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Modelling the seasonal contribution of a CO_2 fertilization effect of the terrestrial vegetation to the amplitude increase in atmospheric CO_2 at Mauna Loa Observatory

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ABSTRACT

An observed increase of the amplitude of the seasonal cycle of atmospheric CO_2 at Mauna Loa Observatory has been examined. Previous global carbon cycle studies seemed to suggest, at least qualitatively, that the observed increase may be entirely due to a CO_2 fertilization effect on the terrestrial biota. The present detailed theoretical investigation shows that a pure CO_2 stimulation of the net primary production may indeed lead to an amplitude increase of 0.15 plus 0.17% yr^{-1} and minus 0.10% yr^{-1} as compared to the measured value of $0.67 \pm 0.25\%$ yr^{-1} for the period between AD 1958 and AD 1987. This result is based on the assumption of a long term fertilization factor $\bar{\beta}$ with a range between 0.15 and 0.60, taken to be equal to the mesaured short term fertilization factor β, obtained in CO_2 enrichment studies with exposure times generally smaller than 1 year. The experimental evaluation of the difference between the relative increase of the summer (peak to trough) and winter (trough to peak) amplitude gives information on the carbon sequestered annually by the terrestrial ecosystems. With the estimated respiration response factor, which characterizes the fraction of the additional production that is consumed by ecosystem respiration, equal to 0.75, and an assumed long-term CO_2 fertilization factor, $\bar{\beta}$, equal to 0.375, acceptable agreement between prediction and measurements is obtained, amounting to a mean annual increase in living biomass of 0.7 Gt C, while a corresponding portion may be stored in soils. The fact that the fertilization alone predicts the observed difference but not the absolute value of both the summer and winter amplitude, leads to the conclusion that other external effects are operative, which are not directly related to the fertilization phenomenon of the vegetation and which influence to an equal extent the summer and winter amplitude. Two such external contributions have been identified; they are both related to the increased fossil fuel carbon input into the Northern Hemisphere: (1) the seasonality of the fossil fuel consumption in the Northern Hemisphere is approximately in phase with the relative uptake or release of CO_2 by the land vegetation and leads to a small contribution to the increase in amplitude, in the range between 0.01 and 0.08% yr^{-1}; (2) the seasonally different transequatorial transport of fossil fuel carbon creates a seasonal behavior which again is approximately in phase with the biota and leads to an additional contribution in the range of 0 to 0.31% per year depending on the wind fields used.

1. Introduction

In early discussions of the "CO_2 problem" the secular increase in atmospheric CO_2 was ascribed almost entirely to CO_2 production by the combustion of oil, coal and natural gas. The fact that the observed atmospheric CO_2 increase was only about half the calculated quantity of CO_2 produced by combustion of fossil fuels was thought to be due to the uptake of excess CO_2 by the

oceans. Woodwell et al. (1978) were among the first to point out that deforestation might contribute a large fraction of the increase in atmospheric CO_2. But, if this were the case, it was hard to see how the oceans could absorb the difference between total CO_2 production from fossil fuel combustion and biogenic sources and the amount remaining in the atmosphere. Keeling (1973), Keeling and Bacastow (1977) and Revelle and Munk (1977) among others, suggested that the biosphere might in fact be a net sink for CO_2 instead of a net source, i.e., that the total biomass of the terrestrial biosphere is actually increasing. Because estimates of terrestrial biomass have such large uncertainties it has been impossible to determine by direct measurement whether this biomass is slightly increasing or decreasing in size. It might be possible to answer the question indirectly, however, by studies of the behavior of atmospheric CO_2, in particular the seasonal cycle of the Northern Hemisphere which reflects mainly biological activities. Controlled experiments in greenhouses and laboratories show that photosynthetic production increases with increasing levels of CO_2 in the atmosphere surrounding the plants. But the effects in natural ecosystems, where many other factors limit organic production, are quite uncertain. Here, also one might hope to learn something from changes in the amplitude of the seasonal CO_2 cycle over extended time periods.

The amplitude of the seasonal atmospheric CO_2 cycle as measured and analyzed by various atmospheric monitoring stations has been increasing over the past three decades. The Mauna Loa Observatory has the longest uninterrupted record and is one of the most distant from major sources and sinks of CO_2 coming from land vegetation; we shall assume that this record is representative of the average changes that have occurred in the Northern Hemisphere, induced both by man and by climatic variations. Heimann et al. (1986), utilizing a three dimensional transport model developed by the Goddard Institute of Space Sciences (GISS), with a windfield derived from a general circulation model of the atmosphere, have established the dominant role of the seasonal vegetation in the observed annual atmospheric CO_2 cycle in the Northern Hemisphere. They found that the Northern Hemisphere land biosphere during an average year contributes 6.87 ppm to the peak-to-peak amplitude at Manuna Loa Observatory with the maximum in the composite signal of the model on 26 April and the minimum on 29 September. The peak-to-peak amplitude on the same dates from all sources including those contributed by the oceans and man was calculated to be 6.26 ppm for AD 1980, while the observed signal for that year was 6.29 ppm (see Fig. 1). The Southern Hemisphere land biosphere makes only a very small contribution of -0.13 ppm, whereas the oceans contribute -1.22 ppm. The latter effect is largely explained by the seasonal heating of the near surface ocean waters which result in a release of CO_2 into the atmosphere during the spring and summer months of the Northern Hemisphere, when most of the CO_2 uptake by land plants occurs. The model seasonal contribution from fossil fuel combustion for AD 1980 is 0.74 ppm. This results mainly because most fossil fuel is consumed in the Northern Hemisphere and greater transequatorial transport of the derived CO_2 in the model occurs in summer than in winter. In a later paper, Heimann et al. (1988) substitute actual wind data for AD 1979 for the model winds used previously and obtain a similar result except that the contribution to the seasonal cycle from fossil fuel is much less, only about 0.2 ppm.

We shall address in this paper the response of the Northern Hemisphere land biota to the secular increase in atmospheric CO_2. We shall see that the CO_2 fertilization effect on the vegetation partly explains the mean annual amplitude increase at Mauna Loa and other observing stations, but that the CO_2 fertilization effect alone does not provide a full explanation. A preliminary analysis, in which other anthropogenically released nutrients in the form of nitrogen, phosphorus and sulfur compounds are considered as well, shows that the nitrogen compounds may indeed contribute an important part to the fertilization of forests and grasslands in low pollution areas (Kohlmaier et al., 1988a). Such a combined CO_2/nitrogen fertilization effect may increase the fertilization factor β, which describes the relative increase in net primary production with respect to the relative increase in CO_2 and other nutrients, from an estimated value of β of 0.375 ± 0.225 for CO_2 alone, to approximately twice this value. However, even such an

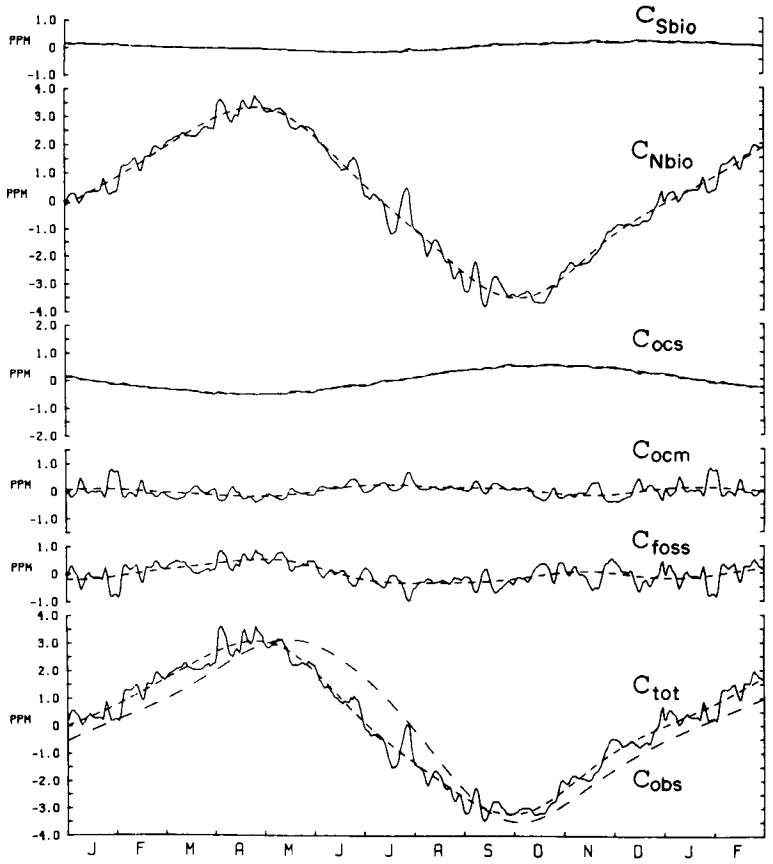

Fig. 1. Simulated daily CO_2 concentration values (solid curves) at Mauna Loa (Heimann et al., 1986). Shown are the various components resulting from the different sources: C_{Sbio}, Southern Hemisphere land biosphere; C_{Nbio}, Northern Hemisphere land biosphere; C_{ocs}, seasonal oceanic CO_2 source; C_{ocm}, stationary oceanic source/sink; C_{foss}, fossil fuel source/sink. A four harmonic fit to the simulated daily values is also shown (short dashed curves). The bottom panel shows the combined signal C_{tot} together with the Mauna Loa data (C_{obs}, long dashed curve). Each component has been shifted so that its annual mean vanishes. The fossil fuel component C_{foss} has been detrended by subtracting a linear increase of 1.68 ppm yr^{-1}.

increased value of the fertilization factor cannot alone explain the observed increase of the seasonal amplitude at the Mauna Loa Observatory, indicating that still other effects are operative, of which changes in climate and land use may be of major importance (Kohlmaier et al., 1988b).

The long-term response of different biomes to increased photosynthetic biomass production is still not well understood (Strain, 1985, and Strain and Cure, 1985), especially with respect to their ability to store the additional production in the living and dead biota. Within the living biota, the world's forests are probably the greatest potential reservoirs for carbon storage while the soils of the temperate and boreal forests and tundra regions may store an even greater amount of carbon provided there is no rise in temperature. It will be shown in this paper that the fraction of carbon sequestered will influence the observed apparent amplitude and its mean annual increase. A particularly simple expression of the dependence of the amplitude on CO_2 fertilization and carbon sequestering is obtained when in addition to the fertilization factor β a heterotrophic respiration response factor ρ, lying between 0 and 1, is

introduced, which defines the fraction of carbon respired to carbon assimilated in excess atmospheric CO_2. In particular, we are able to show by looking at the differences of the gains in the winter (trough to peak) and summer (peak to trough) amplitudes that the present storage of carbon is indeed related to the product of β and $(1-\rho)$. Evaluating the observed difference between the winter and summer amplitudes at Mauna Loa, we estimate that the amount of carbon sequestered should be substantial, on the order of 0.7 ± 0.3 Gt C yr^{-1} in the biota and 0.6 ± 0.35 Gt C yr^{-1} in the humus soil fraction, totalling 1.3 ± 0.7 Gt C yr^{-1} (Kohlmaier et al., 1987).

2. Model for the amplification of the atmospheric CO_2 seasonal cycle within the northern atmosphere, as measured at Mauna Loa Observatory

In the following, we present a model which relates the observed amplitude increase of the atmospheric CO_2 cycle to the stimulation of the photosynthesis of land plants by increasing levels of atmospheric CO_2. Heimann et al. (1986) have shown that the vegetation of the Northern Hemisphere land biota dominates the observed seasonal cycle with a contribution of approximately 90%, hence we shall analyze mainly the changes of the carbon fluxes entering from the Northern Hemisphere atmosphere into the biota, here called F_{npp}, and the corresponding net fluxes from the biosphere into the atmosphere, F_{res}, as the main two exchange processes, shown in Fig. 2. F_{npp} represents the total flux of atmospheric CO_2 entering the Northern Hemisphere biota as a result of gross photosynthesis minus autotrophic respiration of the plants. The index npp is chosen since the annual integral over the flux F_{npp} represents the net primary production (NPP) of all Northern Hemisphere biota. The corresponding flux F_{res} represents the net carbon release from the living biota, litter and soil layer whose annual integral is equivalent to the heterotrophic respiration (RES) by organisms of the detritus and grazing food chain. All other contributions to the seasonal behavior of atmospheric CO_2 in the Northern Hemisphere are modelled by a term F_{ext}, which is small with respect to

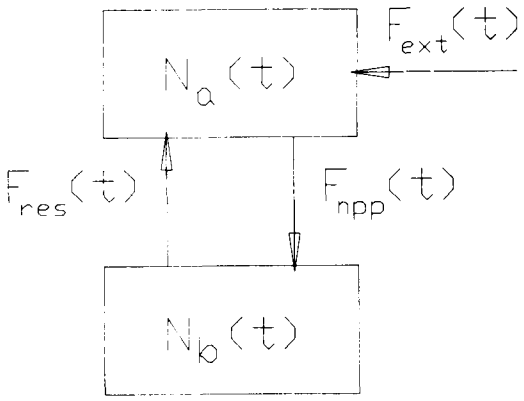

Fig. 2. Model diagram for the seasonal exchange between stored CO_2 in the Northern Hemisphere atmosphere (N_a) and stored carbon in the Northern Hemisphere biota (N_b). F_{res} refers to the flux of CO_2 associated with heterotrophic respiration and F_{npp} to the flux associated with net primary production. $F_{ext}(t)$ denotes seasonally varying additional fluxes which perturb the atmosphere-biota system.

the main fluxes describing the exchange between the Northern Hemisphere atmosphere and the Northern Hemisphere biota. The change with respect to time, t, of the Northern Hemisphere atmosphere carbon content N_a is then given by the differential balance equation:

$$dN_a/dt = F_{res}(t) - F_{npp}(t) + F_{ext}(t). \quad (1)$$

To describe the atmospheric CO_2 behavior in terms of F_{npp}, F_{res}, and F_{ext} during the course of a particular yearly interval, n, we integrate eq. (1) beginning with the day in autumn when the CO_2 concentration is minimal, after removing the slowly varying long term secular increase from the record.

$$N_a(n-1+t) = N_a(n-1) + \int_0^t [F_{res}(n-1+\tilde{t}) - F_{npp}(n-1+\tilde{t})]\,d\tilde{t} + \int_0^t F_{ext}(n-1+\tilde{t})\,d\tilde{t}. \quad (2)$$

For mathematical convenience the yearly interval is started at 29 September, the average day of minimum atmospheric CO_2 concentration for the Mauna Loa record. The year $n = 1$ starts on 29 September 1958 and lasts through 28 September

1959, while any year n starts on 29 September of year $(1957 + n)$ and ends on 28 September of year $(1957 + n + 1)$. In the integration, $t \leqslant 1$ yr and the integration variable is distinguished from t by the symbol $\bar{t}$.

In Fig. 3a typical qualitative smoothed one-year cycles of F_{npp} and F_{res} are shown for two consecutive years. The cycles are estimated from ecological data neglecting other sources into the atmosphere. The atmospheric signal is characterized by a winter season in which F_{res} exceeds F_{npp}, and a summer season in which F_{npp} exceeds F_{res}. The integral of the difference of the two fluxes shows therefore a maximum at the end of the winter season and a minimum at the end of the summer season, as illustrated by the dashed curve in Fig. 3c. Although not necessary for the analysis of the model, we find it convenient to approximate both F_{npp} and F_{res} by periodical step functions (Fig. 3b), with the constraint that the seasonal net inputs are time-invariant (Fig. 3c, curve b), implying that the cross-hatched areas of Figs. 3a and 3b for a season are equal to one another. The fraction of the year in which the atmospheric CO_2 concentration rises is denoted by m_w. For the Mauna Loa record m_w is equal to 0.63. The corresponding fraction where atmospheric CO_2 falls is denoted m_s which for the same record is 0.37. The sum $n + m_w$ refers to 29 April of the year n. The integrals over each of the two fluxes, F_{npp} and F_{res}, taken separately for the winter and summer season, represent the net primary production and heterotrophic respiration respectively for the seasons of a particular year, n.

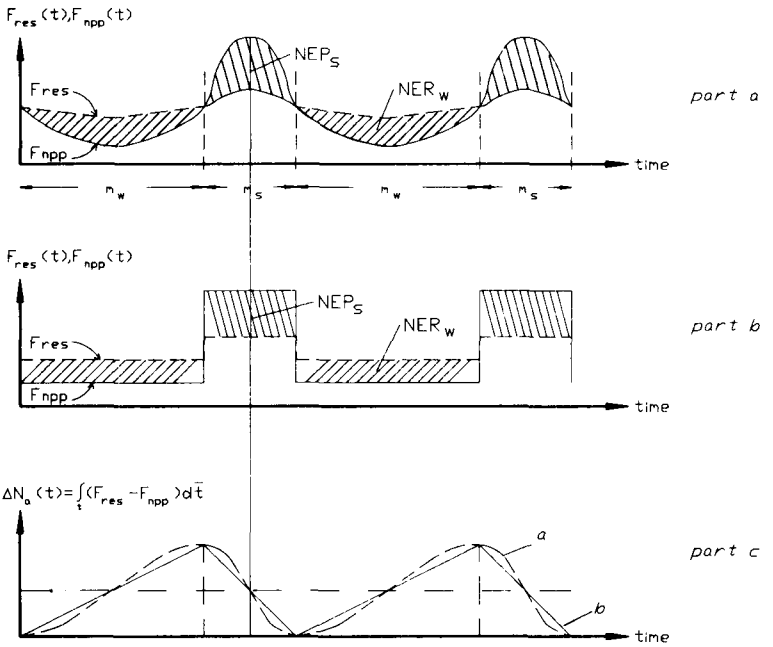

Fig. 3. (a) Seasonal cycle of atmospheric CO_2 as derived from the difference between CO_2 fluxes F_{res} and F_{npp} in a seasonally balanced biosphere. Time intervals, m_s and m_w, refer to the summer and the winter season of the year respectively, as discussed in the text. The cross-hatched areas indicate the net ecosystem respiration in winter, NER_w, and the net ecosystem production in summer, NEP_s. NER_w and NEP_s are set equal. (b) Same as Fig. 3a except that F_{npp} and F_{res} are step functions in time, chosen such that NER_w and NEP_s are equal to the corresponding quantities in 3a. (c) Change in atmospheric CO_2 concentration consistent with Fig. 3a, dashed curve, and Fig. 3b, solid straight lines. The peak to peak amplitudes are the same in both cases.

These four quantities are defined by the following equations.

$$\mathrm{NPP_s}(n) = \int_{m_w}^{1} F_{\mathrm{npp}}(n-1+t)\,\mathrm{d}t \tag{3a}$$

$$\mathrm{NPP_w}(n) = \int_{0}^{m_w} F_{\mathrm{npp}}(n-1+t)\,\mathrm{d}t \tag{3b}$$

$$\mathrm{RES_s}(n) = \int_{m_w}^{1} F_{\mathrm{res}}(n-1+t)\,\mathrm{d}t \tag{3c}$$

$$\mathrm{RES_w}(n) = \int_{0}^{m_w} F_{\mathrm{res}}(n-1+t)\,\mathrm{d}t. \tag{3d}$$

We shall also make use of the integrals over a full year defined by

$$\mathrm{NPP}(n) = \int_{0}^{1} F_{\mathrm{npp}}(n-1+t)\,\mathrm{d}t \tag{3e}$$

$$\mathrm{RES}(n) = \int_{0}^{1} F_{\mathrm{res}}(n-1+t)\,\mathrm{d}t. \tag{3f}$$

The observable trough to peak amplitude:

$$A_w(n) = N_a(n-1+m_w) - N_a(n-1),$$

(winter amplitude) and the corresponding peak to trough amplitude:

$$A_s(n) = N_a(n-1+m_w) - N_a(n),$$

(summer amplitude) of a given year n can be derived within the framework of our model as the sum of a biotic and an external contribution:

$$\begin{aligned} A_w(n) &= N_a(n-1+m_w) - N_a(n-1) \\ &= \mathrm{NER_w}(n) + b(n) + m_w a(n) \end{aligned} \tag{4a}$$

and

$$\begin{aligned} A_s(n) &= N_a(n-1+m_w) - N_a(n) \\ &= \mathrm{NEP_s}(n) + b(n) - m_s a(n). \end{aligned} \tag{4b}$$

The first terms on the right side of eqs. (4a) and (4b) symbolize the net ecosystem respiration in winter defined by

$$\mathrm{NER_w}(n) = \mathrm{RES_w}(n) - \mathrm{NPP_w}(n) \tag{5a}$$

and the net ecosystem production in summer

$$\mathrm{NEP_s}(n) = \mathrm{NPP_s}(n) - \mathrm{RES_s}(n). \tag{5b}$$

Both $\mathrm{NER_w}$ and $\mathrm{NEP_s}$ are non-negative by the choice of m_w and m_s to represent the time of minimal and maximal CO_2 concentration, respectively, in the record, detrended with respect to the long term source increase. The contributions of the external carbon fluxes are characterized by the following two quantities. The first quantity $a(n)$ is the annually integrated external CO_2 input, which in recent years has been positive due to the combustion of fossil fuels:

$$a(n) = \int_{0}^{1} F_{\mathrm{ext}}(n-1+t)\,\mathrm{d}t. \tag{6a}$$

The second quantity is the seasonal component of the external CO_2 input which may be a positive or negative quantity.

$$b(n) = \int_{0}^{m_w} F_{\mathrm{ext}}(n-1+t)\,\mathrm{d}t - m_w a(n). \tag{6b}$$

These additional contributions, $a(n)$ and $b(n)$, represent not only the fossil fuel input but also atmospheric carbon dioxide exchange processes with the oceans and the Southern Hemisphere.

Figs. 4a, 4b and 4c illustrate possible relations between the observable amplitudes $A_w(n)$ and $A_s(n)$, the ecological quantities NER(n) and NEP(n), and the parameters $a(n)$ and $b(n)$ of the external CO_2 contribution. The annual net ecosystem production NEP defined by

$$\mathrm{NEP}(n) = \mathrm{NPP}(n) - \mathrm{RES}(n) \tag{7a}$$

$$= \mathrm{NEP_s}(n) - \mathrm{NER_w}(n), \tag{7b}$$

indicates whether the Northern Hemisphere biota will absorb CO_2 ($\mathrm{NEP}(n) > 0$) or release CO_2 ($\mathrm{NEP}(n) < 0$) over one year. For the pre-industrial state assumed to finish at AD 1750, we assume that the ensemble of all ecosystems of the Northern Hemisphere is approximately in a balanced state (designated by the superscript "o") such that $\mathrm{NEP^o}$ equals 0. In contrast, we will allow (as in Figs. 4a, 4b and 4c) the possibility that the CO_2 fertilization effect will not only bring about an increase in NPP, and as a consequence an increase in RES, but also the sequestration of carbon in the biota and soils, such that

$$\mathrm{NEP}(n) > 0 \quad \text{for all } n \geqslant 1.$$

In addition to $A_w(n)$ and $A_s(n)$, we have plotted in Figs. 4a, 4b and 4c an apparent mean amplitude $A(n)$ which can be expressed in terms of $\mathrm{NEP_s}$ and $\mathrm{NER_w}$ (eqs. 4a, 4b, 7b)

$$A(n) = m_s A_w(n) + m_w A_s(n) \tag{8a}$$

$$= m_s \mathrm{NER_w}(n) + m_w \mathrm{NEP_s}(n) + b(n) \tag{8b}$$

$$= \mathrm{NER_w}(n) + m_w \mathrm{NEP}(n) + b(n), \tag{8c}$$

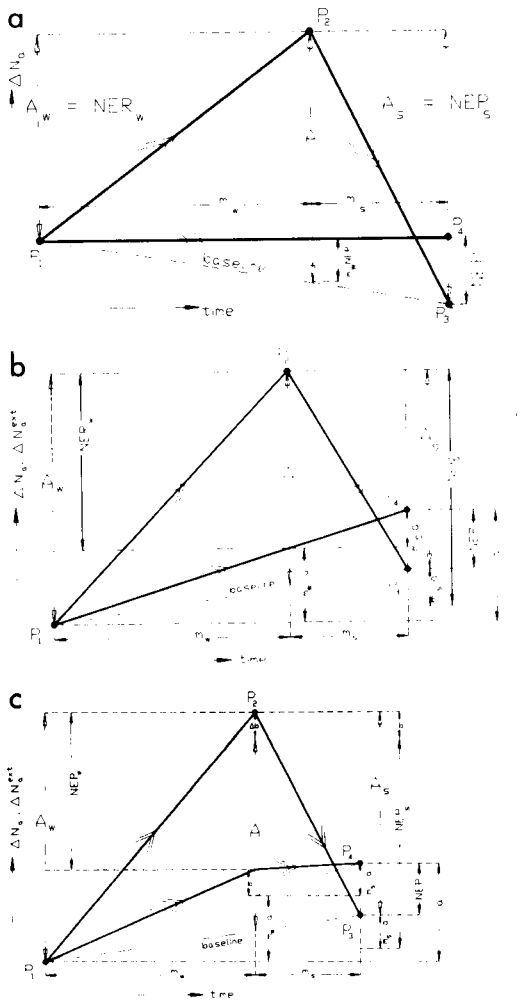

Fig. 4. (a) Seasonal CO_2 cycle showing winter amplitude, A_w, summer amplitude, A_s, and mean amplitude, A, for an unbalanced biosphere where NEP (equal to $NEP_s - NER_w$) is greater than zero and no external input, F_{ext}, is operative. The vertical scale is in units of carbon abundance. (b) Same as Fig. 4a except that a constant external input, F_{ext}, operates during the entire course of the year. (c) Same as Fig. 4b except that F_{ext} is seasonally varying.

and which can be interpreted geometrically as the vertical distance from the peak (P_2) to the base line of the neighbouring troughs (line $P_1 P_3$). The advantage of this definition is the removal of the linear trend $a(n)$ from any external perturbations.

In Fig. 4a we illustrate the limiting case in which there is no external perturbation F_{ext}; in other words, both $a(n)$ and $b(n)$ equal zero. If in addition, no net ecosystem production occurs ($NEP = 0$), the atmospheric CO_2 concentration at the beginning (initial point P_1) and at the end of a one year period (end point P_4) would be equal to one another. If, however, as illustrated, NEP is assumed to be greater than zero, the rise in atmospheric CO_2 concentration from point P_1 to point P_2 during the winter period, with NER_w equal to A_w, is smaller than the corresponding fall in summer from point P_2 to P_3 with NEP_s equal to A_s.

In Fig. 4b, an external perturbation is considered which comprises an external annual contribution $a(n)$, without a seasonal contribution $b(n)$. The winter amplitude A_w in this particular case becomes larger than in the case illustrated in Fig. 4a, while, at the same time, the summer amplitude becomes smaller such that the two effects cancel out in the mean amplitude. In Fig. 4b, two pathways are indicated, namely $P_1 P_4$ associated with the external CO_2 input, and a total resulting pathway $P_1 P_2 P_3$ including the biotic activity; the distance $d(P_3 P_4)$ characterizes the case where NEP is greater than zero. Finally, in Fig. 4c, it is assumed that there is an external CO_2 contribution to the amplitude which is characterized by the excess seasonal contribution $b(n)$ measured at the maximum of the composite signal ($t = m_w$). The path $P_1 P_4$, which describes the external input of CO_2 during the course of the year, is now characterized by the excess seasonality $b(n)$. Superposition of the external contribution onto the biotic activity results in the winter amplitude A_w ($A_w = NER_w + m_w a + b$) and the corresponding summer amplitude A_s ($A_s = NEP_s - m_s a + b$). The path $P_1 P_2 P_3$ shows the resulting CO_2 increase and decrease during the one year cycle, where the apparent mean amplitude is given geometrically by:

$$A = NER_w + b + m_w NEP$$

which is equal to the previously obtained eq. (8c). By substitution of eqs. (5a) and (5b) into eq. (8b), the apparent mean amplitude $A(n)$ can be expressed in terms of NPP_s, RES_s, NPP_w and RES_w:

$$A(n) = m_s[RES_w(n) - NPP_w(n)] + m_w[NPP_s(n) - RES_s(n)] + b(n). \quad (9)$$

In a previous paper, Kohlmaier et al. (1987) showed that both the net primary production (NPP) and the heterotrophic respiration (RES), which are annual integrals of corresponding fluxes, can be expressed as a function of the increasing atmospheric CO_2 levels by introducing the two parameters, the CO_2 fertilization factor $\bar{\beta}$ and the respiration factor ρ discussed above. Choosing a simple linear dependence of NPP on the partial pressure of atmospheric CO_2, the change in NPP with respect to a chosen reference state NPP° at corresponding CO_2° is given by:

$$\mathrm{NPP}(n) = \mathrm{NPP}^\circ\left[1 + \bar{\beta}\frac{\mathrm{CO_2}(1958.24 + n) - \mathrm{CO_2^\circ}}{\mathrm{CO_2^\circ}}\right], \quad (10)$$

where the mean excess CO_2 concentration during the year $n = 1$ (29 September 1958 to 28 September 1959) is characterized by the corresponding concentration of 29 March 1959 (1958.24 + 1). The best exponential fit of the atmospheric CO_2 concentrations during the Mauna Loa period between AD 1958 and AD 1982 has been evaluated by Bacastow et al. (1985):

$$\mathrm{CO_2}(t) = 297.85 + 16.510\exp(0.037808(t - 1957.0)), \quad (11)$$

which is characterized by a starting CO_2 value of 297.85 ppm (different from the preindustrial value of 279 ppm because it fails to account properly for a biotic CO_2 release before AD 1958) and an exponential increase of 0.037808 yr^{-1}.

$\bar{\beta}$ in eq. (10) represents the CO_2 fertilization factor appropriate to the case of a gradual increase in atmospheric CO_2 levels (for details see Kohlmaier et al., 1987). It may be related with caution to the experimental CO_2 fertilization factor β determined in phytotrons, greenhouses, and open top chambers (Strain and Cure, 1985; Rogers et al., 1983; Kimball, 1983), where the CO_2 concentration is held at an elevated level throughout the experiment:

$$\beta(\mathrm{CO_2}) = \frac{[\mathrm{NPP(CO_2)} - \mathrm{NPP(CO_{2\,amb})}]/\mathrm{NPP(CO_{2\,amb})}}{[\mathrm{CO_2} - \mathrm{CO_{2\,amb}}]/\mathrm{CO_{2\,amb}}}. \quad (12)$$

Eq. (12) is formally related to eq. (10) when eq. (10) is solved for $\bar{\beta}$. The β from eq. (12) defines the relative increase in NPP, or yield of annual crops, with respect to the relative increase of CO_2 above the ambient concentration $CO_{2\,amb}$ of 330 to 340 ppm.

In analogy to the net primary production, NPP(n), as given by eq. (10), we accept the expression for the heterotrophic respiration RES(n) obtained by Kohlmaier et al. (1987, eq. 36) within the asymptotic limit of long adaptation times to the perturbation of excess CO_2:

$$\mathrm{RES}(n) = \mathrm{RES}^\circ\left[1 + \rho\bar{\beta}\frac{\mathrm{CO_2}(1958.24 + n) - \mathrm{CO_2^\circ}}{\mathrm{CO_2^\circ}}\right] \quad (13)$$

where the respiration response factor ρ, a parameter within the limits 0 to 1, describes the respiration increase following a stimulation of the NPP. Setting ρ equal to unity implies that NPP(n) and RES(n) increase to an equal extent, allowing no additional storage of carbon, while a ρ of zero implies the very unrealistic situation that the heterotrophic respiration is not changed at all, such that all additional carbon assimilated is sequestered by the ecosystem.

Kohlmaier et al. (1987) have shown that the factor ρ can be interpreted dynamically. For example, if NPP(n) increases in response to an exponentially rising CO_2 input according to eq. 10, while the respiration response of the biota is proportional to biomass, then the respiration response is given by

$$\rho = \frac{1}{1 + k_f\,\tau_B(i)}, \quad (14)$$

where k_f is the rate constant for an exponential CO_2 increase in the atmosphere and where $\tau_B(i)$ is the residence time of carbon in a particular ecosystem i. The quantity τ_B has been previously characterized for four biome types (Kohlmaier et al., 1987): agriculture systems with $\tau_B \cong 1$ yr ($\rho = 0.96$), savanna and other grassland systems with $\tau_B \cong 4$ yr ($\rho = 0.87$), tropical forests with $\tau_B \cong 14$ yr ($\rho = 0.65$) and temperate and boreal forests collectively with $\tau_B \cong 21$ yr ($\rho = 0.56$). As the temperate and boreal forests are major contributors to the seasonality of atmospheric CO_2

observed in the Northern Hemisphere, the respiration response factor ρ most probably lies in the range 0.6 to 0.8, and almost surely lies in the range 0.5 to 1.0. Thus we write:

$$\rho = 0.75 \pm 0.25.$$

If the above relations are generalized in the sense that both the net primary production and the heterotrophic respiration are affected by CO_2 fertilization to an equal extent in summer and winter, then the change of NPP_s or NPP_w between a particular year n and a reference year 0 (beginning 29 September 1957) is given by:

$$\mathrm{NPP}_j(n) - \mathrm{NPP}_j(0) = \mathrm{NPP}_j^\circ \bar{\beta} \left(\frac{\Delta \mathrm{CO}_2(n) - \Delta \mathrm{CO}_2(0)}{\mathrm{CO}_2^\circ} \right) \tag{15a}$$

where $j = $ s or w and $\Delta \mathrm{CO}_2(n) = \mathrm{CO}_2(1958.24 + n) - \mathrm{CO}_2^\circ$.

By defining a mean annual stimulation factor $\bar{\chi}(n)$:

$$\bar{\chi}(n) = \frac{\bar{\beta}}{n} \left(\frac{\Delta \mathrm{CO}_2(n) - \Delta \mathrm{CO}_2(0)}{\mathrm{CO}_2^\circ} \right) = \frac{\bar{\beta}}{n} \left(\frac{\mathrm{CO}_2(n) - \mathrm{CO}_2(0)}{\mathrm{CO}_2^\circ} \right), \tag{15b}$$

eq. (15a) can be written as:

$$\mathrm{NPP}_j(n) - \mathrm{NPP}_j(0) = n \bar{\chi}(n) \, \mathrm{NPP}_j^\circ, \tag{15c}$$

where $j = $ s or w.

Similarly the integral change of the heterotrophic respiration is assumed to be given, following from eq. (13), by

$$\mathrm{RES}_j(n) - \mathrm{RES}_j(0) = n \rho \bar{\chi}(n) \, \mathrm{RES}_j^\circ \tag{16a}$$

where $j = $ s or w.

For the evaluation of the amplitude change in terms of the ecological quantities NPP_j° and NEP_s°, RES_j° in eq. (16a) may be substituted by eqs. (5a) and (5b), assuming that NER_w° equals NEP_s° in the preindustrial state, which results in

$$\begin{aligned} \mathrm{RES}_s(n) - \mathrm{RES}_s(0) &= n \rho \bar{\chi}(n) [\mathrm{NPP}_s^\circ - \mathrm{NEP}_s^\circ] \\ \mathrm{RES}_w(n) - \mathrm{RES}_w(0) &= n \rho \bar{\chi}(n) [\mathrm{NPP}_w^\circ + \mathrm{NEP}_s^\circ]. \end{aligned} \tag{16b}$$

With eqs. (15c) and (16b), the mean annual change of the amplitude (eq. 9) up to the year n of the Mauna Loa record may be evaluated:

$$\begin{aligned} \overline{\Delta_a A}(n) &= \frac{A(n) - A(0)}{n} \qquad (17a) \\ &= \frac{m_s}{n} [(\mathrm{RES}_w(n) - \mathrm{RES}_w(0)) - (\mathrm{NPP}_w(n) - \mathrm{NPP}_w(0))] + \frac{m_w}{n} [(\mathrm{NPP}_s(n) - \mathrm{NPP}_s(0)) - (\mathrm{RES}_s(n) - \mathrm{RES}_s(0))] + \overline{\Delta_a b}(n) \\ &= \bar{\chi}(n) (\rho \mathrm{NEP}_s^\circ + (1 - \rho)[m_w \mathrm{NPP}_s^\circ - m_s \mathrm{NPP}_w^\circ]) + \overline{\Delta_a b}(n) \end{aligned}$$

where:

$$\overline{\Delta_a b}(n) = \frac{1}{n} [b(n) - b(0)]. \tag{17b}$$

The relative mean annual amplitude increase with respect to a reference amplitude A° equal to NEP_s°, assuming a preindustrial reference state, in which NEP_s° equals NER_w°, is given by:

$$\frac{\overline{\Delta_a A}(n)}{A^\circ} = \bar{\chi}(n) \left\{ \rho + (1 - \rho) \left[m_w \frac{\mathrm{NPP}_s^\circ}{\mathrm{NEP}_s^\circ} - m_s \frac{\mathrm{NPP}_w^\circ}{\mathrm{NEP}_s^\circ} \right] \right\} + \frac{\overline{\Delta_a b}(n)}{\mathrm{NEP}_s^\circ}. \tag{18a}$$

The two terms within the square brackets are a function of the partitioning of NPP° and RES° between the summer and winter periods. We will represent this quantity in square brackets with the symbol, σ, and call it the "reference state partition function". Examples of the partitioning are illustrated in Figs. 6, 7, and 8, and are discussed in detail below. We will find it convenient to evaluate σ in terms of the annual production as well as according to its definition. Hence we note that:

$$\sigma = m_w \frac{\mathrm{NPP}_s^\circ}{\mathrm{NEP}_s^\circ} - m_s \frac{\mathrm{NPP}_w^\circ}{\mathrm{NEP}_s^\circ} = \frac{\mathrm{NPP}^\circ}{\mathrm{NEP}_s^\circ} (p_i - m_s) \tag{18b}$$

where

$$p_j = \frac{\mathrm{NPP}^{\circ}_j}{\mathrm{NPP}^{\circ}}, \tag{18c}$$

where $j = \mathrm{s}$ or w, $p_s + p_w = 1$, and $\mathrm{NPP}^{\circ} = \mathrm{NPP}^{\circ}_s + \mathrm{NPP}^{\circ}_w$. The relative amplitude change is then given by the expression:

$$\frac{\overline{\Delta_a A}(n)}{A^{\circ}} = \bar{\chi}(n)\{\rho + (1-\rho)\sigma\} + \frac{\overline{\Delta_a b}(n)}{\mathrm{NEP}^{\circ}_s}. \tag{18d}$$

Similarly the mean relative amplitude changes for the winter and the summer amplitude can be derived from eqs. (4a, 4b), (14a, 14b) and (15):

$$\frac{\overline{\Delta_a A_s}(n)}{A^{\circ}} = \bar{\chi}(n)\left\{\rho + (1-\rho)\frac{\mathrm{NPP}^{\circ}_s}{\mathrm{NEP}^{\circ}_s}\right\} + \frac{\overline{\Delta_a b}(n) - m_s\overline{\Delta_a a}(n)}{\mathrm{NEP}^{\circ}_s} \tag{19a}$$

$$\frac{\overline{\Delta_a A_w}(n)}{A^{\circ}} = \bar{\chi}(n)\left\{\rho - (1-\rho)\frac{\mathrm{NPP}^{\circ}_w}{\mathrm{NEP}^{\circ}_s}\right\} + \frac{\overline{\Delta_a b}(n) + m_w\overline{\Delta_a a}(n)}{\mathrm{NEP}^{\circ}_s} \tag{19b}$$

where

$$\overline{\Delta_a a}(n) = \frac{1}{n}[a(n) - a(0)], \tag{19c}$$

and $A^{\circ} = A^{\circ}_s = A^{\circ}_w \cong \mathrm{NEP}^{\circ}_s$.

Finally, the difference between summer and winter amplitude (eqs. 19a and 19b) gives a particularly simple relation, useful in determining the amount of carbon sequestered in an ecosystem:

$$\frac{\overline{\Delta_a A_s}(n) - \overline{\Delta_a A_w}(n)}{A^{\circ}_s} = \bar{\chi}(n)(1-\rho)\frac{\mathrm{NPP}^{\circ}}{\mathrm{NEP}^{\circ}_s} - \frac{\overline{\Delta_a a}(n)}{\mathrm{NEP}^{\circ}_s}, \tag{19d}$$

where $A^{\circ} = A^{\circ}_s = A^{\circ}_w \cong \mathrm{NEP}^{\circ}_s$ as above.

3. Model distributions for the seasonal uptake and release of CO_2 in the Northern Hemisphere and their relation to the amplitude measured at Mauna Loa Observatory

In Section 2, we have derived equations for the amplitude increase of the seasonal cycle which can be evaluated provided that we know the seasonal rate of uptake and release of CO_2 by the Northern Hemisphere vegetation in its response to increasing CO_2 levels, expressed by the parameters $\bar{\beta}$, the fertilization factor, and ρ, the respiration response factor. In addition we have shown that external perturbations may become important, in particular when the external fluxes exhibit a seasonal behavior, here expressed by the parameter $b(n)$. The above expressions for the amplitude change of the seasonal cycle in the Northern Hemisphere were derived without the explicit coupling of the biotic source-sink terms to a three dimensional atmospheric transport model. Within the approximations made to derive these expressions, the Northern Hemisphere is considered as one well mixed box which reflects the integrated release and uptake of CO_2 by all Northern Hemisphere ecosystems. In Fig. 5a, the monthly rates of net primary production and respiration, $F_{npp}(j)$ and $F_{res}(j)$ ($j = 1, 2, \ldots, 12$) are shown, as calculated by Heimann et al. (1988) for the Northern Hemisphere vegetation. These authors derive the temporal and spatial distribution of F_{npp} from satellite measurements from which they deduced the incoming photosynthetically active solar radiation intercepted by the vegetation canopy. They modelled F_{res} so as to achieve a best fit to atmospheric CO_2 observations under the assumption that no net annual accumulation of carbon occurs locally. They chose F_{res} to be the sum of a constant term and a term depending on the mean daily temperature above a threshold of -10°C. They assumed that every increase of 10°C in temperature near the ground increases the heterotrophic respiration by a factor of 1.5 (i.e., Q_{10} value of 1.5). The difference between the curves of F_{npp} and F_{res} (cross hatched area in Fig. 5a) defines the summer net ecosystem production NEP_s ($F_{npp} - F_{res} > 0$) and the winter net ecosystem respiration NER_w ($F_{npp} - F_{res} < 0$). In Fig. 5b the calculated net uptake or release of CO_2 by the vegetation, based on the data of Fig. 5a, is compared with the corresponding difference signal of the measured integrated atmospheric CO_2 concentration ($N_a(j) - N_a(j-1)$) at Mauna Loa Observatory for the mean seasonal cycle between AD 1958 and AD 1987 shown in Table 1 (uptake of Bacastow and Keeling, 1981, p. 104). A mean delay time of two weeks is assumed between the biogenic sources and the observation point at

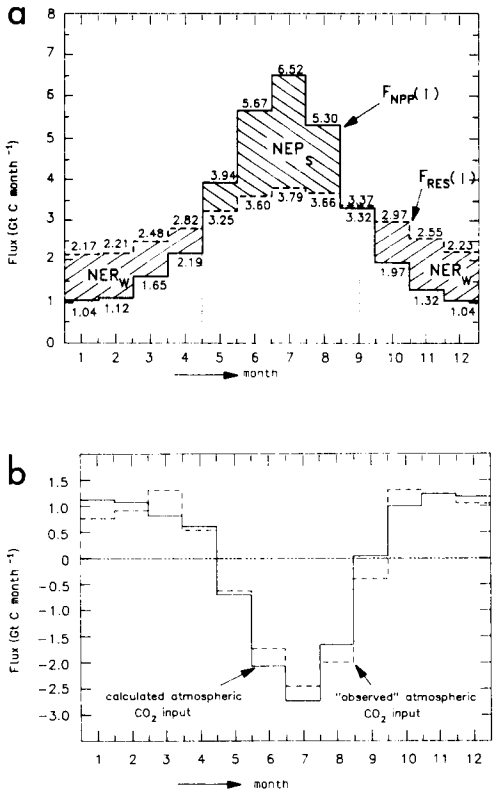

Fig. 5. (a) Predicted CO_2 fluxes of respiration, $F_{res}(j)$, and net primary production, $F_{npp}(j)$, in Gt C for each month, j, of a yearly cycle derived for the Northern Hemisphere from the model of Heimann et al. (1988). A balanced biosphere is assumed with NEP_s equal to NER_w. (b) Comparison of the predicted and observed monthly differences in CO_2 flux between the biosphere and atmosphere of the Northern Hemisphere. A delay time of two weeks is assumed between the biosphere source and the observation station at Mauna Loa. A factor of 1.235 Gt C ppm^{-1} is used to connect the model flux in Gt C $month^{-1}$ to a concentration change in ppm $month^{-1}$.

Table 1. *Average monthly departures in atmospheric CO_2 concentration in ppm from the long-term trend at Mauna Loa Observatory**

Jan	Feb	Mar	Apr	May	Jun
−0.11	0.56	1.33	2.41	2.92	2.28
Jul	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
0.87	−1.13	−2.92	−3.17	−2.05	−0.91

* Based on measurements from March 1958 through 1 January 1987.

Mauna Loa. A comparison of the calculated net fluxes from the biota and the observed source fluxes shows close agreement, lending confidence to our assumption that the seasonal behavior of atmospheric CO_2 is dominated by the land vegetation, and that an amplitude change can be derived mainly from the corresponding vegetation changes. In order to make a direct comparison between the changes in atmospheric CO_2 (measured in ppm) and the net source/sink fluxes of the biota (measured in Gt C) a conversion factor of 1.235 Gt C ppm^{-1} at Mauna Loa observatory was introduced, normalizing the observed Mauna Loa curve to the model. The magnitude of this conversion is reasonable, if we consider that the release of approximately 1 Gt C corresponds to an atmospheric CO_2 increase of 1 ppm, if released and distributed homogeneously within one hemisphere, together with the fact that the Mauna Loa result is perturbed by the attenuation of the signal with height (3400 m) and the small interhemispheric exchange during one season. Eqs. (18a), (18b), (19a), and (19b) summarize the activity of all biomes in the Northern Hemisphere which, however, make different contributions to the amplitude, depending on their seasonality, with the temperate and boreal zones dominating the observed seasonal behavior of atmospheric CO_2. In analogy to the one-biome case, an equivalent expression can be derived for an ensemble of non-interacting biomes in the Northern Hemisphere:

$$\frac{\overline{\Delta_a A}(n)}{A^\circ} = \sum_i \bar{\chi}_i(n)\{\rho_i \mathrm{NEP}_s^\circ(i) + (1-\rho_i)[m_w \mathrm{NPP}_s^\circ(i) - m_s \mathrm{NPP}_w^\circ(i)]\} \frac{1}{\mathrm{NEP}_s^\circ} + \frac{\overline{\Delta_a b}(n)}{\mathrm{NEP}_s^\circ} \tag{20a}$$

where $\bar{\chi}_i$ and ρ_i are the corresponding fertilization and respiration response factors of a particular ecosystem i. When we divide the Northern Hemisphere vegetation into three zones: a combined tropical-subtropical zone between 0° and 31.3°N, a combined temperate-boreal zone between 31.3° and 62.6°N, and an arctic zone between 62.6° and 90°N, the partial contributions to NEP_s are found by the model of Heimann et al. (1988) to be 1.4, 5.5 and 0.6 Gt C yr^{-1} respectively, summarized in Table 2. The total

Table 2. *Calculated average quantities of net primary production (NPP) and net ecosystem production (NEP) in summer and winter, respectively, derived from the model of Heimann et al. (1988)*

Zone	Summer / winter	NPP_s [Gt C]	NPP_w [Gt C]	NEP_s [Gt C]	NPP [Gt C]
0–90°N	4/8	21.4	13.6	7.1	35.1
0–31.3°N	6/6	9.9	6.5	1.4	16.4
31.3°–62.6°N	4/8	13.2	3.9	5.5	17.1
62.6°–90°N	3/9	1.4	0.3	0.6	1.6

For the assumed steady state the heterotrophic respiration is given by $RES_s = NPP_s - NEP_s$, $RES_w = NPP_w + NEP_s$, ($NER_w = NEP_s$).

Northern Hemisphere net ecosystem production in summer, NEP_s, amounts to 7.1 Gt C yr^{-1}, slightly less than the sum for all three zones, because only four months show production exceeding respiration when averaged over all 3 zones combined, while for one month (September) production and respiration are nearly balanced. The global mean net primary production as calculated by the model of Heimann et al. (1988) amounts to 55.9 Gt C yr^{-1}, between the ecological estimates of 53 Gt C yr^{-1} given by Whittaker and Likens (1963) and 60 Gt C yr^{-1} given by Atjay (1980). The model shows that 64% of the global NPP occurs in the Northern Hemisphere and 36% in the Southern Hemisphere, again in fair agreement with the ecological estimates. In eqs. (18) to (20), we showed that only the integrated CO_2 uptake and release during one season need to be considered in calculations. To illustrate this using the model results of Heimann et al. (1988), we show in Fig. 6a an aggregated step function for a CO_2 uptake and release which is characterized by a winter period of 7.5 months (splitting the month of September in which F_{npp} and F_{res} are nearly equal to each other) in which the respiration, RES_w, is equal to 19 Gt C, and thus exceeds the corresponding net primary production, NPP_w, by 7 Gt C. In the 4.5 months of the summer period, NPP_s is equal to 23 Gt C and exceeds the corresponding respiration, RES_s, by 7 Gt C. In this example, the reference state partition function, σ (see equation 18b), is found to be 1.41 (with $NPP^o = 35$ Gt C,

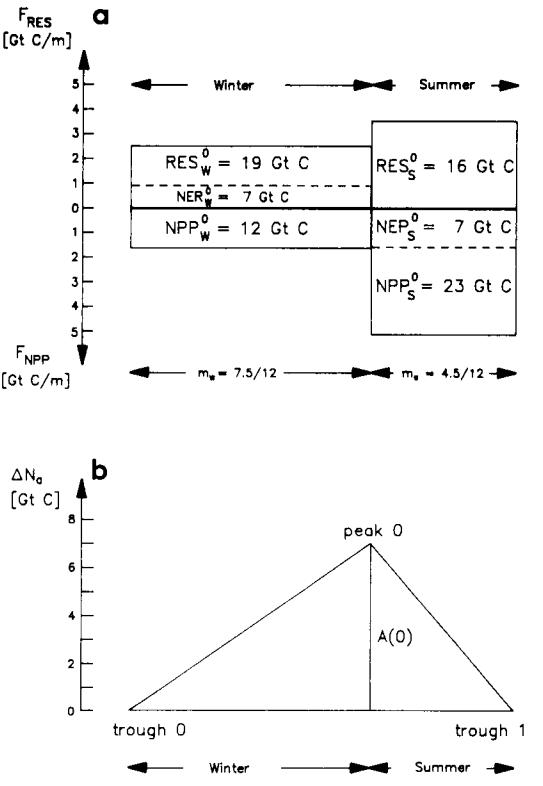

Fig. 6. (a) Aggregated steady state distribution of net primary production in winter and summer, NPP_w^o and NPP_s^o respectively, and heterotrophic respiration RES_w^o and RES_s^o, between 0° and 90°N as derived from the model of Heimann et al. (1988). (b) Resulting amplitude of the annual CO_2 cycle.

$NEP_s^o = 7$, $p_s = 0.66$ and $m_s = 0.375$). The ratio of NPP^o/NEP_s^o is a quantity which is both derived from ecological knowledge of NPP^o and NEP_s^o and from the atmospheric observations of a mean amplitude of the Northern Hemisphere (NEP_s^o). In order to reproduce the presently observed Mauna Loa amplitude of 6.8 ppm we need to postulate a value for NEP_s^o of approximately 7 Gt C. The total Northern Hemisphere production NPP^o, on the other hand, is given by ecological estimates as well as by model considerations with a range

$$NPP^o = 30 \text{ to } 40 \text{ Gt C}$$

such that the ratio of the two quantities NPP^o/NEP_s^o is evidently between 4.3 and 5.7. The resulting amplitude is shown in Fig. 6b, in

which the winter amplitude A_w, equal to NER_w^o, and the summer amplitude A_s, equal to NEP_s^o, are equal to one another, since a balanced state has been assumed.

In Fig. 7a a modified distribution of NPP_j and RES_j ($j = s$ or w) is shown in which RES_s is hypothetically increased by 2 Gt C (approximately 12.5%), while RES_w is decreased by 2 Gt C (approximately 10.5%). This change results in a decrease of both NEP_s^o and NER_w^o by 2 Gt C or 29%, while p_s and m_s are conserved. As illustrated geometrically in Fig. 7b, it follows that the resulting amplitude is also decreased by 29%, showing the high sensitivity of these ecological systems to any shift in phase of CO_2 uptake and release, even when the total annual biotic CO_2 uptake and release is conserved.

The CO_2 fertilization effect for the original distribution is illustrated in Fig. 8. Suppose the system is fertilized in such a way that both NPP_s and NPP_w are increased by 20%, while RES_s and RES_w are kept constant, implying a heterotrophic respiration response factor ρ equal to zero. (The actual annual NPP increase is, of course, much smaller, of the order of 0.01 of the effect illustrated.) The resulting integral amplitude change of the CO_2 cycle is related to the corresponding change in net primary production, ΔNPP, by

$$\frac{\Delta A}{A(0)} = \frac{\Delta NPP}{NPP(0)}[\rho + (1-\rho)\sigma],$$

where eq. (15a) and (15b) have been substituted into eq. (18d), and where the initial state was

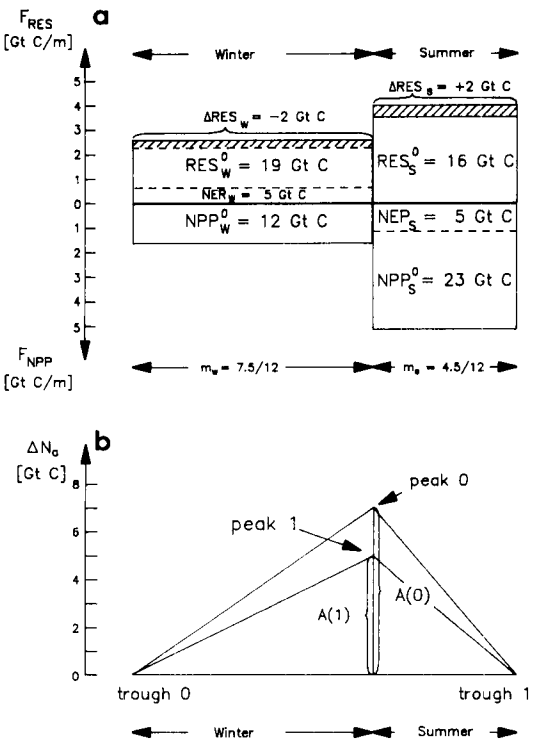

Fig. 7. (a) Steady state distribution of NPP and RES as in Fig. 6a, except that RES_s is increased by 2 Gt C while RES_w is decreased by 2 Gt C, without changing NPP_s or NPP_w. (b) Comparison of the resulting amplitude of the annual CO_2 cycle with the amplitude of Fig. 6b.

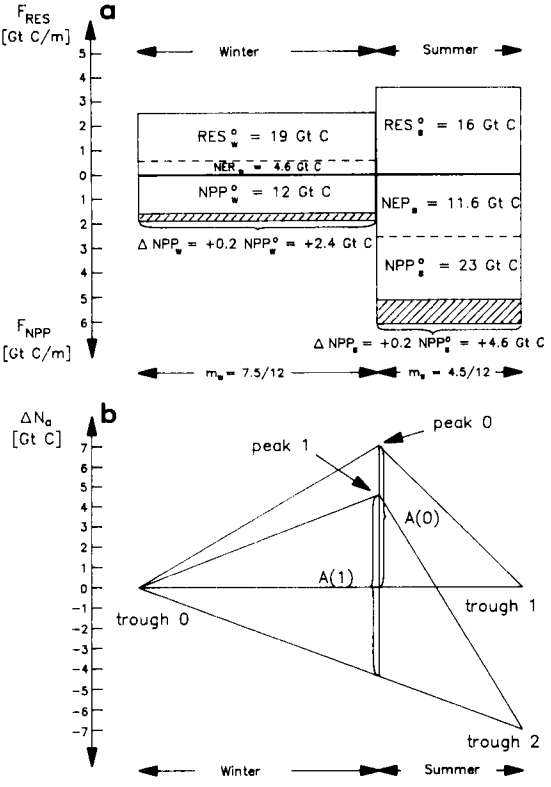

Fig. 8. (a) Distribution of NPP and RES as in Fig. 6a, except that both NPP_s and NPP_w are increased by 20% while RES_s and RES_w are unchanged. (b) Comparison of the resulting amplitude of the annual CO_2 cycle with the amplitude of Fig. 6b.

assumed to be a steady state in which no net ecosystem production occurred (formally achieved by setting the initial state "(0)" equal to the steady state "°"). Both with the above formula and by geometric construction we can show that the amplitude is increased by 28%, provided that ρ is zero, showing that the observed amplitude rise may be larger than the concurrent change in NPP.

4. Interpretation of a CO_2 fertilization effect from the observed amplitude increase at Mauna Loa Observatory

Bacastow et al. (1985) have analyzed the seasonal amplitude increase in atmospheric CO_2 concentration using two principal methods: (1) comparing the consecutive summer (peak to trough) and winter (trough to peak) amplitudes after having removed the long term trend by an exponential function $E(t)$, described by eq. (11); (2) assuming a time-dependent CO_2 concentration $P(t)$, which is the sum of $E(t)$ and a harmonic function $S(t)$, multiplied by the linear gain function $(1+\alpha t)$:

$$P(t) = E(t) + (1+\alpha t)\,S(t), \tag{21a}$$

where $E(t)$ is identical to $CO_2(t)$ as defined in eq. (11), and where

$$S(t) = \sum_k [A_k \sin(2\pi k t) + B_k \cos(2\pi k t)] \tag{21b}$$

with time-invariant parameters α, A_k and B_k ($k = 1, 2, 3, 4$). In an iterative procedure, the data were fitted to $(1+\alpha t)S$ after the long term trend function E had been subtracted from the original data. The residual, in part associated with the El Niño events with an average recurrence time of 4 years, was then fitted to a spline function R, as explained in detail by Bacastow et al. (1985). After the spline function had been determined, it was subtracted from the data, and a new fit of the data to the function $E+(1+\alpha t)S$ was achieved. Using method (1), an average rate of increase of the summer and of the winter amplitude in the period between AD 1958 and AD 1982 was evaluated by Bacastow et al. (1985):

$$\frac{\overline{\Delta_a A_s}(24)}{A(0)} = 0.66 \pm 0.22\% \tag{22a}$$

$$\frac{\overline{\Delta_a A_w}(24)}{A(0)} = 0.47 \pm 0.27\%, \tag{22b}$$

with $A(0)$ in AD 1958 being 5.45 ppm.

The resulting apparent mean amplitude change is then given by:

$$\frac{\overline{\Delta_a A}(24)}{A(0)} = m_w \frac{\overline{\Delta_a A_s}(24)}{A(0)} + m_s \frac{\overline{\Delta_a A_w}(24)}{A(0)} = 0.59 \pm 0.25\%\ \mathrm{yr}^{-1}, \tag{22c}$$

while the difference between summer and winter amplitude is characterized by

$$\frac{\overline{\Delta_a A_w}(24) - \overline{\Delta_a A_s}(24)}{A(0)} = 0.19 \pm 0.35\%\ \mathrm{yr}^{-1}. \tag{22d}$$

For the same data set, using 7-day averages, Bacastow et al. (1985) found with method (2) an annual increase of the mean amplitude of $0.73 \pm 0.09\%$ yr^{-1}, a value only slightly dependent on the stiffness of the spline function R. For direct comparison with the model developed here we shall concentrate on a comparison of the theoretical results with method (1), since in this case the gain factor is directly related to our theoretical development. For the time period between AD 1958 and AD 1982 (corresponding to $n = 0$ to 24) eqs. (18d), (19a) and (19b) were simplified by dropping, in each equation, the final terms. Thus the following equations were evaluated:

$$\frac{\overline{\Delta A}(24)}{A^\circ} = \bar{\chi}(24)[\rho + (1-\rho)\sigma], \tag{23a}$$

$$\frac{\overline{\Delta A_s}(24)}{A^\circ} = \bar{\chi}(24)\left[\rho + (1-\rho)\,p_s \frac{\mathrm{NPP}^\circ}{\mathrm{NEP}_s^\circ}\right], \tag{23b}$$

$$\frac{\overline{\Delta A_w}(24)}{A^\circ} = \bar{\chi}(24)\left[\rho - (1-\rho)\,p_w \frac{\mathrm{NPP}^\circ}{\mathrm{NEP}_s^\circ}\right], \tag{23c}$$

$$\frac{\overline{\Delta_a A_s}(24) - \overline{\Delta_a A_w}(24)}{A^\circ} = \bar{\chi}(24)(1-\rho)\frac{\mathrm{NPP}^\circ}{\mathrm{NEP}_s^\circ}, \tag{23d}$$

noting that $A_s^\circ = A_w^\circ = A^\circ = \mathrm{NEP}_s^\circ$.

The terms $\overline{\Delta_a a}(n)$ and $\overline{\Delta_a b}(n)$ of eqs. (18d), (19a) and (19b) are considered afterwards. For the evaluation of σ, eq. (18b), the following set of parameter ranges are considered:

$p_s = 0.66 \pm 0.10$,

$m_s = 0.375$,

$\mathrm{NPP}^\circ/\mathrm{NEP}_s^\circ = 5 \pm 1.5$.

We have limited the range of p_s by a lower bound of 0.56 by supposing that the monthly rate of heterotrophic respiration in the summer period is equal to or larger than the corresponding rate in winter. For NPP^o/NEP_s^o equal to 5 the lower and upper bounds of p_s correspond to

$$\sigma = \frac{NPP^o}{NEP_s^o}(p_s - m_s) = 1 \text{ to } 2.$$

The response of the plant communities to increasing levels of CO_2 has been expressed in our theoretical development by two parameters, namely $\bar{\beta}$, the CO_2 fertilization factor controlling the net primary production, NPP, and ρ, the respiration response factor controlling the heterotrophic respiration, RES. Lacking better information on the theoretical parameter $\bar{\beta}$, we set it equal to the experimentally derived fertilization factor β. In Table 3 we summarize an analysis (Kimball, 1983) of 770 observations concerning the relative yield increases of mostly agricultural crops in CO_2 enriched environments. A distinction is made between mature crops, where the increase in marketable yield is given, immature crops, where the total biomass increase has been reported, and an arithmetic mean value which approximately corresponds to the entire growth period. From this information, together with the evaluations of Strain and Cure (1983), we conclude that $\bar{\beta}$ is represented by

$$\bar{\beta} = 0.375 \pm 0.225 \ (0.15 \text{ to } 0.60).$$

The parameter range of the respiration response factor ρ is proportionally even less; from the analysis of the preceding section we propose

$$\rho = 0.75 \pm 0.25 \ (0.5 \text{ to } 1.0).$$

The parameter $\bar{\chi}(24)$ is, according to eq. (15b), the product of $\bar{\beta}$ and the expression,

$$\frac{CO_2(24) - CO_2(0)}{nCO_2^o},$$

which according to the Mauna Loa observations has the value $0.358\%\ yr^{-1}$; hence, $\bar{\chi}(24) = 0.134 \pm 0.081\%\ yr^{-1}$.

Using the mean parameter set and its deviations, a most probable (m.p.) amplitude increase as well as its corresponding lower (min) and upper (max) bounds can be evaluated:

$$\left.\frac{\overline{\Delta_a A}(24)}{A(0)}\right|_{m.p.} = 0.148\%\ yr^{-1},$$

$$\left.\frac{\overline{\Delta_a A}(24)}{A(0)}\right|_{min} = 0.053\%\ yr^{-1},$$

$$\left.\frac{\overline{\Delta_a A}(24)}{A(0)}\right|_{max} = 0.379\%\ yr^{-1}.$$

In these expressions, A^o was replaced by $A(0)$ by considering the corresponding amplitude increase of $A(0)/A^o = 1.021$, estimated from the increase in NPP given by eq. (15a) and eq. (11). Similarly, the corresponding winter and summer amplitude increases can be obtained, which, for simplicity,

Table 3. *Estimates of the growth factor, β, derived from 770 observations on plant CO_2 stimulation as collected and analysed for the relative yield increases by Kimball (1983)*

	Mature crops (marketable yield) β	Immature crops (biomass) β	Arithmetic mean for entire growth period β
C_3-grain crops (e.g. wheat)	0.27	0.47	0.37
leaf crops (e.g. cabbage)	0.40	0.44	0.42
fruit crops (e.g. tomato)	0.22	0.56	0.39
fiber crops (e.g. cotton)	0.95	1.16	1.06
legume seed crops (e.g. soy bean)	0.31	0.57	0.44
root and tuber crops (e.g. potato)	0.44	0.77	0.61
non-agricult. C_3-plants	—	0.50	0.50
woody plants	—	0.40	0.40
all C_3-plants (weighted according to the number of observations)	0.29	0.51	0.40
all C_4-plants (e.g. corn)	1.01	0.11	0.56
all species (weighted according to the number of observations)	0.30	0.48	0.39

we present only in terms of the most probable estimate:

$$\left.\frac{\overline{\Delta_a A_s(24)}}{A(0)}\right|_{m.p.} = 0.210\%\ \mathrm{yr}^{-1},$$

$$\left.\frac{\overline{\Delta_a A_w(24)}}{A(0)}\right|_{m.p.} = 0.045\%\ \mathrm{yr}^{-1}.$$

In the theoretical development, the dependence of $\Delta A/A_0$ on the parameter ρ is clearly distinct for the winter and summer amplitudes which show a large difference that may be used as a diagnostic tool for a CO_2 fertilization effect. A comparison of the measured difference between the winter and summer amplitude increase, namely $0.19 \pm 0.39\%\ \mathrm{yr}^{-1}$, with the corresponding calculated one, namely $0.165\%\ \mathrm{yr}^{-1}$, shows that there is a fair agreement between prediction and observation even though both the measured and calculated differences are highly uncertain.

4.1. External seasonal contributions to the amplitude increase

While for the difference between the summer and winter amplitude increases the external contributions drop out, they need to be considered for the mean amplitude increase as well as for the separate analyses of the summer and winter components. It is very difficult to estimate these external seasonal contributions without employing an explicit seasonal atmospheric transport model. However, we may first estimate the contribution from the seasonally differing fossil fuel carbon input into the Northern Hemisphere, as summarized by Rotty (1987). Rotty has given the percentage contribution of each month to the total fossil fuel carbon input into the atmosphere, for a majority of countries north of 30° N latitude, showing that a larger percentage of fossil fuel is emitted in the winter period than in the corresponding summer period. By plotting the cumulative input over one year, starting in 1 October, and comparing the corresponding mean, we find that the excess seasonality of the Northern Hemisphere was approximately 4% of the fossil fuel carbon input in a corresponding year n. Since the total fossil fuel carbon emission increased from 2.3 Gt C in AD 1958 to 5.0 Gt C in AD 1982, the excess seasonal contribution, expressed by $b(n)$, has increased approximately by the same proportion. For our estimate we have used an annual input into the Northern Hemisphere of 85% of the total global fossil fuel carbon input. The calculated mean seasonal contribution of this effect is then given by:

$$\left[\frac{\overline{\Delta_a b(24)}}{\mathrm{NEP}_s^o}\right]_{\text{seas. foss. fuel}} = 0.05 \pm 0.03\%\ \mathrm{yr}^{-1}.$$

This relatively small contribution is somewhat further reduced if the uptake of fossil fuel carbon by the oceans is considered with a mean exchange time of 7 to 10 years.

There may be an additional seasonal CO_2 contribution to the amplitude of the seasonal cycle associated with the seasonality of interhemispheric exchange of the Northern Hemisphere fossil fuel input of CO_2. Heimann et al. (1988) have employed a three dimensional atmospheric transport model which prescribes the wind fields on the basis of winds observed in 1979. They note a considerable difference in the results for this fossil fuel contribution to the amplitude when the observed winds are used (0.2 ppm), as compared to when the average windfields of the GISS general circulation model were used in their earlier study (0.7 ppm; Heimann et al., 1986). If the interhemispheric transport in summer is greater than in winter, this effect again would be approximately in phase with the CO_2 uptake by plants and thus would be registered as an increasing contribution as the total emitted CO_2 increases with time. Heimann et al. (1986), using the GISS model, estimated that this seasonal effect may explain nearly half of the measured increase in seasonal amplitude of CO_2. If we treat the GISS results as an approximate upper limit, but set no lower bound to account for the small effect obtained when using the observed winds, we arrive at the following estimate:

$$\left[\frac{\overline{\Delta_a b(24)}}{\mathrm{NEP}_s^o}\right]_{\text{interhem. transp. foss. fuel}} = 0 \text{ to } 0.31\%\ \mathrm{yr}^{-1}.$$

In conclusion, we believe that direct effects connected with fossil fuel carbon input may account for a non-negligible contribution to the observed amplitude increase, first owing to the seasonal distribution of fossil fuel carbon emission to the atmosphere, and secondly owing to the seasonal difference of interhemispheric transport.

5. Discussion

Our discussion is structured according to Table 4, which is a summary of the relations presented in the derivation of the amplitude change of atmospheric CO_2. Our model is based on the assumption that the main contributions to the observed amplitude increase of the seasonal CO_2 cycle, as observed at the Mauna Loa Observatory, are due to the changing seasonal patterns of CO_2 uptake and release by the Northern Hemisphere land vegetation. As prescribed by relation (I), the change in atmospheric CO_2 of the Northern Hemisphere is described by the time varying fluxes associated with the net primary production and heterotrophic respiration of the land biota, F_{npp} and F_{res}, respectively, while any other time varying effects external to the biota are summarized by the perturbation flux F_{ext}. During each year a winter and a summer period can be distinguished in which F_{res} exceeds F_{npp}, and vice versa. The peak to trough amplitudes during the winter and summer periods depend on the integration of these fluxes (relations II) and of those of external origin (relations III).

The winter amplitude, A_w, and the summer amplitude, A_s, as shown in relation IV, depend on the NPP and RES of the particular season, as well as on the external contributions $a(n)$ and $b(n)$, where n counts the years since the beginning of the Mauna Loa record. The apparent mean amplitude A is independent of any secular trend described by $a(n)$, since $a(n)$ drops out in the weighted mean average. Relations V, which describe the CO_2 fertilization effect, are based on the experimentally supported assumption that increasing levels of atmospheric CO_2 lead to an increase in the photosynthetic rate, in the net primary production NPP, in the standing biomass N_b, in the litter production, which is assumed to increase with the standing biomass, and in the heterotrophic respiration, which is a result of the increased litter production. Net primary production of a particular ecosystem i, NPP_i, as well as the net primary production for the ensemble of all ecosystems, NPP, is chosen here, for simplicity, to be independent of the particular time of the development or of the stage of the plant community. In a previous paper (Kohlmaier et al., 1987), we showed that the dynamic process of growth is better represented when NPP_i is replaced by $NPP_i^\circ(N_{ib}/N_{ib}^\circ)^\delta$, where N_{ib}° and NPP_i° refer to the climax biomass and climax production under standard conditions and δ is a climax parameter which varies between zero and less than one. Two limiting situations of a CO_2 fertilization effect may be envisaged: (1) a process in which all stages of development are equally fertilized, leading to a stimulation of net primary production, characteristic of relation V-A, and (2) a process in which the younger stages are stimulated more than those of the climax state, leading in the limiting formulation to a climax biomass which is equal to the one without stimulation. Since, however, within an ensemble of systems there are always some systems in the development stage, this second effect also leads to a higher standing biomass (Kohlmaier et al., 1986). This second situation is supported by the findings of Table 3, in which immature crops show a higher CO_2-response than the corresponding mature crops. An extension of this concept has been observed in tundra ecosystems exposed in successive years to elevated CO_2 concentrations; apparently, the plant communities adapted to the higher CO_2 concentrations, as the enhanced photosynthesis response decreased in successive years (Oberbauer et al., 1986).

As the CO_2 fertilization effect for a long term response is known practically only within a factor of 2 to 4, the distinction between models (1) and (2) has been neglected here; any model change can be easily accommodated within the chosen value of $\bar{\beta}$. Furthermore, the CO_2 fertilization effect up to the present time can be assumed to depend linearly on increasing CO_2; a saturation formulation by a Michaelis-Menten or logarithmic dependence would not alter the results. Higher order terms in the expansion of these expressions can be neglected at present CO_2 levels which differ not more than 25% from the preindustrial values.

Changes in heterotrophic respiration (relation V-B) are expected to be proportional to those in net primary production. Increased litter production will release more carbon dioxide provided the specific rate of decomposition is not changed appreciably by CO_2 fertilization. Increases in heterotrophic respiration are thus modeled as the product of the stimulation factor $\bar{\chi}$ (dependent on $\bar{\beta}$ and ΔCO_2) and a respiration

Table 4. *Summary of relations presented in the derivation of the amplitude change*

(original equation no.)

I. Differential equation for atmospheric CO_2 balance

$$dN_a/dt = F_{res}(t) - F_{npp}(t) + F_{ext}(t). \quad (1)$$

Winter period of length m_w:

$$F_{res}(t) - F_{npp}(t) > 0,$$

with $n \leqslant t < n + m_w$.

Summer period of length m_s:

$$F_{npp}(t) - F_{res}(t) > 0$$

with $n + m_w \leqslant t < n + 1$; $n = 0, 1, 2 \ldots$; $m_w + m_s = 1$.

II. Seasonal integrations of equation for atmospheric CO_2 balance

For winter season ($t = 0$ to m_w)

$$\int_0^{m_w} [F_{res}(n-1+t) - F_{npp}(n-1+t)]\,dt = RES_w(n) - NPP_w(n) > 0, \quad (3b, d)$$

for summer season ($t = m_w$ to 1)

$$\int_{m_w}^{1} [F_{res}(n-1+t) - F_{npp}(n-1+t)]\,dt = RES_s(n) - NPP_s(n) < 0. \quad (3a, c)$$

Year $n = 1$ starts on 29 September 1958 with the beginning of the winter period and ends 28 September 1959. Integrations are without external perturbations.

III. Contributions to atmospheric CO_2 balance from external perturbations

(A) Annually integrated contribution:

$$a(n) = \int_0^1 F_{ext}(n-1+t)\,dt. \quad (6a)$$

(B) Excess seasonal contribution:

$$b(n) = \int_0^{m_w} F_{ext}(n-1+t)\,dt - m_w a(n). \quad (6b)$$

IV. Seasonal amplitudes of atmospheric CO_2 for $F_{ext} = 0$

$$A_w(n) = RES_w(n) - NPP_w(n) + b(n) + m_w a(n) \quad (4a, 5a)$$

$$A_s(n) = NPP_s(n) - RES_s(n) + b(n) - m_s a(n) \quad (4b, 5b)$$

$$A(n) = m_s A_w(n) + m_w A_s(n). \quad (8a)$$

response factor ρ, assumed to be between zero and one, which describes the fraction of the additional production that is respired.

In a companion paper (Kohlmaier et al., 1988a), we have examined the question of stimulation or retardation (leading in the extreme case to the dieback of vegetation) by enhanced nutrient levels (nitrogen, phosphorus, and sulfur) in addition to CO_2, produced directly or indirectly by the activities of man. Airborne nitrogen compounds (nitrates, ammonium salts, NO_x, nitrous and nitric acid) are the most likely candidates for a stimulation of net primary production, as long as their levels are low and matched by other nutrients important for plant production. Within the industrial belt between 30° and 60°N, we can identify an area of low pollution (about 90% of the total area) that may profit from additional

Table 4—*continued*

(original equation no.)

V. CO_2 fertilization

It influences directly net primary production, NPP_j, and indirectly heterotrophic respiration RES_j.

(A) Effects on NPP_j

$$NPP_j(n) = NPP_j(0) + NPP_j^\circ \bar{\beta}\left(\frac{CO_2(n) - CO_2(0)}{CO_2^\circ}\right) \tag{15a}$$

where j = s or w, the superscript ° refers to the assumed preindustrial (steady) state, and $\bar{\beta}$ is the assumed fertilization factor for the long term response of the primary production.

The mean annual stimulation factor $\bar{\chi}(n)$ is the product of $\bar{\beta}$ and the mean annual CO_2 increase:

$$\bar{\chi}(n) = \frac{\bar{\beta}}{n}\left(\frac{CO_2(n) - CO_2(0)}{CO_2^\circ}\right). \tag{15b}$$

Then:

$$NPP_j(n) = NPP_j(0) + n\bar{\chi}(n)\,NPP_j^\circ. \tag{15c}$$

(B) Effects on RES_j

$$RES_j(n) = RES_j(0) + n\rho\bar{\chi}(n)\,RES_j^\circ \tag{16a}$$

where ρ is the respiration response factor, which lies approximately between zero and one.

VI. Mean annual changes for winter amplitude, A_w, summer amplitude, A_s, and apparent mean amplitude, A

(A) Annual increase in summer amplitude:

$$\frac{\overline{\Delta_a A_w}(n)}{A^\circ} = \bar{\chi}(n)\left\{\rho - (1-\rho)\frac{NPP_w^\circ}{NEP_s^\circ}\right\} + \frac{\overline{\Delta_a b}(n) + m_w\overline{\Delta_a a}(n)}{NEP_s^\circ}. \tag{19b}$$

(B) Annual increase in winter amplitude:

$$\frac{\overline{\Delta_a A_s}(n)}{A^\circ} = \bar{\chi}(n)\left\{\rho + (1-\rho)\frac{NPP_s^\circ}{NEP_s^\circ}\right\} + \frac{\overline{\Delta_a b}(n) - m_s\overline{\Delta_a a}(n)}{NEP_s^\circ}. \tag{19a}$$

(C) Annual increase in mean amplitude:

$$\frac{\overline{\Delta_a A}(n)}{A^\circ} = \bar{\chi}(n)\left\{\rho + (1-\rho)\left[m_w\frac{NPP_s^\circ}{NEP_s^\circ} - m_s\frac{NPP_w^\circ}{NEP_s^\circ}\right]\right\} + \frac{\overline{\Delta_a b}(n)}{NEP_s^\circ}. \tag{18a}$$

(D) Difference between increase in summer and winter amplitude:

$$\frac{\overline{\Delta_a A_s}(n) - \overline{\Delta_a A_w}(n)}{A^\circ} = \bar{\chi}(n)(1-\rho)\frac{NPP^\circ}{NEP_s^\circ} - \frac{\overline{\Delta_a a}(n)}{NEP_s^\circ}$$

$$= \bar{\beta}\left(\frac{CO_2(n) - CO_2(0)}{CO_2^\circ}\right)(1-\rho)\frac{NPP^\circ}{NEP_s^\circ} - \frac{\overline{\Delta_a a}(n)}{NEP_s^\circ}. \tag{19d}$$

nitrogen in about the same order of magnitude as it is stimulated by increased CO_2. If we include these findings in the stimulation factor χ, an average increase of the effective $\bar{\beta}$ by about 50% (leading to a range of $\bar{\beta}$ between 0.2 and 0.9) appears appropriate; however, we cannot give any detailed estimate on this effect, since it requires a worldwide analysis at the biome level of the individual ecosystems. We support the idea that both increased CO_2 and other nutrients are stimulating plant growth, although the ratios between the elements may not always be optimal. We disagree with Melillo and Gosz (1983) who emphasize in their analysis that nitrogen and phosphorus are far more limiting for the present production of all ecosystems than is CO_2. This is almost certainly not true of nitrogen fixing plants, or of forests in which the principal photosyn-

thesis product is cellulose and other components of wood which are very low in nitrogen content (Lemon, 1983).

With the derived changes of NPP and RES, the mean annual changes in winter amplitude A_w, summer amplitude A_s, and apparent mean amplitude A can be calculated (relations VI). It is important to notice here that the relative amplitude changes are only to a first order approximation equal to the stimulation factor χ of NPP, inasmuch as they are modified both by the respiration response factor ρ and by σ, which characterizes the seasonal partitioning of NPP and RES. The difference in the change of summer and winter amplitude defines the extent to which the stimulation of the net primary production will lead to a sequestering of carbon in the biota. Our suggested respiration response factor $\rho = 0.75$, corresponding to a sequestering of 25% of the additional net primary production, and the suggested CO_2 fertilization factor $\bar{\beta}$ of 0.375 leads to a numerically close agreement between the observed summer/winter difference ($\overline{\Delta_a A_s}/A^\circ - \overline{\Delta_a A_w}/A^\circ = 0.19\%\ \mathrm{yr}^{-1}$) and the corresponding predicted difference of $0.17\%\ \mathrm{yr}^{-1}$. The observed difference, however, is highly uncertain so that we cannot ascribe too much importance to this agreement.

In regard to the predicted apparent mean amplitude of the annual change in the seasonal swing, we might argue that the predicted value of $0.15\%\ \mathrm{yr}^{-1}$ is too small compared to the observed mean amplitude change of $0.66\%\ \mathrm{yr}^{-1}$ because our assumed $\bar{\beta}$ factor of 0.375 for CO_2 fertilization is too small. We note, however, that in accordance with eq. (18d), $\bar{\beta}$ needs to be increased to 1.5 or 2.0 to give agreement with the observed mean annual amplitude increase. The difference between the predicted gain in summer and winter amplitude, however, is then also enlarged unless ρ is increased nearly to one, which implies that the proportion of carbon fixed in net primary production sequestered each year is quite small.

External contributions to the amplitude change reflect any changes in the seasonal release or uptake of CO_2 other than those connected with a stimulation of net primary production and heterotrophic respiration. We distinguish between a mean trend $a(n)$ and an excess seasonal contribution $b(n)$. Supposing that it were mathematically possible to filter out the mean secular trend in atmospheric CO_2 we need only to worry about the residual term $b(n)$, contributing to an observed amplitude change. The most obvious external contributions, which have been evaluated quantitatively, are: (1) the contribution of the seasonality of fossil fuel use, which is known, however, to be small, and (2) the seasonally differing transequatorial transfer of CO_2, which may be significant, according to the three dimensional GISS atmospheric transport model. Contributions to the seasonal amplitude may also derive from changes in land use patterns.

Assuming a mean value of $\bar{\beta}$ of 0.375, we concluded in Section 4 that such a CO_2 fertilization factor could explain a contribution to the amplitude increase of $0.15\%\ \mathrm{yr}^{-1}$ out of the total observed amplitude increase of $0.66\%\ \mathrm{yr}^{-1}$ up to the year 1982. External effects not related to the terrestrial biosphere can be identified with respect to the increasing fossil fuel carbon input; the preferential input of fossil CO_2 into the Northern Hemisphere, slight differences in the seasonal input, and seasonal differences in transequatorial transport could explain perhaps another $0.17\%\ \mathrm{yr}^{-1}$ of the observed amplitude increase, which still leaves about half of the observed effect unexplained.

The two most important factors not described up to now are land use changes that have occurred in the biota during the Mauna Loa period and the climatic variability including any possible long term trends. A detailed analysis of these effects, however, cannot be carried out by assuming a uniform trend over the entire Mauna Loa period (1958–1988). We must consider several time periods of the Mauna Loa record separately. The year to year amplitude has not increased in a regular pattern. Hall and Ekdahl (1975) pointed out that the cumulative amplitude increase in the first half of the Mauna Loa period (1958–1973) was quite small. In the second half of the record period, however, the amplitude increase was substantial, giving a value of about $0.67\%\ \mathrm{yr}^{-1}$ for the entire period of 1958–1987. Biota-climate interactions are the most likely candidates to cause such a behavior. But let us first focus on the land transformations. The expansion of agricultural production by more than 2% annually was achieved in the 1960's mainly through increases in the area of cultivated land

(Richards et al., 1983) at the expense of natural ecosystems, while in the second half of the Mauna Loa record, intensive measures (irrigation, fertilizers, pesticides, double cropping) primarily were responsible for increased agricultural production. Although the detailed analysis of the effects of land use changes on the seasonal amplitude of atmospheric CO_2 concentrations will be presented in another communication, the effects may be summarized by saying that increases in agricultural land areas tend to decrease the amplitude, while more intensive cultivation tends to increase it. Tropical deforestation has not exhibited such a bimodal time evolution. Although quite severe in its effects on global ecology and perhaps even on climate, its influence on the annual changes in amplitude will be quite small because of its small seasonality.

Climate influences vegetation/soil systems through changes in temperature (Kohlmaier et al., 1982, 1988b) and in precipitation, which affects soil moisture. The Mauna Loa record was characterized by two consecutive surface temperature regimes, the first period of the record (12 to 15 years) when the temperature fell by 0.15 to 0.30°C, and the second period when the temperatures increased by 0.3 to 0.4°C, summing to a total temperature change during the entire Mauna Loa period of only 0.10 to 0.15°C (Jones et al., 1986). The fall in surface temperature would tend to decrease the amplitude in the first half of the Mauna Loa record, perhaps partly compensating for CO_2 fertilization, while in the second part of the Mauna Loa record, the effects of increasing temperature and CO_2 fertilization would tend to add up, thus at least partly explaining the observed large amplitude increase.

Phase shifts in the seasonality of net primary production and heterotrophic respiration which determine the annual seasonal atmospheric CO_2 cycle are another problem of concern. These shifts could be caused by variability in the seasonal patterns of the climate. We showed in the examples of Fig. 6 and Fig. 7 that the amplitude is very sensitive to any transfer in production or respiration from the summer to the winter season. Although the sensitivity to these shifts is high, we do not believe that changes in seasonality could be a major explanation for the effects observed at Mauna Loa, since, for example, the temperature would tend to shift both photosynthesis and respiration in the same direction such that they would partially compensate each other.

6. Conclusions

In previous sections, we derived an analytical expression for the amplitude of the seasonal cycle of atmospheric CO_2, by considering the seasonally varying fluxes of net primary production, F_{npp}, and heterotrophic respiration, F_{res}, associated with the activity of the terrestrial vegetation. We showed that both the stimulation of the net primary production, expressed by the long term fertilization factor $\bar{\beta}$ and the stimulation of the heterotrophic respiration expressed by the product of $\bar{\beta}$ and the heterotrophic respiration response factor, ρ, are important in the determination of the amplitude change. The extent of the amplitude change is, however, also determined by the particular temporal distribution of the biotic activity expressed here by the reference state partition function σ. This function was derived from the model calculations of F_{npp} and F_{res}, performed by Heimann et al. (1988). They calculated the seasonal net primary production flux of a particular geographical zone from the incoming photosynthetically-active solar radiation and the observed vegetation index, while they determined the heterotrophic respiration flux from the seasonal surface temperature and an estimated CO_2 release response of the litter-soil system. We determined in this paper that the long term CO_2 fertilization factor $\bar{\beta}$ probably lies between 0.15 and 0.60, with a mean of 0.375 when averaged over the different biomes of the earth, implying that a 10% change in atmospheric CO_2 will bring about a 1.5 to 6% change in net primary production. Guided by dynamic model calculations (Kohlmaier et al., 1987), we further determined that the respiration response function, ρ, should vary from about 0.96 for grassland ecosystems to about 0.56 for temperate and boreal forest systems, with ρ of 0.75 (with a range of 0.5 to 1.0) perhaps representing a best estimate for the ensemble of all ecosystems. The theoretical prediction of a CO_2 fertilization effect can be compared either with the apparent mean annual amplitude increase $\overline{\Delta_a A}$, or with the corresponding increases in summer (peak to

trough) and winter (trough to peak) amplitudes $\overline{\Delta_a A_s}$ and $\overline{\Delta_a A_w}$, each taken separately. For the given parameter ranges, we calculated a relative increase of the mean amplitude of the seasonal swings of atmospheric CO_2, as measured at Mauna Loa Observatory from AD 1958 to 1982:

$$\left[\frac{\overline{\Delta_a A}\ (1958 \text{ to } 1982)}{A\ (1958)}\right]_{CO_2 \text{ fert.}} = 0.15\%\ \text{yr}^{-1}$$

(ranging from 0.05 to 0.38% yr^{-1}).

In its mean this result represents less than one quarter of the observed amplitude increase of $0.66\% \pm 0.25\%\ \text{yr}^{-1}$ for this time period. For the difference in the increase of the summer and winter amplitudes, we calculated with the same parametric values an increase of $0.17\%\ \text{yr}^{-1}$, which is in agreement with the measured value $0.19\%\ \text{yr}^{-1}$, the latter, however, characterized by a large experimental mean deviation. We advanced two explanations for the circumstance that CO_2 fertilization does not explain the total mean amplitude change and yet there is good agreement for the difference in winter and summer amplitude change: (A) other effects influence the biotic activity such that our estimates of parameters $\bar{\beta}$ and ρ were not appropriate, and (B) external, non-biotic effects need to be considered.

Let us first consider phenomena related to the biota (explanation A). The mean annual amplitude change in CO_2 is most sensitive to the stimulation factor $\bar{\chi}$, which is equal to $\bar{\beta}\Delta_a CO_2/CO_2^0$. If an ambient CO_2 increase were the only cause of the amplitude increase, we would need to increase $\bar{\beta}$ to 1.5 to 2.0, a factor four times higher than most ecologists are willing to support. At the same time, the difference between the summer and winter amplitude increase (which appears to be predicted correctly using our original parameter set) is most sensitive to the product of $\bar{\chi}(1-\rho)$, and thus implies that an increase in $\bar{\beta}$ is accompanied by a decrease in $(1-\rho)$. If this is true, then the amount of carbon sequestered by the biota will stay approximately constant despite a change in $\bar{\beta}$.

One additional stimulation could occur through anthropogenically released nitrogen, phosphorus or sulfur. This stimulation, however, accounts at most for an increase of $\bar{\chi}$ by a factor of 1.5, and thus implies an effective mean value of $\bar{\beta}$ of 0.55.

We emphasized above that the year to year variability of the CO_2 amplitude was substantial, and that the mean increase in amplitude within the first half of the Mauna Loa period (1958–1973) was considerably lower than the mean increase over the entire period ($0.67\%\ \text{yr}^{-1}$ from AD 1958 to 1987). We suggested that climatic variability is the most likely cause for such a behavior. Lacking detailed knowledge of the influence of the complex climate patterns on the seasonal uptake and release of CO_2 by vegetation and soils, we accepted the global surface temperatures as a principal indicator of climate changes. Global surface temperatures fell during the first half of the Mauna Loa record, while they increased over the second half. Since in general both net primary production and heterotrophic respiration respond to small increases in temperatures with increases in their activities, we expect an amplitude decrease caused by lower temperature in the first half of the record thus compensating for part of the CO_2 fertilization effect, with the opposite being true for the second half of the record.

Land use changes occurring through increased agricultural production and deforestation are also likely to influence the CO_2 amplitude. Increase in agricultural production occurred in the 1960's partly at the expense of natural grassland and forest ecosystems, a transformation which is likely to decrease the amplitude, while in the past 10 to 20 years increased agricultural production was mainly due to intensive measures (irrigation, fertilization, etc.) which would tend to increase the amplitude of the seasonal cycle. The influence of tropical deforestation on the amplitude was probably small because of the low seasonality of tropical ecosystems.

We mentioned above (explanation B) that external, non-biotic phenomena also may be a reason for the large observed amplitude change. In particular, we identified two external seasonal contributions, both related to the increased use of fossil fuel consumption:

(1) the contribution from the seasonal consumption of fossil fuel

(2) the contribution from the seasonally varying interhemispheric transport of excess CO_2 associated with the fossil fuel carbon input into the Northern Hemisphere.

Three dimensional atmospheric transport model calculations, that show a sensitivity to the winds

used in the model, give an overall estimate which includes the seasonality of fossil fuel use:

$$\left[\frac{\overline{\Delta_a A}\ (1958 \text{ to } 1982)}{A\ (1958)}\right]_{\text{atm. transp./seas. } CO_2}$$
$$= 0.05 \text{ to } 0.31\%\ \text{yr}^{-1}.$$

In the mean the external non-biotic effects could thus be responsible for approximately 25% of the observed effect, leaving about 75% to land biota related phenomena.

In summary for the land biota related phenomena, a CO_2 fertilization effect is likely to explain about 25% (ranging from 8 to 64%) of the integral amplitude increase in the seasonal CO_2 signal from 1958 to 1988. Deposition of anthropogenic nitrogen (and to a minor extent phosphorus and sulfur) on land ecosystems, especially within the "industrial belt" between 31.3° and 62.6° N, probably made a positive contribution to the growth of the land biota and to the CO_2 seasonal amplitude in the first part of the Mauna Loa period. With air pollution effects becoming more important in the latter part of the Mauna Loa period, it is estimated that the overall effect of nitrogen, phosphorus, and sulfur for the entire period was perhaps 10 to 20% of the total observed amplitude increase. Of the land use changes considered, the intensification of agricultural practices probably made the most significant contribution to the amplitude increase, while deforestation in the tropics had a small effect because of low seasonality of tropical vegetation. Climate variations certainly influence the uptake and release of CO_2 by land biota, but more detailed models are needed to determine whether any systematic change can be attributed to the climate of the past 25 years.

Carbon sequestration in the land biota and soils is connected with the CO_2 fertilization effect. The observed difference between summer and winter CO_2 amplitudes probably reflects sequestration of approximately 1.3 ± 0.7 Gt C yr^{-1}.

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