Energy balance. The quantity Q, the ratio of fusion power to radiation loss, is important in determining the feasibility of a reactor. Estimates (*10*) for the CBFR are Q = 35 for D-T, 3 for D-^{3}He, and 2.7 for p-^{11}B (*18*). Spin polarization of the fuel would (*13*) increase Q for the p-^{11}B reactor to 4.3, and a further increase may result from the nuclear quadrupole moment (*19*) of ^{11}B. The design of a 100-MW (electric) reactor (*13*) has been considered on the basis of Q = 4.3 by assuming a converter efficiency of 0.9 for α particles, 0.4 for radiation, and 0.7 for accelerators. The coils are assumed to be superconducting and to sustain magnetic fields of about 100 kG. The dimensions of Fig. 3 are based on these calculations.

Conclusions

The main emphasis of fusion research to date has been on the D-T Tokamak because of the large value of Q. Such a value makes the design of such a reactor much easier and much less dependent on exotic technologies. From this research has come most of the considerable body of knowledge required for fusion reactors, including the behavior of beams, which forms the basis of our present research. The purpose of this article has been to indicate another option for fusion reactor development, based on the p-^{11}B reaction. In the light of recent discoveries about the classical behavior of high-energy particles (*4*), the p-^{11}B reactor seems possible and has many engineering advantages concerning size, radioactivity, and maintenance.

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Impact of Lower Atmospheric Carbon Dioxide on Tropical Mountain Ecosystems

F. Alayne Street-Perrott,* Yongsong Huang,† R. Alan Perrott, Geoffrey Eglinton, Philip Barker, Leila Ben Khelifa, Douglas D. Harkness, Daniel O. Olago‡

Carbon-isotope values of bulk organic matter from high-altitude lakes on Mount Kenya and Mount Elgon, East Africa, were 10 to 14 per mil higher during glacial times than they are today. Compound-specific isotope analyses of leaf waxes and algal biomarkers show that organisms possessing CO_2-concentrating mechanisms, including C_4 grasses and freshwater algae, were primarily responsible for this large increase. Carbon limitation due to lower ambient CO_2 partial pressures had a significant impact on the distribution of forest on the tropical mountains, in addition to climate. Hence, tree line elevation should not be used to infer palaeotemperatures.

Most estimates of the cooling of tropical land areas at the last glacial maximum (LGM) are incompatible (*1*) with the much smaller decrease in sea-surface temperatures (≤2°C) estimated from microfossil assemblages in deep-sea cores by CLIMAP (*2*). For example, palaeoecological evidence for a general descent of the upper tree line by 1000 to 1700 m on the tropical high mountains at the LGM has been used to infer a cooling of 5° to 12°C, on the assumptions that temperature was the main control on the forest limit and that environmental lapse rates have remained constant through time (*3*). One possible problem with this interpretation, however, is that glacial aridity (*4*), ultraviolet-B radiation (*5*), and ambient concentrations of CO_2 (*6*, *7*) may also have influenced altitudinal zonation. Here we show that changes in the partial pressure of atmospheric CO_2 (pCO_2) had a significant impact on tropical mountain ecosystems.

At the LGM, pCO_2 was reduced to a level of 190 to 200 μatm, compared with its pre-industrial level of 270 to 280 μatm (*8*). The ecophysiological effects of this large decrease in CO_2/O_2 ratio may have been exacerbated by a small increase in atmospheric O_2 content, resulting from an enhanced burial rate of organic carbon in the glacial ocean (*9*). Plants whose first product of photosynthesis is a three-carbon acid, that is, the C_3 plants, including almost all trees and most shrubs, would have been disadvantaged by increased photorespiration (*10*) and physiological drought (*11*): C_4 plants, including many tropical savanna grasses and sedges, possess a CO_2-concentrating mechanism, making them more efficient than C_3 plants at low pCO_2 with respect to the use of carbon, nitrogen, and water (*12*). Biome modeling suggests that the competitive balance shifted toward C_4 plants at all elevations in the tropics (*7*). Aquatic ecosystems would have been even more susceptible to carbon limitation than they are today because of high diffusional resistances to CO_2 uptake through water (*13*).

The $^{13}C/^{12}C$ ratio in sedimentary organic matter acts as a tracer of the carbon cycle (*14*, *15*), permitting the reconstruction of past changes in the relative abundance of land plants with different metabolic path-

F. A. Street-Perrott and R. A. Perrott are in the Tropical Palaeoenvironments Research Group, Department of Geography, University of Wales Swansea, Swansea SA2 8PP, UK. Y. Huang and G. Eglinton are at the Biogeochemistry Research Centre, Department of Geology, University of Bristol, Bristol BS8 1RJ, UK. P. Barker is at the Hydrodynamics and Sedimentology Laboratory, Department of Geography, Lancaster University, Lancaster LA1 4YB, UK. L. Ben Khelifa and D. O. Olago are at the School of Geography, University of Oxford, Oxford OX1 3TB, UK. D. D. Harkness is with the Natural Environment Research Council Radiocarbon Laboratory, Scottish Enterprise Technology Park, East Kilbride, Glasgow G75 0QF, UK.

*To whom correspondence should be addressed.
†Present address: Department of Geosciences, Pennsylvania State University, University Park, PA 16802, USA.
‡Present address: Department of Geology, University of Nairobi, Post Office Box 30197, Nairobi, Kenya.

ways. Typically, C_3 plants have bulk $\delta^{13}C$ values of −22 to −33 per mil (average −27 per mil) (*16*). In contrast, C_4 plants exhibit $\delta^{13}C$ values of −9 to −16 per mil (average −13 per mil). Crassulacean acid metabolism (CAM) plants—which fix CO_2 in darkness by a process similar to that in C_4 plants—including many succulents, display intermediate ^{13}C contents and are also adapted to low CO_2 and water stress. In aquatic environments, the $\delta^{13}C$ values of algae and submerged macrophytes, most of which use the C_3 pathway, provide an index of the availability of dissolved CO_2 and HCO_3^- to the photosynthesizing cells (*13, 17*). At normal lake water temperatures, the $\delta^{13}C$ values of HCO_3^- are 7 to 11 per mil heavier (more positive) than the values for dissolved CO_2 (*18*).

The $\delta^{13}C$ values of bulk organic matter from East African lake and swamp sediments decreased from glacial to interglacial times by 7 to 17 per mil (*4, 19, 20*). The heavy carbon in sediments of glacial age has been attributed to the spread of C_4 grasses and sedges as a result of drier climate (*19*) or lower atmospheric pCO_2 (*6, 20, 21*). However, the bulk isotope signal in lake sediments reflects a diverse array of carbon sources. It may also be significantly modified by diagenesis (*15*). Compound-specific isotope analysis now permits the measurement of $\delta^{13}C$ values for individual biomarkers representing specific terrestrial, aquatic, and bacterial sources, thereby minimizing the overprint of diagenesis (*22*). Plant material of C_3 and C_4 origin can be readily differentiated, which is an impossible task for pollen analysis alone. Here, we compare the molecular-isotopic stratigraphy of sedimentary lipids from two high-altitude Kenyan lakes with independent palaeoecological data in order to reconstruct the glacial-to-interglacial changes in carbon cycling within the lakes and their catchments.

Sacred Lake, Mount Kenya. Sacred Lake (0°03′N, 37°32′E) occupies an extinct crater at an elevation of 2350 m (*23*) in moist montane rain forest (*24*). Today the tree line lies at 2900 to 3400 m. The lake is small (0.51 km^2), shallow (≤5 m), and oligotrophic. In 1989 it was acidic (pH 5.0 to 6.1) and poorly buffered, with an extremely low salinity (9 to 21 mg of salts per liter). It was surrounded by a floating mat of emergent macrophytes. We recovered two parallel piston cores, SL1 and SL2, of 16.34 and 13.4 m length, respectively, from a water depth of 2.50 m (*25*). The cores consist mainly of carbonate-free lake muds and water lily peats, interrupted by volcanic ashes and debris-flow diamicts (Fig. 1). Fossil root mats indicate that the lake became shallow, usually without desiccation of the deposits. An array of 29 stratigraphically consistent ^{14}C dates and 10 U/Th dates (*26*) suggests that the basal lake sediments (15.13 m in SL1) are ~115,000 years old. Pollen data are available for the last 33,000 ^{14}C years (*24*).

The total organic carbon (TOC) content of the Sacred Lake sediments is high (≤58 %). The diatom content varies from 0 to 10^8 valves per gram of sediment. Remains of the planktonic green alga *Botryococcus braunii* are abundant. Although C/N ratios of 10 to 27 could be used to infer a mixture of aquatic and terrestrial carbon sources (*15*), they should be interpreted with caution because hydrocarbon synthesis by *B. braunii* results in an anomalously high bulk C/N ratio (~36) in this alga (*27*).

The bulk $\delta^{13}C$ values in cores SL1 (Fig. 1) and SL2 vary from −31.5 to −14.1 per mil. The two curves are virtually identical. At least five positive excursions reached −18 to −14 per mil during the early glacial, before 34,000 ^{14}C years before present (B.P.). These peaks are generally associated with alkaliphilous diatoms (*Fragilaria* cf. *construens* var. *venter*, *Cymbella microcephala*, *Gomphonema gracile*, *Epithemia sorex*, and *Synedra acus*) indicative of pH values ≤8.5, although some circumneutral and acidophilous diatoms are present (*Achnanthes microcephala* and *Brachysira brebissonii*).

An interstadial $\delta^{13}C$ minimum (−24 to −22 per mil) is dated at ~34,000 to 24,000 ^{14}C years B.P. It corresponds to a minor peak of dry montane forest pollen (mainly *Podocarpus*) (*24*). Abundant planktonic (*Aulacoseira distans* vars.) and acid-tolerant (*B. brebissonii*) freshwater diatoms show that the lake had expanded.

The last glacial (24,000 to 13,000 ^{14}C years B.P.) is marked by an isotope maximum (−18 to −14 per mil). Abundant

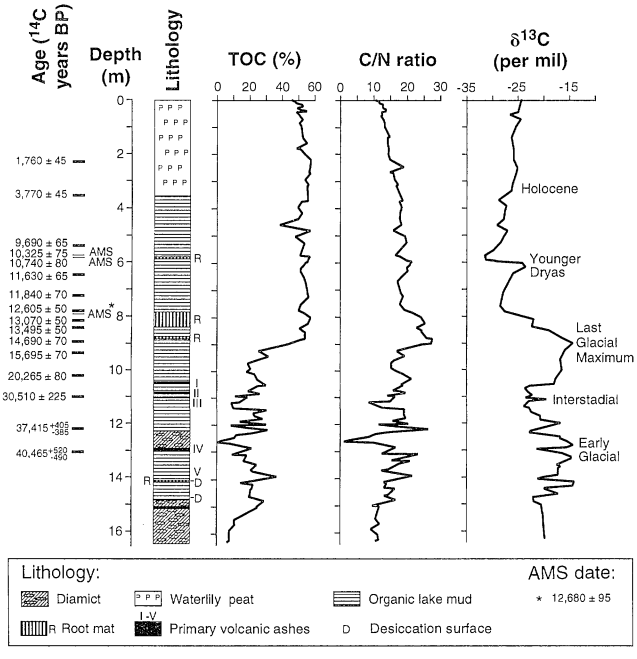

Fig. 1. Stratigraphy and bulk sediment properties of core SL1, Sacred Lake, Mount Kenya. The ^{14}C dates older than 30,000 years B.P. are probably minimum ages.

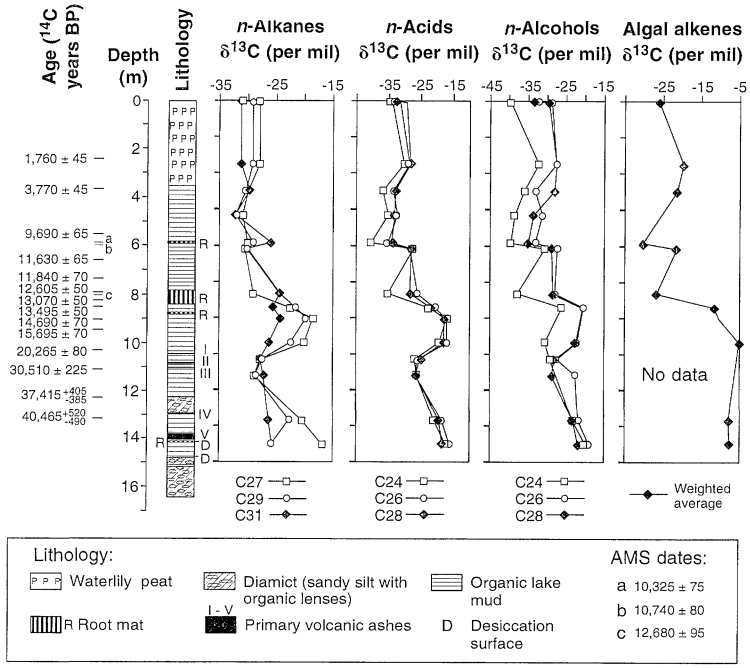

Fig. 2. Molecular-isotopic stratigraphy of core SL1, Sacred Lake, Mount Kenya, showing carbon-isotope values of leaf-wax components and algal alkenes.

pollen of grasses, including large grains typical of C_4 taxa (*28*), found in association with ericaceous shrubs and *Artemisia*, indicate an almost treeless, grassy heathland (*24*). Sedge pollen also increased slightly. If interpreted solely in terms of air temperature, the maximum tree line lowering of 1000 to 1100 m corresponds to a cooling of 5° to 9°C (*24*). The lake was shallow and alkaline (pH 7 to 8.5), with an algal flora dominated by *B. braunii* and the diatom *Fragilaria* cf. *construens* var. *venter*, which is abundant in the modern lakes above tree line (*29*). The chironomid fauna also suggests waters that were alkaline and oligosaline (≤1.5 to 2 g/liter) (*30*).

After 12,000 ^{14}C years B.P., the transition to lower, interglacial δ^{13}C values was interrupted by a positive oscillation (to −23.6 per mil) culminating during the Younger Dryas stadial, just before 10,740 ± 80 ^{14}C years B.P. The following δ^{13}C minimum, −31.5 per mil, is dated at ~10,300 ^{14}C years B.P. This abrupt decrease of ~8 per mil was associated with a rapid ascent of tree line (*24*). Moist montane forest became established at the site. After 3285 ± 60 ^{14}C years B.P., dry forest trees (*Podocarpus* and *Olea*) increased in abundance, and δ^{13}C values rose to a plateau of −27 to −24 per mil. Although *B. braunii* is abundant in the Holocene sediments, diatoms are scarce, partly because of dissolution. However, the dominance of acidophilous taxa (*Eunotia implicata*, *Pinnularia* cf. *brevicostata* var. *sumatra*, and *Cymbella* aff. *cesatii*) suggests generally acidic, freshwater conditions similar to those today.

The lipids we extracted from the sediments of Sacred Lake are of two principal types: leaf waxes from higher plants and algal alkenes (*31*). The former are represented by C_{27} to C_{31} *n*-alkanes with an odd-over-even predominance, and by C_{24} to C_{28} *n*-alcohols and *n*-fatty acids with an even-over-odd predominance. Long chain (C_{27} to C_{31}) *n*-alkanes are particularly resistant to biodegradation (*32*). In core SL1, they range in abundance from 90 to 900 μg per gram dry weight (gdw) (average 318 μg/gdw, n = 15), and the highest concentrations occurred in the last 11,000 years. The abundance of the C_{16} and C_{18} *n*-fatty acids, commonly attributed to phytoplankton, is low compared with their longer chain homologs, probably as a result of early diagenetic degradation (*33*). However, algal biomarkers are represented by at least 15 different botryococcenes: the highly distinctive, branched, isoprenoid hydrocarbons (alkenes) produced by *B. braunii* (*34*). These algal alkenes are present throughout the core except in the interstadial sediments dated at ~34,000 to 24,000 ^{14}C years B.P., but increase to a maximum concentration of ~15 mg/gdw after 4000 ^{14}C years B.P. Bacterial hopanoids are only present in trace amounts. Their δ^{13}C values fall between −23 (glacial) and −30 to −37 per mil (Holocene), in contrast to the highly ^{13}C-depleted hopanoids typically derived from methanotrophic bacteria (*35*). These values rule out the isotopically heavy cogenetic CO_2 produced during methanogenesis as the main source of the high bulk δ^{13}C values during glacial times.

Molecular-level isotope data confirm that the large carbon-isotope variations in TOC reflect both terrestrial and aquatic signals. The δ^{13}C values of leaf wax components of higher plants display an average glacial-to-interglacial shift exceeding 15 per mil. Heavy values for *n*-alkyl lipids (weighted average: −23 to −17 per mil) are found in sediments dated >34,000 and 24,000 to 13,000 ^{14}C years B.P., indicating that the lake received mainly C_4 plant detritus (*36*, *37*) during early- and full-glacial times. In the intervening interstadial, the contribution of C_3 plant debris increased (average: −28 to −26 per mil). At the end of the glacial, the δ^{13}C values of leaf waxes dropped sharply, except for a minor positive excursion during the Younger Dryas. The lowest mean value of −36 to −28 per mil was reached at the beginning of the interglacial, ~10,300 ^{14}C years B.P. It reflects a dominantly C_3 plant source (*37*), compatible with the re-establishment of dense moist montane forest. An increase in the relative contribution of C_4 material is evident after 4000 years B.P.

The δ^{13}C values of algal alkenes vary broadly in parallel with those of leaf wax compounds (correlation coefficient r^2 = 0.63 to 0.88) (Fig. 2). However, the amplitude of variation is larger (>25 versus 15 per mil) and the measured values are 5 to 15 per mil heavier than those of leaf wax components. High values are found in algal alkenes extracted from lake muds of early- and full-glacial age. The highest value (−5.1 per mil) is dated at ~18,200 ^{14}C years B.P., corresponding to the LGM. In contrast, a minimum value of −30.3 per mil was reached ~10,300 ^{14}C years B.P., immediately after a brief positive excursion mark-

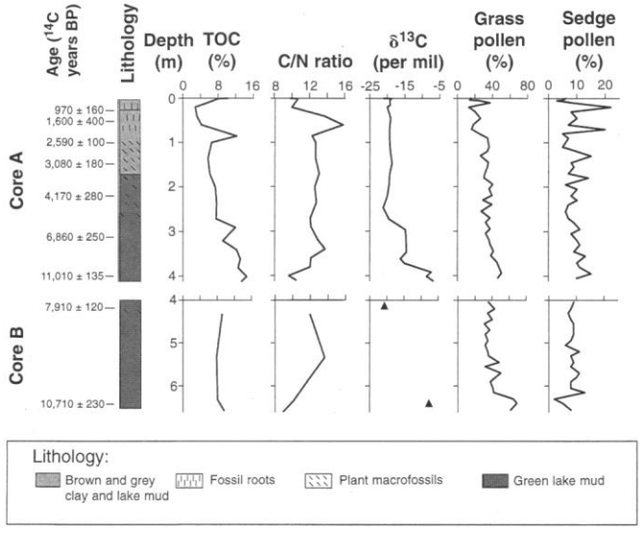

Fig. 3. Stratigraphy, bulk sediment properties, and pollen data for cores A and B, Lake Kimilili, Mount Elgon. Grass and sedge pollen are expressed as percentages of the total pollen. Triangles indicate δ^{13}C values of ^{14}C-dated samples.

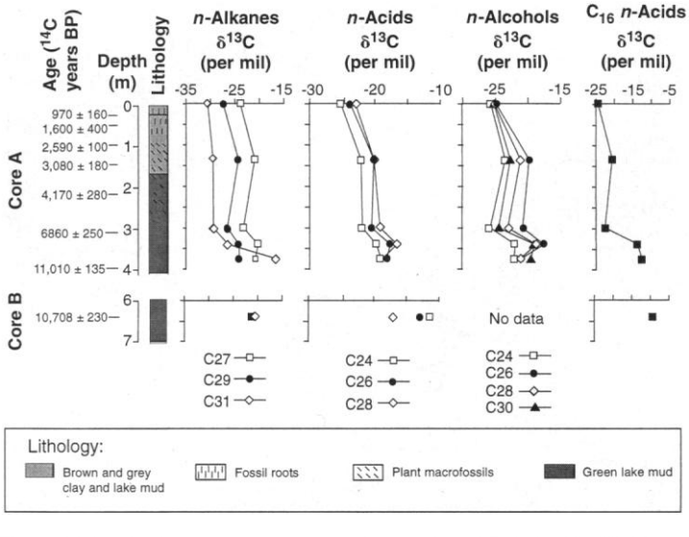

Fig. 4. Molecular-isotopic stratigraphy of cores A and B, Lake Kimilili, Mount Elgon, showing carbon-isotope values of leaf wax components and the C_{16} *n*-acid. The C_{18} *n*-acid could not be measured because of co-elution problems.

ing the Younger Dryas.

Lake Kimilili, Mount Elgon. Lake Kimilili (1°06′N, 34°34′E) lies at an elevation of 4150 m in a glacial cirque, surrounded by sparse Afroalpine vegetation (*4*). When sampled, it covered an area of ~100 m by 50 m and was shallow. No water-chemistry data are available. A 4.10-m-long Hiller core was raised from the exposed lake floor (point A). The base of the sequence (4.05 to 6.55 m) was recorded at point B, where the sediments were considerably thicker. The cores consisted of extremely diatomaceous, carbonate-free lake muds containing 3 to 15% TOC and 1.8×10^9 to 8.0×10^9 diatom valves per gram (Fig. 3). The C/N ratios of 9 to 16 suggest that most of the TOC was derived from algal detritus (*15*). Deposition began at ~11,000 ^{14}C years B.P. The lake shallowed after ~3500 ^{14}C years B.P., as indicated by an increase in clay and the presence of rootlets (*4*).

Heavy bulk carbon-isotope values (−8.8 to −7.0 per mil) were found at the base of both cores (11,000 to 10,000 ^{14}C years B.P.) (Fig. 3). The δ^{13}C values decrease abruptly in two steps, at ~10,000 and at ~7000 ^{14}C years B.P. They then remain steady around a mean value of about −19.5 per mil. The highest δ^{13}C values correspond to a slight maximum in the pollen of grasses and sedges (Fig. 3). The diatom flora in these late-glacial levels is dominated by *Fragilaria* spp., notably *F. pseudoconstruens*, *F. pinnata*, and *F.* cf. *oldenburgiana*. These taxa typically live on minerogenic muds in shallow, neutral to mildly alkaline water bodies. In Arctic Canada, *F. pseudoconstruens* is found in dilute, tundra lakes with low summer water temperatures and a short ice-free growing season (*38*). However, this flora is quite different from that of the perennially frozen, freshwater Lake Hoare in Antarctica (*39*), suggesting that ice cover was seasonal rather than perennial. After 10,000 ^{14}C years B.P., pollen of shrubby C_3 Afroalpine plants such as *Alchemilla* and *Helichrysum* increased (*4*). Since 8600 ^{14}C years B.P., the lake has been dominated by *F. construens* var. *venter* and *F. exigua*. The presence of *F. exigua* suggests that water temperatures (*38*) and phosphorus availability (*40*) had increased. Diatom concentrations also rose, implying that primary productivity was higher, possibly linked to a longer ice-free growing season and increased nutrients.

The concentrations of terrestrial leaf waxes in cores A and B are as much as an order of magnitude lower than those in Sacred Lake, reflecting the much more sparsely vegetated catchment. They also show less temporal variability. Another marked difference is the dominance of C_{16} and C_{18} *n*-fatty acids, attributable primarily to algae, in contrast to C_{26} and C_{28} in Sacred Lake. Bacterial hopanoids are too low in concentration in Lake Kimilili sediments to be measured.

Although the Lake Kimilili sequence does not extend back to the LGM, heavy δ^{13}C values averaging −20 to −17 per mil are found in leaf wax compounds extracted from sediments of Younger Dryas age (11,000 to 10,000 years B.P.) in both cores (Fig. 4), indicating that the contribution of C_4 plant detritus was greater than that found today (*36*, *37*). During the Holocene, the weighted-mean δ^{13}C values of leaf wax components decreased to a modern value of −27 to −24 per mil, in line with the observed expansion of C_3 shrubs.

As in Sacred Lake, algal lipids exhibit even larger changes in isotopic composition than compounds derived from higher plants. For example, the C_{16} *n*-fatty acid that is abundant in *Fragilaria* (*41*) attained values of −13 to −10 per mil during the Younger Dryas, compared with −24 per mil in the surface mud (Fig. 4). Sealed-tube pyrolysis was performed on two samples dated >10,000 years B.P. in order to probe the origin of the highly ^{13}C-enriched organic matter (*42*). These samples yielded a series of hydrocarbons of probable algal origin with very heavy isotope values, including an abundant, highly branched C_{20} isoprenoid alkene monoene attributable to diatoms (*43*) (−4.2 per mil), several other branched or cyclic compounds (−8.4 to −4.2 per mil), and the C_{20} to C_{22} *n*-alkanes (−11 to −7 per mil).

Carbon cycling in terrestrial and aquatic ecosystems. During the last glacial stage, both study sites showed an increase in the proportion of organic detritus derived from plants using the C_4 pathway (*36*). Today, populations of C_4 tussock grasses are found on dry sites up to at least 3370 m on Mount Kenya (*44*) and 3700 m on Mount Elgon (*45*), and C_4 sedges occur up to at least 3525 m on Mount Kenya (*46*) and 3380 m on Mount Elgon (*45*). *Euphorbia* and other succulents are common on the dry north flank of Mount Kenya at altitudes of 1800 to 2100 m, so that a contribution from CAM taxa cannot be ruled out. Expansion of C_4 and CAM taxa, which possess CO_2-concentrating mechanisms at the expense of trees and C_3 grasses, would have been favored by both lower pCO_2 and aridity. However, the significant delay (300 to 600 years) between the δ^{13}C maxima and the lake-level minima recorded by root mats in core SL1 (Fig. 1) suggests that lower pCO_2 played a dominant role.

At both study sites, the isotopic variations in algal biomarkers are even larger than those observed in higher plant leaf waxes. Algal compounds exhibit exceptionally heavy δ^{13}C values during the last glacial stage (−5 to −4 per mil in isoprenoid alkenes, and −13 to −7 per mil in straight-chain lipids). This isotopic signal appears to emanate mainly from green algae (*B. braunii*) in Sacred Lake and from diatoms (*Fragilaria* spp.) in Lake Kimilili. Because the δ^{13}C value of glacial atmospheric CO_2 was about −7 per mil (*47*), and because lipids are isotopically even more depleted than whole cells with respect to the source carbon (*16*), *Botryococcus* and *Fragilaria* must have been using HCO_3^- as a carbon source, that is, they both possessed a CO_2-concentrating mechanism inducible at low concentrations of dissolved CO_2 (*48*). This inference is supported by modern studies of pH drift (*49*).

The extremely heavy glacial-age isotope values in algal biomarkers also imply that isotopic discrimination was very limited with respect to the source carbon. Minimal fractionation is typical of algae affected by severe carbon limitation. This situation may result from low pCO_2; high temperature, pH, or salinity; physical barriers to diffusion such as ice cover or oil films produced by *B. braunii*; or high algal productivity (*50*). For example, δ^{13}C values heavi-

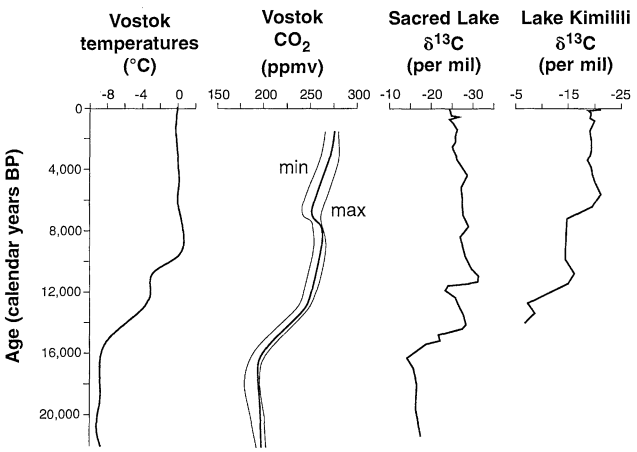

Fig. 5. Variations in δ^{13}C values in TOC from Sacred Lake and Lake Kimilili, Kenya, compared with palaeotemperature anomalies and atmospheric CO_2 variations during the last 22,000 calendar years as recorded by the Vostok ice core, Antarctica (*8*). Note that the isotope scales are reversed.

er than −10 per mil have been found in algae from hot springs, heliothermal brines, seasonally or perennially frozen lakes, and fast-growing cultures (*50, 51*). High productivity is unlikely to have been the main cause of reduced discrimination during glacial times, because the concentrations of algal remains are higher in Holocene sediments. Any explanation for the isotopic variations in algal biomarkers must also account for the marked parallelism exhibited by terrestrial and algal compounds in both lakes (Figs. 2 and 4).

We conclude that the glacial-to-interglacial isotopic shift observed in lacustrine algae was driven by natural variations in dissolved CO_2. During the last glacial stage, the primary control on the concentration of dissolved CO_2 was lower atmospheric pCO_2 (Fig. 5), amplified by local climate-related factors. In Sacred Lake, increased pH and, to a lesser extent, salinity associated with glacial aridity would have intensified carbon limitation. The elimination of forest and floating swamp would have reduced the input of isotopically light, biogenic CO_2 and organic detritus from the vegetation canopy and soils (*52*), suppressing the tendency toward CO_2 supersaturation that is seen in some modern African lakes (*53*). Recycling of C_4 plant detritus would also have shifted the dissolved carbon pool toward heavier isotope values. Whereas there is as yet little evidence for past variations in its pH and salinity, Lake Kimilili lies not far below the modern freezing level (~4790 m) (*54*); during glacial times, seasonal ice cover may have exacerbated the impact of lower pCO_2 on this lake. Both lakes also exhibited variations in productivity during the Holocene, driven by changes in nutrient supply. Together, these local factors may account for the differences in the form of the bulk $\delta^{13}C$ curves from the two sites (Fig. 5).

In agreement with recent model results (*7*) and bulk $\delta^{13}C$ data from the equatorial lowlands (*55*), our isotopic data suggest that glacial-to-interglacial variations in atmospheric pCO_2 had a significant impact on the distribution of tropical rain forests, thus contributing to the decrease in terrestrial biomass at the LGM (*56*). They also reveal the existence of severe carbon limitation in high-altitude lakes during glacial times. Hence, there is a need to reassess palaeoecological and palaeotemperature reconstructions for the LGM, especially those derived from tree-line altitude on the tropical high mountains.

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