TsuBiMo: a biosphere model of the CO$_2$-fertilization effect

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ABSTRACT: Stimulation of photosynthesis at higher CO$_2$ concentrations is repeatedly observed in short-term experiments at the single leaf level. We scaled up from leaf to globe by use of a model of half-degree spatial resolution (ca 50 × 50 km) and came to the conclusion that the CO$_2$-induced increase in the total terrestrial net primary production (NPP) may be described by the same simple formula that has been frequently used over the last 2 decades: 

$$NPP(C_a) = NPP_0 [1 + \gamma \ln(C_a/C_0)]$$

where $C_a$ is the atmospheric CO$_2$ concentration. We also concluded that $NPP_0$ can be set at 61.6 Pg C yr$^{-1}$ and $\gamma$ at 0.35 (for $C_0 = 340$ ppmv) in this formula. Proceeding from aircraft measurements of CO$_2$ concentrations and the isotopic carbon ratio, we assumed that the turnover time of the biological cycle is 19.2 yr, and we estimated the sink induced by CO$_2$ fertilization to be 1.3 Pg C yr$^{-1}$ (averaged for the period 1980–90). It is worth mentioning, however, that the estimate of the turnover time is so sensitive to the average isotopic shift that occurs on air-plant exchange that one can hardly define a feasible confidence interval for it.

KEY WORDS: CO$_2$ fertilization · Biosphere model · Carbon sink

1. INTRODUCTION

The observed increase in the CO$_2$ concentration in the atmosphere is lower than the difference between CO$_2$ emission and CO$_2$ dissolution in the ocean. This imbalance, earlier named the ‘missing sink’, comprises up to 1.1 Pg C yr$^{-1}$, after taking land-use changes into account. The subsequent assessments assume that this sink is caused by some natural changes in terrestrial ecosystems (Houghton 1996).

The simplest explanation for the ‘missing sink’ is CO$_2$ fertilization. Stimulation of photosynthesis at higher CO$_2$ concentrations is repeatedly observed in short-term experiments at the single leaf level. A number of biosphere models take this effect into account for calculating the natural terrestrial sink. The results of such calculations are normally in close agreement with the magnitude of the ‘missing sink’.

The problem with these biosphere models is their validity. Because of the complexity of biological systems, one normally constructs a detailed process-based model. A model of this sort contains a huge number of parameters that are set at ad hoc values. One can easily obtain the desired magnitude of a terrestrial sink by tuning the model parameters, but one can hardly claim that the thus-obtained value of the sink is close to the real one when the settings of the model parameters have not been validated.

The purpose of this study was to construct a demonstrative biosphere model of the CO$_2$-fertilization effect. Every biosphere model is deductive in its nature. One cannot compare the projected and observed dynamics of its state variables—there are no observations of this sort. Hence, a biosphere model should be demonstrative in its form—that is, the logic of transition from level to level should be clear, the number of coefficients should be relatively small and the coefficients should be based on empirical information. In other words, the structure of the model should allow the pro-
cess of deduction to be traced and should reveal the cause-effect links between assumptions and conclusions.

2. MODEL OVERVIEW

We described the CO2-fertilization effect as a linear increase in the rate of light saturated photosynthesis \( P_{\text{max}} \) with the increase of CO2 concentration:

\[
P_{\text{max}}[C_a(t)] = p_0 \left( C_a(t) - C_c \right)\\
\]

where \( C_a(t) \) is CO2 concentration in the atmosphere, \( C_c(t_0) \) is atmospheric CO2 concentration in 1980 and \( C_c \) is CO2 compensation point for photosynthesis.

Then we scaled up from the single leaf to canopy by means of Kuroiwa’s formula of gross primary production (Oikawa 1985, 1986).

\[
\text{GPP} = 2 \cdot D \cdot G \cdot k \cdot \frac{P_{\text{max}}}{K} \ln \left[ \frac{1 + \sqrt{1 + \beta \cdot I_0 / (p_{\text{max}}/K)}}{1 + \sqrt{1 + \beta \cdot I_0 \cdot \exp(-K \cdot \text{LAI}) / (p_{\text{max}}/K)}} \right]
\]

where \( D \) is the average daylength during growing season, \( G \) is the length of growing season, \( I_0 \) is the light intensity at noon, \( \beta \) is the light-use efficiency, \( K \) is the light extinction coefficient, \( \text{LAI} \) is the leaf area index and \( k \) is the constant for conversion assimilated CO2 to synthesized dry matter.

This formula was derived from the assumption that the light dependence of photosynthesis at a single leaf is of the Michaelis-Menten type:

\[
P_{\text{g,leaf}} = \frac{P_{\text{max}} \cdot K \cdot I_{\text{can}}(L)}{p_{\text{max}} / \beta + K \cdot I_{\text{can}}(L)}
\]

where \( P_{\text{g,leaf}} \) is the rate of light-limited photosynthesis at a single leaf, \( L \) is the cumulative leaf area index above the level of the leaf (0 ≤ \( L \) ≤ LAI), and \( I_{\text{can}}(L) \) is the light intensity at this level which is supposed to be equal to \( I_{\text{exp}}(-K \cdot L) \), where \( I_0 \) is the light intensity above the canopy and \( I_{\text{can}} \) is the light intensity at the given level of the canopy. Integration over all leaf layers gives

\[
P_{\text{g,can}} = \frac{P_{\text{max}}}{K} \ln \left[ \frac{1 + \beta \cdot I_0 / (p_{\text{max}}/K)}{1 + \beta \cdot I_0 \cdot \exp(-K \cdot \text{LAI}) / (p_{\text{max}}/K)} \right]
\]

and integration over the daily course of \( I_0(t) \) which is approximated by the formula \( I_0(t) = I_0 \sin^2(\pi t/D) \), gives

\[
\text{GPP}_{\text{daily}} = 2 \cdot D \cdot \frac{P_{\text{max}}}{K} \ln \left[ \frac{1 + \sqrt{1 + \beta \cdot I_0 / (p_{\text{max}}/K)}}{1 + \sqrt{1 + \beta \cdot I_0 \cdot \exp(-K \cdot \text{LAI}) / (p_{\text{max}}/K)}} \right]
\]

The light attenuation coefficient (\( K \)) depends not only on the leaf inclination angle, which is relatively constant for a given species, but also on the mode of foliage distribution (Oikawa & Saeki 1977). We supposed that the mode of foliage distribution is changing in such a manner that \( K \) and LAI are in a specific correspondence \( K_{\text{opt}}(\text{LAI}) \) which gives a maximum of GPP for a given LAI. Kuroiwa’s formula (Alexandrov & Oikawa 1997) suggests that \( K_{\text{opt}}(\text{LAI}) \) is similar to the inverse relationship between \( K \) and LAI observed by Smith et al. (1991) in Pinus contorta stands. This relationship implies minor variations in FPAR (fraction of absorbed photosynthetically active radiation) of continuous vegetation cover. Therefore we set \( \exp(-K \cdot \text{LAI}) \) to be 0.1.

Then we calculated \( \beta \) at 0.06 µmol CO2 µmol\(^{-1}\) photons, we reduced the number of globally varying parameters and rewrote Eq. (2) as follows:

\[
\text{GPP} = 2 \cdot D \cdot G \cdot k \cdot \frac{P_{\text{max}}}{K} \ln \left[ \frac{1 + \sqrt{1 + \beta \cdot I_0 / (p_{\text{max}}/K)}}{1 + \sqrt{1 + \beta \cdot I_0 \cdot \exp(-K \cdot \text{LAI}) / (p_{\text{max}}/K)}} \right]
\]

where \( k = 0.6, \phi = \exp(-K \cdot \text{LAI}) = 0.1, \) and \( p_{\text{K}} = p_{\text{max}}/K \).

\( I_0 \) was calculated from the gridded data set on PAR (Dye et al. 1994); \( D \) was calculated proceeding from latitude (Iqbal 1983). The geographical distribution of \( G \) was derived from the characteristic month averages (1986–88) of the monthly Normalized Difference Vegetation Index (NDVI) (Kinemann & Hastings 1992) and \( T \), mean monthly temperatures (Leemans & Cramer 1991), by use of NDVI > 0.1 and \( T_m > 0\°C \) as a criterion for growth period. In order to identify the global pattern of \( p_{\text{K}} \) at 0.5° × 0.5° resolution we assumed that it is a function of climate: \( p_{\text{K}} = p_{\text{K}}(T, \text{RFL}) \), where RFL is a rain factor (precipitation divided by temperature). The particular form of this function (Eq. 3) we derived (Appendix 1) from the Osnabrück collection of net primary production (NPP) data (Esser et al. 1997):

\[
p_{\text{K}} = 32.3 \cdot \exp \left[ \left( \frac{T - 30}{11.2} \right)^2 \right] \frac{(\text{RFL}/2.6)^{4.57}}{1 + (\text{RFL}/2.6)^{4.57}}
\]

where \( p_{\text{K}} \) is expressed in (µmol CO2) m\(^{-2}\) s\(^{-1}\) and \( T \) and RFL are mean monthly temperature and monthly rain factor averaged over the vegetation period (RFL = P/T, where \( P \) is the monthly precipitation averaged over the vegetation period).

To obtain NPP we used an empirical formula linking NPP and GPP:

\[
\text{NPP} = 3000 \cdot \left[ 1 - \exp(-\text{GPP}/4140) \right]
\]

where NPP and GPP are given in g dry matter m\(^2\) yr\(^{-1}\).

The decrease in the NPP/GPP ratio with GPP is reported in a number of papers on plant productivity. The particular formula was taken from Box (1988).
solved a differential equation for plant biomass to obtain NPP.

3. TERRESTRIAL NPP AND ITS GROWTH FACTOR

\[
NPP(C_a) = NPP_0 \left[ 1 + \gamma \ln \left( \frac{C_a}{C_a^0} \right) \right]
\]  

(5)

Experimental data generally fit this model (Amthor 1995, Wullschleger et al. 1995), but the value of the so-called growth factor (\(\gamma\)) varies from experiment to experiment. Hence, the choice of the growth factor value at the biosphere level is not strictly prescribed by experiments. More than often \(\gamma\) is tuned 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 CO2 and \(\delta^{13}C\) records. Our calculations of the total terrestrial NPP at different CO2 levels suggest that \(\gamma\) should be set at 0.35 (Fig. 1) when Eq. (5) is applied at the biosphere level.

Another factor that may significantly affect the estimates of the sink induced by CO2 fertilization is NPP0 – that is, NPP at 340 ppmv. The modelled NPP ranges from 39.9 to 80.5 Pg C yr\(^{-1}\), with a mean of 54.9 Pg C yr\(^{-1}\) (Cramer et al. 1997). Our estimate is 61.6 Pg C yr\(^{-1}\).

The global pattern of NPP might also be significant, but it is difficult to express it in a form other than a map. Therefore we plotted TsuBiMo-NPP0 (Fig. 2) together with the well-known Miami NPP and NPP derived directly from annual NDVI (TsuBiMo stands for Tsukuba Biosphere Model given by Eqs 1 to 4). At first glance it would seem that there is little difference between them, but a close look at the maps will show some points of controversy between these models even though they were derived from the same NPP data.

4. THE TERRESTRIAL SINK INDUCED BY CO2 FERTILIZATION AND ITS SENSITIVITY TO TURNOVER TIME

Turnover time—the length of time between absorption and release of carbon entering the biological
cycle—essentially affects the terrestrial sink induced by CO\textsubscript{2} fertilization. However, it is more common to test the sensitivity of the terrestrial sink to the uncertainty in turnover time (the range of which is merely assumed). More or less certain estimates of NPP\textsubscript{0} and γ obtained in this study allow us to evaluate the uncertainty in the terrestrial sink which is related to the uncertainty in turnover time.

The terrestrial sink $N_b$ is commonly calculated as the difference between the present and past biomass: $N_b(t) = B(t) - B(t-1)$, where the course of $B$ is obtained from a differential equation of the form

$$\frac{d}{dt} B(t) = \text{NPP} - \frac{B(t)}{\tau_B}$$

(6)

where $\tau_B$ is the turnover time of organic matter (e.g., Kohlmaier et al. 1987, Goudriaan 1992) or a system of differential equations of the same sort regarding the biomass pools (leaves, stems, roots) and the pools of dead organic matter (Kohlmaier et al. 1987, Goudriaan 1992). Disaggregating Eq. (6), biosphere modellers justify their choice of $\tau_B$, but do not totally remove its uncertainty. Solving Eq. (6) for the NPP given by Eq. (5) at NPP\textsubscript{0} = 61.6 Pg C yr\textsuperscript{-1} and $\gamma = 0.35$ and for $C_a(t)$ given by historical CO\textsubscript{2} records of Keeling & Whorf (1994) and Neftel et al. (1994), we calculated the terrestrial sink for $\tau_B$ to range from 5 to 100 yr (Fig. 3). Proceeding from the aircraft measurements of the CO\textsubscript{2} concentrations and isotopic ratio of its carbon in the middle and upper troposphere over Siberia (Nakazawa et al. 1997), we assumed (Appendix 2) that $\tau_B = 19.2$ yr, and finally estimated the sink at 1.3 Pg C yr\textsuperscript{-1}.

5. CONCLUSION

For a particular ecosystem, the abundance of complicated details suggests that the model was formulated thoroughly. However, we considered global vegetation, and this forced us to schematize the model and seek the simplicities behind the details. Thus, we supposed that Kuroiwa’s formula summarizes some detailed models of canopy photosynthesis and that Box’s formula for the GPP-NPP relationship might be supported by some detailed models of dry matter reproduction. Finally, we reduced the results of our calculations of the response of terrestrial NPP to CO\textsubscript{2} increase to the simple formula that has been heavily used for the last 2 decades.

Modellers rarely convert their results into simple formulas to avoid the false impression that their conclusions remain valid outside the domain of model settings. However, such a precaution renders complicated models unsuitable for instantly improving the state of the art in carbon cycle studies. To maintain the balance between credibility and usability of our results, we recorded CD-R containing the information about the settings of our model. This also makes the model open to modification by those who study global change at the level of plant physiology—proceeding from the TsuBiMo on CD, they can easily trace how their findings affect the balance of global budget of carbon.

The global manifestation of the CO\textsubscript{2} fertilization effect is determined by the turnover time of the biological cycle—that is, the average time span between absorption and release of carbon. Considering $^{13}$C as a tracer, we analyzed some data on summertime changes in CO\textsubscript{2} and its isotopic ratio in the troposphere over Siberia and set the turnover time at some plausible value. We cannot be confident of this value because it is sensitive to the average isotopic shift that occurs in air-plant exchanges. The latter must be determined more accurately as at its current accuracy one can hardly define a feasible confidence interval for the turnover time.

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The Osnabrück collection of NPP data, synthesized by H. Lieth and G. Esser, is available at http://www-eosdis.orl.gov/npp/other_files/ods_des.html. We produced from this collection a reference data set (Alexandrov et al. 1999) by selection of the data points that meet the following criteria: 
- contains original estimate of total NPP
- geographical location of data point allows one to specify vegetation zone, mean annual temperature and annual precipitation
- shows normal distribution of NPP within the groups related to vegetation zones.

We added to this data set on NPP the environmental characteristics required by the Kuroiwa’s formula and calculated the contains original estimate of total NPP collection a reference data set (Alexandrov et al. 1999) by gov/npp/other_files/ods_des.html. We produced from this Lieth and G. Esser, is available at http://www-eosdis.ornl.gov/npp/other_files/ods_des.html.

For grasslands, we first calculated the average, maximum and minimum of the observed summertime CO2 concentrations as

\[
\delta_{C_+} = \delta_{C_+} - 0.05(C_+ - C_0).
\]

Let us assume that NPP = xR and set for simplicity x = 2, then

\[
R \cdot \xi = C_+ - C_0.
\]

Assuming next that \(C_+ + C_0 = C_0\), we obtain

\[
\tau_B = \frac{-\epsilon + 0.5C_0}{\delta}. \tag{A7}
\]

Setting \(\delta\) at –0.03‰ yr\(^{-1}\) and \(\epsilon\) at –17‰, we obtain

\[
\tau_B = \frac{-0.05C_0 - 17}{0.03}. \tag{A8}
\]

Substituting the observed value of \(C_0 (C_0 = 351.5 \text{ ppmv})\), we obtain \(\tau_B = 19.1667 \text{ yr.}\)

There are 2 major source of uncertainty in the interpretation of the data. The first is the ratio NPP/R during the period of observation. The second and more important is the value of \(\epsilon\). The assumed values of \(\epsilon\) vary from –14.8‰ (Lloyd & Farquhar 1994) to –20‰ (Quay et al. 1992) and dramatically affect the estimate of \(\tau_B\). The observations of Nakazawa et al. (1997) imply \(\epsilon > -17.5\text{‰}\), which is in general agreement with the Lloyd-Farquhar theory – \(\epsilon = -17.5\text{‰}\) for an ‘all-C3 biosphere’—but must be higher due to the presence of C4 plants. (For C4 plants, \(\epsilon = -3.6\text{‰}\).) However, their particular estimate (–14.8‰) was derived from the contribution of C4 plants to the annual GPP (–17.8‰ \times 0.79 – 36.6‰ \times 0.21), and its relevance to a particular season is questionable. Midsummer (July) is a dry season for many grassland biomes, and so the contribution of C4 plants in that period may be significantly smaller than annual. (Using NDVI [NGDC 1992] as a proxy to NPP seasonality, we concluded that contribution of C4 plants in that period is half as much as their annual contribution.) Assuming also \(\epsilon = -19\text{‰}\) as a typical value for C3 plants, we therefore set \(\epsilon\) in Eq. (A7) to be –17‰ (–19‰ × 0.87 – 36.6‰ × 0.13) as a plausible value for the summer season.
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