Climate-biosphere interactions on glacial-interglacial timescales

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[1] Potential positive feedbacks of the biosphere on glacial-interglacial climate change have been extensively investigated in recent years. In this paper, we summarize these feedbacks and the evidence that they may play a quantitatively significant role. We then attempt to assess the role of biosphere feedbacks in glacial/interglacial climate change by evaluating five lines of empirical evidence: (1) synchroneity of warming during the last glacial termination (expected if the biosphere is important, because of short response times); (2) changes in the $\delta^{18}O$ of O_2, which may reflect the relative fertility of the land and ocean biospheres, (3) changes in the triple isotope composition of O_2, which constrain global rates of photosynthesis in the past; (4) the relationship between atmospheric CO_2 and dust accumulation at Vostok, and (5) indications for the occurrence or absence of Pleistocene-style glacial cycles before the evolution of the land biosphere. The evidence is compatible with a significant role for the biosphere in driving glacial-interglacial change, but unambiguous empirical support is not yet in hand. *INDEX TERMS:* 0315 Atmospheric Composition and Structure: Biosphere/atmosphere interactions; 1620 Global Change: Climate dynamics (3309); 1610 Global Change: Atmosphere (0315, 0325); 4806 Oceanography: Biological and Chemical: Carbon cycling; *KEYWORDS:* ice ages, climate-biosphere interactions

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1. Introduction

[2] At least two modes of climate change over glacial-interglacial timescales are now evident in the Pleistocene record. One involves climate change that is in phase between the hemispheres, although there may be leads and lags whose duration is short compared to periods of climate cycles [e.g., *Imbrie et al.*, 1993; *Sowers and Bender*, 1995]. This mode is representative of climate change on timescales of 10–100 ka. In-phase climate change is characterized by globally warmer (cooler) temperatures, increased (decreased) precipitation, greener (browner) Earth, and decreased (increased) ice volume. These climate variations are due to changes in Earth's radiative balance. They reflect both higher (lower) concentrations of greenhouse gases, and lower (higher) albedo due to three characteristics of the interglacial Earth: decreased extent of glacial ice, increased extent of oceanic area, and a greener land biosphere.

[3] The other mode of climate change is of millennial duration, reflected most conspicuously in the rapid climate change events (interstadial events) observed in the Greenland ice cores [*Dansgaard et al.*, 1993; *Grootes et al.*, 1993; *Mayewski et al.*, 1994]. Between 15 and 75 ka, approximately 20 interstadial events are recorded in the ice cores. Their duration ranges from a few hundred to a few thousand years. Both long and short duration millennial events recorded in GISP2 and GRIP have counterparts in Antarctic ice cores from Vostok and Byrd [*Blunier et al.*, 1998; *Bender et al.*, 1999; *Blunier and Brook*, 2001]. Millennial duration climate change events are primarily out of phase between the hemispheres, or at least the north and south polar regions [*Blunier et al.*, 1998; *Blunier and Brook*, 2001; *Sowers and Bender*, 1995]. Interstadial events appear to be linked to changes in the thermohaline circulation of the oceans and the associated meridional heat transport [*Stocker et al.*, 1992; *Crowley*, 1992; *Oppo and Lehman*, 1995]. An intensification of North Atlantic Deep Water formation removes heat from the southern hemisphere while increasing the oceanic heat flux to the North Atlantic.

[4] The atmospheric CH_4 concentration rose during interstadial events, contributing a small greenhouse forcing [*Chappellaz et al.*, 1993; *Brook et al.*, 1999], but CO_2 concentrations did not change in a uniform way with climate at millennial timescales. Additional small contributions to radiative forcing during interstadial events may have come from albedo decreases resulting from decreases in atmospheric dust loading [e.g., *Mayewski et al.*, 1993, 1994]. Apparently, interstadial climate change was a manifestation of the redistribution of heat fluxes at the Earth's surface. Changes in the global radiative balance were small.

[5] The discovery of glacial-interglacial changes in the CO_2 concentration of air trapped in ice core samples [*Delmas et al.*, 1980; *Neftel et al.*, 1982] stimulated various experimental and modeling studies aimed at understanding the role of the biosphere in ice age climate change. *Broecker* [1982] showed that increased biological drawdown of CO_2, perhaps induced by a ~50% increase of [PO_4^{3-}] in the

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glacial ocean, could account for the observed glacial-interglacial pCO_2 change. His paper introduced the concepts that marine ecosystems could play a major role in glacial-interglacial climate change, and that their effects could be quantitatively evaluated. Subsequent workers suggested other ways in which the ocean biosphere could influence atmospheric pCO_2, including a change in the depth scale over which organic matter is remineralized as it sinks through the thermocline and the deep ocean, a change in the rain ratio of $CaCO_3/CH_2O$, and variations in ocean alkalinity. In 1984, three papers noted the very large reservoirs of underutilized micronutrients in the Southern Ocean, and showed that increases in nutrient uptake in this basin could explain glacial-interglacial CO_2 variations [*Siegenthaler and Wenck*, 1984; *Knox and McElroy*, 1984; *Sarmiento and Toggweiler*, 1984]. *Martin* [1990] followed with his seminal paper starting with the argument that Southern Ocean productivity was largely iron-limited, an assertion that has been amply documented by later work [e.g., *Martin et al.*, 1990; *Moore et al.*, 2000; *Boyd and Law*, 2002]. Martin argued that dissolution of iron from dust particles falling out to the sea surface could be an important iron source for Southern Ocean ecosystems. He noted the general inverse correspondence of CO_2-time and dust concentration-time curves at Vostok, and proposed that a greater dust flux during the ice ages led to Fe fertilization and increased CO_2 drawdown in the Southern Ocean.

[6] *Sigman and Boyle* [2000] recently reviewed the extensive literature aimed at documenting the history of Southern Ocean productivity by studying the sedimentary record. There are two apparently robust signals. First, productivity was lower south of the Polar Front, and higher to the north, during glacial times. Second, the fraction of nutrient utilization was nonetheless higher south of the Polar Front than it is today. Greater fractional nutrient utilization would lower atmospheric CO_2 even if productivity were lower. It seems likely, but remains to be proven, that increased CO_2 drawdown and/or decreased ventilation [*Stephens and Keeling*, 2000] in the Southern Ocean was the major cause of the lower CO_2 concentrations in the glacial atmosphere. One argument to the contrary comes from work of *Archer et al.* [2000], who question the sensitivity of atmospheric CO_2 to Southern Ocean productivity and stratification. They show that the ocean biogeochemistry general circulation models predict a smaller decrease in atmospheric CO_2 than do box models for similar changes in nutrient cycling. They show that the magnitude of diapycnal mixing is larger in published GCM's representations than in box models, they argue that invoking a greater role for diapycnal mixing is appropriate, and they favor the lower GCM sensitivities over the higher box model sensitivities. The issue continues to be under discussion. If Archer et al. are correct, then Southern Ocean changes could have accounted for about half the glacial-interglacial CO_2 variation.

[7] At the global scale, the land biosphere during glacial times was clearly much sparser than today [e.g., *Crowley and Baum*, 1997; *Wyputta and McAvaney*, 2001]. During the last decade, a number of studies have shown that a denser (interglacial) land biosphere has the contradictory effects of reducing albedo (hence inducing warming), and increasing evapotranspiration (hence inducing cooling). Recent experiments, summarized below, suggest that cooling predominates in the tropics while warming wins in the extratropics (our main focal area). Increased vegetation also leads to a decrease in the dust load of the atmosphere. Decreased dust may lower the planetary albedo. A more intriguing consequence is that decreased dust loading will decrease the flux of dust, and iron, to the open ocean, thereby lowering the fertility of the sea.

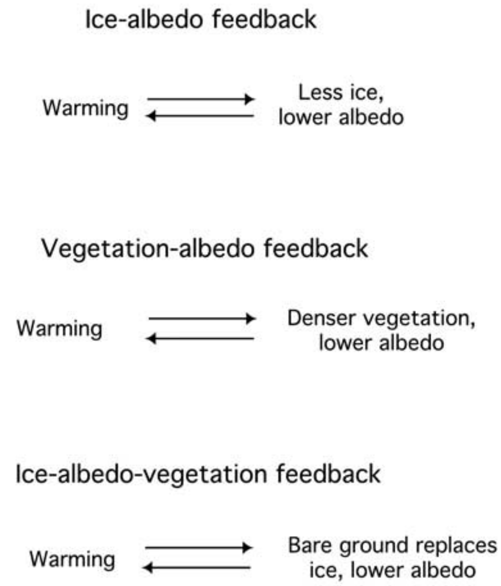

Figure 1. Glacial-interglacial climate feedbacks involving albedo.

[8] Figure 1 illustrates feedbacks among the different processes that influence glacial-interglacial climate change by varying albedo. Figure 1 (top) illustrates the ice-albedo feedback, long regarded as a critical element in glacial-interglacial climate change. Warming induces melting of glaciers; the consequent decrease in albedo causes more warming. Figure 1 (middle) shows that there is a similar feedback between climate and vegetation. Warming causes denser vegetation, by extending the growing season and by increasing evaporation and hence precipitation. Denser vegetation in turn lowers albedo, inducing further warming. Figure 1 (bottom) shows the role of vegetation in the "ice-albedo" feedback. When ice sheets melt, the decrease in albedo is partly due to the disappearance of reflective ice, but also partly due to vegetation replacing barren ground.

[9] Figure 2 illustrates land and ocean biosphere feedbacks involving dust and CO_2. Denser vegetation leads to a lower dust flux to the oceans, greater iron limitation of marine ecosystems, decreased net oceanic production, lower sea surface CO_2 drawdown, and higher atmospheric CO_2 (Figure 2 (top)). Higher CO_2 in turn fertilizes the growth of terrestrial vegetation, thereby closing a positive feedback loop. Figure 2 (bottom) demonstrates the obvious role of climate in the dust-vegetation-CO_2 feedback cycle. Denser vegetation leads to lower dust fluxes, decreased net oceanic production, higher atmospheric CO_2, warmer climate and again denser vegetation.

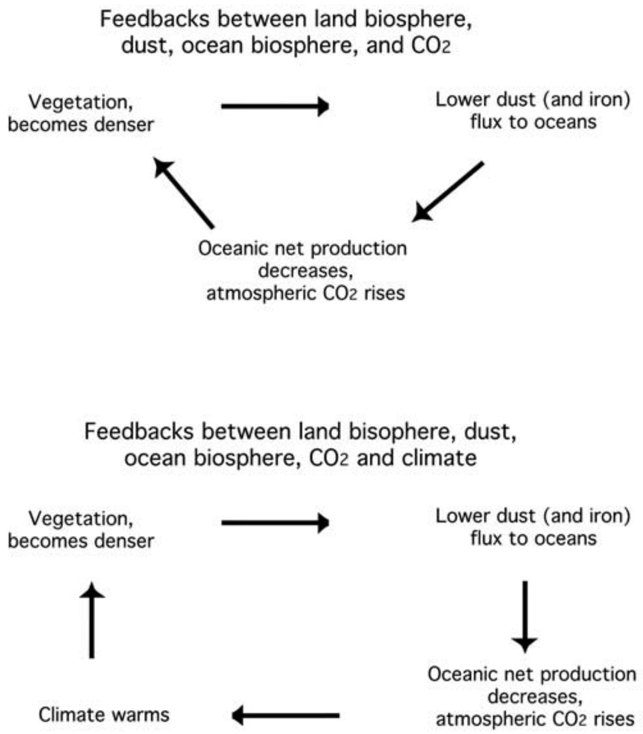

Figure 2. Glacial-interglacial climate feedbacks involving dust and the biosphere.

[10] Several modeling studies have examined the contribution of some of these feedbacks to glacial-interglacial climate change. Typical estimates for climate sensitivity to increased CO_2 would attribute about 2°C of the ~6° C glacial-interglacial temperature change to different greenhouse gas concentrations [*Intergovernmental Panel on Climate Change* (*IPCC*), 2001]. The remainder of the warming was due to a decrease in albedo associated both with retreat of glaciers and with the deglacial greening of the continents. Also, albedo variations due to changes in cloud cover may have made an as-yet unquantified contribution.

[11] The feedbacks identified in Figures 1 and 2 are all positive. Omitted from these diagrams are at least two other positive feedbacks associated with deglaciation: lower albedos due to rising sea level and lesser sea ice. A negative feedback is the deglacial growth of the land biosphere, which sequesters atmospheric CO_2. The early Holocene CO_2 minimum is attributable to this effect. Calculations suggest that the deglacial increase in the land biomass attenuated the CO_2 rise by about 25 ppmv [*Broecker*, 1982; *Sigman and Boyle*, 2000].

[12] This negative feedback notwithstanding, a change in one part of the climate system will induce continued change in the same direction, according to the feedback loops in Figures 1 and 2. The characteristic response times are mostly short. Climate responds instantaneously to changes in radiative forcing, and hydrology responds very rapidly to changes in climate and the land biosphere. The response time of the land biosphere to changes in climate and atmospheric CO_2 is of order 10–100 years. The response time of the Southern Ocean biosphere to increased dust flux is instantaneous if fertilizing iron derives immediately from dissolution of settling dust particles, and decades to centuries if the proximal source of iron is upwelling. Thus climate changes associated with radiative forcing are likely to be in phase globally, on timescales of decades to centuries. The great exception, of course, is associated with glaciated areas of the northern hemisphere, where response times are several millennia. We can expect these areas to warm and cool at the same time as other regions of the planet, but more slowly. In fact a number of studies document such a lagged response of Northern Hemisphere glaciation and deglaciation with respect to other aspects of climate change [*Imbrie et al.*,1993; *Shackleton*, 2000].

[13] This paper seeks to test the following hypothesis: that climate feedbacks involving both the land and ocean biospheres are essential for Pleistocene-type glacial-interglacial cycles. We first review experimental and modeling evidence about the magnitude of the feedbacks. Then we examine observations that give evidence about the role of the biosphere in climate change. Before proceeding, we need to recognize that critical tests are elusive. This paper reports on their current status.

2. Background: Summary of Modeling and Experimental Results

[14] In this section, we summarize selected experimental and modeling studies that indicate the magnitude of the climate forcings of the various feedback loops. The question we address here is whether the individual links in the feedback loops are strong enough to be quantitatively significant in glacial/interglacial climate change.

2.1. Albedo Effect of the Changing Biosphere

[15] Vegetation on land has two counteracting effects on climate, as indicated earlier. First, vegetation promotes evapotranspiration, and the loss of latent heat from the surface. In response, the surface temperature cools and outgoing radiation decreases. Second, vegetation absorbs insolation and decreases albedo, and the surface temperature rises. Various experiments, summarized below, suggest that moderate increases in vegetation lead to cooling in the tropics (increased evapotranspiration predominates) and warming in the extratropics (decreased albedo predominates). At very high densities of vegetation, evapotranspiration cools more than diminished albedo warms. *Kleidon et al.* [2000], for example, used a GCM to calculate global climate for a world in which the entire area of continents is covered with vegetation having a leaf area index of 10. They observed significant global cooling in this "extreme greening" experiment. One can understand this response from the fact that the fraction of absorbed radiation increases asymptotically as leaf area index rises. Evapotranspiration, however, may scale more linearly with leaf area index.

[16] A wide range of studies shows that more moderate increases in the density of extratropical vegetation lead to significant warming [e.g., *de Noblet et al.*, 1996; *TEMPO*, 1996; *Kutzbach et al.*, 1998; *Betts*, 2000]. *Foley et al.* [1994], for example, ran an experiment in which they calculated climate change at 6 ka in response to a 20% expansion of boreal forest. The resulting annually averaged

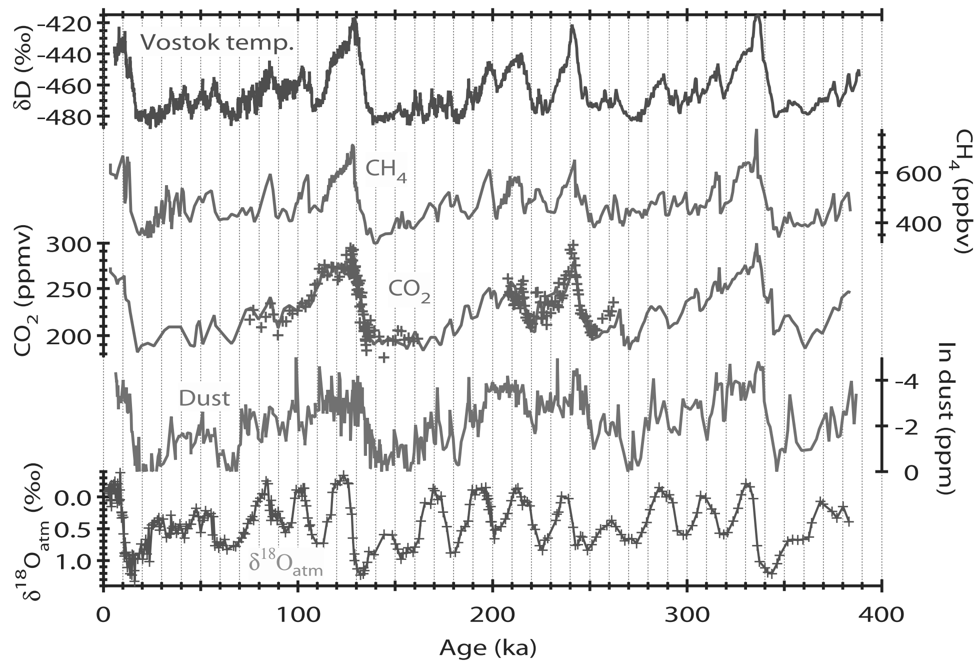

Figure 3. Vostok ice core climate records [*Petit et al.*, 1999; *Fischer et al.*, 1999]. See color version of this figure at back of this issue.

albedo fell and temperature rose by 0.1 and 1.6°C, respectively, from 60°N–90°N.

[17] Four papers have examined the effects of vegetation changes between the last glacial maximum (LGM) and the Holocene on LGM climates [*Crowley and Baum*, 1997; *Kubatzki and Claussen*, 1998; *Levis et al.*, 1999; *Wyputta and McAvaney*, 2001]. Each involved a numerical experiment in which the authors calculated LGM climate for two different assumptions about the LGM land biosphere: (1) that it was identical to the present-day biosphere and (2) that it was identical to the LGM biosphere as inferred from pollen reconstructions or modeling studies. In each case, replacing modern with glacial vegetation led to a warming over much of the tropics. The models calculate that the tropics were cooler during the LGM, but that sparser vegetation attenuated the tropical cooling. Extratropical North American temperatures were unchanged or decreased somewhat with LGM vegetation in the models. Eurasian temperatures dropped significantly for LGM vegetation.

[18] *Kubatzki and Claussen* [1998] tabulated temperature changes in Asia due to the switch from modern to glacial vegetation. The vegetation change led to a temperature decrease of 2.3° in "East Asia" (34°N–68°N, 108°E–145°E) and 1.6° in "Central Asia" (28°N–62°N, 58°E–108°E). Their model calculates that the vegetation change causes summertime temperatures in North America to drop by about 0.5°C from the ice edge to 30°N. *Wyputta and McAvaney* [2001] calculate that the change from modern to glacial vegetation induces an annually averaged cooling of about 2°C south of the glaciers in both Eurasia and North America. The total glacial cooling in these areas is highly variable, but is about 9° in North America and 7° in Eurasia. Thus, vegetation changes in climate models enhance the glacial cooling/deglacial warming by up to 25%. This enhancement would accelerate climate change and amplify its magnitude.

2.2. Effect of Diminished Vegetation on Atmospheric Dust Transport

[19] Several modeling studies calculate that dust fallout during the LGM would have been far higher than today [*Reader et al.*, 1999, 2000; *Mahowald et al.*, 1999; *Harrison et al.*, 2001]. Data for the Vostok ice core [*Petit et al.*, 1999] validate these estimates by showing that dust accumulation during the LGM was about 2 orders of magnitude above Holocene levels (Figure 3). *Mahowald et al.* [1999] diagnosed the cause of the increase by separating it into components due to increased wind speed and glacial (rather than interglacial) vegetation. They found that vegetation is by far the dominant cause of the glacial increase in dust fallout. *Reader et al.* [2000] calculated that average atmospheric lifetimes of dust during the LGM were similar to modern values. Consistent with this result, *Mahowald et al.* [1999] calculated that the change from modern to glacial winds did not lead to a great increase in dust transport to oceans and ice-covered continents (Greenland and Antarctica). Thus it is apparently the aridity and browning of the continents, and the consequent increase in erosion, rather than changes in transport, that caused the dramatic rise in glacial dust deposition. Three models have calculated that glacial dust fluxes to the Southern Ocean were at least an order of magnitude higher than interglacial [*Mahowald et al.*, 1999; *Reader et al.*, 2000; *Harrison et al.*, 2001].

2.3. Dust Fluxes and Southern Ocean Productivity

[20] *Archer and Johnson* [2000] recently summarized results of several modeling studies allowing one to compare

iron fluxes to the surface of the Southern Ocean by upwelling of seawater dissolved iron, and by dissolution from dust fallout [*Duce and Tindale*, 1991; *Tegen and Fung*, 1995; *Mahowald et al.*, 1999]. They attribute a large fraction of the iron source to dust deposition. *Fung et al.* [2000] and *Moore et al.* [2002] used models to estimate regional values of the ratio of Fe supplied by aeolian deposition versus upwelling. Assuming that 2% of aeolian Fe dissolves, their results suggest that aeolian deposition supplies ~10–20% of Fe over much of the Southern Ocean today. The calculated aeolian contribution to the eastern half of the Antarctic Pacific is smaller [*Moore et al.*, 2002].

[21] Modeling studies, supported by ice core data, conclude that dust fallout rates were at least an order of magnitude higher during the LGM (see preceding summary). Clearly, then, it is likely that higher LGM dust fluxes increased the supply of dissolved iron to Southern Ocean ecosystems and (inferentially) enhanced their productivity. The next question is whether lower CO_2 can plausibly be attributed to increased Antarctic productivity driven by a higher dust flux. Many recent papers invoke increased glacial dust as the cause of lower glacial CO_2, and this hypothesis remains a serious candidate. In a recent review, *Sigman and Boyle* [2000] showed that enhanced glacial nutrient utilization in the Antarctic sector of the Southern Ocean, south of the Polar Front, could account for most of the ice age CO_2 drawdown (utilization is the fractional uptake in surface waters). On the other hand, enhanced uptake north of the Polar Front would lead to a far smaller drawdown. They reviewed sedimentary evidence for changes in CO_2 uptake. They concluded that productivity in the Antarctic zone was lower during the LGM, but nutrient and CO_2 utilization were greater. Sigman and Boyle invoked slower vertical mixing to reconcile these two conclusions. Can one invoke increased aerosol Fe input to account for increased nutrient utilization? The conceptual model of *Archer and Johnson* [2000] suggests that Antarctic waters reach the surface with enough Fe to remove about half of the dissolved nutrients, and a corresponding fraction of the CO_2. Additional nutrient utilization requires iron input from dust fallout. According to their model, lower upwelling would lead to increased uptake of nutrients with a constant dust flux, and even greater fractional uptake with an enhanced dust flux. Later we present a simple schematic model linking dust fluxes to Antarctic nutrient drawdown.

2.4. Effect of CO_2 on Temperature and Plant Growth

[22] The effect of CO_2 on global temperature is well documented by studies of anthropogenic impacts. Estimates of climate sensitivity, from modeling studies summarized in the *IPCC* [2001] report, indicate that changing CO_2 likely accounted for about 2°C of global ice age cooling, about a third of the total. The effect of CO_2 on plants is much less well constrained. In many experiments, elevated CO_2 leads to a large immediate enhancement of growth that diminishes with time, as other components of the plant or ecosystem become limiting. The large-scale impact of elevated CO_2 is under debate. Some studies suggest it is minor in the current global change scenario [e.g., *Pacala et al.*, 2001].

[23] Lower CO_2 during the ice ages has the potential to affect the growth of C3 plants in a number of ways. First, the internal CO_2 pool at the site of fixation will be reduced [*Anderson et al.*, 2001], as will the rate of photosynthesis. Plants can compensate for this effect somewhat by up-regulation, making more RuBisCo [*Anderson et al.*, 2001]. This remedy has its physiological costs, however, and must reduce production in N-limited ecosystems. Second, losses will be greater because the rate of photorespiration scales with the O_2/CO_2 ratio [*Farquhar et al.*, 1980]. Third, productivity falls because of lower water use efficiency, which roughly scales with the CO_2 concentration [e.g., *Anderson et al.*, 2001]. These effects are more likely to be important as CO_2 drops than as it rises. Water use efficiency is likely to be a particularly important cause of lower glacial productivity, given the well-documented increase in aridity of the ice age Earth. In fact a number of papers have argued that lower pCO_2 during the ice ages would lead to diminished vegetation cover [*Jolly and Haxeltine*, 1997; *Cowling and Sykes*, 1999; *Street-Perrott et al.*, 1997; *Williams et al.*, 2001; *Bennett and Willis*, 2000]. *Cowling* [1999] nested the Biome 3 model [*Haxeltine and Prentice*, 1996] of the terrestrial biosphere in a GCM, and computed the changes in leaf area index along a meridional line at 82° W. She calculated that lowering CO_2 from preindustrial to LGM values would cause leaf area index to drop by 17% in woodlands, and 46% in xeric ecosystems south of the ice sheet. The effect of lowered pCO_2 on ice age vegetation remains uncertain, but the feedback may well have been important. In summary, modeling and experimental studies demonstrate that feedbacks of the biosphere outlined in Figures 1 and 2 are of a magnitude that may be important in Pleistocene climate change.

3. Empirical Evidence for the Role of the Biosphere in Glacial-Interglacial Climate Change

[24] In the preceding discussion, we examined modeling studies that investigate the strength of various processes in which changes in the biosphere feed back upon climate. If the models were sufficiently comprehensive and accurate, we could use them alone to evaluate the role of the biosphere. However, the models are not yet at this stage. Therefore we use an empirical approach, in which we compare records of climate change with (mostly) global-scale records reflecting the activity of the biosphere. We search for similarities and differences in these two sets of records that reflect the magnitude of climate forcing by the biosphere. Covariations in these two types of records would strengthen the case for the biosphere, but cannot prove it. The absence of covariations would argue against an important role for the biosphere.

3.1. Synchroneity of Climate Change During Termination 1

[25] The last glacial termination began nominally at around 20 ka and was nearly complete at the onset of the Holocene (~10 ka). One can divide the forcings involved in this dramatic climate change into three groups. The first includes variations in surface climate properties with rapid

response times. "Rapid response times" (as used here) are less than a century, much shorter than the deglaciation. Response times of the atmosphere, surface ocean, sea ice, and the land biosphere generally fall within this range. Thus this group includes most forcings in the feedback loops involved in climate-biosphere interactions. If the biosphere has a large impact on climate, then much glacial/interglacial climate change should be globally synchronous. Of course even here one must recognize that there are nonlinearities and thresholds in the climate system that involve leads/lags and mode switches. An example is orbital forcing of rapid monsoonal climate changes in low latitudes [e.g., *deMenocal et al.*, 2000]. The second group of climate forcings involve climate sea-saws. Best understood of these is the north-south sea-saw in which changes in the thermohaline circulation induce out-of-phase climate change between Greenland and Antarctica [*Blunier et al.*,1998; *Blunier and Brook*, 2001].

[26] The third group of climate forcings are those with response times of 1–10 kyr. Two are critical. Boreal and temperate ice sheets have a response time of ~10 kyr [*Imbrie et al.*, 1993] and play a large role in the global climate. Their persistence during deglaciation slows the warming in the ice-free regions to their south. The ocean CO_2 system also has a long response time, order 5 kyr [*Keir*, 1988; *Sigman et al.*, 1998]. This response time is due to $CaCO_3$ compensation and the interaction of seawater with biogenic calcite on the seafloor.

[27] Synchroneity is a natural attribute of the rapid response times of most feedbacks involving the biosphere. Therefore a "necessary but not sufficient" test for the role of the biosphere involves determining the extent to which deglacial climate change is globally synchronous, and synchronous with the deglacial evolution of the biosphere. We address this question by discussing the deglacial climate change beginning at ~17 ka (calendar) B. P. Our discussion is highly selective in omitting many well-dated examples of deglacial climate change that began at some other time. We do not argue that deglacial changes in climate and the biosphere started everywhere at this time. Rather, we show that many important aspects of deglaciation took place at this time: widespread areas of the Earth began warming, greenhouse gas concentrations rose, vegetation became denser, and the dust flux to the Southern Ocean began to fall. We first discuss continental records progressing northward from Antarctica to the Arctic. We then briefly consider marine records.

[28] Data on the timing of deglacial warming in Antarctica come mainly from ice core studies. East Antarctic ice cores Dome C and Vostok, correlated by gas stratigraphy to the well-dated GISP2 core in Greenland, begin to warm at about 17.5 ka [*Petit et al.*, 1999; *Monnin et al.*, 2001]. Byrd, in West Antarctica, warms at ~20 ka, cools, and begins its irreversible deglacial warming at ~18.5 ka [*Blunier and Brook*, 2001].

[29] The deglacial history of Chile and Argentina is known from studies of both glacial geomorphology and pollen. There is a late glacial advance at Canal Beagle, Tierra del Fuego (55°S). Glaciers here reached their maximum extent and began receding by 17.5 ka [*Heusser*, 1998]. In the Chilean Lake District (~42°S), there were repeated glacial advances during the last ice age [*Lowell et al.*, 1995]. The last of these advances occurred between 16.7 and 17.8 ka, with most dates older than 17 ka. Summarizing recent results, *Denton et al.* [1999] date the onset of deglaciation of the Southern Andes at 17.5 ka, with a following pulse at about 15.5 ka.

[30] Pollen studies indicate that warming in the southern extratropics also began at the same time as warming in East Antarctica. At Puerto del Hambre, Patagonia (53°36′S), pollen studies show that southern beech diminishes around 17.0 ka, replaced by "deglacial successional communities" in which grasses, herbs and heath appear [*Heusser et al.*, 2000]. This change is interpreted as a shift to warmer and drier climates. In a number of Chilean sites further to the north (41°S–43°S), pollen studies show evidence of warming at ~17.0 ka. *Moreno et al.* [1999, 2001] document an increase in thermophilous plants (notably Myrtaceae) at about 16.8 ka at Canal de Puntilla. *Heusser et al.* [1996] show pollen evidence that mixed grasses and trees replaced glacial deposits at Mayol (Isla Grande de Chiloé) at about 16.8 ka. They also summarize additional lines of evidence demonstrating the onset of warming in the Chilean Lake District and Chilotan Archipelago at about 16.8 ka.

[31] There is pollen evidence for warming at about 17 ka in the New Zealand and Australia. In New Zealand, afforestation of the North Island began at about this time [*McGlone*, 1995]. A pollen study of Lake Selina, western Tasmania, shows temperate rain forest replacing grasslands at about 17 ka [*Colhoun*, 2000].

[32] Moving north, noble gas paleotemperatures of the Stampriet Aquifer, 27°S and 17°E in southern Africa, begin warming at about 17.9 ka according to radiocarbon dating of the waters [*Stute and Talma*, 1997] (cited by *Gasse* [2000]). There is a deglacial warming at 17 ka recorded in pollen and sedimentary $\delta^{13}C$ of organic carbon sediments of Lake Tritrivakely, Madgascar (19°47′S) [*Gasse and Van Campo*, 1998]. Pollen in a South China Sea core (20°07′N, 117°23′E) records warming starting at about 17.9 ka [*Sun and Li*, 1999].

[33] *Reille and Lowe* [1993] summarize evidence in southwestern France for a "15,000 year (^{14}C) event" (17.9 ka calendar) recorded in pollen and attributed to warming and increased precipitation. At Hidden Lake, Tibet, (29°49′N, 92°23′E) pollen evidence puts warming somewhat later, 15.9 ka [*Tang et al.*, 1999]. Much of the extensive North American climate record is focused on time slices rather than time series. This record is consistent with steady warming by ~17 ka [e.g., *Webb et al.*, 2001].

[34] Margins of the LGM ice sheets varied in North America and Europe as elsewhere. The Laurentide ice sheet reached its maximum extent prior to 20 ka, waned, then readvanced to another maximum (but slightly further north), around 18 ka. At about 17.4 ka, it retreated, and subsequent deglacial advances terminated much further to the north [*Hansel and Johnson*, 1992; *McCabe and Clarke*, 1998; *Karrow et al.*, 2000]. In Europe, deglaciation at this time is marked by a switch from glacial rhythmites to local stream silts at about 17.3 ka in Lake Zurich, and the deglacial origin of Rotsee, in Switzerland, at about 17.1 ka [*Lotter*,

1991; *Lister*, 1988]. In the Arctic, the iconic record is that from the ice cores of Summit, Greenland [*Dansgaard et al.*, 1993; *Meese et al.*, 1997]. There is a small warming at ~15.5 ka, followed by a dramatic warming at the start of the Bolling, at 14.6 ka. In Svalbard, however, *Svendsen et al.* [1996] date onset of retreat from the maximum glacial advance at 17.7 ka.

[35] *Clark et al.* [2002] recently analyzed deglacial warming as recorded by a number of marine records. They assert that there are two modes of deglacial warming. One is an "East Antarctic Mode" (slow warming beginning at about 17.5 ka, as at Vostok and Dome C). The other is a "Greenland mode," marked most obviously by rapid warming at ~14.6 ka and a Younger Dryas cooling. Ocean sites in the Northeastern Pacific, tropical North Atlantic, and South Atlantic have the East Antarctic signal and reflect warming that commences at ~17.5 ka.

[36] Finally, we discuss biogenic greenhouse gases. Deglacial increases in CO_2 CH_4, and N_2O are well documented [e.g., *Raynaud et al.*, 1993]. *Monnin et al.* [2001] recently presented high-resolution CO_2 and CH_4 records for the Dome C ice core. According to their chronology, CO_2 and CH_4 both began rising at 17 ka. By 15.4 ka, CO_2 had risen by 30 ppm. This rise corresponds to 40% of the deglacial CO_2 increase (from 187 ppm to 265 ppm by the start of the Holocene). This sharp initial increase would have contributed to greenhouse forcing and would have stimulated plant growth. It is also accompanied by a synchronous, but small, rise in CH_4. This latter rise signifies the spread of wetlands but would not itself lead to significant temperature feedbacks.

[37] In summary, the period between ~15 and 18 ka was a time when climate, the biosphere, and biogenic greenhouse gases were changing as would be expected given the feedbacks outlined in Figure 1. Starting at ~17 ka, roughly synchronous deglaciation and warming took place over many areas of the Earth from high southern to high northern latitudes. These changes were accompanied by rising concentrations of greenhouse gases and afforestation in many regions. These synchronous changes are consistent with a significant role for the biosphere in promoting climate change, but of course they cannot prove such a role.

3.2. Evidence From Variations in the $\delta^{18}O$ of O_2 in Air

[38] O_2 in air is produced by photosynthesis and consumed by respiration. The isotopic composition of O_2 reflects the steady state balance of production and consumption [*Lane and Dole*, 1956]. The $\delta^{18}O$ of O_2 ($\delta^{18}O_{atm}$) produced by marine photosynthesis (which accounts for ~40% of the total) is close to that of seawater (~ 0‰ on the SMOW scale). O_2 from land photosynthesis is higher, about +5‰, because evapotranspiration leads to an enrichment of heavy isotopes in leaf water [*Craig and Gordon*, 1965; *Farquhar et al.*, 1993]. Respiration discriminates against the heavy isotopes by ~20‰, causing the $\delta^{18}O$ of O_2 to be higher than the source flux by this amount. These factors roughly account for the observed Dole effect of 23.5% [*Lane and Dole*, 1956; *Bender et al.*, 1994]. A number of second order effects are significant at the level of 0.1–1‰ [*Bender et al.*, 1994; *Angert et al.*, 2001].

[39] The preceding discussion of feedbacks suggests that the ratio of terrestrial/marine production should oscillate with climate. The ratio is expected to be higher during interglacial times. At these times, terrestrial production is greatest; marine production may be low because vegetation suppresses the atmospheric dust flux to the ocean. The signal of variable terrestrial/marine production will be recorded in variations of $\delta^{18}O_{atm}$, which can be accessed with ice core studies (Figure 3). However, an indication of the complexity of this approach becomes evident when one asks about the sense of the variations. There are two possibilities. If the magnitude of the leaf water enrichment (currently ~5‰ w.r.t. seawater) is constant, then $\delta^{18}O_{atm}$ will increase as land/ocean production increases. On the other hand, the leaf water enrichment rises as relative humidity falls [e.g., *Craig and Gordon*, 1965]. If glacial times correspond to periods of lower relative humidity, the glacial enrichment in the $\delta^{18}O$ of leaf water could be higher. In this case, $\delta^{18}O$ of O_2 could rise even while land/ocean productivity falls.

[40] *Shackleton* [2000] has elegantly decomposed the $\delta^{18}O$ curve of atmospheric O_2 into constituent parts related to ice volume and orbital variations. He interprets his results as indicating that the $\delta^{18}O_{atm}$ is the sum two components. One reflects $\delta^{18}O_{atm}$ variations of seawater and hence glacial-interglacial variations in ice volume. The second reflects variations in the $\delta^{18}O$ of leaf water and the ratio of land/ocean production. This latter hydrology/biology signal has maximum amplitude of about 0.6 ‰, which would allow significant variations in production on land and in the oceans. It varies in a way that is highly coherent with precession. *Bender et al.* [1994] and *Shackleton* [2000] both argued that the monsoon was the phenomenon linking $\delta^{18}O_{atm}$ and precession. The link would be due to low latitude precipitation, which is greater during periods of stronger summer insolation [*Prell and Kutzbach*, 1987]. The nature of the forcing is such that stronger insolation is linked to increased precipitation, a greener low latitude land biosphere, and lower $\delta^{18}O_{atm}$.

[41] The $\delta^{18}O_{atm}$ variations reflecting changes in the biosphere differ from variations in two key late Pleistocene climate properties: ice volume and CO_2. Both of these properties have periodic variability associated mainly with the 41 and 100 kyr cycles. The implication is that the low-latitude land biosphere is not a key player in glacial-interglacial climate change or its accompanying CO_2 variations. The $\delta^{18}O_{atm}$ record is thus incompatible with hypotheses that the low latitude dust flux to the oceans mediated atmospheric CO_2 by stimulating N_2 fixation and hence increasing the oceanic nutrient inventory [*Falkowski*, 1997]. Such an effect would have lead to a strong precession cycle in the CO_2 record, which is not observed. Of course, a small component of glacial interglacial changes in CO_2 and ice volume are linked to precession [e.g., *Martinson et al.*, 1987], and these could have been influenced by the biosphere. The biosphere must have varied at the period of tilt, if for no other reason that currently productive areas of the continent were periodically covered by ice sheets at this frequency. However, $\delta^{18}O_{atm}$ variations do not reflect changes in the biosphere at this frequency [*Shackleton*, 2000].

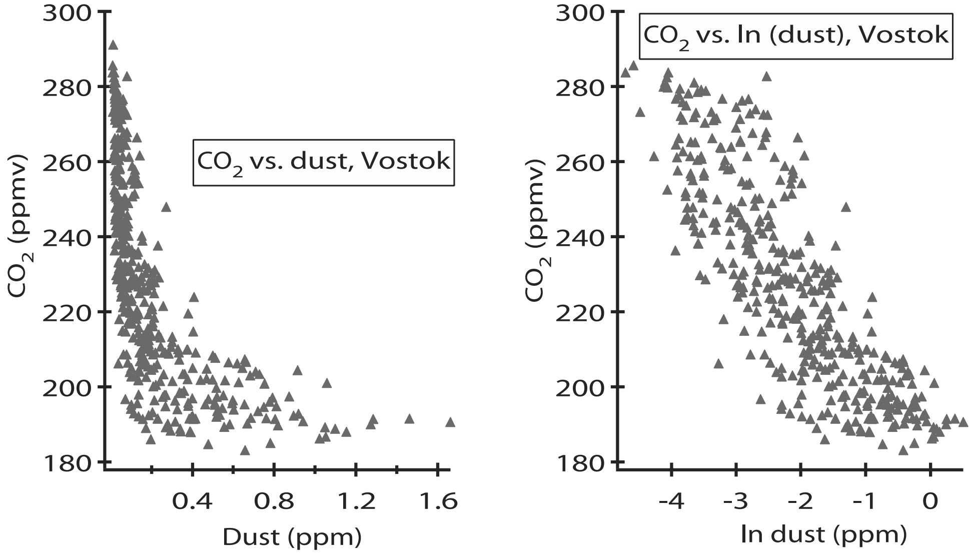

Figure 4. CO_2 versus dust and ln(dust) in the Vostok ice core. Data are from *Petit et al.* [1999], interpolated to 1 kyr resolution. See color version of this figure at back of this issue.

[42] Further evidence that the low latitude land biosphere does not have a major impact on the extent of glaciation (at least) comes from examining rapid climate change events. These events, strongly manifested in Greenland, impact the tropical Atlantic [*Hughen et al.*, 2000; *Peterson et al.*, 2000] and the Asian monsoons [*Wang et al.*, 2001]. However, rapid climate change events are not obviously associated with major changes in ice volume or sea level. For example, sea level rose during the Younger Dryas and Heinrich event 1 [*Hanebuth et al.*, 2000], despite stadial climates in Greenland at these times.

3.3. Evidence From the Triple Isotope Composition of O_2

[43] *Luz et al.* [1999] and *Blunier et al.* [2002] recently reported on use of the triple isotope composition of O_2 in air to constrain past values of the fertility of the planet. Seawater is the ultimate source of O_2. Oceanic photosynthesis produces O_2 by splitting seawater directly. Land photosynthesis splits leaf water, which is ultimately derived from seawater. The difference between the isotopic composition of O_2 and seawater depends on fractionation during hydrologic processes and fractionation by the various pathways of O_2 consumption. These processes all fractionate the $^{18}O/^{16}O$ ratio twice as much as they fractionate $^{17}O/^{16}O$. Absent other influences, the $\delta^{17}O$ of O_2 in air would be 0.5 times $\delta^{18}O$ of O_2.

[44] In fact, $\delta^{17}O$ of O_2 is less than half $\delta^{18}O$. The cause of this anomaly is isotope exchange between O_2 and CO_2 in the stratosphere [*Bender et al.*, 1994; *Luz et al.*, 1999]. In this reaction, ^{17}O is fractionated by (roughly) the same amount as ^{18}O rather than half as much [*Mauersberger et al.*, 2001; *Thiemens et al.*, 1991, 2001; *Alexander et al.*, 2001; *Yung et al.*, 1997]. The magnitude of the anomaly in the term $\delta^{17}O-0.5\ \delta^{18}O$ of O_2 reflects the rate ratio of isotope exchange in the stratosphere to O_2 turnover by photosynthesis and respiration. One can then correct for changes in stratospheric exchange due to CO_2 variations, and calculate variations in rates of photosynthesis and respiration on the planet. *Luz et al.* [1999] and *Blunier et al.* [2002] estimate that the planetary photosynthesis rate during the LGM, and back to $\sim$50 ka, was about 85% of modern.

[45] This rate is obviously consistent with lower productivity of the glacial land biosphere. Is it consistent with ocean iron fertilization, and higher productivity by the ocean biosphere? *Blunier et al.* [2002] attempted to answer this question by adopting values for land productivity calculated using models of the glacial land biosphere. Knowing total and land productivity, they calculated ocean productivity by difference. Their values ranged from about 90% to 140% of modern, depending on the estimate of land productivity. The latter values, in turn, depended largely on assumptions made about the sensitivity of land plant growth to atmospheric CO_2. Model estimates of land biosphere production will need to be more accurate before we can determine if oceanic production was higher during the LGM.

3.4. Relationship Between Atmospheric CO_2 and Dust Accumulation at Vostok

[46] In Figure 4, we plot CO_2 versus concentration of dust in Vostok, and also versus ln (concentration of dust). In this discussion, we equate dust concentration with dust accumulation rate. The ice accumulation rate during glacial times, when dust is high, is about a factor of two lower than during interglacial times. This difference is far less than the concentration change and does not affect the following discussion.

[47] Figure 4a shows that there is a curvilinear relationship between dust and CO_2. Dust concentrations are low for most of the CO_2 range, and high only when CO_2 drops to its lowest values. *Broecker and Henderson* [1998] attributed this relationship to a time lag associated with Fe-induced

nitrogen fixation, which would lower atmospheric CO_2 by eventually increasing the oceanic nutrient inventory.

[48] Figure 4b also shows that CO_2 decreases linearly as the ln of the dust concentration rises, albeit with considerable scatter. We recognize, of course, that correlations do not demonstrate causal relationships. We nevertheless suggest that the log linear relationship is causally significant, and reflects the following mechanism regulating glacial-interglacial CO_2 variations. The basic premise is that the dust flux to the sea surface decreases exponentially as one goes downwind of the source areas. This dependence is evident in the values of surface fluxes computed by the model of *Mahowald et al.* [1999]. We can distinguish three regimes of Fe limitation. Waters close to source areas are Fe-replete. Waters at intermediate distances are Fe-intermediate but still productive, and distal regions are highly Fe-limited, and barren. Now assume that dust fluxes rise by a factor of *e*. Productivity is unchanged in regions proximal to the source, which were already Fe-replete. Productivity is also unchanged in the most distant regions, where the enhanced dust flux remains so small that it does not support significant production. Increased dust enhances production only around the Fe-intermediate region. In the simplest model, increasing the dust flux by *e* converts one scale length of ocean downwind of the source from Fe-intermediate to Fe-replete. It also converts one scale length from "barren" to Fe-intermediate. Such a model accounts for the observed log linear dependence of CO_2 on dust. *Moore et al.* [2002] simulated some aspects of this response in their GCM study of LGM climate and CO_2.

[49] In Figure 3, we plot CO_2, Vostok temperature, and ln (dust) versus age. This plot shows that many maxima in CO_2 concentration have associated minima in dust. Plots of these properties for the glacial terminations (Figure 5) show the close correspondence between falling dust and rising CO_2 during deglacial events. This close correspondence is additional evidence that varying dust fluxes to the Southern Ocean contribute to the glacial-interglacial variability in atmospheric pCO_2.

3.5. Glacial-Interglacial Climate Changes Before the Evolution of the Land Biosphere

[50] This paper examines the hypothesis that climate feedbacks associated with the land biosphere are essential for the climate instability associated with Pleistocene-style glacial-interglacial cycles. ("Pleistocene-style" refers to sea level variations of order 100 m, and periods of the same order as those of the Milankovitch band.) A corollary is that there could not have been Pleistocene-style glacial-interglacial cycles before the land biosphere evolved. This event occurred in the Silurian and Devonian periods. By the Carboniferous (which began at 355 Ma), land plants apparently had a density rivaling that of today.

[51] Were Pleistocene-style glacial-interglacial cycles absent before the Carboniferous? There are, of course, compelling examples of earlier glaciation. Some are very different from Pleistocene cycles. The most dramatic examples are Snowball Earth episodes, which possibly lasted millions of years. Other early glaciations are marked by glacial geomorphic features that do not clearly reflect cyclicity or its absence. However, there are also examples of alternating sedimentary layers, interpreted as reflecting Milankovitch-timescale eustatic variations of sea level, prior to the Silurian. Examples include strata of the Proterozoic Rocknest Formation, N. W. Territories, Canada [*Grotzinger*, 1986]; Cambrian sediments of both the eastern and western United States [*Osleger and Read*, 1991]; and Ordovician sediments of the El Paso group, West Texas [*Goldhammer et al.*, 1993]. The strata are shallow water, passive margin, deposits consisting of alternating shallower (or emergent) and slightly deeper water sediments. The origin of cyclicity is controversial. The authors cited above consider that cyclicity derives from eustatic sea level change. Furthermore, they show that the periodicities, while quite uncertain, are consistent with Milankovitch forcing. The alternative view is that cyclicity derives from changes in local sedimentary regimes in the face of slow subsidence [e.g., *Wilkinson et al.*, 1996]. In any case, the inferred amplitude of the sea level changes is small: order 10 m for the Rocknest, 15–25 m for the Cambrian North American sediments, and 10–25 m for the Ordovician El Paso Group sediments.

[52] There is also at least one case inferred to represent Pleistocene-magnitude sea level variability timed by insolation changes in pre-Carboniferous sediments. This is the case of the Late Ordovician glaciation. *Sutcliffe et al.* [2000] summarize evidence, based on glacial features and sedimentary $\delta^{18}O$ changes, that the magnitude of the Late Ordovician ice sheets was equivalent to a $\sim$100 m lowering of sea level. They document the occurrence of two separate glaciations. They assume eccentricity forcing (100 ka cycle) and date the timespan of the two events accordingly. However, there is no independent evidence for such a timespan. In any case, there are apparently only two Late Ordovician events rather than multiple Pleistocene-type cycles.

[53] In the Permo-Carboniferous, following the evolution of land plants, the situation changes dramatically. Here, well-known cyclothems give strong evidence for cyclic, glacioeustatic, changes in sea level. These are of Pleistocene scale in both period and amplitude. There are many ways in which Permo-Carboniferous climate cycles are recorded in sediments, including variations in diagenetic style [*Soreghan et al.*, 2000] and facies variations in terrestrial deposits [*Fielding and Webb*, 1996]. However, the most important for our purposes are cycles of alternating marine and terrestrial deposits in which the deepest water marine deposits were formed in low energy environments reflecting relatively deep depths on passive margins. *Klein* [1993] and *Heckel* [1995] discuss examples of such Carboniferous cyclothems in the continental United States. *Tandon and Gibling* [1997] show that upper Carboniferous sediments around the Gulf of St. Lawrence conform to this pattern as well. *Klein* [1993] reviewed evidence for the amplitude of glacioeustatic sea level changes implied by Carboniferous cyclothems and concluded they were of order 60 m, with considerable uncertainty. *Heckel* [1995] estimated that glacioeustatic variations were similar, of order 100 m, as did *Soreghan et al.* [2000]. Several authors addressed the issue of cycle period for Permo-Carboniferous climate fluctuations. *Klein* [1990], *Soreghan* [1994], and *Fielding and Webb* [1996] note that periods are compatible with those of Milankovitch cycles (which were somewhat shorter in the

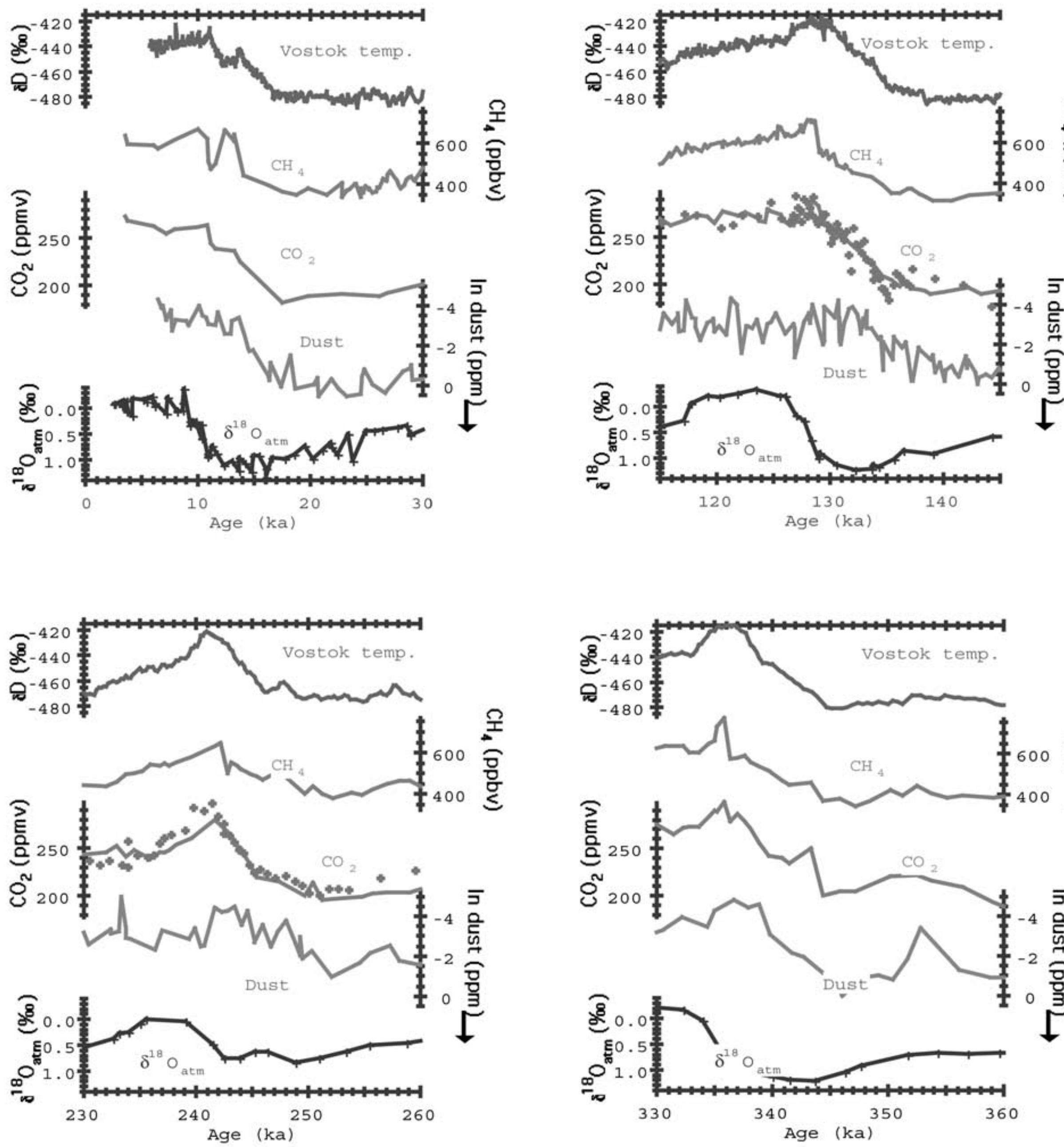

Figure 5. Climate records of the Vostok ice core during glacial terminations. Data are from *Petit et al.* [1999] and *Fischer et al.* [1999]. See color version of this figure at back of this issue.

Paleozoic than today). However, periods are not well constrained and it is difficult to make a compelling case.

[54] In summary, there is currently no evidence for Pleistocene-style glacial cycles before the evolution of the land biosphere. Shortly thereafter, however, there is compelling evidence for such cycles. It is not possible to say that the evolution of the land biosphere was the essential development that enabled the development of Pleistocene-type cycles. It could be that such cycles occurred before the Permo-Carboniferous, but have not yet been detected in the sedimentary record. It may also be that such cycles were absent before this time, not because of the absence of the land biosphere, but because continental configurations and greenhouse gas concentrations were unfavorable for their development. Nevertheless, current knowledge of the sedimentary record is consistent with the idea that feedbacks of the land biosphere are essential for Pleistocene-style glacial cycles.

4. Summary

[55] In today's world, the biosphere has a large impact on climate. The ocean biosphere influences climate pri-

marily by controlling the pCO_2 of surface water and hence the atmosphere. The land biosphere influences climate primarily by lowering albedo and inducing evapotranspiration. Climate variations alter the biosphere. The resulting changes generally have positive feedbacks on climate change. One can therefore consider the possibility that feedbacks involving the biosphere increase the amplitude of glacial-interglacial climate change, and contribute to the instability that is such a dramatic feature of Pleistocene climates. Modeling studies and observations indicate that candidate climate-biosphere feedbacks are large enough to be major influences on global change at glacial-interglacial timescales

[56] We have made five empirical tests of the role of climate-biosphere feedbacks. Widespread deglaciation and warming at ~17 ka is consistent with a large role for surface climate processes and positive feedbacks. Variations in $\delta^{18}O_{atm}$ suggest, on the other hand, that there were important variations in the fertility of the low latitude land biosphere associated with precession that did not have a large impact on glacial/interglacial cycles. The record of the O_2 triple isotope ratios during the past 60 ka are consistent with high ocean fertility during the ice age, as predicted for iron fertilization, but only if one accepts estimates of land biosphere productivity from models invoking a strong response of growth to CO_2. The record of Vostok CO_2 and dust concentration supports a model in which productivity, and atmospheric CO_2 drawdown, rises with the ln of the dust flux. Finally, the Paleozoic record shows that confirmed glacioeustatic cycles, with periods and magnitude comparable to Pleistocene events, probably first occurred after land plants appeared in the Devonian.

[57] Thus sedimentary evidence is generally supportive of a large role for the biosphere in glacial-interglacial climate change, but is not yet definitive. Evaluating the role of the biosphere continues to be a work in progress.

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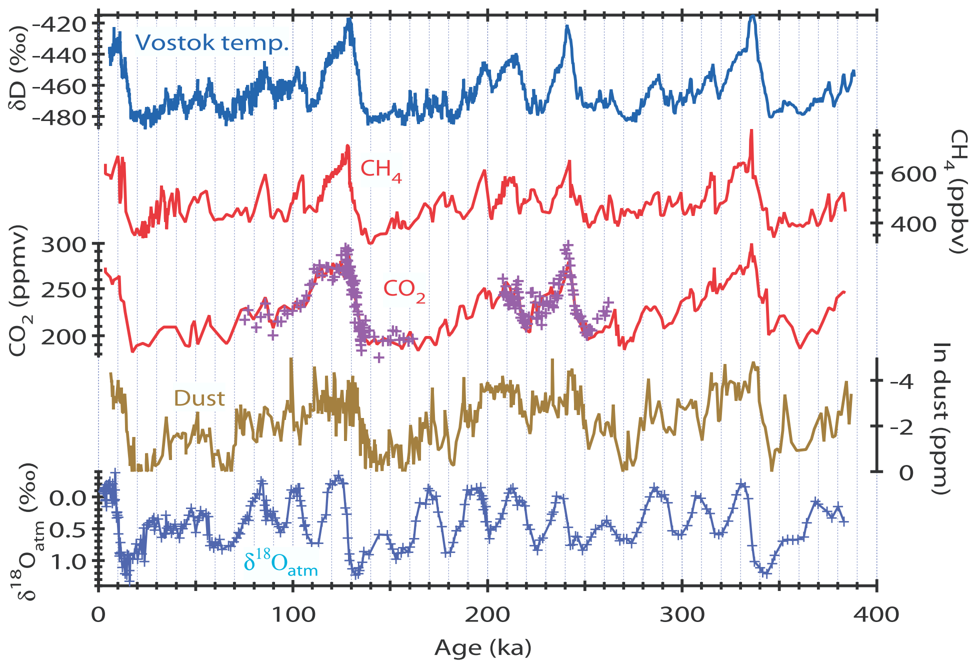

Figure 3. Vostok ice core climate records [*Petit et al.*, 1999; *Fischer et al.*, 1999].

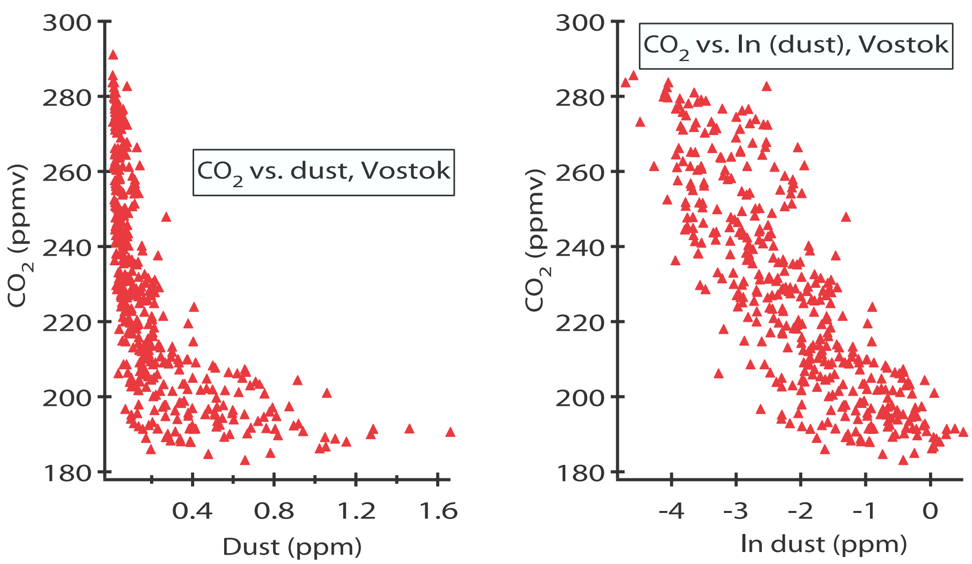

Figure 4. CO_2 versus dust and ln(dust) in the Vostok ice core. Data are from *Petit et al.* [1999], interpolated to 1 kyr resolution.

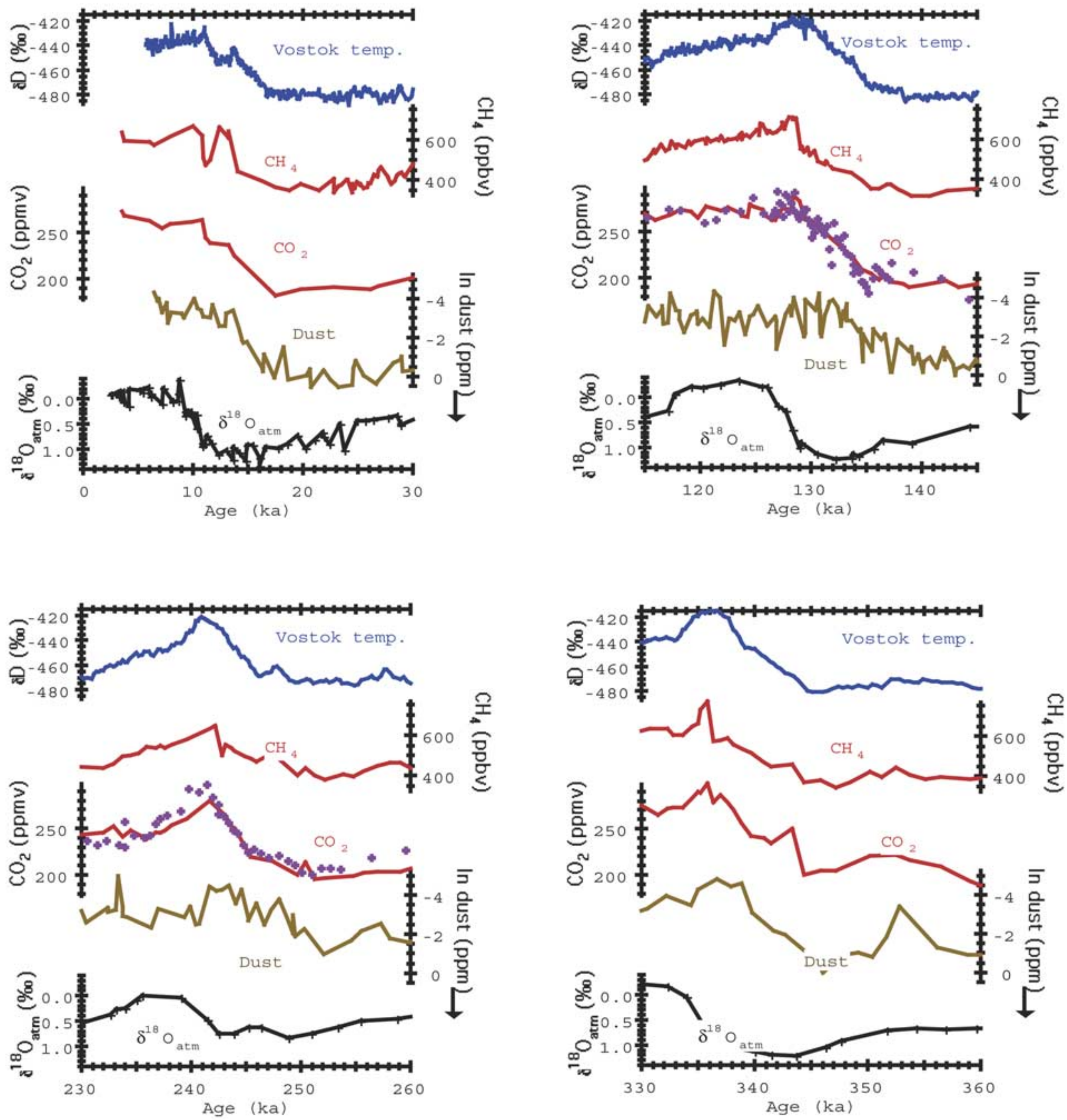

Figure 5. Climate records of the Vostok ice core during glacial terminations. Data are from *Petit et al.* [1999] and *Fischer et al.* [1999].