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Climate dependence of the CO_2 fertilization effect on terrestrial net primary production

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ABSTRACT

The quantitative formulation of the fertilization effect of CO_2 enrichment on net primary production (NPP) introduced by Keeling and Bacastow in 1970s (known as Keeling's formula) has been recognized as a summary of experimental data and has been used in various assessments of the industrial impact on atmospheric chemistry. Nevertheless, the magnitude of the formula's key coefficient, the so-called growth factor, has remained open to question. Some of the global carbon cycle modelers avoid this question by tuning growth factor and choosing the value that fits the observed course of atmospheric CO_2 changes. However, for mapping terrestrial sinks induced by the CO_2 fertilization effect one needs a geographical pattern of the growth factor rather than its globally averaged value. The earlier approach to this problem involved formulating the climate dependence of the growth factor and the derivation of its global pattern from climatic variables (whose geographical distribution is known). We use a process-based model (TsuBiMo) for this purpose and derive the values of growth factor for major biomes for comparison our approach with the earlier studies. Contrary to the earlier prevailing opinion, TsuBiMo predicts that these values decrease with mean annual temperature (excluding biomes of limited water supply). We attribute this result to the effect of light limitation caused by mutual shading inside a canopy, which was considered earlier as unimportant, and conclude that current hypotheses about CO_2 fertilization effect (and thus projections of the related carbon sink) are very sensitive to the choice of driving forces taken into account.

1. Introduction

The most general mechanism lying behind the sequestration of extra CO_2 by terrestrial ecosystems is the fertilization effect of CO_2 enrichment. It was known as far back as in the early 1900s and used in the theory of climate change proposed then by Arrhenius. The quantitative formulation of this mechanism introduced by Keeling and Bacastow in the 1970s (Bacastow and Keeling, 1973) was widely used in the assessments of the industrial impact on atmospheric chemistry and received the name 'Keeling's formula':

$$NPP(C_a) = NPP_0\left[1 + \gamma \ln\left(C_a/C_a^0\right)\right], \quad (1)$$

where C_a is ambient CO_2 concentration, γ is growth factor (β in original notation), C_a^0 is some baseline concentration of CO_2 (e.g. pre-industrial), $NPP_0 = \mathrm{NPP}(C_a^0)$.

Experimental data support Keeling's formula in the sense that observed increment in NPP is normally proportional to the logarithm of CO_2 concentration. However, the magnitude of the coefficient of proportionality (the so-called "growth factor") is not constrained by the experimental data: its value varies widely from one experiment to another. Statistical analysis of available data (Kimball, 1983; Wullschleger et al., 1995) shows that average value of the growth factor measured in controlled-exposure studies falls in the range between 0.35 and 0.6. This does not necessarily mean that the growth factor as a parameter of a global carbon cycle model must lie in the same range. The collections of

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experimental data are prejudiced toward some regions of the world, and hence the value of the growth factor at the global scale is open to question. Global carbon cycle modelers use a wider range of growth factor values: from 0.2 (Oeschger et al., 1975) to 0.6 (Gifford, 1980); they tune it to match the land-use emission estimate (e.g. Kheshgi et al., 1996) and to obtain the same value of net terrestrial uptake as deconvoluted from the CO_2 and $\delta^{13}C$ records.

For mapping terrestrial sinks induced by CO_2 fertilization effect one needs a geographical pattern of the growth factor rather than its globally averaged value[1]. This problem may be approached by considering the climate dependence of the growth factor. Thus, Polglase and Wang (1992) assessed inter-biome differences in growth factor by using a climate dependence that they derived from the formula of Farquhar and von Caemmerer (1992) for the photosynthetic rate of a leaf and Farquhar's formula (Farquhar, 1989) for the temperature dependence of the CO_2 compensation point for gross photosynthesis. This approach is some sort of 'geographic modeling' (Box and Meentemeyer, 1991). As in the case of 'geographical modeling', Polglase and Wang use a model linking the variable under interest with some climatic variables of known geographical distribution, and thus obtain the geographical distribution of the variable under interest.

In this paper we derive the climate dependence of the growth factor by use of a process-based NPP model. First, we simulate the CO_2 effect on NPP along the geographical grid of half-degree resolution. Then, we approximate the results of simulation by Keeling's formula and find corresponding values of growth factor. Next, we plot these values against mean annual temperature to reveal the climate dependence of the growth factor. Finally, we compare our findings with those of Polglase and Wang (1992).

2. Method

We derive the climate dependence of the growth factor by use of TsuBiMo, a process-based NPP model calibrated for use at the global scale. The detailed description of the model and calibration method can be found in our previous papers (Alexandrov et al., 1999; Alexandrov and Oikawa, 2002; Alexandrov et al., 2002). Here, we describe the model briefly, focusing on essential assumptions.

2.1. *The process-based model of CO_2 fertilization effect*

The model proposed by Oikawa (1986) suggests that the light-saturated rate of photosynthesis, p_{max}, is proportional to the atmospheric concentration of $CO_2(C_a)$:

$$p_{max}(C_a) = p_{max}\left(C_a^0\right)\frac{C_a - C_c}{C_a^0 - C_c}, \tag{2}$$

where C_c is compensation point of photosynthesis and C_a^0 is some baseline concentration of CO_2.

The typical value of C_c for C_3 plants under normal conditions is 50 ppmv, but it may vary depending on species and environmental conditions and thus induce variability in the CO_2 fertilization effect on p_{max}. At $C_c = 0$ ppmv (normally assumed for C_4 plants) p_{max} is doubled at $C_a = 2\ C_a^0$, but it would be trebled at doubled CO_2 concentration if C_c were half of C_a^0.

The response of actual photosynthesis is light-limited. The light-limited rate of photosynthesis can not be higher than $K\beta\ I_0$, where I_0 is light intensity, K is light extinction coefficient, and β is light-use efficiency defined as initial slope of the curve "photosynthesis vs. light intensity". If p_{max} is doubled at C_a^* and $K\beta I_0$ is less than $2p_{max}(C_a^0)$, then the light-limited rate of photosynthesis would increase at C_a^* by a factor of

$$\frac{K\beta I_0}{p_{max}\left(C_a^0\right)} < 2$$

at most, if we would assume that photosynthesis at C_a^0 is not already limited at such a low light intensity. In other words, the closer is $p_{max}(C_a^0)$ to $K\beta I_0$, the weaker is the CO_2 fertilization effect on the actual rate of photosynthesis.

Let us denote the ratio of $K\beta I_0$ to p_{max} as S_I:

$$S_I = \frac{\beta I_0}{(p_{max}/K)}. \tag{3}$$

When I_0 approaches zero, S_I also approaches zero, for p_{max} is limited by factors other than I_0. (It is the *light-saturated* rate.) When I_0 tends to infinity, S_I also tends to infinity, for the same reason.

The actual rate of photosynthesis does not tend to infinity: it saturates at some values of S_I, and thus it is expected to be

[1] It is worth to mention here that the scope of this paper is restricted to the response of plant net primary productivity, a starting point of the complicated process that forms a carbon sink at increasing atmospheric concentration of carbon dioxide.

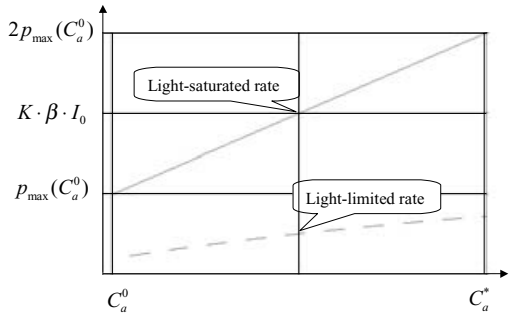

Fig. 1. Light-saturated and light-limited response of photosynthesis to CO_2 enrichment. The solid line shows the CO_2 dependence of light-saturated rate; $p_{max}(C_a^0)$ denotes the light-saturated rate at some baseline CO_2 concentration; C_a^* is the elevated CO_2 concentration at which p_{max} is doubled; I_0 is the light intensity, $K\beta I_0$ is the highest potential rate of photosynthesis at a given I_0; the dashed line shows the CO_2 dependence of the light-limited rate of photosynthesis for I_0.

$$p_{max}\frac{S_I}{1+S_I}.$$

Figure 1 shows the rate of the actual photosynthesis as a function of C_a for $K\beta I_0 = 1.5p_{max}(C_a^0)$. We notice from this figure that photosynthesis at C_a^0 is already light-limited for the light intensity supposed. Taking into account this fact, we can expect that the rate of light-limited photosynthesis will increase at C_a^* by a factor of

$$\frac{p_{max}\left(C_a^*\right)\dfrac{S_I\left(C_a^*\right)}{1+S_I\left(C_a^*\right)}}{p_{max}\left(C_a^0\right)\dfrac{S_I\left(C_a^0\right)}{1+S_I\left(C_a^0\right)}} = \frac{2p_{max}\left(C_a^0\right)\dfrac{0.5S_I\left(C_a^0\right)}{1+0.5S_I\left(C_a^0\right)}}{p_{max}\left(C_a^0\right)\dfrac{S_I\left(C_a^0\right)}{1+S_I\left(C_a^0\right)}}$$

$$= 2\frac{1+S_I\left(C_a^0\right)}{2+S_I\left(C_a^0\right)}$$

which is equal to 1.5 for $S_I(C_a^0) = 2$ [i.e. for $K\beta I_0 = 2p_{max}(C_a^0)$].

For daily canopy photosynthesis,

$$P_g = p_{max}S_f(S_I), \tag{4}$$

where S_f is given by the formula:

$$S_f = \frac{2}{K}\ln\left(\frac{1+\sqrt{1+S_I}}{1+\sqrt{1+\varphi S_I}}\right) \tag{5}$$

where $\varphi = \exp(-K(LAI)$, and LAI is leaf area index (the review of Kuroiwa's theory underlying this formula can be found in the paper of Alexandrov and Oikawa (2002); it is also worth to mention here that p_{max} is the rate per area of leaf, and P_g is the rate per area of land covered by canopy).

Formulas (4) and (5) suggest that when S_I tends to infinity, S_f tends to LAI and thus P_g tends to $p_{max}LAI$, and that when S_I approaches zero, S_f and P_g also approach zero.

Let us now fix I_0 and change C_a. When C_a increases, p_{max} increases and S_I decreases, i.e. one term of formula (4) is elevated with C_a, and the another term falls off. What does this give as a result? It can be shown that at a given $p_{max}(C_a^0)$, β, I_0, LAI and K, P_g is a saturating function of C_a and that its half-saturation point is sensitive to $S_I(C_a^0)$. Thus, in case of tropical forest [where $S_I(C_a^0)$ is the lowest], the half-saturating CO_2 concentration is equal to 450 ppmv, whereas in case of evergreen broad-leaved forest [where $S_I(C_a^0)$ is higher], it is equal to 640 ppmv. Consequently, P_g of tropical forest increases by 39.5% when C_a is doubled, whereas P_g of evergreen broad-leaved forest increases by 47%.

The average values of I_o are roughly the same in both cases, and so the shift of the half-saturation point (and the increase of the relative intensity of the CO_2 fertilization effect) is attributed to the difference in the value of $p_{max}(C_a^0)/K$, a lumped parameter that we derived from NPP data by 'inverting' the NPP model for $\varphi = 0.1$. Since the value of $p_{max}(C_a^0)/K$, or shortly p_K, characterizes canopy productivity, one may say that eqs. (2)–(5) suggest canopies of a lower productivity to be more responsive to CO_2 fertilization than their more productive counterparts.

Another source of variation in the intensity of the CO_2 fertilization effect is efficiency of GPP conversion to NPP. (GPP stands for Gross Primary Production, and NPP for Net Primary Production.) A decrease of NPP/GPP ratio with GPP has been reported in a number of papers on plant productivity. The empirical formula was derived by Box (1988):

$$NPP = 3000[1 - \exp(-GPP/4140)] \tag{6}$$

where NPP and GPP are given in g m^{-2} yr^{-1} (of dry weight). This formula suggests further divergence in the intensity of the CO_2 fertilization effect between ecosystems of low and high productivity. Since the length of growing season is a major determinant of annual GPP, this formula suggests reduction in the intensity of the CO_2 fertilization effect in ecosystems with a longer growing season.

2.2. Globalization of the process-based model

Applying a process-based NPP model [like that given by eqs. (1)–(4)] over the global grid we face the problem of how to calibrate it at this scale. Our approach to this problem was as follows [details can be found in Alexandrov et al. (2002)]. In the first place, we considered the data on NPP as an indirect measurement of model parameters. Secondly, we reduced the number of undefined parameters to a single lumped parameter (SLP). In the third place, we 'inverted' the model and derived the value of the SLP for each data point. In the fourth place, we considered the SLP as some characteristic of vegetation and formulated an empirical model linking SLP and climate averaged over the data points belonging to the same biome. (This model enables us to specify SLP as a function of climate rather than that of vegetation class.) Finally, we globalized the process-based model by assigning an SLP value to each node of the geographical grid proceeding from the climate characteristics of the node.

Applying this scheme to the process-based model proposed by Oikawa (1986) we derived a global scale model of NPP (named TsuBiMo) from the Osnabrück collection of NPP data (Esser et al., 1997) after some filtering (Alexandrov et al., 1999) of this collection. In order to reduce the number of variables, we assumed that the mode of foliage distribution is changing in such a manner that K and LAI are in a specific relationship, $K = K_{\mathrm{opt}}(LAI)$, which gives a maximum of GPP for a given LAI [justification of this relationship can be found in the paper of Alexandrov and Oikawa (1997)]. This relationship implies minor variations in FPAR (fraction of absorbed photosynthetically active radiation) of continuous vegetation cover, and so we set φ at 0.1, assuming that approximately 10% of PAR reaches the ground. Then, we solved eq. (4) with respect to S_{I} and calculated $p_{\mathrm{K}} = p_{\max}(C_{\mathrm{a}}^0)/K$ (that serves as SLP) for each data point by use of eq. (3). Next, we found that p_{K} depends on the average monthly temperature of growing season (T_{v}) and an aridity index ($RFL_{\mathrm{v}} = P_{\mathrm{v}}/T_{\mathrm{v}}$, where P_{v} is the average monthly precipitation of growing season) as follows:

$$p_{\mathrm{K}} = 52.5 \times \exp\left[-\left(\frac{T_{\mathrm{v}} - 30}{11.2}\right)^2\right] \times \frac{(RFL_{\mathrm{v}}/2.6)^{4.57}}{1 + (RFL_{\mathrm{v}}/2.6)^{4.57}}, \quad (7)$$

where p_{K} is expressed in mg CO_2 dm^{-2} h^{-1}. Finally, we globalized the model in use by calculating a p_{K} value for each node of the geographical grid of half-degree resolution.

2.3. Fitting model output by Keeling's formula

Applying TsuBiMo over the geographical grid of half-degree resolution, we calculated the total terrestrial NPP at ten concentrations of the atmospheric CO_2 from 240 to 690 ppmv. Then we found the value of the growth factor that provides the best agreement (in the sense of least squares) between Keeling's formula and model outputs. Similar calculations were done for the parts of the geographical grid representing major biomes.

3. Results

Keeling's formula well approximates TsuBiMo output within certain range of C_{a} (Fig. 2). Stars (TsuBiMo projections for $C_{\mathrm{c}} = 50$ ppmv) fall on the line (Keeling's formula with $\gamma = 0.34$) when C_{a} ranges between 290 and 640 ppmv. Outside this range they fall below the line, which is to say that one should not apply Keeling's formula as an expedient substitution for the process-based model outside certain range of atmospheric CO_2 concentrations. In other words, the use of the Keeling's formula is restricted to the future projections prior to the year 2050.

The growth factor of the total NPP is not sensitive to TsuBiMo setting of C_{c}. It varies from 0.32 to 0.36,

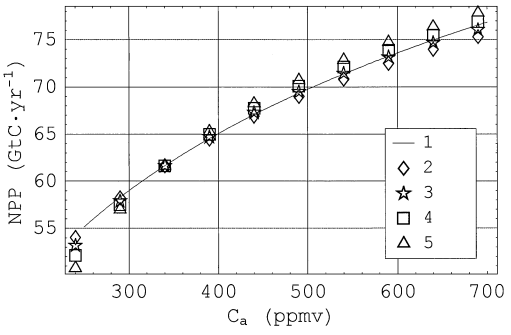

Fig. 2. CO_2 dependence of total terrestrial NPP, comparing Keeling's formula with a process-based model (TsuBiMo) outputs. Legend: (1) Keeling's formula, $\gamma = 0.3417$; (2) TsuBiMo, $C_{\mathrm{c}} = 25$ ppmv; (3) TsuBiMo, $C_{\mathrm{c}} = 50$ ppmv; (4) TsuBiMo, $C_{\mathrm{c}} = 75$ ppmv; (5) TsuBiMo, $C_{\mathrm{c}} = 100$ ppmv.

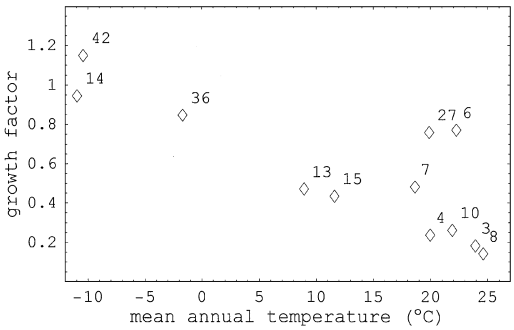

Fig. 3. The climate dependence of growth factor suggested by TsuBiMo. Diamonds mark the mean values of NPP and mean annual temperature of the following biomes: deserts (6), semi-desert scrubs (27), shrublands (7), subhumid woodlands (10), grasslands (15), tundra (42), needle-leaf forests (36), summer-green broad-leaved forests (13), evergreen broad-leaved forests (4), tropical rainforests (8) and rain-green forests (3).

when C_c varies from 25 to 75 ppmv. We can say with reasonable confidence that TsuBiMo implies a growth factor lies in the range from 0.3 to 0.4. This estimate is lower than the value (0.42) that matches land-use emission of 1.6 GtC yr^{-1} in 1980s (Kheshgi et al., 1996), suggesting that the *net* land-use emission in 1980s might be lower than 1.6 GtC yr^{-1}.

The regional values of growth factor apparently correlate with climate (Fig. 3). They decrease with mean annual temperature when water supply is sufficient, and are higher where climate is drier. The positive correlation of growth factor with climate dryness is not surprising. This finding is in line with that of other researchers. However, the negative correlation with mean annual temperature contradicts the prevailing view that warmness amplifies CO_2 fertilization effect, and shows the need for a comparative analysis of model assumptions.

The range of regional estimates (Table 1 and Fig. 3) conforms to theoretical expectations. The values of growth factor predicted by physiological models vary from 0.06 to 1.3 (Luxmore and Baldocchi, 1995), whereas our estimates fall within closer limits, from 0.14 in tropical rainforest to 1.15 in tundra. Nevertheless, it is worth mentioning that we do not consider all the factors of the plant response to CO_2 enrichment. For boreal and polar biomes, there is a reason to think that nitrogen limitation might be more important than that of light. Therefore, the high values of growth factor (i.e. more than 0.5) should be considered as potential values that may be realized under some circumstances.

4. Discussion

The production of organic matter is not a simple process. It is not completely described by a single model: there are alternative explanations for any experimental result. Therefore, it is not surprising that our findings contradict to the hypothesis proposed by Polglase and Wang (1992). The models based on alternative assumptions often contradict each other. This does not necessarily mean that one of them is wrong and another is true. They may merely have different domains.

Table 1. *The values of growth factor that provide a 'best fit' of Keeling's formula to TsuBiMo outputs*

Biome code	Biome name (Box, 1995)	Mean annual temperature, °C	Growth factor
3	Raingreen/semi-evergreen forests	23.9	0.1821
4	Evergreen broad-leaved forests	20.9	0.2370
6	Deserts	22.3	0.7706
7	Shrublands	18.6	0.4820
8	Tropical rainforest	24.6	0.1412
10	Subhumid woodlands	21.9	0.2608
13	Summergreen broad-leaved forests	8.9	0.4705
14	Larch forest	−11.0	0.9451
15	Grasslands	11.6	0.4341
27	Semi-desert scrub	19.9	0.7590
36	Needle-leaved evergreen forests	−1.7	0.8464
42	Tundra	−10.4	1.1489

Polglase and Wang (1992) assumed that the rate of gross photosynthesis is the Michaelis–Menten function of $C_a - C_c$, half-saturating at $3C_c$. Taking into account the temperature dependence of C_c, they supposed that the Michaelis–Menten constant must increase with temperature and concluded that growth factor must also increase with temperature. (The growth factor is proportional to Michaelis–Menten constant, when Keeling's formula is considered as an approximation of a Michaelis–Menten function). This led them to propose that warm climate amplifies the CO_2 fertilization effect.

We also assume that the rate of gross photosynthesis is the Michaelis–Menten function of $C_a - C_c$ and agree that C_c may increase with temperature. We disagree about the Michaelis–Menten constant only. Some set of controlled-exposure studies shows that it depends on light intensity: the lower the light intensity, the lower the level of CO_2 concentration starting from which further CO_2 enrichment has little effect. Therefore, following Kuroiwa's approach, we supposed that Michaelis–Menten constant is proportional to the ratio of potential rate of photosynthesis available at given light intensity to its light-saturated rate at given environmental conditions.

The resulting discrepancy with the conclusions of Polglase and Wang shows that current hypotheses about CO_2 fertilization effect (and thus projections of the related carbon sink) are very sensitive to the choice of driving forces taken into account. Consideration of the light limitation inside a canopy dramatically changes the pattern of climate dependence as derived on the assumption that this factor is not important. What will happen when proper attention will be paid to another factor such as nitrogen limitation, for example? The meta-analysis of CO_2 fertilization effects in case of European forest species (Medlyn et al., 1999) suggests that nitrogen limitation may really take place there: across the 15 field experiments the rate of light-saturated photosynthesis was increased only by 51% at doubled CO_2. Therefore, we may suppose that taking into account nitrogen limitation will significantly reduce our estimates of the growth factor for tundra and boreal forest.

The synergy between the driving factors of the CO_2 fertilization effect offers a challenge to a modeler. However, the drawback to the deeper insight is the lack of crucial experiments, i.e. those allowing no alternative explanations. Such experiments are not easy to devise. For example, when Kellomäki and Wang (2001) found that the "theoretically expected positive effect of the warmer temperature on the CO_2-induced stimulation of growth was not observed," they attributed this fact to the variety of changes in plant growth induced by elevated CO_2 and temperature and concluded that it is not realistic "to extract all these changes from this experiment alone." Nevertheless, experiments of this sort are badly needed for verification of the models, and we hope that the discrepancy between the models displayed in this paper will attract the attention of experimenters.

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