

TsuBiMo: a biosphere model of the CO₂-fertilization effect

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ABSTRACT: Stimulation of photosynthesis at higher CO₂ 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 CO₂-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 CO₂ concentration. We also concluded that NPP_0 can be set at 61.6 Pg C yr⁻¹ and γ at 0.35 (for $C_0 = 340$ ppmv) in this formula. Proceeding from aircraft measurements of CO₂ 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 CO₂ 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: CO₂ fertilization · Biosphere model · Carbon sink

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1. INTRODUCTION

The observed increase in the CO₂ concentration in the atmosphere is lower than the difference between CO₂ emission and CO₂ 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 CO₂ fertilization. Stimulation of photosynthesis at higher CO₂ 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 CO₂-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-

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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_{\max} with the increase of CO₂ concentration:

$$p_{\max}[C_a(t)] = p_0 \frac{C_a(t) - C_c}{C_a(t_0) - C_c} \quad (1)$$

where $C_a(t)$ is CO₂ concentration in the atmosphere, $C_a(t_0)$ 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).

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

where D is the average daylength during growing season, G is the length of growing season, I_0 is the light intensity at noon, β is the light-use efficiency, K is the light extinction coefficient, 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:

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

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

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

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

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

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 $\exp(-K \cdot \text{LAI})$ in Kuroiwa's formula to be 0.1. Setting β at 0.06 $\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photons, we reduced the number of globally varying parameters and rewrote Eq. (2) as follows:

$$\text{GPP} = 2 \cdot D \cdot G \cdot k \cdot p_K \cdot \text{Ln} \left[\frac{1 + \sqrt{1 + \beta \cdot I_0 / p_K}}{1 + \sqrt{1 + \beta \cdot I_0 / p_K}} \right] \quad (2')$$

where $k = 0.6$, $\varphi = \exp(-K \cdot \text{LAI}) = 0.1$, and $p_K = p_{\max}/K$; 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 $T_m > 0^\circ\text{C}$ as a criterion for growth period. In order to identify the global pattern of p_K at $0.5^\circ \times 0.5^\circ$ resolution we assumed that it is a function of climate: $p_K = p_K(T, \text{RFL})$, 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):

$$p_K = 32.3 \cdot \exp \left[- \left(\frac{T - 30}{11.2} \right)^2 \right] \cdot \frac{(\text{RFL}/2.6)^{4.57}}{1 + (\text{RFL}/2.6)^{4.57}} \quad (3)$$

where p_K is expressed in $(\mu\text{mol CO}_2) \text{m}^{-2} \text{s}^{-1}$ 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:

$$\text{NPP} = 3000 \cdot [1 - \exp(-\text{GPP}/4140)] \quad (4)$$

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

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). The advantage of this model is obvious: we need not

solve a differential equation for plant biomass to obtain NPP.

3. TERRESTRIAL NPP AND ITS GROWTH FACTOR

CO₂ fertilization effect is commonly described by

$$\text{NPP}(C_a) = \text{NPP}_0 \left[1 + \gamma \text{Ln} \left(\frac{C_a}{C_a^0} \right) \right] \quad (5)$$

Experimental data generally fit this model (Amthor 1995, Wullschlegel et al. 1995), but the value of the so-called growth factor (γ) 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 γ 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 $\delta^{13}\text{C}$ records. Our calculations of the total terrestrial NPP at different CO₂ levels suggest that γ 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

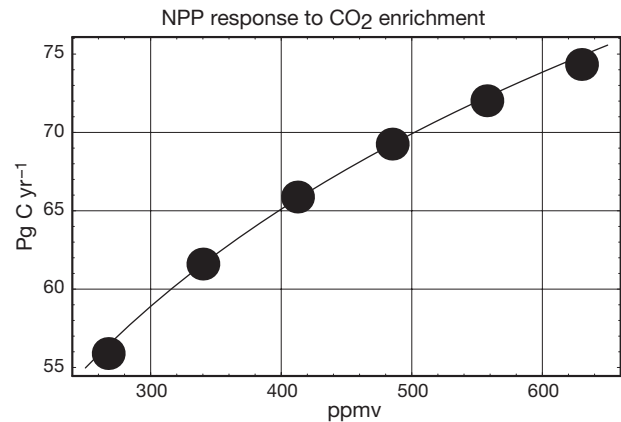


Fig. 1. The TsuBiMo projection (points) of CO₂ dependence of terrestrial NPP fit Eq. (5) well for NPP₀ = 61.6 Pg C yr⁻¹ and $\gamma = 0.35$ (line)

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

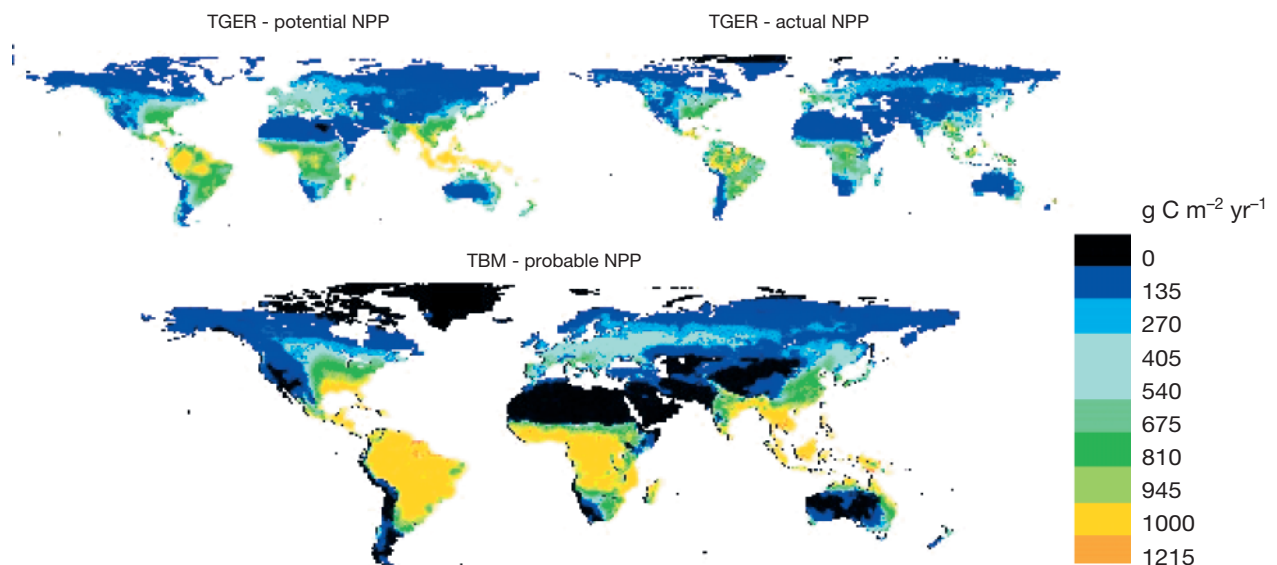


Fig. 2. TsuBiMo-NPP (lower center) plotted against the well-known Miami NPP (upper left) and NPP derived by Box et al. (1994) from annual NDVI (upper right)

cycle—essentially affects the terrestrial sink induced by CO₂ fertilization. However, it is more common to test the sensitivity of the terrestrial sink to the uncertainty in the growth factor (the range of which is known from experiments) than that to the uncertainty in turnover time (the range of which is merely assumed). More or less certain estimates of NPP₀ 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

$$\begin{cases} \frac{dB}{dt} = \text{NPP} - \frac{B}{\tau_B} \\ B(t_0) = \text{NPP}(t_0) \cdot \tau_B \end{cases} \quad (6)$$

where τ_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 τ_B , but do not totally remove its uncertainty. Solving Eq. (6) for the NPP given by Eq. (5) at NPP₀ = 61.6 Pg C yr⁻¹ and $\gamma = 0.35$ and for $C_a(t)$ given by historical CO₂ records of Keeling & Whorf (1994) and Neftel et al. (1994), we calculated the terrestrial sink for τ_B to range from 5 to 100 yr (Fig. 3). Proceeding from the aircraft measurements of the CO₂ 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⁻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

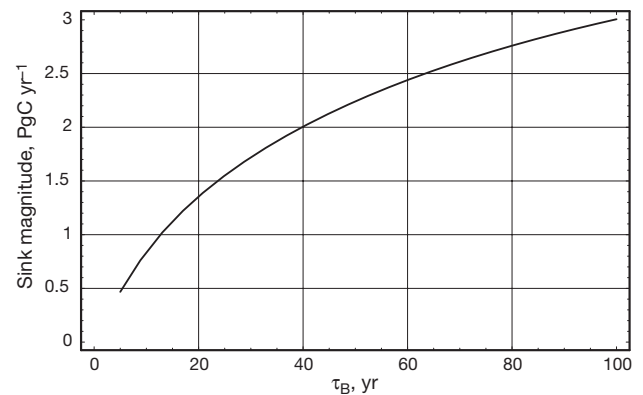


Fig. 3. Effect of turnover time (τ_B) on the magnitude of the terrestrial sink induced by CO₂

calculations of the response of terrestrial NPP to CO₂ 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 CO₂ 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 ¹³C as a tracer, we analyzed some data on summertime changes in CO₂ 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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Appendix 1. The global pattern of light saturated photosynthesis

The Osnabrück collection of NPP data, synthesized by H. Lieth and G. Esser, is available at http://www-eosdis.ornl.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 results given in Table A1, which we put into the basis of the $p_K(T, RFL)$ calibration.

We assumed

$$p_K(T, RFL) = f_1(T) \cdot f_2(RFL) \quad (A1)$$

$$f_1(T) = a_0 \exp \left[- \left(\frac{T - T_{opt}}{\sigma} \right)^2 \right] \quad (A2)$$

$$f_2(RFL) = b_0 \frac{(RFL/\theta)^a}{1 + (RFL/\theta)^a} \quad (A3)$$

set T_{opt} to be 30°C, and fit the data (Table A1) by calibrating the other coefficients (a_0 , b_0 , α , σ , and θ). For this purpose, we calculated a_0 and σ from the data on summergreen broad-leaved forests (Class 13) and needle-leaved evergreen forests (Class 36). (The function f_1 is determined by 2 points, if T_{opt} is known.) Thus calibrated temperature dependence overestimates the value of p_K for grasslands (Class 15). Considering this as a sign of water limitation, we

concluded $f_2(3.1) = 0.647$. Then, supposing that f_2 is close to 1 at RFL = 5 (the value typical for boreal and temperate forests), we calculated α and θ .

Thus Eq. (3) fits well not only the data on the classes that were used for estimating its coefficients but also the data on other classes; a projected value always falls within the confidence interval of the mean value given in the Table A1. However, the suggestion that p_K peaks at 30°C is not strictly dictated by the data. Due to the large uncertainty in p_K of tropical forests (Classes 3, 8 and 10), it might be set also at 25 or 35°C (or even 20°C).

Table A1. p_K (in $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), T and RFL of Box's vegetation classes. N: 3 – raingreen/semi-evergreen forests/woodlands/scrub; 4 – evergreen broad-leaved forests; 7 – shrublands (seasonal/evergreen); 8 – tropical rainforest; 10 – subhumid woodlands/scrub; 13 – summergreen broad-leaved forests and woods; 15 – grasslands; 36 – needle-leaved evergreen forests/woods. NN: number of data points

N	NN	p_K		T		RFL	
		Mean	SE	Mean	SE	Mean	SE
3	8	25.074	11.907	25.6	0.6	5.7	0.2
4	5	14.49	2.898	18.3	2.0	9.8	2.1
7	6	6.237	2.016	21.1	1.5	3.0	0.6
8	3	48.132	33.831	24.4	1.8	8.3	0.8
10	8	31.122	11.151	23.1	1.1	3.9	0.3
13	88	8.253	0.819	16.9	0.3	5.7	0.24
15	11	5.796	1.071	17.3	0.9	3.1	0.3
36	26	3.528	0.441	13.3	0.4	5.2	0.3

Appendix 2. Plausible value of the turnover time

Nakazawa et al. (1997) reported a linear relationship between the CO₂ concentrations observed in the troposphere over Siberia and $\delta^{13}\text{C}$ (-0.05‰ ppmv^{-1}) and concluded that the observed variations in CO₂ were caused by the CO₂ exchange with a single reservoir or with reservoirs with the same $\delta^{13}\text{C}$. The measurements were made in summer, and so they also suggest that the variations in CO₂ were produced by biospheric activities.

Let us denote the average, maximum and minimum of the observed summertime CO₂ concentrations as C_0 , C_+ and C_- , respectively, and the related values of $\delta^{13}\text{C}$ as δ_0 , δ_+ and δ_- , respectively. Then, the suggestions of Nakazawa et al. (1997) may be formulated as follows:

$$\begin{cases} C_+ - C_- = (\text{NPP} - R) \cdot \xi \\ \delta_+ C_+ - \delta_- C_- = (\delta_0 + \varepsilon)(\text{NPP} - R) \cdot \xi + \delta' \tau_B R \cdot \xi \\ \delta_+ = \delta_0 - 0.05(C_+ - C_0) \\ \delta_- = \delta_0 - 0.05(C_- - C_0) \end{cases} \quad (A4)$$

where NPP is net primary production, R is heterotrophic respiration (that is, CO₂ release in the course of organic matter decay), τ_B is the turnover time of the biological cycle, δ' is the rate of $\delta^{13}\text{C}$ depletion ($\delta' \approx -0.03\text{‰ yr}^{-1}$), ε is the isotopic shift that occurs in the course of air-plant exchange and ξ is a conversion factor.

Eq. (A4) implies

$$\delta_0(C_+ - C_-) - 0.05(C_+ - C_-)(C_+ + C_- - C_0) = (\delta_0 + \varepsilon)(C_+ - C_-) + \delta' \tau_B R \cdot \xi \quad (A5)$$

Let us assume that $\text{NPP} = xR$ and set for simplicity $x = 2$, then $R \cdot \xi = C_+ - C_-$. This allows us to rewrite Eq. (A5) as follows:

$$-0.05(C_+ + C_- - C_0) = \varepsilon + \delta' \tau_B \quad (A6)$$

Assuming next that $C_+ + C_- - C_0 \approx C_0$, we obtain

$$\tau_B = \frac{-(\varepsilon + 0.05C_0)}{\delta'} \quad (A7)$$

Setting δ' at -0.03‰ yr^{-1} and ε at -17‰ , we obtain

$$\tau_B = \frac{0.05C_0 - 17}{0.03}$$

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

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 ε . The assumed values of ε vary from -14.8‰ (Lloyd & Farquhar 1994) to -20‰ (Quay et al. 1992) and dramatically affect the estimate of τ_B . The observations of Nakazawa et al. (1997) imply $\varepsilon > -17.5\text{‰}$, which is in general agreement with the Lloyd-Farquhar theory – $\varepsilon \approx -17.5\text{‰}$ for an 'all-C₃ biosphere' – but must be higher due to the presence of C₄ plants. (For C₄ plants, $\varepsilon \approx -3.6\text{‰}$.) However, their particular estimate (-14.8‰) was derived from the contribution of C₄ plants to the annual GPP ($-17.8\text{‰} \times 0.79 - 3.6\text{‰} \times 0.21$), and its relevance to a particular season is questionable. Mid-summer (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 $\varepsilon \approx -19\text{‰}$ as a typical value for C₃ plants, we therefore set ε in Eq. (A7) to be -17‰ ($-19\text{‰} \times 0.87 - 3.6\text{‰} \times 0.13$) as a plausible value for the summer season.

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