The biosphere as a driving force in the global carbon cycle*

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Abstract

Atmospheric CO_2 and growth of green plants affect each other vice versa. Not only is atmospheric CO_2 suboptimal for plant growth, the amount of carbon tied up in biomass is of the same order of magnitude as the amount in atmospheric CO_2. The biosphere maintains strong exchange fluxes of carbon by assimilation and respiration, both on land and in the sea. Cessation of either terrestrial or marine biospheric carbon fixation would lead to doubling of atmospheric CO_2 within a few hundred years.

Past fluctuations of atmospheric CO_2 have probably been strongly amplified or even caused by the biosphere, in interaction with the climatic greenhouse effect of atmospheric CO_2. Depletion of atmospheric CO_2 by the end of the Tertiary was probably a major factor in both the evolution of C_4 plants and the onset of the glacial periods. Geologically, the man-made enrichment of the atmosphere with CO_2 has hardly started, and it is expected to lead to climatic and biospheric changes comparable in size to those leading to transitions between geological periods in the remote past.

Introduction

Atmospheric CO_2 has a central position in the global carbon cycle, because exchange fluxes between the world's major carbon reservoirs are mainly in the form of CO_2. Industrial development, and the corresponding fossil fuel consumption, enhance the natural carbon cycle by the injection of considerable masses of CO_2 into the atmosphere. Since the beginning of the industrial era about 200 years ago, the atmospheric CO_2 content has risen from about 280 cm^3/m^3 via 325 cm^3/m^3 in 1970 to 345 cm^3/m^3 now (Trabalka, 1985). The CO_2 released into the atmosphere is not in-

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ert, but is redistributed over the other carbon reservoirs. The most important absorber of atmospheric CO_2 is the ocean. It reduces the annual increase of atmospheric CO_2 to about 60 % of the amount annually released by combustion of fossil fuels (Bolin et al., 1979). The major fluxes in the natural carbon cycle are more than ten times as large as the man-made injection of CO_2 by burning of fossil fuel. The dynamic equilibrium between the natural fluxes is gradually shifted by this steady man-made addition of CO_2 to the atmosphere.

Potential climatic effects of atmospheric CO_2 are a reason for concern, also on a governmental level in the Netherlands (Gezondheidsraad, 1983; 1986). The expected global warming, known as the greenhouse effect, might lead to an uncomfortable rise of sea level, and to changes of the vegetation zones. In this paper the role of the biosphere as an active driving force in the global carbon cycle will be stressed. On the other hand biospheric activity also depends directly on the atmospheric CO_2 content (Gifford, 1982; Anon., 1985).

CO_2 as a climatic factor

The role of CO_2 in the energy balance of planet Earth can be loosely compared to the action that an envelope of glass would have: it transmits solar radiation to the surface of the earth, but it intercepts the black-body radiation, emitted by the soil surface. Only a part of this radiative energy flux is re-emitted into space, whereas the downward component of this re-emission causes a higher incoming radiative energy level at the earth surface than the solar flux alone. Thanks to this atmospheric action the global average surface temperature is about 15 °C instead of −18 °C (Dickinson, 1982). Because of the analogy this climatic action of CO_2 is called the 'greenhouse' effect. CO_2 is not the only 'greenhouse' gas, in fact water vapour is the most important one, and a number of other gases such as O_3, NO_2, NH_3, and CFKs (freon-like gases) appear to become increasingly important (Chamberlain et al., 1982). By addition of CO_2 to the atmosphere the natural 'greenhouse' effect is enhanced, and the temperature at the earth surface can be expected to increase.

The relation between CO_2 addition and expected temperature increase is a subject of extensive study, mainly by means of climatic modelling (Washington & Parkinson, 1986). Predictions are considerably complicated by the strong greenhouse effect of water vapour, which itself is a climatic factor that will be altered. Increasing air temperature will lead to more evaporation (and consequently precipitation) so that the total water vapour content of the atmosphere is also expected to increase, and the single CO_2 effect will be enhanced. This water vapour feedback factor is estimated to be as large as about 2 or 3. Increased cloud formation may cause some negative feedback.

The best modelling results presently available indicate an average global warming of about 1.5 to 4.5 °C (Schlesinger & Mitchell, 1985). As the temperature increase will be the largest (up to 10 °C) in the cold and dark polar winters, and the smallest in the tropics, the temperature gradients across the globe will be reduced.

The hydrological cycle (evaporation/precipitation) will be intensified by about 10 %. These rainfall effects, however, may be highly regional.

CO_2 as a biotic factor

The importance of air as a carrier of raw material for plant growth has been known since the end of the 18th Century, and was discovered by people like Van Ingen-Housz, Priestly and Senebier. Much earlier, Lucretius preluded on the idea of elemental geophysical cycles when he wrote that the sky, the sea, the earth, the sun, the rivers, the fruits, the forests and living beings all consist of the same elements, albeit interconnected in different ways (Lucretius, 60 BC). We know now that biomass mainly exists of carbon and water, enriched with a small fraction of nutrient elements. Almost all of the carbon in the plant is taken up as CO_2 from the air. The weight fraction of carbon in dry weight of plant material is rather stable between 40 and 50 %, so that there must be 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 level, water supply, nutrient supply and temperature for the processes of growth, photosynthesis and CO_2 assimilation, but also of the concentration of ambient CO_2 itself. In general the normal ambient CO_2 concentration of about 300-330 cm^3/m^3 is suboptimal, and higher growth rates of green plants can be realized at a concentration of about 1000 cm^3/m^3 (Lemon, 1984; Strain & Cure, 1985). At that level the favourable CO_2 effect on growth is practically saturated, and the growth rate may be more than 1.5 times as high as under normal conditions. Small increments of atmospheric CO_2 lead to increments in biomass production that are about 1/2 to 3/4 as large, both expressed as relative changes. Indeed, about 1/10 to 1/6 of the annual increment of world food production is freely obtained as an unrequested side-effect of increasing atmospheric CO_2. The acceleration of growth is not as strong under unsufficient nutrient supply (Goudriaan & de Ruiter, 1983) or may be even absent. Water shortage, on the other hand, does not diminish the relative stimulation by higher CO_2; on the contrary, it may even enhance it (Gifford, 1979). Also under low radiation levels a considerable positive CO_2 effect remains. The generally favourable CO_2 effect is well known in horticulture and has found wide-spread practical application (Enoch & Kimball, 1986).

Global reservoirs and fluxes of carbon (Fig. 1)
Huge amounts of carbon lie tied up in carbonates in the earth crust, but these are only important on very long geological time scales. Much more interesting on the short time scale of decades is the reduced carbon, present as coal, oil and natural gas. Because of its tremendous energy content, it is burnt and relocated from the earth crust into the atmosphere at a rate of about 5×10^{15} g C a^{-1}. When this flux rate is compared to the total amount of carbon in the atmosphere, which is about 700 Gt (1 Gt = 10^{15} g), it is clear that this rate is bound to have a large effect on a time scale of a hundred years or so. The reservoir of fossil carbon on the other hand is much larger, several thousands of gigatonnes C, and perhaps even much larger,
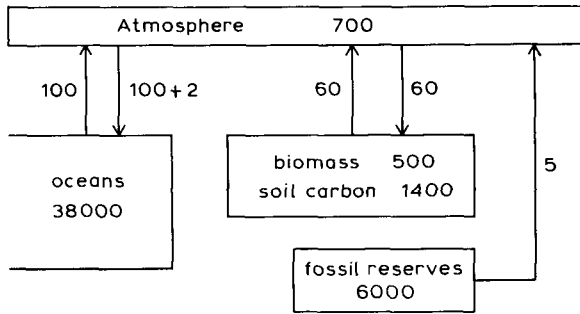
Fig. 1. Global reservoirs of carbon, active in exchange, expressed in Gt C, and their exchange fluxes in Gt a^{-1}. The atmosphere receives 5 Gt C annually from fossil fuel combustion. Because the present atmospheric carbon concentration is out of equilibrium with the ocean, the atmosphere looses 2 Gt a^{-1} more to the ocean than is returned.

dependent on the efficiency of exploration. Anyway, the reserves of fossil fuel are so large that long before they will be exhausted, a large effect of their burning can be expected on the atmospheric CO_2 content.

The net rate of increase of atmospheric CO_2 is at present only about 60 % of the rate of fossil fuel combustion. The other 40 % (about 2 Gt C a^{-1}) is absorbed by the oceans. The amount of carbon present in the ocean is huge, about 38 000 Gt, but this figure is deceptive as a guideline for estimating the redistribution of CO_2 between atmosphere and ocean. First, complete mixing through the deep sea takes time, several hundreds of years. And second, most of the ocean carbon is locked away beyond chemical equilibrium in the form of bicarbonate. The net effect of the carbon chemistry of sea water is that its relative change in carbon content is only one tenth of the relative change of partial pressure of CO_2. This large chemical resistance increases even further with increasing CO_2 uptake. Nevertheless, the ocean is large enough to potentially absorb as much as 85 % of CO_2 injected into the atmosphere. The difference with the present uptake of 40 % is caused by the slow rate of mixing. Eventually the deep sea will take its share. Much of this knowledge on transport in oceans, but also in and between the other pools of carbon, has been obtained by isotope research (Mook, 1986).

The oceanic uptake that we see now is still mainly stored in the surface waters of the ocean. These upper hundred or so meters are internally well mixed, but isolated from the deep sea by thermal stratification. Only in the higher latitudes is the stratification broken, so that exchange occurs. There cooled water sinks down, carrying CO_2 with it. The counter-flow of upwelling deep water is mainly found in the tropics. This slow circular mass flow of water causes a renewal of the deep sea water once every few hundreds of years on the average. When the upwelling cold water is warmed up in the tropics, CO_2 is released, as much as 4 Gt C a^{-1}. Indeed, accurate measurements of atmospheric CO_2 concentration show a persistent equatorial bulge (Gammon et al., 1985).

Almost all biospheric carbon is stored on land, as wood, in leaves, in litter, and also in dead organic matter in humus (Olson et al., 1985). Live biomass is estimated to be close to 600 Gt C, and humus to about 700 Gt C. There is a fairly gradual transition from humus to inert, and practically elemental, carbon in the soil, which is another 700 Gt C. These three subreservoirs together are generally considered as

biotic, and store 2000 Gt C. The residence time of carbon in these reservoirs varies from less than a year for leaves, through some decades in wood and humus, to several centuries or more in the inert carbon in the soil (Kortleven, 1963).

Changes of atmospheric CO_2 over various time scales

On all time scales CO_2 is changing. Usually one is not aware of the sizeable diurnal changes of CO_2 in the lower few meters of the atmospheric boundary layer near the ground. Due to noctural respiration of soil and plants, atmospheric CO_2 reaches a maximum in the morning, and decreases again in the daytime when the photosynthetic uptake is in operation. Especially in still, inversion-like weather the early morning level of CO_2 may reach more than twice the mean value. Soon after sunrise the inversion is usually broken, photosynthesis starts and CO_2 very quickly returns to a value between 320 and 380 cm^3/m^3. During the period of major photosynthetic activity the vegetation is surrounded by air not differing more than 20 cm^3/m^3 from the atmospheric mean.

These strong diurnal fluctuations prevent precise geophysical measurements of average atmospheric CO_2, and so these measurements are done on mountain tops far from local sources. In this way the diurnal cycle is avoided, and a clear annual cycle can be made visible. The famous measurement series from Mauna Loa, Hawaii, shows the annual cycle, superimposed on a decadal time trend caused by fossil fuel combustion (Keeling et al., 1982).

Like the diurnal cycle, also the annual cycle is of biospheric origin. Of course the annual cycle is spatially much more extended than the diurnal one and comprises the full atmospheric column, but it varies considerably with place on earth. Most notably the phases on the Northern and Southern hemisphere are opposite, which shows that the time scale of atmospheric mixing of the two hemispheres is at least one year. The seasonality is most outspoken above the continents in the temperate zones, and almost absent in the equatorial zone (Fig. 2). There are indications that the seasonal amplitude of the CO_2 signal has been increasing over the last decade (Revelle & Kohlmaier, 1986). Several mechanisms may be responsible for this increase, such as an increasing biospheric activity per se, but also a growing time interval between periods of net growth and of net decay. As yet there is no conclusive evidence whether the increasing amplitude has anything to do with the increasing background level of CO_2 itself.

In our own measurements in Wageningen the decadal increase of atmospheric CO_2 is also clearly visible in records since 1970 of measurements of photosynthesis outdoors, done at CABO (Louwerse, pers. comm.).

The Mauna Loa series goes back to the 1950s. Earlier CO_2 data are available from air bubbles, enclosed in polar ice (Neftel et al., 1985). These records show that the CO_2 concentration has been gradually rising from about 280 cm^3/m^3 in 1800. Probably this level is representative for the entire pre-industrial historic period.

Earlier back, during the glacial periods all time, minimum records of about 200 cm^3/m^3 were reached, as shown by the same ice core technique applied in the Antarctic ice cap (Neftel et al., 1982). During the interglacials the CO_2 concentration
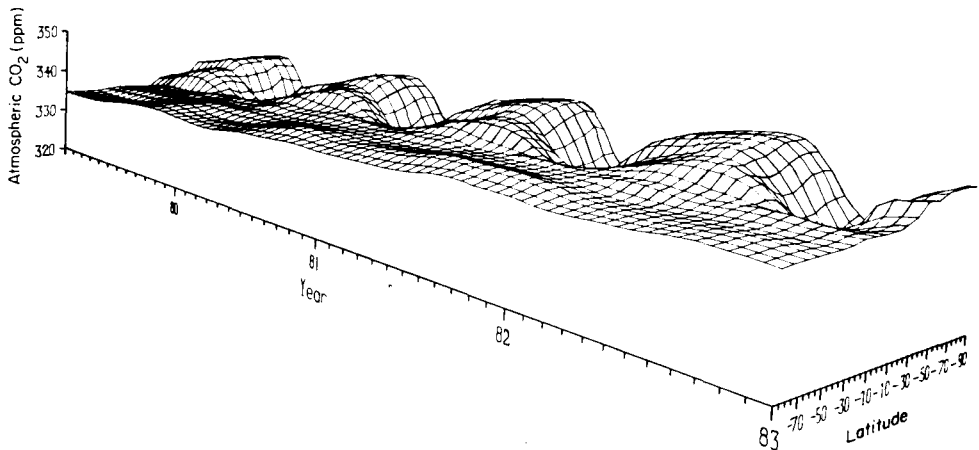
Fig. 2. Annual cycling of atmospheric CO_2 is strongly dependent on latitude. Data from 15 sea-level sites (Harris & Bodhaine, 1983 cited by Gammon et al., 1985). The strong seasonality on the northern hemisphere is due to the large amount of terrestrial vegetation there.

returned to close to 300 cm^3/m^3 with a transition period of only a few hundred years. A close synchrony existed between low temperatures and low CO_2 levels, but the temperature drop was much stronger than expected from the CO_2 drop alone. Therefore other factors, such as increased reflection of solar radiation by the vast ice cover, must have amplified the coupling. Also changes in biospheric activity in the oceans are likely to have been decisive for the flip-flop-like oscillations.

Ever since life began, atmospheric CO_2 has been steadily decreasing until the glacial periods. Fossil coal reserves are witnesses of lush plant growth in the remote past, stimulated by high atmospheric CO_2, that probably lay in the order of percents. In the Cambrium period solar luminosity was about 30 % lower than nowadays, and so the continuous draw-down of atmospheric CO_2 since then by the activity of the biosphere can be viewed as a compensation for the increasingly larger radiation load of the sun. This fortuitous maintenance of life-friendly conditions on our planet by life itself during millions of years has prompted the formulation of a hypothesis of goddess Gaia, who takes well care of herself (Lovelock, 1979). Whether the expected man-made changes of atmospheric CO_2 (Fig. 3) are part of her strategy has not been revealed yet, but it is certain that they are of geological importance.

By the end of the Tertiary, CO_2 was so far depleted that life must have become quite harsh for terrestrial plants. Large stomatal opening was necessary for CO_2 uptake and caused a relatively high transpirational water loss. Frequent drought was more likely, and it is precisely under such conditions that the water-efficient C_4 mechanism gives a large advantage over the regular C_3 mechanism. The low CO_2 level may have been a dominant factor in the evolution of the C_4 species. Indeed, the oldest fossil records of C_4 plants date from the Pliocene, which just preceded the glacial periods (Nambudiri et al., 1978).
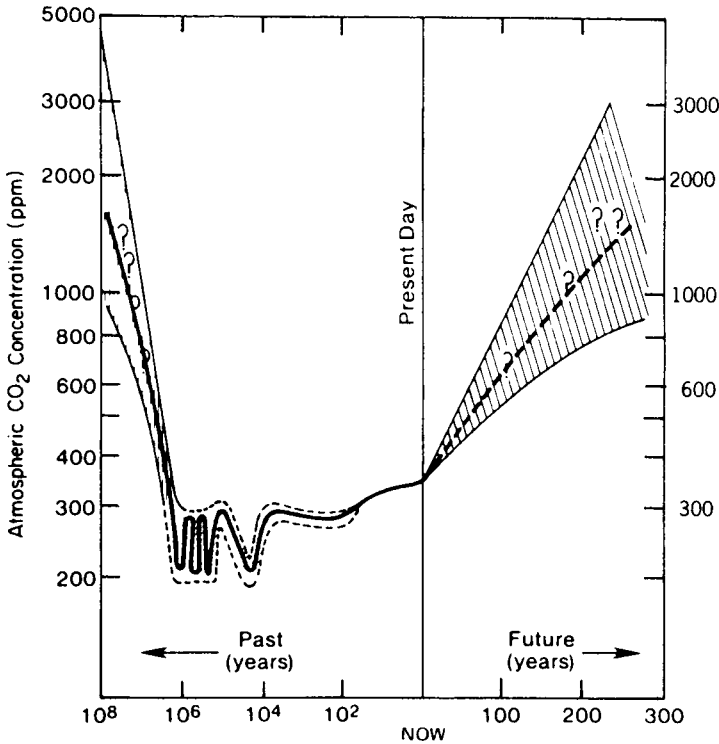
Fig. 3. Time course of atmospheric CO_2 in history and expected in future. Hatching indicates level of uncertainty. Note the logarithmic time scale for the historic data.

The biospheric pumps

The reservoir of biospheric carbon on land is maintained by the equilibrium between photosynthesis and decay. With a global net annual C fixation estimated as 60 Gt and a biospheric carbon pool of 2000 Gt in total, the average life time of carbon in a simple one-box model would be 33 years. In a slightly more complicated model, a parallel-serial circuitry of components is visualized (Fig. 4) with various life times. For humus and inert carbon, this model structure can be derived from the work of Kortleven(1963), who showed that the response of humus level to litter input is of a first order character. For live biomass, this structure is founded on the work of van de Sande Bakhuyzen (1937). A compartmentalized model can much better represent the dynamics of changes than a one-box model. Such changes may be induced by human activities such as deforestation, and slash and burning agriculture. The recognition of different pools with widely different residence times helps to understand 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 mate-
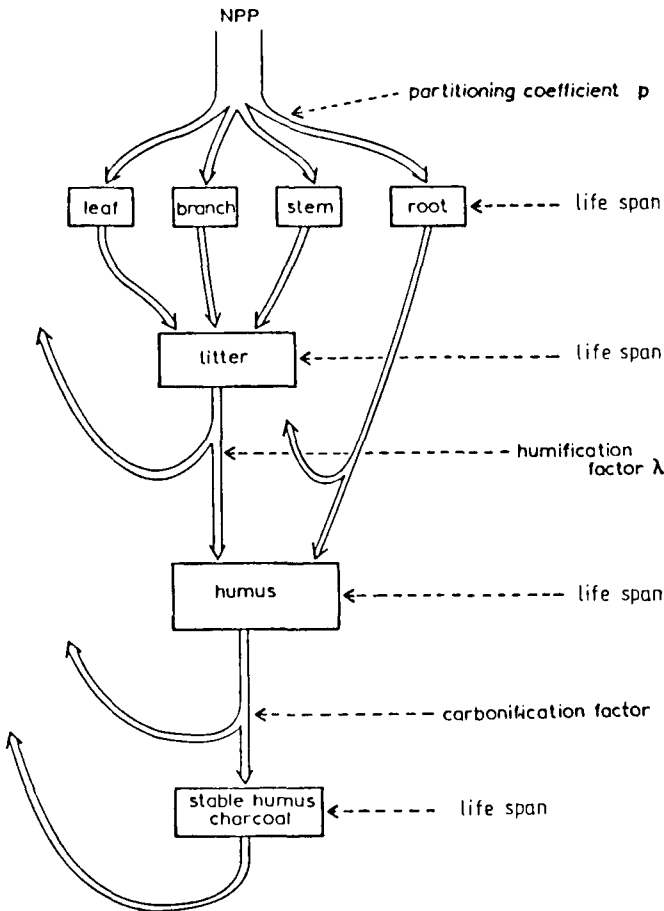
Fig. 4. General diagram of flow of carbon through an ecosystem.

rial burnt into the highly inert charcoal pool (Seiler & Crutzen, 1980). Therefore in the long run repeated burning increases the carbon content of soils, at the expense of the atmospheric and oceanic reservoirs. Studies of the effect of deforestation tend to overestimate the immediately visible destruction, and to underestimate the less spectacular and slow process of regrowth. If the type of land use has not been changed, the area-based net primary productivity (NPP) is not affected and gives rise to regrowth of first pioneer vegetation, gradually changing to mature vegetation types. Except with low ground coverage by vegetation, NPP is hardly coupled to biomass.

On a global scale, NPP is stimulated by atmospheric CO_2. Ranging from water limited to phosphorus limited, the relative stimulus varies between 0.7 and zero. Agriculture enhances soil weathering by digging and ploughing. Together with the

tremendous growth of artificial fertilizer application, this results in a global increase of nutrient availability (eutrophication), which serves as another background stimulus of global NPP.

These factors together (charcoal formation, regrowth, and fertilization by CO_2 and nutrients), are responsible for a compensation of the release rate of CO_2 as caused by deforestation (Goudriaan & Ketner, 1984). Indeed, at present the terrestrial biosphere is a net absorber of carbon at a rate of about 0-0.5 Gt a^{-1}.

The terrestrial biosphere can be considered as a surface phenomenon with a negligible thickness. The thin biospheric crust of carbon-rich material on the earth's surface is spatially highly diversified. Different degrees of aggregation have been used to describe the complexity of the terrestrial biosphere. One of the most sophisticated systems is the databank compiled by Matthews (1983). Remote sensing data have contributed considerably to the mapping of the distribution of green leaf area on earth (Tucker et al., 1986).

Almost all biospheric carbon is concentrated on land, because of the relatively high longevity of wood and humus. In contrast, the lifetime of plankton is not measured in years but in days, and as a reservoir of carbon the plankton is negligible. Still the marine primary productivity is of utmost importance for the regulation of atmospheric CO_2 by its effect on the carbon content of seawater.

Some 20 % of the biotic carbon fixation in the upper ocean layer 'rains' down unobstructed by the thermal stratification. This precipitation rate is estimated at 8 Gt C a^{-1}, and on its way down the organic material is gradually decomposed releasing CO_2 into the deep sea. Only a tiny fraction ultimately reaches the ocean floor. This downward pumping of organic material maintains the carbon content of the deep sea water at a much higher level, than it would have been otherwise. Its potential effect on atmospheric CO_2 is depicted in Fig. 5, which shows a simulation result of a fictive change in the rate of precipitation of organic matter into the deep sea. The model used was the one described by Goudriaan & Ketner (1984). A cessation
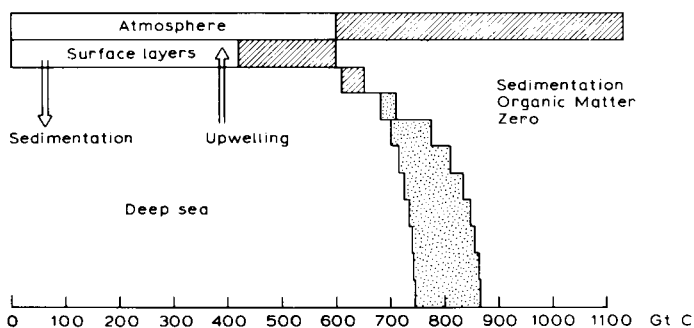

Fig. 5. Distribution of carbon over atmosphere and oceanic depth in two different model simulations. In the first simulation the distribution was in equilibrium with the present downward precipitation of organic matter from the ocean surface towards the deep sea. In the second simulation the precipitation was brought to zero. As a result after two hundred years the deep sea had lost carbon (stippled), whereas the upper layers and the atmosphere had gained carbon (hatched).

of plankton growth would cause a 50 % increase of atmospheric CO_2 in about 200 years time, and a doubling of plankton growth would let it drop to far below 200 cm^3/m^3. Whatever mechanism stimulated the plankton growth, it is likely that such a change has been responsible for the fast changes of atmospheric CO_2 in the Pleistocene.

The biospheric pumps of carbon are intimately connected with nutrient cycles of other elements. Plankton growth is strongly affected by supply rates of phosphorus and nitrogen, welling up from the deep sea (Raymont, 1980). Therefore the atmospheric CO_2 changes were probably caused by changes in circulation patterns (Sarmiento & Toggweiler, 1984; Siegenthaler & Wenk, 1984) in the oceans, which in turn may have been changed by CO_2 itself (Manabe & Bryan, 1985). Once triggered, a single mechanism could not have completed the job, and powerful feedback loops must have amplified the responses.

Man-made changes of the biosphere are inevitable, and whether or not these changes will be amplified, time will surely tell. Human society can better be prepared for the outcome as regarded likely by scientists, but not be taken by surprise if things turn out differently. The global CO_2 experiment that we are all in together is not over yet.

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