Biogeosciences Discussions

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 two semi-empirical models based on the light use efficiency (LUE) and water use efficiency (WUE) concepts, respectively. Results are shown to be broadly consistent with other data sets (grassland above-ground NPP; globally extrapolated gross primary production, GPP) and published analyses. But although both models describe the data about equally well, they predict notably different responses to [CO_2] and temperature. These are illustrated by sensitivity tests in which [CO_2] 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. The [CO_2] response of the WUE model is much larger but is probably an overestimate for dense vegetation as it assumes no increase in runoff; while the [CO_2] response of the LUE model is probably too small for sparse vegetation as it assumes no increase in vegetation cover. In the LUE model warming reduces total NPP with the strongest effect in South China, where the growing season cannot be further extended. In the WUE model warming increases total NPP, again with the strongest effect in South China, where abundant water supply precludes stomatal closure. The qualitative differences between the two formulations illustrate potential causes of the large differences (even in sign) in the global NPP response of dynamic global vegetation models to [CO_2] and climate change. As it is not clear which response is more realistic, the issue needs to be resolved by observation and experiment.

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 and atmospheric carbon dioxide concentration ([CO_2]) and to quantify the feedbacks from climate change to

[CO$_2$] (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 [CO$_2$] increase alone ("CO$_2$ 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 (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 be inconsistent with atmospheric constraints indicating that warming reduces terrestrial carbon storage and increases atmospheric [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), and a smaller data set of grassland NPP measurements, to explore the predictions made by simple, theoretically derived semi-empirical 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 [CO_2] and climate. Because of the relative simplicity of the models we can 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 (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, Caemmerer and Berry (1980) model of photosynthesis. An important assumption of this analysis is that photosynthetic capacity acclimates to environmental conditions so as to maximize daily net photosynthesis at the leaf level (Haxeltine and Prentice, 1996b; Dewar, 1996).

Two simplifying assumptions underpin our approach to developing semi-empirical models based on the WUE and LUE concepts. (1) We assume that light, water and [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) NPP is assumed to be an approximately constant fraction of GPP – that is, annual autotrophic respiration is assumed to be a fixed fraction of GPP or, equivalently, that carbon use efficiency is constant across different environments and climates (Waring et al., 1998). This appears to be contrary to the analysis of Piao 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 is independent of mean annual temperature when the distinction between managed and old-growth forests is taken into account (S. Piao, P. Ciais, personal communication, January 2011). The NPP data we use are from managed forests. Both assumptions are re-examined later.

We began by fitting the simplest possible models, seeking proportionality between annual NPP and either annual water use (evapotranspiration) or annual absorbed PAR (taking account of the considerable spatial variation in fAPAR). We also provide theoretical derivations for closely similar models that take account of how vapour pressure deficit affects WUE, and how the temperature-dependence of the CO$_2$ compensation point affects LUE. These theoretical derivations provide a basis for analysing the responses of the models to environmental changes.

2.2 Data

2.2.1 NPP data

1238 plot-based records of forest NPP observation data 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. The data in Luo (1996) are

provided in tonnes (Mg) dry matter ha^{-1} a^{-1}. We converted the data to g C m^{-2} a^{-1}, using a factor of 0.5 to convert dry matter to carbon content.

We also used 135 records of aboveground NPP (ANPP) compiled by Ni (2004) from field measurements of grasslands in northern China. Although Ni (2004) derived total NPP from these sites, the results are strongly dependent on the estimates used for 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 aboveground NPP measurements in this study, as they are closer to the primary observations. We then examine the implications of our findings for ANPP/NPP ratios.

2.2.2 Environmental 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 $>0\,°C$) of accumulated growing degree days above $0\,°C$ (mGDD$_0$, equivalent to growing-season mean temperature), the total annual incident photosynthetically active radiation during the growing season (PAR$_0$), annual equilibrium evapotranspiration (E_q), and the climatic moisture index (MI = MAP/E_q where MAP is mean annual precipitation). Annual actual evapotranspiration (E_a) was calculated from MI using a minor modification of the Zhang equation: $E_a = E_q$ [1 + MI − (1 + MI^w)$^{1/w}$] with $w = 3$ and with E_q used instead of the Priestley-Taylor potential evaporation E_p as originally used ($E_p = 1.26\,E_q$: Zhang et al., 2004). The soil-moisture accounting algorithm of Prentice et al. (1993) was also tried, with soil water holding

capacities assigned as in Wang, Ni and Prentice (2011). 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 $mGDD_0$, PAR_0, E_q, and MI and E_a estimated from the Zhang equation, are mapped in Fig. 1. The contents of three soil

5 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).

2.2.3 Ecophysiological data

fAPAR represents the fraction of absorbed PAR by green plants, which is an index of foliage cover. We used monthly fAPAR data on a 0.5° grid from SeaWiFS (Gobron et

10 al., 2006) to derive an annual fAPAR field, also in Fig. 1. 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).

Although we have data on fAPAR, a model is required to predict changes in fAPAR

15 with changes in environment. On the assumption that water availability is the main control of annual fAPAR over the study region, we fitted an empirical relationship for fAPAR as a function of MI:

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

using non-linear regression. This function was used to account for variation of fAPAR

20 in the LUE model.

The ratio of internal CO_2 concentration (c_i) to ambient CO_2 concentration (c_a) is an index of the regulation of stomatal conductance. We estimated effective growing-season values of c_i/c_a as follows:

$$c_i/c_a = 0.426 + 0.417\text{MI} \tag{2}$$

25 This expression combines the standard approximation for $\delta^{13}C_{\text{leaf}}$ (Farquhar et al., 1982; Farquhar et al., 1989) with an empirical regression equation for $\delta^{13}C_{\text{leaf}}$ 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). Equation (2) was used to provide estimates of the dependence of c_i/c_a on water availability in both the WUE and LUE models. 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 MI $\geq$ 1. Estimated values of c_i/c_a are mapped in Fig. 1.

The CO_2 compensation point Γ^* 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:

$$\Gamma^* = \Gamma^*_{25}\exp(0.0512\Delta T) \tag{3}$$

where ΔT is the difference between the measurement temperature in degrees Celsius (T_C) and 25°C. We substituted the mean growing season temperature (mGDD$_0$) for T_C in order to estimate an effective growing-season value of Γ^* as mapped in Fig. 1.

2.3 Models

2.3.1 Theoretical derivation of a 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:

$$A = g_s c_a (1 - c_i/c_a) \tag{4}$$

where A is GPP and g_s is stomatal conductance to CO_2. 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.

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

$$E = 1.6 g_s D \tag{5}$$

where E is transpiration and D is the 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 simple WUE model from Eqs. (4) and (5):

$$A = 0.63 q (c_a/D)(1 - c_i/c_a) E_a \tag{6}$$

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

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:

$$D = \xi^2 (1 - c_i/c_a)^2 / (c_i/c_a)^2 \tag{7}$$

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 plants

adapted to dry environments appear to show a weak response to soil water potential. In general, based on analysis of published drying experiments, variations in c_i/c_a with soil moisture appear to be slight compared with its response to D (S. Zhou, R. Duursma, B. Medlyn and I. C. Prentice, unpublished results). Accordingly, we do not consider variation in ξ when estimating D. 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, as they are based on observed ^{13}C discrimination by plants growing in their natural environment.

Substituting Eqs. (7) into (6), we then obtain:

$$A = 0.63q\xi^2 c_a E_a (c_i/c_a)^2/(1 - c_i/c_a) \tag{8}$$

and NPP as a fraction of A. We fitted NPP data first simply by linear regression on E_a, then on the product $E_a (c_i/c_a)^2/(1 - c_i/c_a)$ with c_i/c_a estimated from Eq. (2).

2.3.2 Theoretical derivation of a LUE model

The light use efficiency model as derived here starts 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 is equivalent to assuming the 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:

$$A = \text{fAPAR}\phi_o I (c_i - \Gamma^*)/(c_i + 2\Gamma^*) \tag{9}$$

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where I is incident photosynthetically active radiation (PAR) integrated over the growing season, and ϕ_o is the intrinsic quantum efficiency. The fAPAR term is needed because I applies to a unit of ground area, while only a fraction of I is absorbed by leaves.

It is implicit in this simplified equation that not only the Rubisco capacity (V_{cmax})
5 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_{max}/V_{max} in wild plants (Wullschleger, 1993) supports this assumption. NPP is again assumed to be a fixed fraction of A. We fitted NPP data first by linear regression on the product fAPAR $\cdot I$ with fAPAR estimated
10 by Eq. (1); then on the product fAPAR $\cdot I(c_i - \Gamma^*)/(c_i + 2\Gamma^*)$ with c_i/c_a estimated from Eq. (2) and Γ^* from Eq. (3).

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
15 suitable breakpoints based on histograms of the values) and performed separate per-formed 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).
20 As an additional, independent source of primary production data, we used the glob-ally extrapolated GPP field at 0.5° resolution derived from a global data set of flux measurements by Beer et al. (2010). We fitted the WUE and LUE models to these data and compared the resulting regressions with our regressions using NPP, thus obtaining an estimate of the NPP/GPP ratio as well as an independent check of the models.
25 Grasslands occupy a large area of China and play a significant role in China's ter-restrial carbon cycle. We therefore tested the models' applicability to grasslands as well as forests. We fitted WUE and LUE models using the grassland ANPP dataset, and compared the results with those obtained for forest NPP. If the true relationships of

NPP in forests and grasslands to the predictors were similar then the ratio of the slopes obtained for grassland ANPP and forest NPP would predict the fractions of grassland NPP allocated above ground. We compared these ratios to the results of Hui and Jackson (2006), whose estimates of below-ground NPP were based on 94 site-years of field biomass measurements at twelve grassland sites around the world, as a check on this assumption.

2.5 Statistical analysis

Slopes were estimated using ordinary least-squares linear regression with intercepts fixed to zero (because a non-zero intercept would have no meaning in the context of either the WUE or the LUE model). Model-data agreement was quantified by Pearson correlation coefficients.

2.6 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 ±10 %. We considered changes of each single climatic factor, and both together, under recent $[CO_2]$ (366 ppm) and doubled $[CO_2]$ (732 ppm). For each projected climate and $[CO_2]$ 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

Simple regressions of forest NPP on water used (E_a) and light absorbed ($I \cdot \text{fAPAR}$) are highly significant, and the associated correlation coefficients are closely similar ($r = 0.654$ for both) (Table 1). The theoretically derived WUE and LUE models also yielded highly significant regressions, and correlation coefficients very similar to those from the simple models ($r = 0.649, 0.627$) (Table 1, Fig. 2). That these correlations are slightly smaller than those obtained with the simple regressions suggests that the theoretically derived models could be improved, but the differences are small, and the theoretically derived models are needed for the analysis later on.

Comparisons of regression slopes for different soil nutrient status classes (Table 2, Fig. 3) show some statistically significant difference for P and K, but the differences are small. For example, there is a significant difference between WUE model slopes for low and high P concentration, but the magnitudes differ by only 7.6 %. The largest and most significant percentage difference (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 status classes showed no significant differences.

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 [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 [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: $-40\,\mathrm{g\,C\,m^{-2}\,a^{-1}}$ (WUE model) and $-37\,\mathrm{g\,C\,m^{-2}\,a^{-1}}$ (LUE model) with less precipitation, and $+36\,\mathrm{g\,C\,m^{-2}\,a^{-1}}$ (WUE model) and $+34\,\mathrm{g\,C\,m^{-2}\,a^{-1}}$ (LUE model) with more precipitation. The responses of NPP to precipitation were in the same direction under doubled $[CO_2]$. Both models also indicated a regional heterogeneity in the NPP response to precipitation change. Under recent $[CO_2]$, 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 $-22\,\mathrm{g\,C\,m^{-2}\,a^{-1}}$ (LUE model). But 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 $50\,\mathrm{g\,C\,m^{-2}\,a^{-1}}$ were simulated (Fig. 4). In the WUE model, NPP generally increased by $>25\,\mathrm{g\,C\,m^{-2}\,a^{-1}}$ in South China, with negative 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). 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 $[CO_2]$ response of the WUE 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. The $[CO_2]$ response of the LUE model was smaller, and 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 $<200\,\mathrm{g\,C\,m^{-2}\,a^{-1}}$ 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 [CO_2] whereas the LUE model showed little change under any conditions.

4 Discussion

4.1 Comparison with other analyses

Slopes estimated using Beer et al.'s GPP data were 0.598 and 0.418 (Table 1) with $r = 0.93$ and 0.91, respectively, for the LUE and WUE models. The high correlations are to be expected, as climatic conditions play a leading role in the empirical algorithm used by Beer et al. to extrapolate GPP. GPP values estimated in this way lack natural variability due to possible variations in soil water capacity, nutrient availability, topography or 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. Nevertheless by comparing estimated regression slopes for NPP data and Beer et al.'s GPP we can obtain an implied NPP/GPP ratio of $a = 0.62$ (WUE model) or 0.37 (LUE model), similar to previous estimates. For example, a generic value of 0.5 was suggested by Waring et al. (1998). Zhang et al. (2009) gave a mean value of 0.52 with lower values in dense vegetation (however, note that this is a pure model result, as the MODIS data retrievals contain no information about a). DeLucia et al. (2007) conducted a meta-analysis after compiling 60 data points obtained from 26 papers published since 1975 and suggested the average value of a ranged from 0.32 for old-growth boreal forests to 0.59 for temperate deciduous forests. Piao et al. (2010) indicated a range from 0.3 to 0.5 based on a global forest C-flux dataset developed by Luyssaert et al. (2007). Our results however are consistent with a reduced NPP/GPP ratio in forest stands $>100\,\mathrm{yr}$ old, as predicted e.g. by Mäkela and Valentine (2001).

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). Our predictions were generally consistent with the estimation of Zhu et al. (2011) but lower than the estimates 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. (2010). 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 ($\sim$0.02 mol C mol^{-1} photons) based on their simple carbon cycle model, which was calibrated using observed seasonal cycles of atmospheric CO_2 concentration at different latitudes. This estimate is of a similar magnitude to ours, obtained from the regression slope of forest NPP on annual absorbed PAR. The slope of the fitted LUE model can be interpreted as an estimate of the product $a\phi_o$. With NPP converted to molar units, this slope is estimated here to be about 0.03. If we assume $a = 0.5$ (the mean value of estimations from WUE model and LUE model), the value of $\phi_o = 0.06$ given by Farquhar, Caemmerer and Berry (1980) also yields a similar slope (0.03). The data provide no support for (indeed, they contradict) the hypotheses of Huston and Wolverton (2009) that NPP is lower in the tropics than in temperate regions, and that nutrient availability is the primary control on forest NPP.

The ratios of ANPP to total NPP for grassland were estimated to be 0.59 and 0.31 by the LUE and WUE models, respectively. These values are of a similar magnitude to the range from 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 general consistency of our estimated ANPP/NPP ratios with Hui and Jackson's results suggested that the two semi-empirical models, developed for forests, are applicable to sparse ecosystem types as well. Their underlying theoretical basis applies to all C_3-dominated ecosystems.

The grassland ANPP data come from several different types: typical steppe, meadow steppe, desert steppe, alpine grassland and others, encompassing large differences in ANPP and also very likely in the ANPP/NPP ratio, as well as some C_4-dominated types. A more precise estimation would require separate analysis of different grassland types but the data available are insufficient to support this.

4.2 Contrasting effects of warming

In the 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 χ 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 LUE model, warming reduces NPP through its effect on the CO_2 compensation point (higher at high temperatures). Where warming leads to drying, foliage cover and thus NPP are reduced. On the other hand, warming leads to extension of the growing season, allowing more PAR to be used for photosynthesis, and increasing NPP. In South China, where daily temperature is all above zero all year around, there can be no further positive effect of warming through an extension of the growing season. As a result, warming has only negative effects on NPP in South China according to this model. In colder North China, the effect of an extended growing season outweighs the negative effects of warming. On the Tibetan Plateau, with high PAR but a short growing season, extension of the growing season leads to an especially strong positive effect due to the large positive effect of increasing PAR_0 (Fig. 4).

4.3 Modelled effects of [CO_2] increase

In the WUE model, NPP responds to elevated [CO_2] on the assumption that actual evapotranspiration E_a is independent of [CO_2]. However, because stomatal

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conductance g_s declines with increasing [CO_2] (Ainsworth and Rogers, 2007), then E_a can only be independent of [CO_2] if foliage cover increases to fully compensate for any decline in g_s. This may 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 [CO_2] on productivity.

On the other hand, in the LUE model, foliage cover is assumed not to adjust to the change in [CO_2], as a constant relationship between fAPAR and MI is assumed to hold. This is probably unrealistic for sparse vegetation, but it may be a reasonable approximation for forests. Thus, this 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.

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 [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 MI = 1, so that when MI > 1 warming-induced increases in vapour pressure deficit no longer reduce productivity. In the LUE model, the abrupt change in the temperature response occurs because of the discontinuity in PAR_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 are 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

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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 any 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
5　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.

10　**4.5　Implications for modelling**

This analysis of the qualitative discrepancy between the two formulations highlights the importance of the (generally poorly known) response of foliage cover to $[CO_2]$, both for the effect of $[CO_2]$ on NPP and also for the (controversial) possible effect of $[CO_2]$ on freshwater runoff (Gedney et al., 2006). The contrast between the two models
15　highlights the fact that *effects of $[CO_2]$ 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 $[CO_2]$. This assumption, which is likely to be far from realistic for continuous vegetation, arises because it is assumed a priori that no increase in runoff will occur in response to
20　increasing $[CO_2]$. The LUE model represents the opposite case in which foliage cover maintains a fixed relationship with MI irrespective of $[CO_2]$. This assumption is probably not be realistic for sparse vegetation, but it does carry the implication that runoff in more densely vegetated regions would be expected to increase with increasing $[CO_2]$.

　　Even though this first-principles analysis illustrates a potential cause of the differ-
25　ences (even in sign) in the global NPP response of dynamic global vegetation models to $[CO_2]$ and climate change (Denman et al., 2007), there is no clear evidence for which response is more realistic or how some compromise between these models should be formulated. We therefore conclude that it is important for observational and

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experimental studies to explicitly address the two key differences in the model predictions of [CO_2] response, i.e. the extent to which vegetation cover in different ecosystems increases (or not) and the extent to which runoff increases (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 [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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Table 1. Linear regressions of NPP: correlation coefficients and regression slopes (without intercept).

	A versus E_a		A versus $I \cdot$fAPAR	
	r	*slope*	r	*slope*
Forest NPP	0.6544	1.0712	0.6536	0.2806

$$A = 0.63q\xi^2 c_a E_a \, (c_i/c_a)^2/(1 - c_i/c_a)$$

	r	slope	NPP/GPP	BNPP/NPP
GPP	0.9068	0.4180	0.2589/0.418=	
Forest NPP	0.6485	0.2589	0.62	1−0.1781/0.2589=
Grass ANPP	0.3363	0.1781		0.31

$$A = \phi_o I \cdot \text{fAPAR} \, (c_i - \Gamma^*)/(c_i + 2\Gamma^*)$$

	r	slope	NPP/GPP	BNPP/NPP
GPP	0.9305	0.5980	0.2196/0.5980=	
Forest NPP	0.6268	0.2196	0.37	1−0.0899/0.2196=
Grass ANPP	0.3055	0.0899		0.59

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Table 2. Regression slopes of observed NPP against 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	t-test	
N concentration				<0.2	
<0.2	0.2219	0.0030	775		
>=0.2	0.2152	0.0039	463	1.3633	
P concentration				≤0.05	≥0.15
≤0.05	0.2199	0.0035	515		**2.8518**
0.05~0.15	0.2226	0.0037	275	0.4909	**3.3671**
≥0.15	0.1982	0.0071	144		
K concentration				≤0.5	≥4
≤0.5	0.2133	0.0042	419		**3.9354**
0.5~4	0.2188	0.0029	779	1.0973	**3.8396**
≥4	0.2694	0.0139	40		

Table 3. Regression slopes of observed NPP against 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	0.2295	0.0033	657		**5.7791**
50~100	0.2159	0.0043	348	1.8151	**3.9314**
>100	0.1887	0.0055	233		

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Table 4. Area-weighted average predicted NPP ($g\,C\,m^{-2}\,a^{-1}$) in baseline climate scenarios under recent [CO_2] and relative changes of area-weighted average predicted ($g\,C\,m^{-2}\,a^{-1}$) for six climate scenarios under recent and doubled [CO_2].

	recent [CO_2]		doubled [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 Precipitation −10 %	−48	−59	+273	−8
Temperature +3.5 K Precipitation +10 %	+32	+13	+435	+72
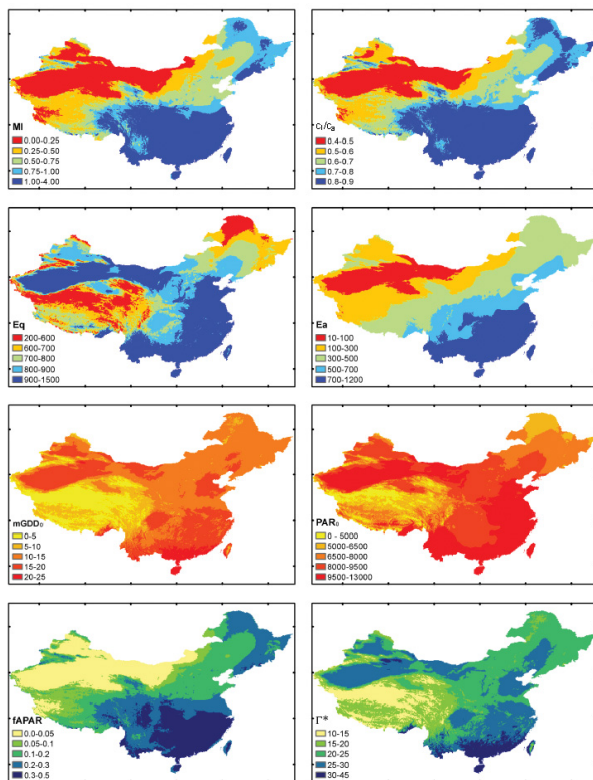
Fig. 1. The distribution pattern of eight environmental or physiological variables: moisture index (MI), ratio of c_i to c_a, equilibrium evapotranspiration (E_q, unit: mm), actual evapotranspiration (E_a, unit: mm), mean temperature of growing-degree days on a basis of 0 centigrade (mGDD$_0$, unit: centigrade), accumulative photosynthetic active radiation during growing season, when daily temperature above 0 centigrade (PAR$_0$, unit: mol photons), fraction of absorbed photosynthetic active radiation (fAPAR), CO_2 compensation point (Γ^*).
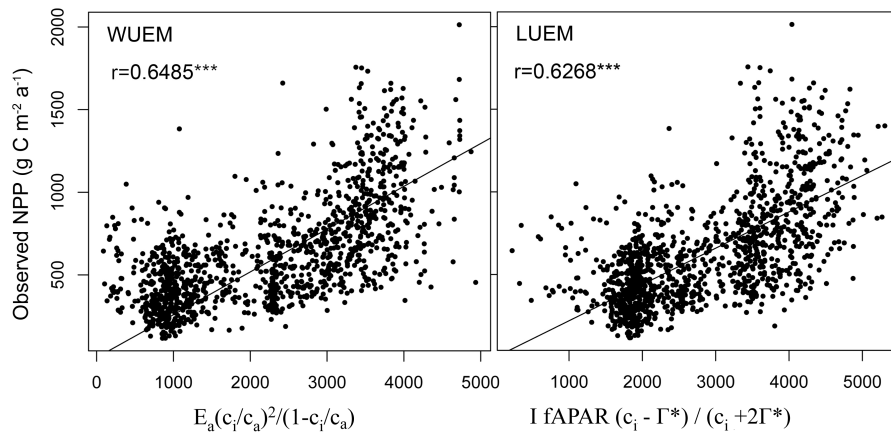
Fig. 2. Relationship between observed NPP and predictors in WUE model and LUE model.

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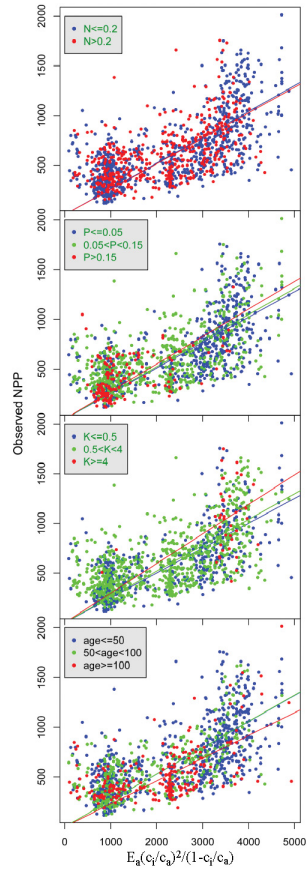
Fig. 3. Relationships between observed NPP and WUE model predictors for different levels of soil Nitrogen (N), Phosphorus (P), Potassium (K) concentrations and stand ages (years).
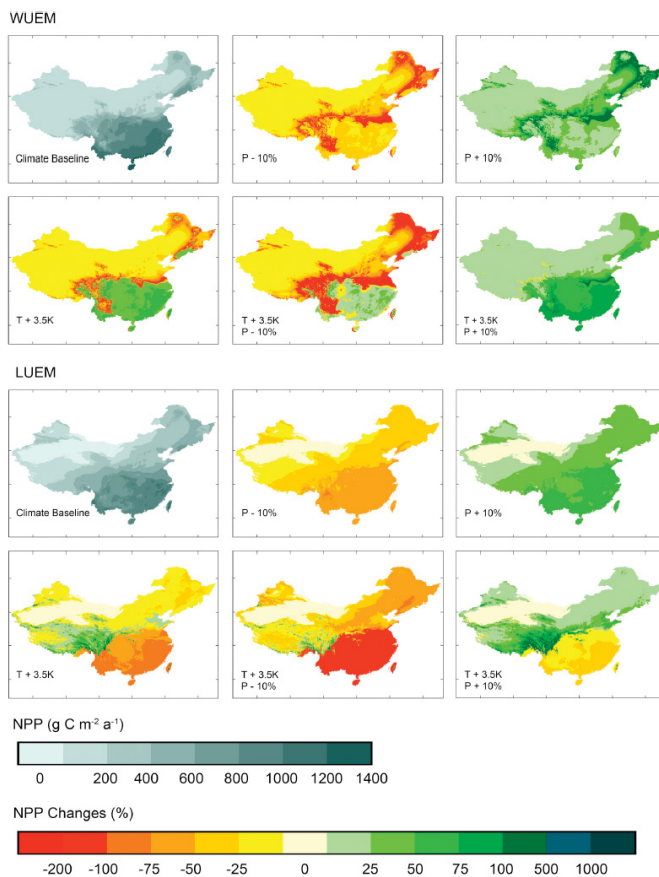
Fig. 4. The distribution pattern of NPP and NPP changes predicted by WUE model and LUE model, in six climatic scenarios under recent [CO_2].
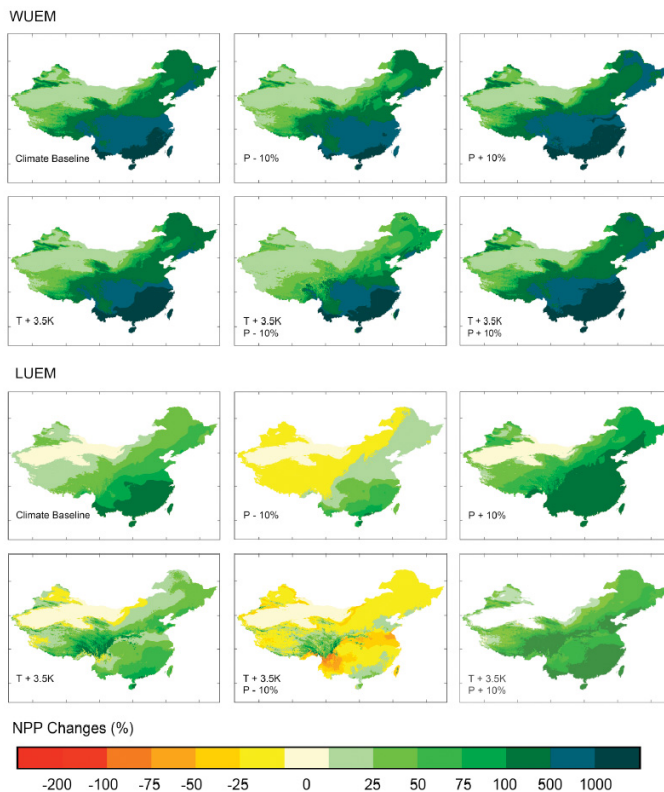
Fig. 5. The distribution pattern of NPP changes predicted by WUE model and LUE model, in six climatic scenarios under doubled [CO_2].
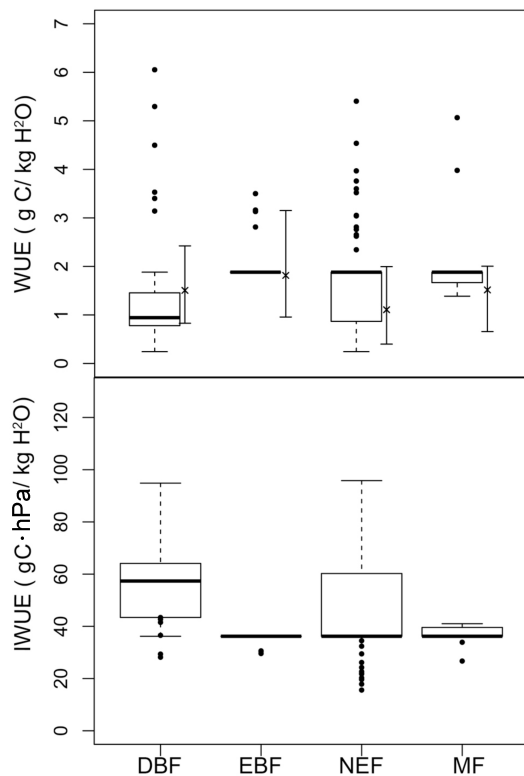
Fig. 6. Boxplot of water use efficiency (WUE) and inherent water use efficiency (IWUE) predicted by WUE model for four forest types: broad-leaved deciduous (DBF), broad-leaved evergreen forest (EBF), needle-leaved evergreen forest (NEF), mixed forest (MF), compared with the results from Beer et al. (2009), indicating by scatter points, and from Zhu et al. (2011), indicating by the line segment (range) with a cross symbol (mean value).