

Transient simulations of Holocene atmospheric carbon dioxide and terrestrial carbon since the Last Glacial Maximum

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[1] Conflicting hypotheses are investigated for the observed atmospheric CO₂ increase of 20 ppm between 8 ka BP and pre-industrial time. The carbon component of the Bern Carbon Cycle Climate (Bern CC) model, which couples the Lund-Potsdam-Jena Dynamic Global Vegetation Model to an atmosphere-ocean-sediment component, is driven by climate fields from time-slice simulations of the past 21 ka with the Hadley Centre Unified Model or the NCAR Climate System Model. The entire Holocene ice core record of CO₂ is matched within a few ppm for the standard model setup, and results are broadly consistent with proxy data of atmospheric ¹³CO₂, mean ocean δ¹³C, and pollen data, within their uncertainties. Our analysis suggests that a range of mechanisms, including calcite compensation in response to earlier terrestrial uptake, terrestrial carbon uptake and release, SST changes, and coral reef buildup, contributed to the 20 ppm rise. The deep sea δ¹³C record constrains the contribution of the calcite compensation mechanism to 4–10 ppm. Terrestrial carbon inventory changes related to climate and CO₂ forcing, the greening of the Sahara, peat buildup, and land use have probably influenced atmospheric CO₂ by a few ppm only. The early Holocene CO₂ decrease is quantitatively explained by terrestrial uptake and calcite compensation in response to terrestrial uptake during the glacial-interglacial transition. The recent hypothesis by *Ruddiman* [2003] that anthropogenic land use caused a 40 ppm CO₂ anomaly over the past 8 ka, preventing the climate system from entering a new glacial, would imply an anthropogenic emission of 700 GtC and a decrease in atmospheric δ¹³C of 0.6 permil. This is not compatible with the ice core δ¹³C record and would require an upward revision of land use emission estimates by a factor of 3 to 4. **INDEX TERMS:** 0322 Atmospheric Composition and Structure: Constituent sources and sinks; 0315 Atmospheric Composition and Structure: Biosphere/atmosphere interactions; 1615 Global Change: Biogeochemical processes (4805); 1610 Global Change: Atmosphere (0315, 0325); **KEYWORDS:** carbon cycle modeling, carbon dioxide, Holocene

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1. Introduction

[2] Ice core CO₂ concentration data show a decrease in atmospheric CO₂ of about 7 ppm from 11 to 8 ka before present (BP). During the later Holocene, after 8 ka BP, CO₂ increases by about 20 ppm to its pre-industrial level of ~280 ppm [*Indermühle et al.*, 1999; *Monnin et al.*, 2000;

Flückiger et al., 2002]. It is generally accepted that the early Holocene CO₂ decrease was caused by terrestrial carbon uptake, particularly in response to forest growth on formerly ice-covered land. The mechanisms behind the subsequent CO₂ increase are however not established.

[3] *Indermühle et al.* [1999] proposed that the main mechanism for the observed CO₂ change is terrestrial carbon uptake and release, in combination with sea surface warming and changes in the calcite cycle. They quantified the contribution of individual mechanisms by means of a double deconvolution [*Joos and Bruno*, 1998] of the ice core CO₂ record together with a limited set of ice core measurements of ¹³CO₂. *Indermühle et al.* [1999] estimated a terrestrial uptake of 110 gigatons of carbon (GtC) in the early Holocene followed by a release of 150 to 200 GtC

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during the past 7 ka. They also implicated a sea surface warming of about 0.5°C between 9 and 6 ka BP that contributed to the observed CO₂ increase.

[4] In contrast, *Broecker et al.* [2001] suggested that the CO₂ rise after 8 ka BP was caused by marine-sediment compensation of the terrestrial carbon uptake during the early Holocene. This mechanism works as follow. First, terrestrial carbon uptake causes the concentration of carbonate ions ([CO₃²⁻]) in the ocean to increase, as terrestrial uptake depletes, through gas exchange, the oceanic content of dissolved inorganic carbon (DIC: [CO₂] + [HCO₃⁻] + [CO₃²⁻]), whereas total ocean alkalinity (carbonate alkalinity: [HCO₃⁻] + 2 [CO₃²⁻]) remains unaffected. Second, the perturbation in CO₃²⁻ (and DIC) is transported to the deep, leading to a deeper saturation horizon of CaCO₃ [*Broecker and Peng*, 1987] and thus to enhanced calcite sedimentation. Under these conditions, the supply of CaCO₃ by weathering is temporarily smaller than the loss by sedimentation, causing a decrease of the carbonate ion concentration in the ocean and an increase in ocean partial pressure of CO₂ and in atmospheric CO₂, until a new equilibrium is reached. The estimated timescale for this CaCO₃ compensation mechanism is of the order of 5000 years [*Broecker and Peng*, 1987; *Keir*, 1988; *Sundquist*, 1990; *Archer et al.*, 1997], as the exchange between ocean water and sediment pore water is slow. Not only compensation of terrestrial uptake during the early Holocene, as postulated by *Broecker*, but also of earlier uptake during the last glacial-interglacial transition (17 to 11 ka BP), as suggested by model results [*Kaplan et al.*, 2002], could have contributed to the Holocene CO₂ rise.

[5] The response of the atmosphere-ocean-sediment system to a pulse-like terrestrial uptake of 100 GtC is illustrated in Figure 1. The ocean responds to the lowered atmospheric partial pressure by releasing carbon until a new equilibrium is reached. The oceanic uptake occurs fast at the beginning and then takes centuries to equilibrate the deep oceanic water masses (left panel in Figure 1). Sediment compensation comes into play on a longer, millennial timescale and is responsible for a slow continuation of the increasing trend in atmospheric CO₂. It is this slow increase shown in the right panel of Figure 1 that emerges as a Holocene CO₂ increase according to the sediment compensation hypothesis. The impact on atmospheric CO₂ of the postulated terrestrial uptake during the deglaciation, corresponding to the first phase of the response curve, is masked by oceanic processes that forced atmospheric CO₂ to increase over the glacial-interglacial transition.

[6] Other hypotheses were formulated more recently. *Ruddiman* [2003] postulates a large release of carbon (and methane) by anthropogenic land use prior to industrialization. He argues, based on the low-resolution Vostok CO₂ data for previous glacial-interglacial cycles, that atmospheric CO₂ would have dropped naturally by 20 ppm during the Holocene and a new glacial would have started if human activities would not have caused a terrestrial carbon release during the Holocene. On the other hand, *Ridgwell et al.* [2003] suggested that coral reef buildup during the last 8 ka could explain the atmospheric CO₂ increase. Potentially, many other mechanisms, such as changes in ocean circula-

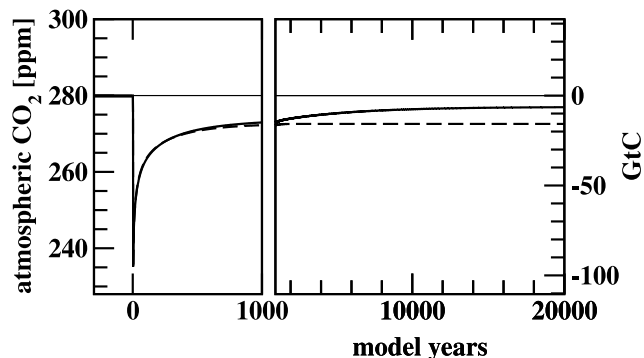


Figure 1. Response in atmospheric CO₂ of the ocean-atmosphere-sediment system to a pulse-like terrestrial uptake of 100 GtC at year 0 as simulated with the standard model setup (solid line). The left panel shows that about 85% of the initial atmospheric perturbation is removed within about 1000 years; then the ocean and atmosphere have roughly reached a new chemical equilibrium (dashed line). Ocean-sediment interaction, governed by a multi-millennial timescale, further reduces the initial CO₂ perturbation. It is the resulting slow rise in atmospheric CO₂ shown on the right panel that emerges as an atmospheric CO₂ increase according to the CaCO₃ sediment compensation hypothesis. The response of the atmosphere-ocean system, excluding ocean-sediment interaction in our model, is shown for comparison (dashed line). Note different x-axis scales for the left and right panel.

tion and stratification, or changes in the marine biological cycle, could have affected atmospheric CO₂ during the Holocene [*Archer et al.*, 2000; *Matsumoto et al.*, 2002]. However, they lack any evidence in the Holocene proxy records.

[7] A range of proxy data has the potential to provide constraints on the proposed mechanisms, but the present situation is unclear. Atmospheric ¹³CO₂ is affected differently by terrestrial carbon uptake in the early Holocene, release in the late Holocene, coral reef growth, or sea surface temperature changes. Unfortunately, the currently available ¹³CO₂ ice core data [*Indermühle et al.*, 1999] are too uncertain to firmly support or reject the different hypotheses, except the land use hypothesis of *Ruddiman* [2003]. For this hypothesis, we find a much larger than observed decrease in atmospheric ¹³CO₂.

[8] The relatively few records of calcite preservation in marine sediments suggest a decrease in the deep ocean carbonate ion concentration during the Holocene in qualitative agreement with the terrestrial and coral reef scenarios [*Broecker and Clark*, 2003]. However, these records do not allow to distinguish between the proposed terrestrial scenarios and the coral reef growth scenarios as each of these scenarios implies a decrease in the deep ocean carbonate concentration during the Holocene.

[9] A mass balance calculation based on δ¹³C measurements on the calcite shells of benthic foraminifera is the most widely accepted data-based method to reconstruct terrestrial carbon inventory changes over glacial-interglacial

cial periods. This method yields a terrestrial biosphere carbon inventory that is reduced by about 300–700 GtC [Shackleton, 1977; Duplessy *et al.*, 1988; Curry *et al.*, 1988; Bird *et al.*, 1994, 1996] at the Last Glacial Maximum (LGM), about 21 ka BP, compared to pre-industrial time. This is a constraint on the overall terrestrial uptake during the last glacial-interglacial transition and the early Holocene and, therefore, on the magnitude of calcite compensation.

[10] Terrestrial pollen data provide information about the biome distribution during the mid-Holocene and the Last Glacial Maximum [Harrison *et al.*, 1998; Jolly *et al.*, 1998; Prentice *et al.*, 2000]. These data can help to evaluate dynamic vegetation models used to simulate terrestrial carbon storage. Estimates of postglacial terrestrial carbon uptake based on pollen data have suggested larger values than the ¹³C mass balance approach (range of best estimates: 700–1400 GtC) [Adams *et al.*, 1990; Van Campo *et al.*, 1993; Crowley, 1995; Adams and Faure, 1998], but these are very approximate due to large gaps in the data considered, and assumptions about the average carbon density of different biomes. For the past 8 ka, Adams and Faure [1998] estimated from pollen data a terrestrial uptake of 170 GtC, in direct contradiction to the terrestrial release postulated by Indermühle *et al.* [1999] and Ruddiman [2003].

[11] Mechanistic modeling studies have addressed Holocene atmospheric CO₂ variations. Brovkin *et al.* [2002] have performed transient simulations over the past 8 ka, forcing their earth system model with orbital variations. They simulated a terrestrial carbon release of 90 GtC, qualitatively in line with Indermühle *et al.* [1999], and they were able to match the ice core CO₂ record by prescribing an additional calcite accumulation in sediments of 270 GtC. Ridgwell *et al.* [2003] forced a multibox ocean model that includes a sediment module with off-line calculated terrestrial carbon emissions [Kaplan *et al.*, 2002] and a coral reef buildup scenario over the past 21 kyrs. They found that coral reef buildup could explain a late Holocene atmospheric CO₂ rise of up to 40 ppm.

[12] Here we present results of transient simulations over the past 21 ka. A fast atmosphere-ocean-sediment-land biosphere carbon cycle model [Joos *et al.*, 2001] is forced with climate fields obtained from time-slice simulations with two ocean-atmosphere general circulation models. The modest CPU requirements of the model allowed us to perform transient sensitivity simulations to explore uncertainties in input climate fields, and to quantify the importance of different carbon-cycle processes for the changes in atmospheric CO₂ over the Holocene. The focus is on changes in the terrestrial system and on the calcite compensation mechanism, whereas coral reef buildup and other sediment-ocean interaction processes are not addressed.

[13] Models and methods are described in the next section. Then we begin our analysis with simulations of terrestrial carbon stock changes over the past 21 kyr (section 3.1) before addressing atmospheric CO₂ variations over the Holocene (section 3.2). In the following subsections, model results for atmospheric ¹³CO₂ (section 3.3), mean ocean δ¹³C (section 3.4), and biome distributions

(section 3.5) are compared with proxy records. The land use scenario by Ruddiman [2003] is discussed in section 4.

2. Models and Methods

2.1. Model Components

[14] The carbon cycle model includes the Lund-Potsdam-Jena Dynamic Global Vegetation Model (LPJ-DGVM) [Sitch *et al.*, 2003], an impulse response function (IRF) substitute of the HILDA ocean model [Siegenthaler and Joos, 1992; Joos *et al.*, 1996] and a well-mixed atmosphere, as in earlier studies [Joos *et al.*, 2001; Gerber *et al.*, 2003]. The equations for ocean carbonate chemistry were adjusted to extend their validity to low CO₂ concentrations. An IRF formulation for ocean-sediment interaction was added, based on the work of Archer *et al.* [1997], to account for the CaCO₃ compensation mechanism operating on glacial-interglacial timescales. The model and its component have been extensively tested in other contexts [Joos *et al.*, 1991, 1997; Joos and Bruno, 1998; Sitch, 2000; McGuire *et al.*, 2001; Dargaville *et al.*, 2002].

[15] The LPJ-DGVM simulates photosynthesis, respiration, fire, and the growth and competition of nine plant functional types (PFT). PFT distributions are constrained by bioclimatic limits for plant survival and regeneration, while the relative performance of PFTs, in competition for light and water, is governed by PFT-specific physiological, phenological, growth, and disturbance-response parameters. The uptake of ¹³C is calculated following Scholze *et al.* [2003] based on work by Lloyd and Farquhar [1994] and Kaplan and Prentice [2002]. The model is driven by atmospheric CO₂ and monthly fields of temperature, precipitation, and cloud cover. The spatial resolution is set here to 3.75° × 2.5°.

[16] The IRF substitute of the HILDA model yields identical results to HILDA, and is used here for computational efficiency. Surface-to-deep tracer transport is described by an IRF. The nonlinearities in air-sea gas exchange and carbonate chemistry are captured by separate equations. The effect of sea surface temperature (SST) variations on carbonate chemistry is included [Joos *et al.*, 1999], whereas the impacts of changes in ocean circulation and in the marine biological cycle on atmospheric CO₂ are neglected. The parameterization of the chemistry of dissolved inorganic carbon [Joos *et al.*, 2001] used in earlier studies has been replaced. Carbonate chemistry and oceanic partial pressure of CO₂ are instead calculated from explicit carbon chemistry equilibrium equations using the solubility coefficient and dissociation constants based on work by Weiss [1974] and Goyet and Poisson [1989], because the parameterization given by Joos *et al.* [2001] has been validated only for a limited range of CO₂ concentrations. Tests revealed, however, that the two methods yield nearly identical results.

[17] CaCO₃ sedimentation is calculated based on an IRF as described in Appendix A. In the standard formulation, 70% of terrestrial carbon uptake is compensated on a e-folding timescale of 5000 years (Figure 1). In sensitivity experiments, the timescale was varied or the IRF was

calculated using three timescales and coefficients and their uncertainties as suggested by *Archer et al.* [1997]. The IRF approach is capturing the response of a 3-D ocean-sediment model for the calcite compensation of a carbon removal (addition) from (into) the atmosphere-ocean-sediment system, while using much less computational power than an explicit model. However, the IRF approach as used here is not adequate to address coral reef buildup or other changes in the ocean-sediment system.

2.2. Climate Boundary Conditions

[18] Changes in precipitation and temperature for the last 21 ka were derived from time-slice simulations with two climate models, the Hadley Centre Unified Model (UM) [*Pope et al.*, 2000; *Hewitt et al.*, 2001] and the NCAR Community Climate Model 1.4—paleo version (CSM) [*Boville and Gent*, 1998; *Otto-Bliesner and Brady*, 2001; *Shin et al.*, 2002; *Liu et al.*, 2003].

[19] The UM consists of the HadSM3 atmospheric circulation model [*Pope et al.*, 2000] coupled to a slab ocean model and a sea-ice model as described by *Hewitt et al.* [2001]. The atmosphere has a resolution of $2.5^\circ \times 3.5^\circ$, with 19 vertical layers. The climate fields used here consist of 19 snapshots carried out roughly every 1000 years up to pre-industrial time. At every time-slice, the model is driven by orbital forcing, observed atmospheric CO₂, and methane concentration. Ice sheet distribution and sea level is prescribed following *Peltier* [1994] until 7 ka BP and for present conditions thereafter. Land surface conditions were varied, by coupling the model asynchronously with the BIOME4 equilibrium vegetation model [*Kaplan et al.*, 2002]. The ocean heat flux convergence was held in all simulations at present-day values.

[20] The NCAR paleo-CSM [*Boville and Gent*, 1998] consists of a coupled atmosphere and ocean general circulation, a dynamic sea-ice model, and a land-surface biophysics model. It has a spectral resolution of T31 for the atmosphere and land-surface and a spatially variable 3-D grid for the ocean and the sea-ice components [*Otto-Bliesner and Brady*, 2001]. One simulation was done with boundary conditions for 21 ka BP [*Shin et al.*, 2002] (sea level, ice sheet distributions, and low greenhouse gas concentrations). Further simulations were performed over the course of the Holocene at 11, 8.5, 6, 3.5, and 0 ka (pre-industrial) BP [*Liu et al.*, 2003]. Only the orbital parameters were varied in these Holocene simulations. Hence the two simulations in the early Holocene must be interpreted with caution as ice sheet extent was considerably different at 11 ka and 8 ka BP compared to present conditions. Carbon cycle model results obtained with CSM climate output are disregarded for the first half of the Holocene (10.5 to 6 ka BP). Although the model set-up is not ideal for the early Holocene, simulations with the CSM climate fields allow an independent check on various results obtained with the UM climate fields as the typical memory of the ocean-atmosphere-terrestrial system is 1 ka or less and the exact evolution of terrestrial carbon inventory variations is not crucial for the overall magnitude of the calcite compensation mechanism (see section 3.2).

[21] For the LGM, simulated global mean temperature is approximately 4°C lower and global mean SST about 2°C

lower than today in both models (Figure 2). The models also yield comparable changes in land temperature for different latitude bands between the LGM and today. The relative high temperatures simulated with the CSM at 11 and 8.5 ka BP are probably influenced by the unrealistic assumption of a present-day ice sheet boundary. Precipitation simulated with the two climate models is comparable on a global scale for the LGM. The CSM yields a more pronounced reduction in precipitation over land areas between 30°N and 90°N than the UM. In the late Holocene, both models show a decreasing trend in precipitation over land.

[22] The monthly temperature, precipitation, and cloud-cover fields applied to force the LPJ-DGVM were obtained by summing (1) monthly mean deviations from the pre-industrial state, (2) a monthly climatology based on observations and (3) monthly interannual anomalies. First, the monthly values of each time-slice were averaged over the length of the simulation to obtain monthly means. Then, the time-averaged monthly values of the pre-industrial reference simulation were subtracted from those of each time-slice. The resulting monthly mean climate deviations were linearly interpolated in time between the midpoints of the time slices to obtain continuous records for the period from 21 ka BP to present for both the UM and the CSM model. Second, the monthly values of a present-day mean climatology [*Leemans and Cramer*, 1991; *Cramer et al.*, 2001] were added to the monthly mean deviations. Third, interannual anomalies were determined for individual months by detrending observational data [*New et al.*, 2000] for simulations with the UM climate fields or from the first 50 years of the pre-industrial run for simulations with the CSM fields. Then, the interannual anomalies were added repeatedly over the 21 ka period. Cloud-cover data for the CSM simulations were not available. The pre-industrial cloud fields as derived from the UM model output were therefore used in all simulations with CSM temperature and precipitation fields. The deviations in global mean SST used to force the HILDA ocean model were calculated from the mean deviations of each time slice with respect to the pre-industrial global mean SST. Climate and SST variations at multidecadal or centennial timescales such as the Younger Dryas or the 8.2 ka BP event are implicitly neglected. Similarly, changes in interannual variability, as far as not captured in the averaged anomaly fields, are neglected, but changes in the seasonality as simulated by the climate models over the past 21 ka are taken into account. Interannual variability is a necessary driver for the model's fire module, but magnitude and timing of fire fluxes depend on the amount of material available for burning and the neglect of changes in interannual variability is not considered as critical for this application.

[23] The ice sheet and ocean-land mask of the UM was used to identify areas suitable for plant growth. During the deglaciation, this area increased by $7.7 \times 10^{12} \text{ m}^2$ (Figure 3). The loss of land by sea level increase was outweighed by the gain of land from ice sheet retreat. The carbon stored on a grid cell that becomes flooded due to sea level rise is assumed to enter the atmosphere with an e-folding timescale

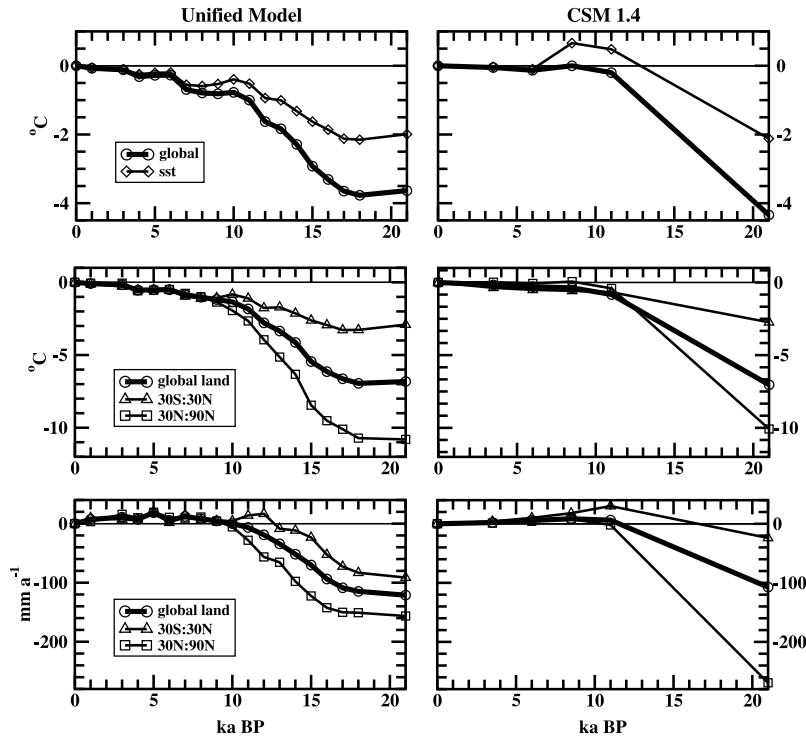


Figure 2. Temperature and precipitation anomalies from time slice simulations with the Hadley Centre UM and the NCAR CSM. Changes are given as mean deviation relative to the pre-industrial control simulation. The symbols represent individual time slice simulations. (top) Global averaged surface and sea surface temperature. (middle) Surface temperature over land. Global averages, excluding Antarctica, and averages for the latitudinal bands between 30°S and 30°N, and between 30°N and 90°N, are shown. (bottom) Changes in precipitation over land, global, and for two latitudinal bands.

of 100 years. Sensitivity experiments have shown that the long-term evolution of atmospheric CO₂ is not affected, whether terrestrial carbon stored initially on a submerged grid cell is released to the atmosphere immediately or gradually.

2.3. Spin-Up, Atmospheric CO₂, and Transient Simulations

[24] The LPJ-DGVM is spun up from bare ground for 1000 years under glacial conditions, i.e., the climate fields for 21 ka BP and atmospheric CO₂ of 186 ppm. Soil carbon stock was calculated based on litter input and mean decomposition rate after 400 years in order to reduce the time required to approach equilibrium. The IRF ocean substitute does not require a spin-up. Total carbon storage is 2100 GtC at the LGM.

[25] Two types of transient simulations were performed. In the set of experiments presented in sections 3.1, atmospheric CO₂ was prescribed during the last deglaciation and the Holocene according to ice core data [Monnin et al., 2000; Flückiger et al., 2002] in order to investigate changes in terrestrial carbon storage and vegetation distribution under realistic CO₂ forcing. In a second set of experiments presented in section 3.2, the evolution of atmospheric CO₂ during the Holocene is modeled and the mechanisms responsible for the simulated Holocene CO₂ variations are quantified. Again, atmospheric CO₂ is prescribed during the

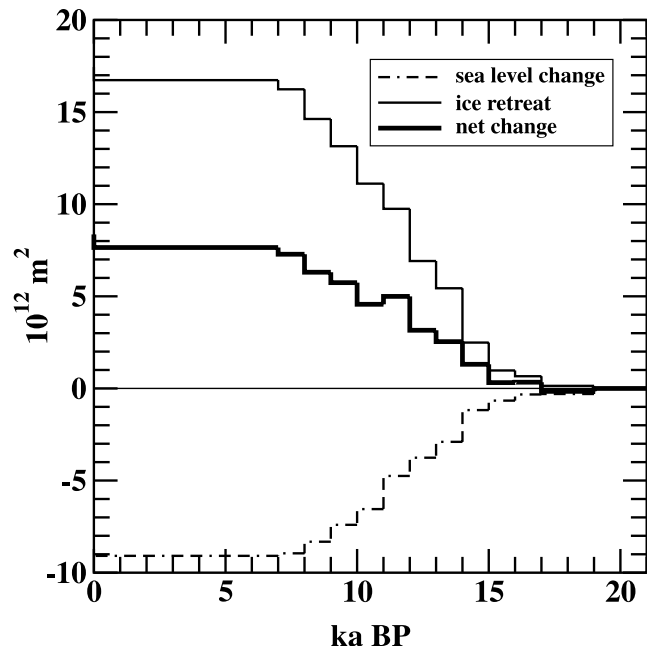


Figure 3. Changes in land available for plant growth relative to 21 ka BP in response to ice sheet retreat (thin solid line) and sea level rise (dash-dotted line) and the resulting net change (thick solid line).

Table 1. Model Setup and Boundary Conditions for the Various Simulations^a

Simulation	T, ka BP	Model Setup
<i>Atmospheric CO₂ Prescribed From LGM (21 ka BP) Until Pre-Industrial Time (0 ka BP)</i>		
P1; P1-CSM		atmospheric CO ₂ from Dome C ice core
P2; P2-CSM		atmospheric CO ₂ set constant to 280 ppm
<i>Atmospheric CO₂ Simulated During the Holocene^b</i>		
S1	10.5	standard simulation
S2; S2-CSM	8.0	CaCO ₃ compensation only (timescale: 5 ka), SST and terrestrial carbon inventory kept constant after <i>T</i>
S2a; S2a-CSM	8.0	CaCO ₃ compensation only (timescales varied between 1 and 50 ka)
S2b; S2b-CSM	8.0	CaCO ₃ compensation only (multiple timescales)
S3	8.0	CaCO ₃ compensation and SST, terrestrial carbon inventory kept constant after <i>T</i>
S4	10.5	CO ₂ fertilization shut off during the whole simulation
S5	10.5	CO ₂ fertilization shut off after <i>T</i>
S6	10.5	no changes in ice sheet ocean land mask after <i>T</i>

^aSimulations, where the CSM climate fields were applied are labeled “CSM”; otherwise the UM climate fields were used.

^bStart of simulation at LGM; atmospheric CO₂ is prescribed until *T* and simulated thereafter.

last deglaciation, as we are not in a position to model the CO₂ variations during the deglaciation with our model setup. A summary of the various experiments is provided in Table 1.

3. Results

3.1. Changes in Terrestrial Carbon Stock

[26] We start our discussion by analyzing the simulated evolution of terrestrial carbon storage over the past 21 kyr. The multimillennia timescales governing calcite compensation imply that the amount and timing of terrestrial carbon uptake during the glacial-interglacial transition and the Holocene must be estimated to quantify

the overall effect of terrestrial stock changes on Holocene CO₂ variations.

[27] In Table 2 the simulated changes in terrestrial carbon inventory and the contribution of different forcing factors and regions to these changes are summarized for selected periods. The LPJ-DGVM was forced by changes in climate and atmospheric CO₂ in simulations P1 and P1-CSM, whereas atmospheric CO₂ was held constant at the pre-industrial value of 282 ppm in the simulations P2 and P2-CSM. Thus simulation P2 (P2-CSM) shows the effect of climate change on terrestrial storage. The difference between P1 and P2 (P1-CSM minus P2-CSM) is due to CO₂ fertilization. Differences in global terrestrial stock changes between simulations with the UM and the CSM climate

Table 2. Factorial Analysis of Changes in Terrestrial Carbon Inventory During the Past 21 ka^a

Simulation	UM				CSM			
	Ice Retreat	Sea Level	Remaining Area	Total Change	Ice Retreat	Sea Level	Remaining Area	Total Change
21–11 ka BP								
P1 CO ₂ and climate	352	–133	460	679	342	–144	367	565
P2 climate only	364	–181	–70	113	353	–198	–176	–21
P1–P2 CO ₂ fertilization	–12	48	530	566	–11	54	543	586
11–8 ka BP								
P1 CO ₂ and climate	139	–67	30	102	140	–66	53	127
P2 climate only	145	–61	21	105	144	–68	50	126
P1–P2 CO ₂ fertilization	–6	–6	9	–3	–4	2	3	1
8–6 ka BP								
P1 CO ₂ and climate	13	–6	4	11	11	–4	76	83
P2 climate only	13	–6	–36	–29	11	–4	46	53
P1–P2 CO ₂ fertilization	0	0	40	40	0	0	30	30
6–0 ka BP								
P1 CO ₂ and climate	0	0	28	28	0	0	75	75
P2 climate only	0	0	–88	–88	0	0	–25	–25
P1–P2 CO ₂ fertilization	0	0	116	116	0	0	100	100
21–0 ka BP								
P1 CO ₂ and climate	610	–193	403	820	603	–199	446	850
P2 climate only	609	–259	–249	101	602	–269	–200	133
P1–P2 CO ₂ fertilization	1	66	652	719	1	70	646	717

^aFor both the UM and the CSM climate fields, simulations with variable (simulation P1, P1-CSM), and a simulation with constant atmospheric CO₂ (simulation P2, P2-CSM) have been performed. CO₂ fertilization is taken as the difference between the two simulations. The changes are distinguished for land covered by ice at the beginning of each period (Ice Retreat), land that has been flooded (Sea Level), and the remaining land, where changes in carbon inventories are driven only by changes in temperature, precipitation, cloud-cover, and atmospheric CO₂. We note that the CSM simulations at 11 and 8 ka BP consider changes in orbital forcing only, whereas otherwise present-day boundary conditions are applied; the numbers for the period 21 to 11 ka BP, 11 to 8 ka BP, and 8 to 6 ka BP must be interpreted with caution and are given here for completeness. The area affected by ice retreat and the size of the remaining area is different for the different evaluation periods, and the data shown in the columns “Ice Retreat” and “Remaining Area” are not additive over periods.

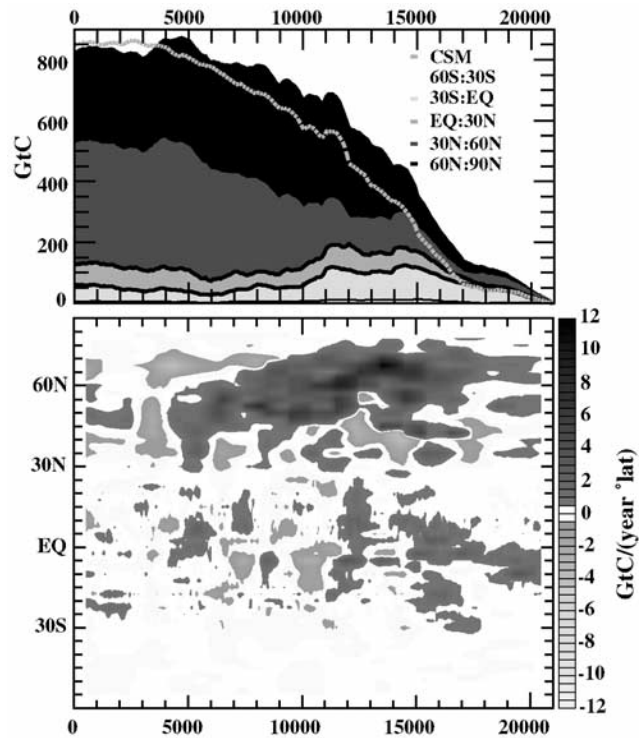


Figure 4. Simulated changes in terrestrial carbon inventory. (top) Cumulative change for different latitude bands for the UM climate anomalies (simulation P1) and global changes for the CSM climate anomalies (dotted line, simulation P1-CSM). The results have been smoothed by a 50-year running mean filter to remove high-frequency variability. (bottom) Zonally integrated net ecosystem uptake (1000-year running means) for the UM climate anomalies (simulation P1). See color version of this figure at back of this issue.

anomalies are generally surprisingly small, not only for the overall change, but also with respect to the contribution of different forcing factors during different periods.

[28] Kaplan *et al.* [2002] performed transient simulations with LPJ-DGVM applying the UM climate anomalies for the past 21 ka and the global inventory changes for simulation P1 and P2 are broadly similar to their results. Here modeled land carbon inventory changes are evaluated for formerly ice-covered areas, for areas flooded by sea level rise, and for the remaining land to quantify the impact of ice sheet retreat, sea level rise, temperature, precipitation, and cloud-cover changes on terrestrial carbon storage (Table 2).

[29] For the period from the LGM to pre-industrial time, the modeled total terrestrial uptake is 820 GtC for the UM climate anomalies (simulation P1) and 850 GtC for the CSM anomalies (P1-CSM). About 80% of the modeled LGM-pre-industrial uptake occurs between 17 ka and 11 ka BP (Figure 4) when changes in the driving variables are large. The LGM-pre-industrial change is comparable [François *et al.*, 1999; Otto *et al.*, 2002] or somewhat higher than the results obtained by others

[Esser and Lautenschlager, 1994; Friedlingstein *et al.*, 1992; François *et al.*, 1998; Beerling, 1999] who have forced terrestrial carbon models with model derived LGM climate fields and atmospheric CO₂. CO₂ fertilization contributes most (~700 GtC) to the simulated total change, as also found in previous studies with biogeochemical models [Esser and Lautenschlager, 1994; François *et al.*, 1998, 1999; Otto *et al.*, 2002]. During the transition, CO₂ fertilization leads to a modeled terrestrial uptake of ~540 GtC in areas not affected by inundation or ice retreat. A role for CO₂ fertilization in determining terrestrial carbon storage at concentrations of CO₂ within the glacial-interglacial range (180 to 280 ppm) has support from a range of data-based studies [Peng *et al.*, 1998; DeLucia *et al.*, 1999; Bennett and Willis, 2000; Cowling and Field, 2003]. The magnitude of the CO₂ fertilization response in our model is consistent with the recent amplification of the seasonal cycle in atmospheric CO₂ [McGuire *et al.*, 2001; Dargaville *et al.*, 2002] and with the enhancement of net primary production shown in Free Air Carbon Dioxide Enrichment experiments [e.g., DeLucia *et al.*, 1999; T. Hickler, unpublished results, 2003].

[30] Climate forcing factors have a substantial impact on terrestrial storage on a regional level. However, carbon uptake in response to vegetation growth on formerly ice-covered areas is partly compensated by carbon loss due to sea level rise and due to changes in temperature and precipitation elsewhere. These compensating fluxes explain the modest contribution (100 and 130 GtC, simulations P2 and P2-CSM) from the combined climate forcings to the global carbon uptake. Vegetation growth on formerly glaciated areas leads to an uptake of more than 600 GtC for both the UM and the CSM climate anomalies, whereas sea level rise leads to a loss of ~260 GtC during the transition and the early Holocene. Changes in temperature and precipitation lead to a carbon loss of 250 and 200 GtC for the UM and the CSM anomalies, on areas not affected by sea level rise and ice sheet retreat, respectively. This loss is caused by higher turnover rates of the litter and soil pools under a warmer climate, whereas the total amount of carbon stored in vegetation on these areas remained almost constant between 21 ka and 8 ka BP. The simulated climate driven uptake is comparable to estimates of Prentice and Fung [1990] as revised upward by Friedlingstein *et al.* [1995] and those of Friedlingstein *et al.* [1992], who combined climate model output for the LGM and bioclimatic schemes, without considering CO₂ fertilization effects.

[31] During the past 8 ka, simulation P1 (in which both climate and CO₂ fertilization effects are included) yields a terrestrial carbon uptake of ~40 GtC. This is in contradiction to the release postulated by Indermühle *et al.* [1999], but it is bracketed amply by earlier model results that range from a terrestrial release of 90 GtC to an uptake of 370 GtC during the late Holocene [Foley, 1994; François *et al.*, 1999; Beerling, 2000; Brovkin *et al.*, 2002; Kaplan *et al.*, 2002]. CO₂ fertilization is mostly responsible for the uptake in simulation P1, whereas changes in sea level and ice sheet extent have a negligible impact. On the other hand, simu-

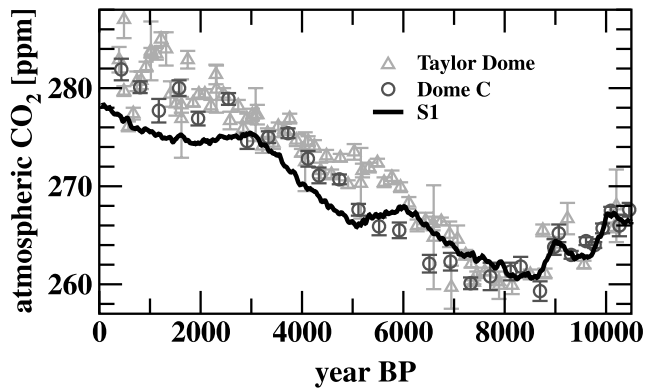


Figure 5. Simulated atmospheric CO₂ (solid line) versus the Holocene ice core CO₂ record (symbols). Model results are for the standard simulation S1 using the UM climate anomalies and have been smoothed by 50-year running means. Climate anomalies have been linearly interpolated between time-slice simulations. This results in step-like changes in the atmospheric CO₂ growth rate. Ice core data are from Dome C (circle) *Flückiger et al.* [2002] and Taylor Dome (triangle) *Indermühle et al.* [1999]. The differences in the ice core data between 7 and 5 ka BP arise from uncertainties in the age scale of the two ice cores [*Stauffer et al.*, 2002].

lation P2 (in which CO₂ fertilization is suppressed) yields a terrestrial release of ~ 120 GtC. A release, albeit smaller, was also obtained in simulation P2-CSM for the period 6 to 0 ka BP (recall that we are disregarding the CSM-based carbon simulations for the early Holocene). The simulated uptake of 100 GtC (Simulation P1) between 11 ka and 8 ka is mainly driven by ice sheet retreat and sea level rise and is in agreement with the atmospheric data-based estimate of 110 GtC by *Indermühle et al.* [1999].

[32] In conclusion, terrestrial carbon storage is simulated to increase over the Holocene in the standard setup (Simulations P1 and P1-CSM). Terrestrial uptake since the LGM is above the range of 300 to 700 GtC estimated from $\delta^{13}\text{C}$ mass balance calculations. We note, however, that a variety of mechanisms have been suggested which could increase this range [e.g., *Crowley*, 1991; *Spero et al.*, 1997; *Maslin and Thomas*, 2003]. On the other hand, terrestrial uptake in the climate-only simulation (P2) is below the data-based range. Hence simulations with the coupled model comparable to P1 and P2 as presented in the next section 3.2 will provide high and low estimates for the influence of sediment compensation on late Holocene CO₂.

3.2. Holocene Atmospheric CO₂

[33] The modeled Holocene evolution of atmospheric CO₂ in the standard simulation S1 matches the ice core data within a few ppm (Figure 5). The early CO₂ decrease of around 6 ppm from 10.5 to 8 ka BP is well reproduced. The relatively steep increase between 8 and 3 ka BP and the increase in the latest part of the Holocene are slightly underestimated; the simulated pre-industrial CO₂ concentration of 278 ppm is at the lower end of the observed range

of ~ 278 to 284 ppm. Next, we present a set of sensitivity experiments to quantify the contribution of individual mechanisms to the changes simulated in S1.

3.2.1. Sediment Compensation

[34] In simulation S2, SST and terrestrial storage are kept constant after 8 ka BP. Atmospheric CO₂ then increases only by 11 ppm during the past 8 ka, much less than the observed 20 ppm increase (Figure 6). The modeled CO₂ increase of 6 ppm between 8 and 6 ka BP is comparable to that shown in the ice core data; however, the sediment compensation mechanism fails to explain the observed CO₂ increase after 6 ka BP.

[35] The sensitivity of these results to variations in the IRF of the sediment component was tested. The timescale, τ , was varied in simulations S2a over a range from 1 ka to 50 ka in steps of 1 ka (Figure 7, top). The simulated atmospheric CO₂ change for the 8 to 0 ka BP period increases from 5 ppm for $\tau = 1$ ka, to 11 ppm for the standard model setup ($\tau = 5$ ka), to approach a value of 14 ppm at large values of τ . Changes are slightly less when applying the CSM anomalies (simulation S2a-CSM). We also tried multiple timescales of 5.5 ka, 8.2 ka, and 200 ka (simulations S2-b) instead of a single timescale of 5000 years; the relative weights of the three timescales were varied within their uncertainties (0.4–0.6, 0.1–0.28, and 0.3–0.32) (see Appendix A). The simulated CO₂ increase was then higher by 0.3–1.1 ppm than the 11 ppm obtained with the standard sediment model setup.

[36] The rather low sensitivity of simulated CO₂ changes during the past 8 ka to the choice of the compensation timescale can be understood by analyzing the fraction, f , that is available between 8 ka BP and 0 ka BP for compensation under the assumption that the terrestrial uptake occurred at time t' (before 8 ka BP),

$$f(t', \tau) = 0.7 \times 0.15 \times \left[\exp \frac{-(8 \text{ ka BP} - t')}{\tau} - \exp \frac{-(0 \text{ ka BP} - t')}{\tau} \right]. \quad (1)$$

The factor 0.15 on the right-hand side arises as only $\sim 15\%$ of a perturbation of the atmosphere-ocean system remains airborne, while the rest is removed by the ocean. This airborne fraction increases with the background level of atmospheric CO₂ due to the nonlinear carbon chemistry [*Joos et al.*, 1996] and a value of 15% is a good approximation for the Holocene situation. A simulation with HILDA model where 100 GtC of carbon were removed from the atmosphere-ocean system yields an equilibrium airborne fraction of 15.8% for a background CO₂ level of 280 ppm as shown in Figure 1 (dashed line). The factor 0.7 represents the fraction of the perturbation in the combined ocean-atmosphere system that is available for sediment compensation; the rest of the perturbation is removed by the weathering cycle operating on a 200 ka timescale [*Archer et al.*, 1997]. We have varied τ between 1 and 40 ka and t' between 17 ka BP and 11 ka BP (Figure 7, bottom). Then the fraction available for sediment compensation during the past 8 ka is typically between 2 and 4%. This may be compared with the fraction of 2.9% simulated in the standard run (S1). These calculations suggest that

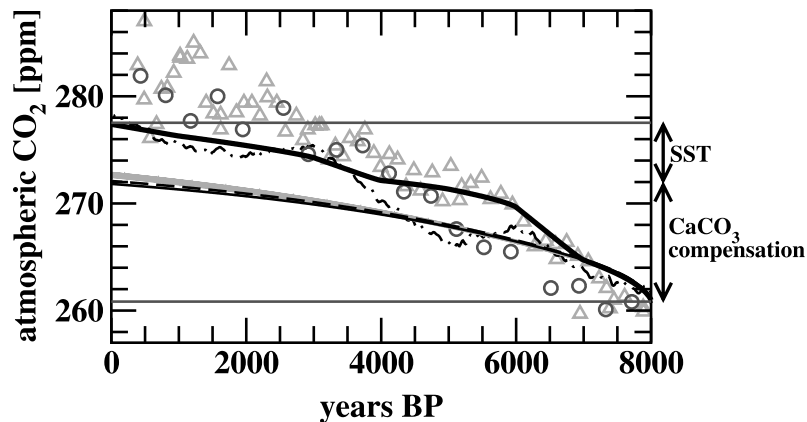


Figure 6. Contribution of the CaCO₃ compensation mechanism, sea surface warming, and of changes in terrestrial storage to the simulated CO₂ increase for the last 8 ka. In simulation S2 (thin solid line), only CaCO₃ compensation is simulated, whereas terrestrial storage and SST are kept constant after 8 ka BP. CaCO₃ compensation leads to a CO₂ increase of about 11 ppm during the past 8 ka. SST is also allowed to vary in simulation S3 (dash-dotted line) and atmospheric CO₂ increases by an additional 5 ppm until the pre-industrial time (difference between S3, dash-dotted line, and S2, thin solid line). The difference between the standard simulation S1 (thick solid line) and simulation S3 (dash-dotted line) is caused by changes in terrestrial carbon storage; a terrestrial uptake and subsequent release is simulated between 7 and 3 ka BP. The arrows on the right-hand side denote the contribution of the CaCO₃ mechanism and the effect of SST on the simulated CO₂ increase from 8 to 0 ka BP. Differences between different sediment compensation only simulations (S2, thin solid line; S2-CSM, dashed line; S2b, shaded area) are negligible as the terrestrial uptake until 8 ka is similar for the CSM and the UM anomalies, and simulated atmospheric CO₂ increase is not sensitive to the exact choice of the timescales governing sediment compensation. The CSM anomalies are applied in simulation S2-CSM (dashed line) instead of the UM anomalies (S2, thin solid line). The shaded area covers the range of results for simulations where three timescales instead of a single timescale have been used to calculate the IRF for sediment compensation and the coefficients for the IRF have been varied within their uncertainties (simulations S2b) for both the UM and the CSM climate anomalies. Ice core data are from Dome C (circle) *Flückiger et al.* [2002] and Taylor Dome (triangle) *Indermühle et al.* [1999].

uncertainties in the timescales of sediment compensation and the exact temporal evolution (as opposed to the magnitude) of terrestrial carbon uptake lead to an uncertainty of about $\pm 30\%$.

[37] In summary, the CO₂ increase between 8 and 0 ka BP in response to sediment compensation is about 3% of the terrestrial uptake during the transition and the early Holocene. Uncertainties in the timescales of sediment compensation lead to an uncertainty of about $\pm 30\%$. In our simulations, only slightly more than half of the observed CO₂ increase is explained by sediment compensation.

3.2.2. Sea-Surface Temperature

[38] In simulation S3, the effect of varying SST on CO₂ solubility is included as well as the CaCO₃ sedimentation mechanism. SST is varied according to the results from the UM model, while terrestrial carbon storage is still kept constant after 8 ka BP. The increase in SST by about 0.6°C occurs mainly between 7 and 6 ka BP and leads to an additional oceanic outgassing of about 6 ppm. Using the CSM model SST makes little difference: The difference in simulated CO₂ changes between S3-CSM and S3 over the past 6 ka is <2 ppm.

3.2.3. Terrestrial Uptake

[39] The simulated change in terrestrial storage during the past 8 ka is small. Consequently, the differences in atmo-

spheric CO₂ between the standard simulation S1 and the simulation S3, where terrestrial storage was kept constant, are slight. The terrestrial biosphere modulates the evolution of CO₂ during the past 8 ka by taking up carbon between 6 and 5 ka, and between 3 and 2 ka BP, and releasing carbon between 5 and 3 ka, and 2 and 0 ka BP.

3.2.4. CO₂ Fertilization

[40] CO₂ fertilization on land affects the modeled evolution of Holocene atmospheric CO₂ in two opposing ways. First, CO₂ fertilization promotes a large terrestrial uptake during the deglaciation when CO₂ increased from 186 to 265 ppm. This leads to a large CaCO₃ compensation and thus leads to longer-term outgassing of CO₂ during the Holocene. Second, CO₂ fertilization acts as a negative feedback in the coupled land-atmosphere-ocean carbon cycle system by enhancing terrestrial uptake during times of increasing atmospheric CO₂. Thus CO₂ fertilization acts to dampen any atmospheric CO₂ increase, including increases driven by, for example, CaCO₃ compensation or sea-surface warming.

[41] This balance is explored by inhibiting CO₂ fertilization in simulation S4. This is done by setting the CO₂ concentration in the model's photosynthesis module to 267 ppm over the entire simulation. Simulation S4 yields a much larger decrease in CO₂ between 10.5 and 8 ka BP

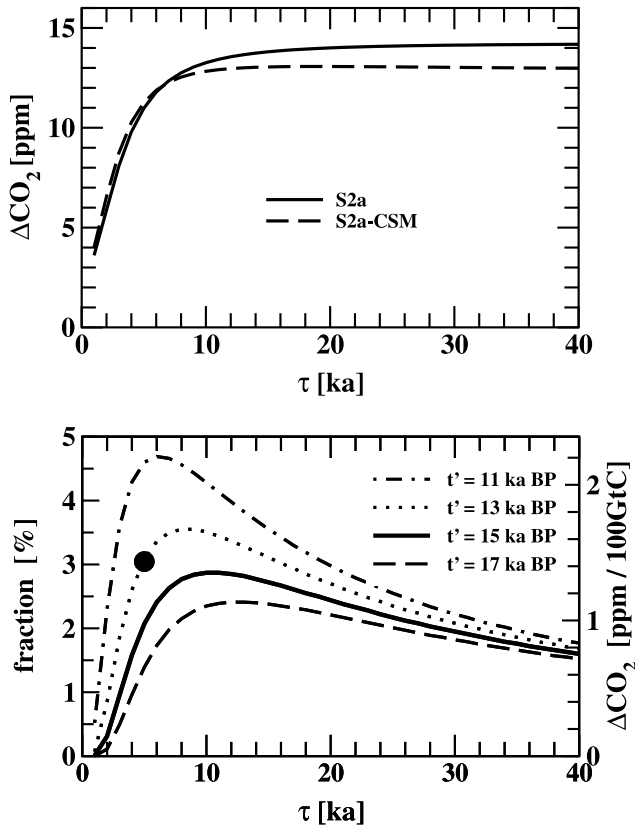


Figure 7. (top) CO₂ increase (8 to 0 ka BP) by CaCO₃ compensation. The timescale τ that governs sediment compensation has been varied between 1 and 40 ka in steps of 1 ka for both the UM (simulation S2a, solid line) and the CSM anomalies (simulation S2a-CSM, dashed line). (bottom) Fraction available for sediment compensation in the period 8 to 0 ka BP. The fraction has been calculated from equation (1) as a function of τ and the time of the terrestrial carbon uptake, t' . The solid circle gives the fraction that is compensated between 8 and 0 ka BP for the standard simulation S1 as calculated by dividing the atmospheric increase of 11 ppm by the terrestrial uptake of 781 GtC \times 0.47 ppm/GtC for 21 to 8 ka BP (Table 2). An e-folding timescale of 5 ka is applied in the standard simulation S1.

(Figure 8) than the standard simulation S1. This is incompatible with observations. Sediment compensation, which partly compensates the terrestrial uptake during 10.5 to 8 ka BP in the standard simulation S1, is strongly reduced in S4. After 8 ka BP, the growth rates in atmospheric CO₂ are similar as in the standard simulation and only slightly lower than observed. A terrestrial carbon release during the past 8 ka is mainly responsible for the CO₂ increase in S4.

[42] In simulation S5, we kept the CO₂ concentration in the model's photosynthesis module constant at 267 ppm after 10.5 ka BP. Thereby, fertilization occurs during the deglaciation, but further CO₂ fertilization during the Holocene is prevented. The simulated decrease in CO₂ at the beginning of the Holocene is still larger than in the standard

simulation and in the data (Figure 8). However, the terrestrial release in combination with CaCO₃ compensation of the uptake during the deglaciation and the early Holocene results in a total CO₂ increase of 20 ppm after 8 ka BP, which is consistent with the ice core data.

[43] Simulations S1 and S4 lead us to several conclusions. First, S4 (with inhibited CO₂ fertilization) is compatible with the *Indermühle et al.* [1999] hypothesis that terrestrial release in combination with sea surface warming caused atmospheric CO₂ to rise during the past 8 ka. However, the modeled change in terrestrial storage during the deglaciation and the early Holocene (Table 2, simulation P2) in S4 was lower than data-based reconstructions, and the CO₂ drawdown in the early Holocene was overestimated by \sim 4 ppm. Second, the magnitude of the CO₂ fertilization mechanism as implemented in LPJ appears not to be critical in order to simulate the observed CO₂ increase after 8 ka

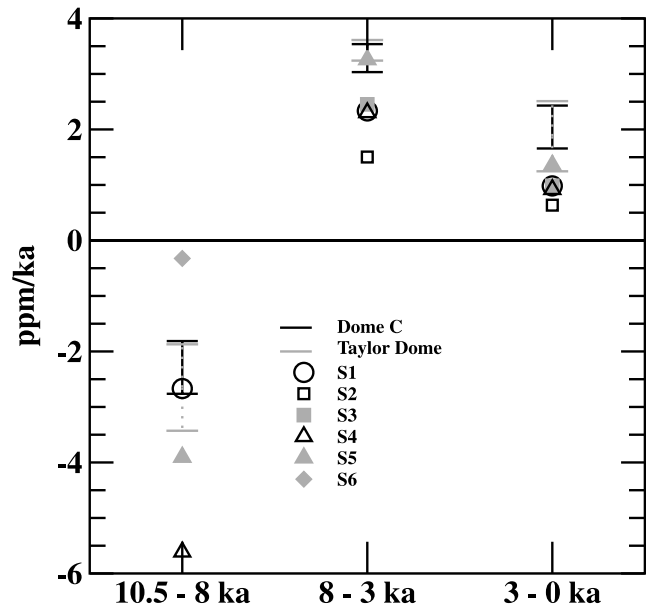


Figure 8. Reconstructed versus simulated atmospheric CO₂ growth rates. The average growth rates have been estimated with linear regression for different Holocene periods for both the Dome C (black solid error bar) [Flückiger *et al.*, 2002] and the Taylor Dome (shaded error bar) [Indermühle *et al.*, 1999]. The bars denote 1 standard deviation determined from the error of the estimated slope, taking into account the analytical uncertainties of the data. Modeled growth rates are given for the standard simulation (S1, solid circle), the simulations S2 with CaCO₃ compensation only after 8 ka BP (open square), the simulation S3 (solid square) where only CaCO₃ compensation and SST changes are considered after 8 ka BP, while terrestrial storage is kept constant, simulation S4 (open triangle) where CO₂ fertilization is suppressed over the entire 21 ka period, simulation S5 (solid triangle) where CO₂ fertilization is suppressed during the Holocene only, and simulation S6 (solid diamond) where ice sheet extent is kept constant after 10.5 ka BP.

BP, but has implications for the mechanistic explanation of the increase. In the standard simulation S1, CaCO₃ compensation is the dominant process explaining about half of the observed increase. In S4, with CO₂ fertilization suppressed, terrestrial carbon release was the dominant process and the role of CaCO₃ compensation was less. The simulated changes in terrestrial storage between the LGM and pre-industrial times, 820 GtC in S1, 100 GtC in S4, span more than the range of 300 to 700 GtC derived from $\delta^{13}\text{C}$ mass balance calculations. Hence the two simulations might roughly be considered as providing upper and lower limits for the strength of the CaCO₃ compensation mechanism.

3.2.5. Ice Sheet Retreat

[44] The decrease in atmospheric CO₂ between 10.5 and 8.5 ka is mainly caused by the establishment of boreal forest following ice sheet retreat. This is demonstrated by simulation S6, where vegetation has been prevented from growing on formerly ice-covered land. Simulated atmospheric CO₂ decreases only by about 1 ppm during the early Holocene in S6, compared to a 6 ppm decrease in the standard simulation and in the ice core data. As noted above, terrestrial uptake on formerly ice-covered land is partly off-set by sediment compensation. In this simulation, SST changes contribute little to the simulated CO₂ changes between 10.5 and 8 ka BP.

3.3. Holocene Atmospheric $\delta^{13}\text{C}$

[45] Atmospheric ¹³CO₂ has the potential to give additional constraints on carbon cycle processes governing the evolution of atmospheric CO₂ during the Holocene [Indermöhle *et al.*, 1999]. Fluxes associated with the CaCO₃ sedimentation have a very small impact on atmospheric $\delta^{13}\text{C}$, whereas terrestrial carbon release and sea-surface warming both tend to increase atmospheric $\delta^{13}\text{C}$. Simulated atmospheric $\delta^{13}\text{C}$ increases by 0.2‰ from 10.5 ka BP until about 6 ka BP, in response to terrestrial uptake and sea surface warming (simulation S1; Figure 9). After 6 ka BP, $\delta^{13}\text{C}$ remains relatively stable. Small changes were also found by Brovkin *et al.* [2002]. The amplitude of the simulated $\delta^{13}\text{C}$ changes is small compared to the data range of about 0.4‰. Sea surface warming causes $\delta^{13}\text{C}$ to increase by 0.07‰ after 8 ka BP (simulation S3). Simulation S4 with suppressed CO₂ fertilization yields a decrease of slightly more than 0.1‰ after 5 ka BP, caused by terrestrial release. These results illustrate the fact that the precision of $\delta^{13}\text{C}$ data needs to be $\pm 0.1\%$ or better for a reliable separation of land and ocean processes.

3.4. Mean Changes in Oceanic $\delta^{13}\text{C}$

[46] Release of isotopically light, organic carbon leads to a lower $\delta^{13}\text{C}$ signature in the ocean and in the whole ocean-atmosphere-land biosphere-reactive sediment system. The mean $\delta^{13}\text{C}$ signature of dissolved inorganic carbon (DIC) in the ocean was lower during the LGM as compared to today, consistent with a lower terrestrial carbon inventory at the LGM. Duplessy *et al.* [1988] estimate from marine sediment data that $\delta^{13}\text{C}$ of DIC was on average lower by 0.32‰ over the water column in the Pacific. Curry *et al.* [1988] estimate LGM-Holocene changes in the deep water isotopic compo-

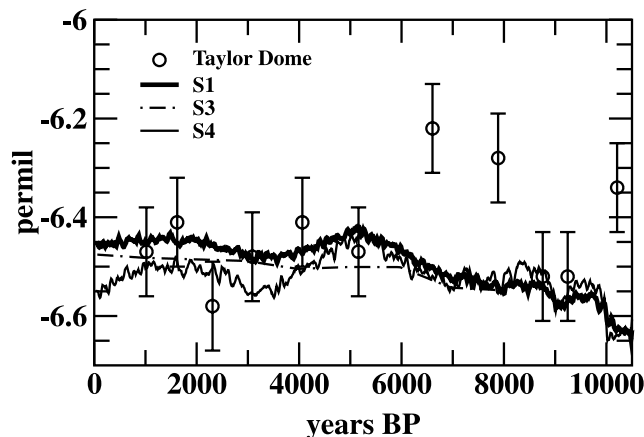


Figure 9. Simulated $\delta^{13}\text{C}$ in atmospheric CO₂ versus the Holocene $\delta^{13}\text{C}$ ice core record. Ice core data are from Taylor Dome (circle) [Indermöhle *et al.*, 1999], and the error bars are estimates of their reproducibility (1 standard deviation). Model results are from the standard simulation (S1, thick solid line), simulation S3 where SST changes and CaCO₃ compensation only is considered after 8 ka BP, and simulation S4 where CO₂ fertilization is suppressed. Atmospheric $\delta^{13}\text{C}$ is only simulated after 8 ka BP in Simulation S3. Results have been smoothed by 50-year running means.

sition between 0.28‰ (Indian) and 0.81‰ (Southern Ocean) and a mean deep ocean change of 0.46‰. These numbers have been used to estimate the LGM-Holocene change in terrestrial carbon stocks to be 300 to 700 GtC [Bird *et al.*, 1994, 1996].

[47] We estimated the temporal evolution of the average $\delta^{13}\text{C}$ signature of DIC from the modeled terrestrial changes in carbon and ¹³C, taking into account changes in the distribution of C₃ and C₄ plants, changes in the air-biota isotopic fractionation, net export of carbon and carbon isotopes by sedimentary burial, and dilution of the isotopic perturbation by the atmosphere, by the land biosphere, by the reactive ocean sediment layer, and by the marine carbon pools, but neglecting changes in the size of the marine organic carbon pool (see Appendix B). Modeled $\delta^{13}\text{C}$ of DIC is 0.50‰ lower at the LGM than today for the standard case where simulated terrestrial storage was 820 GtC lower at the LGM (simulation P1) (Figure 10, bottom).

[48] Changes in the mean terrestrial isotopic signature have a minor impact on the modeled changes in $\delta^{13}\text{C}$ of DIC. The reason is that the biospheric C inventory is about 15 times smaller than the total carbon inventory in the ocean-atmosphere-land biosphere-reactive sediment system. The simulated mean $\delta^{13}\text{C}$ difference between the terrestrial and atmospheric carbon stocks decreased by 1.1‰ from the LGM to the Holocene (Figure 10, top; simulation P1). An increase in boreal trees that leads to a higher ratio of carbon assimilated by C₃ versus C₄ plants has contributed to this shift. The estimated oceanic $\delta^{13}\text{C}$ shift is 0.05‰ smaller than in the standard case, if the land biosphere-atmosphere $\delta^{13}\text{C}$ difference is kept at the Holo-

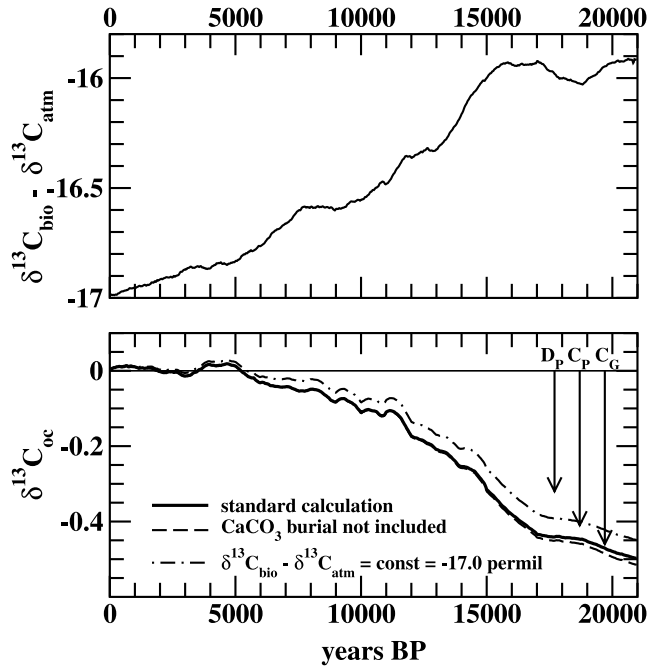


Figure 10. Modeled LGM-Holocene changes (top) in the mean $\delta^{13}\text{C}$ difference between the terrestrial and atmospheric carbon stocks and (bottom) in the average isotopic signature of the carbon stored in the ocean-atmosphere-land-reactive sediment system (solid line). Values are for simulation P1 and in permil units. Changes in the atmosphere-land biosphere $\delta^{13}\text{C}$ difference and the export of carbon by sediment burial have a small influence on the modeled oceanic $\delta^{13}\text{C}$ perturbation as illustrated by calculations where the atmosphere-land biosphere $\delta^{13}\text{C}$ difference was kept constant (dash-dotted line) or calcite burial neglected (dashed line). Thin arrows indicate data-based estimates of the average LGM-Holocene change for the whole Pacific (D_P [Duplessy et al., 1988]), and for deep waters only in the Pacific (C_P) and globally (C_G) [Curry et al., 1988].

cene value of -17‰ . Even smaller deviations relative to the standard are found when carbon export to ocean sediments is neglected.

[49] A major caveat in the above calculations is the unknown fate of the marine organic carbon pool. Marine organic carbon has a similar isotopic signature to the organic carbon on land. Hence the observed isotopic change in marine sediments is only indicative of the total net change in organic carbon, but allows no distinction between changes in the oceanic versus the terrestrial organic pools. Here we have assumed that the organic carbon pool of 700 GtC remained constant over time, similar to calculations of terrestrial carbon stock changes [Bird et al., 1994, 1996]. Marine sediment $\delta^{13}\text{C}$ data and our modeled estimate of the mean oceanic $\delta^{13}\text{C}$ change would come into agreement if the organic carbon pool in the ocean was larger by 100 to 500 GtC at the LGM than today.

3.5. Changes in Plant Type Distribution

[50] Vegetation reconstructions based on pollen and plant macrofossil data show that global biome distributions at the LGM were markedly different from present [Wright et al., 1993; Prentice et al., 2000]. The differences can be broadly explained by the presence of ice sheets, a global reduction in land-surface temperature, and a reduced water cycle in concert with lower C_3 plant productivity and plant water-use efficiency directly due to the low atmospheric CO_2 concentration [Harrison and Prentice, 2003]. Vegetation reconstructions also show differences between mid-Holocene and present biomes [Wright et al., 1993; Prentice et al., 2000], although these are less extensive at a global scale. In order to assign the simulated abundances of the PFTs to biome types, we use the simple algorithm summarized in Figure 11. The simulated potential natural vegetation for pre-industrial time (Figure 12) shows the main features indicated in global maps [e.g., Haxeltine and Prentice, 1996; de Fries et al., 1999]. The simulated mid-Holocene biome distribution also shows qualitative features of late Holocene vegetation change (Figure 12) as indicated by pollen

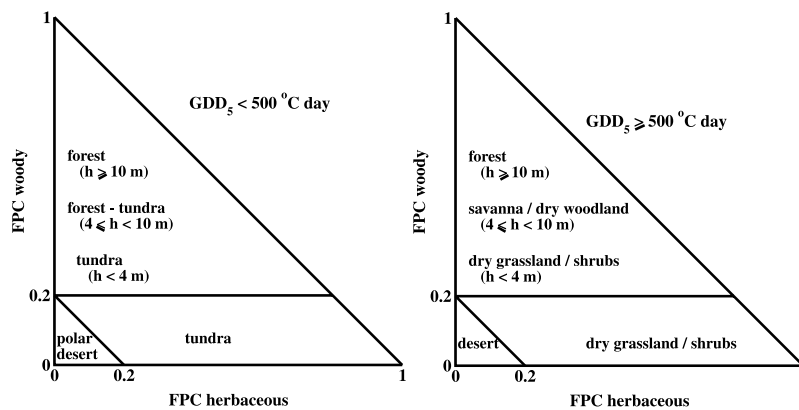


Figure 11. Scheme used to assign biome types from the simulated fractional plant cover (FPC) of woody and herbaceous species and simulated stand height (h).

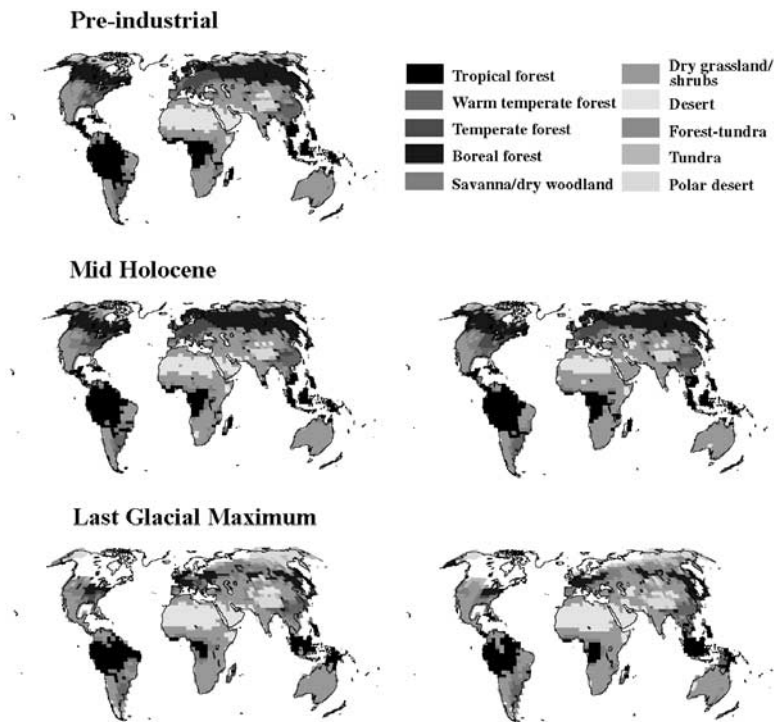


Figure 12. Simulated biome distribution for the LGM (21 ka BP), the Mid-Holocene (6 ka BP), and the pre-industrial time (0 ka) for the UM climate anomalies (left, simulation P1) and the CSM climate anomalies (right, simulation P1-CSM). The distribution at pre-industrial time is nearly identical for simulations with the UM and the CSM anomalies (not shown). See color version of this figure at back of this issue.

analysis data at sampling points, whose density, however, varies considerably among regions [Prentice *et al.*, 2000]. The Central African tropical forest is reduced; this is supported by the limited observational evidence from this region, and has been attributed to a moisture shift of the intertropical convergence zone [Harrison *et al.*, 1998]. A slight simulated increase in precipitation to the north of the Sahel produces a northward encroachment of shrubs and grass into areas which are desert today. This is qualitatively consistent with extensive evidence [Jolly *et al.*, 1998], and can be explained by an increase in monsoon penetration due to the greater than present land-sea contrast in the Northern Hemisphere [Kutzbach and Street-Perrott, 1985]. However, the simulated vegetation shift rarely exceeds one latitudinal band (2.5°); the CSM produces a slightly more pronounced northward shift. Neither model reproduces the full magnitude of reduction of the Sahara desert shown by data [Jolly *et al.*, 1998]. This underestimation is to be expected because the UM simulation lacks the positive feedback caused by circulation changes in the Atlantic [Kutzbach and Liu, 1997; Braconnot *et al.*, 1999] while the CSM simulation lacks the positive feedback caused by vegetation-atmosphere interactions [e.g., Broström *et al.*, 1998; Braconnot *et al.*, 1999; de Noblet-Ducoudré *et al.*, 2000].

[51] The observed slight northward shift in the arctic treeline [Prentice *et al.*, 2000; Bigelow *et al.*, 2003; Kaplan

et al., 2002] is too small to be represented well with the coarse model resolution, but it is indicated by a few grid cells in the northern circumpolar region. In the midlatitudes, few changes in vegetation distribution are simulated. The extent of temperate forest in North America, Europe, and China nearly remain unchanged, and the observed northward extension of temperate treelines in Europe and China [Prentice *et al.*, 2000] is not resolved.

[52] The simulated biome distribution for the LGM differs radically from the present-day or mid-Holocene distribution and reproduces the broad features observed in paleodata. Strong reduction in temperatures in northern latitudes produced a southward displacement and major reduction in area of the boreal forest, while reduced precipitation over midlatitude Eurasia caused a fragmentation of the temperate forests. These features are consistent with observations, as summarized, for example, by Prentice *et al.* [2000]. However, despite the reduced precipitation, the simulations show forest over much of western Europe whereas the data show even drier conditions with steppe predominant. The reconstructions also show a reduced extent of tropical forests and increased extent of grasslands and shrublands. The UM especially appears to overestimate low-latitude tree cover.

[53] In conclusion, the main changes in simulated and reconstructed biome distributions agree moderately well with data for the LGM and the mid-Holocene. The largest

differences arise in the tropics, where the simulated extent of tropical forests is overestimated at the time of the LGM, and the modeled reduction of the Sahara desert is underestimated in mid-Holocene time.

4. Potential Impact of Land Use Emissions

[54] The grand hypothesis by *Ruddiman* [2003] that human activities prevented the climate system to enter a glacial during the Holocene has been discussed in two editorials [*Crowley*, 2003; *Crutzen and Steffen*, 2003]. A part of the hypothesis is that land use prevented atmospheric CO₂ to drop and that anthropogenic land use emissions are responsible for a 40 ppm atmospheric anomaly. In the following we scrutinize this part of the overall hypothesis.

[55] First, we estimate a lower limit for the anthropogenic emissions needed to raise atmospheric CO₂ by 40 ppm over the Holocene. The ocean is roughly in equilibrium with the atmosphere on a millennial timescale, and about 85% of the carbon emission into the atmosphere must have been removed by the ocean, leaving only ~15% airborne (Figure 1). This yields a cumulative carbon emission by land use of 566 ppm (40 ppm × 2.123 GtC ppm⁻¹ × 100/15). The effective emissions to explain a 40 ppm rise must be higher as ocean sediment interaction would have further reduced the atmospheric perturbation. We note that the equilibrium airborne fraction is well constrained, as ocean carbonate chemistry and ocean volume, the two primary governing factors, are well known. Second, a lower limit for the atmospheric δ¹³C perturbation is estimated by applying equation B2 of Appendix B. This yields a decrease in atmospheric δ¹³C of 0.3‰. Third, a transient simulation with HILDA model (coupled to the IRF sediment model and a box-type biosphere) is carried out to take into account system dynamics. Prescribing a linear increase from 240 to 280 ppm over the past 8 ka yields a cumulative carbon emission of 710 GtC and an atmospheric δ¹³C decrease of 0.6‰.

[56] Both the isotopic perturbation and the carbon emissions by land use implied by the *Ruddiman* hypothesis are in conflict with other data. The 0.6‰ isotopic perturbation is not compatible with the ice core data that suggest an atmospheric δ¹³C decrease of about 0.25‰ during the last 8 ka (Figure 9). Historical cumulative carbon losses due to changes in land use have been estimated to be 180 to 200 GtC by comparing carbon storage for natural vegetation distribution and present-day land cover [*Matthews*, 1983; *de Fries et al.*, 1999]. This is 3 to 4 times less than required for a millennial-scale 40 ppm increase.

[57] Early human-induced land use change might have contributed by a few ppm to the observed pre-industrial CO₂ rise. World population increased by more than an order of magnitude from about 300 million to 5 billion during the last millennium. The vast majority of the population increase occurred during the past 150 years, driving a land use flux of about 120 GtC [*Houghton*, 1999]. Subtracting this estimate from the estimated 180 to 200 GtC total cumulative land use loss yields a pre-1850 emission of 60 to 80 GtC. Such an emission causes atmospheric CO₂, after re-equilibration with the ocean, to rise by 4 to 6 ppm (60 to 80 GtC ×

0.47 ppm/GtC × 0.15). In conclusion, it is unlikely that the small population that lived during the Holocene could have forced a CO₂ rise of more than a few ppm.

5. Discussion and Conclusions

[58] Possible mechanisms responsible for the evolution of Holocene atmospheric CO₂ are explored by forcing the Bern CC carbon cycle model, which includes the Lund-Potsdam-Jena Dynamic Global Vegetation Model and an ocean-sediment component, with results from time-slice simulations from comprehensive climate models over the past 21 ka. The focus is on terrestrial carbon storage, calcite compensation, and changes in SST, whereas the buildup of coral reefs, peat formation, and anthropogenic land use activities have not been included in the model. The simulated atmospheric CO₂ concentrations match the ice core data within a few ppm and the model results are broadly consistent with proxy data of atmospheric ¹³CO₂, mean ocean δ¹³C, and pollen data, within their uncertainties.

[59] CaCO₃ compensation and SST increase are the main factors driving the simulated CO₂ increase during the past 8 ka. Carbon uptake on formerly ice-covered land, partly compensated by a loss of terrestrial carbon due to sea level rise and CaCO₃ compensation, is responsible for the simulated early Holocene decrease of CO₂. This conclusion differs from that of *Broecker et al.* [2001], who assigned the entire late Holocene CO₂ increase to sediment compensation, or *Indermühle et al.* [1999], who postulated a terrestrial carbon release as the main cause.

[60] A conceivable alternative explanation emerges when considering the results from simulations in which the CO₂ fertilization mechanism is suppressed. In this case, a terrestrial carbon release in response to temperature and precipitation changes in combination with sea-surface warming and sediment compensation explains the 20 ppm CO₂ increase during the past 8 ka. This result is qualitatively consistent with the proposal by *Indermühle et al.* [1999]. However, the early Holocene CO₂ decrease is overestimated in the simulation by 4 ppm, and total terrestrial uptake during the past 21 ka is only about 100 GtC for the past 21 ka, well below any recent estimate.

[61] Sensitivity analyses and a comparison with data-based reconstructions of the terrestrial uptake suggest that only about half of the observed CO₂ increase of 20 ppm (8 to 0 ka BP) can be explained by CaCO₃ compensation in response to earlier terrestrial carbon uptake. The impact of sediment compensation on atmospheric CO₂ during the past 8 ka is principally determined by the total amount of terrestrial carbon uptake during the glacial-interglacial transition and the early Holocene. We find that its contribution to the atmospheric CO₂ increase between 8 and 0 ka BP corresponds to 3 ± 1% of this terrestrial uptake. The data-based range of 300 to 700 GtC implies a late Holocene CO₂ rise between 4 and 10 ppm (3% × 0.47 ppm/GtC × 300 to 700 GtC) due to this mechanism.

[62] A relatively strong contribution to the Holocene CO₂ rise by SST change is found here in contrast to *Brovkin et al.* [2002], who suggest a negligible contribution by this

mechanism. *Brovkin et al.* [2002] applied a model of intermediate complexity, neglecting forcing by ice sheet retreat. Here a box-type ocean model is forced by spatially averaged SST changes obtained from the output of the HadSM3 atmosphere model coupled to a slab ocean model, a sea-ice model, and prescribed orbital, greenhouse gas, and ice sheet forcing. Our results might be biased toward high values as communication between the surface and the deep ocean is not represented by the slab model, and results are influenced by a change in the land-sea mask between 7 and 6 ka in the UM time slice simulations. The contribution of SST changes to the Holocene CO₂ rise requires further investigations.

[63] The hypothesis by *Ruddiman* [2003] that land use prevented atmospheric CO₂ from dropping and that anthropogenic land use emissions are responsible for a 40 ppm increase is dismissed based on the ice core δ¹³C record and other well-founded land use emission estimates [*Matthews*, 1983; *de Fries et al.*, 1999]. We estimate that early human-induced land use emissions might have contributed 4 to 6 ppm to the observed CO₂ rise.

[64] Other processes not represented in our simulations might have contributed to the Holocene CO₂ evolution. (1) *Ridgwell et al.* [2003] show that coral reef buildup is likely to play an important role for the late Holocene CO₂ evolution. (2) Beside CaCO₃ compensation of terrestrial uptake and coral reef buildup, other sediment-ocean interactions have the potential to increase atmospheric CO₂ during the Holocene. These include changes in the rain-ratio of calcite and organic carbon and changes in the silica cycle in response to the glacial-interglacial reorganization [*Archer and Maier-Reimer*, 1994; *Matsumoto et al.*, 2002]. (3) The greening of the Sahara desert as reconstructed for 6 ka BP is not simulated in our model setup, similar to other models that do not include climate-vegetation feedbacks. However, *Indermühle et al.* [1999] estimated that the desertification of the Sahara caused a terrestrial release of about 30 GtC during the past 6 ka (until pre-industrial time). This implies that only 2 ppm of the rise can be explained by the Late Holocene expansion of the Sahara. (4) Long-term changes in solar irradiance, which were not considered in the UM and CSM simulations, might conceivably have contributed to a warmer climate and to a terrestrial release of a few ppm. *Gerber et al.* [2003] suggested that solar irradiance changes caused atmospheric CO₂ variations of about 6 ppm during the last millennium. However, the residual ¹⁴C tree ring record [*Stuiver et al.*, 1998] suggests little long-term changes in solar irradiance. (5) The 8.2 ka cold event in the North Atlantic region, not represented in the UM and CSM simulations, might have caused additional terrestrial uptake of up to a few tens of GtC around 8.2 ka BP and a subsequent release thereafter. (6) On the other hand, peat buildup in high northern latitudes may have sequestered additional carbon on land. A recent estimate [*Gajewski et al.*, 2001, 2002] suggests that about 400 GtC have been stored in northern peat land during the past 8 ka and 200 to 320 GtC during the past 3 ka. Such high estimates are, however, in conflict with the ice core records for atmospheric CO₂ and δ¹³C.

[65] In summary, the early Holocene CO₂ decrease has been quantitatively explained by terrestrial uptake and calcite compensation. CO₂ fertilization and forest growth on formerly ice covered areas are mainly responsible for the simulated uptake of 820–850 GtC over the past 21 ka, whereas changes in climate alone would lead to a terrestrial carbon loss. A range of mechanisms, including calcite compensation, terrestrial carbon uptake and release, SST changes, and coral reef buildup, contributed to the 20 ppm late Holocene CO₂ rise. We constrained the contribution of calcite compensation (in response to terrestrial uptake during the transition and the early Holocene) to 4 to 10 ppm. Terrestrial carbon inventory changes related to climate and CO₂ forcing, the greening of the Sahara, peat buildup, and land use have probably influenced CO₂ by a few ppm only. SST variations contributed between 0 and 6 ppm. The land use scenario by [*Ruddiman*, 2003] is highly unlikely and not compatible with the ice core δ¹³C record. The potentially large contribution of coral reef buildup needs to be further explored with 3-D ocean-sediment models.

[66] A high-precision ice core δ¹³C record with a high temporal resolution would have the potential to shed further light on the Holocene CO₂ problem. Our simulations suggest that the precision of the record must be better than 0.1‰.

Appendix A: Representation of CaCO₃ Compensation

[67] The IRF substitute for the HILDA ocean model is described elsewhere [*Joos et al.*, 1996, 2001]. Here these equations are complemented by an IRF representation of the impact of CaCO₃ sediment compensation on atmospheric CO₂ [*Archer et al.*, 1997].

[68] CaCO₃ dissolution and sedimentation affects both the balance of dissolved inorganic carbon (DIC, ΣCO₂) and of alkalinity in the ocean. For simplicity, the impact of alkalinity changes on the partial pressure of CO₂ and atmospheric CO₂ is formally factored into changes in the concentration of DIC, here termed δΣCO₂^{*}. The asterisk superscript refers to the inclusion of the impact of alkalinity changes, and δ denotes the change since the start of the simulation. This simplification does not affect simulated atmospheric CO₂.

[69] The flux of ΣCO₂^{*} from the sediment (*sed*) to the ocean (*oc*) is given by the convolution integral

$$F_{sed,oc}(t) = \int_{t_0}^t dt' \frac{a}{\tau} F_{a-oc,out}(t') e^{-\frac{t-t'}{\tau}}, \quad (\text{A1})$$

where $F_{a-oc,out}$ is the net flux of carbon leaving the ocean-atmosphere system. For example, $F_{a-oc,out}$ is the net flux into the terrestrial biosphere minus fossil carbon emissions. Here t_0 denotes the time at the start of the simulation, and a denotes the fraction of the ocean-atmosphere perturbation that is eventually removed by CaCO₃ compensation with the governing timescale τ . The values of a and τ are set to 0.7 and 5000 years in the standard model setup [*Archer et al.*, 1997]. The convolution integral is reformulated for computational efficiency, and the flux from the sediment at

Table A1. Timescales and Coefficients for the Sediment Compensation IRF

<i>i</i>	τ_i , years	a_i		
		Mean	Fast	Slow
1	5500	0.54	0.6	0.4
2	8200	0.14	0.1	0.28
3	200,000	0.32	0.3	0.32

time t is calculated from the flux from the sediment at the previous time step and the net flux leaving the system,

$$F_{sed,oc}(t) = F_{sed,oc}(t - \Delta t)e^{-\frac{\Delta t}{\tau}} + \frac{\Delta t}{\tau} a_i F_{a-oc,out}(t - \Delta t)e^{-\frac{\Delta t}{\tau}}, \quad (A2)$$

where Δt is the length of the model time step.

[70] The multicentury timescale of ocean overturning is small compared to the timescale of sediment compensation, and the $\Sigma\text{CO}_2^*(t)$ concentration is uniformly lowered throughout the ocean,

$$\delta\Sigma\text{CO}_2^*(t) = \delta\Sigma\text{CO}_2^*(t - \Delta t) + \frac{10^6}{V_{oc} \rho} F_{sed,oc}(t) \Delta t. \quad (A3)$$

Here, V_{oc} is the ocean volume ($1.38 \cdot 10^{18} \text{ m}^3$) and ρ is the density of ocean water. $F_{sed,oc}$ and $F_{a-oc,out}$ are in units of mol yr^{-1} ($1 \text{ GtC} = 8.33 \cdot 10^{13} \text{ mol}$), and $\delta\Sigma\text{CO}_2^*$ is in units of $\mu\text{mol kg}^{-1}$. $F_{sed,oc}$ and $\delta\Sigma\text{CO}_2^*$ are initialized to zero at the start of the transient simulation. This change in DIC due to sediment compensation, $\delta\Sigma\text{CO}_2^*(t)$, is added to the change in DIC due to air-sea gas exchange in the HILDA IRF model [Joos *et al.*, 1996, equation (3)] before evaluating sea surface partial pressure.

[71] In sensitivity experiments, the IRF is refined, according to the timescales given by Archer *et al.* [1997]. Then equation (A1) changes to

$$F_{sed,oc}(t) = \int_{t_0}^t \sum_{i=1}^3 \frac{a_i}{\tau_i} F_{a-oc,out}(t') e^{-\frac{t-t'}{\tau_i}} dt'. \quad (A4)$$

[72] Uncertainties associated with the a_i are considered by determining a ‘‘fast’’ compensation, where a_1 is set to the highest feasible value and a_3 to the lowest, and a ‘‘slow’’ compensation, with a_1 low and a_3 high. Here a_2 is set that $\Sigma a_i = 1$. The coefficients applied are given in Table A1.

Appendix B: Mean Ocean $\delta^{13}\text{C}$ Signature

[73] Release of isotopically light organic carbon perturbs the isotopic signal in the relatively fast (<1000 years) exchanging carbon reservoirs, land biosphere, atmosphere, ocean, and reactive sediments. This perturbation is calculated from the modeled changes in the terrestrial carbon stock and the modeled changes in the mean land biosphere-atmosphere $\delta^{13}\text{C}$ difference, $\delta^{13}\text{C}_{b-a}$.

[74] The mass balance for ^{13}C is [Heimann and Maier-Reimer, 1996]

$$\frac{d}{dt} [N_a \cdot \delta^{13}\text{C}_a + N_b \cdot \delta^{13}\text{C}_b + N_{o,DIC} \cdot \delta^{13}\text{C}_{o,DIC} + N_{o,OC} \cdot \delta^{13}\text{C}_{o,OC} + N_{rs} \cdot \delta^{13}\text{C}_{rs}] - F_w \cdot \delta^{13}\text{C}_w + F_s \cdot \delta^{13}\text{C}_s = 0, \quad (B1)$$

where N denotes a carbon inventory, $\delta^{13}\text{C}$ is the $^{13}\text{C}/^{12}\text{C}$ isotopic ratio expressed in permil units, the indices $a, b, o,$

and rs refer to the atmosphere, biosphere, ocean, and reactive sediments, DIC is dissolved inorganic carbon, OC is organic carbon, F_w is the carbon input by weathering, F_s the carbon loss by burial, and $\delta^{13}\text{C}_w$ and $\delta^{13}\text{C}_s$ the isotopic signatures of these fluxes.

[75] Equation (B1) is solved for the mean perturbation in the system, $\Delta\delta^{13}\text{C}_m$, by assuming that (1) the pool of organic carbon in the ocean remains constant, (2) its isotopic difference relative to DIC remains constant, (3) the isotopic perturbation in response to the terrestrial change is equal in all reservoirs, (4) the carbon input by weathering is balanced by the loss to the sediment and that the weathering flux is isotopically unperturbed, whereas the burial flux carries the mean isotopic perturbation, and (5) $\delta^{13}\text{C}$ changes other than those from the terrestrial perturbation, for example, due to SST changes or changes in the marine biological cycle, can be neglected [Smith *et al.*, 1999]. The estimated overall LGM to Holocene $\Delta\delta^{13}\text{C}_m$ change is not sensitive to assumptions (2) to (5) within reasonable, data-based limits, whereas a change in the isotopically depleted organic carbon inventory in the ocean would influence the results similarly as an equal change in the terrestrial carbon inventory. This yields

$$\begin{aligned} \frac{d}{dt} \Delta\delta^{13}\text{C}_m = & \frac{-1}{N_a + N_b + N_{o,DIC} + N_{o,OC} + N_{rs}} \\ & \cdot \left[(\delta^{13}\text{C}_{a,0} + \Delta\delta^{13}\text{C}_m) \cdot \frac{d}{dt} N_a + (\delta^{13}\text{C}_{a,0} + \delta^{13}\text{C}_{b-a} \right. \\ & + \Delta\delta^{13}\text{C}_m) \cdot \frac{d}{dt} N_b + N_b \cdot \frac{d}{dt} \delta^{13}\text{C}_{b-a} \\ & + (\delta^{13}\text{C}_{o,DIC,0} + \Delta\delta^{13}\text{C}_m) \cdot \frac{d}{dt} N_{o,DIC} \\ & \left. + (\delta^{13}\text{C}_{rs,0} + \Delta\delta^{13}\text{C}_m) \cdot \frac{d}{dt} N_{rs} + F_s \cdot \Delta\delta^{13}\text{C}_m \right]. \end{aligned} \quad (B2)$$

[76] Equation (B2) is evaluated backward in time for a pre-industrial atmospheric signature, $\delta^{13}\text{C}_{a,0}$, of -6.4‰ , the modeled land-atmosphere isotopic difference, $\delta^{13}\text{C}_{b-a}$ (Figure 10, top), the pre-industrial signatures of DIC and of reactive sediments of 0‰ , a total carbon inventory of $43\,020 \text{ GtC}$ ($N_{a,0} = 600 \text{ GtC}$; $N_{b,0} = 2\,920 \text{ GtC}$; $N_{o,DIC,0} = 38\,000 \text{ GtC}$; $N_{o,OC,0} = 700 \text{ GtC}$; $N_{rs,0} = 800 \text{ GtC}$), the prescribed change in the atmospheric carbon inventory from the ice core data, the modeled change in the terrestrial carbon inventory (Figure 4, top), a burial flux of 0.2 GtC yr^{-1} , and by setting the combined change in the DIC and reactive sediment carbon inventories equal to the change in the atmospheric plus terrestrial inventory.

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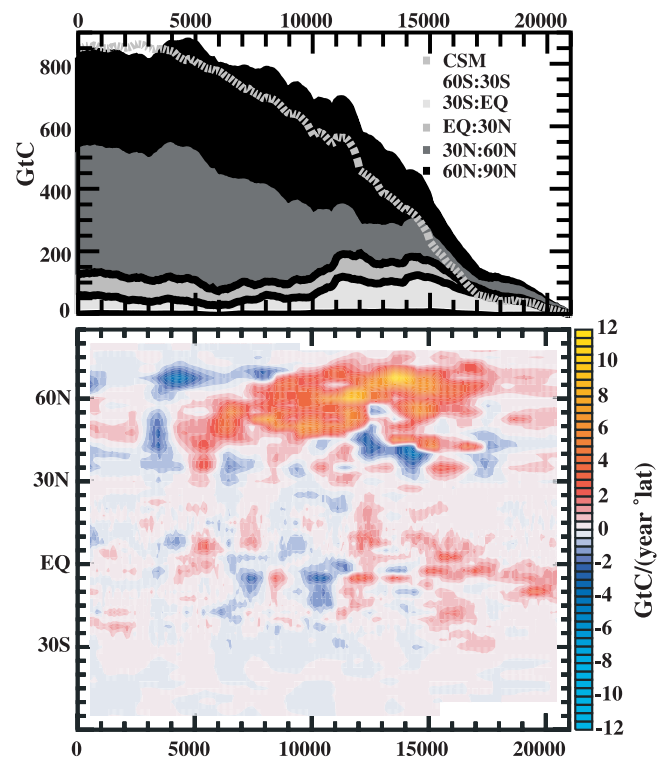


Figure 4. Simulated changes in terrestrial carbon inventory. (top) Cumulative change for different latitude bands for the UM climate anomalies (simulation P1) and global changes for the CSM climate anomalies (dotted line, simulation P1-CSM). The results have been smoothed by a 50-year running mean filter to remove high-frequency variability. (bottom) Zonally integrated net ecosystem uptake (1000-year running means) for the UM climate anomalies (simulation P1).

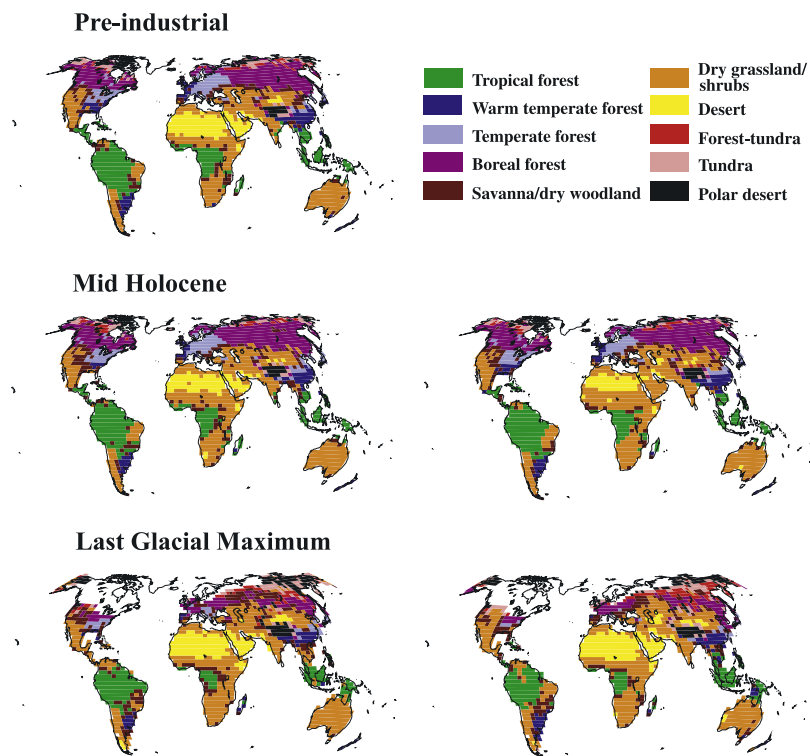


Figure 12. Simulated biome distribution for the LGM (21 ka BP), the Mid-Holocene (6 ka BP), and the pre-industrial time (0 ka) for the UM climate anomalies (left, simulation P1) and the CSM climate anomalies (right, simulation P1-CSM). The distribution at pre-industrial time is nearly identical for simulations with the UM and the CSM anomalies (not shown).