogeochemistry models) are equally important in their abilities for accurate simulations. With the current climate and CO₂ concentration, the vegetation distribution simulated by KBIOME presents a fair agreement with observed vegetation (κ = 0.423). This agreement is obviously lower than the results from simulations (VEMAP Members, 1995) of other biogeography models for the conterminous U. S. (κ > 0.69). The better agreement in modeling the U. S. vegetation distribution was achieved by tuning the models in both ecophysiological and resource constraints to the regional conditions. However, the vegetation simulation by KBIOME for China was derived from the model’s global simulation. Therefore, the model is lack of adjustments for the special regional complexity.

With the three GCM projected climate scenarios under doubled CO₂(612 ppmv), TEM estimates a greater NPP response with simulated vegetation redistribution (29%-33%) than with fixed natural vegetation types (19%-23%) at the country-level (with 519 ppmv CO₂)(Xiao et al., 1998). About 10% higher NPP seems to be due to the vegetation changes and the higher CO₂ concentration, both appear to be responsible for the additional NPP response.

To compare other modeling exercise done for the conterminous U. S. using TEM and BIOME2 (an updated version of BIOME, Haxeltine and Prentice (1996) under the OSU, GFDL-R30 and UKMO climate scenarios and doubled CO₂ (710 ppmv), the estimated NPP increases of 26% to 35% with the fixed potential vegetation types, and
27% to 39% with the BIOME2 simulated vegetation redistribution; the difference seems only up to 4%. The structural response of NPP ranges from −4% to 12%, and functional response from 27% to 31%. To compare the NPP predictions at the two continents, structural response plays a greater role in China than in the U.S., while the functional response plays a greater role in the U.S. than in China. In China, KBIOME predicted the area expansion of forests (+8% to +10%) and grasslands (+25% to +32%), and the reduction of tundra (−30% to −46%) and shrublands/desert (−3% to −15%) for the GCM scenarios with doubled CO₂. The replacement of less productive tundra and shrublands/desert by more productive forests and grasslands accounts for the large structural response of NPP in China. In contrast, BIOME2 predicted forest increase only under the GFDL-R30 climate (+10%) in the conterminous U.S. Under the OSU and UKMO climates forests decreased by 14% (VEMAP Members, 1995). BIOME2 also predicted eastward extension of grasslands or savanna into the eastern broadleaf forests for all scenarios. As a result, there are slightly negative structural responses of NPP except for the GFDL-R30 climate that has a positive structural response (12%). Improved N availability caused by warming (+3 °C to +6.7 °C) may have also contributed to the greater role of the functional response. The different NPP response patterns in the two continents illustrate the spatial variability projected by the global GCMs.

5.3 Sensitivities of structural and functional responses

The vegetation distributions simulated by the KBIOME are sensitive to changes in climate and CO₂; and the NPP estimated by TEM sensitive to changes in climate, CO₂; and vegetation. However, the various spatial patterns among the three GCM climates in China do not seem to affect the general patterns of vegetation redistribution and NPP response. An overall warming in all GCM scenarios, despite the different extents and distributions, shifts the boundaries of all forests northward because temperature is a key ecophysiological constraint in determining the distribution of woody plants (VEMAP Members, 1995). In addition, a generally wetter conditions in all the GCM scenarios change the boundaries of grasslands, shrublands, and tundra because water availability is an important limiting resource that determines the major distribution of vegetation. Although drier conditions occur in the center of northwestern China and along the southern coast with GFDL-Q climate, and in southern China with GISS climate, these changes have no effect on the vegetation types in the northwest desert, or the forest boundaries in the south. Therefore, the general patterns of vegetation redistribution are quite consistent under the three scenarios, such that the structural response of NPP estimated by TEM is quite similar for the three climate change scenarios.

The great variations in the GCM climates may influence effectively the functional responses of NPP. However, in TEM, doubled CO₂ mitigates divergence in NPP estimates caused by climate change only (Xiao et al., 1998; VEMAP Members, 1995). There is a strong interaction between elevated CO₂ and climate responses that enhance NPP and carbon storage in TEM estimates. Thus, the NPP response patterns under changed climates at doubled CO₂ are less diverse than the GCM scenarios illustrate.

5.4 Coupled models

In this study, we used one pair of model (KBIOME and TEM) for the model coupling experiments and got the consistent predictions of the country-level responses under the three GCM scenarios. In VEMAP (VEMAP Members, 1995), three biogeography models and three biogeochemistry models were used to generate 9 pairs of “coupled models” for predicting NPP responses in the conterminous U.S. under the three GCM scenarios. Their results show that total NPP responses for the conterminous U.S. range from 0% to 40% with functional responses ranging from −22% to 31%, and structural responses ranging from −4% to 28%. The uncertainties in model
predictions may come from several sources: 1) differences in the GCM projected scenarios; and 2) differences in model assumptions used to describe ecosystem structure and function by the biogeography and the biogeochemistry models (VEMAP Members, 1995). More comparison work with alternative biogeography and biogeochemistry models may be needed to study China so that we can document the uncertainty related to differences in the conceptualizations of controls over structure and function of China’s vegetation.

5.5 Limitations in this study

Our study on the effects of climate change and elevated CO₂ on terrestrial ecosystems in China have several limitations. First, the simulations only make projections about steady-state or equilibrium conditions that are hypothesized to exist today and at some time in the future with doubled CO₂ and altered climate. However, the increasing concentration greenhouse gases and the response of climate system to the associated radiative forcing occur dynamically. Functional changes could be rapid and directly correspond to the changes in climate and CO₂, however, the structural changes may occur over a longer period and not keep pace with rapid environmental change (Melillo et al., 1996). Interactions between ecosystem structure and function through time will cause NPP responses that could not be predicted by the equilibrium analysis in this study. The coupling of biogeography and biogeochemistry in this study is only unidirectional without any type of feedback between ecosystem structure and function, and obviously not realistic. The development of comprehensive dynamic ecosystem models (DEMOs), which can realistically link ecosystem structure and function dynamics with all interactions and information exchanges and incorporate transient dynamics, are critical goals in study of terrestrial ecosystem response to climate changes (VEMAP Members, 1995). Several comprehensive ecological models have been developed recently (Woodward et al., 1995; Foley et al., 1996, Daly et al., 2000). However, the models, which are sophisticated enough to include all important vegetation processes and biogeochemical processes, are still far from complete at this stage.

Another limitation presented in this China study is that our results pertain only to potential vegetation so that agricultural areas which currently occupy about 11% of the total land area and an even larger percentage in the highly productive southeastern part of China have not been considered in this study. The issues of incorporating actual land cover types and developing crop models for agriculture lands should be considered in the future model experiments. These issues are especially crucial for making realistic regional predictions in countries with intensive land-use such as China and India.

6 Conclusions

Although several limitations exist, this study presents the preliminary estimates of a range of vegetation changes and NPP responses under potential future climate equilibria in China. Geographically-referenced biogeography and biogeochemistry models are shown as useful tools in examining spatial patterns of distribution in vegetation and other important functional variables (e.g. NPP), and integrating ecological information at different scales. The KBIOME is more advanced than models which are only based on correlations with environmental constrains such as Holdridge Scheme; and TEM is more robust than statistically-based models for predicting ecological responses under the novel environmental conditions. The coupling of the models enabled us to investigate two aspects of ecological responses simultaneously, and evaluate how the vegetation change can affect ecosystem NPP with a spatial perspective. Such analyses are not usually done because biogeography models and biogeochemistry models have been generally developed independently and focused on different interests. Future improvements on this China study will rely on model development and data refinement. A transient version of TEM (4.1 version) has been completed and tested.
in a few experiments (Melillo et al., 1996; McGuire et al., 1997; 2000). Linking the transient TEM with a dynamic vegetation model (DVM), TEM-DVM, is in an early stage of development and will be used for a future China study. With the cooperation of Chinese colleagues, we expect to calibrate TEM using data from intensively studied sites in China provided by the Chinese Ecosystem Research Network (CERN). This network includes 45 long-term experimental stations representing major terrestrial ecosystem types in China. The new parameterizations of TEM will help improve the accuracy of the simulations of NPP and other biogeochemical variables for terrestrial ecosystems of China.

References


### Explanation of plates

**Plate I** Contemporary distributions of (a) annual mean temperature (°C), (b) total annual precipitation (mm), and (c) annual mean cloudiness (%).

**Plate I** The contemporary (a) vegetation distribution simulated by KBIOME, (b) net primary production (g C·m$^{-2}$·a$^{-1}$) simulated by TEM.

**Plate II** Vegetation redistributions under GFDL-Q, GISS, and OSU climate scenarios, simulated by the model KBIOME.

**Plate IV** Responses of NPP (gC·m$^{-2}$·a$^{-1}$) to changes in climates (GFDL-Q, GISS and OSU scenarios) and doubled atmospheric CO$_2$.

**Plate V** Responses of NPP (%) to changes in climates (GFDL-Q, GISS and OSU scenarios) and doubled atmospheric CO$_2$.