Modelling biospheric control of carbon fluxes between atmosphere, ocean and land in view of climatic change

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ABSTRACT. The amount of carbon in the atmosphere is less than in the terrestrial biosphere and much less than in the ocean. The level of atmospheric CO_2 is the result of a delicate balance in exchange fluxes with ocean and biosphere. Climatic change has the potential to alter this balance.

A model for the global carbon cycle was used for assessment of the importance of a number of biosphere and ocean characteristics that control atmospheric CO_2. This model included CO_2 feed back on the exchange fluxes, but no temperature feed back.

According to this model covering previously bare land with vegetation would lower atmospheric CO_2 by only 1.5 ppm for each 10^{12} m^2(100 Mha) of land additionally covered. At the present size of the terrestrial biosphere a global doubling of longevity of soil carbon would cause a decrease of 65 ppm of atmospheric CO_2.

The accumulated net biospheric release of carbon to the atmosphere during the last 120 years is estimated at about 30 Gt C. This figure is consistent with measured data of carbon isotopes and with data of atmospheric CO_2.

Marine photosynthesis is responsible for building up high phosphate and carbonate levels in the deep sea by precipitation of organic material. Marine photosynthesis is mostly limited by phosphate in the surface waters, and therefore an increase in total phosphate in the sea would lower atmospheric CO_2. Precipitated fraction and phosphate content of organic material are equally important.

The present difference in chemical composition between the Atlantic ocean on one hand and the Indian and Pacific oceans on the other can be explained by a much larger mixing rate between deep and surface water in the Atlantic ocean. Reducing this mixing rate in the Atlantic to that in the Pacific, would cause atmospheric CO_2 to drop by 25 ppm within a few hundred years time. Similarly, a sudden increase in mixing rate at the glacial-interglacial transitions could explain the strong and fast rise in atmospheric CO_2.

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1.INTRODUCTION

1.1 Reservoirs and fluxes

Three major reservoirs of carbon, the atmosphere (700 Gt C), the oceans (39000 Gt C) and the terrestrial biosphere (2000 Gt C, including soil) constantly exchange carbon in the form of CO_2. The biosphere acts as a powerful driving force in the exchange of carbon between atmosphere, ocean and land. Modelling these fluxes is necessary for a quantitative assessment of the effects of the present and continuing injections of CO_2 into the atmosphere. It should also lead to a better understanding of the large and fast changes of atmospheric CO_2 at glacial-interglacial transitions(Oescher and Stauffer,1986).

Broecker(1984) pointed at the importance of nutrient levels in ocean water for marine photosynthesis, and for atmospheric CO_2, but he also noted that the rapidity of the glacial-interglacial transitions dismisses total nutrient contents as the prime factor. Ocean ventilation rate is more likely a candidate.

Terrestrial photosynthesis is also potentially able to sequester large amounts of carbon, but compared to the enormous reservoir of carbon in the oceans the role of the terrestrial biosphere is modest. In absence of other disturbances, an external injection of carbon will eventually be partitioned over atmosphere, ocean and terrestrial biosphere in the ratio's 0.11,0.71 and 0.18 respectively.

With industrialization, fossil carbon is more and more being injected into the global carbon cycle. At present the oceans absorb a fraction of only 0.4 of this man-made addition and not of 0.71, due to lack of time for redistribution.

Reclamation of land for agriculture and for other human utilization also causes release fluxes of CO_2. These fluxes are due to oxidation of soil carbon, and to decomposition of long-lived biomass such as wood. Simultaneous regrowth of biomass in other regions, and a global stimulus of growth by increased CO_2 largely restore the balance.

1.2 Model development

In this paper a model for the global carbon cycle(Goudriaan and Ketner,1984) will be used and further developed to investigate the controlling potential of some factors. The model performance for the present situation will be discussed and the importance of some of the model parameters for control of atmospheric CO_2 will be investigated. The model will be validated with published data sets such as depth profiles of chemical constituents in the oceans, time series of carbon isotopes and of atmospheric CO_2. The effect of climatic change will not be explicitly modelled, but some potential points of impact will be indicated.

2. MODELLING THE TERRESTRIAL BIOSPHERE

2.1 Disaggregation with respect to residence time

The average residence time of carbon in a simple one box model would be

about 40 years. A more realistic model consists of a parallel-serial circuitry of components with various residence times. For humus and dinert carbon this type of structure can be derived from the work of Kortleven (1963) and of Olson (1963), who both showed that the response of humus level to litter input is of a first order character. Schlesinger (1986) reviewed several data sources, leading to support of first order dynamics of humus. He mentioned considerable losses in soil carbon upon reclamation of virgin land (from an equilibrium of 20 kg C m^{-2} to a new equilibrium of 15 kg C m^{-2}, to be reached after several decades).

In simulation models such losses are reproduced, by virtue of a shorter residence time of humus in agricultural soil (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.

2.2 Geographical disaggregation

The potential distribution of ecosystems on earth is primarily governed by climate. The Holdridge classification scheme (Holdridge,1967) uses climate variables to map vegetation, and can be exploited for an analysis of the effects of climatic change (Warrick et al.,1986a). Amounts of carbon stored in soils can be mapped in the Holdridge diagram (Fig 6.2 in Houghton et al.,1985) which enables a direct estimation of potential carbon sequestering in soils upon a change in climate.

A much higher degree of complexity of disaggregation was realized in the description by Matthews(1983) who compiled a high resolution data base of the geographical distribution of ecosystems. Remote sensing data have contributed considerably to the mapping of the distribution of green leaf area on earth (Tucker et al.,1986).

In the model of Goudriaan and Ketner(1984) only 6 ecosystems were distinguished, to represent the major features of the geographical distribution of biotic terrestrial carbon.

2.3 Human disturbance of ecosystems

Human activities such as agriculture, forest logging, pollution and urbanization have strongly altered vegetation and will continue to do so. They are locally clearly visible and tend to mask the physiological and climatic effects of rising atmospheric CO_2 on ecosystems.

Forest logging can be done with two purposes that must be clearly distinguished. One possibility is that the land is going to be permanently used as agricultural land, the other one is just removal of wood, perhaps with the intention of a temporary agricultural utilization. Both types of disruption can be modelled by a transition matrix that represents the annual area to be transferred from one ecosystem to another.

If no change in land destination occurs, the annually treated land

area occurs on the diagonal of this transition matrix. Its effect was here modelled as a sudden release of most of the above ground carbon to the atmosphere (burning). A small fraction of the biomass, however, becomes long-lasting charcoal, and is so excluded from atmospheric circulation for a long time. This effect reflects the twofold consequence of burning: it not only immediately releases CO_2 into the atmosphere, but it also fixes a small fraction of the carbon of the material burnt into the highly inert charcoal pool (Seiler and Crutzen, 1980). Therefore repeated burning of forests, agricultural land and savanna's increases the carbon content of soils, at the expense of the atmospheric and oceanic reservoirs.

When the land use destination is changed as well, the contents of the soil carbon reservoirs are transferred to the corresponding reservoirs of the new ecosystem type, usually agricultural land. The residence time of humus in agricultural land is shorter, resulting in a considerable loss of soil carbon during the next decades. For instance, in tropical forests the mean areal density of carbon is 140 ton C ha^{-1} in contrast with only 50 ton C ha^{-1} in agricultural land. A rate of transfer of 12 Mha yr^{-1} therefore means that about one Gt C will be released in total for each year that this deforestation occurs.

However, this release is not immediate but distributed in time. With a residence time of humus in agricultural soil at 20 years, the release rate is overestimated if immediate release is assumed. With a dynamic simulation model such a delay can be easily taken into account.

2.4 Terrestrial photosynthesis as affected by CO_2

The weight fraction of carbon in dry weight of plant material varies only between 40 and 50%, so that there is a close connection between CO_2 assimilation and dry weight gain. Plant physiological and agricultural research has shown the importance of environmental factors such as radiation, temperature, water and nutrient supply for primary production (De Wit et al.,1979; Johnson,1981). Aereal CO_2 itself has been proven to be important as well (Lemon,1984; Warrick et al.,1986b).

In general, the normal ambient CO_2 partial pressure of about 300-330 μbar is suboptimal (Strain and Cure,1985) for C_3-plants which form 95% of the biomass. Stimulation of seasonal dry weight gain by increasing ambient CO_2 continues up to about 1000 μbar partial pressure. Over a large range of CO_2(200- 1000 μbar) the response of dry weight gain to CO_2 is logarithmic:

$$NPP = NPP_o \, (1 + \beta \log(CO_2/CO_{2,Q})) \qquad (1)$$

where : NPP net annual primary production (g m^{-2} yr^{-1})
NPP_o NPP in the reference situation at 300 μbar.
The value of the response factor β is about 0.7 under good growth conditions otherwise(Goudriaan et al.,1985), but declines with increasing nutrient shortage (Goudriaan and De Ruiter,1983). Under water shortage (Gifford,1979; Rosenberg,1981) the growth stimulating effect of atmospheric CO_2 is not reduced, but may even be enhanced. This interaction with water shortage is caused by partial stomatal closure

under increased CO_2. In this situation C_4-plants benefit from increased CO_2 just as much as C_3-plants.

Ideally, the value of β should be separately determined for each type of ecosystem, but up to now in modelling the global carbon cycle a single value is used, usually between 0.2 and 0.5 . Goudriaan and Ketner(1984) whose model will be used here, adopted 0.5. This relatively high value was chosen to allow for eutrophication as well.

2.5 Terrestrial photosynthesis as affected by biomass

The logarithm of the growth rate of a free standing individual plant is often linearly related to the logarithm of plant size itself: an allometric relationship. This relationship has been used in a number of models as reviewed by Bolin(1986). However, this relationship cannot be used on the scale of a field, and even less on that of an ecosystem,. Because of competition between plants, the effect of biomass on growth should then rather be described in terms of fraction of radiation absorbed by green leaf area (Milthorpe and Moorby,1979). Due to mutual shading of leaves, the fraction of absorbed radiation is soon saturated with increasing leaf area. Above a leaf area index (LAI) of 3 m^2(leaf area) m^{-2}(land area), which corresponds with a leaf dry weight of 150 g m^{-2}(land area) no further increase of NPP can be expected with increasing leaf biomass. Positive feedback of biomass on NPP is further weakened by increased partitioning of growth to non-photosynthesizing organs such as stems and branches, after the soil has been sufficiently covered with green leaf area. Therefore models that use an allometric relationship between NPP and biomass on a global scale tend to overestimate the positive feedback with biomass. Only in case of clustering of vegetation in bushes, as often occurs in dryland vegetation, does the photosynthesis-biomass relationship continue much longer, but it does so at the expense of growth rate per unit land area. In this situation bush coverage and green leaf coverage within the bushes must be separately modelled (Goudriaan,1986). For a global scale model however such a refinement is not warranted.

Expansion of vegetation onto previously bare land is something else and should be explicitly modelled as area growth of ecosystem coverage. It is clear that such processes can be important when the climate changes (see 5.2.1).

Thanks to pioneer vegetation, carbon fixation is not much reduced after removal of biomass. As far as modelling of carbon is concerned, it does not matter what the type of vegetation is that takes up the carbon from the atmosphere. It will take decades however, to restore carbon pools with long residence times, such as stem wood. The time course of net ecosystem production (NEP) after deforestation typically shows an overshoot. After some decades the losses of slowly decaying dry matter increase in reservoirs with long residence times (stems in particular) and they finally consume almost all production.

Both the cyclic (diagonal component of the transition matrix) and permanent (triangular component of transition matrix) forms of land use change grow at a global scale. Thanks to regrowth the cyclic components of deforestation and of other forms of biomass removal from ecosystems

do not have much influence on atmospheric CO_2 (see 4.3)

3. MODELLING THE OCEAN

3.1 Compartmentalization

Reviews of some of the existing models for carbon exchange between ocean and atmosphere can be found in Björkström(1986), Sarmiento(1986), Broecker and Peng(1982),Baes et al.(1985). As Björkström(1986) pointed out, some of these models have presently been compartmentalized to the extent that they need as many as 600 parameters. The work presented here aims at compromising the needs for high resolution on one hand and for simplicity on the other. In the model presented by Goudriaan and Ketner(1984) the ocean was compartmentalized into 10 strata, of which the top one was further split into three zones : a high latitude zone (after Viecelli et al.,1981) and a low latitude zone consisting of two strata. Diffusion was permitted between all strata ($K=4000\ m^2\ yr^{-1}$), and the Gordon circulation was simulated by a mass flow sinking from the high latitude surface zone. This mass flow was equally distributed over the nine deep strata, where it forced an upwelling into the low latitude surface zone. The circulation was closed by continuous mass flow from the low to the high latitude surface zone.

In modification of the Goudriaan and Ketner(1984) model, the surface zones were considered to be internally well-mixed (K infinite), but a resistance of 0.25 yr m^{-1} was modelled for exchange with the atmosphere. The size of this resistance was chosen by calibration with the rate of decline of the ^{14}C-peak after the nuclear tests in the early sixties (Fig 6). It means that an annual molar flux of CO_2 can pass through the surface, equivalent to the total carbon content of 4 meters of sea water. Because of the small size of the chemical capacitance, however, an approximately ten times(Revelle factor) larger depth is annually involved in chemical equilibration.

In the 1984 model marine photosynthesis was added as a fixed driving force. The decomposition of precipitated organic material could account for observed features such as high partial pressure of CO_2 in deep sea water, followed by CO_2 release in the upwelling zone and net uptake in the high latitude downwelling zone.

Since this model considered the ocean as one stratified unit, it could not account for the large observed differences between the Atlantic ocean on one hand and the Pacific and Indian on the other. In glacial periods these oceans may have been more alike (Broecker and Peng,1982). To investigate the effect of realization of this possibility by simulation, it was necessary to separate the two ocean systems in the model, and characterize them with their own parameters.

In the modified model the two ocean systems differed mainly by their rate of internal turning over of deep and surface water, which is much higher in the Atlantic than in the Pacific&Indian ($2\ 10^{15}\ m^3\ yr^{-1}$ versus $0.2\ 10^{15}\ m^3\ yr^{-1}$) (Baes et al.,1985).

The two ocean systems were connected, via the atmosphere for carbon dioxide and for oxygen, and via the Antarctic Sea for phosphate, oxygen

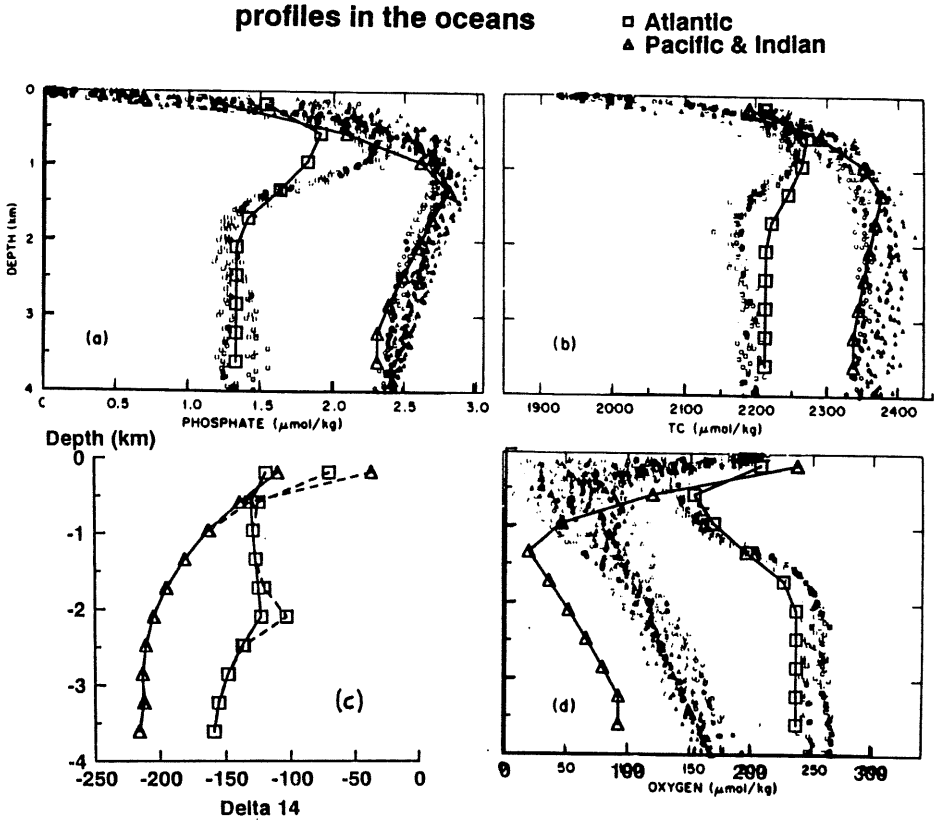

Figure 1 Measured and simulated (large connected symbols) depth profiles of phosphate(a), of total carbon (b) and of oxygen(d) in the Atlantic and in the Pacific and Indian. These simulation results are presented as an overlay on Fig 5.6 in Baes et al.(1985). For $\delta^{14}C$ (c) simulated profiles are given before the nuclear tests and for the year 1972 (dashed lines)

and total carbon. The exchange via the atmosphere is obvious, but the one via the Antarctic Sea needs some explanation. A strong circumpolar flow of surface water around Antarctica was modelled, connecting both oceanic systems. Some exchange of deep sea water may occur as well, but was not included in the model. At the 45.2 °/oo isopycnal a strong gradient is observed of many characteristics (GEOSECS data in Broecker and Peng,1982), which means that there is little exchange between the deep waters of the Antarctic and the oceans.

The downward water flow from the Antarctic Sea towards the deep sea of both ocean systems stems from a common source of cold surface water

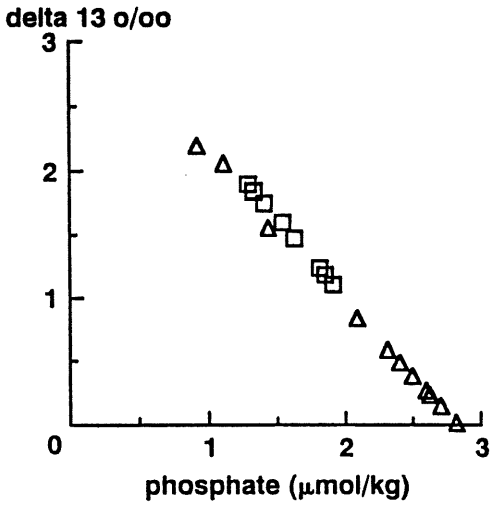

Figure 2 Simulated δ^{13} (°/oo) versus phosphate concentration in both ocean systems.

in the circumpolar flow. This feature, in combination with different ventilation rate could generate the large differences in chemical compositions in both ocean systems, as are also observed in reality. The precipitation of organic material, originating from marine photosynthesis was essential in maintaining this difference.

3.2 Marine photosynthesis

Since nutrients strongly affect marine photosynthesis, it was necessary to include nutrient transport. Phosphate is considered as the main limiting factor. The total amount of ocean phosphate was initialized as an input parameter (92 Gt P, on basis of Baes et al,1985), but the distribution of phosphate was established by simulation. The ratio between downward precipitation of organic material, fixed in marine photosynthesis, and phosphate concentration of the upper layer was given as a model parameter (278 g C g P^{-1} m yr^{-1}). This parameterization leads to a downward flux of approximately 3 Gt C yr^{-1} in total, sinking through the 400 m depth level. The phosphorus content of organic material, and its oxygen demand upon decomposition was taken according to the Redfield equation (Baes et al.,1985;pp 88), leading to 0.024 g P $g^{-1}C$ and 3.47 g O $g^{-1}C$ respectively.

Surface layers received phosphate from the deeper layers by upwelling and by diffusion. The precipitating organic material was allowed to decompose between 400 and 1500 m depth, thereby raising the phosphate and carbonate levels and consuming oxygen (Fig 1). The profiles generated in this way are similar to observed profiles (Baes et al,1985).

This biotic pump is independent of atmospheric CO_2, since carbon is not a limiting factor for marine photosynthesis. Assuming that the ocean profiles have been in equilibrium with this process before atmospheric

CO_2 started to rise, marine photosynthesis plays no role in enhancing the rate of carbon uptake by the oceans. However, if the rate of marine photosynthesis is increased by eutrophication or for other reasons, its role can be significant.

3.3 Carbon isotopes

Exchange of isotopes within the sea was modelled analogous to other passive admixtures. Between sea and air a second flux component was modelled, driven by the difference between isotope ratio's in water and air, and by their discrimination upon solution. This flux component faces the total amount of carbon for isotopic equilibration, and is therefore about ten times(Revelle factor) slower than chemical equilibration. As a result of this method the prenuclear equilibrium of $\delta^{14}C$ in the surface ocean layers was simulated to be about -100 °/oo (Fig 1c). The long residence time of water in the deep Pacific shows up in low values of $\delta^{14}C$. The simplified model structure for massflow generated a tongue of downwelled water in the Atlantic at a depth of about 2000 m.

The assumed discrimination of ^{13}C in photosynthesis (Mook,1986) caused a correlation between $\delta^{13}C$ and phosphate (Fig 2), practically the same as observed in reality(See Fig 6-12 in Broecker and Peng,1982).

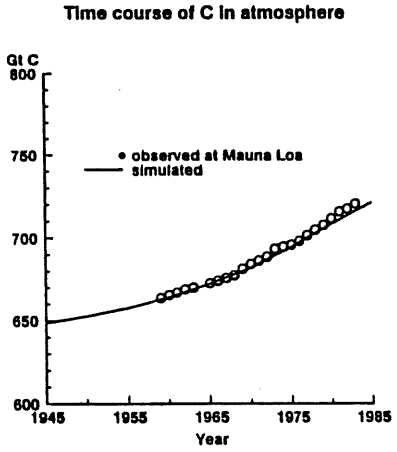

Figure 3. Simulated and measured time courses of atmospheric CO_2.

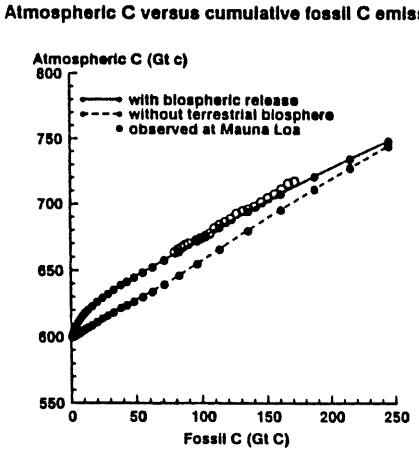

Figure 4. Simulated and measured atmospheric CO_2 versus cumulative injection of fossil carbon, every five years, the last one in 1995. The simulated results are given with and without biospheric exchange.

4 MODEL BEHAVIOUR FOR THE MODERN TIME

4.1 Atmospheric CO_2 concentration and airborne fraction

Observed and simulated atmospheric CO_2 are given in Fig 3. The fossil emission to the atmosphere was based on the data of Rotty and Masters (1985), with extrapolation to the near future. The simulation was started in 1780 at 285 μbar (599.6 Gt C).

Atmospheric CO_2 is highly correlated with cumulative fossil fuel emission (Fig 4). The slope of this graph is the so-called marginal airborne fraction α_m (Bolin,1986). Over the period 1960-1980 it has an observed value of 0.576, whereas values of 0.564 and 0.634 were simulated with and without terrestrial biosphere respectively (Fig 4). The difference was caused by a net positive biospheric uptake in the last decades.

To be able to compare models with and without biosphere, Bolin introduced the term "total airborne fraction" which stands for atmospheric increase divided by the sum of biospheric and fossil fuel emissions. Of course, net biospheric emission should be used in this calculation and not the gross emission. The difference can be considerable, if one considers that the simulated gross biospheric emission between 1860 and 1980 was 122 Gt C, in contrast to 30 Gt C net emission. If the atmospheric increase over this period is divided by the sum of gross biospheric and fossil fuel emission, α can be found to be less than 0.3 . Such a low value of α seems to indicate an unrealistically high capacity of the biosphere to absorb carbon, which was a reason for Bolin(1986) to criticize the model of Goudriaan and Ketner(1984). However, he should have used net emission, not gross. Gross emission generates ample ecological space for regrowth.

If net biospheric emission is used, α becomes a characteristic of ocean uptake only. Between 1960 and 1980 the net biospheric emission was simulated to be negative, so that the simulated total airborne fraction was higher, not lower, than the "marginal" one and became 0.595 . This value is not the same as was simulated without biosphere, as one might have thought. However, the different time path of atmospheric CO_2 in both simulation runs affected ocean uptake.

4.2 Carbon isotopes

Due to an assumed $\delta^{13}C$ of -25°/oo for fossil carbon and a fractionation of -19°/oo in photosynthesis, the simulated atmospheric $\delta^{13}C$ decreased with 1.47 °/oo between 1860 and 1980, with a continuing rate of decrease in 1980 of 0.03 per year. These figures practically coincide with the data recorded by Freyer(1986) (Fig 5a), but they show a faster rate of decrease than Stuiver(1986) has found. For atmospheric ^{14}C a similar, but much stronger, decrease (the Suess effect) was simulated, from -23.5 °/oo in 1860 down to -46 °/oo in 1950. These model simulations fall in line with the data as given in Broecker and Peng (1982) and Bolin(1986) (Fig 5b). The modelled decline of atmospheric radiocarbon after the nuclear tests is presented in Fig 6.

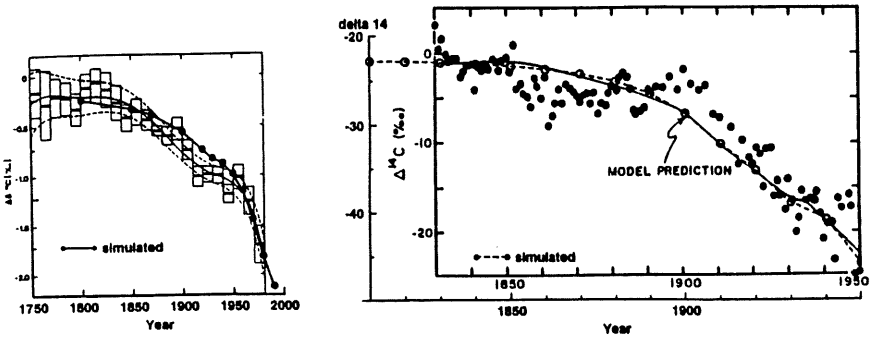

Figure 5. Simulated and measured time courses of carbon isotope ratio's. The simulation results are presented as overlays.
a) For $\Delta^{13}C$ on the data given by Freyer (1986) in his Figure 7.5.
b) For $\Delta^{14}C$ on the data given by Broecker and Peng (1982) in their Figure 10-23. Their "MODEL PREDICTION" and my "simulated" results practically coincide.

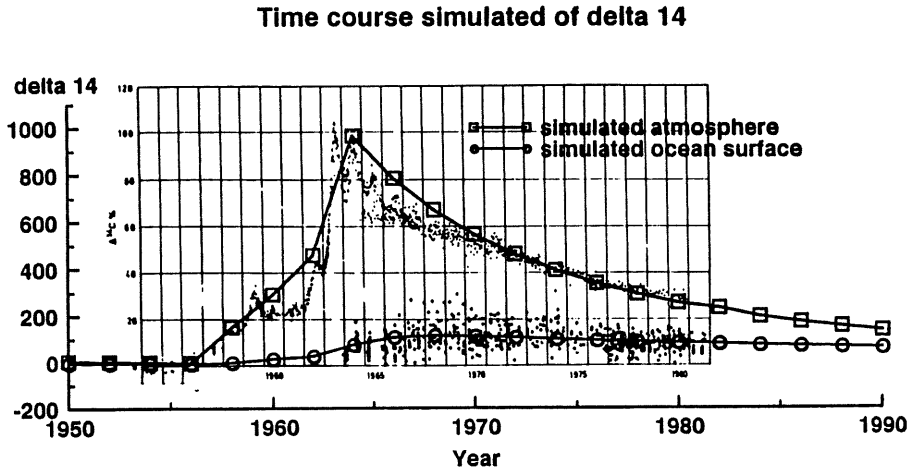

Figure 6. Simulated and observed time courses of $\Delta^{14}C$ in the atmosphere and in the sea surface water at low latitudes, for the period after the nuclear tests. The simulation results are presented as an overlay on the data given by Bolin (1986) in his Figure 3.6

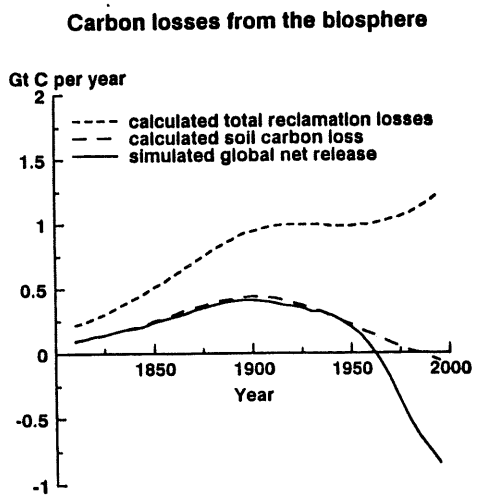

Figure 7. Calculated losses are based on statistics only. The simulated rate of net biospheric release of carbon includes the effect of growth stimulation by atmospheric CO_2.

4.3 Biospheric release

A detailed review of the subject was given by Houghton(1986). It highlights the uncertainties of current estimates, both of current carbon contents and of the timing of the releases.

In modification to the model given by Goudriaan and Ketner(1984), a faster rate of land reclamation around the turn of this century was assumed, and a smaller rate at present. This larger emphasis on early reclamation represents the colonial expansion in that period. The net 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 Mha=10^{12} mPw2), 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 Mha yr^{-1} to agricultural land and another 6 Mha yr^{-1} to grassland.

A straighforward method of estimating biospheric releases is to use the rate of annual land transfer from virgin land to agricultural soil, and to multiply it with the difference between soil carbon content typical for both ecosystems. The result of this method, calculated for the data used in our simulation model, is given in Fig 7 as "calculated soil carbon loss". The high rate of reclamation around 1900 is clearly visible. The cross-over around 1980 is caused by increasing reclamation from tropical forest land, which has a low soil carbon content.

Similarly the rate of removal of above ground biomass can be calculated by multiplying carbon areal density with the areal rate of permanent deforestation. Added to "calculated soil carbon loss" this rate gives the "calculated total reclamation losses" in Fig 7. The strong increase in recent times is caused by much faster deforestation in the tropics. In this procedure the estimates of Brown and Lugo (1984)

were used, which are lower (about half) than assumed before. Naturally the estimates for biomass releases are smaller as well.

However, for a global estimate of net carbon release from the terrestrial biosphere to the atmosphere these type of calculations are unsufficient. First, a considerable portion of deforested land becomes grassland, with a much higher soil carbon content than arable land. Second, the soil carbon is not released immediately, but it is gradually decomposed over a period of decades. Third, partial humification and charcoal formation reduce the losses by 10 to 20% . Fourth, elsewhere reclamation of dry land occurs by irrigation. In these places soil carbon is increased, not decreased. Fifth, and most important, a global stimulus of NPP may be assumed due to rising atmospheric CO_2(see 2.4). This slowly changing global background does not produce dramatic sights, but it still has large consequences. Without it, the terrestrial biosphere (including soil carbon) would now contain about 50 Gt C less. In other words, the photosynthetic stimulus has delayed the rising curve of atmospheric CO_2 by about ten years time.

It is central to this model result that the longevity of the various biospheric components is not decreased. As long as longevity is the same, carbon storage will be proportional to increased NPP. This assumption is not unrealistic, and it may even be to conservative. The observed lowered nitrogen contents connected with increased CO_2 may even lead to larger longevities.

Together, these factors explain the difference between "calculated total reclamation losses" and "simulated global net release" in Fig 7. The difference is the more striking as the same rates of land transfer were used.

Beside permanent transfer of land between ecosystems, biomass is also temporarily removed by litter burning and by deforestation for shifting cultivation. An assumed rate of annual burning of biomass (mainly litter) on grassland and agricultural land may seem large (800 Mha yr^{-1}) as it causes a release of about 5 Gt C per year. However, when this litter burning was set at zero, the simulated atmospheric CO_2 concentration in 1980 was very little affected (6 ppm lower). This small effect on net biospheric release is not amazing, considering that the litter would have decomposed anyway during the year to come. Whether or not shifting cultivation is considered did not have a large effect either: a simulated concentration that is only 1 ppm lower in 1980.

Between 1860 and 1980 the accumulated loss of biospheric carbon was simulated to be no more than 30 Gt C. This figure is much lower than others have found on basis of isotopic data. However, the simulation results presented here give no reason to assume larger releases(Fig 5).

Several reasons may exist for the deviation between my rather low estimate and earlier larger ones. First, differences of differences ($\Delta^{13}C$ versus $\Delta^{14}C$) are inaccurate. Second, in my estimate of the resistance of the atmosphere-ocean interface, based on the rate of decline of $\Delta^{14}C$, I allowed for the simultaneous dilution in the biosphere. My resistance estimate was therefore larger than without allowance for this dilution. A larger resistance leads to a faster decline of $\Delta^{13}C$, and requires a smaller release of biospheric carbon for compatibility

with observed rates of decline of $\Delta^{13}C$. Several other small model differences may also have contributed.

5 POTENTIAL GLACIAL-INTERGLACIAL PARAMETER CHANGES

5.1 Redistribution of CO_2 released into the atmosphere

Total terrestrial biotic carbon can be estimated at about 2000 Gt C for a prehuman situation. Since the cascade of biospheric components driven by terrestrial NPP was described by linear equations, the equilibrium level of their contents will follow the logarithmic response of Eqn 1 as well. The carbon content of the oceans is about 39000 Gt C, responding with a Revelle factor of about 10 to atmospheric CO_2, which reduces their effective content to 3900 Gt C. Starting with an atmosphere with 600 Gt C, a quick calculation shows that CO_2 emission into the atmosphere will eventually be partitioned as 11% to the atmosphere, 18% (for β=0.5) to the terrestrial biota and 71% to the ocean.

Therefore the ocean must be included in even a simple model for the effect of biospheric changes, but on the other hand the biosphere can be omitted if just first order effects of ocean parameter changes are studied. This consideration was followed below.

5.2 Terrestrial biosphere

5.2.1 Change in vegetated area

A dramatic increase of the vegetated area by 1000 Mha (10. 10^{12} m^2) from bare land to grassland and forest did not have a large impact on atmospheric CO_2. Such an increase would cause a carbon sequestering of some 230 Gt C (23 kg C m^{-2}). Growth of stemwood and accumulation of soil carbon being a rather slow process, atmospheric CO_2 dropped never more than 25 ppm below the starting level of 285 ppm. It reached an equilibrium after one thousand years, which was only 15 ppm lower than the initial level. This result means that about 200 Gt of the required 230 Gt C must have been released by the ocean in response to the decreased partial pressure of CO_2 in the atmosphere.

5.2.2 Change in longevity of soil carbon

Longevity of soil carbon (humus and charcoal) is of large importance. When its value was instantaneously doubled, atmospheric CO_2 dropped from 285 to around 220 ppm within a few decades, and remained at that level. About 1000 Gt C was sequestered in the soil, of which 840 Gt C was extracted from the sea, and 140 Gt C from the atmosphere.

The wetness of climate has a large effect on the amount of soil carbon. Doubling the precipitation/evaporation ratio also practically doubles soil carbon (Fig 6.2 in Houghton et al,1985). A globally mean wetter climate could therefore induce a large drop in atmospheric CO_2.

5.3 Ocean

5.3.1 Changes in marine photosynthesis

Two model characteristics dominate marine photosynthesis: the phosphate content of organic material (Redfield ratio) and the effect of phosphate concentration in the surface waters on precipitation of organic material. When this effect was tripled, precipitation instantaneously tripled as well. However, phosphate was then withdrawn at a much faster rate, and soon the phosphate in the water became more depleted. Because of this feedback mechanism the effect of the precipation-phosphate ratio was much less than proportional. A similar mechanism operated when the Redfield ratio was reduced: decreased withdrawal of phosphate caused some accumulation of phosphate in the surface layers, thereby stimulating photosynthesis and carbon precipitation to the deep sea. Only when the Redfield ratio and precipitation-phosphate ratio were simultaneously altered, could a lasting strong effect on atmospheric CO_2 be observed (Table 1).

Of course, a direct change in the total amount of phosphate in the ocean had also a large effect: about 1 ppm decline of atmospheric CO_2 per percent of total ocean phosphate.

Table 1 Simulated effect of parameters affecting marine photosynthesis on atmospheric CO_2(control 285 ppm)

		Precipitation/phosphate ratio (g C g P^{-1} m yr^{-1})	
		278	834
Redfield ratio	0.024	285 ppm	236 ppm
Redfield ratio	0.01	247 ppm	160 ppm
Total phosphate	92 Gt P	285 ppm	
Total phosphate	101 Gt P	277 ppm	

5.3.2 Changes in ocean ventilation

The model behaviour was remarkably insensitive to the size of the Circumpolar flow, connecting both ocean systems. If it was decreased from 2 to 0.1 10^{15} m^3 yr^{-1}, the difference between the ocean systems was largely maintained, and atmospheric CO_2 dropped from 285 to 278 ppm.

A much stronger effect resulted from changes in the massflow ventilation within each ocean system. If the Gordon flow in the Atlantic was reduced from 2. to 1. 10^{15} m^3 yr^{-1}, atmospheric CO_2 dropped from 285 to 276 ppm and a further reduction to 0.2 10^{15} m^3 yr^{-1} resulted in an atmospheric CO_2 of 260 ppm.

This effect can be explained by decreased upwelling, a lowering of the phosphate concentration in the surface layer of the Atlantic and increase of both phosphate and total carbon in the deep Atlantic. In the Pacific very little changed.

Similarly, if the ventilation in the Pacific was increased from 0.2 10^{15} m^3 yr^{-1} in the control run to 2. 10^{15} m^3 yr^{-1}, the atmospheric concentration was increased from 285 up to 344 ppm in 500 years time.

The relaxation time of these changes was about 200 years.

Changing the depth at which the downwelling water of the Atlantic enters the deep sea from 1500 to 3500 m reduced the residence time of the deep water (as signified by ^{14}C) but almost nothing otherwise. This lack of importance of the reentering depth is connected with the assumed complete decomposition of precipitated organic material in the upper 1500 m, below which almost no gradient remained.

6. CONCLUSION AND DISCUSSION

During the glacial periods atmospheric CO_2 was much lower than during interglacials, whereas the vegetated area was presumably much smaller. Although soil carbon may have been higher in the tropics than at present, it seems unlikely that it could have compensated for the loss of terrestrial carbon in the high latitudes. Climatic wetness stimulates accumulation of soil carbon, but during the glacials climate was probably dryer, not wetter. From a physiological point of view the dryness was accentuated by low atmospheric CO_2 which stimulates stomatal opening and transpiration. Dry and CO_2 poor conditions definitely favoured C_4-species, and have probably stimulated their evolution. In view of these considerations it is most likely that the terrestrial carbon pool was much smaller during the glacials than in between. In addition to going the wrong way, it is hard to see how the terrestrial biosphere could have caused the rapidity of the changes of atmospheric CO_2.

Marine photosynthesis itself can probably not be altered much in its response to the limiting nutrient phosphate. However, it is the precipitated fraction that matters for carbon accumulation in the deep sea. Also the mean depth at which it decomposes is important. These factors are probably biology-linked and controlled by species composition. If release of phosphate upon decomposition of precipitating organic material could occur faster than of carbon, the remaining material would be depleted in phosphate. Such a shift would cause a further drawing down of atmospheric CO_2.

The main actor on atmospheric CO_2 must have been the ocean circulation. Changes in ocean ventilation have a very large and quick effect. The question remains what has initiated them to change their pattern or magnitude. The temperature feedback on solubility of CO_2 in sea surface water was estimated to amplify an externally caused change in atmospheric CO_2 by a factor 1.5 .

According to the ocean model presented here the differences between the major ocean systems can be explained without deep sea currents from the Atlantic to the Pacific. Such currents further strengthen the nutrient-enriched character of the deep Pacific as compared to the waters of the Atlantic (Broecker and Peng,1982).

Model parameters are always uncertain. For instance, the assumed value of the biotic growth factor β of 0.5 may be a little too high, which is also suggested by Fig 4. The eutrophication effect, which was included in the value of β, should be treated separately.

The simulation results of carbon isotopes give no reason to believe that the net accumulated carbon release from the biosphere during the

last century has been larger than about 30 Gt C. Both the isotopic data and the CO_2 data themselves are consistent with this limited net release of biotic carbon. 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 imbalance may be due to increasing atmospheric CO_2, as assumed here, but other environmental factors may be involved as well.

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