

Carbon cycle, Vegetation and Climate Dynamics in the Holocene: Experiments with the CLIMBER-2 Model

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Abstract

Multiple proxy data reveal that the early to middle Holocene, ca. 8 to 6 kyr BP, was warmer than the pre-industrial period in most regions of the northern hemisphere. This warming is presumably explained by the higher summer insolation in the northern hemisphere owing to changes in the orbital parameters. Subsequent cooling in the late Holocene was accompanied by significant changes in vegetation cover and an increase in atmospheric CO₂ concentration. The essential question is whether it is possible to explain these changes in a consistent way accounting for the orbital parameters as the main external forcing for the climate system. We investigate this problem using the computationally efficient model of climate system, CLIMBER-2, which includes models for oceanic and terrestrial biogeochemistry. We found that changes in climate and vegetation cover in the northern subtropical and circumpolar regions can be attributed to the changes in the orbital forcing. Explanation of the atmospheric CO₂ record requires an additional assumption of excessive CaCO₃ sedimentation in the ocean. The modeled decrease in the carbonate ion concentration in the deep ocean is similar to that inferred from CaCO₃ sediment data [Broecker *et al.*, 1999]. For 8 kyr BP, the model estimates the terrestrial carbon pool ca. 90 Pg higher than its pre-industrial value. Simulated atmospheric $\delta^{13}\text{C}$ declines during the course of the Holocene similar to $\delta^{13}\text{C}$ data from the Taylor Dome ice core [Indermühle *et al.*, 1999]. Amplitude of simulated changes in $\delta^{13}\text{C}$ is smaller than in the data, while a difference between the model and the data is comparable with the range of data uncertainty.

An edited version of this paper was published by AGU.
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Global Biogeochemical Cycles, 2002, 16(4), 1139,
doi:10.1029/2001GB001662.

1. Introduction

Ice-core based reconstructions of past climate changes [Jouzel *et al.*, 1987], [Grootes *et al.*, 1993], [Blunier and Brook, 2001] estimate the onset of the current interglacial epoch, the Holocene, to ca. 11.5 thousand years before present (kyr BP). Multiple proxy data (pollen data, macrofossils) reveal that the summer climate in the northern hemisphere was warmer in the early to middle Holocene (ca. 8 to 6 kyr BP) relative to the pre-industrial climate [Velichko *et al.*, 1997], [Prentice *et al.*, 2000]. This warming has been explained by variations in orbital forcing: the northern hemisphere received more solar radiation in the boreal summer during the mid-Holocene than at present [Berger, 1996]. The orbital forcing hypothesis for the mid-Holocene has been successfully tested with climate models of different complexity [Kutzbach *et al.*, 1996], [Hewitt and Mitchell, 1996], [Pollard *et al.*, 1998], [Ganopolski *et al.*, 1998], [Crucifix *et al.*, 2002].

Expanded vegetation cover in the northern circumpolar region and in the northern subtropics suggests that the amount of carbon stored in the vegetation and soils during the mid-Holocene was higher than at pre-industrial (see, e.g., [Adams *et al.*, 1990]). Moreover, ice core data from the Vostok [Barnola *et al.*, 1993] and the Taylor Dome [Indermühle *et al.*, 1999] show that the atmospheric CO₂ concentration during 9 to 8 kyr BP was about 20 ppmv lower than the pre-industrial level. Analyzing the $\delta^{13}\text{C}$ record from the Taylor Dome, Indermühle *et al.* [1999] suggested that an increase in the atmospheric CO₂ concentration during the course of the Holocene was mainly caused by the decay of terrestrial carbon accumulated in the early Holocene. Alternatively, Broecker *et al.* [1999] suggested that the increase in the atmospheric CO₂ concentration during the Holocene can be explained by accounting for a carbonate compensation mechanism in the ocean which operates on a time scale of the order of 5 thousand years. Presumably, CO₂ release from the ocean during glacial-interglacial transition [Archer, 2000] led to an increase in the carbonate ion concentration in the deep ocean and a deepening of saturation horizon for calcite. The oceanic carbonate system had reacted by excessive accumulation of CaCO₃ sediments and restoring of the carbonate ion concentration in the deep ocean. As a result, total ocean alkalinity declined, CO₂ solubility decreased, and atmospheric CO₂ concentration increased. The latter hypothesis is supported by analysis of carbonate sediments in the deep tropical ocean

and broad-scale evidence of excessive accumulation of CaCO₃ in the ocean during the Holocene [Milliman, 1993].

These hypotheses can be tested by using of prognostic models of the global carbon cycle. The essential task is to explain the changes in carbon cycle during the Holocene in a way consistent with climate and vegetation changes, assuming that variations in the orbital parameters are the only external forcing. We investigate this problem with the climate system model CLIMBER-2 which includes dynamic atmosphere, ocean and vegetation models, as well as oceanic biogeochemistry model.

The paper is organized in the following way. First we describe the terrestrial and oceanic biogeochemical components and present results for the pre-industrial simulation AOVC-0K (Atmosphere-Ocean-Vegetation-Carbon simulation with boundary conditions at 0 kyr BP, see Table 1 for experiment acronyms). Then we discuss equilibrium simulations for 8 kyr BP. Finally, we present results of transient simulations from 8 kyr BP till the pre-industrial (see Table 2) and compare them with available proxy.

2. Model Description and Performance for Present-day Climate

CLIMBER-2 is a climate system model of intermediate complexity [Petoukhov *et al.*, 2000]. It includes a 2.5-dimensional dynamical-statistical atmosphere model with a coarse spatial resolution of 10° in latitude and 51° in longitude, a multi-basin, zonally-averaged ocean model, including a sea ice model, which operates with latitudinal resolution of 2.5° and a terrestrial vegetation model. Results of CLIMBER-2 compare favorably with data of the present-day climate [Petoukhov *et al.*, 2000], with paleoclimatic reconstructions [Ganopolski *et al.*, 1998], [Claussen *et al.*, 1999a], [Kubatzki *et al.*, 2000] and with results from sensitivity experiments undertaken with comprehensive models [Ganopolski *et al.*, 2001].

2.1. Atmosphere-Vegetation Coupling

In CLIMBER-2, the vegetation model interacts with the atmospheric model. At the end of the simulation year, output of the atmospheric model (temperature and precipitation fields) is used for simulating vegetation cover and the terrestrial carbon cycle. In turn, the vegetation cover and the maximum of leaf area index (LAI) are accounted for in calculating the surface albedo, roughness, and evapotranspiration

during the following simulation year. The land surface component in CLIMBER-2 has daily time step; it treats land as a fractional composition of simple land surface types (trees, grass, desert, and ice). The description of land surface processes is based on the biosphere-atmosphere transfer scheme by *Dickinson et al.* [1993].

2.2. Terrestrial Biosphere

The model for the terrestrial biosphere VECODE [Broukin *et al.*, 2002], [Cramer *et al.*, 2001] was designed specifically with the purpose of interactive coupling with a coarse resolution atmospheric model for long-term simulations. It is a reduced-form dynamic global vegetation model (DGVM), which simulates changes in vegetation structure and terrestrial carbon pools on a time scale from decades to millennia. Plant functional types (PFTs, see e.g. [Prentice *et al.*, 1992], [Chapin *et al.*, 1996] for PFT conception) are used to describe vegetation cover (section 2.2.1). For any given climate, there is a unique stable composition of PFTs corresponding to the climate (in this context, we refer to climate as long-term averaged atmospheric fields). If climate changes, then the vegetation model simulates the transition from the equilibrium for the previous climate to a new equilibrium with the new climate (section 2.2.3). The time scale of this transition is determined from the carbon cycle model (section 2.2.2).

2.2.1. Bioclimatic Classification. A fractional bioclimatic classification [Broukin *et al.*, 1997] is developed in order to adapt discrete bioclimatic classifications (e.g. Life Zones by *Holdridge* [1947] or BIOME by *Prentice et al.* [1992]) for coarse resolution climate models. Two basic PFTs are used: trees and grasses. The sum of tree fraction, f , and grass fraction, g , is equal to vegetation fraction, v ; the rest is desert fraction, $d = 1 - v$. These transient fractions are different from equilibrium fractions (vegetation in equilibrium with climate), denoted by \hat{f} , \hat{v} . Semi-empirical parameterizations for \hat{f} (Eq. A11) and \hat{v} (Eqs. A12-A14) are based on regularities of distribution of forest and desert in climatic space [Lieth, 1975] which have ecophysiological basis [Woodward, 1987]. Vegetation map by *Olson et al.* [1985] and updated version (Cramer, pers. comm.) of climate dataset by *Leemans and Cramer* [1991] were used in the validation procedure.

CLIMBER-2 is able to simulate the basic global patterns of the present-day potential vegetation cover: A boreal forest belt, tropical forests (see Fig. 1,a),

subtropical deserts in Africa and Eurasia (Fig. 1,c). Grasses occupy a significant part of high latitude regions as well as subtropical areas (Fig. 1,b). In mid-latitudes in Northern America, the model overestimates the tree fraction due to the coarse model resolution: the strong west-east gradient in precipitation is not represented by the mean value across the continent.

2.2.2. Carbon Cycle. Carbon in vegetation is aggregated into two compartments: a 'fast' pool of green biomass (leaves), C_{Φ}^1 , and a 'slow' pool of structural biomass (stems, roots), C_{Φ}^2 . Dead organic matter is described by two pools: a 'fast' compartment (woody residues), C_{Φ}^3 , and a 'slow' compartment (humus), C_{Φ}^4 . Variables C_{Φ}^i are simulated separately for trees and grass. The dynamics of the carbon pools are integrated with an annual time step (Eqs. A1-A4). These equations are written in general form for ^{12}C and ^{13}C . Net primary productivity (NPP), Π , is simulated on an annual basis following the semi-empirical parameterization (Eq. A5) by *Lieth* [1975] which is often used for first-guess estimations on a global scale [Post *et al.*, 1997]. Eq. (A5) compares favorably with bulk measurements for NPP for present-day climate everywhere except in the dry subtropical regions where it overestimates productivity. In these regions NPP is corrected by accounting for the vegetation fraction (Eq. A12) as NPP averaged over the grid cell is equal to $\Pi \cdot v$. Dependence of NPP on the atmospheric CO_2 concentration, C_{atm} , is taken into account by the biotic growth factor in a logarithmic form (Eq. A5) [den Elzen *et al.*, 1995].

NPP allocation between green and structural biomass is estimated as a function of NPP, with increased allocation to C_{Φ}^2 relative to C_{Φ}^1 as NPP increases (Eq. A6). For calibration of this function we used an empirical dataset of NPP and carbon storage from about 500 sites in the northern Eurasia, collected by *Bazilevich* [1993]. The same data were used for calibrating parameterizations for the turnover time of biomass τ_{Φ}^i , $i = 1, 2$, which is assumed to be a function of NPP (Eq. A7). The turnover time of soil carbon τ_{Φ}^i , $i = 3, 4$, is a function of the mean annual temperature following the approach by *Schimel et al.* [1994]. The annual maximum of LAI is assumed to be proportional to the green biomass.

For simulation of the global ^{13}C budget the grass fraction is diagnostically separated into fractions of C_3 and C_4 types, g_3 and $g - g_3$ correspondingly, applying a coldest month temperature threshold similar to Eq. (A17) of *Haxeltine and Prentice* [1996]. The

only simulated difference between C_3 and C_4 grasses is ^{13}C fractionation (see Table 3). Results for the terrestrial carbon cycle from the AOVC-0K simulation are presented in the Figs. 2, 3. For potential vegetation (without historical deforestation), the model estimates global NPP of 56 PgC yr^{-1} and biomass and soil carbon of 850 and 1080 PgC , respectively. Most of the carbon (ca. 85%) is allocated to the C_3 -photosynthesis pathway and the remaining carbon (15%) to the C_4 -pathway. The globally averaged $\delta^{13}\text{C}$ fractionation factor for terrestrial biosphere is 0.984.

2.2.3. Vegetation Dynamics. To account for the sub-grid scale processes of vegetation succession, we apply linear equations (A8-A9) for simulating the dynamics of the PFT fractions. The model implies that the vegetation cover reacts to any climate change with a relaxation towards a new equilibrium with a time scale determined by the turnover time of the structural biomass. For instance, if the climate becomes more wet and the equilibrium fraction of trees increases, then the trees become more successful in competing with grasses and occupy an additional fraction of land within the large grid cell with a time scale of tree growth. In vicinity of an equilibrium, Eq. (A8) is a linearized version of the evolutionary model for vegetation dynamics [Svirezhev, 1999] which accounts for competition between trees and grasses in the idealized form. With respect to the dynamics of the northern treeline under CO_2 -induced climate change, VE-CODE shows similar performance to other dynamic global vegetation models [Cramer *et al.*, 2001].

2.3. Ocean Biogeochemistry

We account for the biogenic production and the subsequent remineralization of organic and inorganic matter (calcium carbonate shells) in the ocean. Sources from riverborne material and aeolian dust, sinks due to sedimentation are neglected. The biogeochemical tracers (Γ) considered in the model are phosphate (PO_4), oxygen (O_2), alkalinity (ALK), dissolved inorganic carbon (DIC, concentration denoted as C_{dic}), two types of dissolved organic carbon (DOC, concentration denoted as C_{doc}^f and C_{doc}^s for fast and slow pools, respectively), as well as the carbon isotopes (^{13}C and ^{14}C) for DIC and DOC. The conservation equation (B1) is solved for every tracer Γ , where $A_d(\Gamma)$ is advective, diffusive, and convective transports and $J_{org}(\Gamma)$ and $J_{car}(\Gamma)$ are internal sources and sinks associated with organic and inorganic (CaCO_3) carbon, respectively. Equations for DIC and DOC are written in general form for ^{12}C and

^{13}C . For radiocarbon $J(\Gamma)$ includes the third term, $J_r(\Gamma)$, associated with radiocarbon decay.

The global mean phosphate and alkalinity values of $2.08 \mu\text{eq kg}^{-1}$ and $2,373 \mu\text{eq kg}^{-1}$, respectively, were obtained from the WOA94 [Conkright *et al.*, 2000], GEOSECS and the TTO data sets. These global mean values are in accordance with previous used values (e.g. [Shaffer, 1996], [Bacastow and Maier-Raimer, 1990]).

At the sea surface, DIC and O_2 are exchanged with the atmosphere. The concentration of O_2 in the upper ocean layer is assumed to be saturated. For CO_2 and its isotopes the surface exchange is determined from the difference in the partial pressure of CO_2 in the air and in the surface water with the gas exchange coefficient of $0.06 \text{ mol m}^{-2} \text{ yr}^{-1} \mu\text{atm}^{-1}$ derived by balancing the air-sea gas exchange of ^{14}C with the total decay of ^{14}C in the ocean [Siegenthaler, 1986]. The $p\text{CO}_2$ in the surface water is calculated from surface temperature, salinity, DIC and ALK in accordance with Millero [1995]. Eqs. (30-34) from [Marchal *et al.*, 1998] are used to account for the temperature dependence of ^{13}C fractionation factor on DIC components. Biological fractionation factor, α_{org}^{13} , depends on $\text{CO}_2(\text{aq})$ in accordance with Rau *et al.* [1989].

Biological processes in the euphotic zone (the upper 100 meters in the model) are explicitly resolved using the model for plankton dynamics by Six and Maier-Reimer, [1996], see Eqs. (B2-B18). This model is modified to account for a slow DOC pool with time scale of 40 years. Globally averaged concentration of the slow DOC is about $5 \mu\text{mol kg}^{-1}$; a small fraction (10%) of the detritus produced in the photic layer is allocated into this pool (Eq. B17).

It is widely assumed that the availability of nitrate and, in some places, of iron governs biological productivity. However, the utilization of nitrogen is accompanied by phosphate uptake, and stoichiometric ratio of nitrogen to phosphorus in biological production is almost constant. We follow a simplified approach by Six and Maier-Reimer [1996] that the phytoplankton productivity is limited by phosphate. Remineralization of particulate organic carbon (POC) and dissolution of CaCO_3 in the aphotic layer are functions of depth (Eqs. B19-B22) following the approach by Yamanaka and Tajika [1996] and Martin *et al.* [1987]. The mass balance for POC and CaCO_3 is satisfied by remineralization of the flux reaching the ocean floor in the deepest model cells in accordance with approach by Marchal *et al.* [1998]. During remineralization of organic matter we assume fractionation between

nutrients and carbon such that C:P ratio, $\eta_{dic}(z)$, increases non-linearly from the traditional Redfield value (106) at the surface to 125 below 2000 meters depth [Shaffer *et al.*, 1999]. The O₂:P ratio, $\eta_{O_2}(z)$, changes almost linear from -138 at the surface to -170 below 2500 meters depth (Eq. B24) in accordance with Shaffer *et al.*, [1999]. The mass balance in the vertical column is conserved by decreasing values for $\eta_{dic}(z)$ and $\eta_{O_2}(z)$ in the depth interval from 100 to 500 m to ca. 103:1 and 133:1 for C:P and O₂:P, respectively.

The results for AOVC-0K are shown in Fig. 4. Global oceanic NPP is about 44 PgC yr⁻¹, POC is 7.2 PgC yr⁻¹, CaCO₃ flux is ca. 0.7 PgC yr⁻¹. The advective and diffusive transport of DOC from the surface layer is 2 PgC yr⁻¹ for the labile DOC-pool, which has a half life of less than one year, and about 2 PgC yr⁻¹ for the slowly decomposing DOC-pool.

Distributions of PO₄, DIC, and ALK within three ocean basins are presented in Fig. 5. These distributions are determined by ocean circulation fields provided by the circulation model as well as by the biological processes simulated by the model for marine biota. In general, the model tends to overestimate near-surface concentration of phosphate in the tropical regions (Fig. 4, A, B). Introducing of slow pool of DOC within the model reduces the nutrient trapping in agreement with Marchal *et al.* [1998]. However, the usefulness of this approach is limited because a high level of nutrients transport with slow DOC leads to unrealistically diffusive spatial structure of the tracer fields. In the intermediate to deep ocean, distributions of phosphate, DIC (Fig. 4, C,D) and ALK (see Fig. 4, E,F) are in good agreement with the data. Distribution of O₂ (not shown) reflects the distribution of PO₄; the minimum of oxygen concentration (10-50 $\mu\text{mol kg}^{-1}$) is reached below the euphotic layer in the tropical Pacific and Indian.

A scheme for global carbon cycle for (AOVC-0K) is presented in Fig. 6. The oceanic and terrestrial carbon storages are 38,320 and 1,930 PgC, respectively. Although oceanic storage of DIC is much larger than terrestrial carbon pool, oceanic and terrestrial net primary productivities are similar (44 and 55 PgC yr⁻¹, respectively).

3. Carbon Cycle Simulation for the Holocene

3.1. Equilibrium simulations for 8 kyr BP

We choose 8 kyr BP as a time for initial conditions because of features of atmospheric CO₂ record inferred from the Taylor Dome ice core [Indermühle *et al.*, 1999]. This period was a turning point in atmospheric CO₂ dynamics: after a gradual decline to 260 ppmv the CO₂ concentration started to increase again. The atmospheric CO₂ concentration was nearly constant during 8,800-8,000 yr BP, such that the processes with time scales of up to several hundred years were in equilibrium with atmospheric CO₂ concentration around 8 kyr BP.

In the equilibrium simulation for the Holocene (AOVC-8K, see Table 1) the atmospheric CO₂ concentration is fixed to 260 ppmv. For atmospheric $\delta^{13}\text{C}$ we use a value -6.4‰ (following spline estimate for the Taylor Dome data at 8 kyr BP, see Figure 2 in [Indermühle *et al.*, 1999]). Orbital forcing is prescribed following Berger [1996]. Sea level and inland ice distribution are the same as in (AOVC-0K). With these boundary conditions and initial conditions taken from (AOVC-0K), we simulate 10,000 years of the coupled atmosphere, ocean, vegetation and biogeochemistry modules until equilibrium is approached.

3.1.1. Changes in climate. Spatial distribution of temperature and precipitation changes (AOVC-8K minus AOVC-0K) is presented in Fig. 7. System response is determined by seasonal asymmetry in orbital forcing, lowered atmospheric CO₂ concentration, and interaction between atmosphere, ocean, and vegetation [Ganopolski *et al.*, 1998]. The northern winter season is slightly cooler (0.5-1°C) in a zone from 30°S to 60°N, especially over the continents (Fig. 7,A). This cooling was not observed in the mid-Holocene simulation with the previous CLIMBER-2 version [Ganopolski *et al.*, 1998], particularly because now we account for decreased atmospheric CO₂ concentration that corresponds to ca. 0.2°C global cooling. However, similar to our previous results, there is a winter warming up to 2°C over the Arctic ocean and continents north of 70°N, which is explained by the decreased sea ice area and sea ice-albedo feedback amplified via forest-temperature feedback. In this season (austral summer), there is a decline in precipitation over land in the tropics, which is especially significant (up to 1 mm day⁻¹) over Southern America. This is mainly explained by a decrease in the land-ocean temperature gradient. As a result, lat-

eral monsoon weakens and moisture convergence over continents decreases.

During the northern summer, a warming of up to 3°C is pronounced over land in the northern hemisphere and tropical land in the southern hemisphere. A warming due to increased summer insolation is amplified by feedbacks between the components of the climate system (Fig. 7,B). Due to the large heat capacity of the ocean, seasonal changes in solar radiation result in much smaller temperature changes over the ocean than over the land. Summer precipitation increases significantly (by $1\text{-}1.5\text{ mm day}^{-1}$) in the North Africa and in the Asian subtropical regions (Fig. 7,D), mainly as a result of intensified monsoon-type circulation which is amplified by vegetation-precipitation feedback [Claussen and Gayler, 1997; Ganopolski et al., 1998]. The wetter conditions in the northern East Asia are explained by intensified monsoon-type circulation, increased forest cover, and subsequent increase in moisture convergence.

In southern Europe, summer precipitation are lower by 0.5 mm/day due to several reasons. First, westerlies in the middle latitudes in the Northern hemisphere are reduced in summer due to: (a) a decrease in the equator-to-pole temperature difference; (b) development of a cyclone-type component of atmospheric circulation around North Africa in response to a lowering of the sea level pressure. Weakening of westerlies reduces eastward moisture flux in spite of intensified evaporation over Atlantic. Second, a development of the ascending branch of vertical velocity in low and middle troposphere over North Africa is compensated in the model via formation of correspondent descending branch over southern Europe, which suppress precipitation over the latter region. Third, an increase in the surface air temperature over the land is more pronounced than over the ocean. All factors contribute to a noticeable decrease in the relative humidity over southern Europe.

Changes in the annual near surface air temperature are 0.1°C and 0.2°C for the globe and the northern hemisphere, respectively. Changes in the temperature over the southern hemisphere and global sea surface temperature (SST) are negligible. The hypothesis of decreased SSTs during the early Holocene discussed by Indermuhle et al. [1999] is not supported by CLIMBER-2 simulation. The thermohaline circulation in the Northern Atlantic is slightly weaker (by 0.2 Sv).

3.1.2. Changes in vegetation cover and terrestrial carbon balance. Changes in the vegetation structure (AOVC-8K minus AOVC-0K) are presented in Fig. 8. Most remarkable changes in terms of vegetation cover are seen in the Afro-Asian northern subtropical regions, north-eastern Asia and high northern latitudes.

Changes in vegetation cover are the most noticeable in the Sahel/Sahara region (Fig. 8,A). The desert fraction inside the Sahara declines to 0.2, the rest of the area is covered by a mixture of C_3 (80%) and C_4 (20%) grasses. More abundant vegetation in the Sahara in the early Holocene is evident from different proxy data [Hoelzmann et al., 1998], [Jolly et al., 1998], [Prentice et al., 2000]. The intensified monsoon-type circulation leads to an increase in tree fraction in the Sahel region, southern and eastern Asia (see Fig. 8,B). Due to a warmer summer the tree fraction increases by up to 0.3 in the northern subpolar region (averaged increase in the zone $60\text{-}70^{\circ}\text{N}$ is 0.2). This warming is partly explained by forest-temperature feedback in the region (presence of forest modifies the radiative balance during the snow season, see [Otterman et al., 1984], [Foley et al., 1994], [TEMPO Members, 1996], [Texier et al., 1997], [Levis et al., 1999]). At the same time, in southern Europe the tree fraction is lower by 0.1 due to an increase in the summer aridity. Similar changes reveal in subtropical regions in the southern hemisphere.

Increased summer aridity and the subsequent decrease in tree fraction in southern and central Europe is explained by a decrease in relative air humidity during the summer season. Pollen reconstructions of vegetation cover reveal reverse changes in southern Europe, for example enhanced deciduous forest cover in the circum-Mediterranean region at the mid-Holocene [Cheddadi et al, 1997], [Tarasov et al., 1998], [Prentice et al., 2000]. At the same time, at several sites in central and south-eastern Europe where present-day "potential" vegetation is forest, a paleosol reconstruction method indicates early Holocene formation of black soil (Schwarzerde or Chernozem), a typical grassland soil [Bork et al., 1998], [Alexandrovsky and Chichagova, 1998]. Similar to the model results, the paleoreconstruction methods reveal that the amplitude of changes in forested area in the region was not considerable.

Changes in NPP are shown in Fig. 8,C. NPP increases significantly in North Africa and in East Asia (up to 0.3 kgC m^{-2}) as a result of wetter climate. At the same time, NPP in southern Europe and in the

southern subtropics slightly decreases. This decrease is caused by a decline in precipitation and a lower atmospheric CO₂ concentration. Globally integrated NPP is higher by 3.1 PgC yr⁻¹.

Changes in vegetation cover and NPP transform into a complex picture of changes in total carbon storage (see Fig. 8,D). Global carbon storage increases by 90 Pg. The most significant increase in the total carbon storage (from 1 to 8 kgC m⁻²) occurs in northern subtropical regions due to decreased aridity. In the Sahara region, soil carbon storage increases by 2.5 kgC m⁻² while changes in biomass are much lower (0.4 kgC m⁻²). In the Sahel, storage increases by 2 and 4 kgC m⁻² for biomass and soil, respectively. Similar increase is seen in South Asia. In southern Europe the losses due to increased aridity are 1.3 and 1.4 kgC m⁻² for biomass and soil, respectively. The southern tropical regions (0-20°S) are a source of carbon as well, due to a decrease in NPP.

In the northern high latitudes, the increase in carbon storage is not as pronounced as the increase in tree fraction. In terms of mean values over the zone 60-70°N, the biomass increases by 1.3 kgC m⁻² while the soil carbon decreases by 0.5 kgC m⁻². The latter is caused by a replacement of tundra with forest, as simulated soil carbon storage for trees is on average by 3 kgC m⁻² lower than the soil carbon storage for grass.

Two additional sensitivity experiments are performed to analyze the relative role of changes in climate and CO₂ in altering the terrestrial and oceanic carbon budget. Our approach is similar to the method by *Cramer et al.*, [2001]. In the first simulation (AOVC-0K-co2), the carbon cycle is driven by a CO₂ concentration of 260 ppmv while the physical climate components simulate the pre-industrial climate from AOVC-0K simulation (see Table 1). In the second simulation (AOVC-8K-clm), the terrestrial carbon responds to a pre-industrial CO₂ concentration (280 ppmv) while the atmosphere/ocean components simulate AOVC-8K climate. The AOVC-0K-co2 simulation reveals effect of changes in atmospheric CO₂ concentration ("CO₂ only"), while the AOVC-8K-clm simulation demonstrates an effect of climatic changes ("climate only"). Changes in terrestrial carbon balance in the simulations are presented in Table 5. In the AOVC-0K-co2 simulation, lower atmospheric CO₂ lead to a decrease in NPP by 1.5 PgC/yr (see Eq. A5). Consequently, carbon storage in biomass and soil decreases, and total terrestrial carbon storage eventually reduces by 49 PgC (see Table 5). In

contrast, the "climate only" simulation reveals an increase in NPP, biomass, and soil carbon, with total gain in 145 PgC. Therefore, changes in the atmospheric fields are more important for the terrestrial carbon budget than the changes in the atmospheric CO₂.

We compare our results with other model assessments of the terrestrial carbon budget for the early to middle Holocene. Inverse modeling approach by *Indermühle et al.*, [1999] (which is based on double deconvolution of Taylor Dome data) revealed a higher terrestrial carbon storage by 195 Pg at 8 kyr BP relative to pre-industrial. In comparison with this estimation, changes within CLIMBER-2 (90 PgC) are smaller in amplitude while qualitatively in the same direction. Regarding experiments with prognostic models for the terrestrial biosphere, differences in the design of experiments are so significant that direct comparison can be misleading. Most simulations were done with "off-line" climate change scenarios, i.e. without accounting for biogeophysical feedbacks. For example, *Foley* [1994b] found a 40 PgC increase in terrestrial carbon storage in an experiment with the DEMETER model using a mid-Holocene climate simulated by the GENESIS model (atmospheric CO₂ was not changed). *Francois et al.* [2000] using the CARAIB model simulated a lower terrestrial carbon storage by 132 PgC and 31 PgC at 6 kyr BP relative to pre-industrial for the climate changes simulated by the ECHAM and LMD-LSCE models, respectively (atmospheric CO₂ concentration was changed from 280 to 260 ppmv). *Beerling* [2000] found a decrease in the terrestrial carbon storage of 265-370 PgC in experiments using the SDGVM model for the climate changes simulated by the UGAMP model for the mid-Holocene. In the latter experiment, a significant part of the carbon loss was presumably a response to a decrease in the atmospheric CO₂ concentration from 350 ppmv to 280 ppmv.

Changes in atmospheric δ¹³C, alteration in vegetation distribution and productivity, all lead to changes of δ¹³C in the terrestrial carbon storage. Replacement of C₃ plants with C₄ plants and vice versa are especially noticeable in the Sahara/Sahel region. In the Sahel, ca. 20% of C₄ grasses are replaced by C₃ trees. In Sahara, C₄ grasses make up 25% of the vegetation cover. On a global scale, changes in distribution of C₃-C₄ plants lead to a slight decrease of terrestrial ¹³C by 0.05‰. However, because of an increase in atmospheric δ¹³C by 0.1‰ in the simulation, the overall effect is an increase in terrestrial

^{13}C by $0.05^\circ/\text{‰}$.

3.1.3. Changes in oceanic biogeochemistry.

Alterations in the distribution of biogeochemical tracers in the ocean follow changes in physical fields (oceanic circulation, temperature) as well as changes in the atmospheric CO_2 . In response to warmer SSTs in the North Atlantic, global oceanic NPP increases by 0.5 PgC/yr and new production increases by 0.1 PgC/yr . Simulated changes in the alkalinity and phosphate distributions are insignificant. In response to the prescribed increase in atmospheric $\delta^{13}\text{C}$ by $0.1^\circ/\text{‰}$ the average oceanic $\delta^{13}\text{C}$ increases by the same value. The total DIC storage in the ocean is 250 PgC lower than in (AOVC-0K) while changes in the DOC inventory are insignificant (increase of 2 PgC).

The relative role of changes in climate and CO_2 for the ocean carbon cycle is explored in the sensitivity simulations AOVC-0K-co2 (CO_2 only) and AOVC-8K-clm (climate only). In the AOVC-0K-co2 simulation, DIC decreases by 240 Pg (see Table 5) due to a lower atmospheric CO_2 concentration. In the AOVC-8K-clm simulation, the oceanic DIC and DOC storages decrease by 10 Pg due to changes in SST and biogeochemical fields. Therefore, changes in the CO_2 boundary conditions are more important for the oceanic carbon budget than the changes in the SST and biogeochemical fields.

3.1.4. Initial conditions for the transient simulation. Summarizing the global carbon balance, there is 200 Pg carbon less in (AOVC-8K) relative to (AOVC-0K) due to changes in the oceanic, terrestrial and atmospheric carbon storages of -250 , 90 , and -40 Pg , respectively (see Table 6). If the biogeochemical fields from the AOVC-8K simulation were taken as initial conditions for the transient simulation from 8 kyr BP to pre-industrial, the initial deficit of 200 PgC would be transformed into too low carbon content of every compartment at the end of the simulation. With a sensitivity of the oceanic DIC storage to the atmospheric CO_2 of 240 Pg C per 20 ppmv (see Table 5, simulation AOVC-0K-co2), the final CO_2 concentration for the pre-industrial would be about 270 ppmv instead of 280 ppmv (neglecting carbonate compensation).

Another important point is that the carbonate ion concentration in the deep ocean is increased by $5 \mu\text{mol kg}^{-1}$ in the simulation AOVC-8K against the pre-industrial simulation (see Table 1). This increase is explained by a decrease in the oceanic DIC storage while the alkalinity was kept constant. If the carbonate compensation were accounted for, the ocean

alkalinity and DIC storage would be lower than in the AOVC-8K simulation. This would lead to even larger carbon imbalance in comparison with the AOVC-0K simulation. However, proxy for the carbonate ion concentration [Broecker *et al.*, 1999] suggest that its value was higher during the early Holocene. Presumably, this increase is explained by CO_2 release from the ocean during glacial-interglacial transition and a deepening of saturation horizon for calcite. The oceanic carbonate system had reacted by excessive accumulation of CaCO_3 sediments and restoring of the carbonate ion concentration in the deep ocean. Because of the long time scale of this process (ca. $5,000 \text{ yr}$), at the early Holocene the oceanic carbonate system was not in equilibrium and the carbonate compensation led to the excessive carbonate accumulation during the Holocene [Milliman, 1993]. Another mechanism for explaining alkalinity changes during the Holocene could be a regrowth of coral reefs [Milliman, 1993].

While modeling of ocean sediments and regrowth of coral reefs is not implemented into the current version of CLIMBER-2, we imitate these processes by removing a fraction of the biogenic CaCO_3 flux above the lysocline (assumed to be at 3.5 km depth). This process immediately removes dissolved carbon in proportion of one mole of DIC per two moles of ALK. On a long time scale, an additional DIC is outgassing to the atmosphere due to decreased alkalinity (this process is simulated explicitly). Consequently, ALK and DIC must be increased for simulation of the initial conditions.

It is also necessary to equalize the total carbon storage for the initial and final time slices. Accounting for the DIC storage sensitivity to the alkalinity and a ratio between the alkalinity and CaCO_3 , we found that with a mean oceanic alkalinity increased by $33 \mu \text{ eq kg}^{-1}$ (ca. 1.3%) the total oceanic carbon storage within the model is higher by 220 Pg than in (AOVC-0K). Changes in the global carbon cycle components in this simulation AOVC-8K-H (H is for high alkalinity) are shown in Table 6. The total amount of carbon in (AOVC-8K-H) is the same as in (AOVC-0K) including excessive CaCO_3 sediments, therefore it can be used as initial conditions for the transient simulation through the Holocene. Sedimentation of CaCO_3 (270 PgC) is necessary to decrease the ocean alkalinity to the pre-industrial value. The difference in the carbonate ion concentration between (AOVC-8K-H) and (AOVC-0K) for the deep tropical ocean is ca. $8 \mu \text{ mol kg}^{-1}$ (see Table 1). The latter is similar

to an estimate of $11 \pm 2 \mu\text{mol kg}^{-1}$ obtained from size distribution of the early Holocene oceanic carbonate sediments by *Broecker et al.* [1999].

3.2. Transient simulations from 8 kyr BP to pre-industrial

In the transient simulation AOVC-T all the components of the climate system (atmosphere, ocean, land vegetation, oceanic and terrestrial carbon cycles) evolve interactively under the slow changes in the orbital forcing. A scenario of oceanic CaCO_3 sedimentation is another external forcing in the simulation. We assume that a fraction of the CaCO_3 flux does not dissolve above the lysocline:

$$f_{sed} = p_{sed} \exp\left(-\frac{t}{\tau_{sed}}\right), \quad (1)$$

where τ_{sed} is a time scale of carbonate compensation (5,000 years) and p_{sed} is taken as 0.18 in order to accumulate 270 PgC during the whole simulation. The initial conditions are taken from (AOVC-8K-H).

3.2.1. Climate, carbon, and vegetation dynamics on a global scale. Results of the transient simulation relative to (AOVC-0K) in terms of zonal average over the land for several model characteristics (insolation, summer warmth, tree fraction and total carbon) are presented in Fig. 9. The changes in summer insolation due to alteration in orbital parameters is especially noticeable at the northern temperate and high latitudes (up to 30 W/m^2 at 8 kyr BP, see Fig. 9,A), where insolation declined smoothly from early Holocene to present [*Berger*, 1996]. The changes in insolation during the last 2,000 years are insignificant. Summer warmth expressed in terms of degree-days above 0 (GDD0) steady declines in middle and high northern latitudes. In the early to middle Holocene, northern subtropical regions are slightly cooler than at the end of the simulation particularly because of expanded vegetation cover and larger evapotranspiration. During the last 2,000 years, changes in GDD0 are negligible (see Fig. 9,B).

On a global scale, annual mean surface air temperature is nearly steady between 8 and 6 kyr BP; it declines by 0.1°C during the next 2,000 years and remains steady after 4 kyr BP (see Fig. 10,A). In the northern hemisphere, the temperature follows the trend of global temperature between 8 and 4 kyr BP, then has minimum around 3 kyr BP and increases again to the pre-industrial value around 500 yr BP (Fig. 10,B). Southern hemisphere exhibits a different kind of dynamics. Temperature reaches a maximum

around 6 kyr BP, then declines and stays almost constant for last 3,000 years (Fig. 10,C). The response of the global mean SST is similar to the response of the southern hemisphere temperature but with smaller amplitude (0.05°C , see Fig. 10,D).

The changes in zonally averaged tree fraction are most significant in the northern high latitudes. Decline in the tree fraction follows the trend of GDD0 in this region (Fig. 9,C). Similarly, in the northern subtropics changes in tree fraction follow changes in precipitation (not shown). At the same time, changes in the southern subtropics are opposite because the region is drier in the early Holocene.

On a global scale, the area covered by trees declines during 8 to 4 kyr BP from 64 to 57 mil. km^2 and remains nearly constant during last 2,000 years (Fig. 11,A). Desert area grows significantly from 15 to 23 mil. km^2 (excluding Antarctica) with most of the changes occurring during 6 to 4 kyr BP (Fig. 11,C). A decrease in grass area (from 58 to 56 mil. km^2) is less significant than the reduction in tree area, because a decrease of grass area in Sahara is compensated by the replacement of trees by grass in Sahel and increase in tundra area at the northern high latitudes. Most of the changes in grass area occur during 6 to 4 kyr BP following aridization of North African climate (Fig. 11,B).

In terms of terrestrial carbon storage, changes are more significant in the subtropical regions than in the northern high latitudes (Fig. 9,D). Decline in carbon storage in the northern hemisphere is followed by a simultaneous buildup of carbon storage in the southern hemisphere. During the last 3,000 years of the simulation the storages are relatively steady. This is explained by simultaneous changes in climate and atmospheric CO_2 . On a global scale, most significant changes in the terrestrial carbon storage occur during 7 to 4 kyr BP, while the last 2,000 years the storages are nearly constant (Fig. 12).

Changes in C_{atm} (Fig. 13,A) are explained by changes in the terrestrial and the oceanic carbon pools (Fig. 12,A). During 8 to 7 kyr BP, the terrestrial carbon pool declines due to changes in vegetation cover and C_{atm} increases by 4 ppmv during that period, well in line with Taylor Dome data. During 7 to 4 kyr BP the decline in land carbon storage of ca. 80 Pg leads to an increase in C_{atm} by additional 10 ppmv (Fig. 13,A) and simultaneous decline in atmospheric $\delta^{13}\text{C}$ by $0.05^\circ/\text{‰}$ (Fig. 13,B). During the next 4,000 years, the oceanic total carbon storage (including CaCO_3 sediments) slowly grows due to absorption of the re-

leased terrestrial carbon. Atmospheric $\delta^{13}\text{C}$ in this period remains steady as $\delta^{13}\text{C}$ emitted by land is absorbed by the ocean (see Fig. 12, B).

During the last thousand years of simulation C_{atm} approaches 280 ppmv. At the end of the simulation the carbon storages are nearly steady: terrestrial biosphere carbon uptake is 0.02 PgC/yr, while release from the ocean is 0.025 PgC/yr. Let us note that we do not account for anthropogenic, solar and volcanic forcings which influenced the climate considerably during the last 1,000 years [Brovkin *et al.*, 1999], [Crowley, 2000].

3.2.2. Regional vegetation dynamics. In the two land regions simulated to have the most pronounced vegetation changes, i.e. northern Africa and the northern high latitudes, we compare the model results with available continuous records of proxy data.

In the Sahara region, vegetation fraction within the model declined from ca. 0.8 at 8 kyr BP to almost 0 at 3 kyr BP. The decrease in vegetation cover is especially rapid during 6 to 4.5 kyr BP. This desertification is a result of a more arid climate amplified by vegetation-atmosphere interaction. Comprehensive analysis of the model performance in the Sahara region (e.g. role of ocean interaction in the system dynamics) is presented in detail in [Claussen *et al.*, 1999b]. Model results compare favorably with the recently analyzed record of aeolian sedimentation at the coast of West Africa which reveals a rapid termination of the African Humid period at the time around ca. 5,500 yr BP [deMenocal *et al.*, 2000].

In the northern high latitudes, pollen data and macrofossils are the main proxy data available for comparison with the model [Velichko *et al.*, 1997], [MacDonald *et al.*, 2000]. Here, we present two continuous Holocene pollen records in lake sediments analyzed recently at the Alfred-Wegener-Institut für Polar- und Meeresforschung in Potsdam. Selected pollen taxa are shown in Fig. 14. The Lama Lake (70°N, 90°E) is situated in the northern taiga near the northern limit of present-day treeline and the Levinson-Lessing Lake (74°N, 98°E) is located in the southern tundra near the boundary with typical Arctic tundra. At the first site, *Picea obovata* (siberian spruce) pollen is abundant in the pollen records for the period from 8 kyr BP to ca. 3 kyr BP and its percentage declines after 3 kyr BP, while *Larix* (larch) pollen percentage shows some increase after 4 kyr BP (Fig. 14,A). The total tree pollen fraction declines after 4 kyr BP. For the last 2,000 years, there is a significant variability in total tree pollen fraction while

its mean level is rather low in comparison with the early Holocene.

At the second site, *Alnus fruticosa* (shrub alder), the main arboreal representative in the pollen records, shows significant decline in the pollen percentage during 8 to 4 kyr BP (Fig. 14,B). Similar changes are seen for *Betula sect. Nanae* (dwarf birch). During the last 3 thousand years, the tree and shrub pollen percentages show little changes, reflecting a treeless environment around the site.

Because of the coarse model's spatial resolution and high spatial variability of vegetation cover in the area, data and model can be compared only in qualitative terms. Changes in the simulated averaged tree fraction in the zone 60-70°N are shown in Fig. 14. Qualitatively, a decline in tree cover evident from the pollen records is in line with the model results. Simulated tree fraction exhibits gradual decline from 0.6 to 0.4, with main changes occur during 8 to 3 yr BP (Fig. 14,C). The main driving force for this decline is the slow cooling over the area which is most pronounced in summer. Climatic reconstruction based on the pollen data from the Taymyr peninsula [Andreev and Klimanov, 2000] reveals gradual summer cooling from the the early Holocene to present-day; changes in winter temperature are not so pronounced in the reconstruction. Besides, the reconstruction shows high interannual variability in climate. Let us note that simulated climate variability is less than the observed variability as the model was designed to simulate the mean climate trend.

3.2.3. Transient simulation with the "ocean only" carbon source scenario. Since submitting this paper, an article by Broecker *et al.* [2001] about causes of the rise of the atmospheric CO_2 content during the last 8,000 years has been published in the *G³*, an electronic journal of the AGU. Broecker *et al.* [2001] supported their previous hypothesis that the rise of the atmospheric CO_2 was caused by the oceanic carbonate compensation with additional proxies. They also presented a scenario of changes in the atmospheric CO_2 and $\delta^{13}\text{C}$ in accordance with their hypothesis. Although release of 90 PgC of terrestrial carbon in the AOVC-T simulation is a result consistent with the simulated climatic changes, it is interesting to compare the scenario by Broecker *et al.* [2001] with CLIMBER-2 results for the "ocean only" carbon source scenario. We performed additional transient simulation (AOVC-T-O) in which an influence of terrestrial biosphere on the carbon balance was neglected for both, atmospheric CO_2 and

$\delta^{13}\text{C}$. Because in this case the land source of 90 PgC was not accounted for, the initial conditions for alkalinity were changed in order to equalize initial and final values of the total carbon storage. Applying procedure similar to the AOVC-8K-H simulation, we found that with the mean alkalinity of $2,421 \mu \text{ eq kg}^{-1}$ the total carbon storage is equal to the total amount of carbon in the AOVC-0 simulation plus 390 PgC of carbonate sediments which are necessary for the alkalinity changes. The sedimentation forcing during transient simulation was prescribed by Eq. 1 where p_{sed} was taken as 0.25 in order to accumulate 390 PgC during the whole simulation. Another equilibrium simulation, (AOVC-8K-O), was done to provide the transient simulation with the initial conditions (see Table 1). The increase of carbonate ion concentration in the deep ocean in this simulation is $9.5 \mu \text{ mol kg}^{-1}$. This value is nearly identical to an estimate of $10 \mu \text{ mol kg}^{-1}$ presented by *Broecker et al.* [2001].

Results of the AOVC-T-O simulation are shown in Fig. 13. Simulated atmospheric CO_2 concentration is generally in line with the Taylor Dome data, although after 5,000 yr BP the simulated trend is at the bottom of the data scatter. Similar to the scenario by *Broecker et al.* [2001], atmospheric $\delta^{13}\text{C}$ is not significantly affected (Fig. 13,B) because: (i) $\delta^{13}\text{C}$ of carbonate is similar to an average oceanic $\delta^{13}\text{C}$; (ii) fractionation of $\delta^{13}\text{C}$ due to sea surface - atmosphere CO_2 exchange is not considerably changed.

Comparing results of AOVC-T and AOVC-T-O simulations, it is difficult to decide which of them is more consistent with the available proxy data. Regarding initial carbonate ion concentration, the AOVC-T-O simulation is more closed to the proxy while the difference between the simulations ($1.5 \mu \text{ mol kg}^{-1}$) is smaller than the proxy precision ($2 \mu \text{ mol kg}^{-1}$, [*Broecker et al.*, 1999]). Trend of the atmospheric CO_2 concentration is nearly identical in both simulations until 6 kyr BP, while later the AOVC-T simulation is more close to the observations (see Fig. 13,A). The difference between simulations has maximum around 4 kyr BP when most of the terrestrial carbon storage is released within the model (see Fig. 12). However, the amplitude of this difference (3 ppmv) is comparable with the scatter of the data. Atmospheric $\delta^{13}\text{C}$ is declining in the AOVC-T simulation, similar to the proxy data, but the amplitude of changes is much smaller than in the data (Fig. 13,B). The AOVC-T-O simulation does not reveal changes in $\delta^{13}\text{C}$, contrary to the proxy. However, the argu-

ment made by *Broecker et al.* [2001] about technical difficulties with measurement of $\delta^{13}\text{C}$ is in favor of possibility that there was no measurable trend in $\delta^{13}\text{C}$ of atmospheric CO_2 during the last 8,000 years. Let us note that the difference between AOVC-T and AOVC-T-O simulations is less than the uncertainty in measuring $\delta^{13}\text{C}$.

We conclude that the difference between two transient simulations is comparable with an uncertainty in the proxy data. Based on the available proxies for the atmospheric CO_2 , $\delta^{13}\text{C}$, and oceanic carbonate ion concentration, it is not possible to answer on the question whether the atmospheric CO_2 rise during the last 8,000 years was caused by the ocean response only or decay of terrestrial carbon has contributed to this rise as well. More proxies are needed to address this question.

4. Discussion and Conclusions

1. Our transient experiment is to our knowledge the first simulation of the global carbon cycle within the framework of a climate system model on a millennium time scale. The simulation is different from experiments on a century time scale [*Cox et al.*, 2000], [*Dufresne et al.*, 2001] because slow long-term processes in the global biogeochemistry (e.g. carbonate sedimentation) are important on a millennium time scale. We set up the initial conditions for the transient experiment in two steps. First, we conducted two equilibrium experiments for initial and final time slices and estimated changes in the oceanic and terrestrial carbon storages while the atmospheric CO_2 concentration was prescribed to the observed values. Then we used an assumption about long-term processes to equalize the total carbon storage for both time slices. Thus, initial conditions guarantee us a proper amplitude of changes in atmospheric CO_2 concentration while changes in $\delta^{13}\text{C}$ are not controlled by the experiment design.

2. Our major conclusion is that changes in the orbital forcing could explain most of the observed long-term dynamics of climate-vegetation system during the Holocene. The most significant changes in vegetation cover during Holocene occurred in monsoon regions in the northern subtropics, above all in the North Africa. Model results compare favorably with the proxy data which reveals very rapid desertification of the Sahara/Sahel region during 6 to 5 kyr BP [*deMenocal et al.*, 2000]. This abruptness can be explained by the atmosphere-vegetation interac-

tion which amplifies the decrease in precipitation due to changes in the orbital forcing [Claussen *et al.*, 1999b]. In eastern Asia, a simulated increase in tree fraction in middle Holocene due to intensified monsoon circulation is in line with proxy data [Prentice *et al.*, 2000].

The northern circumpolar region is another region with a remarkable change in vegetation cover during the Holocene. Continuous pollen records for Taymyr peninsula reveal a decrease in tree pollen during 8 to 3 kyr BP while rather stable vegetation cover during the last 3,000 years. Qualitatively, model results are in line with data. Decline in tree fraction within the model could be interpreted as either a southward retreat of the treeline or a reduction in forest density, or a combination of the two. In North America, the model shows a significant decrease in tree fraction during the Holocene due to summer cooling of 1-2°C. However, proxy data reveal little shift in tree-line position in the Arctic [Prentice *et al.*, 2000]. One possible explanation for this difference is the impact of a relatively late decay of the Laurentide ice sheet on regional climate and soil formation which we neglect in our simulation.

3. The model simulations reveal that terrestrial carbon storage at 8 kyr BP was 90 PgC higher than pre-industrial storage. Most of these changes are explained by changes in vegetation cover in the northern subtropics where more humid climate was favorable for plant productivity. Changes in vegetation cover in the circumpolar region, although significant, were not subsequently followed by a significant increase in carbon storage because of relatively low productivity of plants in the arctic environment. In some other regions, especially in the Southern hemisphere, terrestrial carbon storage was reduced due to the low atmospheric CO₂ concentration during the early Holocene.

With a pre-industrial value for the mean ocean alkalinity the model can not reproduce the amplitude of CO₂ changes in the Holocene recorded in the ice cores. Accounting for excessive CaCO₃ sedimentation in the ocean is necessary to explain the atmospheric CO₂ trend inferred from the ice cores. A higher concentration of carbonate ion in the deep ocean during the early Holocene is in accordance with sediment data [Broecker *et al.*, 1999]. Presumably, carbonate sedimentation process in the ocean during the Holocene led to a decrease in the carbonate ion concentration. As a consequence of declining alkalinity, the ability of the ocean to absorb carbon emitted by the terrestrial biosphere was reduced. Hence, in accordance to

our model results, the ocean was a source of carbon during the late Holocene.

4. In the transient simulation AOVC-T, atmospheric $\delta^{13}\text{C}$ decreases by 0.05‰ during the first half of the simulation in response to a decline in the terrestrial carbon storage. While this decrease is qualitatively in line with Taylor Dome data, the amplitude of changes in the model is much smaller than in the data (ca. 0.35‰). Possible explanations include: (i) uncertainties in the measurements of ^{13}C (ca. 0.08‰); (ii) long-term variability in oceanic or atmospheric circulation, which was not considered in our experiments; (iii) the biogeochemical processes neglected in the model, for example, methane emissions, which could considerably influence the atmospheric $\delta^{13}\text{C}$. Accounting for methane production as well as accumulation and decay of carbon in wetlands should improve carbon balance estimates in future model simulations.

5. "Ocean only" carbon source scenario is addressed in the transient simulation AOVC-T-O. Simulation results are in line with a scenario of changes in the atmospheric CO₂ and $\delta^{13}\text{C}$ recently published by Broecker *et al.* [2001]. The difference between two transient simulations, AOVC-T and AOVC-T-O, is comparable with an uncertainty in the proxy data. Based on the available proxies for the atmospheric CO₂, $\delta^{13}\text{C}$, and oceanic carbonate ion concentration, it is not possible to conclude whether the atmospheric CO₂ rise during the last 8,000 years was caused by the ocean response only or decay of terrestrial carbon has contributed to this rise as well. More proxies are needed to address this question.

Appendix A: Equations for Terrestrial Carbon Cycle

$$\Phi = \{t, g\},$$

$$\frac{dC_{\Phi}^1}{dt} = k_{\Phi}^1 \Pi \alpha_{\Phi}^* R^* - \frac{C_{\Phi}^1}{\tau_{\Phi}^1}, \quad (\text{A1})$$

$$\frac{dC_{\Phi}^2}{dt} = (1 - k_{\Phi}^1) \Pi \alpha_{\Phi}^* R^* - \frac{C_{\Phi}^2}{\tau_{\Phi}^2}, \quad (\text{A2})$$

$$\frac{dC_{\Phi}^3}{dt} = k_{\Phi}^2 \frac{C_{\Phi}^1}{\tau_{\Phi}^1} + k_{\Phi}^3 \frac{C_{\Phi}^2}{\tau_{\Phi}^2} - \frac{C_{\Phi}^3}{\tau_{\Phi}^3}, \quad (\text{A3})$$

$$\frac{dC_{\Phi}^4}{dt} = k_{\Phi}^4 \frac{C_{\Phi}^2}{\tau_{\Phi}^2} + k_{\Phi}^5 \frac{C_{\Phi}^3}{\tau_{\Phi}^3} - \frac{C_{\Phi}^4}{\tau_{\Phi}^4}, \quad (\text{A4})$$

$$\Pi(T_a, P_r, C_{atm}) = \Pi_{max} \min\left\{\frac{1}{1 + e^{(\nu_1 - \nu_2 T_a)}}, \right.$$

$$1 - e^{\nu_3 P_r} \} (1 + \beta \log \frac{C_{atm}}{C_{atm}^0}), \quad (\text{A5})$$

$$k_{\Phi}^1(\Pi) = n_{\Phi}^1 + \frac{n_{\Phi}^2}{1 + n_{\Phi}^3 \Pi}, \quad (\text{A6})$$

$$\tau_{\Phi}^i = \begin{cases} m_{\Phi}^{i,1} + \frac{m_{\Phi}^{i,2}}{1 + m_{\Phi}^{i,3} \Pi} & i = \{1, 2\}, \\ m_{\Phi}^{i,4} e^{-m_{\Phi}^{i,5} T_a} & i = \{3, 4\}, \end{cases} \quad (\text{A7})$$

$$\alpha_{\Phi}^* = R^* = 1 \text{ for } {}^*C = {}^{12}C; \alpha_t^* = \alpha_3^{13}, \alpha_g^* = \alpha_3^{13} g_3 + \alpha_4^{13} (1 - g_3), R^* = \frac{{}^{13}C_a}{C_a} \text{ for } {}^*C = {}^{13}C,$$

$$\frac{df}{dt} = \frac{1}{\tau_t^2} (\hat{f} - f), \quad (\text{A8})$$

$$\frac{dv}{dt} = \frac{1}{\tau_v} (\hat{v} - v), \quad (\text{A9})$$

$$\tau_v = \begin{cases} \tau_g^2 & v_{min} \leq v \leq 1, \\ \tau_t^2 & v < v_{min}, \end{cases} \quad (\text{A10})$$

$$g = v - f, \hat{f}(G_0, P_r) = f_{max} (1 - e^{-c(G_0 - G_{min})}) \cdot \frac{(P_r)^a}{(P_r)^a + a_{for} (G_0 - G_{min})^2 e^{b(G_0 - G_{min})}} \quad (\text{A11})$$

$$\hat{v}(G_0, P_r) = \begin{cases} 0 & P_r \leq P_r^{min}, \\ \min[1, \hat{V}] & P_r > P_r^{min}, \end{cases} \quad (\text{A12})$$

$$\hat{V} = 1 - \frac{1}{1 + a_{des} (P_r - P_r^{min})^2 e^{b(G_0 - G_{min})}} \quad (\text{A13})$$

$$P_r^{min} = P_r^0 e^{b_2(G_0 - G_{min})} \quad (\text{A14})$$

Appendix B: Equations for Oceanic Carbon Cycle (except sea surface-air exchange)

$$\frac{\partial \Gamma}{\partial t} = A_d(\Gamma) + J_{org}(\Gamma) + J_{car}(\Gamma), \quad (\text{B1})$$

$$\Gamma = \{C_{dic}, C_{doc}^i, {}^{13}C_{dic}, {}^{13}C_{doc}^i, {}^{14}C_{dic}, P, O_2, ALK\}, i = \{f, s\},$$

$$\frac{dC_p}{dt} = \Pi - G - (d_p + \gamma_p) C_p', \quad (\text{B2})$$

$$\frac{dC_z}{dt} = \epsilon_{her} \zeta G - (d_z + \gamma_z) C_z', \quad (\text{B3})$$

$$\Pi = r(T, L) \frac{P}{P + P^0} C_p, \quad (\text{B4})$$

$$G = g_T(T) \frac{C_p'}{C_p + C_p^0} C_z, \quad (\text{B5})$$

$$E(z) = (1 - \epsilon_{her}) G + d_p C_p' + (1 - \epsilon_{can}) d_z C_z', \quad (\text{B6})$$

$$J_{org}(C_{dic}) = F_{dic} + D^f + D^s, \quad (\text{B7})$$

$$J_{org}(C_{doc}^i) = F_{doc}^i - D^i, \quad (\text{B8})$$

$$J_{org}(P) = \frac{F_{dic}}{\eta_{dic}(z)} + \frac{D^f + D^s}{\eta_{doc}}, \quad (\text{B9})$$

$$J_{org}(O_2) = -F_{dic} \frac{\eta_{O_2}(z)}{\eta_{dic}(z)} - (D^f + D^s) \frac{\eta_{O_2}(z_{eup})}{\eta_{doc}}, \quad (\text{B10})$$

$$J_{org}(ALK) = -F_{dic} \frac{\eta_N}{\eta_{dic}(z)}, \quad (\text{B11})$$

$$J_{car}(ALK) = 2F_{car}, \quad (\text{B12})$$

$$D^i = r_{doc}^i C_{doc}^i, \quad (\text{B13})$$

$$C_p' = C_p - C_p^{min}, \quad (\text{B14})$$

$$C_z' = C_z - C_p^{min}, \quad (\text{B15})$$

functions $r(T, L)$ and $g_T(T)$ are Eqs. (1-4) from [Sitch and Maier-Reimer, 1996],

sources in euphotic layer:

$$F_{dic} = (-\Pi + \epsilon_{her}(1 - \zeta)G + \epsilon_{can} d_z C_z') \alpha_{org}^* R^*, \quad (\text{B16})$$

$$F_{doc}^i = l_f^i (\gamma_p C_p' + \gamma_z C_z') \alpha_{org}^* R^*, \quad (\text{B17})$$

$$F_{car} = -\kappa(z) R_r E(z) R^*, \quad (\text{B18})$$

sources in aphotic layer:

$$F_{dic} = \frac{\partial \theta}{\partial z} \alpha_{org}^* R^* \int_0^{z_{eup}} E(z) dz, \quad (\text{B19})$$

$$F_{car} = \frac{\partial \kappa}{\partial z} R_r R^* \int_0^{z_{eup}} E(z) dz, \quad (\text{B20})$$

$$\theta(z) = \left(\frac{z}{z_{eup}}\right)^{a_{\theta}} \quad (\text{B21})$$

$$\kappa(z) = e^{\left(-\frac{z - z_{eup}}{d_{\kappa}}\right)} \quad (\text{B22})$$

$$F_{doc}^i = 0, \quad (\text{B23})$$

$$J_{org}(O_2) = -F_{dic} \frac{\eta_{O_2}(z)}{\eta_{dic}(z)} - (D^f + D^s) \frac{\eta_{O_2}(z_{eup})}{\eta_{doc}}, \quad (\text{B24})$$

$$J_r({}^{14}C_{dic}) = -\lambda^{14} C_{dic}, \quad (\text{B25})$$

$$\alpha_{org}^* = R^* = 1 \text{ if } \Gamma = \{C_{dic}, C_{doc}^i\}, \alpha_{org}^* = \alpha_{org}^{13}, R^* = \frac{{}^{13}C_{dic}}{C_{dic}} \text{ if } \Gamma = \{{}^{13}C_{dic}, {}^{13}C_{doc}^i\}.$$

Acknowledgments.

The authors thank Stephen Sitch, Wolfgang Cramer and David Beerling for constructive comments regarding terrestrial carbon cycle. Discussions with David Archer, Colin Prentice, Wolfgang Knorr, Alexander Alexandrovsky, Hans-Rudolf Bork, and Pavel Tarasov were very fruitful. The authors are grateful to David Archer and two anonymous reviewers for their thoughtful comments on the manuscript. Jørgen Bendtsen was funded by the Danish National Science Research council.

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Received , 2001; revised , ; accepted , .

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Figure 1. Vegetation cover in CLIMBER-2. A. Tree fraction; B. Grass fraction; C. Desert fraction.

Figure 2. Scheme of the terrestrial carbon cycle in CLIMBER-2, (AOVC-0K). Units are Pg for carbon storages and Pg yr^{-1} for carbon fluxes.

Figure 3. Map of vegetation characteristics in CLIMBER-2, (AOVC-0K). A. Maximum LAI; B. NPP (kgC m^{-2}); C. Total biomass (kgC m^{-2}); D. C. Total soil carbon (kgC m^{-2}).

Figure 4. Scheme of the oceanic carbon cycle in CLIMBER-2, (AOVC-0K). Units are Pg for carbon storages and Pg yr^{-1} for carbon fluxes. Dotted lines are for boundaries of the photic surface layer. Dashed arrow represents fast DOC which is physically transported and remineralized in the deep ocean.

Figure 5. Distribution of the biogeochemical tracers (PO_4 , DIC, ALK) in the ocean basins, (AOVC-0K). A, model PO_4 concentration, $\mu\text{mol kg}^{-1}$; C, model DIC concentration, $\mu\text{mol kg}^{-1}$; E, model alkalinity, $\mu\text{eq kg}^{-1}$; B, D, F, GEOSECS data, zonally averaged and interpolated onto the model grid for PO_4 , DIC, and ALK, correspondingly.

Figure 6. Scheme of the global carbon cycle in CLIMBER-2, pre-industrial steady state. Units are Pg for carbon storages and Pg yr^{-1} for carbon fluxes.

Figure 7. Climatic difference between (AOVC-8K) and (AOVC-0K). (A) and (B) are for change in near-surface air temperature (in $^{\circ}\text{C}$) for northern hemisphere winter (December-February) and summer (June - August), respectively. (C) and (D) are the same as (A) and (B), respectively, but for change in precipitation (mm/day).

Figure 8. Difference in vegetation characteristics between (AOVC-8K) and (AOVC-0K). A, desert fraction; B, tree fraction; C, NPP (kgC m^{-2}); D, carbon storage (kgC m^{-2}).

Figure 9. Changes in climate, vegetation and carbon characteristics, difference between (AOVC-T) and (AOVC-0K). A, summer irradiation (W m^{-2}), external forcing; B, growing-degree days (GDD0); C, tree fraction; D, carbon storage (kgC m^{-2}).

Figure 10. Changes in mean annual surface temperature ($^{\circ}\text{C}$), difference between (AOVC-T) and (AOVC-0K). A, globe, B, northern hemisphere, C, southern hemisphere, D, global SST.

Figure 11. Global vegetation cover (10^6km^2), (AOVC-T). A, trees, B, grasses, C, desert.

Figure 12. Changes in oceanic (incl. CaCO_3 sediments) and terrestrial carbon storages, (AOVC-T). A, total carbon, PgC; B, ^{13}C , $\text{PgC } \text{‰}$

Figure 13. Comparison of Taylor Dome data [Indermühle *et al.*, 1999] and transient simulations for atmospheric CO_2 and $\delta^{13}\text{C}$. A, dynamics of atmospheric CO_2 concentration (ppmv), solid line for (AOVC-T) simulation (both terrestrial and oceanic carbon sources) and dashed line for (AOVC-T-0) simulation (oceanic carbon source only), dots with $1-\sigma$ error bars and thin line for the ice core data; B, the same as (A) but for $\delta^{13}\text{C}$ (in ‰).

Figure 14. Comparison of pollen records and CLIMBER-2 results for Taymyr region. (A) Pollen diagram for the Lama Lake (70°N , 90°E). Black shaded area is for percentages of pollen content of selected tree species and total pollen percentage of trees against herbs pollen and spores percentages. (B) The same as (A), but for the Levinson-Lessing Lake (74°N , 98°E). (C) Simulated tree fraction, (AOVC-T).

Table 1. Summary of equilibrium simulations^a

Acronym	Simulation purpose	Time slice	Atm. CO ₂ , ppmv	$\delta^{13}\text{C}_{\text{ATM}}$, ‰	Changes in CO ₃ ⁼ , $\mu\text{ eq/kg}$	Mean ocean ALK, $\mu\text{ eq/kg}$
<i>Reference</i>						
AOVC-0K	Reference for 0K	Pre-industrial ^c	280	-6.5	-	2,373
AOVC-8K	Reference climate for 8K	8,000 yr BP ^d	260	-6.4 ^e	5	2,373
<i>Carbon cycle sensitivity</i>						
AOVC-0K-co2	Sensitivity to atm. CO ₂	Pre-industrial	280/260 ^f	-	-	2,373
AOVC-8K-clm	Sensitivity to climate	8,000 yr BP	260/280 ^f	-	-	2,373
<i>Initial conditions for transient simulations</i>						
AOVC-8K-H	Initial conditions for AOVC-T	8,000 yr BP	260	-6.4	8	2,406
AOVC-8K-O	Initial conditions for AOVC-T-O	8,000 yr BP	260	-6.4	9.5	2,421

^a The simulations are done for 10,000 yr with prescribed boundary conditions (insolation, CO₂, ALK)

^b Changes in pressure-corrected carbonate ion concentration in deep tropical ocean in comparison with AOVC-0K

^c The simulation corresponds to present-day climate and pre-industrial carbon cycle

^d Insolation changes are prescribed in accordance with *Berger* [1996]

^e $\delta^{13}\text{C}_{\text{ATM}}$ is prescribed following a spline estimate for the Taylor Dome data at 8,000 yr BP, see Figure 2 in *Indermühle et al.* [1999]

^f Atmospheric CO₂ concentration for climate / carbon cycle models

Table 2. Summary of transient simulations from 8 kyr BP to pre-industrial

Acronym	Simulation purpose	Initial/final atm. CO₂,^a ppmv	Initial/final $\delta^{13}\text{C}_{\text{ATM}}$, ‰	Initial/final mean ocean ALK, $\mu\text{eq/kg}$	CaCO₃ sedimentation, Pg C
AOVC-T	Baseline transient	260/280	-6.4/-6.45	2,406/2,373	270
AOVC-T-O	“Ocean only” carbon source	260/280	-6.4/-6.4	2,421/2,373	390

^a Atmospheric CO₂ is interactive with terrestrial and oceanic carbon cycle; total carbon amount in the system (incl. ocean sediments) is conserved

Table 3. Variables and Parameters of the Carbon Cycle Model

Variable, parameter	Term	Value	Units
<i>Land</i>			
Tree fraction	f	var.	
Equilibrium tree fraction	f^*	var.	
Vegetation fraction	v	var.	
Equilibrium vegetation fraction	v^*	var.	
Grass fraction	g	var.	
Relative fraction of C ₃ -type grass	g_3	var.	
Carbon storage	C_{Φ}^i	var.	kgC m ⁻²
Carbon lifetime	τ_{Φ}^i	var.	yr
NPP	Π	var.	kgC m ⁻² yr ⁻¹
NPP allocation factor	k_{Φ}^1	var.	
Parameters of carbon allocation	$k_{\Phi}^i, i \geq 2$	const.	
Parameters of allocation dependences	$n_{\Phi}^i, m_{\Phi}^{i,j}$	const.	
Mean annual surface air temperature	T_a	var.	°C
Growing degree-days above 0	G_0	var.	degree-days
Annual mean precipitation	P_r	var.	mm yr ⁻¹
Bioclimatic parameters	$a, a_{for}, a_{des},$ b, b_2, c	const.	
Maximum tree fraction	f_{max}	0.95	
Minimum precipitation for vegetation	P_r^{min}	var.	mm yr ⁻¹
Threshold in v time scale	v_{min}	0.1	
Minimum GDD0 for trees	G_{min}	800	degree-days
Atmospheric CO ₂ concentration	C_{atm}	var.	ppmv
Reference atmospheric CO ₂ concentration	C_{atm}^0	280	ppmv
Maximum NPP for C_{atm}^0	Π_{max}	1.4	kgC m ⁻² yr ⁻¹
NPP regressional parameters	ν_i	const.	
Factor of NPP dependence on C_a	β	0.2	
Carbon isotopic fractionation factor during photosynthesis	α_{Φ}^*	var.	
Atmospheric carbon isotopic ratio	R_{Φ}^*	var.	
¹³ C fractionation factor for C ₃ plants	α_3^{13}	0.982	
¹³ C fractionation factor for C ₄ plants	α_4^{13}	0.995	
<i>Ocean</i>			
Tracer source minus sink due to cycle of organic matter	$J_{org}(\Gamma)$	var.	
Tracer source minus sink due to cycle of CaCO ₃	$J_{car}(\Gamma)$	var.	
DIC concentration	C_{dic}	var.	μ mol kg ⁻¹
DOC concentration	C_{doc}^i	var.	μ mol kg ⁻¹
PO ₄ concentration	P	var.	μ mol kg ⁻¹
O ₂ concentration	O_2	var.	μ mol kg ⁻¹
Alkalinity concentration	ALK	var.	μ eq kg ⁻¹
Phytoplankton concentration	C_p	var.	μ mol kg ⁻¹

Table 3. (continued)

Variable, parameter	Term	Value	Units
Zooplankton concentration	C_z	var.	$\mu \text{ mol kg}^{-1}$
Net primary productivity	Π	var.	$\mu \text{ mol kg}^{-1} \text{ s}^{-1}$
Grazing	G	var.	$\mu \text{ mol kg}^{-1} \text{ s}^{-1}$
Sea surface temperature	T	var.	$^{\circ}\text{C}$
Incoming surface shortwave radiation	L	var.	W m^{-2}
NPP dependence on T and L	$r(T, L)$	var.	
Grazing dependence on T	$g_T(T)$	var.	
Half-saturation constant for nutrient uptake	P^0	0.016	$\mu \text{ mol P kg}^{-1}$
Half-saturation constant for phytoplankton ingestion	C_p^0	3.5	$\mu \text{ mol C kg}^{-1}$
Egestion as fecal pellets from herbivores	$1 - \epsilon_{her}$	0.1	
Egestion as fecal pellets from carnivores	$1 - \epsilon_{can}$	0.95	
Specific mortality rate for phyto- and zooplankton	d_p, d_z	0.008	day^{-1}
Exudation rate of DOC	γ_p	0.03	day^{-1}
Excretion rate of DOC	γ_z	0.06	day^{-1}
Assimilation efficiency	ζ	0.6	
Shifted C_p, C_z	C'_p, C'_z	var.	$\mu \text{ mol kg}^{-1}$
New production flux	$E(z)$	var.	$\mu \text{ mol kg}^{-1} \text{ s}^{-1}$
Depth of euphotic layer	z_{eup}	100	m
DOC remineralization	D^i	var.	$\mu \text{ mol kg}^{-1} \text{ s}^{-1}$
POC remineralization	F_{dic}	var.	$\mu \text{ mol kg}^{-1} \text{ s}^{-1}$
DOC source	F_{doc}^i	var.	$\mu \text{ mol kg}^{-1} \text{ s}^{-1}$
CaCO ₃ source	F_{car}	var.	$\mu \text{ mol kg}^{-1} \text{ s}^{-1}$
DOC:P ratio	η_{doc}	106	
N:P ratio	η_N	16	
DIC:P ratio for $E(z)$	$\eta_{dic}(z)$	Table 4	
O ₂ :P ratio for remineralization of $E(z)$	$\eta_{O_2}(z)$	Table 4	
DOC allocation factor	l_f^s	0.1	
Remineralization allocation	$\theta(z)$	var.	
Remineralization parameter	a_{θ}	-0.858	
Carbonate allocation	$\kappa(z)$	var.	m
Mean dissolution depth	d_{κ}	3000	m
Rain ratio	R_r	0.1	
DIC carbon isotopic ratio	R^*	var.	
¹³ C fractionation factor for photosynthesis	α_{org}^{13}	var.	
Decay constant for ¹⁴ C	λ^{14}	3.84e^{-12}	s^{-1}

Functions $r(T, L)$ and $g_T(T)$ are Eq. 1-4 from [Six and Maier-Reimer, 1996]; grazing rate g_0 in Eq. 4 is increased to 1.0. Parameter ζ corresponds to $zinges$ in [Six and Maier-Reimer, 1996]. Parameter $1 - \epsilon_{her}$ is chosen between 0 and 0.2 (Katharina Six, personal communication)

Table 5. Changes in the carbon balance, difference between sensitivity simulations and (AOVC-0K)

Simulation	NPP, PgC yr ⁻¹	Biomass, PgC	Soil, PgC	Total carbon, PgC	DIC, PgC
AOVC-8K-co2	-1.5	-17	-31	-48	-240
AOVC-8K-clm	5.4	63	79	142	-10
AOVC-8K	3.7	44	46	90	-250

Table 6. Changes in global carbon balance, difference between (AOVC-8K-H) and (AOVC-0K)

Compartment	Carbon content, Pg
Atmosphere	-40
Ocean DIC and DOC	220
Ocean CaCO ₃ sediment	-270
Land biosphere	90
Total	0

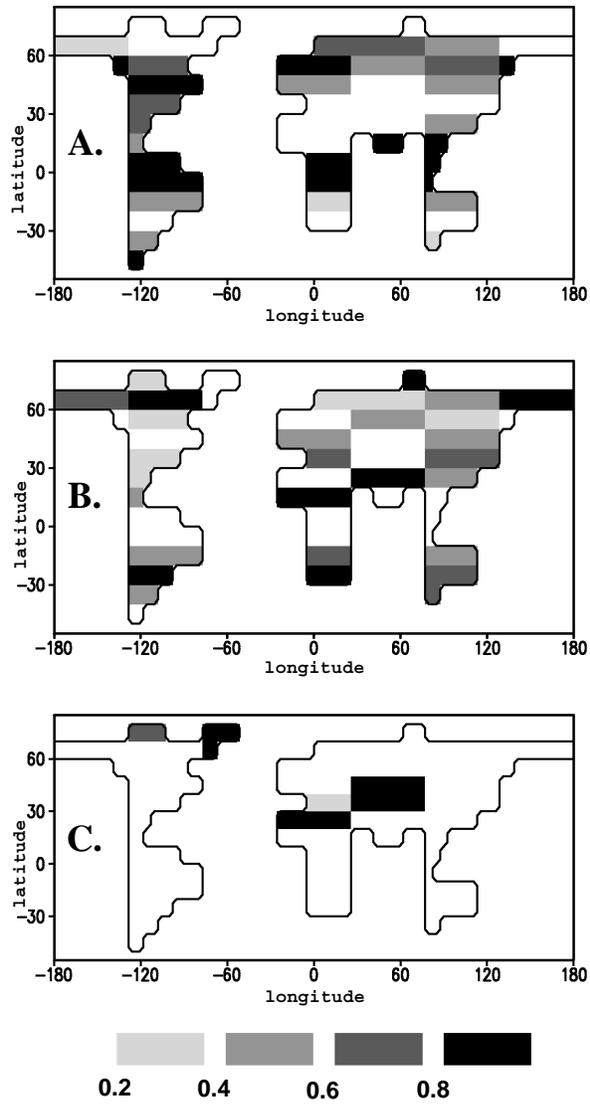


Fig.1

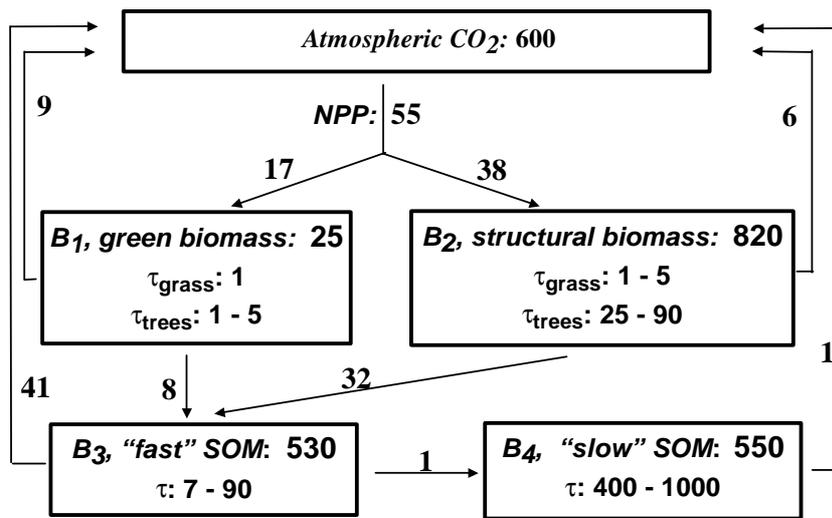


Fig. 2

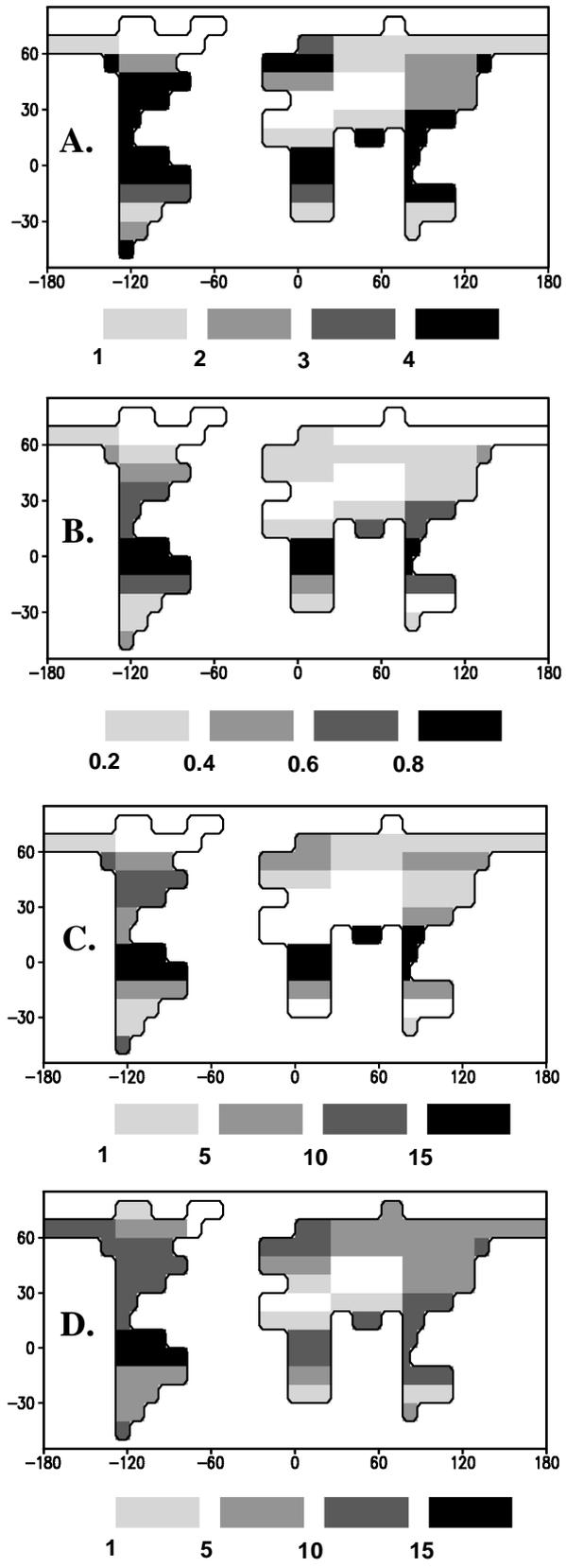


Fig. 3

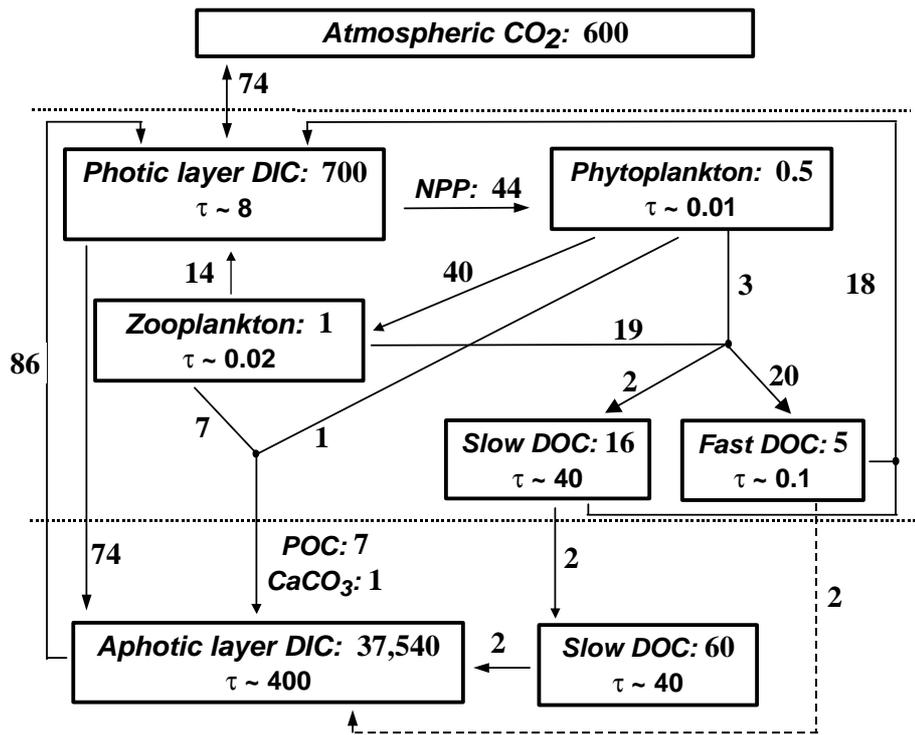


Fig. 4

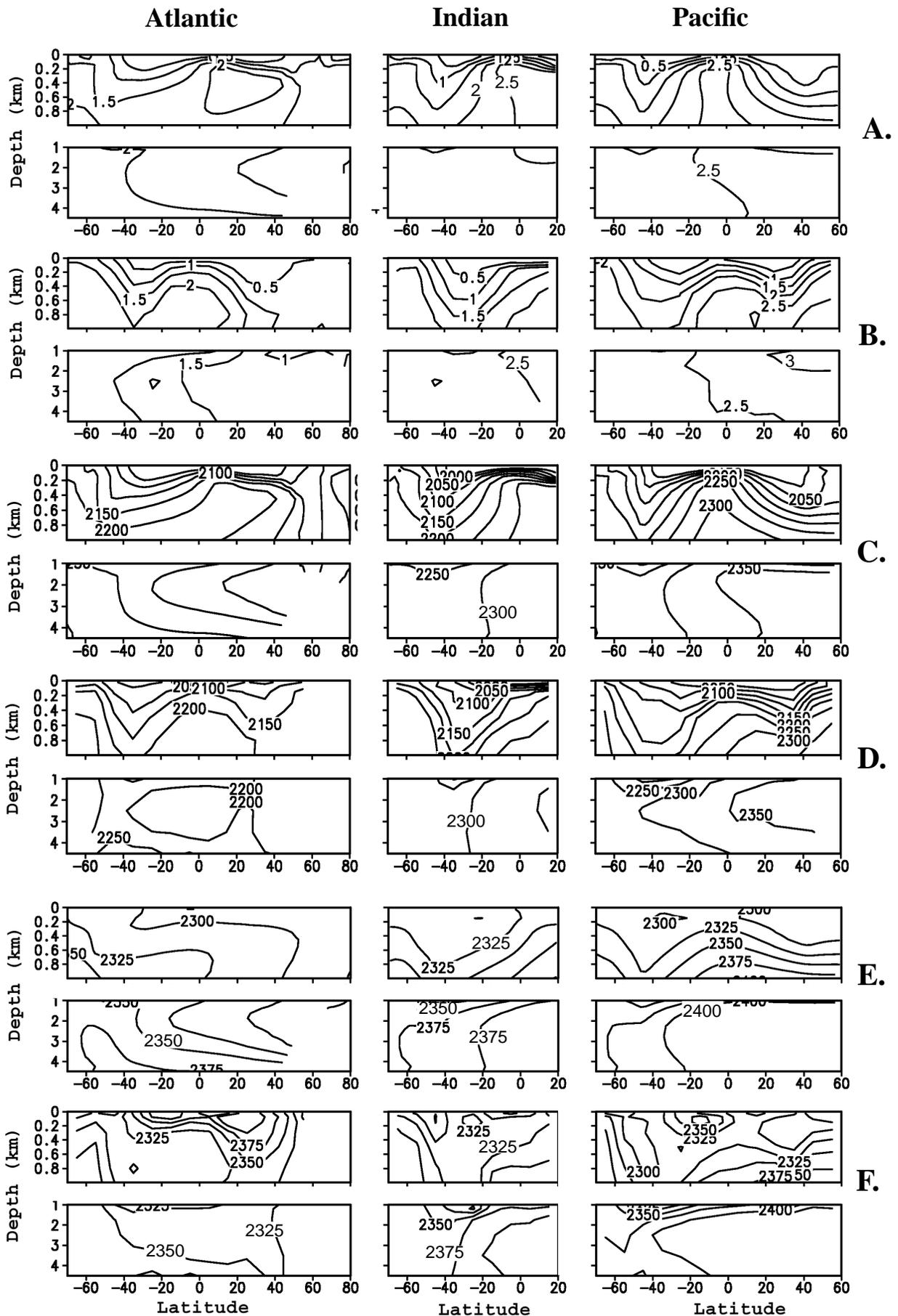


Fig. 5

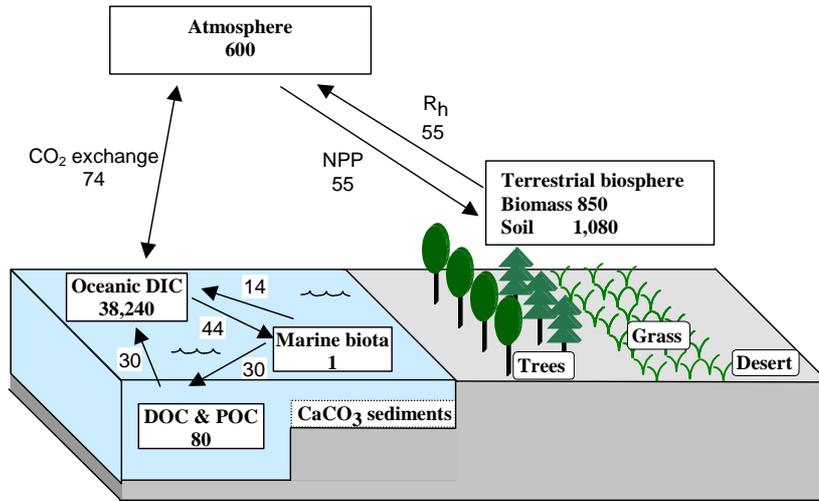


Fig. 6

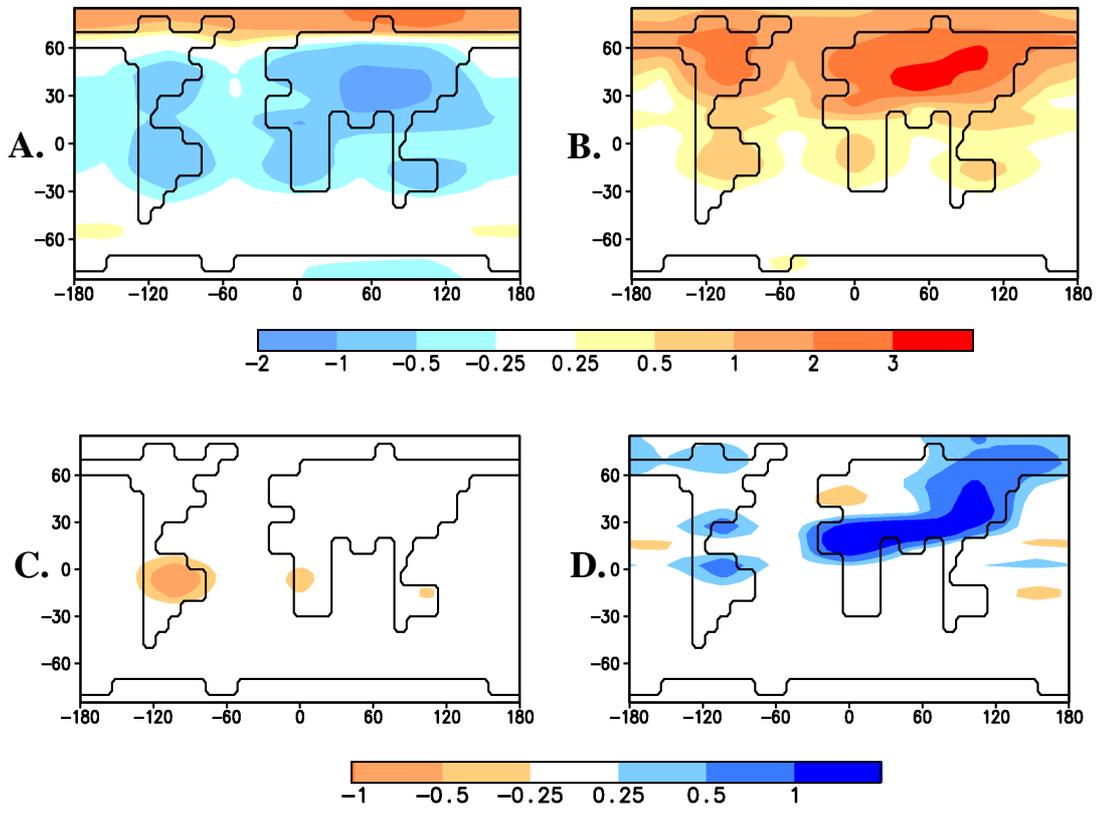


Fig. 7

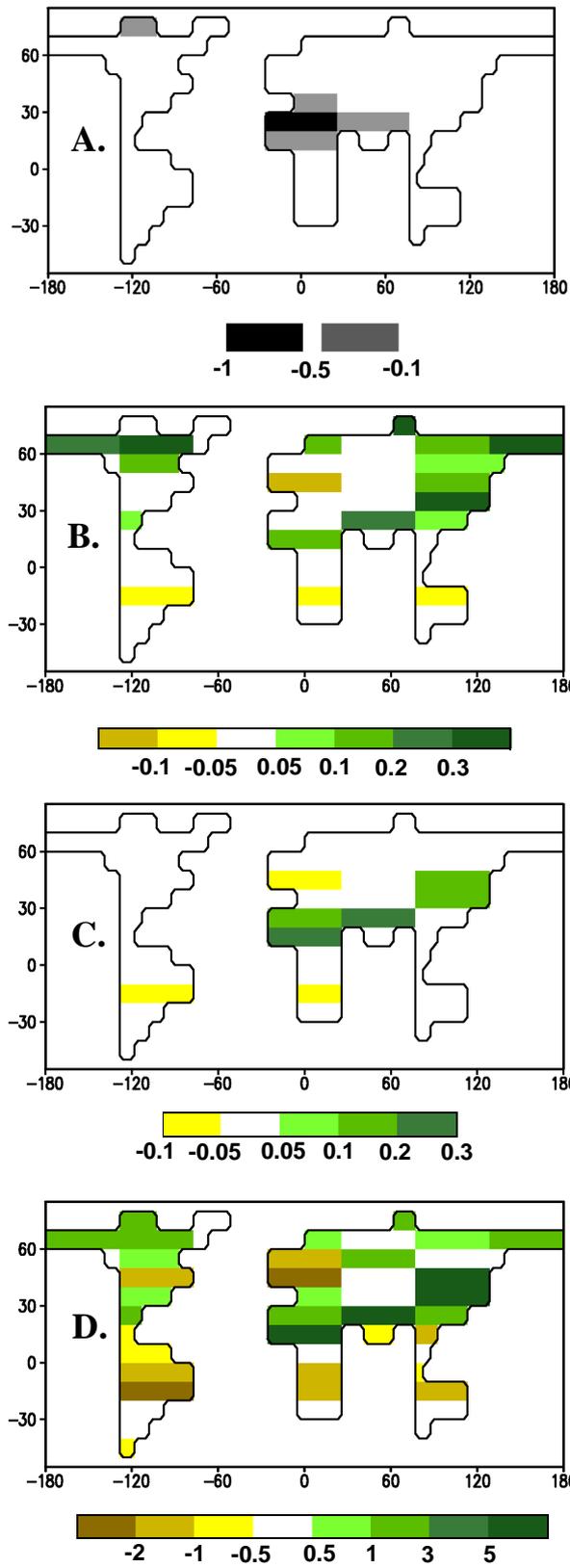


Fig. 8

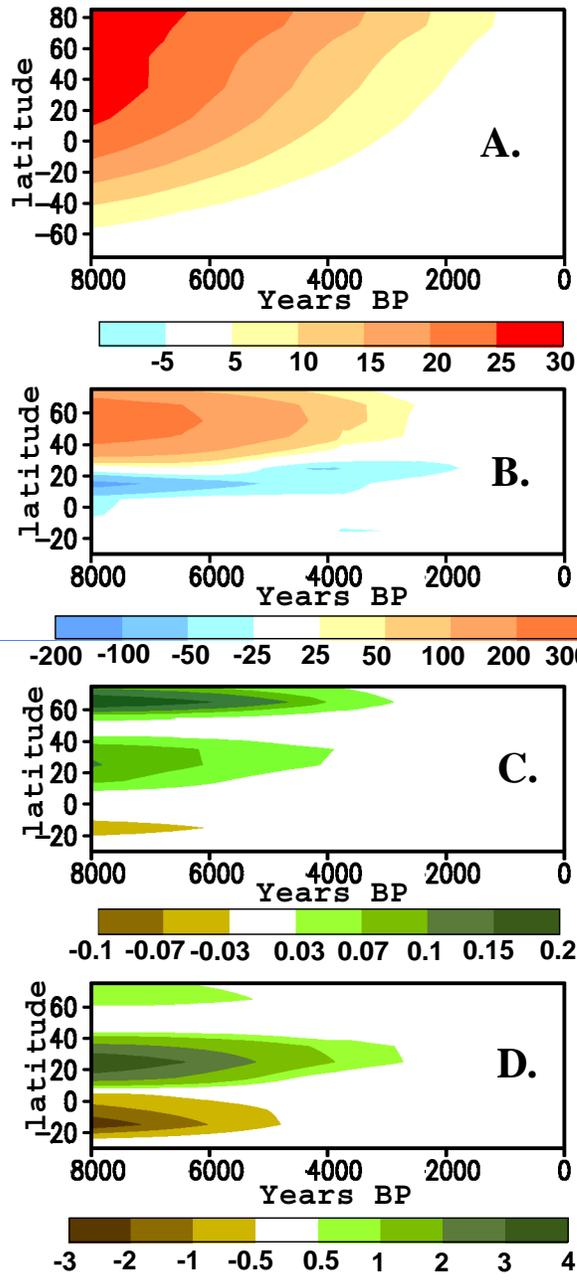


Fig. 9

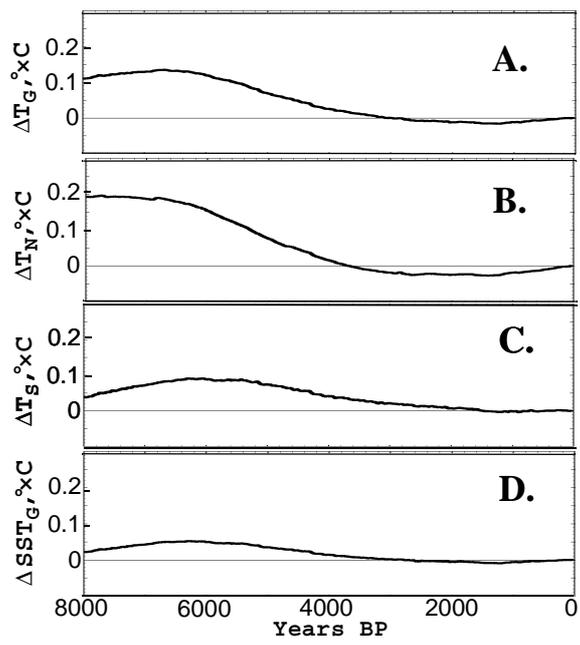


Fig. 10

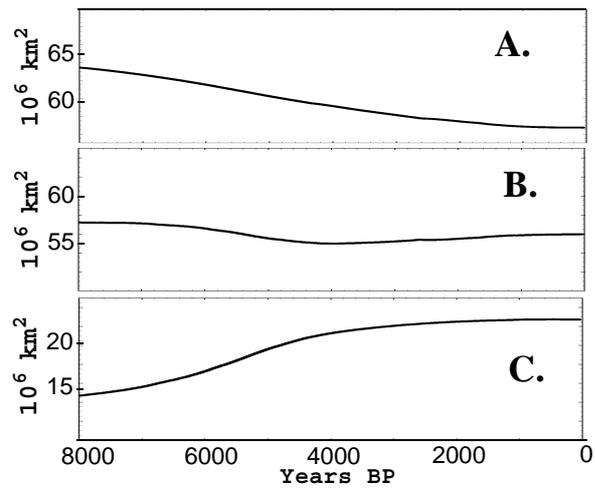


Fig. 11

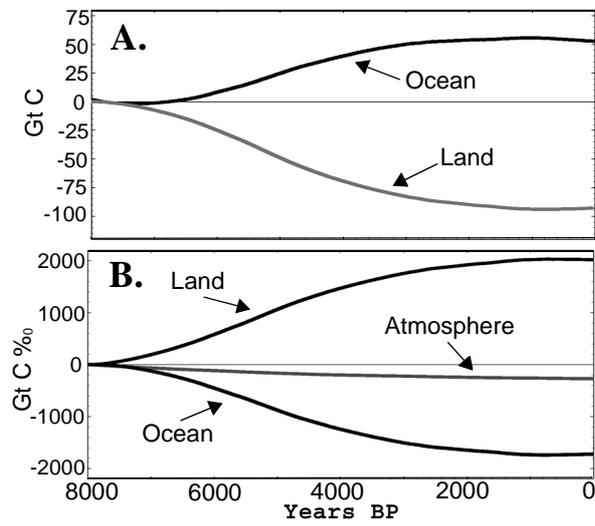


Fig. 12

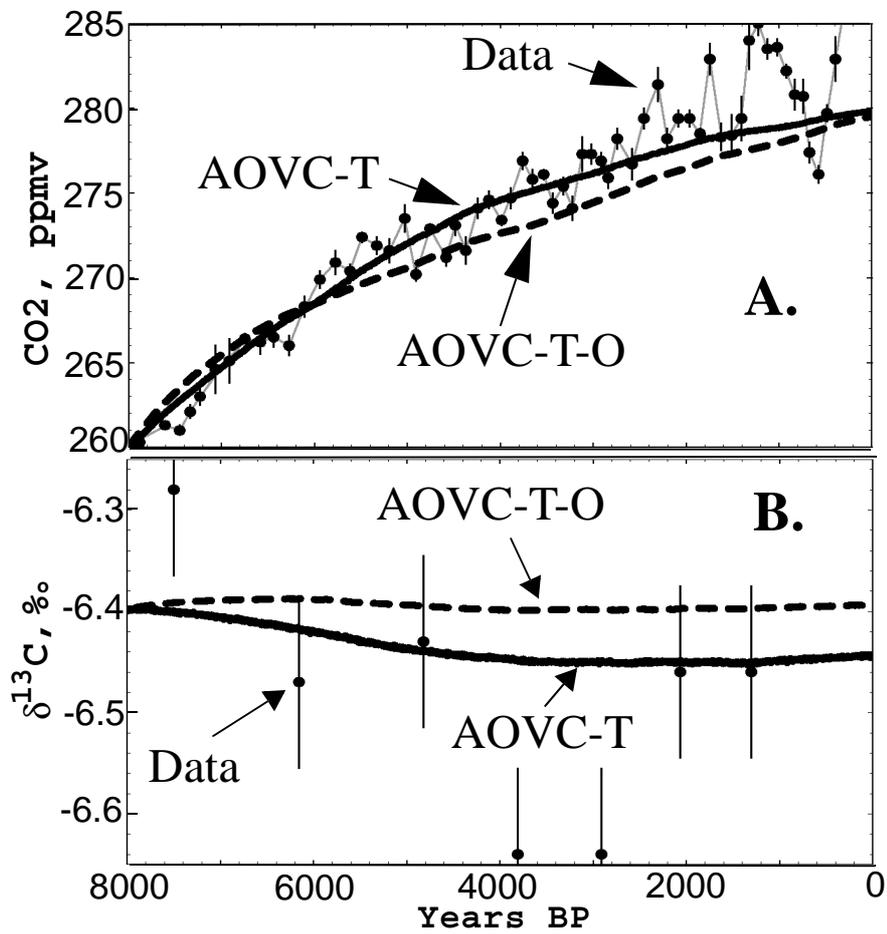


Fig. 13

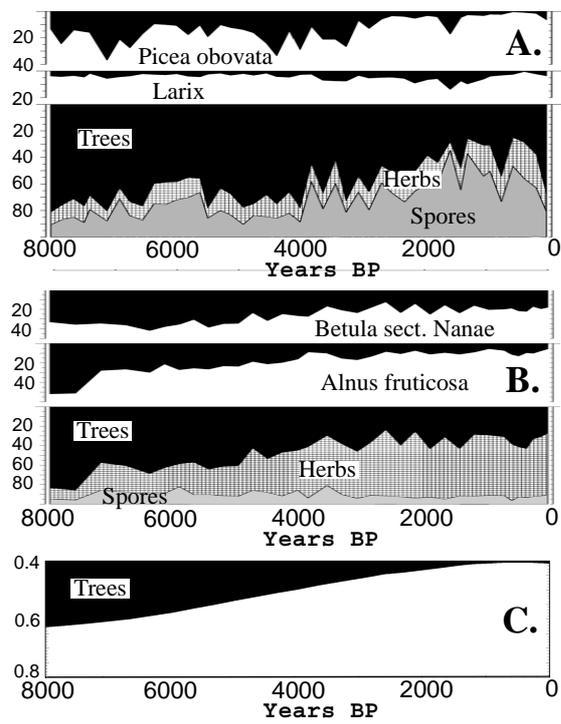


Fig. 14