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Sensitivity of potential natural vegetation in China to projected changes in temperature, precipitation and atmospheric CO_2

Han Wang · Jian Ni · Ian Colin Prentice

Abstract A sensitivity study was performed to investigate the responses of potential natural vegetation distribution in China to the separate and combined effects of temperature, precipitation and [CO_2], using the process-based equilibrium terrestrial biosphere model BIOME4. The model shows a generally good agreement with a map of the potential natural vegetation distribution based on a numerical comparison using the ΔV statistic ($\Delta V = 0.25$). Mean temperature of each month was increased uniformly by 0–5 K, in 0.5- or 1-K intervals. Mean precipitation of each month was increased and decreased uniformly by 0–30%, in 10% intervals. The analyses were run at fixed CO_2 concentrations of 360 and 720 ppm. Temperature increases shifted most forest boundaries northward and westward, expanded the distribution of xeric biomes, and confined the tundra to progressively higher elevations. Precipitation increases led to a greater area occupied by mesic biomes at the expense of xeric biomes. Most vegetation types in the temperate regions, and on the Tibetan Plateau, expanded westward into the dry continental interior with increasing precipitation. Precipitation decreases had opposite effects. The modelled effect of CO_2 doubling was to partially compensate for the negative effect of drought on the mesic biomes and to increase potential ecosystem carbon storage by about 40%. Warming tended to counteract this effect, by reducing soil carbon storage. Forest biomes showed substantial resilience to climate change, especially when the effects of increasing [CO_2] were taken into account. Savannas, dry woodland and tundra biomes proved sensitive to temperature increases. The transition region of grassland and forest, and the Tibetan plateau, was the most vulnerable region.

Keywords Biogeography model · Sensitivity analysis · Climate change · CO_2 fertilization · Carbon storage · China

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Introduction

Temperature and precipitation play decisive roles in controlling the distribution of vegetation on large spatial scales. Heat and moisture are requirements for plant life and are the key factors that select for diverse plant traits and life forms (Harrison et al. 2010). Other environmental factors, including topography, disturbance and herbivory, with non-negligible effects on plants at fine spatial scales are overwhelmed by the combined effects of temperature and moisture in controlling the structure and physiognomy of the regional vegetation. Because of this fundamental fact, large-scale models for vegetation distribution—from the empirical world climate zones of Köppen (1931) to dynamic global vegetation models (Prentice et al. 2007) based on ecophysiological mechanisms—are based on temperature and precipitation as key environmental inputs.

The anthropogenic [CO$_2$] increase is expected additionally to alter the distribution of vegetation both indirectly through its influence on global temperatures and precipitation patterns and directly through the physiological effects of [CO$_2$]. These arise because of the essential role of CO$_2$ as the substrate for photosynthesis. Over the past 0.8 million years, [CO$_2$] varied between warm interglacial periods with maxima of 280–300 ppm and cool glacial periods with minima of 170–200 ppm (Siegenthaler et al. 2005; Lüthi et al. 2008; Prentice and Harrison 2009). Since the Industrial Revolution, however, [CO$_2$] has been increasing close to exponentially and has recently exceeded 390 ppm (http://www.esrl.noaa.gov/gmd/ccgg/trends/). CO$_2$ is the anthropogenic greenhouse gas with the highest radiative forcing (Forster et al. 2007) and is thus principally responsible for continuing global climate change (Parry et al. 2007) with consequences for species and ecosystems (Fischlin et al. 2007). On the other hand, (a) the capacity of C$_3$ plants to fix CO$_2$ through photosynthesis is not saturated even at the current atmospheric concentration and (b) stomatal behaviour ensures that plants conserve water more effectively at higher CO$_2$ concentrations. Thus, physiological CO$_2$ effects can influence the growth and competition of different plant functional types (PFTs) and thereby influence vegetation productivity, competition, structure and biome boundaries. Free Air Carbon dioxide Enrichment (FACE) experiments demonstrate the direct effect of CO$_2$ on productivity (Norby et al. 2005), while evidence from the last glacial maximum has been used to show its effects at the level of vegetation compositional changes and biome shifts (Bond et al. 2003; Harrison and Prentice 2003; Prentice and Harrison 2009; Prentice et al. 2010). Nevertheless, the extent to which physiological effects of CO$_2$ influence vegetation is more controversial (e.g. Fischlin et al. 2007) than the effects of temperature and precipitation, because the latter are directly observable on the modern landscape.

Several national-scale studies (Ni et al. 2000; Ni 2003; Fang et al. 2003; Piao et al. 2009; Piao et al. 2010a, b) have analysed the patterns of vegetation and vegetation function across China. It has been estimated that Chinese vegetation served as a net carbon sink of atmospheric CO$_2$ during the 1980s and 1990s at a rate of 0.19–0.26 PgC year^{-1} (Piao et al. 2009). Fang et al. (2003) and Piao et al. (2005) showed a positive response of China's terrestrial net primary productivity (NPP) to increases in temperature, precipitation and [CO$_2$]. Piao et al. (2010a) summarized the trends of climate change in the recent decades and their possible impacts on agriculture. However, to date, few studies have been conducted to investigate the potential for future climate change and further increases in [CO$_2$] to impact on natural vegetation structure, distribution and properties. Analyses have been either focused on particular

regions (Ni 2000a; Song et al. 2005) or have limited in the scope of scenarios they consider (Gao et al. 2000; Ni et al. 2000). Gao et al. (2000) analysed the response of terrestrial ecosystems in China to eight climatic scenarios involving perturbations from the present climate with [CO$_2$] doubling, year-round warming by 2 K and year-round increasing precipitation by 20%. Here, we use a well-established global vegetation model, BIOME4, to assess the potential for combined impacts of different degrees of climate and [CO$_2$] change to influence vegetation structure across the country. We test the present-day BIOME4 simulation against the potential natural vegetation distribution using the ΔV statistic (Sykes et al. 1999) to indicate the reliability of the simulation. Projections of the carbon cycle and climate change during the 21st century have indicated an increase in [CO$_2$] to between 540 and 970 ppm under different scenarios from the IPCC Special Report on Emissions Scenarios (Nakicenovic et al. 2000), a rise in mean annual temperature of 0.5–7.5 K, increases in both winter and summer precipitation in most part of China, but a decrease in precipitation in some parts of the interior (Cruz et al. 2007). Piao et al. (2010a) noted that although climate models have generally projected increases in precipitation in northern China, the recent historical trend has actually been a decline. To reflect the broad possible range of outcomes, we show results from running BIOME4 with temperature increased stepwise in the range of 0.5–5 K and precipitation either increased or decreased in the range of 10–30%. We compare the geographical range and area occupied by each vegetation type between imposed and current climate conditions. The simulations are performed under both recent and doubled [CO$_2$] to bracket the range of possibilities. The analysis under current [CO$_2$] can be regarded as an extreme sensitivity experiment in which it is hypothesized that the plants derive no benefit from increased [CO$_2$]. The analysis under doubled [CO$_2$] represents the assumption that [CO$_2$] reaches a high level and that the response of plants is as modelled in BIOME4.

Methods

The BIOME4 model

BIOME4 (Kaplan 2001) is a development from the BIOME3 model of Haxeltine and Prentice (1996). BIOME4 uses a small set of bioclimatic constraints to select potential PFTs under a given climate condition. The particular traits of each PFT, together with physical soil properties and atmosphere CO$_2$ concentration, are used to capture key plant physiological processes including photosynthesis, stomatal behaviour and transpiration. Competition between

PFTs is simulated implicitly, as a function of relative values of NPP. An optimization algorithm is used to calculate the maximum sustainable leaf area index (LAI) of each PFT and its associated NPP. Based on the competition results, the most successful and second most successful PFT and their sustainable LAI are used to generate an assignment of each model grid cell to a biome, based on a set of semi-empirical rules.

BIOME4 predicts the distributions of 27 biomes altogether (tropical evergreen rainforest, tropical semi-deciduous forest, tropical deciduous forest, warm-mixed forest, temperate deciduous forest, temperate conifer forest, cool mixed forest, cool conifer forest, cold mixed forest, evergreen taiga/mountain forest, deciduous taiga/mountain forest, tropical savanna, temperate sclerophyll woodland, temperate broadleaved savanna, open conifer woodland, tropical xerophytic shrubland, temperate xerophytic shrubland, tropical savanna, temperate savanna, temperate grassland, desert, barren, graminoid-forb tundra, shrub tundra, dwarf shrub tundra, prostrate shrub tundra and cushion forb-lichen-moss tundra). These have been grouped here into nine mega-biomes (Harrison and Prentice 2003): tropical forest, warm-temperate forest, temperate forest, boreal forest, savanna and dry woodland, grassland and dry shrubland, desert, dry tundra and tundra. For simplicity of analysis, we use these mega-biomes to represent vegetation types in China, following the assignment scheme used by Harrison and Prentice (2003). We made a single amendment to the model: in order to capture more accurately the boundary of tundra and forest vegetation on the Tibetan Plateau, we set a minimum heat requirement for boreal evergreen and boreal deciduous trees at 500 growing degree days (5°C base), similar to the criterion imposed in the LPJ dynamic global vegetation model (Sitch et al. 2003). BIOME4 accurately simulates polar treelines without this criterion (based on low-simulated NPP of woody vegetation types beyond the treeline), but tends to overestimate the elevation of alpine treelines at lower latitudes. Thus, reliance on an NPP criterion alone is probably too simple, as in reality trees must have sufficient warmth as well as an adequate carbon balance for net growth (Harrison et al. 2010).

Input data

Model inputs are [CO_2] (one global value), monthly means of three climate variables (temperature, precipitation and "cloudiness" or more precisely the percentage of possible hours of bright sunshine) and soil texture data for all grid cells located by latitude and longitude coordinates. The model was run at 0.1° resolution.

Baseline climate input data were generated from interpolated climate records of mean monthly temperature, precipitation and percentage of possible sunshine hours from 1814 meteorological stations (740 stations have observations from 1971–2000 and the rest from 1981–1990, China Meteorological Administration unpublished data) using three-dimensional thin-plate spline interpolation (ANUSPLIN version 4.36, Hutchinson and Hancock 2006). Soil data (available water holding capability and percolation index) were derived from the Food & Agriculture Organization digital soil map of the world obtained by reading directly from Reynolds global soils data set (Reynolds et al. 1999) at 0.1° resolution. [CO_2] was fixed at 360 or 720 ppm.

Sensitivity experiments

Mean temperature of each month was increased uniformly up to a warming of 5 K, in 0.5 intervals from the baseline condition to 2 K and in 1-K intervals from 2 to 5 K. Mean precipitation of each month was both increased and decreased uniformly by up to 30% in 10% intervals. The percentage area change (i.e. the simulated increase or decrease in area occupied by a mega-biome under a given climate-[CO_2] scenario, relative to the simulated area occupied under recent climate and [CO_2]) is used to indicate the sensitivity of that mega-biome to changes in climate and [CO_2].

Model testing

The potential distribution of natural vegetation derived from the 1:1 million vegetation map of China (Hou 2001) was used to test the biogeographic simulation with BIOME4 using the ΔV statistic to compare data and model results. The 573 actual vegetation types in the vegetation map were re-assigned to the 27 potential biome types in the model according to floristic and bioclimatic criteria. Cultivated vegetation types were assigned to potential natural vegetation using bioclimatic criteria. The dissimilarity between data and model at each grid point (ΔV value) was measured using the attribute-based method introduced by Sykes et al. (1999) based on the relative importance of different plant life forms in each biome and attributes of each life form with a weight for each attribute. Grid-point ΔV values were area-weighted and averaged to form a whole-region ΔV value. This value indicates the dissimilarity between two maps and ranges from 0 (perfect agreement) to 1 (nothing in common). The definitions of plant life forms and attributes, and the assignment of importance values, attribute values and attribute weights, are based on the study by Ni et al. (2000) with minor extensions to deal with the change from BIOME3 as used by Ni et al. (2000) to BIOME4. For those model grid cells containing vegetation types classified to more than one biome, we selected the biome with the smallest ΔV.

Estimation of potential carbon storage

Although many estimates of terrestrial carbon storage change have been made by assigning fixed vegetation and soil carbon per unit area to each biome (e.g. Ni 2000a, b for China), such estimates overlook climate-dependent variation within biomes and exclude a priori any effect of CO_2 concentration on carbon storage (Prentice and Harrison 2009). Here, we use a simple alternative method to estimate the potential (steady-state) carbon storage from BIOME4. The method incorporates the influence of climate and CO_2 on productivity and the influence of temperature on soil decomposition rate.

Consistent with the assumption of steady state in BIOME4, we consider the rate of carbon transfer from vegetation to soil by litter production and that from soil organic matter to atmosphere by decomposition both to be equal to NPP, which is the rate of carbon transfer from atmosphere to vegetation. The sizes of the vegetation (C_{veg}) and soil carbon (C_{soil}) pools in steady state are then determined by NPP and the rates of turnover of these pools, expressed as turnover times (τ_{veg}, τ_{soil}):

$$C_{veg} = NPP.\tau_{veg} \tag{1}$$

$$C_{soil} = NPP.\tau_{soil}. \tag{2}$$

The turnover time of vegetation carbon is controlled above all by the vegetation type, while that for soil carbon is strongly influenced by temperature. Carbon storage of vegetation and soil under recent climate and [CO_2] conditions has been estimated from published field measurements (Yang et al. 2008; Li et al. 2004; Ni 2003, 2004; Zhou et al. 2003; Wu et al. 2003; Luo et al. 2002; Ni et al. 2001; Jiang et al. 1999; Fang et al. 1998). We assigned typical values for each mega-biome (Table 1) and calculated their turnover times from Eqs. 1 and 2 using the average-simulated NPP for each mega-biome. τ_{veg} is

treated as constant for a mega-biome, since it is assumed to depend mainly on the life history of the plants. τ_{soil} is assumed to depend on temperature, with a multiplier given by exp $[-k(T - T_{ref})]$ where T is the temperature and T_{ref} is the reference temperature. We use the new global generic estimate of $k = 0.034$, which corresponds to a Q_{10} of 1.4 (Mahecha et al. 2010). For each scenario, we thus calculate the total carbon storage in vegetation and soil for each mega-biome and for all mega-biomes together, using the simulated NPP, constant τ_{veg} and temperature-dependent τ_{soil}.

Results

ΔV statistic

Under present climate, BIOME4 simulates the occurrence of 25 biomes in China (all of the 27 possible, except for open conifer woodland and tropical grassland). Comparison of predicted mega-biome distributions (Fig. 1) with their observed natural equivalents (Fig. 2) shows general agreement, with a ΔV value of 0.25 calculated as described previously. The model captures most biome distributions and boundaries accurately. The model predicts a large area in the subtropical zone with warm-temperate forest, transitioning southward to tropical forest along the south coast of China and northward to temperate forest in the wetter part of the temperate zone. It successfully captures the desert boundary although the mosaic nature of the distribution of deserts and grasslands in the transition zone between them is lost. In comparison with the simulation with BIOME3 (Ni et al. 2000), it simulates temperate deciduous forest more accurately, although it still shows a tendency to underestimate the extension of temperate forests to the north and west. It also simulates the

Table 1 Typical values of carbon storage for Chinese mega-biomes, based on a synthesis of published measurements

Mega-biome	C_{veg} (kgCm^{-2})	C_{soil} (kgCm^{-2})	Ratio (−)	NPP (kgCm^{-2} year^{-1})	τ_{veg} (year)	τ_{soil} (year)
Tropical forest	34	9	0.26	1.40	24	6
Warm-temperate forest	18	10	0.56	1.22	15	8
Temperate forest	9	13	1.40	0.88	10	15
Boreal forest	12	23	1.90	0.46	26	50
Grassland/dry shrubland	2	8	4.00	0.52	4	15
Savanna/dry woodland	4	14	3.50	0.98	4	14
Desert	1	2	2.00	0.11	9	18
Dry tundra	4	5	1.30	0.20	20	25
Tundra	4	12	3.00	0.35	11	34

C_{veg} and C_{soil} are carbon storages in vegetation and soil, respectively. Ratio = C_{soil}/C_{veg} = τ_{soil}/τ_{veg} where the τ are turnover times, calculated using Eqs. 1 and 2 with net primary productivity (NPP) as simulated by BIOME4 under recent climate and [CO_2]

Fig. 1 Mega-biomes simulated under recent [CO_2] and six climatic scenarios
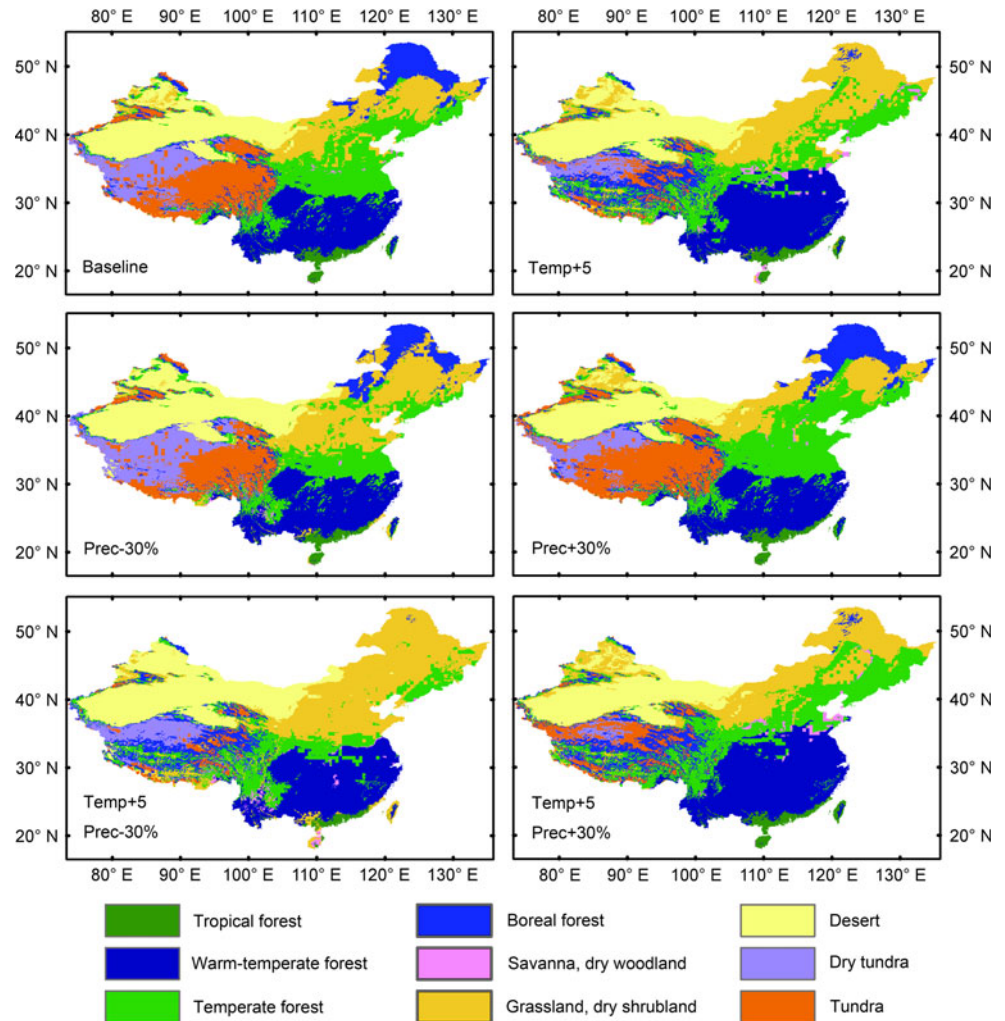

distinctive dry tundra and tundra biomes above the elevational treeline in the Tibetan Plateau. (Note that we use the terms tundra and dry tundra here consistently with the usage in BIOME4 and other global models and maps to include treeless alpine vegetation types such as those occurring on the Tibetan Plateau, although they have usually been classified differently in the Chinese literature). The boundary between tundra and dry tundra is less well captured. This may be a matter of definition—in any case, the model correctly predicts the dominance of dry tundra in the north-western part of the plateau.

Sensitivity study

Increasing temperature shifts most forest boundaries northward and westward, expands the distribution of savanna, dry woodland, grassland, dry shrubland and desert and confines tundra on the Tibetan Plateau to progressively higher elevations (Fig. 1). Except for tropical rainforest, most forest biomes in China are simulated to experience a substantial shift in their distribution. When temperature

increases by as much as 5 K, warm-temperate forest moves its northern boundary forward from the Yangtze River almost to the Yellow River (Fig. 3) and moves up to higher elevations in the mountains while the western boundary does not change. In the south-western part of its distribution area, temperate forest replaces tundra at lower elevations on the Tibetan Plateau and the Hengduan Mountains, while expanding slightly in the north-east part of its distribution, mainly in the Changbai Mountains, but also losing ground in parts of this region to warm-temperate forest and grassland. Temperate forest in China becomes confined to a long narrow zone from the Changbai Mountains and Greater Higgnan Mountains in north-east China across the North China Plain and the Loess Plateau to the eastern and southern margins of the Tibetan Plateau and the Hengduan Mountains. Boreal forest in the northern part of China, especially in the Greater Higgnan Mountains, shrinks to a scattering of small fragments on elevated hilltops, while boreal forest in north-west China and on the Tibetan Plateau expands its range to include most of the area of the Tianshan Mountains, the Altai Mountains, the Qilian Mountains and

Fig. 2 Natural distribution of potential vegetation in China. The vegetation types from the Vegetation Atlas of China at a scale of 1:1 million (Hou 2001) were regrouped into mega-biomes based on floristic and bioclimatic criteria
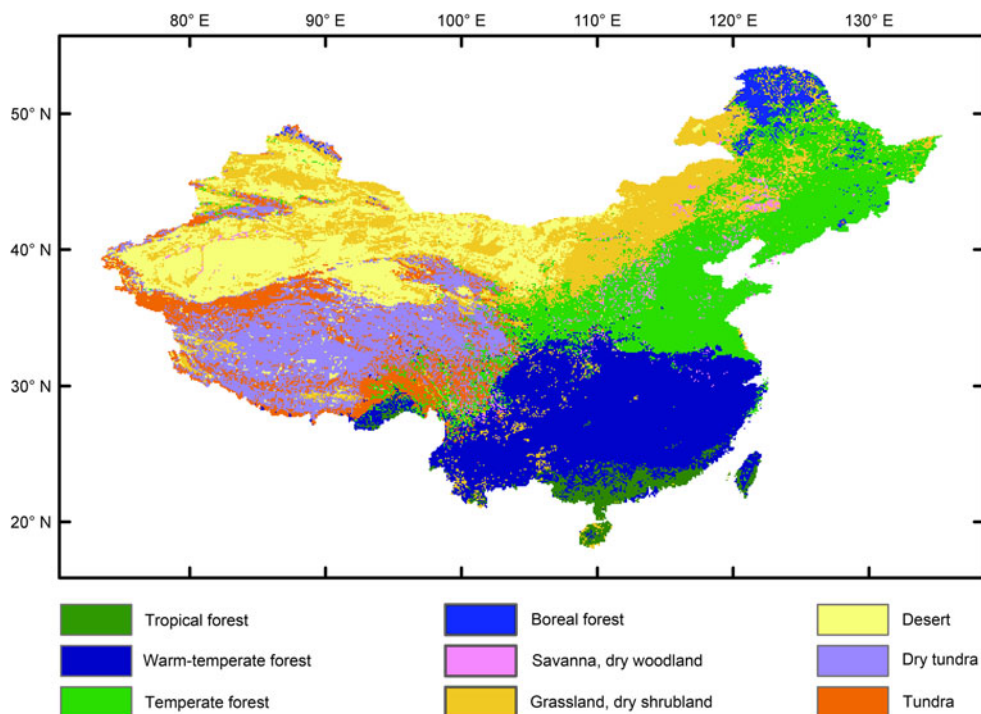

Fig. 3 Elevation map of China (Farr et al. 2007), showing major mountain ranges and rivers mentioned in the text
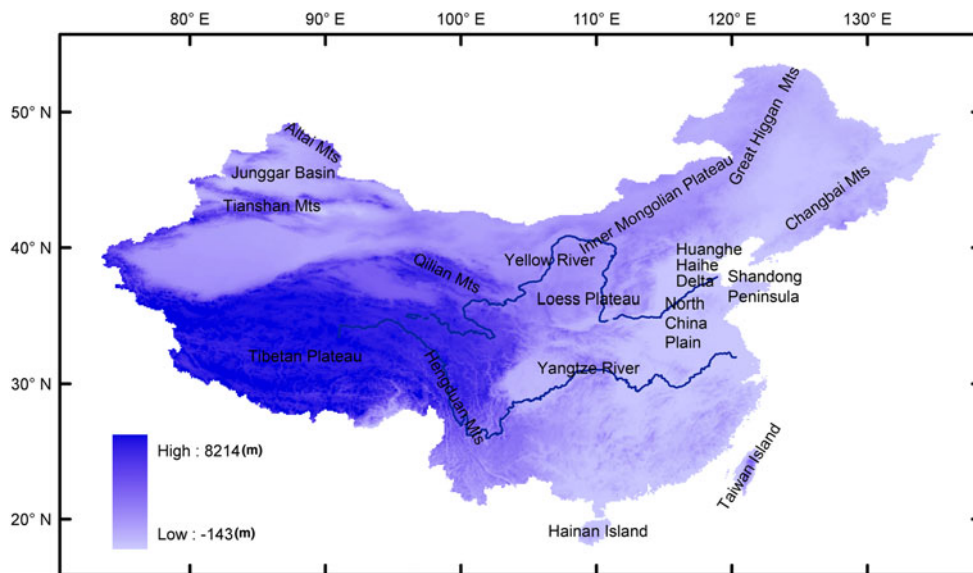
the interior of the Plateau. Due to these contrasting impacts in different boreal forest regions, the total area of boreal forest at first decreases and then gradually increases in response to warming (Fig. 5). Tundra vegetation is consequently squeezed to the north-western area of Tibetan Plateau in the high-temperature scenario. Tropical rainforest proves the most robust forest type, its distribution largely remaining in its original area with less than 10% area changes under most warming scenarios. The only replacement of tropical rain forest happens along the west coast of

Hainan Island, where savanna and dry woodland come to dominate; these more xeric vegetation types also appear at the boundaries of temperate forest with warm-temperate forest and temperate grassland in relatively arid areas and some calcareous or salinized soils around the coast of the Shandong Peninsula. With increasing temperature, grassland and dry shrubland benefit strikingly in competition with boreal and temperate forest in north China, but only slightly in competition with desert, as manifested by a more-or-less stable western boundary of grassland and dry

**Fig. 4** Mega-biomes simulated under doubled [CO_2] and six climatic scenarios
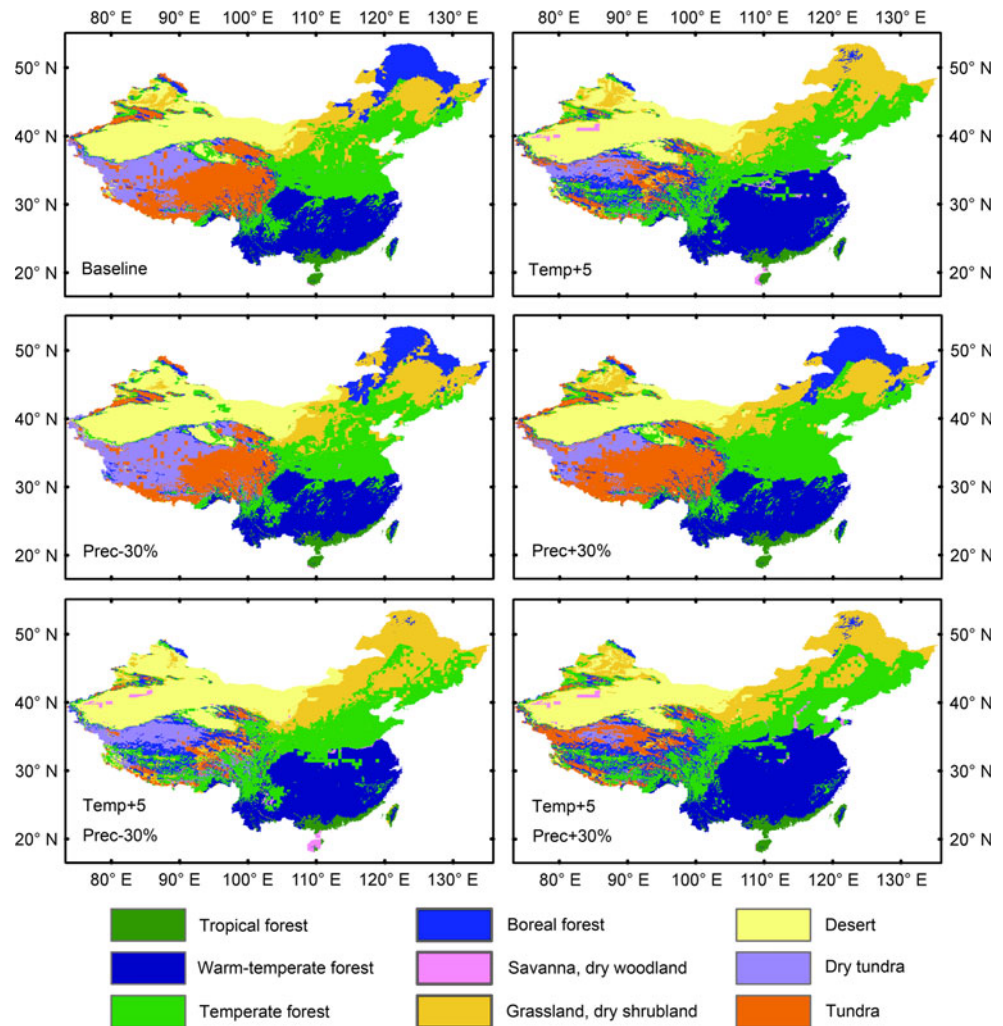
shrubland. This mega-biome thus shows a net positive response of total area to warming (Fig. 5).

Precipitation increases lead, as expected, to a greater area occupied by mesic biomes (forests and tundra), at the expense of xeric biomes (savanna, dry woodland, grassland, dry shrubland, desert, dry tundra) (Figs. 1, 5). Most vegetation types in the temperate region and on the Tibetan Plateau expand westward into the dry continental interior with increasing precipitation. Precipitation decreases have the opposite effect. Occupying the regions that have the highest precipitation today, tropical and warm-temperate forests shows less than 20% change in area whether precipitation increases or declines (Fig. 5). In regions of intermediate precipitation, however, changing precipitation has a powerful influence. Increasing precipitation benefits mesic vegetation (temperate, boreal forest and tundra) at the expense of xeric vegetation (grassland, dry shrubland and dry tundra). The boundaries of the mesic biomes shift westward towards the dry continental interior. Grassland and dry shrubland are thus pushed westwards due to the

competition with forest, but also themselves expand into desert regions so that their boundary with desert shifts westwards e.g. into the interior of the Junggar Basin. Again, the effects of reduced precipitation are broadly opposite to those of increased precipitation.

The modelled effect of CO_2 doubling is to partially compensate for the negative effect of drought on the mesic biomes (Figs. 4, 5). Drought can be produced by either precipitation decrease or temperature increase (which increases potential evapotranspiration and therefore increases water loss from vegetation). Elevated [CO_2] to some degree protects temperate forest against losses to grassland and dry shrubland due to warming and/or drying. In the temperate region, the effect of CO_2 doubling on biome distribution is sufficient to counteract the effect of approximately a 10% decrease in precipitation (Fig. 5). The CO_2 effect as modelled is stronger in drier regions. However, the distribution of boreal forest in north-eastern China shows little effect of elevated CO_2, consistent with Hickler et al.'s (2008) analysis suggesting a relatively
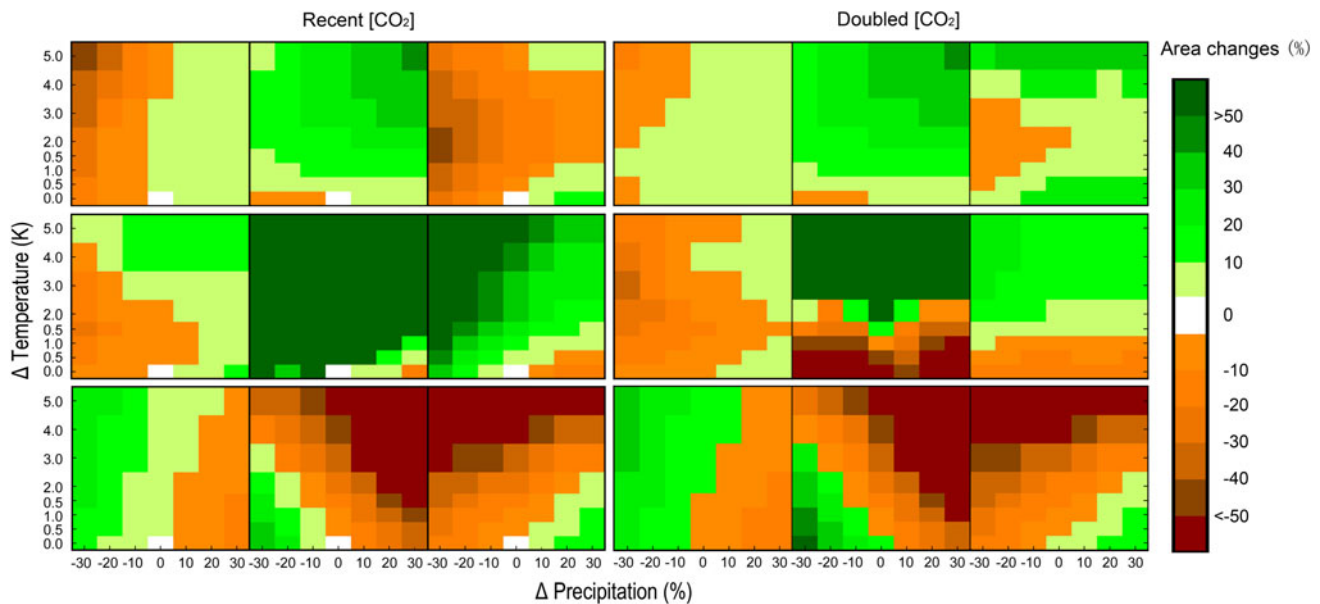
Fig. 5 Climatic sensitivity of the distribution areas of nine mega-biomes under recent (*left*) and doubled (*right*) [CO$_2$]. Within each half of the Figure, mega-biomes are presented in the following order: *top left* tropical forest, *top middle* warm-mixed forest, *top right* temperate forest, *middle left* boreal forest, *middle* savanna/dry woodland, *middle right* grassland/dry shrubland, *bottom left* desert, *bottom middle* dry tundra, *bottom right* tundra

minor CO$_2$ effect on forest productivity under the climatic conditions characteristic of boreal forest.

The most severe reductions of mesic biomes are shown when temperature increases are combined with precipitation decreases under unchanged CO$_2$ concentration (Fig. 1). Under this highly unfavourable combination of conditions, grassland and dry shrubland spread to occupy most of north China, leaving forest confined to refugia in the Changbai Mountains (for temperate forest) and the Tianshan and Altai Mountains (for boreal forest). In this scenario, grassland and dry shrubland even appear in Taiwan Island, in the western part of the original tropical rainforest area and to the south-east of the Tibetan Plateau. Tundra vegetation on the Tibetan Plateau is restricted to almost the same region as in the extreme warming condition, but with a different pattern of competition between dry tundra and tundra because dry tundra is more tolerant of the water shortage. The rest of China becomes mainly occupied by warm-temperate forest, with northern and western boundaries to temperate forest and the southern boundary connecting to tropical rainforest. As reflected by the percentage area changes, desert, savanna and dry woodland, grassland and dry shrubland all tend to increase in area towards the high-temperature, low-precipitation extreme, while tropical rainforest and tundra show the opposite trend (Fig. 5).

Generally in these simulations, forest biomes show considerable resilience to climate change, especially when the physiological effects of increased CO$_2$ concentration are taken into account (Fig. 5). The areas occupied by all

forest vegetation types vary by less than 50% among all scenarios. The most floristically diverse forest biomes—warm-temperate forest and tropical rainforest—are the two biomes that most closely maintain their original distributions. With the physiological CO$_2$ effects considered, temperate forest also can largely maintain its distribution, with some encroachment of warm-temperate forest in the south. Savanna and dry woodland increase their distributional area by more than 50% with temperature increases >1.5 K or precipitation decreases. Tundra vegetation types are the most sensitive to temperature increases, declining in area by as much as 60% in about a third of simulated cases.

The grassland–forest transition regions and the Tibetan plateau emerge as the regions most vulnerable to climate change, showing large-scale replacement of biomes (forests giving way to grasslands and tundra giving way to forest) under many scenarios (Fig. 4).

NPP and carbon storage

Warming alone has little overall effect on modelled NPP and biomass (Fig. 6). However, warming has a strong negative effect on soil carbon storage, so that the effect of warming alone on total carbon storage is negative.

Elevated CO$_2$ produces a general positive response of NPP under all climate scenarios. Biomass and soil carbon storage increase by roughly 40% due to CO$_2$ doubling. But the CO$_2$ and climate effects are not additive because the physiological effect of increasing [CO$_2$] is greater at higher temperatures. With elevated CO$_2$, warming at first causes

Fig. 6 Climatic sensitivity of China's net primary productivity, potential carbon storage in biomass and soil and total carbon storage under recent (*left*) and doubled (*right*) [CO₂]
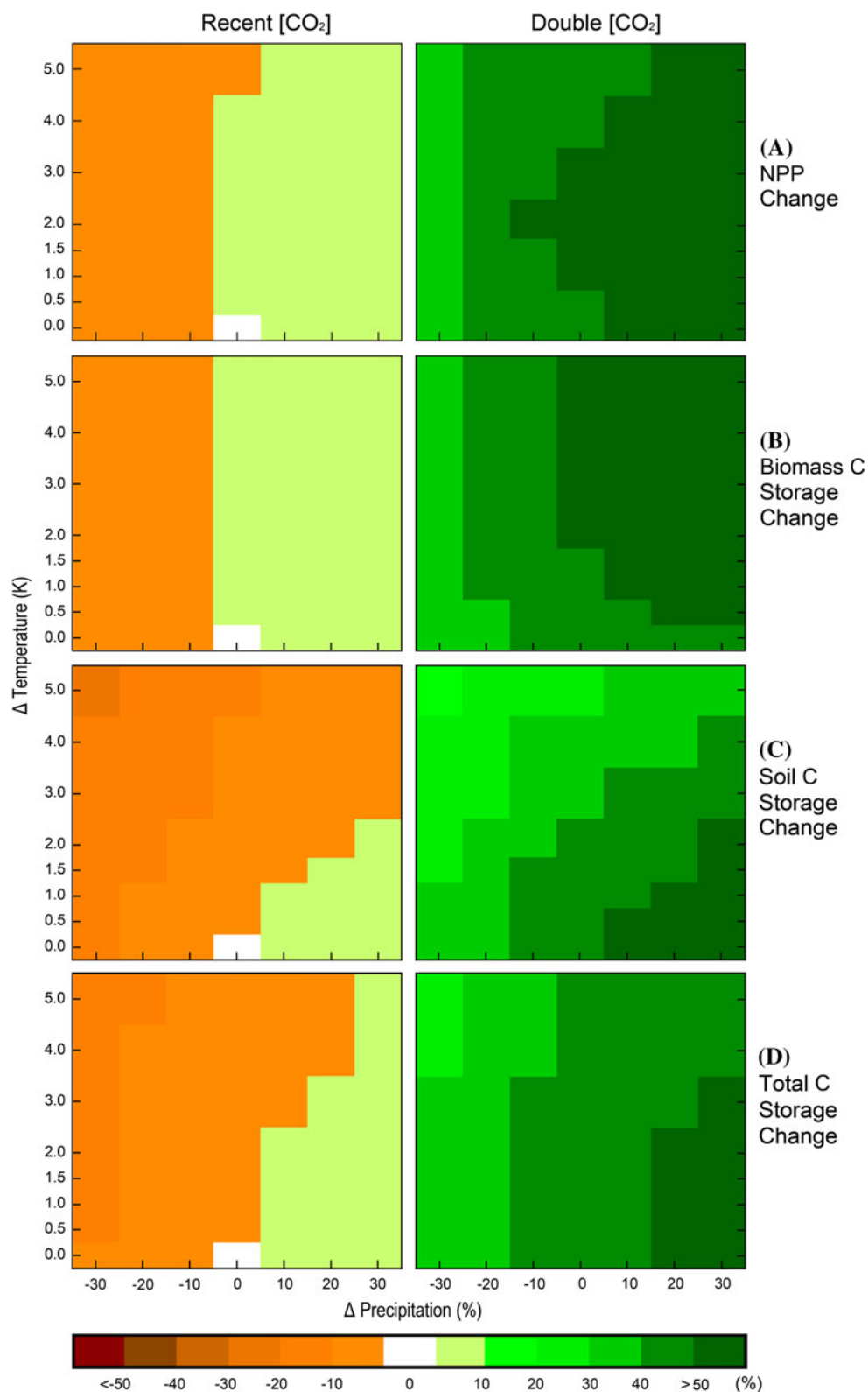
an increase in NPP, but then for warming greater than 2 degrees, NPP begins to decrease again. Biomass also increases with warming up to 2 degrees and then stabilizes.

For soil carbon, the effect of warming is to progressively counteract the increase caused by higher NPP at elevated CO₂. Total carbon storage under elevated CO₂, although

always higher than it would be without CO_2 effects, becomes less at higher temperatures, especially if these are accompanied by reduced precipitation.

Discussion

The results presented here are consistent with an emerging general understanding of the effects of temperature increases, precipitation changes and rising CO_2 concentration on global vegetation distribution (Fischlin et al. 2007), productivity and carbon storage (Friedlingstein and Prentice 2010).

1. Forest vegetation is expected to respond to anthropogenic climate change by shifting polewards and uphill, but tropical rainforests may behave differently. Evidence from a worldwide study on rainforests (Hilbert et al. 2002) and especially recent intensive studies on Amazon rainforest (Malhi et al. 2008; Phillips et al. 2009, 2010; Salazar et al. 2007; Laurance et al. 2009) have shown that tropical forests are potentially vulnerable to a warmer, drier climate, particularly if more strongly El Niño-like conditions develop. Tropical forests would then be partially replaced by savannas, a shift that is also shown in our study. However, the failure of tropical rainforest in China to expand much under any of the climate changes we consider may be more fundamentally connected with the steep climate gradient across its boundary with warm-temperate forest, due to the mountains in this area increasing abruptly in elevation with distance inland. A similar topographical cause can also explain why warm-temperate forest in high-precipitation scenarios does not shift its western boundary very far. Loarie et al. (2009) considered this topographical effect and noted that the horizontal velocity of temperature change is several orders of magnitude lower in mountainous regions, compared with flat regions. The simulated trend of temperate forest shift is consistent with a projection that the areal coverage of broad-leaved/Korean pine forests will decrease by 20–35%, with a significant northward shift (Wu 2003). It is also consistent with the findings of Peng et al. (2009) on the forest carbon balance under future climate change in north-eastern China, suggesting that towards the end of the century, only forest ecosystems in mountain regions are likely still to be net carbon sinks.

2. Due to its unique location, elevation and climate (Zhang 1983), the Tibetan Plateau is a regional of special physical and biological interest. Our results highlight the fact that this region is also exceptionally vulnerable to climate change. In particular, the characteristic tundra and dry tundra (meadow) vegetation are at risk of conversion to either forest (due to warming), grassland or desert (due to drying). This intrinsic vegetation vulnerability is exacerbated because temperature here is expected to increase much faster than that in the rest of China; some major climate "jumps" have already been detected in the past 40 years (Niu et al. 2004).

3. The grassland, dry woodland and desert biomes all increase in scenarios that involve rising temperature, decreasing precipitation and unchanged CO_2. This increase takes place at the expense of adjacent forest biomes. However, doubling $[CO_2]$ somewhat offsets the climate change effect. This is in part due to the differences in the photosynthetic pathway of their dominant species. C_3 plants (most woody plants and temperate grasses) and C_4 plants (especially tropical grasses) differ in their responses to CO_2, with C_3 plants benefiting more than C_4 plants. In addition, rising CO_2 confers increased water use efficiency and may help trees to compete with grasses. In our study, with CO_2 fertilization included, the total area of grassland and dry shrubland declines by more than 60%, compared with the same climate scenario with unchanged $[CO_2]$, while the area of tropical, warm-temperate and temperate forests enlarges by more than 10%. The projections by Peng et al. (2009) on forest carbon balance under future climate change in north-eastern China also support a positive effect of increased $[CO_2]$ on forest growth in this region.

Our results suggest that although climate changes in the range that may occur during the present century are likely to be a primary driver for changes in vegetation distribution, physiological CO_2 effects are potentially important as well and may be expected to influence vegetation composition, LAI, structure and vegetation boundaries by modifying the growth and competition of different PFTs. This underlying assumption in current models is supported by the palaeorecord. Jolly and Haxeltine (1997), for example, used BIOME3 (Haxeltine and Prentice 1996) to analyse the effects of changing CO_2 concentration and found that a large elevational extension of the heath belt on East African mountains during the last glacial maximum was predictable due to the low CO_2 concentration. Harrison and Prentice (2003) quantified global CO_2 effects on vegetation at the last glacial maximum and concluded that the observed glacial/interglacial changes in forest distribution could not be explained without them. Thus, based partly on palaeoevidence, it seems reasonable to accept that CO_2 increase has some mitigating effects on biome shifts caused by drought, as suggested by our model results.

According to the modelled results for potential carbon storage, elevated [CO_2] not only exerts an impact on vegetation structure but also greatly affects vegetation function, although this positive response is counteracted to some extent by the negative effect of warming. Our results concerning the combined effect of climate change and CO_2 elevation on carbon storage are broadly consistent with previous analyses. For example, Cao et al. (2003) indicated that China's terrestrial ecosystems were taking up carbon but their uptake capacity was being undermined by continuing climate change. Peng et al. (2009) and Ni (2000b) both showed overall increases in NPP and carbon storage in biomass and soil.

We have considered the effect of warming through its direct (positive and negative) and indirect (evapotranspiration-mediated) effects on NPP and also through enhancement of heterotrophic respiration (Lloyd and Taylor 1994; Kirschbaum 1995). Some consistency emerges from this and previous modelling of the effect of warming on carbon storage: climate change (at least, up to some level) tends to increase China's total NPP (Peng et al. 2009; Cao et al. 2003; Ni 2000b) while reducing soil carbon storage (Peng et al. 2009; Cao et al. 2003). However, the effect of warming on carbon storage may well be more complicated than this. The modelled temperature effect would be greater if a larger Q_{10} value had been used, as was typical in earlier studies (Friedlingstein et al. 2006; Lenton and Huntingford 2003). The new generic value (Mahecha et al. 2010) applies to total ecosystem respiration, including plant respiration, which appears to respond less steeply to temperature (Piao et al. 2010b), and thus, the generic value may be a lower bound. Furthermore, the data used to estimate this generic value are from flux measurements and thus dominated by the dynamics of short-lived carbon pools. Knorr et al. (2005) suggested that the longer-lived soil carbon pools may be even more sensitive to temperature than the short-lived pools; this prediction now has clear empirical support (Craine et al. 2010). On the other hand, if nitrogen availability effects were taken into consideration, warming-induced soil decomposition enhancement (especially in cooler climates) could increase the movement of nitrogen from soil with a lower C:N ratio to plants with a higher C:N ratio, thereby supporting increased carbon storage (e.g. Rastetter et al. 1992). These are some of the issues that continue to cause large uncertainty in the magnitude of the climate-carbon cycle feedback (i.e. warming leading to CO_2 release from ecosystems and thereby adding to the warming) at global as well as regional scales (Friedlingstein and Prentice 2010).

This study indicates about 40% increase in total carbon storage in ecosystems due to [CO_2] fertilization in the case of a doubling of [CO_2]. The fact that this effect is larger than the simulated temperature effect is consistent with many other model analyses (Friedlingstein et al. 2006; Friedlingstein and Prentice 2010). However, it should be noted that this value is a calculation for potential carbon storage; croplands store less carbon than natural vegetation and would not be expected to increase as much in carbon storage as a consequence of increasing [CO_2] (Piao et al. 2010a).

Considering the most likely future climate change alongside the influence of human activity, the response of natural vegetation in China to future environmental change is characterized by substantial regional differences. According to future climate trends summarized in Cruz et al. (2007), warming over all China will be greater during winter than summer, and the warming will be especially strong on the Tibetan Plateau and in semi-arid regions. Mean precipitation will likely increase in most of China but decrease in some western areas. Thus, the most severe possible scenarios for China's mesic vegetation may not come true: forests with their important functions in carbon sequestration, water retention and high biodiversity will likely continue to be the predominant natural vegetation cover in a large area of China. Higher winter temperature will also help some forest vegetation types to expand their distribution northward and upward. However, the potential retreat of tundra vegetation and its replacement by forests in parts of the Tibetan Plateau in response to increasing temperature and precipitation may signal a problem for livestock grazing in this vulnerable region. Similar problems could also apply to the arid area in north-western China owing to the projected expansion of desert, the least productive biome, in response to drying and warming.

Already subject to intensive grazing and land use pressures, the transitional region between grassland and forest on the Inner Mongolian Plateau is likely to be a hotspot of potential losses of grassland productivity and even desertification, if suitable measures are not taken to prevent overgrazing (Li and Zhou 2001; Qiu et al. 2001). Finally, the Huanghe-Haihe delta is a vulnerable area. Deltas are diverse ecosystems often with unique assemblages of plants and animals, located in different climate regions (Hassol 2005).The forest in the Huanghe-Haihe delta region is projected to degrade into savanna and dry woodland. The problems of this region may be exacerbated by more frequent and higher-level inundation due to storm surges and floods, potentially putting communities, biodiversity and infrastructure at risk of damage. Such impacts could be even more pronounced if natural ground subsidence is enhanced by human activities (Cruz et al. 2007).

Thus, faced with a high degree of uncertainty in climate change and vegetation impacts (Piao et al. 2010a) and some potentially highly unfavourable outcomes for certain regions, it is important to enhance our understanding of the relationship between vegetation, climate and [CO_2]

changes through the analysis of recent observations during the past decades of actual vegetation response to climate change, combined with field experiments, and analysis of the palaeorecord.

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