

# Estimating the carbon transfer between the ocean, atmosphere and the terrestrial biosphere since the last glacial maximum

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## ABSTRACT

Carbon dioxide records from polar ice cores and marine ocean sediments indicate that the last glacial maximum (LGM) atmosphere CO<sub>2</sub> content was 80–90 ppm lower than the mid-Holocene. This represents a transfer of over 160 GtC into the atmosphere since the LGM. Palaeovegetation studies suggest that up to 1350 GtC was transferred from the oceans to the terrestrial biosphere at the end of the last glacial. Evidence from carbon isotopes in deep sea sediments, however, indicates a smaller shift of between 400 and 700 GtC. To understand the functioning of the carbon cycle this apparent discrepancy needs to be resolved. Thus, older data have been reassessed, new data provided and the potential errors of both methods estimated. New estimates of the expansion of terrestrial biomass between the LGM and mid-Holocene are 700 GtC ± > 300 GtC, using the ocean carbon isotope-based method, compared with of 1100 GtC ± > 500 GtC using the palaeovegetation estimate. If these estimates of the carbon shift to the terrestrial biosphere are equilibrated with the dissolved carbon in the oceans, and the CaCO<sub>3</sub> compensation of the ocean is taken into account, then the glacial atmospheric CO<sub>2</sub> would have been between 50 (±30) ppm and 95 (±50) ppm higher. The glacial atmosphere therefore should have had a CO<sub>2</sub> partial pressure of between 330 and 375 µatm. Hence, a rise of between 130 and 175 µatm in atmospheric CO<sub>2</sub>, rather than 80 µatm, at the end of the last glacial must be accounted for.

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## INTRODUCTION

Research on ice cores has shown that the carbon dioxide level in the Earth's atmosphere has closely paralleled the changes in global climate over at least the last 160,000 yr (Barnola *et al.*, 1987). During the Last Glacial Maximum (LGM) 20,000–18,000 yr BP, the atmospheric CO<sub>2</sub> level was about 80–90 ppm

lower than during the present (Holocene) interglacial (Barnola *et al.*, 1987). This amount of CO<sub>2</sub> represents a difference of about 160 Gt (160 billion tonnes) in the total amount of carbon in the atmosphere, and it must have been released from either the oceanic, terrestrial or (perhaps) geologic reservoirs. Recently, interest has focused mainly on explaining possible internal changes within the oceans that might have controlled such CO<sub>2</sub> fluctuations (Siegenthaler, 1986), and the feedback effects these may have had on the climatic.

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The terrestrial system, in contrast, has been largely neglected, despite its potential importance as a dynamic carbon store and its effect on atmospheric CO<sub>2</sub>. At the end of the last glacial period the terrestrial biosphere expanded; this decreased the CO<sub>2</sub> content of the atmosphere in opposition to the documented rise in atmospheric pCO<sub>2</sub>. The real rise in atmospheric pCO<sub>2</sub> must have larger than the 80–90 ppm observed in the ice core records. Broecker and Peng (1993) from carbon isotope composition of benthic and planktonic foraminifera suggested that the ocean–atmosphere system contained  $1.4 \pm 0.2\%$  more carbon during interglacials. When this is equilibrated with the dissolved carbon in the oceans, Broecker and Peng (1993) suggest that it would cause the glacial atmosphere to have had 47 ppm more CO<sub>2</sub>. Even when the CaCO<sub>3</sub> compensation is taken into account, Broecker and Peng (1993) estimate there was a rise of 25 ppm. So the real increase in the atmosphere CO<sub>2</sub> since the last glacial according to Broecker and Peng (1993) was 105 µatm, rather than the observed 80 µatm.

The purpose of this paper is to review the different approaches for estimating the shifts in terrestrial carbon storage since the LGM. As only when we have reliable estimates of the expansion of the terrestrial biosphere can we assess its importance in modulating atmospheric CO<sub>2</sub> and thus fully understand the causes of the increase of atmospheric CO<sub>2</sub> documented in the ice core records.

## RECONSTRUCTION OF PAST ENVIRONMENTS USING PALAEO-ECOLOGICAL DATA

In the present-day world there are clear relationships between particular vegetation types, and the amount of carbon

stored in the vegetation and soil. To estimate the glacial-to-interglacial carbon shift an obvious approach is to estimate present-day vegetation carbon storage and to compare this to changes in the extent of the different vegetation types in the past. This approach, although relatively simple, involves a number of assumptions which might or might not be well founded.

At the most basic level, there is still a considerable degree of uncertainty over the distribution of vegetation during the past, especially during the considerably different global climate of the last glacial period (COHMAP, 1988). Plant fossil data, the most direct and trustworthy source of information on past vegetation, are still very patchy for around the time of the LGM. For large areas of the world, for instance Indo-China and the interior of the Amazon and Congo Basins, there are still virtually no pollen or macrofossil data from this period. The general quality of the plant fossil record improves greatly for the Holocene, but there are still large gaps in our knowledge to leave considerable room for uncertainty regarding the vegetation cover of many regions during the early to-mid Holocene.

Fortunately, it is possible to use other sources of data as proxy indicators of past vegetation conditions. Particular species of animals are associated strongly with particular vegetation conditions in the present world, so their fossils can be used as a rough indicator of the ecology of an area in the past, whilst bearing in mind the possibility that such relationships do sometimes shift unexpectedly over time (Adams and Woodward, 1992). Sedimentological processes of the present day are often dependent on vegetation cover, either in the area of sediment deposition or the area where it is being eroded from. A particular type of sediment grade or depositional structure can often give clues as to the type of vegetation that once existed there, although once again the interpretation can be misled by the complexities of processes in the past giving the same result by different means. Finally (and most tenuous and controversial) there are biogeographical clues based on the present-day distributions of animals and plants, which may partly be a

legacy of the changed vegetation and climate conditions which existed during the last glacial period.

Each of these sources, including the more direct plant fossil evidence, has to be treated with caution as they can easily give misleading results. Sometimes, plant fossils can be transported for long distances or concentrated selectively to give a misleading impression of the general vegetation types which actually existed. Good dating of the evidence is often lacking, especially for sedimentary deposits where there is little surviving organic matter that can be used for  $^{14}\text{C}$  dating. Fortunately, the range of direct and correlative dating techniques is expanding and the accuracy of existing methods is also improving. Nevertheless, many sites which have been taken as revealing conditions under the LGM remain poorly dated or without any strong age control. Obviously, such sources of evidence have been treated with more caution than those which have been dated.

Mapping of palaeovegetation for the LGM is still at a preliminary stage, but there are now sufficient data to map many of the salient features of global vegetation, with a fair degree of confidence. Adams *et al.* (1990) were the first to use this palaeovegetation approach to reconstruct the global vegetation pattern during the LGM and they compared it to the (pre-industrial) present. From the average per unit area carbon storage estimated for each vegetation type, Adams *et al.* (1990) estimated the global carbon storage for each time-slice. Here their original dataset is extended, and global vegetation patterns have been reconstructed for the LGM (20 kyr to 18 kyr BP) and the mid to late Holocene (5 kyr to Present, see Fig. 1). Carbon transfer to the terrestrial biosphere from another reservoir between the LGM and the mid-Holocene is estimated at about 1100 GtC (Table 1).

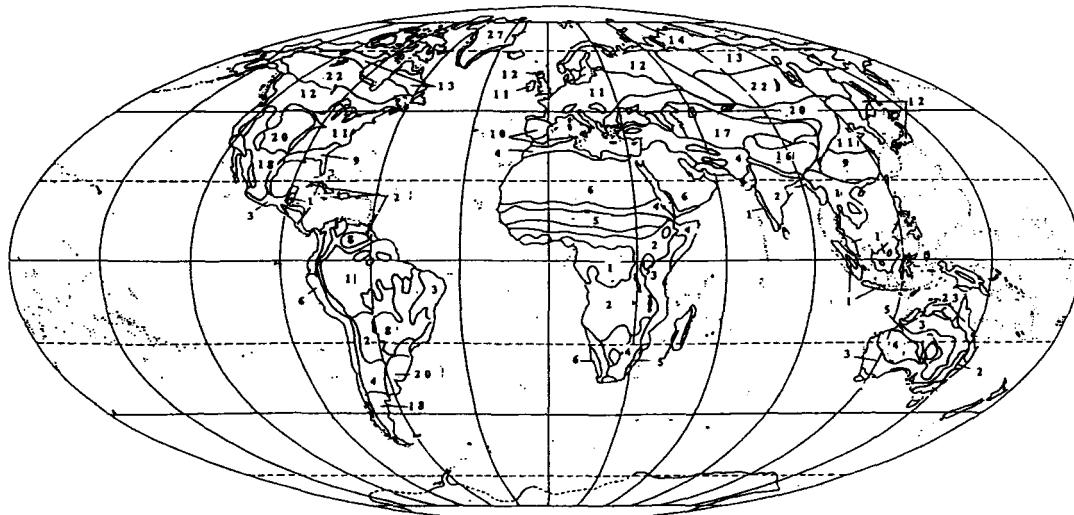
#### UNCERTAINTIES OF THE PALAEOVEGETATION CARBON STORAGE ESTIMATES

The first source of uncertainties is the spatial inaccuracies of the vegetation maps, as there may be thousands of miles between data points. Because there is

never a complete coverage of data for the past, it is necessary to interpolate between the widely spaced data points. This is not necessarily as much of a problem as one might think, because present-day world vegetation types often tend to be fairly uniform, grading into one another over hundreds of kilometres. When the landscape is broken up into a complex mosaic by variable topographical or soil factors, the task of reconstructing the general pattern from a few localized data is far more difficult. However, from the knowledge of present-day vegetation cover, it can be seen that very often the same or a similar mosaic occurs over broad areas (Olson *et al.*, 1983), and that analogous but somewhat shifted mosaics would most likely have occurred in the past.

To estimate the extent of this spatial uncertainty, extreme interpretations of the palaeovegetation data were made, and the carbon transfer was recalculated. The maximum and minimum estimates were 1250 GtC and 950 GtC. A second source of error is the effect of spatial heterogeneity of biomass and soil carbon on the average area carbon storage values per unit; a conservative estimate of this uncertainty is  $\pm 30\%$  (Olson *et al.*, 1983), causing a maximum error of  $\pm 30\%$  in the carbon transfer estimate ( $\pm 400$  GtC). A considerable amount of work has since been done, on both soils and vegetation, so this error is probably somewhat reduced. A third source of error lies in the fact that vegetation with a similar composition to the present might have differed significantly from their modern analogue in their carbon storage during different climatic conditions. Some LGM vegetation types have no modern analogue (Adams and Woodward, 1992) so that their carbon storage has to be estimated by approximation to the nearest analogue. An important example is the steppe-tundra that covered a significant area during the LGM; there is no present-day vegetation type to compare this with in terms of carbon storage. The best reconstruction of the steppe-tundra is based on the abundant plant species, indicating an open ground habitat, and general sedimentological evidence. These suggest that the steppe-tundra was arid and desert-like, rather than moist like the present-day

(a)



(b)



**Fig. 1.** General summary of this study's global vegetation reconstruction of the Late Holocene (a) and the Last Glacial Maximum (18,000 yr BP) (b). Numbers represent vegetation type and are listed in Table 1.

tundra or steppe. The reliance on the 'modern analogue' causes additional problems, because present vegetation types perceived to be 'natural' may have been considerably altered by human activity (Brown *et al.*, 1991). For instance, it now seems that most tropical rainforests and temperate forests have been altered by humans for centuries, resulting in a subtle but significant depletion in carbon storage. More uncertainties may

have been induced by the effects of time lags between climate change and vegetation and soil development (Schlesinger, 1984), and by the difficulties of estimating the timing and extent of peat development (Neustadt, 1982; Zoltai, 1991). Our best estimate of the carbon transfer and its errors using the palaeovegetation approach is  $1120 \text{ GtC} \pm 500 \text{ GtC}$ . To improve this estimate additional palaeodata are required, especially from Indo-

china, and the interior of the Amazon and Congo Basins.

#### ESTIMATING THE EXPANSION OF THE TERRESTRIAL BIOSPHERE FROM THE CARBON ISOTOPE SHIFT FOUND IN DEEP-SEA CORE RECORDS

The principle of deriving the size of changes in the terrestrial biomass

**Table 1.** The mean estimate of the global carbon storage of different vegetation types vegetation for the late Holocene (0–5 kyr BP) and the Last Glacial Maximum (18–20 kyr BP).

Vegetation type	Carbon storage late Holocene	(GtC) LGM	Shift
1 Tropical equatorial forest	237	144	93
2 Tropical woodland	73	118	55
3 Thorn scrub	96	98	-2
4 Tropical semi-desert	21	23	-2
5 Tropical grassland	16	20	-4
6 Tropical extreme desert	4	8	-4
7 Montane tropical forest	12	5	7
8 Savanna	20	69	-49
9 Temperate evergreen forest	141	22	119
10 Mediterranean forest	18	5.3	12.7
11 Temperate deciduous forest	314	51	263
12 Closed boreal conifer forest	214	41	173
13 Open temperate woodlands	142	75	67
14 Tundra	118	0*	118
15 Southern steppe-tundra	0*	103	103
16 Polar desert/northern steppe	0.7	3.4	2.7
17 Temperate desert	25	56	-31
18 Temperate semi desert	56	110	-54
19 Coniferous rainforest	19	0*	19
20 Temperate/montane grasslands	117	18	99
21 Wooded steppe & tundra	7	36	-29
22 Main taiga	205	0*	205
23 Monsoon forest	59	18	41
24 Open wetland/peatland	130	0*	130
25 Swamp forest	0*	0*	0*
26 Bog forest	0*	0*	0*
27 Ice	0	0	0
28 Alpine	0*	0*	0*
29 Lake	0	0	0
Total	2145	1023.3	1121.7

\* Represent a value less than 0.5 GtC.

using deep ocean  $\delta^{13}\text{C}$  in carbonate is simple (Shackleton, 1977): one calculates how much material with a  $\delta^{13}\text{C}$  composition of average terrestrial biosphere is required to change the value of the total dissolved inorganic carbon ( $\Sigma\text{CO}_2$ ) in the oceans by the observed amount. A value of  $-25\%$  (wood; Craig, 1953, 1954) is commonly used as an average of terrestrial biomass. The total mass of the ocean total dissolved carbon ( $\Sigma\text{CO}_2$ ) has been estimated between 3740 GtC (Broecker and Peng, 1982; Siegenthaler, 1986) and 4200 GtC (Berger and Vincent, 1986), with an average  $\delta^{13}\text{C} = 0$ . Though simple, this approach has produced a large range of estimates (see Table 2 and Fig. 2), mainly due to uncertainties of this approach.

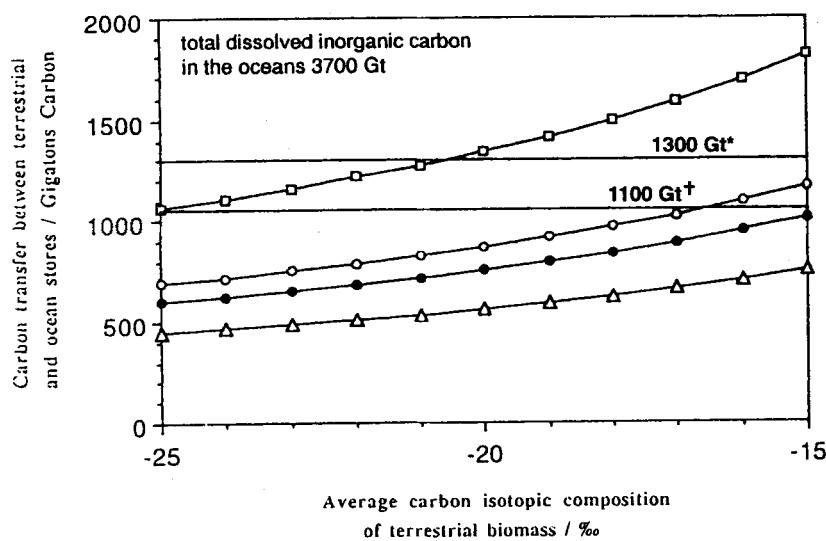
#### UNCERTAINTIES IN ESTIMATING THE CARBON SHIFT USING DEEP-SEA CARBON ISOTOPES

##### Benthic foraminifera $\delta^{13}\text{C}$ and the carbon budget

Estimates of the change in average  $\delta^{13}\text{C}$  value of  $\Sigma\text{CO}_2$  globally must be derived from observations on cores, which give us local values for surface and deep waters (from planktonic and benthic foraminifera), e.g. Duplessy *et al.* (1988) and Curry *et al.* (1988). The  $\delta^{13}\text{C}$  values of planktonic foraminifera are determined by the removal of  $^{12}\text{C}$  from the surface water by photosynthesis, leaving  $^{13}\text{C}$  preferentially in dissolved inorganic carbon, which is used in shell

construction by planktonic foraminifera (which are thus isotopically heavy), e.g. Wefer and Berger (1991). Therefore, and because of the much larger volume of the deep ocean, benthic foraminiferal isotopic records from the largest ocean, the Pacific, are used to estimate the average global value of  $\delta^{13}\text{C}$  in  $\Sigma\text{CO}_2$ . Problems induced by non-equilibrium secretion of the test are circumvented by analysing specimens from a single species. However, the  $\delta^{13}\text{C}$  values of benthic foraminifera not only depend upon the world's average  $\delta^{13}\text{C}$  in  $\Sigma\text{CO}_2$ , but also vary with local productivity and global patterns of deep water circulation (Kroopnick *et al.*, 1977). Export productivity determines the volume of  $^{13}\text{C}$ -depleted organic matter deposited locally into bottom waters where it oxidizes to  $^{13}\text{C}$ -depleted  $\Sigma\text{CO}_2$ . Global deep water circulation determines where the deep waters have been out of contact with the atmosphere for the longest time and how long this is, i.e. where the deep waters are the oldest, and have collected the ' $^{13}\text{C}$ -depleted rain' of organic material longest: the oldest waters are the most depleted in  $^{13}\text{C}$ . At the present time values of  $\delta^{13}\text{C}$  in  $\Sigma\text{CO}_2$  in the deep northern Pacific are about 1‰ lighter than those in the northern Atlantic, because deep water circulation moves from the northern Atlantic (youngest) to northern Pacific (oldest). The turn-over rate of deep waters (presently about 1000–1500 years; Worthington, 1972) is important because it determines the maximum age (i.e. maximum  $^{13}\text{C}$  depletion) of deep waters in the oceans.

Global productivity, productivity patterns, deep water turnover rate and deep water circulation patterns all affect the oceanic carbon cycle and were probably all different during the last glacial period (e.g. Labeyrie *et al.*, 1992; Imbrie *et al.*, 1993). Stable isotope and trace element data indicate that the relative volumes of intermediate and deep water formed in the North Atlantic differed, with more intense formation of intermediate water masses, and less active ventilation of the deep North Atlantic during glacial periods (e.g. Boyle, 1992). The circulation between Atlantic and the Pacific may have been less asymmetric than today, with intermediate water formation occurring in the North Pacific.



**Fig. 2.** Estimates of the glacial-interglacial carbon transfer from terrestrial biosphere into the oceans, using different estimates of the net change in carbon composition of total dissolved inorganic carbon, and assuming a total mass of total dissolved inorganic carbon of 3700 Gt. Horizontal lines show estimates of Adams et al. (1990)(\*) and this study(†). □ Shackleton (1977); ○, Curry et al. (1988); ●, Berger and Vincent (1986); △ Duplessy et al. (1988).

Globally, oceanic primary productivity was probably higher during glacials as indicated by an overall greater difference between  $\delta^{13}\text{C}$  values of benthic and

planktonic foraminifera ( $\Delta\delta^{13}\text{C}$ ; e.g. Broecker and Peng, 1982, 1993; Broecker, 1982; Berger and Vincent, 1986; Duplessy, 1986; Duplessy et al., 1988;

Curry et al., 1988; Boyle, 1992; Herguera, 1992). This greater productivity may have contributed to lower atmospheric  $\text{pCO}_2$ , by speeding up the biological carbon pump and depositing carbon from the atmosphere into the deep ocean. For comparison Broecker and Peng (1993) estimated that, for today's ocean, if all the nutrients available were extracted by surface-dwelling plants then the atmosphere's  $\text{CO}_2$  content would be 150 ppm; in contrast, if the oceans were sterile then the atmosphere's content would be 470 ppm. This is compared with a pre-industrial atmospheric  $\text{CO}_2$  content of 280 ppm.

Reduced ventilation of the deep ocean may have assisted in keeping the carbon in the deep ocean and in ocean sediments (Sarmiento and Toggweiler, 1984; Duplessy et al., 1988; Boyle, 1992). Both greater productivity and reduced deep water ventilation, as well as a lower average  $\delta^{13}\text{C}$  value of dissolved inorganic carbon (resulting from the transfer of terrestrial organic matter into the oceans), would have contributed to lower  $\delta^{13}\text{C}$  values in benthic foraminifera during the glacials. The absolute and relative size of the contributions of these different factors is not clear (e.g. Berger and Vincent, 1986; Heinze et al., 1991).

**Table 2.** Estimates of the expansion of the terrestrial biosphere between the LGM and the mid Holocene, and its effect on atmospheric  $\text{CO}_2$  content.

	$\delta^{13}\text{C}$ air (PDB‰)	$\delta^{13}\text{C}$ ocean (PDB‰)	Carbon Transfer (GtC)	$\Delta\text{pCO}_2$ (μatm)*	$\Delta\text{pCO}_2$ (μatm)-20 μatm ( $\text{CaCO}_3$ compensation)*
Atmospheric $\text{CO}_2$ change					
Barnola et al. (1987)			160	80 μatm (direct obs. of ice-cores)	
Palaeovegetation Studies					
Adams et al. (1990)			1300	130	110
Maslin et al. (this study)			1120 ± > 500	115 ± > 50	95 ± > 50
Carbon Isotopic Studies					
Shackleton (1977)	-0.70	1000	100	80	
Duplessy et al. (1984)	-0.15	220	23	3	
Berger and Vincent (1986)	-0.40	570	58	38	
Curry et al. (1988)	-0.46	650	66	46	
Duplessy et al. (1988)	-0.32	450	45	25	
Leuenberger et al. (1992)	-0.30				
Marino et al. (1992)	-0.61	-0.35	162–556	16–56	3–36
Herguera (1992)			400–700	40–70	20–50
Broecker and Peng (1993)		-0.35	425	47	25
Maslin et al. (this study)		-0.40 ± 0.14	700 ± > 300	70 ± > 30	50 ± > 30
Climate Modelling Studies					
Prentice and Fung (1990)			-30 ± 50	-30 ± 50	-30 ± 50

\*Calculations of  $\Delta\text{pCO}_2$  and the  $\Delta\text{pCO}_2$  including the  $\text{CaCO}_3$  compensation of the ocean ( $\approx -20 \mu\text{atm}$ ) are based on Broecker and Peng (1993) assuming the ocean-atmosphere total carbon to be 32,000 GtC.

It has been proposed that much of the higher productivity at higher latitudes during glacial times, especially in the Southern Oceans, contributed significantly to globally higher oceanic productivity and lower atmospheric pCO<sub>2</sub> (e.g. Knox and McElroy, 1984; Sarmiento and Toggweiler, 1984). Yet several palaeoceanographic tracers in the Southern Oceans indicate that there was no such increased productivity at the high latitudes, and that belts of higher productivity shifted towards lower latitudes (e.g. Mortlock *et al.*, 1991; Charles and Fairbanks, 1990; Charles *et al.*, 1991; Kumar *et al.*, 1993). Glacial productivity at latitudes 50–60°N in the Atlantic Ocean was also lower (Jasper *et al.*, 1993; Thomas *et al.*, in press). In low latitude regions, however, glacial productivity was higher by a factor of 1.5–2 in the Pacific (Herguera and Berger, 1991; Herguera, 1992; Herguera *et al.*, 1992) and Atlantic (Sarnthein *et al.*, 1988). Observations on the oceanic record thus suggest that the primary productivity in the oceans was especially enhanced in the mid and low latitudes, whereas it was reduced in the higher latitudes (Mix and Fairbanks, 1985; Sarnthein *et al.*, 1988).

There are other possible means by which ocean productivity could have increased, strengthening the biological pump. The first involves changing the ratio of carbon to phosphorus and carbon to nitrogen in marine organic matter (Broecker, 1982). If these ratios had changed during the last glacial then the biological pump could have increased. The near uniformity of these ratios in today's ocean (Broecker *et al.*, 1985) makes this scenario unlikely (Broecker and Peng, 1993). The second way is increasing the input of nutrients to the ocean; Broecker and Peng (1982) suggested this could have been achieved by erosion of the continental shelves during periods of low sea-level.

What is required is more detailed spatial information from many cores in different ocean basins to quantitatively estimate the net changes in productivity from glacial to interglacial periods.

#### Explaining the deep-sea carbon isotope shift

Most probably there was some transfer from the terrestrial biosphere (depleted

in <sup>12</sup>C) into the ocean-atmosphere system (e.g. Siegenthaler, 1986), because the oceans as well as the atmosphere became isotopically lighter during the last glacial, but the magnitude of change is not well constrained (Marino *et al.*, 1992; Leuenberger *et al.*, 1992; see Table 2). If the low glacial atmospheric pCO<sub>2</sub> had been fully determined by the oceanic productivity increase, the atmosphere would have been expected to have been heavier isotopically during periods of oceanic productivity, instead of lighter.

The mean global δ<sup>13</sup>C shift is comparatively small compared to the inaccuracies of the analysis which is usually quoted as ±0.09‰ (Hall and Shackleton personal communication, 1993). We have taken the 'best' estimate of the global mean oceanic δ<sup>13</sup>C shift to be 0.4‰, an average of the most recent values (Berger and Vincent, 1986; Curry *et al.*, 1988; Duplessy *et al.*, 1988; Sarnthein *et al.*, 1988; Herguera *et al.*, 1992); the standard deviation of these five separate estimates is ±0.06‰.

The simple box model requires the use of an average isotopic value for global terrestrial biomass (including soil carbon). Errors are introduced by the difficulty in estimating the average δ<sup>13</sup>C value of the terrestrial biomass, as well as the assumption that this value was constant with time. Many authors (e.g. Shackleton, 1976; Crowley, 1991; Herguera *et al.*, 1992) assumed a figure of –25‰, from the isotopic composition of wood by Craig (1953) (Shackleton and Crowley, pers. comm.), but estimates of biomass are sensitive to the value of average δ<sup>13</sup>C (see Fig. 2).

Estimating the average isotopic composition of the terrestrial biomass is difficult because of immense spatial variation. The two main types of higher plants have different isotopic ranges. The C3 photosynthetic pathway is used by most higher plants (δ<sup>13</sup>C values from –23‰ to –35‰; Anderson and Arthur, 1983). The C4 pathway is used mainly by tropical grasses (δ<sup>13</sup>C values ranging –10‰ to –14‰; Cerling *et al.*, 1993). The relative abundances of these two plant types, and the isotopic variation within each group, are poorly documented on a global scale. The general isotopic composition of the organic matter stored in the world soils, which

comprises 2/3–3/4 of the terrestrial biomass, is not known (Schlesinger, 1984; Siegenthaler, 1986; Tappan, 1986; Walker and Kasting, 1992). Our present best estimate of the global mean δ<sup>13</sup>C of the terrestrial biomass is –22‰ with an error of at least ±3‰ (unpublished data).

The average isotopic value of the terrestrial biomass may not be constant through time because under lower atmospheric pCO<sub>2</sub> and/or low humidity conditions C4 plants out-perform C3 plants, and the reverse is true for high pCO<sub>2</sub> and high humidity conditions (Cerling *et al.*, 1993; Melillo *et al.*, 1993). Therefore, the C3/C4 ratio during the glacials (at lower pCO<sub>2</sub> and humidity) may have been lower than today, leading to an average biomass which was heavier isotopically, and to <sup>12</sup>C enrichment of the atmosphere and the oceans. An overall global expansion of C4 vegetation in the late Miocene has been proposed to cause the global δ<sup>13</sup>C shift of about 1‰ (Cerling *et al.*, 1993). Such a change in floral composition could thus have made the transfer of less biomass necessary to explain the oceanic record, making the estimates in Table 2 maximal.

Taking into account the many quantifiable errors, the estimate of carbon transfer between the LGM and the mid-Holocene using the ocean based carbon isotope method is 700 GtC ± > 300 GtC, compared to a palaeovegetation estimate of 1120 GtC ± > 500 GtC.

#### IMPLICATIONS OF THE TERRESTRIAL BIOSPHERE EXPANSION SINCE THE LAST GLACIAL ON THE CO<sub>2</sub> CONTENT OF THE ATMOSPHERE

Broecker and Peng (1993), calculated that an estimated expansion of the terrestrial biosphere of 425 GtC would have caused a decrease in the atmospheric CO<sub>2</sub> content of 25 ppm. In summarizing all the major contributions to the glacial to interglacial increase in atmospheric CO<sub>2</sub> content, they found that the 80 ppm increase observed in the ice cores could only be achieved under the following assumptions (see Table 3).

1 The deposition of CaCO<sub>3</sub> in coral reefs during the marine transgression

during the deglacial compensated for the expansion of the terrestrial biosphere during the early Holocene (Berger, 1982; Odyke and Walker, 1992).

2 The average salinity of the world's ocean lowered by about 3% at the end of the last glacial, this would have lowered the atmospheric CO<sub>2</sub> content by 11 ppm. This could have been countered by the increased role of brine formation caused by the expansion of sea ice during the last glacial in the North Atlantic and Antarctica. If so then the salinity of the polar waters would have been lower relative to the ocean's average during the deglacial and this could have easily offset the impact of the ocean-wide salinity increase.

If the estimates of the carbon shift to the terrestrial biosphere presented in this review are equilibrated with the dissolved carbon in the oceans then their effect on atmospheric pCO<sub>2</sub> can be calculated (Broecker and Peng, 1993). Broecker and Peng (1993) also calculated that the CaCO<sub>3</sub> compensation of the oceans was about 20 ppm. The ΔpCO<sub>2</sub> values, with and without CaCO<sub>3</sub> compensation, for each of the various estimates of the expansion of the terrestrial biosphere in the literature, as well as those from the calculations presented here, are given in Table 2.

The estimates of the expansion of the terrestrial biosphere presented in this review are larger than those calculated by Broecker and Peng (1993), i.e. 700 GtC ± > 300 GtC and 1120 GtC ± > 500 GtC.

Their effect on the glacial atmospheric CO<sub>2</sub> content is correspondingly larger, between 50 (±30) ppm and 95 (±50) ppm. The glacial atmosphere therefore should have had a CO<sub>2</sub> partial pressure of between 330 and 375 μatm. Hence, a rise of between 130 and 175 μatm in atmospheric CO<sub>2</sub>, rather than 80 μatm, at the end of the last glacial must be accounted for. When these estimates are added to the models of Broecker and Peng (1993) then it is not possible to achieve the 80 ppm increase in atmospheric CO<sub>2</sub> content observed in the ice cores (see Table 3). This implies that any of the following mechanisms have been under-estimated: the deposition of coral reefs during the deglacial, the extent and effect of sea ice during the last glacial, the strength of the biological pump during the last glacial, and/or the magnitude of reduction of the deep sea CO<sub>3</sub><sup>2-</sup> since the last glacial. There may well be other mechanisms which increase atmospheric CO<sub>2</sub> content as yet unaccounted for.

## CONCLUSIONS

In summary, taking into account those errors which are quantifiable, the best estimates of carbon transfer to the terrestrial biosphere between the LGM and the mid-Holocene is 700 GtC ± > 300 GtC using the ocean-based carbon isotope method, and 1120 GtC ± > 500 GtC using the palaeovegetation

approach. The apparently significant discrepancy between the two methods may be caused by the assumptions and complexities of each method. Considering the huge differences between the techniques, it is encouraging that the final results are in fact so close. Similar large, apparent discrepancies occur in estimates of the rate of CO<sub>2</sub> uptake by the oceans using different techniques (Tans *et al.*, 1993), illustrating a similar lack of understanding of the carbon cycle at shorter time-scales. Estimates of the terrestrial biosphere presented here suggest that its effect on atmospheric CO<sub>2</sub> content over this time-scale was much greater than previously thought (between 50 and 95 ppm). This suggests that either the mechanisms used to explain the atmospheric CO<sub>2</sub> increase observed in the ice cores have been underestimated, or that there are other mechanisms which have not yet been accounted for.

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Table 3. Four scenarios of the possible contributions to the glacial to interglacial CO<sub>2</sub> increase (i.e. from ~200 μatm during the last glacial to 280 μatm during the mid Holocene) (based on Broecker and Peng, 1993).

	Broecker and Peng (1993)		This study	
	ΔpCO <sub>2</sub>	ΔpCO <sub>2</sub>	ΔpCO <sub>2</sub>	ΔpCO <sub>2</sub>
Increased biomass	-25 <sup>A</sup>	0†	-50 <sup>B</sup> / -95 <sup>C</sup>	-25 <sup>B</sup> † / -70 <sup>C</sup> †
Temperature rise (~2°C)	+ 18	+ 18	+ 18	+ 18
Salinity drop (g L <sup>-1</sup> )	-11	0‡	-11	0‡
Reduced deep sea CO <sub>3</sub> <sup>2-</sup> (10 μM kg <sup>-1</sup> )	+ 20	+ 20	+ 20	+ 20
Increased ΔCO <sub>3</sub> = surface-deep*	+ 40	+ 40	+ 40	+ 40
Total	+ 48	+ 78	+ 17 / -28	+ 53 / +8

\*As a result of a reduction in the power of the biological pump and the redistribution of nutrient between the intermediate and deep waters.

†Assumes that the deposition of CaCO<sub>3</sub> in coral reefs during the marine transgression which accompanied the last deglaciation partially compensated for the expansion of the terrestrial biosphere. Broecker and Peng estimate the effect was approximately + 25 μatm.

‡Assumes that the polar sea ice effect compensated for the ocean-wide salinity change

<sup>A</sup>calculated assuming a carbon transfer of 425 GtC (Broecker and Peng, 1993)

<sup>B</sup>calculated assuming a carbon transfer of 700 GtC based on the ocean carbon isotope method (this study)

<sup>C</sup>calculated assuming a carbon transfer of 1100 GtC based on the palaeovegetation reconstruction method (this study)

## REFERENCES

- Adams J., Faure H., Faure-Denard L., McGlade J. and Woodward F. (1990) Increases in terrestrial carbon storage from the Last Glacial Maximum to the present, *Nature*, **348**, 711–714.
- Adams J.M. and Woodward, F.I. (1992) The past is the key to the future, *Adv. Ecol. Res.*, **22**, 257–314.
- Anderson T. and Arthur M. (1983) Stable isotopes of oxygen and carbon and their application to sedimentological and paleoenvironmental problems. In: *SEPM Short Course No. 10: Dallas Stable isotopes in Sedimentary Geology* (ed. by T. Anderson and M. Arthur). University of Dallas, Dallas, USA.
- Barnola J.M., Raynaud D. and Korotkevich, Y. S. (1987) Vostok ice core provides, 160,000 year record of atmospheric CO<sub>2</sub>, *Nature*, **329**, 408–414.
- Berger W. H. (1982) Increase of carbon dioxide in the atmosphere during deglaciation, the coral reef hypothesis, *Naturwissenschaften*, **69**, 87–88.
- Berger W. H. and Vincent E. (1986) Deep sea carbonates, reading the carbon isotope signal, *Geol. Rndsch.*, **75**, 249–269.
- Boyle E.A. and Keigwin, L.D. (1982) Deep circulation of the North Atlantic over the last, 200,000 years, geochemical evidence, *Science*, **218**, 784–787.
- Boyle E.A. (1992) Cadmium and δ<sup>13</sup>C paleochemical ocean distributions during the stage 2 glacial maximum, *Ann. Rev. Earth Planet. Sci.*, **20**, 245–287.
- Broecker W. (1982) Ocean chemistry during glacial times, *Geochim. Cosmochim. Acta*, **46**, 1689–1705.
- Broecker W.S. and Peng T-H. 1982) *Traces in the Sea*. Eldigino Press, New York.
- Broecker W.S. and Peng T-H. (1993) What caused the glacial to interglacial CO<sub>2</sub> change. In: *The Global Carbon Cycle*, NATO ASI Series, Vol. 15 (ed. by M. Heimann). Springer, Berlin.
- Broecker W.S., Takahashi T. and Takahashi T. (1985) Sources and flow patterns of deep-ocean waters as deduced from potential temperature salinity and inital phosphate concentrations, *J. geophys. Res.*, **90**, 6925–6939.
- Brown S., Gillespie A.J.R. and Lugo A.E. (1991) Biomass of tropical forests of south and south-east Asia, *Can. J. Forest Res.*, **21**, 111–117.
- Cerling T., Wang Y. and Quade J. (1993) Expansion of C4 ecosystems as an indicator of global ecological change in the late Miocene, *Nature*, **361**, 344–345.
- Charles C. and Fairbanks R. (1992) Evidence from Southern Ocean sediments for the effects of North Atlantic deep-water flux on climate, *Nature*, **355**, 416–419.
- Charles C., Froelich P., Mortlock M. and Morley J.J. (1991) Biogenic opal in Southern Ocean sediments over the last, 450, 000 years, implication for surface water chemistry and circulation, *Paleoceanography*, **6**, 697–728.
- COHMAP members (1988) Climatic Change of the last, 18,000 years, Observations and model simulations, *Science*, **241**, 1043–1052.
- Craig H. (1953) The geochemistry of stable isotopes of carbon, *Geochim. Cosmochim. Acta*, **3**, 53–72.
- Craig H. (1954) Carbon 13 in plants and the relationships between carbon-13 and carbon-14 variation in nature, *J. Geol.*, **62**, 115–149.
- Crowley, T.J. (1991) Ice Age carbon, *Nature*, **352**, 575–576.
- Curry W.B., Duplessy, J-C., Labeyrie L.D. and Shackleton N.J. (1988) Changes in the distribution of δ<sup>13</sup>C of deep water ΣCO<sub>2</sub> between the last glaciation and the Holocene, *Paleoceanography*, **3**, 327–337.
- Duplessy J-C., Shackleton N.J., Matthews R.K., Prell W., Ruddiman W.F., Caralp M. and Hendy C. (1984) δ<sup>13</sup>C record of benthic foraminifera in the last interglacial ocean , implication for the carbon cycle and the global deep water circulation, *Quat. Res.*, **21**, 225–243.
- Duplessy J-C. (1986) CO<sub>2</sub> air sea exchange during glacial times , importance of deep sea circulation changes. In: *The Role of Air-Sea Exchange in Geochemical Cycling* (ed. by P. Buat-Menard), pp. 249–267. Reidel, Dordrecht.
- Duplessy J-C., Shackleton N.J., Fairbanks R.J., Labeyrie L.D., Oppo D. and Kallel N. (1988) Deepwater source variation during the last climatic cycle and their impact on the global deepwater circulation, *Paleoceanography*, **3**, 343–360.
- Heinze C., Maier-Reimer E. and Winn N. (1991) Glacial pCO<sub>2</sub> reduction by the world ocean, experiments with Hamberg carbon cycle model, *Paleoceanography*, **6**, 395–430.
- Herguera J.C. and Berger W.H. (1991) Paleoproductivity from benthic foraminifera abundance , glacial to post glacial change in the west-equatorial Pacific, *Geology*, **19**, 1173–1176.
- Herguera J.C. (1992) Deep sea benthic foraminifera and biogenic opal, glacial to postglacial productivity changes in the western equatorial Pacific, *Mar. Micropaleont.*, **19**, 79–98.
- Herguera J.C., Jansen E. and Berger W.H. (1992) Evidence for a bathyal front at 2000 m depth in the glacial Pacific, based on a depth transect on Ontong Java Plateau, *Paleoceanography*, **7**, 273–288.
- Imbrie J. et al. (1993) On the structure and origin of major glaciation cycles. The 100,000-year cycle, *Paleoceanography*, **8**, 699–737.
- Jasper J.P., Sikes E.L., Mix A.C., Prahl F.G., Keigwin L.D. and Hayes J. (1993) Molecular isotopic evidence of deglacial decline in CO<sub>2aq</sub> concentrations in the North Atlantic and control of the late Quaternary atmospheric pCO<sub>2</sub>, *SEPM Meeting: The stratigraphic record of Global Change, August 1993, Penn State University, University Park, PA*, 37pp.
- Jasper J.P. and Hayes J. (1990) A carbon isotope record of CO<sub>2</sub> level during the late Quaternary, *Nature*, **347**, 462–464.
- Kier R.S. (1988) On late Pleistocene ocean geochemistry and circulation, *Paleoceanography*, **3**, 413–445.
- Knox F. and McElroy M.B. (1984) Changes in atmospheric CO<sub>2</sub>, Influences of the marine biota at high latitudes, *J. geophys. Res.*, **89**, 4629–4637.
- Kroopnick P.M., Margolis S.V. and Wong C.S. (1977) δ<sup>13</sup>C variations in marine carbonate sediments as indicators of the CO<sub>2</sub> balance between the atmosphere and oceans. In: *The Fate of Fossil Fuel CO<sub>2</sub> in the Oceans* (ed. by N.R. Andersen and A. Malahoff), pp. 295–321. Plenum Press, New York.
- Kumar, N., Gwiadza R., Anderson R.F. and Froelich P.N. (1993) 3231 Pa/230Th ratios in sediments as a proxy for past changes in Southern Ocean productivity, *Nature*, **362**, 45–48.
- Labeyrie L. D., Duplessy, J-C., Duprat J., Juillet-Leclerc A., Moyes J., Michel E., Kallel N. and Shackleton, N. J. (1992) Changes in the vertical structure of the North Atlantic Ocean between Glacial and Modern times, *Quat. Sci. Rev.*, **11**, 401–414.
- Leuenberger M., Siegenthaler U. and Langway C.C. (1992) Carbon isotope composition of atmospheric CO<sub>2</sub> during the last ice age from an Antarctic ice core, *Nature*, **357**, 488–490.
- Marino B., McElroy M., Salawitch R.J. and Spaulding W.G. (1992) Glacial to interglacial variations in the carbon isotopic composition of atmospheric CO<sub>2</sub>, *Nature*, **357**, 461–466.

- Melillo J.M., McGuire A.D., Kicklighter D.W., Moore III B., Vorosmarty C.J. and Schloss, A.L. (1993) Global climate change and terrestrial net primary production, *Nature*, **363**, 234–240.
- Mix A.C. and Fairbanks R.G. (1985) North Atlantic surface water control of Pleistocene deep water circulation, *Earth Planet. Sci. Lett.*, **73**, 231–243.
- Mortlock R.M., Charles C.D., Froelich P.N., Zibello M., Saltzman J.L., Burckle D. and Hays J.D. (1991) Evidence for lower productivity in the Antarctic Ocean during the last glaciation, *Nature*, **351**, 220–222.
- Neustadt M.I. (1982) Holocene peatland development. In: *Quaternary Environments in the Soviet Union* (ed. by A.A. Velirchio), Ch. 19, pp. 201–206. Springer, Berlin.
- Olson J.S., Watt J.A. and Allinson L.J. (1983) *Carbon in Live Vegetation in Major World Ecosystems*, Vol. No. 1997. Environmental Sciences Division Publication, Oak Ridge National Laboratory, TN
- Opdyke B.N. and Walker J.C.G. (1992) The return of the coral reef hypothesis, Glacial to interglacial partitioning of basin to shelf carbonate and its effect on Holocene and atmospheric pCO<sub>2</sub>, *Geology*, **20**, 733–736.
- Prentice K.C. and Fung I.Y. (1990) The sensitivity of terrestrial carbon storage to climate change, *Nature*, **346**, 48–51.
- Sarmiento J.L. and Toggweiler J.R. (1984) A new model for the role of the oceans in determining atmospheric CO<sub>2</sub>, *Nature*, **308**, 621–624.
- Sarnthein M., Winn K., Duplessy J.-C. and Fontugne M. (1988) Global variations of Surface Ocean Productivity in Low and Mid latitudes, *Paleoceanography*, **3**, 361–398.
- Schlesinger, W.H. (1984) Atmospheric CO<sub>2</sub> and feedback effects on climate. In: *Role of Terrestrial Vegetation in the Global Carbon Cycle*, SCOPE 23 (ed. by G.M. Woodwell), pp. 109–111. Springer, Berlin.
- Shackleton N.J. (1977) C-13 in Uvigerina; Tropical rainforest history and the equatorial Pacific carbonate dissolution cycles. In: *The Fate of Fossil Fuel CO<sub>2</sub> in the Oceans* (ed. by N.R. Andersen and A. Malahoff), pp. 401–427. Plenum Press, New York.
- Siegenthaler U. (1986) Carbon dioxide, its natural cycle and anthropogenic perturbation. In: *The Role of Air-Sea Exchanges in Geochemical Cycling* (ed. by P. Buat-Ménard), pp. 209–247. Reidel, Dordrecht.
- Tans P.P., Berry J.A. and Keeling R.F. (1993) Oceanic <sup>13</sup>C/<sup>12</sup>C observations, a new window on ocean CO<sub>2</sub> uptake, *Global Biogeochem. Cycles*, **7**, 353–368.
- Tappan H. (1986) Phytoplankton, below the salt at the global table, *J. Paleontology*, **60**, 545–554.
- Thomas E., Booth L., Maslin M. and Shackleton N.J. (1995) Benthic foraminifera assemblages in the North East Atlantic in the last, 40,000 years, *Paleoceanography*, **10**.
- Walker J.C.G. and Kasting J.F. (1992) Effect of fuel and forest conservation on future levels of atmospheric carbon dioxide, *Paleogeogr. Paleoclim. Paleoecol. (Global Planet. Change Section)*, **97**, 151–189.
- Wefer G. and Berger W.H. (1991) Isotope paleontology, growth and composition of calcareous species, *Mar. Geol.*, **100**, 207–248.
- Worthington L.V. (1972) *On the North Atlantic Circulation*, Vol. 6. John Hopkins Oceanographic Studies, Baltimore
- Zoltai S.C. (1991) Estimating the age of peat samples from their weight, *Holocene*, **1**, 68–73.

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