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Reconstruction of past terrestrial carbon storage in the Northern Hemisphere from the Osnabrück Biosphere Model and palaeodata

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ABSTRACT: Until now the reconstruction of past carbon storage from data has often been done by using modern carbon databases. The results are likely a rough approximation of the reality, and can be improved by the use of biosphere models. These models usually need to be parameterized by a large number of environmental inputs, which are often not available from palaeodata. The empirical Osnabrück Biosphere Model (OBM) needs as input only 3 environmental parameters, easily derivable from pollen data. We adapted it to reconstruct the past terrestrial carbon storage from palaeodata. Sensitivity experiments performed by uniformly decreasing the mean annual temperature, average annual precipitation and/or CO_2 concentration suggest that temperature and CO_2 concentration affect the carbon storage more than does precipitation. The use of the only palaeodata available at a global scale shows that only a weakening of CO_2 fertilization must be invoked to reconstruct the Last Glacial Maximum (LGM) carbon storage, which is an intermediate situation between the no-fertilization effect assumed by previous studies and the fertilization effect based on modernist empirical equations. The terrestrial carbon storage in the Northern Hemisphere for this period ranged from 910 to 1270 Pg, which represents an increase of 330 to 710 Pg (a planetary increase of 470 to 1014 Pg from the LGM to the present). This result is similar to our previous reconstruction and agrees broadly with the values estimated on the basis of 0.32‰ change obtained for global deep ocean $\delta^{13}C$.

KEY WORDS: Terrestrial carbon storage · Biosphere model · Palaeodata · Sensitivity experiment

INTRODUCTION

Studies of Antarctic ice cores have shown that the atmospheric concentration of CO_2 during the Last Glacial Maximum (LGM) was ~80 ppmv (parts per million by volume) lower than the ~280 ppmv value of the pre-industrial period (Barnola et al. 1987). Biogeochemical processes that can modulate atmospheric CO_2 concentration and the ocean-atmosphere carbon distribution have been explained in 2 different ways. The first model invokes a greater biological pump efficiency which involves greater sinking fluxes of organic carbon relative to upwelling of total CO_2 (Broecker 1982, Volk & Hoffert 1985). The second model invokes alkalinity mechanisms which increase the concentration of $(CO_3)^{2-}$ in glacial surface waters (Broecker & Peng 1989). Both models emphasize changes in $\delta^{13}C$ of atmospheric CO_2 between glacial and interglacial conditions. Marino et al. (1992) attribute isotopically light glacial atmospheric CO_2 to a combination of factors including not only decreased productivity of the polar ocean but also reduced terrestrial biomass. Leuenberger et al. (1992) presented analyses of past carbon isotope composition of atmospheric CO_2 from Antarctic ice; they also considered change in land biomass among the factors producing observed changes in atmospheric $\delta^{13}C$. The hypothesis that less carbon was stored on the continents at the LGM was first formulated by Shackleton (1977), based on studies of the $\delta^{13}C$ changes of benthic foraminifera in the equatorial Pacific. A further estimate of the mean $\delta^{13}C$ content of the global ocean during the LGM, 0.32‰ lower than today, suggests there has been a 400 to 500 Pg post-glacial increase in the level of terrestrial carbon storage (Duplessy et al. 1988).

A great effort has been made to reconstruct the LGM terrestrial carbon budget. Simulations using atmospheric general circulation models (AGCMs) and various bioclimatic approaches yielded estimates for post-LGM increases varying from ±50 Pg (Prentice & Fung 1990) to 300 Pg (Friedlingstein et al. 1992). A 300 to 700 Pg range was recently obtained by Prentice et al. (in press), who used a global biome model (Prentice et al. 1992) derived from modern climate data (Leemans & Cramer 1991), and the Hamburg AGCM simulations for the LGM and for today. The first estimate of post-LGM increase based on land data, 1350 Pg, was given by Adams et al. (1990), who used continental palaeodata to produce a global map of LGM vegetation. A second estimate of terrestrial carbon storage was produced by Van Campo et al. (1993) using modern and LGM CLIMAP (Climate/Long Range Investigation Mapping and Prediction) compilations of both land and sea surface conditions. This new estimate indicates an increase of 715 Pg (range 430 to 930 Pg) from the LGM to the present, which is more consistent with both the Prentice et al. (in press) modelling results and the ocean-based approach.

All the available model- or data-based estimates suffer severe limitations. They imply not only an equilibrium state between the vegetation, soil and climate, but also carbon densities for each ecosystem similar to modern values. Possible low-fertilization effects of low atmospheric CO_2 concentration on the net primary production cannot be taken into account. Therefore, the combined use of palaeodata (Peterson et al. 1979, CLIMAP Project Members 1981, Frenzel et al. 1992) and of a biosphere carbon cycle model is required to reconstruct the dynamics of vegetation and soil carbon storage under changing global boundary conditions.

On the basis of the underlying processes of photosynthesis, respiration, transpiration, nitrogen cycling and carbon-nitrogen feedbacks, several terrestrial biogeochemical models have been recently developed to estimate the dynamics of terrestrial ecosystem production, biomass and soil organic matter at regional and global scales (Raich et al. 1991, McGuire et al. 1992, Melillo et al. 1993, Parton et al. 1993, Potter et al. 1993). But these process-based terrestrial biogeochemical models are difficult to use for investigating the glacial terrestrial carbon budget, because: (1) the complexity of interactions among terrestrial biogeochemical processes during the glacial-interglacial is poorly understood, and (2) few data sets are available to parameterize these models. The Osnabrück Biosphere Model (OBM) (Esser 1987, 1991) contains more empirical relationships than process-based equations, but needs only a few input parameters, which can be easily calculated from the available palaeodata. Moreover, it improves estimates of the carbon density of the various ecosystems. For these reasons, it has been used to estimate past terrestrial carbon dynamics in response to past climatic changes (Peng et al. 1994, Esser & Lautenschlager 1993).

We present here an adapted version of the OBM developed by Esser (1987, 1991), which considers the CO_2 fertilization effect. LGM terrestrial carbon is estimated from temperature, precipitation and ecosystem distribution provided by palaeodata and not by AGCM simulation as in Esser & Lautenschlager (1993). Our results are compared with the CLIMAP-data-based estimate of Van Campo et al. (1993) and the AGCM simulation of Esser & Lautenschlager (1993) at the Northern Hemisphere scale.

MODEL AND DATA

The Osnabrück Biosphere Model. We use a version of the OBM adapted to a 0.5° × 0.5° grid. The model calculates the carbon fluxes and pools of the terrestrial biosphere depending on mean annual temperature, total annual precipitation and the atmospheric CO_2 concentration. A detailed description of the model construction and a discussion of its ability to be applied to present conditions can be found in the original papers. Here we mainly highlight some important points and modifications introduced in this study.

The OBM model includes herbaceous and woody live biomass, litter from herbaceous and woody material, and soil organic carbon. The carbon fluxes are net primary production (NPP), allocation of assimilates to the compartment of live biomass, litter production, litter decomposition, soil organic carbon production, and soil organic carbon decomposition.

The NPP, which is the rate at which the vegetation in an ecosystem fixes carbon from the atmosphere (gross primary productivity) minus the rate at which it returns carbon to the atmosphere (plant respiration), represents the net carbon input from the atmosphere into the biosphere. The NPP calculated by OBM is an equilibrium prediction. The model assumes that vegetation changes in response to climatic change have been completed. The productivity share of the potential vegetation is basically limited either by temperature or precipitation and can be estimated by the MIAMI model (Lieth 1975), which is calibrated on 52 sites from North America, the Caribbean, Western Europe, Africa and Asia; it is modified by soil fertility (F_{soil}) and by the CO_2 fertilization effect (F_{CO_2}) (Esser 1991).

The CO_2 fertilization effect is very important for understanding the glacial biospheric carbon budget.

The CO_2 fertilization factor, F_{CO_2}, represents the influence of the entire complex of ecological effects of atmospheric CO_2 concentration; it depends on the atmospheric CO_2 concentration (CO_2) and soil fertility (F_{soil}). The CO_2 fertilization effect as described by Esser (1991, Eq. 31.5) can be reliably used in the case of modern higher CO_2 concentrations, but the extrapolation of this equation to lower glacial CO_2 concentrations is still speculative. In consequence, we consider 2 basic scenarios to examine the CO_2 fertilization effect on terrestrial carbon storage at the LGM as in Esser & Lautenschlager (1993).

In the OBM, the vegetation biomass is calculated by an empirical relationship between NPP and mean stand age of vegetation. Mean stand age is derived from DATAVW (a few gaps are filled using the method of ranking) (Esser 1984), and represents approximately the average turnover time of the vegetation. Litter production and decomposition, and soil organic carbon production and decomposition, are functions of mean annual temperature, total annual precipitation, atmospheric CO_2 concentration, soil fertility, and vegetation types.

To estimate the potential carbon storage in vegetation, in litter and in soil pools, we do not take into account the land-use effect. The losses of dissolved and particulate organic carbon through leaching or deposition are generally negligible (Schlesinger & Melack 1981, Schlesinger 1985).

Model inputs. The CO_2 concentration of the atmosphere was set to a value of 280 ppmv for the pre-industrial period (present), and to 200 ppmv for the LGM, in agreement with the CO_2 measurements from the Vostok ice core (Barnola et al. 1987). The sea level reduction for the LGM was assumed to be −130 m (CLIMAP Project Members 1976), leading to a continental area of 18.71 million km^2 for the Northern Hemisphere. Given that the atmosphere acts as an unlimited carbon source to fill the pools, we calculated the initial values for each pool using a fixed atmosphere CO_2 concentration. The pre-run procedure indicated that 1500 yr were needed to stabilize the large soil pools and prevent model drift in the continued model run.

The input data sets of the model were mean annual temperature, total annual precipitation, potential vegetation types and soil types at each grid cell.

The IIASA climatic database (Leemans & Cramer 1991) provides mean annual temperature (T_{0k}) and total annual precipitation (P_{0k}) for a grid of 0.5° × 0.5°. We considered 17 vegetation types (Table 1) defined as in the biome model of Prentice et al. (1992). The mean stand age of each biome and the factor needed to calculate the proportion of herbaceous and woody production were taken from Esser (1991, Table 31.6).

The soil data (Zobler 1986) were based on a soil map of the world (FAO-UNESCO 1974) given for a 1° × 1° grid. The soil units of this map were interpolated at the 0.5° × 0.5° gridpoints as required by the model. The soil fertility factor, F_{soil}, was derived by comparing the measured NPP of the soil with NPP calculated from climate only (Esser 1991). The soil types not given in Table 31.4 in Esser (1991) were assumed to have an F_{soil} of 1 (McGuire et al. 1993).

We limited our study to the Northern Hemisphere, where the input data needed were available for the LGM. The Northern Hemisphere represents about 70% of global terrestrial carbon storage (Van Campo et al. 1993) and thus plays a large role in the global carbon budget. The boreal forest represents the largest reservoir of soil carbon and is second, behind broadleaf humid forests, in vegetation carbon storage (Lashof 1989). Tans et al. (1990) hypothesized that mid-latitude ecosystems of the Northern Hemisphere are accumulating carbon at an annual rate of 2.0 to 3.4 Pg.

PRESENT CARBON STORAGE IN THE NORTHERN HEMISPHERE

The latitudinal distribution of the total carbon storage in the Northern Hemisphere (Fig. 1) shows that the

Table 1. The 17 biomes as defined by Prentice et al. (1992). The mean stand age of each biome and the biomass share factor for herbaceous production, H_h, were derived from Esser (1991, Table 31.6). (The biomass share factor for woody production is simply calculated as $1 - H_h$)

Code	Biome	Mean stand age (yr)	H_h
TUND	Tundra	5	0.48
COGS	Cool grass/shrub	1	1.0
WTUN	Wooded tundra	10	0.7
TAIG	Taiga forest	100	0.34
CLMX	Cold mixed forest	100	0.36
CLDE	Cold deciduous forest	100	0.38
COMX	Cool mixed forest	130	0.29
COCO	Cool conifer forest	130	0.29
WAMX	Warm/evergreen mixed forest	130	0.29
WADE	Temperate deciduous	150	0.38
XEWS	Xerophytic woods/shrub	20	0.4
SEDE	Semidesert	15	0.85
SAWO	Tropical savanna	5	0.98
TRDF	Tropical dry forest	80	0.4
HODE	Hot desert	5	0.85
WAGS	Warm grass/shrub	1	1.0
EQEG	Tropical rain/seasonal forest	200	0.37

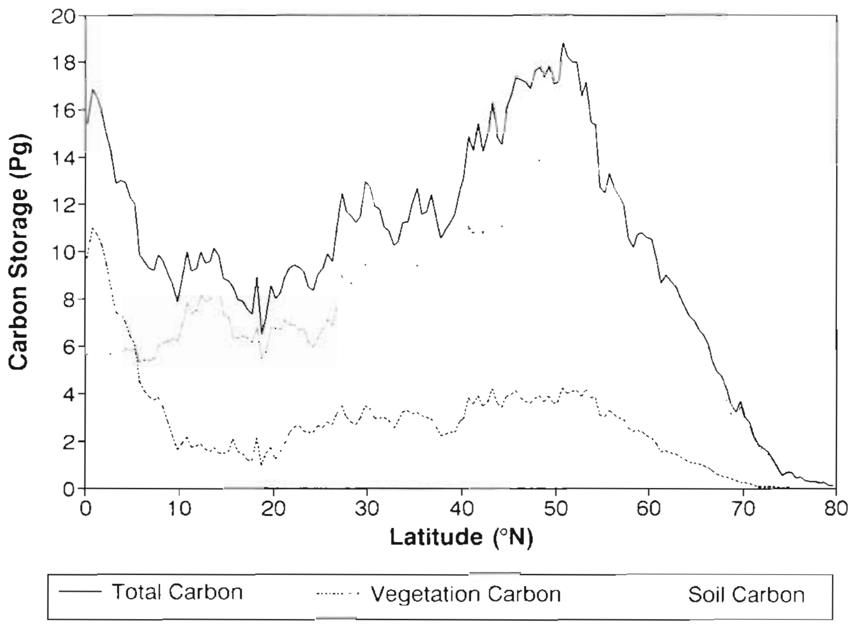

Fig. 1. Present-day zonally averaged distribution of total carbon, vegetation carbon, and soil carbon by 0.5° latitude band

highest amount is stored at about 52° N, where climate and nutrients are favorable for temperate and boreal forests on a large continental area. This result is similar to that of Van Campo et al. (1993).

The maximum vegetation carbon storage occurs in the equatorial humid forest with high biomass; the lowest vegetation carbon storage is found between 10° and 20° N, corresponding to open vegetation and desert, and between 65° and 80° N, corresponding to tundra-steppe and polar desert.

The soil carbon storage increases continuously from 20° to 50° N due to a gradual temperature decrease. The largest soil carbon storage appears at about 45° to 53° N, corresponding to temperate and boreal forests (with high carbon storage in peat bog soil). Tropical forest soil contains less carbon than other forest types, because high temperature and sufficient precipitation amplify the soil respiration.

The distributions of area and of carbon storage for each ecosystem are shown in Fig. 2. The higher carbon

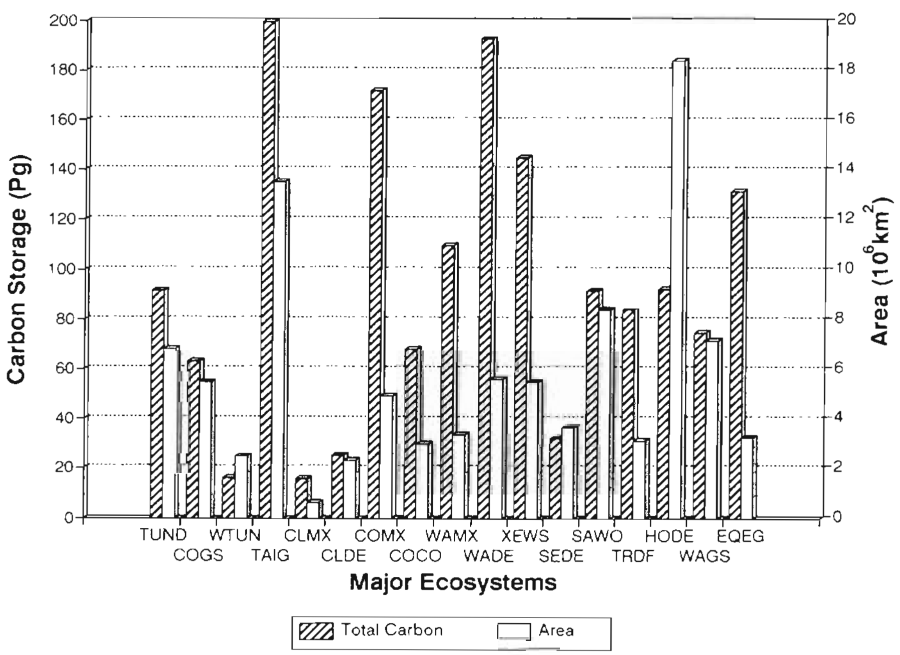

Fig. 2. Present-day distribution of total carbon storage and area among the major ecosystems. See Table 1 for ecosystem abbreviations

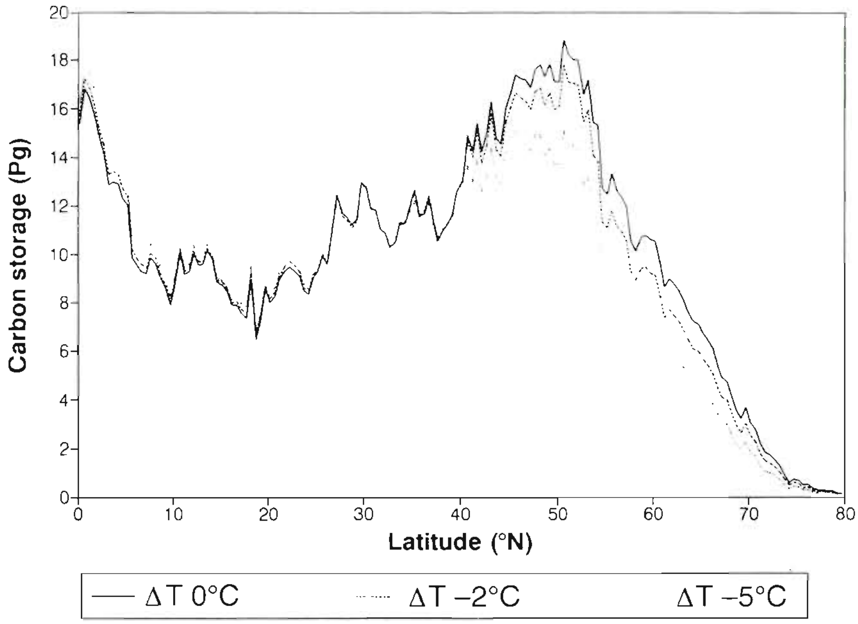

Fig. 3. Zonally averaged values of total carbon storage for temperature variations of 0 °C (present-day situation), −2 °C and −5 °C, by latitude

storages occur respectively in taiga (TAIG) with 199 Pg, temperate deciduous forest (WADE) with 193 Pg and cool mixed forest (COMX) with 172 Pg, due to their larger area. The lower carbon storages are found in the cool mixed forest (CLMX) with 16 Pg, wooded tundra (WTUN) with 16 Pg and cool deciduous forest (CLDE) with 25 Pg, due to their smaller area. The hot desert (HODE) occupies the largest area with 18×10^6 km^2, but it has a low carbon storage (about 92 Pg).

Total carbon storage in the Northern Hemisphere (see Table 3) was 1604 Pg for the studied area of 101×10^6 km^2, with 431 Pg in the vegetation and 1173 Pg in the soil. As carbon storage in the Northern Hemisphere is about 70 % of the global carbon storage (Van Campo et al. 1993), this result broadly agrees with calculations by Esser & Lautenschlager (1993) and is higher than estimations by Schlesinger (1977), Atjay et al. (1979) and Olson et al. (1985) for global terrestrial ecosystems with land-use disturbances (about 560 Pg in vegetation and 1500 to 1600 Pg in soil).

SENSITIVITY EXPERIMENTS

In order to examine how changes in temperature, precipitation and CO_2 concentration would affect carbon storage, several sensitivity studies were carried out with the OBM by altering the 3 factors individually (Esser 1987, McGuire et al. in press).

The atmospheric CO_2 concentration was about 200 ppmv at the LGM (Barnola et al. 1987). The palaeoclimatic data (CLIMAP Project Members 1976, Peterson et al. 1979) suggest that the unglaciated land surface at 18000 yr BP was generally colder and drier than at present. The differences in temperature were from −1 to −12 °C and even larger, while precipitation differences were more variable. The mean difference was about −5 °C for temperature and −30 % for precipitation. We studied the overall effect of climate on the carbon storage by successively decreasing: (1) temperature at each gridpoint, by 2 °C and 5 °C; (2) precipitation, by 10 % and 30 %; and (3) atmospheric CO_2 concentration, by 30 ppmv and 80 ppmv.

Sensitivity to temperature

Temperature was decreased successively by 2 °C and 5 °C while precipitation and CO_2 concentration were maintained at modern values. Fig. 3 shows that the carbon storage increased from 0° to 30° N and decreased from 30° to 80° N due to the ice sheet and the open vegetation extensions. Cooling reduces soil respiration more than vegetation photosynthesis between 0° and 30° N. In contrast, vegetation photosynthesis decreased more than soil respiration between 30° and 80° N. The range of response was evidently larger for the 5 °C decrease than for the 2 °C decrease; the change in carbon storage was especially dramatic in the high-latitude regions, where temperature is a strong limiting factor. The total carbon storage (Table 2) decreased by about 3.3 % for $\Delta T = 2$ °C (28 Pg in vegetation and 25 Pg in soil), and by 9.2 % for $\Delta T = 5$ °C (74 Pg in vegetation, 73 Pg in soil). As the LGM at high and middle latitudes was much cooler than simulated in these experiments, it is likely that the LGM carbon storage was reduced by more than 20% due to temperature alone.

Sensitivity to precipitation

The total carbon storage was slightly altered by precipitation decreases of 10 and 30%. Table 2 shows that the total carbon storage was decreased by 0.7% and 1.8% respectively. In fact, vegetation carbon storage decreased by 21 and 72 Pg respectively, but soil carbon increased by 11 and 42 Pg, because in these complex ecological interactions, the decrease in soil moisture limits soil metabolic activity, which might lead to a reduction of the soil heterotrophic respiration. At the scale of the Northern Hemisphere, the net effect is negative, although it is slightly positive between 58° and 75° N (Fig. 4).

Sensitivity to CO_2 concentration

Fig. 5 and Table 2 show that decreases in CO_2 concentration by 30 and 80 ppmv had a strong effect on carbon storage, leading to reductions of 8.1% (36 Pg in vegetation, 92 Pg in soil) and 24.9% (109 Pg in vegetation, 290 Pg in soil) respectively. In the OBM calculations, NPP is affected directly by F_{CO_2} which, as described above, depends on CO_2 concentration and soil fertility. This explains why CO_2 concentration is the most important limiting factor in the changes of carbon storage.

Table 2. Vegetation, soil, and total carbon storage (vegetation C + soil C) for various experiments with the OBM. Sensitivity experiments were performed by simply decreasing the values of temperature (-2°C and -5°C), precipitation (-10% and -30%), and CO_2 concentration (-30 ppmv and -80 pppmv) with respect to the present climate dataset. Cumulative effects represent the effects of decreasing temperature, precipitation and CO_2 concentration. Values in parentheses are the differences between the results and present-day values. Values are given in Pg carbon

Sensitivity experiment	Veg. C	Soil C	Total C	Change
Present climate	431	1172	1604	
Temperature -2°C	403 (-28)	1148 (-25)	1551 (-53)	-3.3%
Temperature -5°C	357 (-74)	1099 (-73)	1456 (-147)	-9.2%
Precipitation -10%	410 (-21)	1183 (+11)	1593 (-10)	-0.7%
Precipitation -30%	359 (-72)	1215 (+42)	1574 (-30)	-1.8%
CO_2 concentration -30 ppmv	395 (-36)	1080 (-92)	1475 (-128)	-8.1%
CO_2 concentration -80 ppmv	322 (-109)	883 (-290)	1205 (-399)	-24.9%
Cumulative effects (-5°C, -30%, -80 ppmv)	249 (-182)	851 (-322)	1100 (-504)	-31.4%

Sensitivity to all 3 factors

We examine now the cumulative effects of changes in temperature (-5°C), precipitation (-30%) and CO_2 concentration (-80 ppmv), as they should better reflect the LGM conditions.

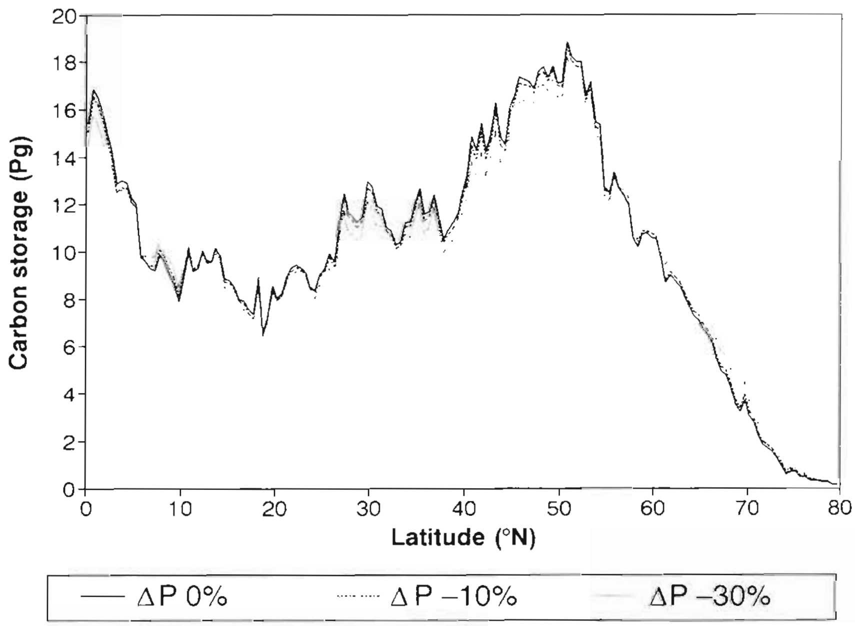

Fig. 4. Zonally averaged values of total carbon storage for precipitation variations of 0% (present-day situation), -10% and -30%, by latitude

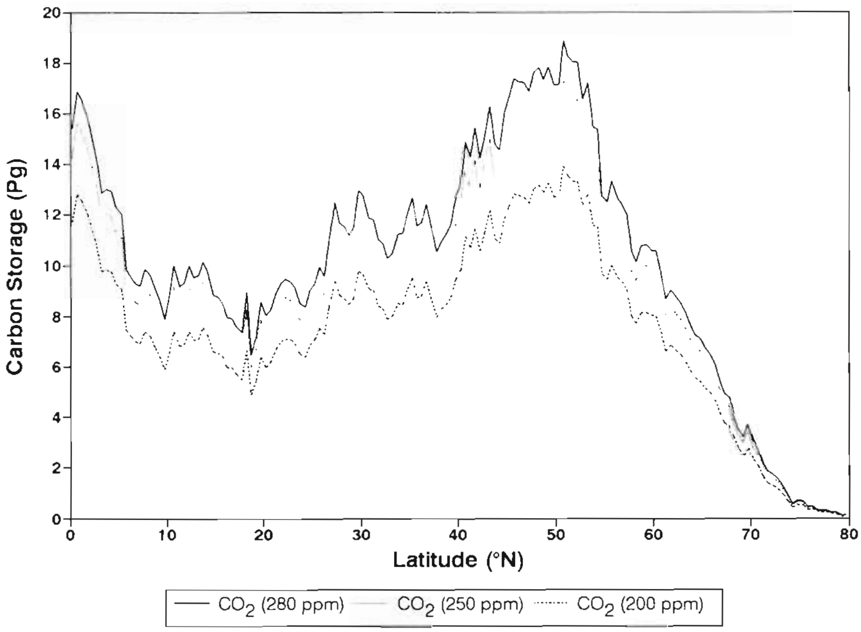

Fig. 5. Zonally averaged values of total carbon storage for several CO_2 concentrations, by latitude. The value of 280 ppmv represents the preindustrial CO_2 concentration

Fig. 6 shows that the greatest decrease of carbon storage was located at mid-latitudes, about 35° to 55° N, where temperature and precipitation are both limiting factors for temperate and boreal forests. Moreover, the CO_2 decrease amplifies the climatic effect through reduction of NPP. The second most sensitive zone was the equatorial band (0° to 5°N), where precipitation and CO_2 concentration were the most limiting factors. Table 2 shows that the total carbon storage was decreased by ~32 % (182 Pg in vegetation, 322 Pg in soil). If we consider the extension of the ice caps and the more pronounced temperature decrease which occurred at the middle latitudes during the LGM, these carbon storage values certainly represent an upper limit. This must be tested now with more realistic anomalies.

A MORE REALISTIC TEST FOR THE LGM IN THE NORTHERN HEMISPHERE

Vegetation and climatic LGM palaeodata at each gridpoint are necessary to run the OBM, but very few data are available. On the one hand, the CLIMAP re-

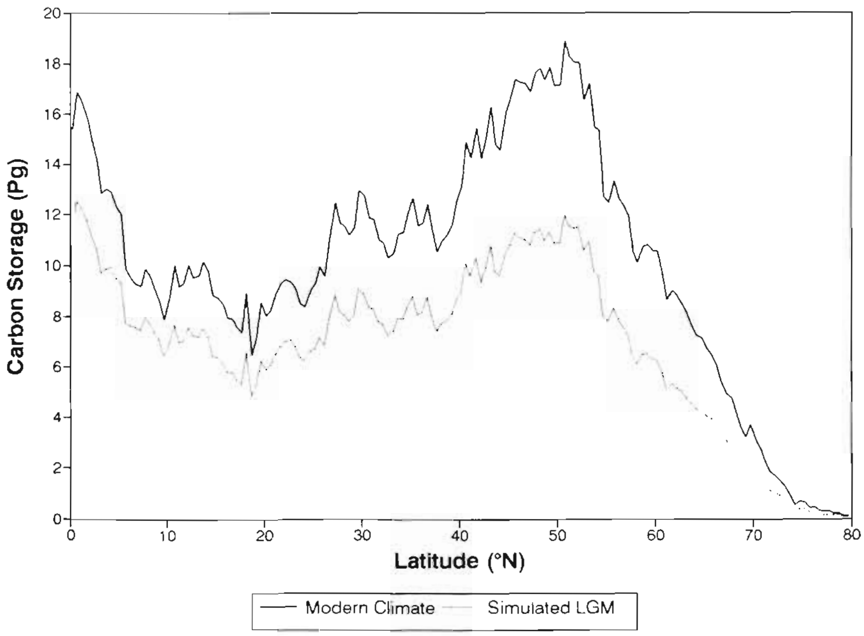

Fig. 6. Zonally averaged values of total carbon storage, by latitude, for the present-day situation and for variations in several factors (simulated LGM: ΔT = −5 °C, ΔP = −30 %, CO_2 concentration = 200 ppmv)

constructions of the earth's surface at the LGM (CLIMAP Project Members 1981) provide main vegetation types, but not the mean annual temperature or total annual precipitation on the continents. On the other hand, the atlas of Frenzel et al. (1992) provides these 3 necessary variables, although the data, methods and stratigraphy on which the reconstructions are based are not clearly shown and their reliability is not indicated. However, the LGM period, with a vegetation dominated by steppes and tundra, is certainly more reliably reconstructed than any other periods presented in this atlas. In the absence of more recent reconstructions based on global palaeoecological databases, we used this atlas to perform an additional test of the OBM.

Climate reconstruction

The anomalies of the mean annual temperature (ΔT_{18k}), and total annual precipitation (ΔP_{18k}) for the LGM were digitized at the 0.5° × 0.5° gridpoints from the atlas of Frenzel et al. (1992). The mean annual temperature (T_{18k}), and total annual precipitation (P_{18k}) were obtained by adjusting the IIASA modern climate (Leemans & Cramer 1991) database values (T0k, P0k) using the gridded anomalies:

$$T_{18k} = T_{0k} + T_{18k}$$
$$P_{18k} = P_{0k} + P_{18k}$$

Vegetation reconstruction

The map of ecosystems proposed by Grichuk (Frenzel et al. 1992) provides the distribution of 9 main vegetation types which were digitized at the 0.5° × 0.5° grid level for the LGM. They correspond to a subset of the biomes of Prentice (Table 1): (1) preglacial tundra vegetation (TUND), (2) preglacial steppe vegetation (COGS), (3) boreal forest (TAIG), (4) broad-leaved and mixed conifer forest (COMX), (5) steppe and desert vegetation (SEDE), (6) subtropical savanna vegetation (SAWO), (7) tropical forests (TRDF), (8) tropical desert steppe vegetation (HODE), (9) high mountain (alpine) vegetation (TUND). The mean stand age (years) of each vegetation type and the factor needed to calculate the proportion of herbaceous and woody production were derived from Esser (1991, Table 31.6) assuming that these values are the same as those of the present for corresponding vegetation types.

Soil data

Because of the lack of soil information for the LGM, we simply used the same soil map as for the present and the same fertility factor (F_{soil}), assuming that F_{soil} stays constant under modern climatic conditions and LGM boundary conditions. We have no reason to think that such an assumption has important consequences for carbon storage, since F_{soil} values are in fact empirical correction factors which are defined as the ratio of the NPP measured on a given soil type to the NPP calculated from the MIAMI model (Lieth 1975).

Estimation of carbon storage

Because the potential fertilization effect of CO_2 is not fully understood and certainly depends on factors not considered here, we chose 2 basic scenarios for estimating LGM carbon storage, as in Esser & Lautenschlager (1993): Scenario 1, CO_2 fertilization effect considered; Scenario 2, no CO_2 fertilization effect.

Scenario 1. At 200 ppmv CO_2, the total carbon storage was estimated to be about 910 Pg (193 Pg in vegetation, 717 Pg in soil). This result indicates a 694 Pg increase in vegetation and soil since the LGM in the Northern Hemisphere, which is much more than the carbon storage increase (400 to 500 Pg) obtained for the whole globe based on ocean $\delta^{13}C$. Thus, the OBM certainly overestimates the CO_2 fertilization reduction during the LGM (Esser & Lautenschlager 1993).

Scenario 2. Neglecting the CO_2 fertilization effect gave carbon storage estimates of about 1276 Pg (251 Pg in vegetation, 1025 Pg in soil), which implies a 327 Pg increase in vegetation and soil since the LGM in the Northern Hemisphere, due solely to climate improving. This result is closer to the estimates of Van Campo et al. (1993). Considering that the carbon storage of the Northern Hemisphere contributed about 70% of the global carbon budget at the LGM as calculated by Van Campo et al. (1993), this result agrees with the 400 to 500 Pg post-glacial increase in global terrestrial carbon storage estimated by deep ocean $\delta^{13}C$ (Duplessy et al. 1988). This scenario shares with all the previous approaches (Adams et al. 1990, Prentice & Fung 1990, Friedlingstein et al. 1992, Van Campo et al. 1993, Prentice et al. in press) the assumption that the modern carbon densities for each ecosystem can be extrapolated to the LGM.

DISCUSSION AND CONCLUSION

The sensitivity experiments suggest that temperature and atmospheric CO_2 concentration have important effects on terrestrial carbon storage. The CO_2 fertilization factor, which depends on the CO_2 concentration and soil fertility, involves complex processes. Although the CO_2 fertilization effect as modified by

Esser (1991) is reliable for the modern CO_2 concentration, extrapolation to the lower glacial CO_2 concentration (200 ppmv) at the LGM is still highly speculative and probably unreliable (Esser & Lautenschlager 1993).

The carbon storage of Scenario 1 is close to the low carbon storage estimates of Van Campo et al. (1993), whereas the result of Scenario 2 is most similar to their median estimate (Table 3). In fact, large parts of North America, Europe and Asia were covered by herbaceous vegetation (Melillo et al. 1990). C4 plants were more extensive than C3 plants during the LGM, for several reasons: C4 plants are not only more competitive (Patterson & Flint 1990) but also have a higher net photosynthesis (Taiz & Zeiger 1991) than C3 plants at low CO_2 concentrations. Considering C4 plants' physiological and ecological mechanisms and metabolism, the NPP of vegetation dominated by C4 plants should have been less reduced at the LGM than that constituted mainly by C3 plants. The carbon storage at the LGM should thus have been greater than suggested by Scenario 1 (Esser & Lautenschlager 1993). But, although the result of Scenario 2 is more similar to that of Van Campo et al. (1993), neglecting CO_2 fertilization is not realistic either. Rather, the reality must have been between these 2 extremes. A realistic estimate of carbon storage in the Northern Hemisphere at the LGM, therefore, is between 910 and 1270 Pg.

If we compare the results of our 2 scenarios with the estimates of Esser & Lautenschlager (1993) using the previous assumption that the carbon storage of the Northern Hemisphere contributed about 70% of the global carbon budget during the LGM, as calculated by Van Campo et al. (1993), we find (Table 3) that the carbon storage levels under 2 scenarios of Esser & Lautenschlager (in press) are higher than those reported both in this study and in Van Campo et al. (1993). Especially the results of Scenario 2 of Esser & Lautenschlager (1993) (i.e. 19.2% increase from LGM to present) are in disagreement with both the global deep ocean $\delta^{13}C$ data and our Scenario 2 result (i.e. 20.6% decrease). The main reason for this is that the AGCM model simulations generally overestimate precipitation in tropical and subtropical regions at the LGM, leading not only to a great reduction in the areas simulated as deserts and an extension of other biome types, but also to an increase in carbon content (Van Campo et al. 1993).

In Fig. 7, a comparison of the distribution of carbon storage among several major ecosystems is made between Scenario 2 of this study and the Van Campo et al. (1993) study (both without CO_2 fertilization effects). The figure shows that the greatest differences occur for the tundra and the tropical dry forest ecosystems, but in opposite directions. For the latter ecosystem, the

Table 3. Carbon storage budget from the LGM to the present in the Northern Hemisphere as reported in this study, Van Campo et al. (1993) and Esser & Lautenschlager (1993). The percentage change was calculated according to the mean present value. The areas do not include the ice and polar deserts. In the columns for Esser & Lautenschlager (1993), the values in parentheses are related to areas which were inundated due to rising sea level, the values for soil C include carbon storage in litter and the areas are estimated by assuming that the area of the Northern Hemisphere contributed about 75% of the global area as calculated by Van Campo et al. (1993)

	This study			Van Campo et al. (1993)				Esser & Lautenschlager (1993)		
		LGM			LGM				LGM	
Times:	Present	Scenario 1	Scenario 2	Present	Low	Median	High	Present	Scenario 1	Scenario 2
Area (× 10^6 m^2)	100.96	96.71	96.71	100.96	96.71	96.71	96.71	102.30	95.33	95.33
Veg C (Pg)	431	194	251	500	205	272	370	496	329 (74)	432 (99)
Soil C (Pg)	1173	716	1025	1242	739	978	1201	1188	980 (152)	1274 (202)
Total C (Pg)	1604	910	1276	1742	944	1250	1571	1684	1309 (226)	1706 (301)
LGM – present		−694	−328		−798	−492	−171		−149	+323
Change		−43.3%	−20.6%		−45.8%	−28.2%	−9.8%		−8.8%	+19.2%

difference is due to the difference in the area reconstructed (Fig. 7a, TRDF). For the tundra, Olson et al. (1985) ascribe a higher carbon density than estimated by the OBM, which is likely unable to simulate the high carbon content in tundra soil.

The OBM is inherently limited, because it is a regression-based empirical model which hardly takes into account possible geophysical feedback between decomposition and productivity (McGuire et al. 1993). Moreover, because of the lack of systematic soil information for the LGM, it is probably simplistic to assume the same soil fertility factors from the LGM to the present. A further limitation lies in our insufficient knowledge of palaeoclimate and palaeovegetation distribution at the LGM. The alternative is to couple a biosphere model to an AGCM simulation, as was done by Esser & Lautenschlager (1993), but this approach also has limitations (low resolution, rough parameterization and approximate boundary conditions) and must be validated by data, which justifies our approach.

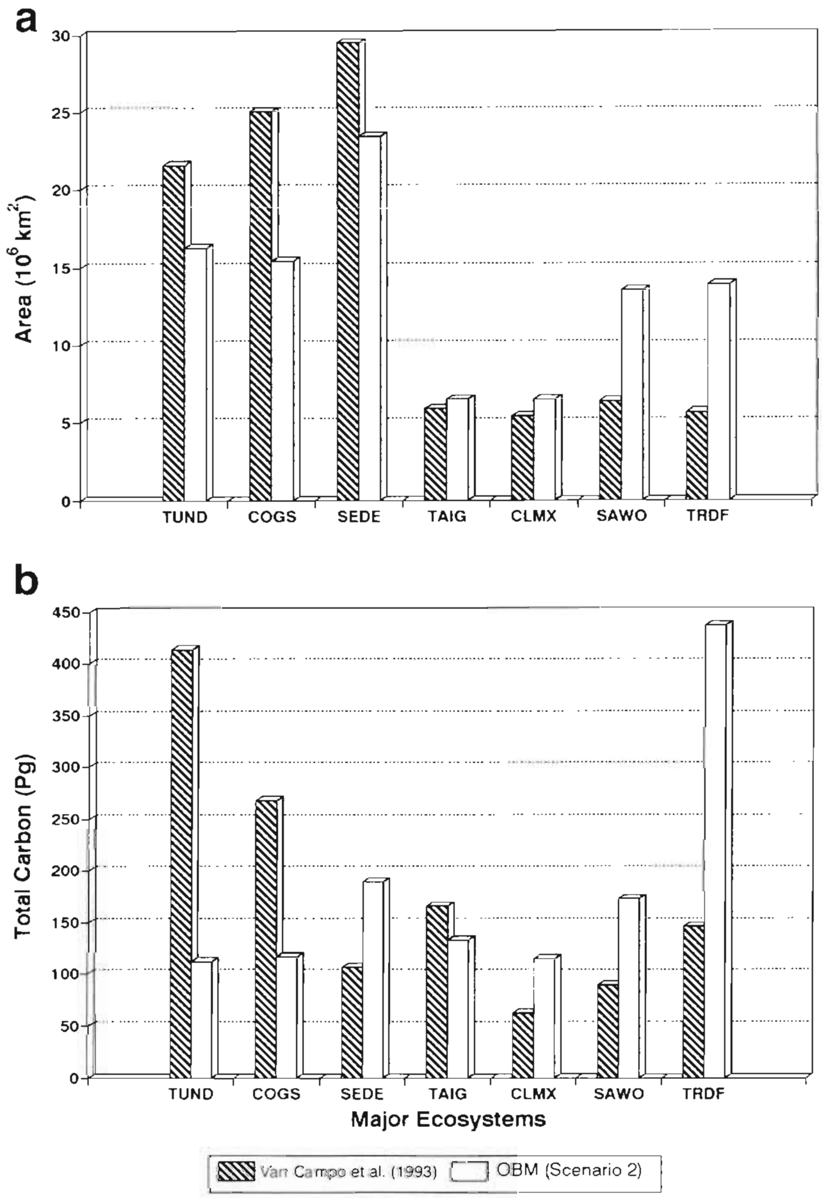

Fig. 7. Comparison between the results of Van Campo et al. (1993) and those of Scenario 2 of this study (no CO_2 fertilization), showing (a) area, and (b) total carbon storage of the major ecosystems at the LGM (see Table 1 for ecosystem codes). Here TRDF includes EQEG; SEDE includes HODE; CLMX includes COMX, WADE and CLDE. The other ecosystems are not represented at the LGM

In summary, our sensitivity experiments suggest that the changes in temperature and in CO_2 concentration affect carbon storage more than changes in precipitation. It appears that a weakening of CO_2 fertilization must be invoked to obtain a realistic estimate of LGM carbon storage. At the scale of the Northern Hemisphere, our reconstruction (i.e. low terrestrial carbon storage at the LGM combined with low CO_2 concentration) implies that the terrestrial biosphere acted as a sink for the CO_2 released by the ocean during the post-glacial atmospheric CO_2 increase. The size of this sink, based on our reconstruction from the Osnabrück Biosphere Model and palaeodata, agrees broadly with the values estimated on the basis of 0.32‰ change obtained for global deep ocean $\delta^{13}C$.

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