

Interaction of ocean and biosphere in their transient responses to increasing atmospheric CO₂

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Abstract

Increasing atmospheric CO₂ induces a net uptake of carbon in the ocean by a shift in chemical equilibrium in seawater, and in the terrestrial biosphere by a stimulated photosynthesis and productivity. The fractions absorbed in both biosphere and ocean decline with increasing dynamics of the release rate of CO₂ into the atmosphere. However, the relative portion of ocean absorption descends much faster with annual growth rate of CO₂ release than biospheric absorption does, due to a difference in dynamics. The equilibrium absorption capacity of the biosphere is estimated to be only one quarter of that of the ocean, but the current sink size of the biosphere is about half of that of the ocean.

Apart from CO₂-stimulated carbon fixation, the biosphere releases CO₂ as a result of land use changes, in particular after deforestation. Both of these fluxes are of the order of 1–1.5 Pg of carbon per year. The CO₂-fertilization effect and regrowth together have turned the terrestrial biosphere as a whole from a source into a sink.

Introduction

The rate of increase of atmospheric CO₂ is about 2.5 Pg of carbon per year less than the flux released by fossil fuel burning. The traditional view was that this difference is absorbed by the ocean (Oeschner *et al.* 1975; Bolin *et al.* 1986). Additional release fluxes of CO₂ of the order of 1–2 Pg yr⁻¹ from large scale deforestation created the problem of the so-called 'missing carbon.' because the ocean was not considered to be able to absorb this flux as well.

Plant physiological and agronomical work has shown that rising ambient CO₂ will stimulate the rate of CO₂ assimilation, and subsequent biomass accumulation (Kimball 1983; Lemon 1984; Strain & Cure 1985; Cure & Acock 1986). Using a realistic CO₂-fertilization effect based on evi-

dence of this kind, the role of the biosphere was included in a comprehensive model for the global carbon cycle (Goudriaan & Ketner 1984), resulting in a simulated realistic time trend of atmospheric CO₂.

In this paper the size of the biospheric sink will be further considered. The sink will be separated from CO₂ sources caused by deforestation. The interaction between CO₂ absorption by ocean and biosphere will be investigated, and in particular how the interaction is influenced by the dynamics of the CO₂ emission rate to the atmosphere.

Reservoirs and fluxes in the terrestrial biosphere

The flux of assimilated CO₂ passes through various biospheric pools, from where the carbon is

eventually recirculated to the atmosphere (Fig. 1). The subsequent fluxes are defined and named as follows:

Gross Primary Productivity (GPP) is the gross carbon fixation of the photosynthetically active organs (mostly the leaves), for global studies usually expressed in Pg of C yr^{-1} . This flux is hard to estimate, but probably ranges between 80 and 200 Pg C yr^{-1} .

Net Primary Productivity (NPP) is equal to *GPP* minus the respiratory losses of the plants themselves. It is equal to the flux of plant material that becomes available to the other organisms that live on it (heterotrophic consumption), e.g. by grazing or by decomposition of dead material. This flux is estimated to be 40–60 Pg C yr^{-1} .

Net Ecosystem Production (NEP) is equal to *NPP* minus the heterotrophic consumption. It presents the net growth of an ecosystem during an undis-

turbed period. Globally this flux is about 4–7 Pg C yr^{-1} .

Net Biospheric Uptake (NBU) is equal to *NEP* minus loss by fire and direct human disturbance. This flux is between 0–1 Pg C yr^{-1} .

The basic ecosystem structure in modelling is given in Fig. 2, starting with *NPP* as a driving force. Each ecosystem has its own characteristic parameters (Goudriaan 1990). The outflow of each state variable in this scheme is calculated as content divided by a constant longevity, so that its equilibrium content is simply the product of longevity and inflow. The outflows cascade down to litter, humus, and resistant soil carbon. From biomass to humus a considerable fraction of carbon is lost by respiratory processes, and also from humus to resistant soil carbon. The complement of this fraction returns to the atmosphere as respiratory CO_2 .

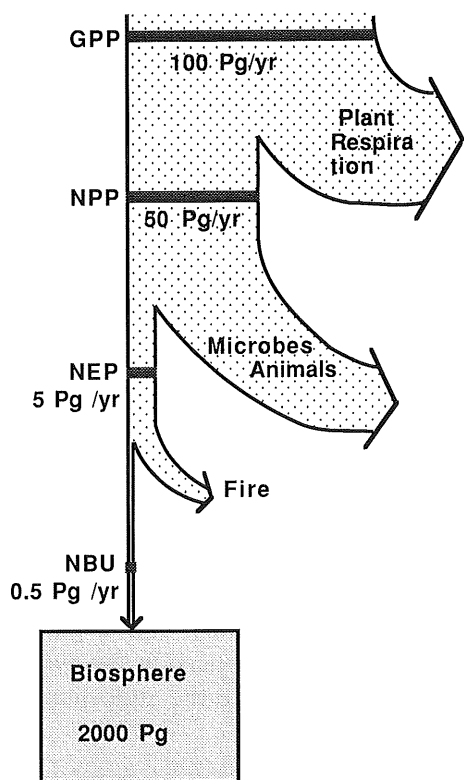


Fig. 1. Major terrestrial carbon fluxes, as consumed by the plants themselves, by heterotrophic organisms and by fire. Net biospheric uptake is the remainder of large positive and negative fluxes.

A simplified ecosystem structure

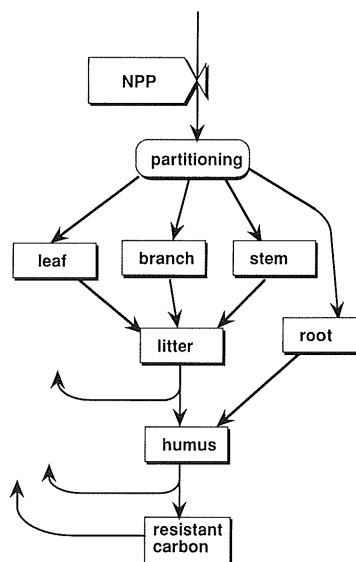


Fig. 2. Simplified model structure for an ecosystem. Each box itself is described by first order decay. Characteristics such as *NPP*, its allocation, reservoir longevity and transfer (respiratory) losses depend on ecosystem type.

The biosphere model

The biosphere model is best understood as an extension of a very simple linear model: $NPP = 50 \text{ Pg C yr}^{-1}$, mean biomass 500 Pg C (Bolin *et al.* 1979), so that the mean longevity must be 10 years. In equilibrium the decomposing flow is equal to the Net Primary Productivity. After one year about 30 % of litter is still present (Jenkinson *et al.* 1991). This influx to humus must be 30 % of NPP or 15 Pg C yr^{-1} . For a total humus reservoir of about 750 Pg C the mean longevity arrives at 50 years. The other 70 % is released in the form of CO_2 into the atmosphere. Representation of the dynamics on a time scale of one hundred years or more requires still an other and much slower reservoir: resistant soil carbon. Its content is also 750 Pg C , and if its through flow is 10 % of the flow of decomposing humus or 1.5 Pg C yr^{-1} , the corresponding time coefficient is 500 years. This simple, crude model for the total biosphere comprises 2000 Pg of carbon, the correct order of magnitude. The term 'linear' refers to the dependence of fluxes on reservoir contents, not to shape of time trends which tend to show exponential declines.

The empirical basis for this linear structure of the dynamics of humus and resistant carbon was given by Kortleven (1963) and Olson (1963). Losses of soil carbon after land use changes can also be fit into this model. A drop of soil carbon after reclamation of virgin land from an equilibrium of 20 kg C m^{-2} to a new equilibrium of 15 kg C m^{-2} after several decades (Schlesinger 1986) can be simulated by using a shorter residence time for humus in soil under arable cultivation (20 yr) than in grassland or in forest (50 yr). Resistant carbon (residence time 500 years) which amounts to about 10 kg C m^{-2} , is included in total soil carbon, and is much less affected by these land use changes, at least in the short term.

Above-ground biomass consists of leaves, stemwood, roots, branches and litter (Fig. 2). Combination of the driving forces and residence times leads to a steady state distribution of surface densities of carbon for a biosphere model consisting of six different ecosystem types as pre-

sented in Fig. 3 (Goudriaan 1990). In this figure the width of each bar represents the area of the vegetation type, and the height of each bar the carbon areal density. The high density of soil carbon in temperate forest and in grasslands as compared with 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. A global biosphere model along these lines can be constructed in varying degrees of spatial and ecosystem resolution. A number of six ecosystems is about the minimum to have a reasonable range and to include deforestation effects (Goudriaan & Ketner 1984). Esser (1987) developed a gridded model with as many as 2433 grid points to represent detailed geographic information. Here the low number of six ecosystems will be maintained for easier interpretation of the model results.

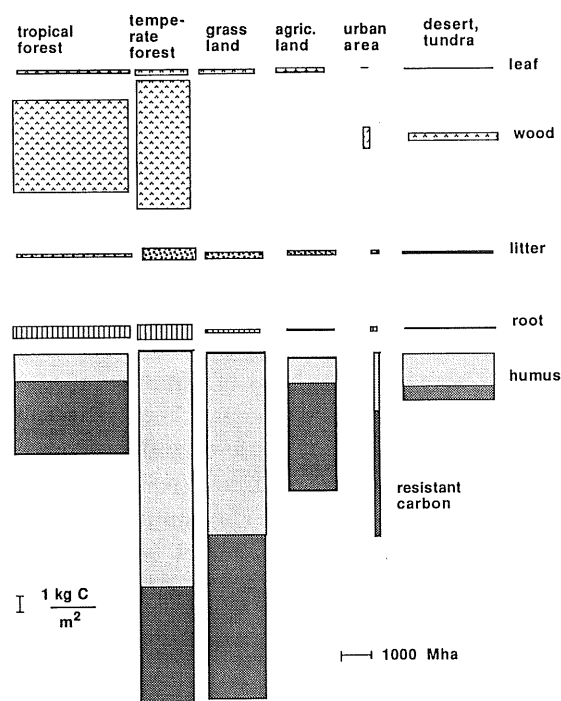


Fig. 3. Simulated carbon areal density (heights of the columns) and land area for each vegetation type (widths of the columns). In this representation the areas of the columns are proportional to the simulated amounts of carbon.

Stimulation of primary productivity

Green plants need CO₂ to grow. A higher concentration of atmospheric CO₂ will stimulate the photosynthetic process, promoting plant growth and productivity. Also the efficiency of plant water use is increased, so that this growth stimulation is possible without an increase of the water demand for transpiration (Goudriaan & Unsworth 1990).

Respiration is not directly stimulated by higher CO₂, if anything it is reduced (Amthor 1991). Yet, respiration will follow the *GPP* indirectly as respiration is proportional to both growth rate and biomass. Therefore the CO₂-enrichment effect is approximately proportionally transmitted from *GPP* to *NPP*. Over a large range of CO₂ (200–1000 ppmv) *NPP* to CO₂ can be described by a logarithmic response function (Goudriaan *et al.* 1985)

$$NPP = NPP_0 \{1 + \beta \log(CO_2/CO_{2,0})\}$$

where *NPP* is the net annual primary productivity, and *NPP*₀ is *NPP* in the reference situation (here at 300 ppmv).

The value of the response factor β is about 0.7 under good conditions for growth, but declines with increasing nutrient shortage (Goudriaan & de Ruiter 1983). Under water shortage (Gifford 1979; Rosenberg 1981) the growth-stimulating effect of atmospheric CO₂ is not reduced, but may even be enhanced. In this situation C₄ plants benefit from increased CO₂ just as much as C₃ plants. There is a large body of experimental data (Kimball 1983; Goudriaan & Unsworth 1990) which shows that the CO₂ fertilization effect on average is about 0.5 % stimulus per % increase of total atmospheric CO₂. This stimulus is effective in agricultural circumstances and probably also in many natural ecosystems. Although there is no direct evidence that the CO₂-enrichment effect can be extrapolated to the major forest ecosystems of the world, the zero hypothesis presumably is that all plants and trees have a similar reaction and do respond positively. Therefore, for modelling purposes, the value of the relative CO₂-fertilization factor β was fixed at 0.5 for all

ecosystems likewise. This value is a bold extrapolation, but it does produce realistic results for the observed CO₂ trend in the atmosphere. In fact, the agreement with the observed time trend of atmospheric CO₂ is almost perfect when a value of 0.45 is used (Goudriaan 1990). In that model the ocean-atmosphere transfer rate was calibrated with carbon isotope evidence. In the study presented here the figure of 0.5 was used to keep the approximating calculations simple. Obviously, all numbers in the presented tables will undergo a slight modification when the more appropriate value of 0.45 is used in the model.

Equilibrium carbon sequestering

In the biosphere

In the simple biospheric model given before, a 10 % increase in atmospheric CO₂ will stimulate the biosphere by 5%: *NPP* becomes 52.5 Pg C yr⁻¹, and equilibrium carbon content of the biosphere rises by 100 Pg to 2100 Pg C. The pre-industrial atmospheric CO₂ content was about 600 Pg of carbon, and so an increment of 10 % is about 60 Pg. From this calculation we can see that eventually the redistribution over biosphere and atmosphere will occur in a ratio of 100/60.

A concise way of expressing the equilibrium redistribution ratio $\Delta B/\Delta A$ is by the simple equation $(\beta B_0)/A_0$ where *A*₀ and *B*₀ are the initial amounts in atmosphere and biosphere. Most of the storage ΔB however, must be realized in the slow soil compartments and it will take centuries to reach the new equilibrium. Therefore the current biospheric increment is much smaller than the one reached in equilibrium.

In the ocean

About 39000 Pg of carbon is present in the ocean, mainly in the form of dissolved bicarbonate ions. When atmospheric CO₂ rises, the concentration of CO₂ dissolved in sea water will go up, and a new equilibrium will be reached. However, at the pH of seawater (about 8.2) the concentration of bicarbonate ions is much higher than that of dis-

solved CO_2 and of undissociated carbonic acid. An increase of dissolved CO_2 slightly shifts the chemical equilibrium, lowering the pH and preventing a proportional increase of the dominating bicarbonate concentration. As a result the total carbon content of sea water does not rise proportionally to atmospheric CO_2 at all. The value of the actual relative response of total carbon to atmospheric CO_2 , ζ , is about 1/10. The same equation as used for biospheric uptake, adapted for the ocean to $\Delta O/\Delta A = (\zeta O_0)/A_0$, gives a value of about 6.

When biosphere and ocean are considered together, they act in parallel. The redistribution will then occur in the following ratio's: an a priori fixed amount of 60 Pg C in the atmosphere will lead to an absorption of 390 Pg C in the ocean and 100 Pg C in the biosphere. This means that only 11 % will remain in the atmosphere, 71 % will be taken up by the ocean and 18 % by the biosphere. This calculation shows that ocean and biosphere together can absorb almost 90 % of CO_2 released to the atmosphere, but this process will take at least a 1000 years or more to do so due to slowness of the large reservoirs both in the deep sea and in soils of terrestrial ecosystems. It is necessary to consider transient behaviour as well if we want to know what is happening now and in the near future.

Transient response

When considered over the last 100 years, the rate of anthropogenic release of CO_2 to the atmosphere has grown approximately in an exponential fashion, at a relative annual rate of about 2.4 % per year. Our analysis can be simplified by using the mathematical rule that each component in a linear system will grow by the same exponential rate as the exponentially growing driving force does. As a consequence, the *disturbances* from the equilibrium of all rates and reservoirs grow at the same exponential rate, and the ratio between these disturbances will remain constant during the transient process. As a first approximation both ocean and biosphere are fairly rep-

resented by this theoretical linear model. This expectation is confirmed by the stability of the observed remanent fraction in the atmosphere: about 55 % for a long time.

For the ocean the principle of linearity applies to the *disturbance* of dissolved inorganic carbon. This disturbance occurs against a background of about 26 g C m^{-3} which forms by far the larger part of the ocean carbon content (about 39000 Pg C). Marine photosynthesis is not affected by atmospheric CO_2 as phytoplankton mainly uses the abundantly available bicarbonate as a carbon source. Yet photosynthesis lowers the carbon content close to the surface (down to about 24 g C m^{-3}), and enriches it in the deep sea where precipitating and decomposing organic material produces a high carbon content far in excess of equilibrium with atmospheric CO_2 (up to about 28 g C m^{-3}). The resulting depth profiles of carbon and phosphate contents could be realistically simulated (Goudriaan 1990), by using phosphate as a driving force for marine primary productivity. The dynamics of the ocean absorption depends on transport processes from surface to deep sea. A model with 12 layers was used, thermohaline circulation was included, sea surface/atmosphere exchange was calibrated with post-nuclear ^{14}C data.

The global carbon cycle with both ocean and biosphere was run with a compartmentalized biosphere model with 6 ecosystem types (Goudriaan 1990) driven by an exponentially increasing rate of emission of CO_2 . Deforestation was not included in order not to confound its effects with those of the feed-back driven sink effect. The model results are presented in Fig. 4.

The interaction of biosphere and ocean through their common access to the atmosphere is best illustrated by calculating the fraction that each absorbs out of a total release rate. For the biosphere this fraction is $\Delta B/(\Delta B + \Delta O + \Delta A)$. This fraction can be written as $(\Delta B/\Delta A)/(\Delta B/\Delta A + \Delta O/\Delta A + 1)$, so that it can be easily calculated from the model results given in Fig. 4.

We then see (Fig. 5) that the remanent fraction (p_a) in the atmosphere strongly increased with increasing dynamics, as could be expected on

1980 was about 12 Mha per year, and with a loss of carbon (including soil carbon) of about 14 kg C m^{-2} , a flux of release of carbon due to deforestation can be expected of about 1.7 Pg C yr^{-1} (including soil carbon losses). This figure is well within the range of a recent estimate of Houghton (1991).

There are, however, a number of processes that reduce the rate of emission from the biosphere as a whole. First, loss of soil carbon does not occur instantaneously but it is delayed in time. A dynamic simulation model takes such a delay into account, in contrast with statistical calculations that assume immediate release. To give an impression of the effect of this delay: assuming a time coefficient of 20 years for soil carbon and a relative growth rate of deforestation of 2 % per year, the rate of release is reduced by a factor 1.5. Surely the soil carbon will eventually be released, but the model deals with the *current* rates. Secondly, not all standing biomass is immediately oxidized, part of it is even conserved in the form of charcoal, which has a much longer longevity than biomass. As a third factor, regrowth of forests occurs in particular in the temperate parts of the world (Brouwer *et al.* 1991). The total rate of regrowth is probably of the order of one third of the rate of tropical deforestation. In the model these processes together reduced the net rate of global carbon release due to land use changes to about 0.6 Pg C yr^{-1} .

This net rate of release was counteracted by a current CO_2 -fertilization flux of 1.1 Pg C yr^{-1} , which was derived from model output using the same method as for the accumulated amounts, given in Table 1. This model result can be approximately understood as follows: The annual rate of increase of atmospheric CO_2 is about 0.4 % per year, leading to an assumed CO_2 fertilization effect of 0.2 % per year for *NPP*. In the simple biosphere model explained in the beginning of this text, the resulting annual increase of equilibrium should then be 4 Pg yr^{-1} , based on 2000 Pg present. The effect of the slowness of the different compartments can be estimated from Fig. 4 as a reduction in $\Delta B/\Delta A$ from 1.56 at 0 % growth to about 0.46 at 2.4 % growth. This leads

from 4 Pg yr^{-1} to about 1.2 Pg yr^{-1} and is very close to the actual model result of 1.1 Pg yr^{-1} .

The result for the terrestrial biosphere as a whole is a *net uptake rate of carbon of 0.5 Pg yr^{-1}* . The rate of emission due to fossil fuel burning was about 5.2 Pg C yr^{-1} . When this flux is added to the biospheric release rate of 0.6 Pg yr^{-1} , we find a total emission rate of about 5.8 Pg C yr^{-1} . The rate of absorption by the ocean was simulated to be 2.0 Pg C yr^{-1} , and so the remaining rate of accumulation in the atmosphere was 2.7 Pg C yr^{-1} . The remanent fraction based on *current* emission rates is now found to be 0.46, very close to the figure based on accumulated amounts over the past 200 years. This small difference emphasizes that the actual increase over time for the combined fossil/biosphere emission has been very close an exponential one. Yet, the time patterns of biospheric emission and fossil fuel emission separately have not been identical. Around the turn of the century the biospheric emission was larger than the fossil fuel emission was, whereas nowadays the situation has reversed. Over the past 200 years together the biosphere has been a net source, but somewhere during the past decades it must have turned into a net sink. This switch is the result of the steadily increasing CO_2 -fertilization effect.

The dual character of the biosphere in being both a source and a sink is undeniable. The biosphere may not be quite as strong a sink as the ocean is, but it is well capable of counteracting its own role as a source (Lugo & Brown 1986).

Discussion

There are different ways to calculate the remanent fraction in the atmosphere. The classical method is simply to take the ratio of atmosphere increment divided by fossil fuel emission, which yields a value of 0.69. This number is too high, since the biospheric emission is not included. But which contribution should we use? Based on *total* biospheric emission (159 + 90) we find a value of 0.44, but based on *net* biospheric emission (159 + 39) we find a value of 0.55. It seems to me that both methods are valid. When only the ocean is

considered as a sink, the value of remanent fraction is identical to $1/(1 + \Delta O/\Delta A)$, to be read from Fig. 4. A comprehensive carbon cycle model can produce this value if one uses the sum of *net* release from the biosphere and fossil carbon emission as denominator. This leads to a remanent fraction of 0.55. When also the sink response of the biosphere is included, the remanent fraction is identical to the fraction p_a given in Fig. 5. This quantity is smaller and arrives at a value of 0.46.

Biospheric release fluxes of CO_2 that are caused by periodic fires in savannas e.g. should not be added to the base of the calculation. These fluxes do not constitute a permanent transfer of carbon from the biosphere to the atmosphere, but are part of the system itself in much the same way as decomposition and respiration are. Bolin's criticism (1986) on the model of Goudriaan & Ketner (1984) for yielding too low a remanent fraction (0.3 as he calculated) must therefore be dismissed.

Climatic change per se has not been discussed at all in this manuscript, partly because it is such a complicated issue, and partly because rising atmospheric CO_2 must be effective already, which we cannot say unequivocally about climatic change. In contrast to geographically diverging climatic effects, the increase of atmospheric CO_2 is ubiquitous. Although the size of the CO_2 -enrichment effect may geographically vary, its direction does not and leads almost certainly to increased carbon fixation. The large increase of carbon storage since the Last Glacial Maximum (Adams *et al.* 1990) must have been a combined effect of warming up and increased atmospheric CO_2 . This historical evidence suggests a trend that may well be resumed in the near future.

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