



Primary production in forests and grasslands of China: contrasting environmental responses of light- and water-use efficiency models

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Abstract. An extensive data set on net primary production (NPP) in China's forests is analysed with the help of two simple theoretically derived models based on the light use efficiency (LUE) and water use efficiency (WUE) concepts, respectively. The two models describe the data equally well, but their implied responses to [CO₂] and temperature differ substantially. These responses are illustrated by sensitivity tests in which [CO₂] is kept constant or doubled, temperatures are kept constant or increased by 3.5 K, and precipitation is changed by ±10%. Precipitation changes elicit similar responses in both models. But NPP in South China, especially, is reduced by warming in the LUE model, whereas it is increased in the WUE model. The [CO₂] response of the WUE model is much larger than that of the LUE model. It is argued that the two models provide upper and lower bounds for this response, with the LUE model more realistic for forests. The differences between the two models illustrate some potential causes of the large differences (even in sign) in the global NPP response of different global vegetation models to temperature and [CO₂].

and atmospheric carbon dioxide concentration ([CO₂]) and to quantify the feedbacks from climate change to [CO₂] (Cramer et al., 2001; Prentice et al., 2001; Friedlingstein et al., 2006; Sitch et al., 2008). But large uncertainties persist, due to the differences among the predictions of different models.

The Fourth Assessment Report (AR4) of the Intergovernmental Panel on Climate Change (IPCC) (Denman et al., 2007) re-analysed results from Friedlingstein et al. (2006), breaking down the models' aggregate global responses to environmental changes into components representing different processes. This analysis revealed large disagreements at a fundamental level. Although all models showed a positive response of global NPP to [CO₂] increase alone ("CO₂ fertilization"), the magnitude differed by a factor of five between the smallest and the largest modelled response. The response of NPP to global warming (and other associated climate changes) was positive in some models but negative in others. All models showed a negative effect of climate change on the overall terrestrial carbon balance ("climate-carbon cycle feedback"), but the modelled responses differed by a factor of 7.5. Subsequent DGVM development, particularly the inclusion of an interactive terrestrial nitrogen cycle in several models (e.g. Sokolov et al., 2008; Thornton et al., 2009; Zaehle and Friend, 2010), has failed to reduce this uncertainty. Some models have even shown an increase in terrestrial carbon storage with global warming (Thornton et al., 2009; Sokolov et al., 2008), although this appears to

1 Introduction

Dynamic global vegetation models, either "offline" or coupled with climate models, have been used extensively to predict the response of global net primary production and the terrestrial carbon balance to scenarios of future climate

be inconsistent with atmospheric constraints indicating that warming reduces terrestrial carbon storage and increases atmospheric $[\text{CO}_2]$ (Friedlingstein and Prentice, 2010).

One possible approach to narrowing the uncertainties in DGVMs is to test simpler, stand-alone models for the component processes. We suggest that the important differences in the ways in which models represent processes might be reducible to a small set of contrasting assumptions. We focus here on the controls of primary production, the most fundamental of all terrestrial ecosystem processes. We exploit a large data set of forest NPP measurements spanning the range of forest types in China (Luo, 1996), supplemented by a smaller data set of grassland NPP measurements, to explore the predictions made by simple but theoretically derived models based on the concepts of water-use efficiency (WUE) and light-use efficiency (LUE) respectively. We find that the observations can be fitted by both types of model, while revealing important differences in their predictions for the responses of NPP to changes in $[\text{CO}_2]$ and climate. Because of the relative simplicity of the models we can begin to analyse their differences, and suggest which aspects of the responses might need to be better characterized empirically.

2 Materials and methods

2.1 Background

Carbon dioxide assimilation through the stomata of vascular plants inevitably entails simultaneous loss of water to the atmosphere. The concept of WUE (the ratio of carbon assimilated to water lost) quantifies this trade-off. WUE has attracted increased interest recently, with the surge in popularity of the eddy covariance technique to quantify carbon gain and water loss at the ecosystem level (Baldocchi, 1994; Kuglitsch et al., 2008; Jassal et al., 2009). The idea of using water use (via WUE) to predict assimilation has been used for modelling crop growth (GLAM, Challinor et al., 2004) and large-scale gross primary production, GPP (Beer et al., 2007).

The concept of LUE (the ratio of carbon assimilation to absorbed photosynthetically active radiation, PAR) also emerged from studies of crop growth (Monteith and Moss, 1977). LUE gained popularity as a way to calculate GPP from incident PAR and remotely sensed measurements of the fraction of absorbed PAR green plants (fAPAR) (e.g. Prince and Goward, 1995; Running et al., 2004). The LUE concept is used in the Lund-Potsdam-Jena (LPJ) DGVM (Sitch et al., 2003) and its derivatives. LPJ relies on a theoretical analysis (Haxeltine and Prentice, 1996a) to predict LUE as a function of environmental controls, based on a simplified version of the Farquhar et al. (1980) model of photosynthesis. An important assumption of this analysis is that photosynthetic capacity acclimates to environmental conditions so as to maxi-

mize daily net photosynthesis at the leaf level (Haxeltine and Prentice, 1996b; Dewar, 1996).

In applying the WUE and LUE concepts, we proceed in two steps (Table 1):

- First we fit “Level 0” or empirical models, in which simple proportional relationships between measured annual forest NPP and either an estimate of annual evapotranspiration (WUE), or an estimate of annual PAR absorption (LUE), are fitted statistically. Annual evapotranspiration for the Level 0 WUE model is derived from annual precipitation and annual equilibrium evapotranspiration (a measure related closely to potential evapotranspiration) using a well-established relationship in hydrology, derived from the so-called Budyko framework in which evapotranspiration is taken to vary smoothly between two end-states representing control by water availability (in dry climates) and control by energy availability (in wet climates). Annual PAR absorption for the LUE model is obtained as the product of annual incident PAR and a satellite-derived estimate of annual fAPAR, the fraction of incident PAR that is absorbed by green plants.
- Second, in order to perform sensitivity experiments in which environmental factors including CO_2 concentration are varied, we develop “Level 1” or semi-empirical models. These are based on explicit theoretical derivations of the WUE and LUE concepts. The Level 1 models are also statistically fitted with the same forest NPP data set, but the predictor variables (annual evapotranspiration and annual PAR absorption, respectively) are modified to take into account additional expected effects of environmental variation on WUE and LUE. Specifically, the Level 1 WUE model takes into account the effect of vapour pressure deficit on stomatal conductance. We estimate this effect indirectly, using a previously published empirical relationship between leaf $\delta^{13}\text{C}$ and a climatic moisture index. The Level 1 LUE model takes into account the known dependence of the photosynthetic CO_2 compensation point on temperature, and an empirical relationship between the climatic moisture index and fAPAR.

The derivations of both of the Level 1 models rely on two simplifying assumptions. (1) We assume that light, water and $[\text{CO}_2]$ are the primary controls on GPP; and therefore, that soil nutrient availability is a secondary consideration (contrary to some interpretations, e.g. Huston and Wolverton, 2009). (2) Although not pre-assigned any particular fraction, NPP is implicitly assumed to be approximately a constant fraction of GPP – that is, annual autotrophic respiration is assumed to be a fixed fraction of GPP or, equivalently, carbon use efficiency is taken to be constant across different environments and climates (Waring et al., 1998). This second assumption appears to be contrary to the analysis of Piao

Table 1. Fitted linear regression models with dependent variables, explanatory variables, correlation coefficients (r) and regression slopes (without intercept).

Models	Dependent variables	Explanatory variables	r	Slope
Level 0 models	forest NPP	E_a	0.6544	1.0712
	forest NPP	$IPAR_0 \cdot fAPAR$	0.6638	0.2633
Level 1 WUE model	forest NPP	$E_a(c_i/c_a)^2/(1 - c_i/c_a)$	0.6485	0.2589
	Beer et al. GPP	$E_a(c_i/c_a)^2/(1 - c_i/c_a)$	0.8890	0.4513
Level 1 LUE model	Grassland ANPP	$E_a(c_i/c_a)^2/(1 - c_i/c_a)$	0.3363	0.1781
	Forest NPP	$IPAR_0 \cdot fAPAR (c_i - \Gamma^*)/(c_i + 2\Gamma^*)$	0.6268	0.3516
	Beer et al. GPP	$IPAR_0 \cdot fAPAR (c_i - \Gamma^*)/(c_i + 2\Gamma^*)$	0.8843	0.6168
	Grassland ANPP	$IPAR_0 \cdot fAPAR (c_i - \Gamma^*)/(c_i + 2\Gamma^*)$	0.3055	0.1442

et al. (2010); however, subsequent re-analysis of the available co-located NPP and GPP data has revealed that the ratio of autotrophic respiration to GPP becomes independent of mean annual temperature when the distinction between managed and old-growth forests is taken into account (S. Piao and P. Ciais, personal communication, 2011). The NPP data we use are from managed forests of various ages. Both assumptions are re-examined later on.

Since the NPP data we exploit here refer to mean annual productivity, the entire approach is for “equilibrium” conditions. All the formulas involved in the estimation of water use and light use are intended to be valid at an annual scale, not for any shorter period.

2.2 Data

2.2.1 NPP data

1238 plot-based records of forest total (above- plus below-ground) NPP were obtained from a dataset constructed by Luo (1996) and Ni (2003), which in turn was based on the Chinese literature from the 1970s to 1990s and the continuous forest-inventory plots of the State Forestry Administration during the period of 1989 to 1993. Most of the plots are managed forest, while only 17 % plots are “old-growth” forest (> 100 yr old). The data in Luo (1996) are provided in tonnes (Mg) dry matter $\text{ha}^{-1} \text{a}^{-1}$. We converted the data to $\text{g C m}^{-2} \text{a}^{-1}$, using a factor of 0.5 to convert dry matter to carbon content.

We also used 135 records of above-ground NPP (ANPP) compiled by Ni (2004) from field measurements of managed semi-natural grasslands in northern China. All the grasslands are grazed, but heavily disturbed sites were avoided. Ni (2004) derived total NPP from these sites, but the results are strongly dependent on the estimates used for below-ground carbon allocation. This is especially true for the driest and coldest sites where the bulk of the production occurs below ground. We have used only the above-ground NPP measurements in this study, as they are closer to the primary observa-

tions. We then examine the implications of our findings for ANPP/NPP ratios.

We have also used the globally extrapolated GPP data of Beer et al. (2010) at 0.5° resolution as a way to obtain an independent estimate of the WUE and LUE of GPP at the grid cells where we have NPP measurements. By comparing results obtained from Chinese forest NPP measurements with results obtained for the global GPP data set, we are able to get a rough estimate of the actual ratio of NPP to GPP for forests in the region. Even though the dataset of Beer et al. (2010) is a modelled product, this dataset can still be used as an independent check of our models, since it is based on observations (eddy-covariance flux measurements) that are independent of our NPP data.

2.2.2 Environmental data

The bioclimatic variables used in all of the Level 0 and Level 1 models were calculated from spatially interpolated (gridded) climatological data. Mean monthly values of temperature, precipitation, and percentage of possible sunshine hours were derived from 1814 meteorological stations across China (740 stations have observations from 1971–2000, the rest from 1981–1990: China Meteorological Administration, unpublished data). These data were interpolated at 0.1° grid resolution for mapping, and to the specific locations and elevations of the forest NPP plots, using three-dimensional smoothing splines (ANUSPLIN version 4.36: Hancock and Hutchinson, 2006). Bioclimatic variables were then calculated as in Prentice et al. (1993, 2011): the daily mean temperature during the growing season (the period with daily-interpolated temperatures $> 0^\circ\text{C}$) (mGDD_0 , $^\circ\text{C}$), the total annual incident photosynthetically active radiation during the growing season ($IPAR_0$, $\text{mol m}^{-2} \text{a}^{-1}$), annual equilibrium evapotranspiration (E_q , mm a^{-1}), and the climatic moisture index ($MI = \text{MAP}/E_q$ where MAP is mean annual precipitation, mm a^{-1}).

Equilibrium evapotranspiration is defined as the stable rate of evapotranspiration that is approached when air passes over a homogeneous, well-watered surface under constant

environmental conditions. Although these conditions are hypothetical, E_q is a well understood physical quantity whose value depends only on temperature and net radiation according to the expression $\lambda E_q = R_n [s/(s + \gamma)]$ where λ is the latent heat of vaporization of water (a weak function of temperature), R_n is net radiation, s is the slope of the Clausius-Clapeyron relationship between the saturated vapour pressure of water and temperature (this slope itself increases with temperature), and γ is the psychrometer constant. E_q forms the basis for the widely used Priestley-Taylor equation for potential evapotranspiration, $E_p = 1.26E_q$. Based on the Budyko framework, the equation $E_a = E_p [1 + MI - (1 + MI^w)^{1/w}]$ (Zhang et al., 2004), where w is a single empirical parameter with a limited range of values, makes it possible to estimate annual actual evapotranspiration (E_a , mm a^{-1}) from MI and E_q . For simplicity, we set w to a single generic the value of 3, appropriate to forest, and $E_p = E_q$.

To test the robustness of this method to calculate E_a , we compared its results with an alternative, more explicitly process-based method based on soil-moisture accounting, as described by Prentice et al. (1993). This method requires soil water-holding capacities to be assigned to grid cells: in this we followed Wang et al. (2011). In the soil-moisture accounting algorithm, daily E_a is computed using an analytical expression for the integral over the 24-h cycle of the lesser of two quantities: a demand function, which is E_q , and a supply function. The supply function takes a maximum value of 1 mm h^{-1} which is diminished in proportion to the fractional volumetric soil water content, in order to mimic the observed reduction in transpiration rate as soils dry out. The soil is treated as a single water store to which precipitation is added and from which evapotranspiration is removed. If the store is full, the excess water runs off. The annual cycle is iterated until a stable seasonal cycle of evapotranspiration is reached. This algorithm yielded values of E_a that were larger by a factor 1.17 but with a very high correlation ($r = 0.98$) to the estimates made with the Zhang equation.

The variables mGDD_0 , IPAR_0 , E_q , and MI and E_a estimated from the Zhang equation, are mapped in Fig. 1. The contents of three soil nutrient elements phosphorus, potassium and nitrogen at the forest NPP observation plots were obtained from the digitized 1 : 1 million soil map of China (Shi et al., 2004).

2.3 Models

2.3.1 The simple (Level 0) WUE model

Our Level 0 WUE model assumes simple proportionality between NPP and E_a . We fitted this model to the forest NPP data by ordinary least-squares linear regression of NPP (observations) against E_a (from the Zhang equation), with the intercept fixed to zero (Table 1).

2.3.2 Theoretical derivation of a (Level 1) WUE model

Due to the resistance of stomata to the inward diffusion of CO_2 and the photosynthetic drawdown of CO_2 in the leaves, c_i in illuminated leaves is always less than c_a . From the diffusion equation, the relationship between net photosynthesis and the CO_2 concentration gradient across the leaf epidermis is:

$$A = g_s c_a (1 - c_i/c_a) \quad (1)$$

where A is GPP and g_s is stomatal conductance to CO_2 (usually expressed in $\text{mol C m}^{-2} \text{ s}^{-1}$). At the whole-ecosystem level as considered here, g_s is a bulk conductance, which depends on foliage cover as well as on the average leaf-level stomatal conductance.

The ratio of internal CO_2 concentration (c_i , $\mu\text{mol mol}^{-1}$ or ppm) to ambient CO_2 concentration (c_a , in the same units) is an index of the regulation of stomatal conductance. We estimated effective growing-season values of c_i/c_a as follows:

$$c_i/c_a = 0.426 + 0.417\text{MI}. \quad (2)$$

This expression combines the standard approximation for $\delta^{13}\text{C}_{\text{leaf}}$ (Farquhar et al., 1982, 1989) with an empirical regression equation for $\delta^{13}\text{C}_{\text{leaf}}$ as a function of MI for C_3 plants, based on field measurements ranging from dense forests to desert (MI from 0.17 to 0.96) along the North East China Transect (Prentice et al., 2011). Since stomatal conductance is regulated in a way that maintains c_i/c_a typically around 0.7 to 0.9 in C_3 plants under conditions of moderate vapour pressure deficit (D) and adequate soil moisture (Wong et al., 1979), we assumed that c_i/c_a does not increase beyond a maximum value of 0.843 for $\text{MI} \geq 1$. Estimated values of c_i/c_a are mapped in Fig. 1.

Diffusion through the stomata also controls plant water loss according to:

$$E = 1.6g_s D \quad (3)$$

where E is transpiration and D is the (dimensionless) vapour pressure deficit at the leaf surface. Here again g_s is a bulk conductance. For simplicity we assume that evaporation from bare ground and interception from leaves add up to an approximately constant fractional loss of water to the plants, with evaporation from bare ground more important in sparsely vegetated environments and interception more important in forests. We thus derive a WUE model from Eqs. (1) and (3):

$$A = 0.63q(c_a/D)(1 - c_i/c_a)E_a \quad (4)$$

where E_a is actual evapotranspiration (including bare ground evaporation and interception), and q (≤ 1) is the fraction of E_a that is transpired.

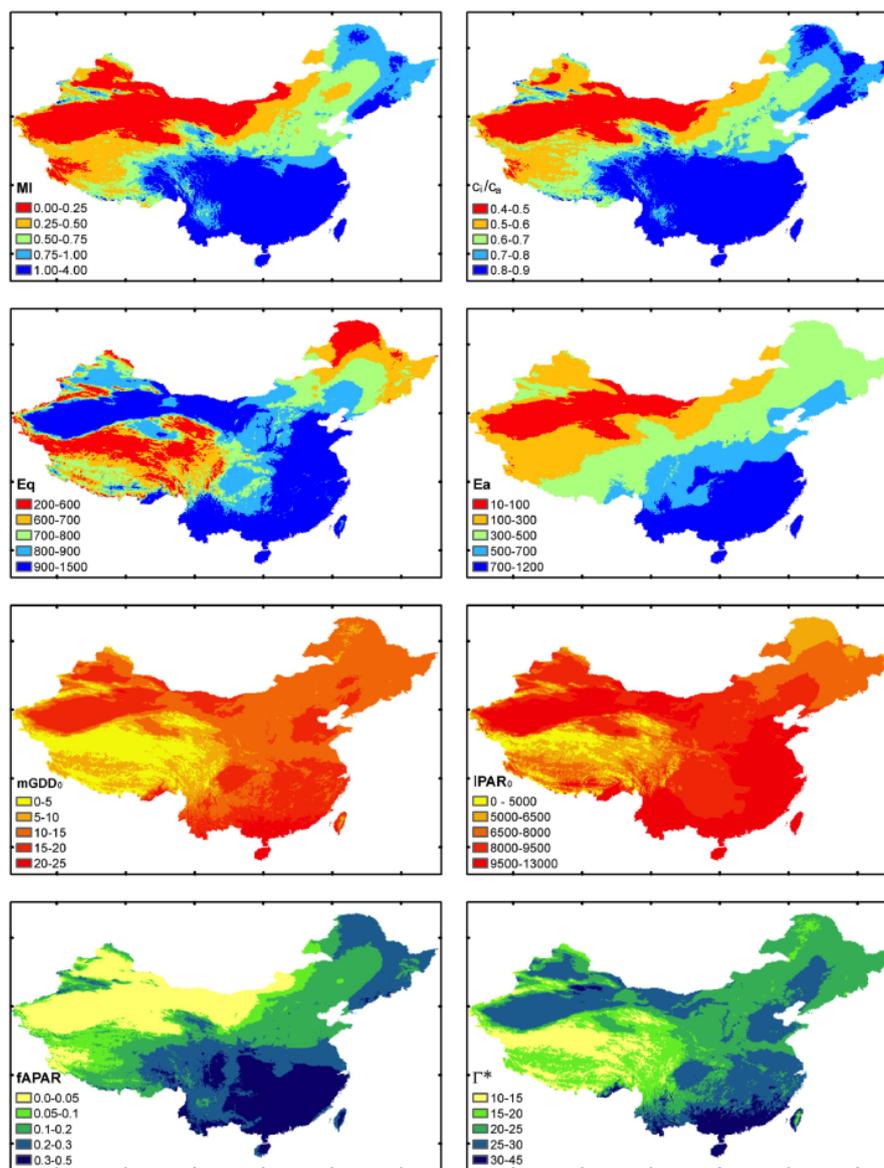


Fig. 1. The distribution pattern of eight environmental or ecophysiological variables: moisture index (MI), c_i/c_a ratio, equilibrium evapotranspiration (E_q ; mm a^{-1}), actual evapotranspiration (E_a ; mm a^{-1}), mean temperature of the period above 0°C (mGDD₀; $^\circ\text{C}$), accumulated photosynthetic active radiation during the period above 0°C (IPAR₀; $\text{mol m}^{-2} \text{a}^{-1}$), fraction of absorbed photosynthetic active radiation (fAPAR), CO₂ compensation point (Γ^* ; ppm).

The effective, growing-season value of D is unknown and not easily calculated from meteorological measurements. Many models require D to be specified as an external variable in a similar way to temperature or precipitation. However, D is not really independent of ecosystem properties; it is controlled by evapotranspiration and the dynamics of the planetary boundary layer, which in turn are determined by energy exchanges at the land surface as well as by conditions in the free troposphere (Raupach, 1995). Furthermore, stomatal optimization theory (Medlyn et al., 2011) implies a

functional relationship between D and c_i/c_a :

$$D = \xi^2 (1 - c_i/c_a)^2 / (c_i/c_a)^2 \quad (5)$$

where ξ is a parameter. There is some evidence that ξ varies among species (Medlyn et al., 2011) and with leaf or soil water potential (Manzoni et al., 2011), but based on an analysis of available data from drying experiments, the response of c_i/c_a to soil moisture appear to be relatively slight compared with its response to D (Zhou et al., 2012). Accordingly, we do not consider variation in ξ when estimating D . This simplification can be justified on two further grounds. First,

because of the dependence of atmospheric water vapour content on transpiration, soil moisture index and D (as the two controls of c_i/c_a) must themselves be mutually correlated, and therefore it is reasonable to expect a correlation between long-term values of c_i/c_a and D . Second, and most importantly for our analysis, the estimates of c_i/c_a from Eq. (2) implicitly include variation in ξ with species and soil moisture to the extent this occurs. This is because they are based on observed ^{13}C discrimination by plants growing in their natural environment.

Substituting Eq. (5) into Eq. (4), we then obtain:

$$A = 0.63q\xi^{-2}c_a E_a (c_i/c_a)^2 / (1 - c_i/c_a) \quad (6)$$

Eq. (6) is our Level 1 WUE model, which could be fully expressed as:

$$A = 0.63q\xi^{-2}c_a E_p [1 + \text{MI} - (1 + \text{MI}^w)^{1/w}] \quad (7)$$

$$(0.426 + 0.417\text{MI})^2 / (0.574 - 0.417\text{MI})$$

by substituting E_a with the Zhang equation and c_i/c_a with Eq. (2).

We fitted this model by ordinary least-squares linear regression of forest NPP data against the product $E_a (c_i/c_a)^2 / (1 - c_i/c_a)$ with the intercept fixed to zero (Table 1).

2.3.3 The simple (Level 0) LUE model

Our Level 0 WUE model assumes simple proportionality between NPP and the product of incident PAR and annual fAPAR. We fitted this model to the forest NPP data by ordinary least-squares linear regression of NPP (observations) against the product $\text{IPAR}_0 \times \text{fAPAR}$, with the intercept fixed to zero. To estimate annual fAPAR, we used monthly fAPAR data on a 0.5° grid from the SeaWiFS satellite product (Gobron et al., 2006). Annual fAPAR is the ratio of total annual absorbed PAR to total annual incident PAR, and is therefore properly calculated as a weighted average of monthly values (weighted by each month's total incident PAR) (Fig. 1).

2.3.4 Theoretical derivation of a (Level 1) LUE model

We start from the assumption that the photosynthetic capacity of leaves at any level in the canopy acclimates spatially and temporally during the course of the growing season to the prevailing daytime incident PAR, so as to be neither in excess (which would entail additional, non-productive maintenance respiration) nor less than required for full exploitation of the available PAR (Haxeltine and Prentice, 1996a; Dewar, 1996). This assumption implies co-limitation of photosynthesis by carboxylation and electron transport under typical daytime conditions. It leads to the simplification that effects of environmental changes (water availability, temperature, c_a) can be expressed through a simplified equation for electron-transport limited photosynthesis:

$$A = \text{fAPAR} \phi_0 \text{IPAR}_0 (c_i - \Gamma^*) / (c_i + 2\Gamma^*) \quad (8)$$

where ϕ_0 is the intrinsic quantum efficiency of photosynthesis and Γ^* is the CO_2 compensation point. It is implicit that not only the Rubisco capacity (V_{cmax}) but also the maximum capacity for electron transport (J_{max}) acclimates to PAR, so that A never approaches light saturation due to J_{max} limitation under typical daytime conditions. The relative conservatism of the ratio $J_{\text{max}}/V_{\text{max}}$ in wild plants (Wullschlegel, 1993) supports this.

Equation (7) is our Level 1 LUE model. But although we have data on present-day fAPAR, a model is required to predict changes in fAPAR with changes in environment. Annual fAPAR is a remotely sensed quantity proportional to the green foliage projective cover (FPC). It is related to leaf area index (LAI) through Beer's law such that fAPAR is approximately proportional to LAI at low values of LAI (< 1), approaching 1 at high values of LAI. It has long been known (e.g. Specht, 1972) that water availability is the dominant control of evergreen (or growing-season) FPC, and more recent analyses (e.g. Nemani and Running, 1989, Ker-goat, 1998) have shown that large-scale patterns of growing-season LAI are close to equilibrium with water supply. Based on this knowledge, we fitted a country-wide empirical relationship for fAPAR as a function of MI:

$$\text{fAPAR} = 0.53\{1 - \exp[-0.7(\text{MI} - 0.15)]\} \quad (9)$$

using non-linear regression of the gridded SeaWiFS annual fAPAR data against MI. Equation (8) then allowed us to estimate fAPAR from MI.

The CO_2 compensation point Γ^* (ppm) depends strongly on temperature. Bernacchi et al. (2003) fitted the Arrhenius equation to measurements in vivo of Γ^* at different temperatures. This relationship can be re-expressed to a close approximation, for the relevant range of temperatures, as an ordinary exponential function:

$$\Gamma^* = \Gamma_{25}^* \exp(0.0512\Delta T) \quad (10)$$

where ΔT is the difference between the measurement temperature in $^\circ\text{C}$ (T_C) and 25°C . We substituted the mean growing-season temperature (mGDD_0) for T_C to estimate effective growing-season values of Γ^* . These are mapped in Fig. 1.

Therefore, our Level 1 LUE model could be fully expressed as:

$$A = 0.53\{1 - \exp[-0.7(\text{MI} - 0.15)]\} \phi_0 \text{IPAR}_0 \quad (11)$$

$$\{0.426c_a + 0.417c_a \text{MI} - \Gamma_{25}^* \exp(0.0512\Delta T)\} /$$

$$\{0.426c_a + 0.417c_a \text{MI} + 2\Gamma_{25}^* \exp(0.0512\Delta T)\}$$

by substituting in Eq. (8) with c_i/c_a from Eq. (2), fAPAR from Eq. (9) and Γ^* from Eq. (10).

To fit the model, we performed a linear regression of the NPP data on the product $\text{fAPAR} \times \text{IPAR}_0 (c_i - \Gamma^*) / (c_i + 2\Gamma^*)$ with c_i/c_a estimated from Eq. (2), fAPAR from Eq. (8), Γ^* from Eq. (9), and the intercept fixed to zero.

2.4 Additional tests

To test for a possible dependence of NPP on soil nutrient availability, we categorized the soil P, K and N concentrations for each forest NPP measurement site (identifying suitable breakpoints based on histograms of the values) and performed separate regressions of NPP on the light- and water-based predictors for the different categories. To test for a possible dependence of NPP on stand age, we also performed separate regressions for three stand age classes (< 50 yr, 50–100 yr and > 100 yr).

We also fitted the Level 1 WUE and LUE models to the GPP dataset of Beer et al. (2010) (Table 1). Using GPP data, the regression slope of the WUE model can be interpreted as an estimate of $0.63q\xi^{-2}c_a$ and the regression slope of the LUE model can be interpreted as an estimate of ϕ_o . Furthermore, by comparing these slopes with those obtained from fitting the forest NPP data, we could obtain a rough estimation of the average ratio of NPP to GPP in the forest plots.

Grasslands occupy a large area of China and play a significant role in China's terrestrial carbon cycle. We tested the models' applicability to grasslands as well as forests. We fitted Level 1 WUE and LUE models to the grassland ANPP data of Ni (2004) and compared the results with those obtained with the forest NPP data (Table 1). If the true relationships of NPP to the predictors were similar in forests and grasslands, then we would expect the ratios of the slopes to indicate the fraction of grassland NPP allocated above ground. We therefore compared these ratios to the results of Hui and Jackson (2006), whose estimates of belowground NPP were based on 94 site-years of field biomass measurements at twelve grassland sites around the world.

2.5 Sensitivity experiments

Regional averages of temperature and precipitation projections under the A1B scenario for 2080 to 2099 from IPCC AR4 (Christensen et al., 2007) were used to suggest simple sensitivity experiments as follows. For all 0.1° grid cells the mean temperature of each month was increased by 3.5 K and the mean precipitation of each month altered by $\pm 10\%$. We considered changes of each single climatic factor, and both together, under recent $[\text{CO}_2]$ (366 ppm) and doubled $[\text{CO}_2]$ (732 ppm). For each projected climate and $[\text{CO}_2]$ level, we mapped the changes from the baseline state, and also calculated the area-weighted average NPP across all grid cells.

3 Results

3.1 Analysis of forest NPP data

Both Level 0 models (WUE and LUE) yielded highly significant regressions, with closely similar correlation coefficients ($r = 0.650$ for WUE model and 0.664 for LUE model) (Table 1).

The Level 1 WUE and LUE models also yielded highly significant regressions, and correlation coefficients similar to those from the Level 0 models ($r = 0.649, 0.627$) (Table 1, Fig. 2). That these correlations are slightly smaller than those obtained with the Level 0 models suggests that the theoretically derived models could be improved. This is not surprising as a number of additional assumptions were made in the derivations. But the differences are small.

When different soil nutrient classes were analysed separately using the Level 1 models, some statistically significant differences were found among the regression slopes (Table 2, Fig. 3). There is a significant difference between the WUE model slopes for low and high P concentration, but the magnitudes differ by only 7.6%. The largest percentage difference in slopes (20.8%) was between soils with low and high K concentration. The results generally indicate a greater slope for higher nutrient availability, except for the highest level of P in the LUE model, which breaks this trend. Low and high N classes showed no significant differences in slope.

There were small but significant differences in the regression slopes for the different age classes, with the > 100 yr age class showing a slope reduced by 14% (Table 3, Fig. 3).

3.2 Modelled responses of NPP to changes in climate and $[\text{CO}_2]$

Precipitation changes elicited similar responses in both models: increasing NPP with more precipitation, and decreasing NPP with less (Table 4, Fig. 4). Under recent $[\text{CO}_2]$, the WUE model estimated an area-weighted average NPP of $369 \text{ g C m}^{-2} \text{ a}^{-1}$ and the LUE model $393 \text{ g C m}^{-2} \text{ a}^{-1}$. The modelled changes of NPP between baseline and 10% precipitation change were similar: $-40 \text{ g C m}^{-2} \text{ a}^{-1}$ (WUE model) and $-37 \text{ g C m}^{-2} \text{ a}^{-1}$ (LUE model) with less precipitation, and $+36 \text{ g C m}^{-2} \text{ a}^{-1}$ (WUE model) and $+34 \text{ g C m}^{-2} \text{ a}^{-1}$ (LUE model) with more precipitation. The responses of NPP to precipitation were in the same direction under doubled $[\text{CO}_2]$. Both models also indicated a regional heterogeneity in the NPP response to precipitation change. Under recent $[\text{CO}_2]$, both models showed larger absolute NPP changes in wet regions. But the WUE model indicated the highest sensitivity region at the transition between wet and dry regions, while the LUE model indicated the highest sensitivity in wet regions.

Warming was predicted to have a negative effect on area-weighted average NPP, with a change of -7 (WUE model) or $-22 \text{ g C m}^{-2} \text{ a}^{-1}$ (LUE model). The regional patterns of response differed between the models. In the LUE model, warming reduced NPP over most of China, with the strongest effect in South China. Exceptions were for a large area in Tibetan Plateau, and a small area in the transition between the wet and dry regions. Reductions of more than $75 \text{ g C m}^{-2} \text{ a}^{-1}$ were simulated (Fig. 4). In the WUE model, NPP generally increased by $> 25 \text{ g C m}^{-2} \text{ a}^{-1}$ in South China, with negative

Table 2. Regression slopes of observed NPP against Level 1 WUE and LUE model predictors for different soil nutrient levels, and t-values for all pairwise comparisons among the levels (bold: $P < 0.05$ or better).

WUE model	slope	standard error	sample size	pairwise t-values	
N concentration				< 0.2	
< 0.2	0.2600	0.0037	775		
≥ 0.2	0.2565	0.0053	463	0.5555	
P concentration				≤ 0.05	≥ 0.15
≤ 0.05	0.2555	0.0041	515		2.0691
0.05–0.15	0.2618	0.0049	579	0.9727	0.9728
≥ 0.15	0.2765	0.0124	144		
K concentration				≤ 0.5	≥ 4
≤ 0.5	0.2503	0.0051	419		2.7688
0.5–4	0.2598	0.0039	779	1.4612	2.1652
≥ 4	0.2978	0.0151	40		
LUE model	slope	standard error	sample size	pairsie t-values	
N concentration				< 0.2	
< 0.2	0.3552	0.0030	775		
≥ 0.2	0.3445	0.0039	463	1.3633	
P concentration				≤ 0.05	≥ 0.15
≤ 0.05	0.3520	0.0035	515		2.8518
0.05 ~ 0.15	0.3563	0.0037	275	0.4909	3.3671
≥ 0.15	0.3173	0.0071	144		
K concentration				≤ 0.5	≥ 4
≤ 0.5	0.3414	0.0042	419		3.9354
0.5 ~ 4	0.3502	0.0029	779	1.0973	3.8396
≥ 4	0.4312	0.0139	40		

Table 3. Regression slopes of observed NPP against Level 1 WUE and LUE model predictors for three stand age classes, and t-values for all pairwise comparisons among the three classes (bold: $P < 0.05$ or better).

WUE model	slope	standard error	sample size	pairwise t-values	
stand age				< 50	> 100
< 50	0.2639	0.0040	657		4.3565
50–100	0.2654	0.0059	348	0.2146	3.9092
> 100	0.2290	0.0072	233		
LUE model	slope	standard error	sample size	pairwise t-values	
stand age				< 50	> 100
< 50	0.3674	0.0033	657		5.7791
50–100	0.3456	0.0043	348	1.8151	3.9314
> 100	0.3021	0.0055	233		

responses elsewhere, and no increase in the Tibetan Plateau region.

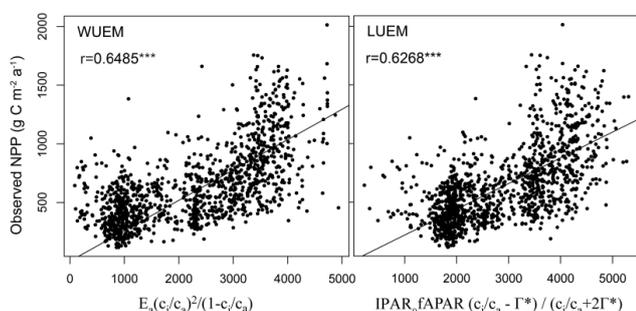
When warming and changes in precipitation were combined, both models indicated a similar tendency: the effect of precipitation change was stronger than that of warming in the north, but weaker in the south (Fig. 4). But the geographic response patterns were different. In the LUE model, warming and reduced precipitation together led to an overall NPP

reduction. Higher NPP in the north was approximately balanced by lower NPP in the south. In the WUE model warming and increased precipitation enhanced overall NPP.

The area-weighted average NPP indicates a much larger [CO₂] response of the WUE model than the LUE model (Table 4), enhancing the positive effect of precipitation increase and warming in the south while counteracting the negative effect of precipitation decrease and warming in the north. In

Table 4. Area-weighted average predicted NPP ($\text{g C m}^{-2} \text{a}^{-1}$) in baseline climate scenarios under recent $[\text{CO}_2]$ and relative changes of area-weighted average predicted ($\text{g C m}^{-2} \text{a}^{-1}$) for six climate scenarios under recent and doubled $[\text{CO}_2]$.

	recent $[\text{CO}_2]$		doubled $[\text{CO}_2]$	
	WUE model	LUE model	WUE model	LUE model
Baseline	369	393	+370	+50
Temperature +3.5 K	-7	-22	+357	+33
Precipitation -10 %	-40	-37	+290	+10
Precipitation +10 %	+36	+34	+442	+87
Temperature +3.5 K	-48	-59	+273	-8
Precipitation -10 %				
Temperature +3.5 K	+32	+13	+435	+72
Precipitation +10 %				

**Fig. 2.** Relationship between forest NPP and predictors in the Level 1 WUE and LUE models.

contrast, the $[\text{CO}_2]$ response of the LUE model was not large enough to counteract the negative effect of warming and/or reduced precipitation in some regions (Fig. 5).

Desert, widely distributed in interior northwestern China, is the least productive ecosystem type with $< 200 \text{ g C m}^{-2} \text{a}^{-1}$ WUE modelled NPP (Fig. 4). The two models showed completely different responses of desert NPP. The WUE model showed a positive response to both precipitation increase and doubled $[\text{CO}_2]$ whereas the LUE model showed little change under any conditions.

4 Discussion

4.1 Comparison with other analyses

The Level 1 LUE and WUE models were additionally fitted to Beer et al.'s GPP data, yielding slopes of 0.617 and 0.451 (Table 1) with $r = 0.88$ and 0.89 , respectively. The high correlations are to be expected, as climatic conditions play a leading role in the algorithms used by Beer et al. to extrapolate GPP. GPP values estimated in this way lack natural spatial variability due to variations in soil water capacity, nutrient availability, topography and land-use history. Such variability is not included either in Beer et al.'s procedure or

in our models, while being inherent in field NPP measurements.

By comparing estimated regression slopes for the forest NPP data and for Beer et al.'s GPP data we can obtain some approximate information about the ratio of NPP to GPP. The comparison yields an implied NPP/GPP ratio of 0.57 in both the Level 1 models (0.2589/0.4513 in the WUE model and 0.3516/0.6168 in the LUE model). The value of 0.57 can be compared e.g. with the generic value of 0.5 was suggested by Waring et al. (1998) and the mean value of 0.52 given by Zhang et al. (2009), with lower values in dense vegetation. (However, note that this is a pure model result, as the MODIS data retrievals contain no information about the NPP/GPP ratio). NPP/GPP ratios estimated by Zhang et al. (2009) for China ranged from 0.45 in the south to 0.7 in the interior. DeLucia et al. (2007) in a meta-analysis indicated NPP/GPP ratios ranging from 0.32 in old-growth boreal forests to 0.59 in temperate deciduous forests. Piao et al. (2010) indicated a range from about 0.3 to 0.5, based on a global forest NPP and CO_2 flux dataset compiled by Luysaert et al. (2007).

When the forest sites were divided into age classes, forests > 100 yr old (Fig. 3, Table 3) show lower regression slopes than the younger age classes. Lower slopes are consistent with lower GPP, and/or a reduced NPP/GPP ratio (e.g. Makela and Valentine, 2001), in old-growth forests. Either way, it is likely that somewhat higher overall values of LUE and WUE have been obtained from this managed forest data set than would be obtained for semi-natural forests with greater average age and biomass.

We compared our modelled values for forest WUE (defined as the ratio of predicted NPP to E_a) with independent determinations for the main forest types (broad-leaved deciduous, broad-leaved evergreen, needle-leaved evergreen, mixed) by Beer et al. (2009) and Zhu et al. (2011). Zhu et al. (2011) used the integrated Biosphere Simulator (IBIS) to simulate GPP and E_a in China between 2002 and 2006. WUE was calculated as the ratio of GPP to evapotranspiration for different vegetation types. The study of Beer et al. (2009) used eddy covariance data to calculate both

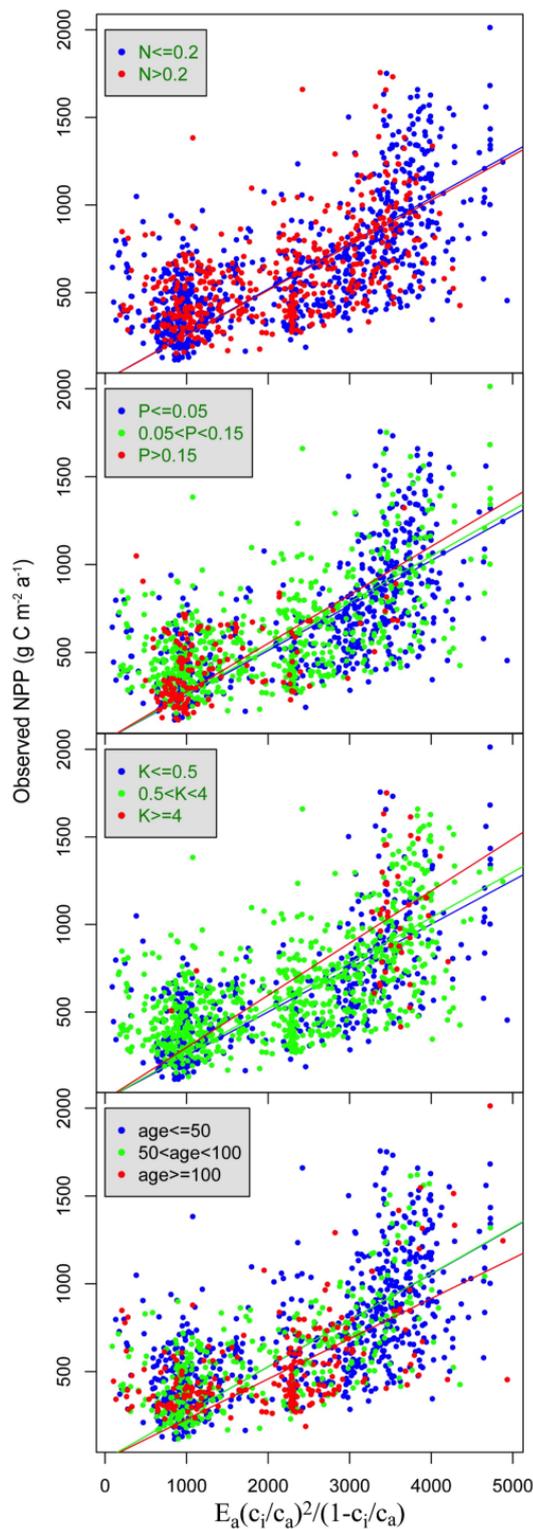


Fig. 3. Relationships between forest NPP and Level 1 WUE model predictors for different levels of soil nitrogen (N), phosphorus (P), potassium (K) concentrations, and stand ages (years).

WUE and “inherent WUE” (the product of WUE and vapour pressure deficit) for different vegetation types. Our estimates of WUE were generally consistent with those of Zhu et al. (2011) but lower than those of Beer et al. (2009) (Fig. 6). This discrepancy is likely caused by the fact that data from rainy days, which would be characterized by high interception losses, were excluded from analysis by Beer et al. (2009). The close similarity of our fitted values for WUE for evergreen broadleaved, needle evergreen and mixed forests may arise because we assumed constant c_i/c_a ratios for $MI \geq 1$.

Knorr and Heimann (1995) obtained a global LUE for NPP of $\sim 0.02 \text{ mol C mol}^{-1}$ photons based on their simple carbon cycle model, which was driven by fAPAR data and calibrated using observed seasonal cycles of atmospheric CO_2 concentration at different latitudes. This is similar to our estimated value of $0.0293 \text{ mol C mol}^{-1}$ photon, obtained from the regression slope of forest NPP on annual absorbed PAR in the Level 1 LUE model ($0.3516 \text{ g C mol}^{-1}$ photon: Table 1).

Our analyses provide no support for the hypotheses of Huston and Wolverton (2009). Huston and Wolverton hypothesized that forest NPP is lower in the tropics than in temperate regions. We find the opposite, i.e. for all models, there is a strong positive relationship between forest NPP and evapotranspiration or PAR – both variables that systematically increase from temperate towards tropical regions (Fig. 1). Huston and Wolverton also proposed that nutrient availability is the primary control on forest NPP. However, our results show that effects of nutrient availability – when considered over a large climatic range – are secondary to those of energy (whether expressed in terms of evapotranspiration or PAR) and water availability. This is clear from inspection of the relevant plots in Fig. 3, where the effects of nutrient status classes are dwarfed by the range of NPP values corresponding to the x-axis predictors (which reflect the influence of energy and water in both models). Interestingly, the largest differences in regression slopes were for K rather than for P or N, which are much more widely discussed as potential controls of productivity in ecological contexts.

The ratios of ANPP to total NPP for grassland were estimated to be 0.59 ($1 - 0.1442/0.3516$) and 0.31 ($1 - 0.1781/0.2589$) by the Level 1 LUE and WUE models, respectively (Table 1). The former value is within while the latter value is below the range of 0.40 to 0.86 estimated by Hui and Jackson (2006) based on independent field data, with the lowest values applying to the driest sites. The grassland ANPP data come from a large range of vegetation types including typical steppe, meadow steppe, desert steppe and alpine grassland, so they encompass large differences in ANPP; and also very likely in the ANPP/NPP ratio, as they include sites ranging from wet to extremely dry climates. The available data are insufficient to support a more detailed analysis. So for the present, we can have less confidence in our models’ applicability to non-forest vegetation types.

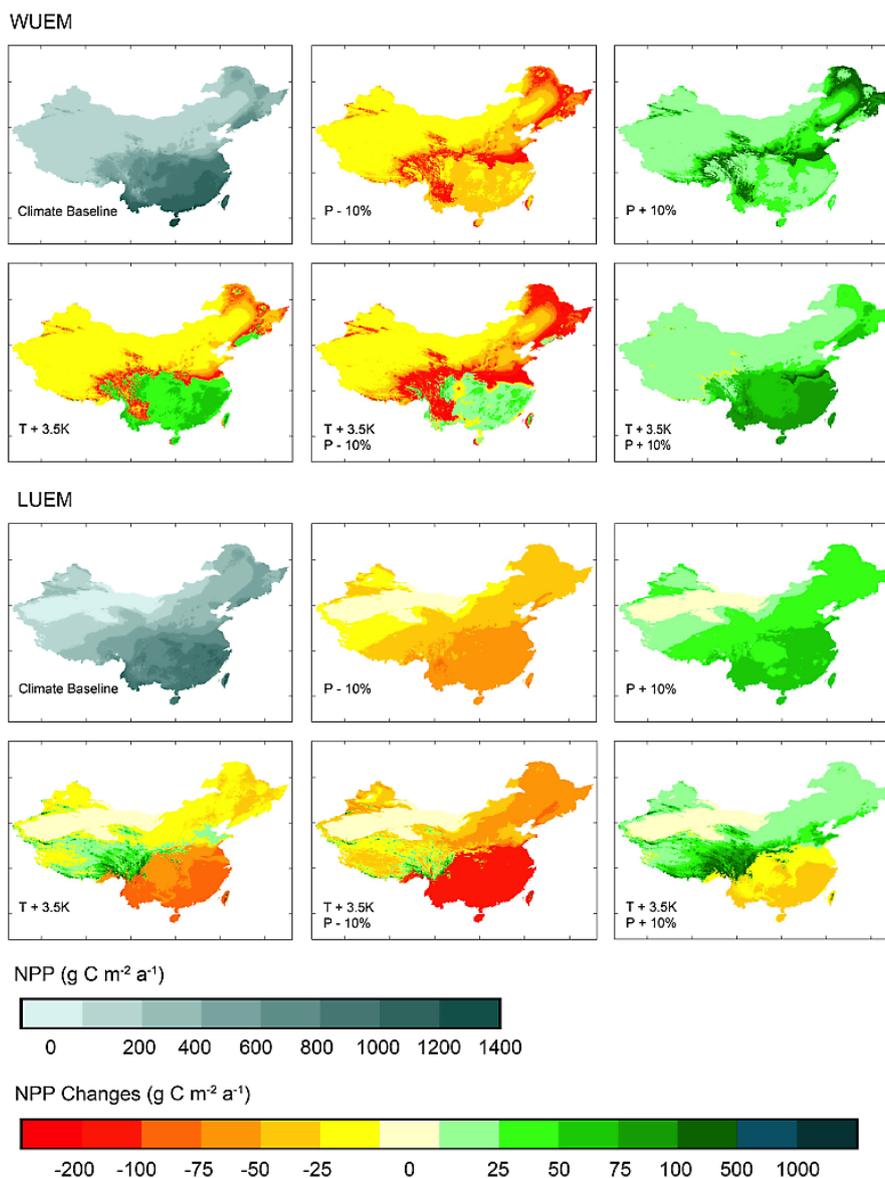


Fig. 4. The distribution pattern of NPP and NPP changes predicted by WUE model and LUE model, in six climatic scenarios under recent $[\text{CO}_2]$.

4.2 Contrasting effects of warming

In the Level 1 WUE model warming induces higher equilibrium evapotranspiration and annual plant water use, which (if all else were equal) would imply greater CO_2 uptake. However, warming also tends to increase drought, and therefore to increase the atmospheric vapour pressure deficit, resulting in stomatal closure, lower c_i/c_a ratio and reduced CO_2 uptake. The net effect of these two competing effects is to increase modelled NPP in humid South China while decreasing it in drier North China (Fig. 4).

In the Level 1 LUE model, warming reduces NPP through its effect on the CO_2 compensation point, which is higher at

high temperatures. Where warming also leads to drying, foliage cover and thus NPP are further reduced. On the other hand, since the driving variable IPAR_0 is defined as the total incident PAR integrated over the growing season, an extension of the growing season because of warming will allow more PAR to be used for photosynthesis; thus increasing NPP. In South China, where daily temperature is all above zero all year around, there can be no further extension of the growing season and therefore no positive effect on production through IPAR_0 ; but there will still be a small negative effect of warming, due to the higher CO_2 compensation point. As a result, warming has only negative effects on NPP in South China, according to this model. By contrast,

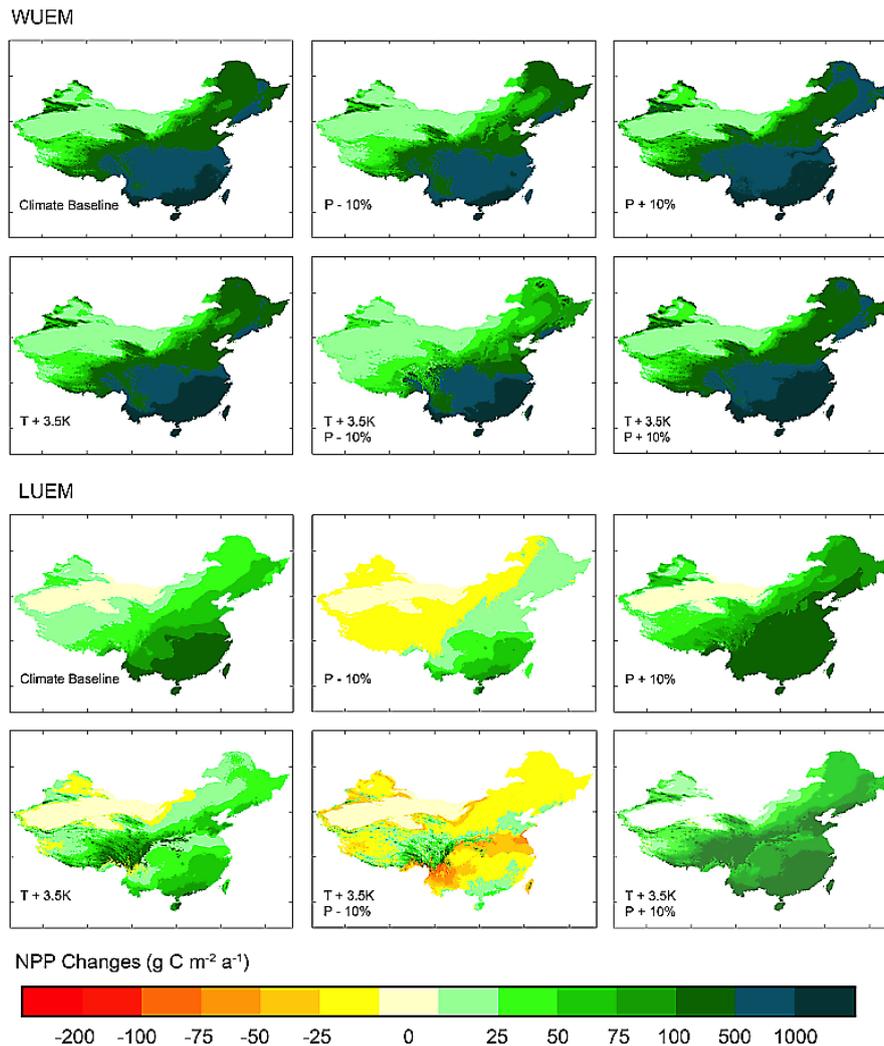


Fig. 5. The distribution pattern of NPP changes predicted by WUE model and LUE model, in six climatic scenarios under doubled $[\text{CO}_2]$.

in colder North China, warming will lead to an extension of the growing season, and this positive effect on production can easily outweigh other effects. Especially on the Tibetan Plateau, which is a high-radiation environment with a short growing season, extension of the growing season leads to an especially strong positive effect due to the large effect of increasing IPAR_0 (Fig. 4).

The modelled responses of NPP to mean annual temperature and precipitation are represented as response surfaces in Fig. 7. Even though both WUE and LUE models suggest the existence of an optimal temperature for NPP, this optimal temperature is affected differently by precipitation in the two models. In the WUE model, increased precipitation strongly shifts the optimal temperature to a higher value. In the LUE model the optimal temperature is more conservative, and modelled NPP declines with temperature above the optimum even under the warm and wet conditions found in southeastern China.

4.3 Modelled effects of $[\text{CO}_2]$ increase

In the Level 1 WUE model, NPP responds to elevated $[\text{CO}_2]$ on the assumption that actual evapotranspiration E_a is independent of $[\text{CO}_2]$. However, because stomatal conductance g_s declines with increasing $[\text{CO}_2]$ (Ainsworth and Rogers, 2007), then E_a can only be independent of $[\text{CO}_2]$ in reality if foliage cover increases to fully compensate for any decline in g_s . This might possibly be realistic for sparse vegetation, but it is very unlikely to be true for forests, where foliage is already absorbing a large proportion of the incident PAR. So the WUE model is expected to provide an upper bound for the effect of $[\text{CO}_2]$ on productivity.

On the other hand, in the Level 1 LUE model, foliage cover is explicitly assumed not to adjust to the change in $[\text{CO}_2]$ as a constant relationship between $f\text{APAR}$ and MI is assumed to hold. This is probably unrealistic for sparse vegetation, but it may be a reasonable approximation for forests. Thus, this

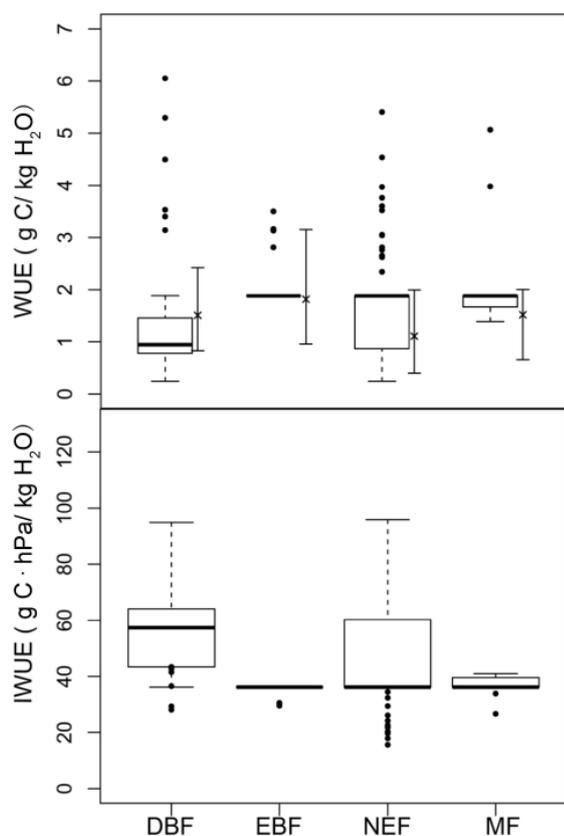


Fig. 6. Boxplot of water use efficiency (WUE) and inherent water use efficiency (IWUE) predicted by the Level 0 WUE model for four forest types: broad-leaved deciduous (DBF), broad-leaved evergreen forest (EBF), needle-leaved evergreen forest (NEF), mixed forest (MF), compared with the results from Beer et al. (2009), indicated by scatter points, and from Zhu et al. (2011), indicated by the line segment (range) with a cross symbol (mean value).

application of the LUE model will yield a lower bound for the CO_2 effect (in so far as the CO_2 response is not additionally constrained by other factors, such as nutrient availability), and may be reasonably realistic for forests.

The response surfaces (Fig. 7) imply that the effect of $[\text{CO}_2]$ elevation in the models does not greatly modify the pattern of NPP response to climate, but does affect the sensitivity of NPP to climate.

4.4 Caveats

Both models have been implemented in a very simple way, probably leading to unrealistically abrupt spatial changes of sign in the responses of NPP to temperature and $[\text{CO}_2]$. In the WUE model, the abrupt change in the temperature response occurs because the assumed values of the c_i/c_a ratio have an imposed discontinuity at $\text{MI}=1$, so that when $\text{MI} > 1$ warming-induced increases in vapour pressure deficit no longer reduce productivity. In the LUE model, the abrupt

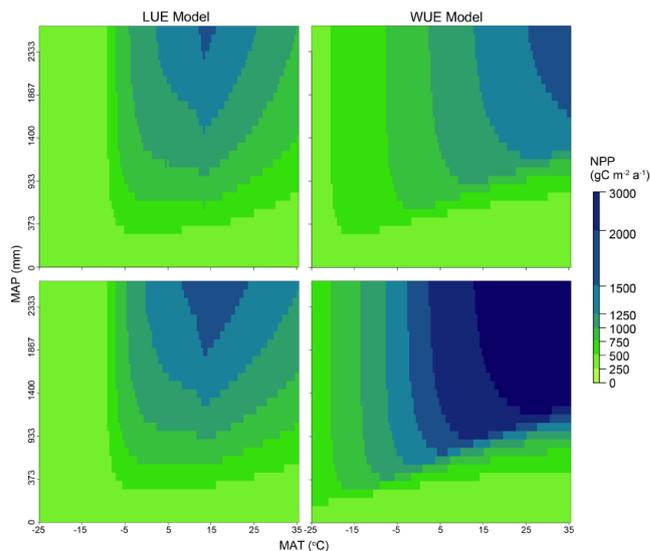


Fig. 7. Annual NPP responses to mean annual temperature (MAT) and mean annual precipitation (MAP) predicted by the LUE and WUE models under recent (upper panel) and doubled (lower panel) $[\text{CO}_2]$. Seasonal cycles of monthly values corresponding to each value of MAT were obtained by adding a constant to the mean seasonal cycle across all the NPP mensuration plots. Monthly values corresponding to each value of MAP were obtained by multiplying the mean seasonal cycle by a constant. These conventions provide a reasonable approximation to the range of climatic conditions found in China.

change in the temperature response occurs because of the discontinuity in IPAR_0 when all days are included in the growing season. The calculation ignores variability within the colder months; if included, this variability would probably induce a smoother transition between temperature-limited and unlimited growing seasons lengths and would allow the growing-season length to continue increasing even when the mean temperature of the coldest month is greater than 0°C .

Nevertheless, the simple formulations adopted here seem qualitatively reasonable. The discontinuities in both models' responses occur along the natural boundary between the warm-temperate (predominantly evergreen) forests of South China and the temperate (deciduous and mixed) forests of North China. The c_i/c_a ratio is likely to be well below 1, as it can only be equal to 1 in the absence of net photosynthesis. Some cut-off or asymptote in the response of c_i/c_a to water availability is therefore inescapable. It is also undeniable that in sufficiently warm climates, with evergreen vegetation, further warming will no longer add to growing season length and therefore to utilized PAR. Thus, even if more realistic formulations allowed for smooth transitions between regimes, there would still be two regimes for each model and the sign of the responses of the two models would still be opposite in the warm, wet region of South China and in the colder, drier regions to the north and west.

4.5 Implications for modelling

Our analysis of the qualitative discrepancy between two alternative simple model formulations highlights the importance of the response of vegetation cover to $[\text{CO}_2]$, which is not well studied. The results have implications not only for the effect of $[\text{CO}_2]$ on NPP but also for the (controversial) possible positive effect of $[\text{CO}_2]$ on freshwater runoff (Gedney et al., 2006). The reason is simply that if vegetation cover increases to compensate for reduced g_s , as is implicitly assumed by the WUE model, then there will be no increase in runoff. On the other hand if vegetation cover does not increase in response to $[\text{CO}_2]$, as is explicitly assumed by the LUE model, then reduced g_s would be expected to lead to an increase in runoff. Thus, the contrast between the two models highlights the fact that effects of $[\text{CO}_2]$ in increasing foliage cover and increasing runoff are complementary. The WUE model represents one extreme case, in which foliage cover is allowed to increase as required to increase NPP in proportion to $[\text{CO}_2]$. The LUE model represents the opposite case in which foliage cover maintains a fixed relationship with MI irrespective of $[\text{CO}_2]$.

Even though this first-principles analysis illustrates a potential cause of the differences (even in sign) in the global NPP response of dynamic global vegetation models to $[\text{CO}_2]$ and climate change (Denman et al., 2007), there is no clear evidence for which response is more realistic in all vegetation types, or how some compromise between these models should be formulated. We therefore conclude that it is important for observational and experimental studies to explicitly address the two key differences in the model predictions of $[\text{CO}_2]$ response, i.e. the extent to which vegetation cover in different ecosystems increases (or not) and the extent to which water use decreases (or not), and the sign and magnitude of the NPP response to warming in the warmer and colder regions.

4.6 Implications for global change impacts on NPP in China

Some tentative conclusions can be drawn about the response of NPP of China's ecosystems to global environmental change. Some positive effect of increasing $[\text{CO}_2]$ is to be expected generally. The effect on NPP is likely to be greater in semi-arid regions where foliage cover can increase, whereas the effect on runoff is likely to be greater in wetter regions. The effect of precipitation changes will depend directly on the sign of those changes, which may well be opposite in different regions (Meehl et al., 2007). The response to warming however remains unresolved.

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