

# Biosphere Structure, Carbon Sequestering Potential and the Atmospheric $^{14}\text{C}$ Carbon Record

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## ABSTRACT

The behaviour of a numerical model for the global carbon cycle is elucidated by a simple analytical model for the biosphere. In the period 1980–1990 the ocean is estimated to have absorbed 33% of the total  $\text{CO}_2$  emission to the atmosphere in that same period. Net deforestation was responsible for 12–17% of this total emission rate, whereas the  $\text{CO}_2$ -fertilization effect caused a re-absorption of 20–25%.

Aggregation of the above-ground biosphere into a single pool in the model caused an overestimation of the  $\text{CO}_2$ -fertilization effect. Also, the estimate of this rate increased when the fraction of carbon assumed to remain after the transformation of litter into humus was increased, but the rate was little influenced by the model structure for soil organic carbon.

A larger estimate for carbon uptake in the biosphere (Tans, Fung, and Takahashi, 1990) must be compensated by a reduced uptake in the ocean to arrive at a carbon balance. To do this, either the exchange rate between the upper mixed ocean layer and deep sea, or between ocean surface and atmosphere, should be reduced. In addition, a good match to the observed time-course of  $^{14}\text{C}$  carbon in the atmosphere must be preserved by the model. The  $^{14}\text{C}$  time-course did not remain well-matched if the atmosphere–ocean surface exchange was reduced, but it was hardly disturbed at all if the exchange rate with the deep sea was reduced.

**Key words:**  $\text{CO}_2$ -fertilization, global carbon cycle.

## INTRODUCTION

A rising concentration of atmospheric  $\text{CO}_2$  will stimulate plant growth and productivity through increased photosynthesis and the improved efficiency of utilization of scarce resources. Most notably, the efficiency of plant water use is increased, so that growth rate can be stimulated without an increase in the water demanded for transpiration.

This paper investigates some of the expected consequences of increased biospheric productivity on carbon cycling and possibly carbon-sequestering, in the biosphere. It will consider the extent to which carbon isotope data can help us trace back pathways of carbon in the global carbon cycle. The effect of climatic warming will not be considered. In contrast to rising atmospheric  $\text{CO}_2$ , climatic changes may be regionally diverse and, moreover, they have not been observed yet and their effects are much harder to predict.

The major carbon pools of the world are the ocean (39 000 Gt C), the terrestrial biosphere (2000 Gt C), the atmosphere (700 Gt C) and fossil fuel reserves (> 6000 Gt C). The carbon in the terrestrial biosphere consists of 450–600 Gt C in living biomass and 1200–

1400 Gt C in various forms of soil organic matter. The gross exchange rates of  $\text{CO}_2$  between atmosphere on one hand, and ocean and biosphere on the other, are of the order of 50–100 Gt C  $\text{yr}^{-1}$ , much larger than the rate of fossil fuel burning (in 1990 about 6 Gt C  $\text{yr}^{-1}$ ). The conventional view has it that the ocean is the largest sink and the biosphere plays only a minor role. Recently, Tans *et al.* (1990) argued that the ocean cannot absorb carbon dioxide at the rate required in this view. In their opinion the net sink strength of the biosphere is larger, a point which shall be discussed further.

Simple analytical models will assist us to understand the results of a more complex numerical simulation model.

## CARBON CYCLE MODEL

The basis of the simulation of the biospheric carbon content is an ecosystem structure as given in Fig. 1 (Goudriaan, 1990), with characteristic parameters for each ecosystem (Table 1). In this scheme the outflow of each state variable is calculated as the content divided by

## A simplified ecosystem structure

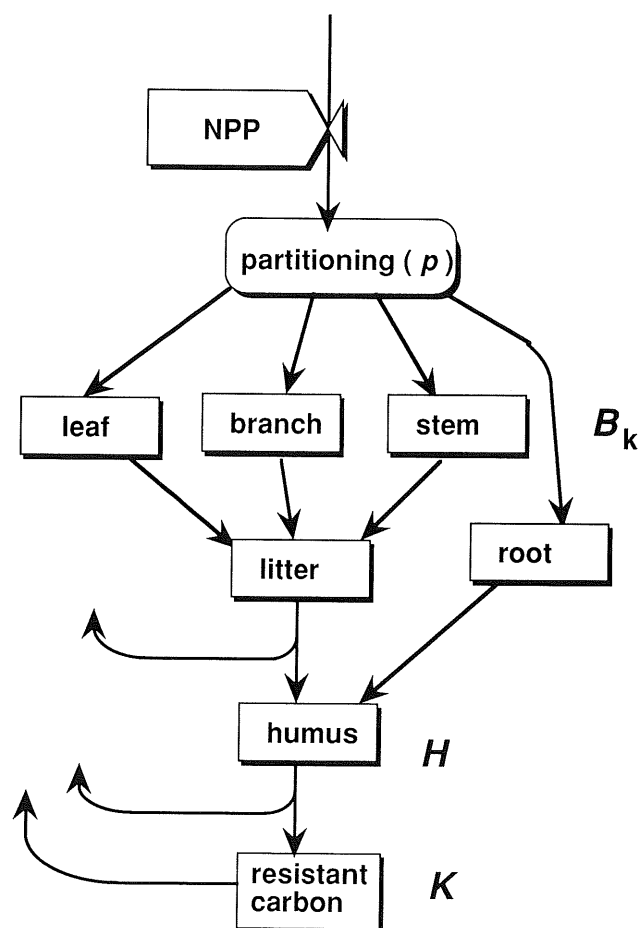


FIG. 1. Generalized model structure for an ecosystem. Each box itself is described by first order decay.  $NPP$ , Net Primary Productivity, its allocation fraction  $p$ ; longevity  $\tau$  and transition fractions  $\phi$  from one box to the next are characteristic ecosystem properties.

a constant longevity, so that its equilibrium content is simply the product of longevity and inflow. This is called a *linear* system because the rates are proportional to the driving contents. The outflows cascade down to litter, humus, and resistant soil carbon. In the transition from biomass to humus a considerable fraction of carbon is lost by respiratory processes and also in the transition from humus to resistant soil carbon. The respired fraction returns to the atmosphere as respiratory  $\text{CO}_2$ .

For humus and resistant carbon this linear structure (Kortleven, 1963; Olson, 1963) can also be used to represent the effects of soil disturbance upon reclamation. Schlesinger (1986) stated that considerable losses in soil carbon occurred when virgin land was reclaimed; soil carbon moved from an equilibrium value of  $20 \text{ kg C m}^{-2}$

to a new equilibrium value of  $15 \text{ kg C m}^{-2}$ , after several decades. Such losses can be represented by using a shorter residence time for humus in agricultural soils (20 yrs) than in grassland or in forest (50 yrs). Resistant carbon (residence time 500 yrs) which amounts to about  $10 \text{ kg C m}^{-2}$ , is included as a component of total soil carbon, but this component is much less affected by such changes in land use.

Six major types of vegetation ('ecosystems') were distinguished, to represent the major features of the geographical distribution of biotic terrestrial carbon. Others (Matthews, 1983; Tucker, Fung, Keeling, and Gammon, 1986; Esser, 1987) have worked at a much more refined scale for mapping the distribution of vegetation.

Combination of the material flow rates and residence times led to a steady-state distribution of surface densities of carbon ( $\text{kg C m}^{-2}$ ) (Fig. 2). In this Figure the width of each bar represents the area of the vegetation type, and the height of each bar is the carbon surface density. The high density of soil carbon in temperate forest and in grassland, as compared to agricultural land and tropical forests, is noteworthy. Leaves in forests receive 30% of the  $NPP$ , but because of their short longevity they make up less than 5% of the forest biomass.

### Deforestation

The effect of deforestation was modelled as a release of most of the above-ground carbon to the atmosphere (burning and decomposition). However, a small fraction of the biomass is converted into long-lasting charcoal (5% of leaves, 10% of branches and 20% of stems), and is then excluded from atmospheric circulation for a long time. Therefore, the repeated burning of forests, agricultural land, and savannas increases the carbon content of soils at the expense of the atmospheric and oceanic reservoirs. In the model, the charcoal was included in the pool of resistant carbon (residence time 500 yrs). Simulation showed that without this charcoal formation, atmospheric  $\text{CO}_2$  would currently be at a level of about  $5 \mu\text{mol mol}^{-1}$  higher and increase at a 5% faster rate. After the removal of biomass, carbon fixation is not greatly reduced, at least on a time-scale longer than one year, because pioneer vegetation takes over. As far as modelling of the carbon balance is concerned, it does not matter what type of vegetation fixes the carbon, but several decades are needed, however, to restore carbon pools such as stem wood.

The assumed rate of annual burning ( $800 \text{ Mha yr}^{-1}$ ) of biomass (mainly litter) on grassland and agricultural land may seem large, in that it causes about  $5 \text{ Gt C}$  per year to be released, which is of the same order as fossil fuel burning. However, this litter would have decomposed anyway, and for the carbon cycle it hardly matters whether litter is burnt now, or decomposed one year later. Shifting cultivation in tropical forests ( $15 \text{ Mha yr}^{-1}$ ) does

TABLE 1. Characteristics used as model input for the six major vegetation types, based on Ajtay, Ketner, and Duvigneaud (1979) and on Brown and Lugo (1984)

	Tropical forest	Temperate forest	Grassland	Arable land	Urbanized area	Sparsely vegetated
Net Primary Productivity ( <i>NPP</i> ) per unit land area ( $\text{kg C m}^{-2} \text{ yr}^{-1}$ )	0.4	0.51	0.57	0.43	0.1	0.07
Partitioning of <i>NPP</i> , and life spans (or residence times) in yr of living biomass						
Leaf	0.3//1	0.3//2	0.6//1	0.8//1	0.3//1	0.5//1
Branch	0.2//10	0.2//10	0.0//10	0.0//10	0.2//10	0.1//10
Stem	0.3//50	0.3//50	0.0//50	0.0//50	0.3//50	0.1//50
Root	0.2//1	0.2//10	0.4//1	0.2//1	0.2//1	0.3//2
Resident times (yr) of dead biomass:						
Litter	1	2	2	2	1	2
Humus	10	50	50	20	50	50
Resist. carbon	500	500	500	500	500	500
Fraction of litter that becomes humus						
	0.4	0.6	0.6	0.2	0.5	0.6
Areas (Mha)						
1780	4400	1900	1700	1000	10	3100
1980	3729	1700	1793	1717	176	2992

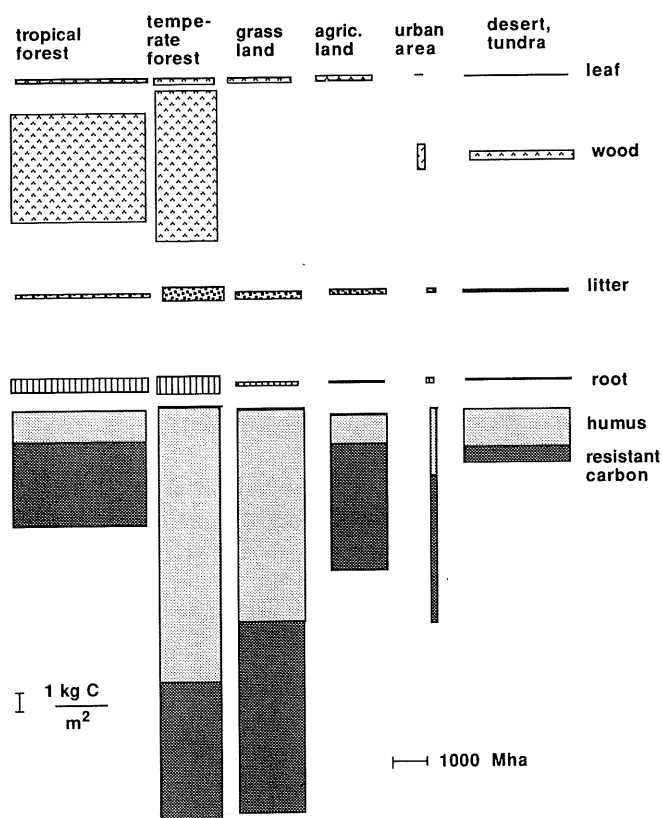


FIG. 2. Simulated equilibrium distribution of carbon surface densities (heights of the columns) on the areas of each vegetation type (widths of the columns).

not have a large effect either: if it did not occur, the simulated atmospheric  $\text{CO}_2$  concentration in 1980 would have been only  $1 \mu\text{mol mol}^{-1}$  lower. These release fluxes are almost entirely compensated by simultaneous regrowth on recently treated areas and, therefore, they have not been added to the figures for deforestation flux given later.

However, a clear distinction must be made with deforestation in which forests are permanently converted to land under arable cultivation. When this happens, the contents of the soil carbon reservoirs are transferred to the corresponding reservoirs in agricultural land. The residence time of humus in agricultural land is shorter than in forest soil and this results in a considerable loss of soil carbon during the subsequent years. For instance, in soils of tropical forests the simulated mean areal density of carbon was  $14 \text{ kg m}^{-2}$  in contrast to  $8 \text{ kg m}^{-2}$  for agricultural land. A rate of transfer of  $12 \text{ Mha yr}^{-1}$ , therefore, means that about  $0.7 \text{ Gt C}$  will eventually be released for each year that this deforestation occurs. The net modelled effect of these land use changes was that during the last 200 years the area of agricultural land rose from 1000 to 1800 Mha ( $100 \text{ Mha} = 10^{12} \text{ m}^2$ ), mainly at the expense of tropical forests. Temperate forests were also reduced (by 100 Mha), but grassland area increased (by 140 Mha). The assumed present rate of deforestation is about  $6 \text{ Mha yr}^{-1}$  to agricultural land and another  $6 \text{ Mha yr}^{-1}$  to grassland.

A straightforward method of estimating biospheric releases is to use the rate of annual transfer from virgin land to agricultural soil and to multiply it by the difference

between soil carbon content typical for both types of land use. The rate of removal of above-ground biomass must also be included. This method leads to an estimate of the global rate of release of about  $1.3 \text{ Gt C yr}^{-1}$  in 1980 (on the basis of  $15 \text{ Mha yr}^{-1}$  and a reduction in carbon surface density of  $0.08 \text{ Gt C Mha}^{-1}$ , or of  $8 \text{ kg C m}^{-2}$ ) and  $1.5 \text{ Gt C yr}^{-1}$  in 1990.

However, calculated in this way reforestation and widespread regrowth on abandoned land is not included. It also ignores the slowness of the release of soil carbon, which delays the release  $\text{CO}_2$  by several decades, because of the longevity of humus. These two factors, together, reduce the release rate to an estimated  $0.7 \text{ Gt C yr}^{-1}$ .

#### The $\text{CO}_2$ -fertilization effect

The third factor, which turns the biosphere from a source into a sink, is the stimulation, worldwide, of photosynthesis by rising atmospheric  $\text{CO}_2$ , the so-called  $\text{CO}_2$ -fertilization effect. Over a large range of  $\text{CO}_2$  ( $200\text{--}1000 \mu\text{mol mol}^{-1}$ ) the response of seasonal dry matter gain per unit ground area (surface density of  $NPP$ ) to  $\text{CO}_2$  can be described by a logarithmic response function (Goudriaan, van Laar, van Keulen, and Louwerse, 1985)

$$\sigma_{NPP} = \sigma_{NPP_0} (1 + \beta \log(\text{CO}_2/\text{CO}_{2,0})) \quad (1)$$

where  $\sigma_{NPP}$  is the surface density of net annual primary productivity ( $\text{kg m}^{-2} \text{ yr}^{-1}$ ), the subscript 0 referring to the reference situation (here at  $285 \mu\text{mol mol}^{-1}$ ). If  $\beta$  has the same value for all ecosystems the  $\text{CO}_2$  effect can be brought outside the summation and global  $NPP$  (abbreviated as  $P$ ) can be written as:

$$P = P_0 (1 + \beta \log(\text{CO}_2/\text{CO}_{2,0})). \quad (2)$$

The value of the response factor ( $\beta$ ) is about 0.7 under favourable conditions of growth, but declines with increasing nutrient shortage (Goudriaan and de Ruiter, 1983). Under water shortage (Gifford, 1979; Rosenberg, 1981) the growth-stimulating effect of atmospheric  $\text{CO}_2$  is not reduced, but may even be enhanced. In this situation,  $\text{C}_4$  plants benefit from increased  $\text{CO}_2$  just as much as  $\text{C}_3$  plants. There is a large body of experimental data (Kimball, 1983; Goudriaan and Unsworth, 1990) which shows that the  $\text{CO}_2$ -fertilization effect may be as large as a 0.5% response per 1% increase of total atmospheric  $\text{CO}_2$ . At present, the rate of increase of atmospheric  $\text{CO}_2$  is  $1.5/350$  or about 0.5% per year. Thus, an annual growth rate of 0.5% of  $\text{CO}_2$  can be translated into an increase of 0.25% per year of the storage capacity in the terrestrial biosphere, equivalent to about  $4 \text{ Gt C}$  of additional storage capacity per year. However, as explained further in this article, this increased capacity is not realized instantaneously, because the slow ecosystem compartments generate a lag. Numerical simulation shows that the nature of the distribution of residence times, ranging from that used for leaves to that for resistant soil

carbon, reduces the calculated  $\text{CO}_2$  fertilization effect to about  $1.1 \text{ Gt C yr}^{-1}$  in 1980 and  $1.4 \text{ Gt C yr}^{-1}$  in 1990. Together with the estimate for regrowth, the global terrestrial biosphere is estimated to act as a net sink of about  $0.4 \text{ Gt C yr}^{-1}$  in 1980 and  $0.7 \text{ Gt C}$  in 1990.

Because of natural heterogeneity, this storage is not practically measurable or visible in terms of biospheric carbon content. Its actual existence can only be inferred from what is known from plant physiology.

#### Effect of model structure of the biosphere on the simulated rate of carbon uptake

It is clear that the amount of detail put into a carbon cycle model influences its performance. The Standard Model given above had a considerable amount of detail with six ecosystem types, each having four biomass components, one litter pool, and two soil organic carbon pools. We could study the importance of the degree of aggregation by using the same complete numerical carbon cycle model, which includes the ocean. However, the picture is then blurred by feedback of the altered simulated rate of  $\text{CO}_2$  increase in the atmosphere. For an explanatory analysis it is better to impose the rate of increase of atmospheric  $\text{CO}_2$  as a given driving variable and see how the rate of sequestering of carbon is affected by the model structure. A simple and clear approximation of the rate of increase of atmospheric  $\text{CO}_2$  is via an exponential function in time. Although we may not catch the fine details of the actual observed rate, we can approximate closely the actual time-curve by choosing the proper parameters. A suitable description for our purpose is:

$$C = C_0 + C_1 \exp(r t) \quad (3)$$

where  $t$  = time since 1980;  $C_0$  = initial steady-state;  $C_1$  = accumulated increment in the year 1980;  $r$  = relative rate of increase.

A realistic set of parameters is:  $C_0 = 285 \text{ ppmv}$  (or  $600 \text{ Gt}$ );  $C_1 = 52 \text{ ppmv}$  (or  $109.5 \text{ Gt}$ );  $r = 0.024 \text{ yr}^{-1}$ . This parameter choice means an imposed rate of increase of  $r C_1$  in the year 1980 of  $1.25 \text{ ppmv yr}^{-1}$  ( $2.63 \text{ Gt C yr}^{-1}$ ).

A convenient property of the exponential time-curve is that the response of all model components of the carbon cycle also follow an exponential curve with the same time parameter  $r$ . The only condition for this property is that all model components are linear. This condition is satisfied as long as the longevities (inverse of relative rates of decay) are constant and, of course, also if the response of the  $NPP$  to  $\text{CO}_2$  is linear. This last condition may seem to produce a problem, but so long as the increase is not too large the beta-type response can be linearized to:

$$P = P_0 (1 + \beta(C_1/C_0) \exp(r t)). \quad (4)$$

This means that the excess  $NPP$  in the reference year

1980 is given by:

$$P_1 = \beta(C_1/C_0) P_0. \quad (5)$$

A simplified parameter choice is  $P_0 = 50 \text{ Gt C yr}^{-1}$ , and  $\beta = 0.5$ , so that  $P_1$  is equal to  $4.561 \text{ Gt C yr}^{-1}$ .

In the most simplified biosphere model we will have one box  $B$  with a longevity  $\tau_B$  of 40 years. The steady-state amount of biomass ( $B_0$ ) is equal to inflow  $P_0$  times longevity  $\tau_B$ , or  $2000 \text{ Gt C}$ . The differential equation for biomass  $B$  is given by:

$$dB/dt = P - B/\tau_B. \quad (6)$$

When  $P$  is written as  $P_0 + P_1 \exp(r t)$  and  $B$  as  $B_0 + B_1 \exp(r t)$ , we can write this last equation as:

$$r B_1 \exp(r t) = P_0 + P_1 \exp(r t) - B_0/\tau_B - B_1 \exp(r t)/\tau_B. \quad (7)$$

We can split this equation into two parts: the steady-state equation  $P_0 = B_0/\tau_B$ , and the dynamic equation that contains the exponential factor in it. After dividing by this exponential factor throughout the dynamic part we obtain:

$$r B_1 = P_1 - B_1/\tau_B. \quad (8)$$

The Net Biospheric Uptake ( $NBU$ ) is equal to  $r B_1$ , but to express this rate in terms of known factors we must first solve the above equation in  $B_1$ :

$$B_1 = P_1/(r + 1/\tau_B). \quad (9)$$

Substituting the parameter values gives a rate of sequestering of  $2.327 \text{ Gt C yr}^{-1}$  in the year 1980.

#### Series circuiting

We can split the biosphere into two parts joined in series: live biomass  $B$  ( $500 \text{ Gt C}$  steady-state) and soil organic matter (humus)  $H$  ( $1500 \text{ Gt C}$ , steady-state). The longevity of biomass,  $\tau_B$ , is 10 years.

In addition to biomass we now have the following equation for humus  $H$ :

$$dH/dt = \phi B/\tau_B - H/\tau_H \quad (10)$$

where  $\phi$  is the fraction of carbon that is entering the humus pool. Typically this fraction is 0.3, so that  $15 \text{ Gt C}$  enters the humus pool annually. Its mean longevity is, therefore, 100 years.

Using the same algebraic methodology as above we now find the set of equations given in Table 2a. When we set the humification factor  $\phi_H$  at 1, so that no carbon is lost upon humification, the longevity  $\tau_H$  must be 30 years when we want to have  $1500 \text{ Gt C}$  of humus in steady-state. We now have a series circuiting of live biomass with 10 years longevity and humus with 30 years longevity, adding up to 40 years in total. It is interesting to see that the calculated  $NBU$  for this scheme at  $2.422 \text{ Gt C yr}^{-1}$  is slightly larger than the one calculated for a single pool of 40 years longevity, with  $H_1 = 64.155 \text{ Gt C}$ . How-

TABLE 2. Parameters, equations and variables for the analytical solution

Initial Net Primary Productivity	$P_0 = 50 \text{ Gt yr}^{-1}$	
CO <sub>2</sub> -fertilization factor	$\beta = 0.5$	
Initial CO <sub>2</sub> concentration	$C_0 = 285 \text{ ppmv}$	
Accumulated addition of CO <sub>2</sub> in the year 1980	$C_1 = 52 \text{ ppmv}$	
Relative annual growth rate of C <sub>1</sub>	$r = 0.024 \text{ yr}^{-1}$	
Longevity of live biomass	$\tau_B = 10 \text{ yr}$	

(a) One live biomass compartment and one soil compartment  $H$  with 1500 Gt initially

$B_0 = P_0 \tau_B$	500 Gt	
$P_1 = \beta(C_1/C_0)P_0$	4.561 Gt yr <sup>-1</sup>	
$B_1 = B_0 (P_1/P_0)/(1 + r \tau_B)$	36.782 Gt	
$r B_1$	0.883 Gt yr <sup>-1</sup>	
$H_0 = \phi_H P_0 \tau_H$	1500 Gt	
Humification factor	$\phi_H = 1$	$\phi_H = 0.3$
Longevity of soil carbon	$\tau_H = 30$	$\tau_H = 100$
$H_1 = H_0 (B_1/B_0)/(1 + r \tau_H)$	64.155	32.455 Gt
$r H_1$	1.540	0.779 Gt yr <sup>-1</sup>
$NBU = r (B_1 + H_1)$	2.422	1.662 Gt yr <sup>-1</sup>

(b) Soil is subdivided into humus  $H$  and charcoal  $K$ , each 750 Gt initially

Humification factor $\phi_H$	0.3	
Carbonization factor $\phi_K$	0.1	
Longevity of humus $\tau_H$	50 yr	
Longevity of charcoal $\tau_K$	500 yr	
$H_0 = \phi_H P_0 \tau_H$	750 Gt	
$H_1 = H_0 (B_1/B_0)/(1 + r \tau_H)$	25.079 Gt	
$r H_1$	0.602 Gt yr <sup>-1</sup>	
$K_0 = \phi_K \phi_H P_0 \tau_K$	750 Gt	
$K_1 = K_1 (H_1/H_0)/(1 + r \tau_K)$	1.929 Gt	
$r K_1$	0.046 Gt yr <sup>-1</sup>	
$NBU = r (B_1 + H_1 + K_1)$	1.531 Gt yr <sup>-1</sup>	

ever, a large loss of carbon occurs in the transformation process of litter into soil organic carbon, and a humification fraction of about 0.3 (Jenkinson, Adams, and Wild, 1990) is typical. This gives a value of  $NBU$  of only  $1.662 \text{ Gt C yr}^{-1}$ , considerably less than the  $2.327 \text{ Gt C yr}^{-1}$  that was calculated for the undivided biosphere reservoir. The real reason that  $NBU$  was reduced, however, is not the series circuiting in itself, but the introduction of a large loss of carbon upon entering the humus pool.

We can continue this subdivision into humus  $H$  and charcoal  $K$  (Fig. 1), whereby  $H_0$  is reduced to  $750 \text{ Gt C}$ , and  $H_1$  to  $25.079 \text{ Gt C}$  (Table 2b). When we add the equations for charcoal (Table 2b), the  $NBU$  is now  $1.531 \text{ Gt C yr}^{-1}$ . The soil accounts for about  $0.648 \text{ Gt C yr}^{-1}$  and live biomass for  $0.883 \text{ Gt C yr}^{-1}$ .

This calculation shows that further serial subdivision of the soil does reduce its uptake potential, but it has a much smaller effect than subdividing the above-ground biomass. The reason for this tiny effect is the very long time-scale of the charcoal pool, strongly exceeding the decadal time-scale of the imposed CO<sub>2</sub> dynamics. For the same reason, the value of the residence time of charcoal is not terribly important. For instance, one might argue that its residence time should be 1000 years rather than 500 years. Obviously, the initial amount  $K_0$  would remain the same, and  $K_1$  is now approximately halved to

1.003 Gt C. Consequently, the uptake rate of soil is reduced from 0.648 to 0.626 Gt C  $\text{yr}^{-1}$ . This change is irrelevant, and it shows that it hardly matters whether we choose a longevity of 500 or of 1000 years for the most resistant soil carbon pool.

#### Parallel compartmentalization

Living biomass had an annual uptake rate of 0.883 Gt  $\text{yr}^{-1}$ , but it was considered as one homogeneous pool. In reality it consists of components such as leaves, branches, stems, and roots, each with very different longevities. Let us denote the partitioning fractions to these organs with the symbol  $p$  and subscripts l, b, s, and r, respectively. For each of the four components the equations of Table 2a are applicable. Suitable parameters for this situation, consistent with the total of 500 Gt assumed before, are given in Table 3. The rate of increase of living biomass carbon is now  $0.024 \times 26.952$  or 0.647 Gt C  $\text{yr}^{-1}$ . The parallel compartmentalization has caused a reduction of the rate of uptake of carbon in live biomass by about 25% as compared to a single homogeneous pool. However, the through-flow to the soil has increased because of the fast turnover of the leaves. The equation for  $H_1$  (Table 2b) must be replaced by:

$$H_1 = H_0 \left( \frac{\sum B_{1,k}/\tau_{B,k}}{\sum B_{0,k}/\tau_{B,k}} \right) / (1 + r \tau_H) \quad (11)$$

where  $k$  stands for the plant organ index. This equation gives 26.687 Gt C for  $H_1$ , instead of the previous value of 25.079 Gt C. Also  $K_1$  has now increased by the same ratio, from 1.929 Gt C in Table 2b to 2.053 Gt C. Together they account for an uptake rate of 0.690 Gt C  $\text{yr}^{-1}$  in the soil. The total uptake rate of the biosphere is 1.337 Gt C  $\text{yr}^{-1}$ .

A similar parallel structure is possible for soil organic carbon, by partitioning the humified flow of 15 Gt C  $\text{yr}^{-1}$  to humus and charcoal in a parallel fashion. The calculation (not given here) shows that the uptake rate becomes slightly larger than in the standard series-circuited model, but only by 0.03 Gt C  $\text{yr}^{-1}$ . It is much more important to have the correct above-ground aggregation than that below-ground.

TABLE 3. An example of a possible disaggregation of the biospheric reservoir

$B_0$  is the amount in the initial steady-state, and  $B_1$  is the amount accumulated by enrichment in the reference year 1980

	$p_k$ (—)	$\tau_k$ (yr)	$B_{0,k}$ (Gt C)	$B_{1,k}$ (Gt C)
Leaves	0.2	1	10	0.8908
Branches	0.3	5	75	6.1085
Stems	0.2	40	400	18.6163
Roots	0.3	1	15	1.3362
Together	1.0	10	500	26.952

#### STANDARD MODEL

This 'Standard Model' is roughly identical to the one described by Goudriaan and Ketner (1984) and by Goudriaan (1990). In contrast to what others (e.g. Bolin, 1986) have found, in this Standard Model *there is no so-called lost carbon*. Using the analytical model we found a  $\text{CO}_2$  enrichment effect of 1.337 Gt C  $\text{yr}^{-1}$  for the year 1980. The more detailed numerical simulation model gave a slightly lower value: about 1.2 Gt C  $\text{yr}^{-1}$ , the reduction being due to a further parallel disaggregation into ecosystems. The simulated rates and accumulated uptakes and losses for the year 1980 are summarized in Table 4.

In spite of deforestation which is included in our model, the global carbon balance is closed, on account of  $\text{CO}_2$  stimulated global productivity. According to this Standard Model, the total terrestrial biosphere has shown a net decrease of 41 Gt C in the period 1780–1980 and 83 Gt C was absorbed by the oceans. Out of the 200 Gt emitted to the atmosphere in total, 117 Gt or 58% has remained there. In this model the ocean absorbs 33% of total  $\text{CO}_2$  emission to the atmosphere, the biosphere emits 15% on one hand and absorbs 20% on the other. At present, the model calculates the biosphere to be a small net sink for carbon and not a net source.

#### Is a much larger sequestering of carbon in the biosphere possible?

Tans *et al.* (1990) concluded on the basis of the North–South gradient of atmospheric  $\text{CO}_2$  that biospheric carbon uptake must be larger and ocean uptake must be smaller than hitherto believed. If they are right, some considerable modifications must be made in the Standard Model (Table 5). First of all  $\beta$  must be larger: about 0.7 instead of 0.5. For an effect of this magnitude to occur there is also a need to postulate decreased decomposition and increased areal coverage as well as stimulated photosynthesis. Although not impossible from an ecological point of view, there is also an observational constraint. If the biosphere absorbs more carbon, the ocean must absorb less to keep the carbon balance in order. If this is what happens it could show up in the time-course of  $^{14}\text{C}$ .

#### Carbon isotope data

In principle, carbon isotopes provide an additional tool to discern complementary paths of carbon exchange, because the ratio of carbon isotopes in source carbon reservoirs are different, and because the photosynthetic process has a slight preference for the lighter  $^{12}\text{C}$  isotope. Fossil carbon reserves, having been formed through photosynthesis, are depleted in the stable isotope  $^{13}\text{C}$  by about 25 parts per thousand. Obviously,  $^{14}\text{C}$  is totally absent in fossil carbon. For this reason the records of both isotopes in the atmosphere have exhibited a down-

TABLE 4. *Balance of carbon fluxes and their accumulated amounts for the year 1980<sup>a</sup>*

The fluxes are very close to the accumulated amounts multiplied by the relative rate of increase of  $0.024 \text{ yr}^{-1}$ . However, this cannot be done for fossil release and deforestation release separately. Although their sum has shown an approximately exponential increase, they have been out of phase with fossil release coming up much more recently.

Fossil release, accumulated and rate	159 Gt C	5.0 Gt C $\text{yr}^{-1}$
Deforestation accumulated and rate	91 Gt C	1.0 Gt C $\text{yr}^{-1}$
Total release, accumulated and rate	250 Gt C	6.0 Gt C $\text{yr}^{-1}$
Ocean uptake, accumulated and rate	83 Gt C	2.0 Gt C $\text{yr}^{-1}$
Biosphere uptake, accumulated and rate through $\text{CO}_2$ enrichment	50 Gt C	1.2 Gt C $\text{yr}^{-1}$
Remaining in atmosphere, accumulated and rate	117 Gt C	2.8 Gt C $\text{yr}^{-1}$

<sup>a</sup> For the year 1990 the numbers are about 20% larger.

TABLE 5. *Two simulated hypotheses for the year 1990*

In the Standard Model the relative stimulus of atmospheric  $\text{CO}_2$  with respect to terrestrial net photosynthesis had a value of 0.5, in the second model it was set at 0.7, and the exchange rate at the air-sea interface was halved to arrive at the same atmospheric  $\text{CO}_2$ -concentration. When, alternatively, the exchange rate between deep sea and mixed layer was halved while maintaining the exchange rate at the ocean surface, the desired shift in  $\text{CO}_2$  flux from sea to biosphere was realized while the atmosphere contents of total  $\text{CO}_2$  and isotope records stayed almost identical to those of the Standard Model (data not printed).

Variable	Initial 1780	Observed	Standard Model	Reduced ocean surface exchange
$F_{\text{fossil} \rightarrow \text{atm}}$	0	5.80	5.80	5.80 Gt C $\text{yr}^{-1}$
$F_{\text{atm} \rightarrow \text{sea}}$	0	?	2.32	1.81 Gt C $\text{yr}^{-1}$
$F_{\text{atm} \rightarrow \text{biosph}}$	0	?	0.75	1.28 Gt C $\text{yr}^{-1}$
$d\text{Atm}/dt$	0	2.7	2.73	2.72 Gt C $\text{yr}^{-1}$
$[\text{CO}_2]_{\text{atm}}$	285	350	349.7	349.8 ppmv
$^{13}\delta_{\text{atm}}$	-6.0	-8.0	-7.93	-8.18 parts per thousand
$^{14}\delta_{\text{atm}}$	-23.0			parts per thousand
1950:		-46	-46.9	-35.7 parts per thousand
1970:		450	533	677 parts per thousand
1980:		220	216	349 parts per thousand
1990:		?	93	199 parts per thousand
Biosphere increment	1895	?	1862	1887 Gt C
Ocean increment	—	?	-32.6	-7.5 Gt C
		?	109.6	84.3 Gt C

ward trend, which is completely in agreement with the results of simulation. It is worthwhile to explore the effects of the present hypothesis of stimulated biospheric uptake on simulated isotopic ratios:

- When the ocean absorbs less carbon, its ability to dilute the isotopically depleted fossil carbon is also getting smaller, and so the isotopic record should show a faster decline.
- On the other hand, the biosphere preferentially takes up the lighter C-isotope, and with a faster biospheric growth, isotopically enriched  $\text{CO}_2$  will remain in the atmosphere. This effect will reduce the downward trend of the atmospheric isotope content.

These two processes are opposite in direction and appear to cancel each other out almost completely with respect to  $^{13}\text{C}$ . Therefore,  $^{13}\text{C}$  isotope abundance is of little use

to discriminate between the pathways of carbon into biosphere and ocean.

However, for the  $^{14}\text{C}$  record the results were more complicated (Table 5). Firstly, there are two very different periods in the  $^{14}\text{C}$  record. Until about 1955 the  $^{14}\text{C}$  record showed a gradual decline from about -23 to about -50 parts per thousand, due to dilution with fossil carbon which does not contain radiocarbon at all. Suddenly, as a result of atmospheric hydrogen bomb-tests in the early sixties, the amount of  $^{14}\text{C}$  in the atmosphere was almost doubled and the level was raised to about +900 parts per thousand in 1965. When these tests were banned (1963) an almost exponential decline in the  $^{14}\text{C}$  levels began.

Using this decline, the gross carbon exchange rate at the ocean surface was calibrated at  $38 \text{ Gt C yr}^{-1}$  in the standard model. Together with an  $\text{NPP}$  of  $50 \text{ Gt C yr}^{-1}$ ,



the relaxation time of radiocarbon in the atmosphere (700 Gt C in 1980) is calculated as  $700/(38 + 50) = 8$  years. However, about half of the *NPP* flows to the short-lived leaves and roots which return their carbon in almost the same season, and so the effective relaxation time is  $700/(38 + 25) = 11$  years. Although description of the  $^{14}\text{C}$  pulse by a single exponential decline is not possible in the mathematical sense, as it is really a composition of various relaxation times, we can reasonably approximate the simulation results for  $\delta^{14}\text{C}$  in Table 5 by  $900 \exp(t - 1965)/11$  for the results of the standard model, where  $t$  is the year.

When the reduced ocean uptake was achieved by a lower surface exchange rate, the relaxation time of the pulse became too large (Table 5). Therefore, the only way that we can hypothesize a lower ocean uptake rate that is compatible with both total atmospheric  $\text{CO}_2$  and  $^{14}\text{C}$ , is by reducing the exchange rate of the mixed layer with the deep sea. This mixed layer contains so much carbon (about 2200 Gt C) that it can absorb the isotope pulse on the time-scale of a few decades almost completely. For total  $\text{CO}_2$ , the absorption capacity is much more limited because of the chemical 'buffering resistance'. This buffering resistance is the reason why a lower exchange rate between mixed layer and deep sea can reduce total absorption of  $\text{CO}_2$  almost without affecting the  $^{14}\text{C}$  record. When the large-scale circulation of water in the Atlantic ocean was halved (of course with initial conditions in the ocean re-adapted to steady state) a  $\text{CO}_2$  flux shift of the size required was realized. For carbon isotopes and for atmospheric  $\text{CO}_2$  the results were almost identical to those of the standard model and, therefore, they have not been given in Table 5.

## DISCUSSION

The  $\text{CO}_2$ -fertilization effect does not have to be expressed just as an increase in the surface density of net primary productivity. It is equally possible that decreased decomposition of wood and soil organic matter play a role. Nutrient contents of organic material formed under higher  $\text{CO}_2$  are lower and may well slow down the rate of decomposition. Vegetated areas may also be increased, when plant life becomes possible in climatic regions that were hitherto uninhabitable.

These mechanisms may occur simultaneously and can complement each other numerically. Simulated carbon isotope records were not sensitive to which of these mechanisms predominated in the model and can, therefore, not be used to distinguish between them. Field work, remote sensing work and physiological work will be needed to assess the contribution of these mechanisms to the global  $\text{CO}_2$ -fertilization effect. A more detailed distinction in geographic and structural pool components is probably also needed.

Even a slight imbalance in the growth of terrestrial

ecosystems, on a global scale, is sufficient to absorb the carbon released by deforestation (Lugo and Brown, 1986). Such an uptake is most likely caused by increasing atmospheric  $\text{CO}_2$ , but eutrophication may also play a partial role. Detection of this fertilization effect by sampling methods in the field is extremely difficult, because of the large natural heterogeneity that exists on practically every spatial scale.

Deforestation is a significant source of  $\text{CO}_2$  at a rate of about 0.5 to 1 Gt C  $\text{yr}^{-1}$ . On the other hand, this rate of release can be more than compensated by global stimulation of growth by atmospheric  $\text{CO}_2$ . From the point of view of the activity of the biosphere, a net biospheric uptake of 0.5–1.0 Gt C  $\text{yr}^{-1}$ , as expressed in the standard model, is plausible. A higher biospheric (and lower ocean) uptake can be reconciled with the observed record of  $^{14}\text{C}$  in the atmosphere, if the proper mechanism in the model is altered. An increased  $\text{CO}_2$ -fertilization effect of the terrestrial biosphere must be accompanied by a smaller exchange rate between deep sea and the mixed surface layer of the ocean.

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