

Vegetation changes over palaeo-time scales in Africa

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ABSTRACT: The record of palaeovegetation dynamics in Africa generally extends back to 30 000 yr BP, and longer records, where they do exist, tend to be characterised by hiatuses, giving a broken slide-show of vegetation dynamics in the past. A few specific sites on, for example, Mount Kenya and the Burundi Highlands in the equatorial tropics offer much longer and continuous records. Pollen analysis of lake, peat, swamp sediments and other materials have largely formed the basis of vegetation and climatic reconstruction on the continent. These pollen diagrams indicate depression of highland vegetation to lower altitudes relative to their positions today, fragmentation of lowland forests, and concomitant expansion of grassland prior to 14 000 yr BP, with maximum impact occurring between 22 000 and 14 000 yr BP. The period 14 000 to 10 000 yr BP was a time of transition, with vegetation recovering to present-day distributions by 10 000 yr BP. These are generalisations, and significant differences do occur from region to region; in particular, vegetation change in southern Africa has been largely asynchronous with the rest of the African continent, save for the peak of the last glacial maximum at 18 000 yr BP. Based on the changes in vegetation, the period prior to 14 000 yr BP is viewed as less humid (with exceptions in southern Africa) and cooler than present, with maximum aridity and temperature depressions (estimated to be between 4 and 7°C lower than today, occurring between 22 000 and 14 000 yr BP). A climatic amelioration followed thereafter, reaching optimal warm and humid conditions at about 10 000 yr BP in the equatorial regions, and about 2000 to 5000 yr later in the subtropical regions. Temperature has been generally viewed as being the major factor driving climate change. Following the recent discovery, from polar ice cores, that atmospheric CO₂ concentrations have also changed through time, current palaeovegetation studies have focused on both pollen and, to probe the physiological effect of changing atmospheric CO₂ on vegetation, on bulk and compound-specific stable carbon isotope analysis of organic sediments. These studies have yielded much valuable information on the relationship between the climatic drivers of vegetation change, namely, temperature, precipitation and atmospheric CO₂ changes. They suggest that CO₂ rather than temperature was the main driving force of vegetation change in the tropics during the glacial-interglacial period, and that vegetation may have responded much more sensitively to humidity changes based on physiological responses to lowered CO₂ concentrations. These conclusions are supported by modelling experiments, and indicate that previous estimates of temperature depression in the tropics are overestimated and need to be revised in light of these new discoveries.

KEY WORDS: Palaeovegetation · Palaeoclimate · Africa

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1. INTRODUCTION

It is now evident, from the numerous palaeoclimatic and palaeoenvironmental studies that have been carried out worldwide, that the temporal climatic and environmental changes characteristic of the low lati-

tude regions during the late Quaternary and other earlier periods can be linked to a combination of earth-extrinsic and earth-intrinsic climate-forcing mechanisms, e.g. changes in the orbital parameters and the resultant changes in the radiation balance and hence earth surface temperatures, changes in sea surface temperatures and ocean and atmospheric circulation patterns, high latitude meltwater inputs particularly in

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the North Atlantic, global variations in atmospheric CO₂ concentrations, etc. Regional factors, such as topography and the precipitation-evaporation balance, also influence the environmental response to climate change. The relative importance of these factors which drive climate change and the extent of the linkages between them are still unclear, particularly in the low latitude regions, where there is a dearth of palaeoclimatic and palaeoenvironmental data. This paper reviews the palaeovegetation changes in Africa, and discusses earlier proposed mechanisms of change

(temperature and precipitation) in the light of the relatively new data on changing atmospheric CO₂ contents over geological time scales.

2. MODERN PHYSIOGRAPHY, CLIMATE AND VEGETATION OF AFRICA

Africa is the world's second largest continent, most of which lies below 2000 m save for a few highland areas, namely, the Atlas mountains, Tibesti mountains in cen-

Table 1. Principal vegetation types and characteristic pollen taxa of the major floristic zones of Africa (from Street-Perrott & Perrott 1993, after White 1983). Zones XV (Zanzibar-Inhambane) and XVI (Tongaland-Pongaland) not discussed

Zone	Type	Characteristic vegetation
I	Mediterranean	Broad-leaved sclerophyllous forest with evergreen <i>Quercus</i> (oak); coniferous forest with <i>Pinus</i> (pome), <i>Cedrus</i> (cedar) etc., deciduous <i>Quercus</i> forest
II	Pre-Saharan	Sclerophyllous forest with <i>Juniperus</i> (juniper), <i>Olea</i> (olive), <i>Pistacia</i> (pistachio) and others; scrub forest, bushland and shrubland; tussock grasslands (steppes) with <i>Artemisia</i> (sage-brush), <i>Lygeum spartum</i> and abundant dryland taxa
III	Saharan	Desert; certain plants characteristic of wadis (e.g. <i>Tamarix</i>) and of shady, rocky, gravelly or saline faces (e.g. <i>Cornulaca</i> , <i>Calligonum</i> , <i>Fagonia</i>); Saharomontane vegetation (Ahaggar, Tibesti) includes Mediterranean/Pre-Saharan elements such as <i>Olea laperrini</i> , <i>Artemisia</i> , <i>Ephedra</i> , <i>Erica arborea</i>
IV	Sahelian	Semi-desert grassland and thorny shrubland (north) to wooded grassland and bushland (south), with <i>Acacia</i> spp., <i>Commiphora africana</i> , <i>Balanites aegyptiaca</i> , Euphorbiaceae, and abundant dryland taxa
V	Sudanian	Woodland and dry forest, with <i>Celtis integrifolia</i> , <i>Hymenocardia acida</i> , <i>Lannea</i> , <i>Prosopis africana</i> , <i>Mytragyna inermis</i> , etc.
VI	Sudano-Guinean	Mosaic of dry, peripheral, semi-evergreen rainforest and woodland or secondary grassland, transitional between Zones V and VII
VII	Guinea-Congolian	Lowland rainforest and swamp forest with very diverse endemic flora including <i>Chlorofora</i> , <i>Holoptelea</i> , <i>Uapaca</i> , <i>Musanga</i> and <i>Elaeis guineensis</i> (oil palm); montane rainforest and grassland (above 1000 m altitude) with <i>Olea hochstetteri</i> , <i>Podocarpus</i> and <i>Ilex</i>
VIII	Lake Victoria regional mosaic	Similar to Zone VI; dry, peripheral, semi-evergreen rainforest and scrub forest with <i>Celtis</i> spp., <i>Holoptelea</i> , and <i>Rhus natalensis</i> ; wooded grassland with <i>Acacia</i> and palms (<i>Borassus</i>)
IX	Zambezo-Congolian	Similar to Zone VI
X	Somali-Masai	Deciduous bushland and thicket similar to Zone IV, grading upward into Zone XVIII through semi-evergreen to evergreen bushland and thicket with <i>Cordia</i> , <i>Croton</i> , etc.
XI	Zambezian	Dry forest and woodland (bushveld) with <i>Brachystegia</i> (miombo), <i>Burkea africana</i> , Combretaceae and Proteaceae (<i>Protea</i> , <i>Faurea</i>)
XII	Kalahari-Highveld	Wooded grassland and bushland (Kalahari thornveld) with <i>Acacia</i> spp., Caparidaceae, Tar-chonantheae (Compositae) and <i>Aloe</i> ; upland grassland (highveld) with abundant Gramineae (grasses), Cyperaceae (sedges), Compositae (daisy family) and Ericaceae (heaths)
XIII	Karoo-Namib	Semi-desert shrubland and desert; few relevant pollen data
XIV	Cape	Sclerophyllous shrubland (fynbos, machia) with Asteraceae, Restionaceae, Proteaceae, Eri-caceae, <i>Artemisia</i> , <i>Cliffortia</i> , <i>Myrica</i> , <i>Stoebe</i> , etc.
XVII	Afromontane	Dry montane forest with <i>Podocarpus</i> , <i>Juniperus</i> and <i>Olea</i> ; wet montane forest with <i>Afrocrania</i> , <i>Macaranga</i> , <i>Neoboutonia</i> , <i>Prunus</i> , <i>Ilex</i> , etc.; montane veld with <i>Celtis</i> and <i>Rhus</i> (southern Africa)
XVIII	Afroalpine and Austroafroalpine	Ericaceous bushland and shrubland with <i>Cliffortia</i> , <i>Erica arborea</i> , and other giant heathers (lower part, eastern Africa); high altitude shrubland and grassland, similar to paramo in South America, with <i>Dendrosenecio</i> , <i>Lobelia</i> , <i>Artemisia afra</i> , <i>Alchemilla</i> , and <i>Helichrysum</i> (everlasting flowers) (upper part, eastern Africa); alpine veld with fynbos elements (Eri-caceae, <i>Passerina</i> , <i>Cliffortia</i> , etc.) (southern Africa)

tral Sahara, Ethiopian mountains, East African mountains and the Drakensburg mountains in southern Africa. It is unique in that it sits astride the equator, and this, coupled with its relatively simple physiography, results in a more or less symmetrical distribution of climate about the equator (Thompson 1965), which is modified by regional factors such as topography and large water bodies (Thompson 1965, Ogallo 1989). As a result of its latitudinal span (27° N to 34.5° S), there is a zonal distribution of climate from the meteorological equator northwards and southwards. The equatorial zone experiences the confluence of airflows from the northern and southern hemispheres, and the confluence zone migrates northward to about 15° to 24° N in June to August, and southward to about 8° N to 16° S in December to February, giving rise to humid climate with a double rainfall maximum, flanked on the north and south by broad belts of monsoonal climates characterised by summer rains and winter drought (Street-Perrott & Perrott 1993). The monsoonal climate belts are flanked to the north by the arid Sahara and to the south by semi-arid (e.g. Namib desert) and savannah regions. The temperate northern and southern extremities of the continent, which project into the belts of mid-latitude westerlies, experience westerly cyclonic disturbances which give rise to high winter precipitation (Street-Perrott & Perrott 1993).

The principal controls on the distribution of vegetation in Africa (Table 1) are total annual rainfall and the timing, duration and intensity of the dry seasons (Street-Perrott & Perrott 1993). It has been noted that, according to the partly floristic and partly physiognomic vegetation classification of White (1983), the vegetation of Africa bears a close relationship to the large-scale climate of the continent (Street-Perrott & Perrott 1993). The similarity of precipitation and vegetation distributions is immediately apparent (Figs 1 & 2).

3. PAST VEGETATION OF AFRICA

There is a relatively much higher abundance of pollen data from the humid tropics and the continental extremities, as compared to the arid and semi-arid subtropics, such as the Sahel-Sahara zone and southern Africa. This is mainly due to the scarcity of rich pollen-bearing deposits such as lacustrine sediments and peats (Scott 1984) and the paucity of continuous pollen records where such deposits exist due to their hydrologically very sensitive settings, where there are periodic desiccations and cessation of sedimentation. There also exist some problems in interpreting pollen diagrams due to a lack of data on modern

pollen production and dispersal mechanisms, for example on Mt. Kenya (van Zinderen Bakker & Coetzee 1972). This problem has been partly resolved by the study of modern pollen dispersion at selected sites of interest (e.g. Hamilton 1972, Hamilton & Perrott 1980, 1981). The identification of pollen types poses another problem, since many pollen types can only be identified to family or genus level, for example the grass pollen of Africa (Scott 1984). Furthermore, the role of environmental variables such as temperature and humidity in controlling the distribution of plant species is not well known—this has resulted in contentious interpretations of the palaeoecological significance of some species: for example, in eastern Africa, *Artemisia* pollen was assumed to be an indicator of cool, dry conditions (Coetzee 1967), while Street-Perrott & Perrott (1993) maintain that its climatic significance is not well understood. In addition, lowland lake sediment records are beset by hiatuses as compared to highland lake and swamp sediment records, presumably mainly due to the relatively low precipitation: evaporation ratio in the lowlands.

Dating of the sediments has also been problematic, particularly in sequences in arid and semi-arid areas, by, for example, frequent hiatuses, lack of sufficient

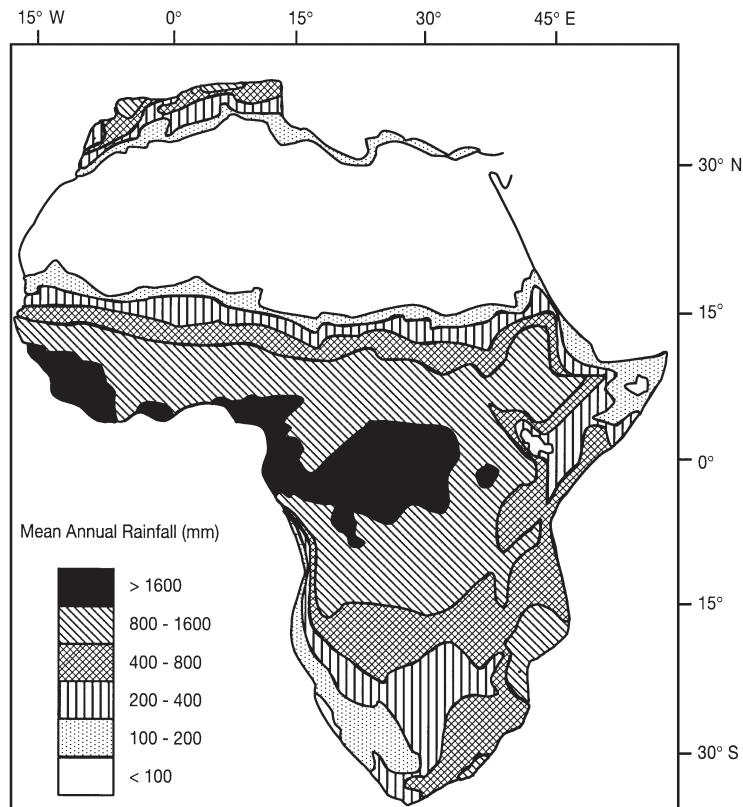


Fig. 1. Rainfall map of Africa (from Street-Perrott & Perrott 1993; after Nicholson 1980)

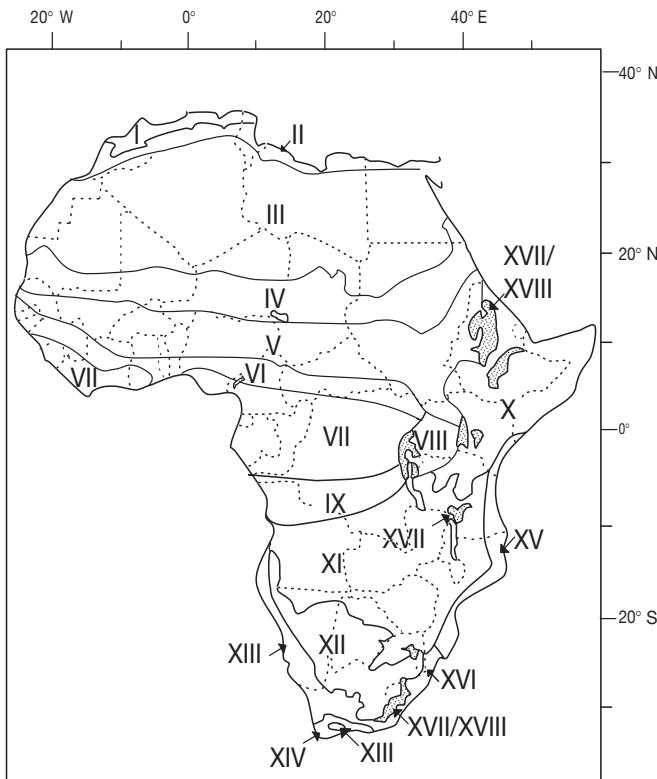


Fig. 2. Major floristic regions of Africa (from Street-Perrott & Perrott 1993; after White 1983)

organic matter, contamination by juvenile CO₂, contamination by younger organic matter. The records of vegetation change do not, generally, date beyond 40 000 yr BP, and in most cases they cover only the period 30 000 yr BP to the present day. In the last few years, however, concerted efforts have been made to obtain longer, continuous, and radiometrically well-constrained cores (e.g. Sacred Lake) to better understand the dynamics of tropical climate and environment over the last glacial-interglacial cycle.

3.1. Northern Africa

Floristic Zones I and II. Climate in the area of the Middle Atlas, Morocco, is strongly seasonal: total mean annual precipitation 930 mm resulting from western cyclonic disturbances; falls mainly during the winter months of October to May.

3.1.1. 22 000 to 14 000 yr BP

The record of a 21 m core from Lake Tigalmamine (32° 54' N, 5° 21' W; 1628 m a.s.l; mean annual precipitation 930 mm), Middle Atlas, Morocco, indicates that

between 18 000 and 8000 yr BP the area was dominated by herb-rich grassland (Gramineae—Chenopodiaceae—*Artemisia* assemblage), suggesting that low moisture conditions prevailed at the time (Lamb et al. 1989). The dates in the littoral 21 m core are, however, tenuous because of depositional breaks prior to 4000 yr BP (Lamb & van der Kaars 1995).

3.1.2. 14 000 to 10 000 yr BP

Between 14 000 and 12 000 yr BP, scattered evergreen oaks occurred in the region. Pollen analysis of marine cores from Gulf of Gabès and near Kneiss and Kerkennah islands, reflecting vegetation change in Tunisia, also indicates the spread of both deciduous and evergreen oaks and pine forests from 12 000 yr BP (Brun 1991). A second, continuous, well-dated, 16 m core from Tigalmamine, covering the Holocene, gives better information on vegetation change (Lamb & van der Kaars 1995). *Quercus* forest had already surrounded the lake by 10 500 yr BP (basal age of the core); *Artemisia* and Gramineae counts at the base of the core are thought to record the transition from the arid late Pleistocene to humid Holocene environment (Lamb & van der Kaars 1995).

3.1.3. 10 000 to 0 yr BP

From 6200 yr BP, low levels of *Cedrus* pollen is found in the record, accompanied with a rise of *Pinus* pollen at a time when the diatom assemblage and ostracod Mg/Ca profile suggests a change from shallow to deeper lake conditions, and decreased water salinity or decreased temperatures, respectively (Fig. 3) (Lamb & van der Kaars 1995). *Artemisia* decreased at the same time in response to the increase in effective moisture (Lamb & van der Kaars 1995). These results are consistent with those from Tunisia marine cores, which show an increase of shrub vegetation with *Oleo-lentis-cetum* from 12 000 yr BP accompanied with an increase in hygrophilous plants until 4000 to 5000 yr BP (Brun 1991). *Quercus canariensis* and *Cedrus* increased at about 4600 yr BP, indicative of moister conditions; the increase in *Q. canariensis* was interrupted by a brief but marked decline coinciding with the arid interval from ca 4500 to 4000 yr BP (Lamb & van der Kaars 1995). From 4000 yr BP, *Cedrus atlantica* appears in the record (Lamb et al. 1989, Lamb & van der Kaars 1995): it currently occupies cooler, moister parts of the Atlas Mountains than those where *Quercus* grows alone, implying a slight fall in temperature (Lamb et al.

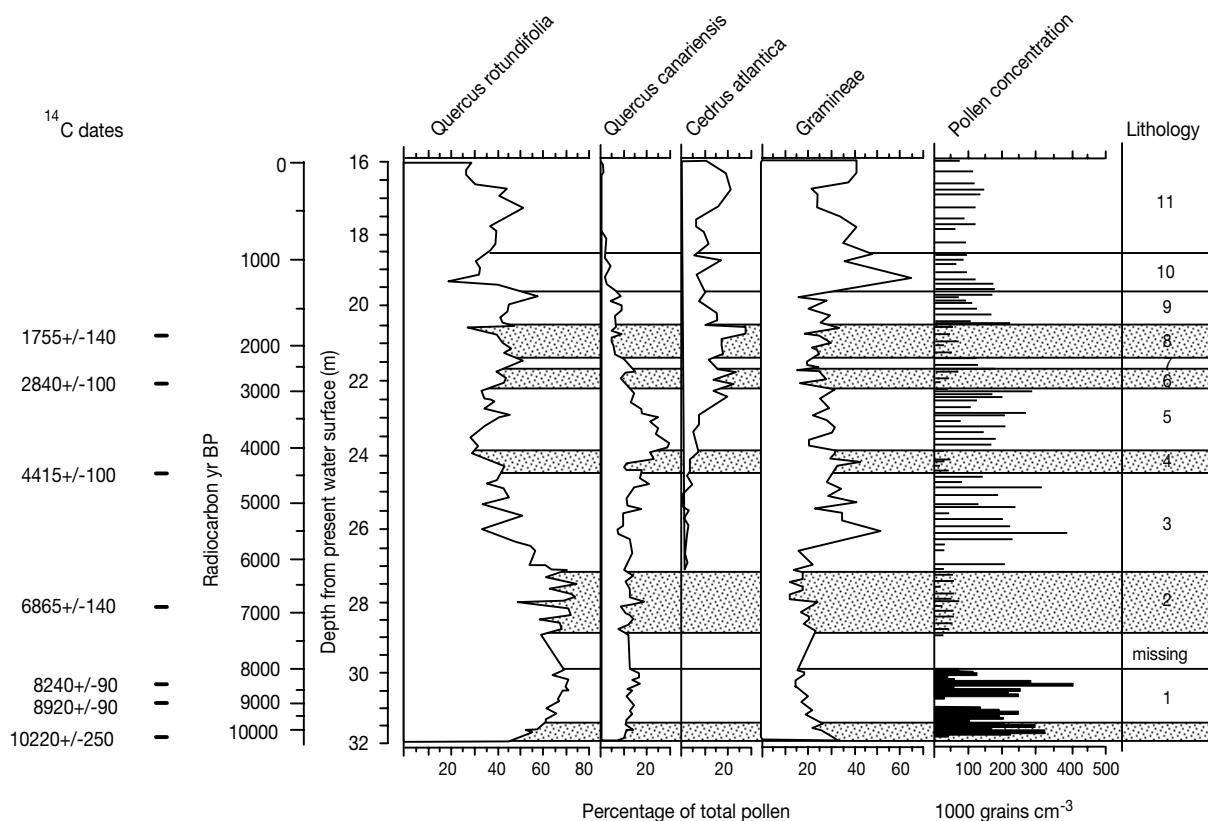


Fig. 3. Pollen stratigraphy of major taxa, Tigalmamine core C86. Shallow water phases inferred from palaeoecological data are indicated by shading (Lamb et al. 1994)

1989). Concordant with the appearance of *C. atlantica*, however, is an increase in $\delta^{18}\text{O}$ on marl, which suggests a temperature increase: these observations are accounted for by change in the source and amount of precipitation, with western storm tracks bringing winter rain to the area (Lamb et al. 1989). The decline of *Fraxinus* and *Q. canariensis* at 2250 yr BP reflects the first anthropogenic influence in the area (Lamb et al. 1989, Lamb & van der Kaars 1995).

The sequence of vegetation change in North Africa (Tigalmamine) from evergreen oak to deciduous oak and then cedar during the Holocene may be interpreted to be due to a progressive increase in available moisture (Lamb & van der Kaars 1995). The contrast between the marked lacustrine response and the very muted vegetation response to short-term climatic events suggests that, during the arid intervals (lasting between 150 and 400 yr), precipitation may have remained sufficient to sustain plant growth in the summer growing season, whereas reduced precipitation in winter (normally the wettest season) resulted in depletion of the groundwater aquifer, leading to a lowered lake level without affecting vegetation because the

mountain winters are too cold for plant growth (Lamb & van der Kaars 1995, Lamb et al. 1995). The rapid response time of the lake level changes in Tigalmamine are thought to reflect higher frequency sub-Milankovitch climatic variations, while the vegetation responded to a lower frequency climate signal, probably modulated by orbital forcing (Lamb & van der Kaars 1995). The regressions, representing short-term decreases in winter rainfall, may be related to sea surface conditions in the North Atlantic (Lamb et al. 1995).

3.2. The Sahara-Sahel-Sudan Region

Floristic Zones III, IV and V. The dominance of high pressure conditions is marked by below average precipitation. Mean annual precipitation is <25 mm over most of the Sahara except for the high plateaux of Ahaggar and Tibesti, which receive >100 mm mean annual precipitation. At present nearly all rains falling in the Sahel zone are monsoonal in origin. In summer (July-August) these rains reach the Ahaggar and Tibesti mountains. Over the central Sahara, available

rains tend to fall during the spring (March to June) and Autumn (September to December), and are linked with tropical depressions. Southwesterly air may penetrate far north in summer in the southern Sahara and produce short-lived low pressure centres (Maley 1987, Barry & Chorley 1992).

3.2.1. 22 000 to 14 000 yr BP

Maximum aeolian activity in the central Sahara occurred between 20 000 and 18 000 yr BP, and subsequently appears to have spread southwards (van Zinderen Bakker 1980). The peak of aridity in the southern Sahara was reached after 18 000 yr BP, probably correlated with the minimum evaporation of equatorial oceans, while the northern flank tended to become more humid as a result of the southward displacement of the Atlantic baroclinic zone and of the accompanying rain-producing eddies, supported by surface cooling and lower local evaporation (Flohn & Nicholson 1980).

3.2.2. 14 000 to 10 000 yr BP

The period 14 000 to 10 000 yr BP is characterised by abrupt warm/cold episodes with marked vegetation changes (Flohn & Nicholson 1980).

3.2.3. 10 000 to 0 yr BP

Two wet periods are documented to have occurred in the Sahara during the Holocene: at 9500 yr BP and 6000 yr BP (Flohn & Nicholson 1980). From 9000 to 5000 yr BP, a fauna with tropical and more humid affinities lived in the northern Sahara and was afterwards replaced by biota typical of drier open country: southern savannah vegetation invaded from the south, and Mediterranean vegetation invaded from the north (Flohn & Nicholson 1980, Neumann 1991). Pollen analysis of lacustrine sediments from Senegal and Mauritania, from areas which are, at present, of Sahelian and Saharan nature, show rapid extension of humid vegetation towards the north from ca 9000 yr BP with maximum intensity at ca 8500 yr BP, and are correlated with the intensification of the Atlantic monsoon (Lézine 1989). The maximum intensity is dated at 8500 yr BP and corresponds with a large body of evidence on lacustrine extensions in the Sahelian and Saharan subtropical latitudes (Lézine 1989). Tropical savannahs shifted 500 to 700 km northwards of their present range between 7000 and 6500 yr BP (this appears to have occurred simultaneously in the east-

ern and central Sahara), receding slightly after 6000 yr BP to 300–400 km north of their present range (Neumann 1991). From 5200 yr BP onwards, aridity increased and the savannah formations retreated to the south until the present status was reached by 3300 yr BP (Neumann 1991). The interval 4000 to 2000 yr BP was more humid in Senegal and Mauritania (Lézine 1989). In the Mauritania-Senegal region, forest destruction occurred at about 2000 yr BP, when the present-day semi-arid environment was established (Lézine 1989).

In this region, climatic factors responsible for the increased humidity during the early to middle Holocene were: a weakening of the subtropical high pressure cells, an interplay of the influences of the Azores and the St. Helena anticyclones, a weakening of the upwelling off the west coast, and a higher evaporation from the ocean surface (Flohn & Nicholson 1980). Due to the interplay of these factors, southern summer rains and northern winter rains alternated and overlapped considerably in area (Flohn & Nicholson 1980).

3.3. Western and Central Africa

Floristic Zones VI, VII and IX. The West African Monsoon Trough generally oscillates between annual extreme locations of about 2° and 25° N (Barry & Chorley 1992). In accordance with the annual migration of quasi-permanent circulation systems, the regions nearest to the equator experience rainfall all year round, but the semi-arid desert fringe only at the height of the boreal summer, while double-peaked precipitation regimes with various timings are characteristic of the intervening latitudes (Hastenrath 1991).

3.3.1. >22 000 yr BP

Palynological investigations of temporally long records in marine sediment cores off the West African coast indicate that forest and woodland are more important during interglacial periods, while, during glacial periods, they are progressively replaced from north to south by grassland (e.g. Agwu & Beug 1984). From 35 000 yr BP through to the early Holocene, there were drastic reductions of forest, freshwater swamps and moist savannah communities in the Niger delta owing to adverse climatic conditions (Sowunmi 1981). During this period, forests in western and central Africa occurred in 3 isolated refugia; Upper Guinea, Cameroon-Gabon and eastern Zaïre, and are thought to have served as a buffer between Sudanian savannah to the north and Zambezian savannah to the south (Maley 1987).

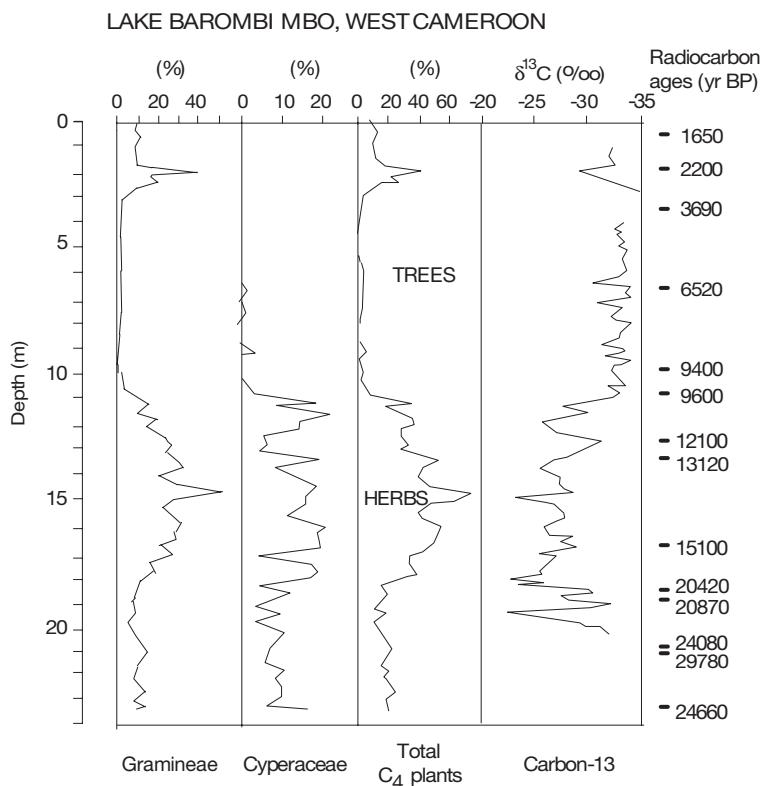


Fig. 4. Pollen and stable carbon isotopes in Lake Barombi Mbo, West Cameroon. From Giresse et al. (1994)

The $\delta^{13}\text{C}$ curve of a 23.5 m core from Lake Barombi Mbo, Cameroon (Fig. 4) ($4^{\circ}40' \text{N}$, $9^{\circ}24' \text{E}$; 300 m a.s.l.), exhibits an almost linear correlation with the curve of the total grass pollen, which forms the main part of the C_4 biomass; it has isotopically relatively light values, indicating a forest environment with some montane flora from 25 000 to 20 000 yr BP (Giresse et al. 1994).

3.3.2. 22 000 to 14 000 yr BP

A mosaic of forest and savannah around Lake Barombi Mbo, accompanied by a fall in the lake level and colonisation of the shores by Cyperaceae and other aquatic plant species, is inferred from pollen and carbon isotope data for the period 20 000 to 13 000 yr BP (Fig. 4) (Giresse et al. 1994). In Lake Bosumtwi, Ghana, a dry, semi-deciduous type of forest, similar to the present-day type, existed at the Pleistocene-Holocene boundary (Talbot & Hall 1981). Pooid grasses (identified by grass cuticle analysis), and *Olea hochstetteri* pollen at the Pleistocene-early Holocene boundary imply palaeotemperatures several degrees lower than today in southern Ghana (Talbot et al. 1984). The $\delta^{13}\text{C}$ values in Lake Bosumtwi (Talbot & Johannessen 1992) and Lake Barombi Mbo (Giresse et

al. 1994) support pollen evidence of grassland (C_4 grasses) expansion during the last glacial maximum.

In response to both lowered temperatures and changes in humidity, montane biotopes of Ghana and West Cameroon (both forested and open) spread to low altitude, replacing the lowland forests, which occurred in 3 isolated refugia: Upper Guinea, Cameroon-Gabon, and eastern Zaïre (Maley 1987). The changes in temperature between the last glacial maximum and present (lowered by 5 to 8°C relative to present), in western Africa, are attributed to the interaction between tropical Atlantic upwelling and cloud formation: stratiform cloud cover produced by the cold Atlantic waters (maximum lowering during the last glacial maximum of 8 to 9°C) caused a cooling and drying of the adjacent land areas (Maley 1987). These clouds formed persistent cover which produced little or no rain, but intercepted solar radiation, causing lower temperatures (Maley 1987).

3.3.3. 14 000 to 10 000 yr BP

From 13 000 to 10 000 yr BP, there was forest extension in the Lake Barombi Mbo area (Giresse et al. 1994). Two short dry phases, marked by positive $\delta^{13}\text{C}$ spikes, are dated by interpolation at 11 200 and 10 300 yr BP (Giresse et al. 1994). In the region of Congo, the forest underwent major expansion from ca 12 000 yr BP (Giresse & Lanfranchi 1984).

3.3.4. 10 000 to 0 yr BP

A dramatic rise in the abundance of arboreal pollen in Lake Barombi Mbo suggests that forest rapidly replaced grassland after 9000 yr BP (Talbot et al. 1984); maximum forest density, with average $\delta^{13}\text{C}$ values of -32‰ , occurred between 9500 and 3000 yr BP (Giresse et al. 1994). Continuous forest became established between 7500 and 5000 yr BP in Lake Bosumtwi (Talbot & Hall 1981); the early stages are concomitant with the more humid conditions recorded in the Niger Delta between ca 7600 and 6960 yr BP, when freshwater swamp and rainforest components increase in the pollen assemblages (Sowunmi 1981). Palynological and sedimentological records from Lake Barombi Mbo show climatic deterioration between 4000 and 3000 yr BP and between 2500 and 2000 yr BP (Maley 1992),

with temporary forest openings reflected during the latter period by $\delta^{13}\text{C}$ excursion above -30‰ (Giresse et al. 1994). Reduction in rain forest communities after 3000 yr BP in the Niger Delta is attributed to human disturbance through agricultural practices (Sowunmi 1981).

3.4. Eastern Africa

Floristic Zones VIII and X. During December to February, the northeast monsoon sweeps down the western Indian Ocean and adjacent East Africa, extending to well south of the equator. During July and August, the southeast trades of the southern hemisphere recurve near the equator and form the origin of the northern hemisphere southwest monsoon. Most rain occurs during the passage of the Intertropical Convergence Zone (ITCZ). Deep westerlies originating from the Atlantic Ocean and the moist Zaïre Basin between June and August are associated with widespread cloudy and rainy weather in western parts of East Africa (Jackson 1961, Thompson 1965, Hastenrath & Lamb 1979, Hastenrath 1984, Ogallo 1989).

3.4.1. $>22\,000$ yr BP

Perhaps the longest continuous records so far retrieved from East Africa are those from Sacred Lake, Mount Kenya (Coetzee 1967, Olago 1995, Street-Perrott et al. 1997, Olago et al. 1999), and Rukiga Highlands (Taylor 1990), spanning the period from 115 000 yr BP and $>42\,000$ yr BP to present, respectively. Prior to 42 000 yr BP, the Sacred Lake site was characterised by unstable vegetation consisting of Ericaceous belt taxa with elements of humid forest (Fig. 5) (Coetzee 1967, Olago 1995), while in the Rukiga Highlands around Muchoya Swamp ($1^{\circ}17' \text{S}$, $29^{\circ}48' \text{E}$; 2260 m a.s.l.), moist lower montane forest vegetation (indicated by, e.g., *Croton* comp., *Ilex*, *Neoboutonia*, *Minulopsis* comp., Urticaceae, Myrtaceae, *Macaranga*, *Nuxia* and *Filcahoa*) existed, prior to 42 000 yr BP, suggesting that conditions were similar then to those existing today (Taylor 1990).

Between 42 000 and 22 000 yr BP, $\delta^{13}\text{C}$ values in Sacred Lake indicate a co-dominant C₃-C₄ ecosystem, reflecting open forest vegetation at the lake (Coetzee 1967, Olago 1995, Olago et al. 1999). A *Hagenia* dominated treeline existed at the altitude of the lake with Ericaceous belt elements (van Zinderen Bakker & Coetzee 1972, Street-Perrott & Perrott 1993, Olago 1995). The period between 42 000 and 34 000 yr BP on Mount Kenya (Olago 1995) was relatively dry, following which humid conditions occurred. Other evidence of dry con-

ditions in East Africa before 30 000 yr BP come from Lake Abiyata ($7^{\circ}10' \text{N}$, 37°E ; 1600 m a.s.l.), Ethiopia, which indicates a generally semi-arid environment almost similar to present-day conditions with slight temperature changes (Lézine 1982), and Karimu Mire basin ($0^{\circ}30' \text{S}$, $36^{\circ}41' \text{E}$; 3040 m a.s.l.), Aberdare range, Kenya, where clay deposition and the absence of organic matter before 32 000 yr BP imply that vegetation was absent or sparse in the surrounding area, while analysis of pollen indicates that shortly thereafter, dry conditions depressed vegetation belts: *Hagenia* (indicating forest-edge conditions) and *Olea* (Olive) dominated, while *Juniperus* (Cedar), *Podocarpus* (Yellow-Wood) and Urticaceae were virtually absent (Perrott & Street-Perrott 1982). Until 32 000 yr BP in the Rukiga Highlands, Ericaceous belt species such as *Anthospermum*, *Cliffortia*, *Artemisia* and *Stoebe* are found, indicating a substantial altitudinal depression of vegetation belts, and a cold, dry period relative to the present (Taylor 1990). At the Burundi site (Kashiru Swamp, $3^{\circ}28' \text{S}$, $29^{\circ}34' \text{E}$; 2104 m a.s.l.), temperatures were estimated at about 4°C colder than now prior to 30 000 yr BP (Bonnefille et al. 1990), in association with the occurrence of montane evergreen (gymnosperm) forest (*Cliffortia*, with *Podocarpus*, *Macaranga*, and *Olea* common) above 2200 m, and the development of Ericaceae around the swamp (Bonnefille & Riollet 1988, Bonnefille et al. 1990). It was also wetter than present (Bonnefille & Riollet 1988, Bonnefille et al. 1990). $\delta^{13}\text{C}$ data for the period 30 000 to 22 000 yr BP in the Rukiga and Burundi Highlands indicate that C₄ plants were dominant (Aucour & Hillaire-Marcel 1993, Aucour et al. 1994) and are supported by the pollen diagram for Kashiru Swamp (Fig. 5) which shows a sharp decline in forest taxa at 29 000 yr BP and an increase in Gramineae (Bonnefille & Riollet 1988). A warm phase occurred ca 26 000 yr BP as evidenced by fossil pollen from the Cherangani Hills in Kenya (1°N , $35^{\circ}28' \text{E}$; 3292 m a.s.l.), with temperatures between 2 and 4.1°C lower than at present (Coetzee 1967).

3.4.2. 22 000 to 14 000 yr BP

A wet episode, characterised by increases in Compositae, *Alchemilla* and *Hypericum* (St. Johns wort) pollen, and a decrease in Gramineae and Cyperaceae pollen, is recorded at $21\,500 \pm 1250$ yr BP at Kashiru (Bonnefille & Riollet 1988). In Muchoya Swamp, the pollen spectra of 5 cores (ranging between 8 and 10 m) indicate that *Hagenia* forest dominated between 25 000 and 17 000 yr BP (the dates are based on an extrapolation of 3 radiocarbon dates along the profile of the longest core) (Morrison 1968). In Muchoya Swamp, the *Hagenia* forest was replaced by Erica-

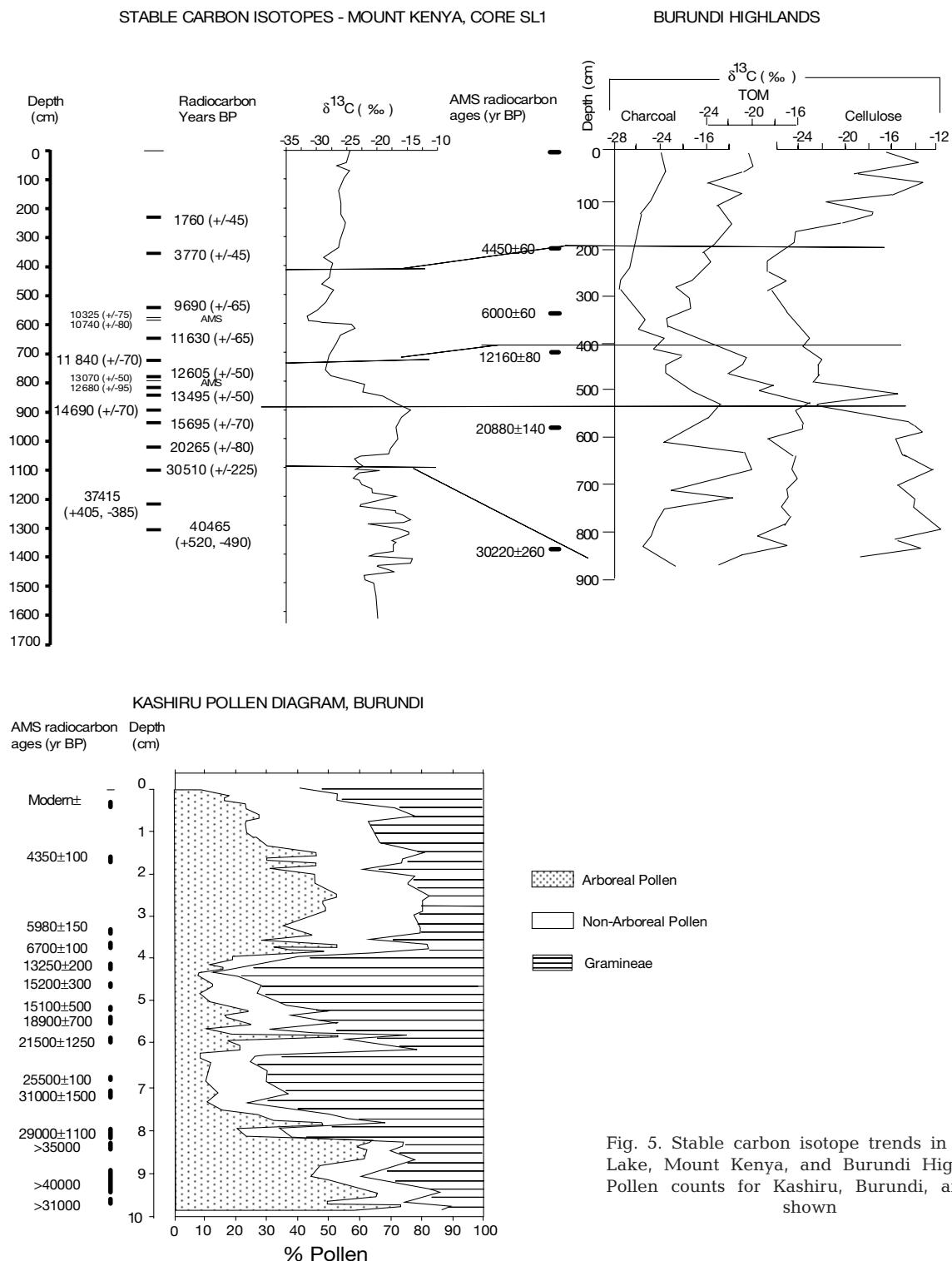


Fig. 5. Stable carbon isotope trends in Sacred Lake, Mount Kenya, and Burundi Highlands. Pollen counts for Kashiru, Burundi, are also shown

ceous belt vegetation (Morrison 1968, Taylor 1990), with *Stoebe kilimandscharica* and much grass pollen persisting through to 11 000 yr BP, suggesting a mean annual temperature between 5 and 8°C lower than today (Morrison 1968). Dry montane scrub (*Anthosper-*

mum, *Ericaceae* and *Hagenia*) persisted around Ahakagyezi Swamp in the Rukiga Highlands between 21 000 and 14 000 yr BP (Taylor 1990). In the Burundi Highlands, an altitudinal depression of between 1000 and 1500 m compared to the present occurred (Bon-

nefille et al. 1990). The extension of montane grasslands (characterised by high percentages of Gramineae and Compositae) in the pollen record is observed between 22 000 and 15 000 yr BP in Kashiru (Roche & Bikwemu 1989). The persistence of the tree taxa *Podocarpus* and *Olea*, and the occurrence of *Myrica*, *Ilex*, *Syzygium*, and *Canthium* during the glacial period, point to the existence of local refuges in the neighbourhood of the Kashiru site (Bonnefille & Riollet 1988). Temperatures in Burundi were correspondingly cool (Bonnefille et al. 1990).

On Mt. Elgon, the extent of the forest and macrophyllous thicket was much less than at present between >23 000 and <14 000 yr BP, and there is evidence of a depression of vegetation belts (Hamilton 1987). At the Cherangani site, Afroalpine vegetation became established (Coetzee 1967). Dry cool conditions persisted in Karimu Mire until ca 11 000 yr BP (Perrott & Street-Perrott 1982). In Lake Naivasha ($0^{\circ} 45' S$, $36^{\circ} 20' E$; 1890 m a.s.l.), the arid glacial (immediately prior to 20 290 yr BP to about 12 270 yr BP) was characterised by Chenopodiaceae, Amaranthaceae, Compositae, and *Anthospermum* (indicators of dry conditions), with low *Olea* and *Podocarpus* pollen (Maitima 1991). Gramineae, Chenoams, Compositae and *Sesbania* dominate prior to 18 000 yr BP (Maitima 1991). A short episode of moderately wet climate and moderate forest expansion on the Aberdare mountains is inferred between ca 17 000 and 15 000 yr BP and is characterised by slightly higher percentages of the forest taxa *Podocarpus*, *Olea*, *Celtis*, *Anthospermum* and *Hagenia*; these pollen types, with the exception of *Podocarpus*, decline sharply towards the end of this episode (Maitima 1991). Street-Perrott & Perrott (1993) note that, during the early part of this period in Sacred Lake, there were rapid shifts in major pollen types, changing from *Hagenia* to *Podocarpus* to *Cliffortia*, and suggest that this could signal the beginning of cold climate with initially dry conditions. Distinguishing features at Sacred Lake during this period are: a gradual decline of *Cliffortia* and *Stoebe* pollen percentages and a concomitant rise in Ericaceae and *Artemisia* pollen, possibly indicating a lowering of higher altitude vegetation, drier climate and a continued decrease in temperature at the altitude of the lake (Coetzee 1967, van Zinderen-Bakker & Coetzee 1972). The $\delta^{13}\text{C}$ values indicate a change in catchment vegetation from open forest to C_4 -dominated grasslands up to about 13 500 yr BP, when there was a resurgence of C_3 species at a time of lake desiccation (Fig. 5) (Olago 1995, Olago et al. 1999). The initial abrupt shift in the $\delta^{13}\text{C}$ values (from lighter to heavier values) at 22 000 yr BP is consistent with the observation of the rapid shift in pollen types (Olago 1995, Olago et al. 1999). A cool dry climate with *Cliffortia* and a decrease in *Hagenia*

(reflecting treeline depression) persisted to 14 050 yr BP (Street-Perrott & Perrott 1993). The trends in Sacred Lake are similar to those observed in Lake Rutundu, Mount Kenya: alpine zone vegetation consisting mainly of grassland mixed with *Artemisia*, other Compositae and scattered Ericaceae represent a cold, dry climate between ca 18 000 and ca 10 800 yr BP, with very dry climate being characteristic of the period up to ca 11 600 yr BP (Coetzee 1967).

Bonnefille et al. (1990) used multivariate statistical analysis (based on an extensive modern data set [356 sites] from East and Central Africa between latitudes $4^{\circ} S$ and $12^{\circ} N$ and longitudes 28° to $42^{\circ} E$, covering desert, subalpine grassland and all forest types) on a 40 000 yr (radiocarbon dated) pollen profile from Kashiru Swamp to derive quantitative estimates of past temperatures in tropical Africa. They derived, for the last glacial period, a temperature decrease of $4 \pm 2^{\circ}\text{C}$, which is slightly lower than previously inferred values, and a simultaneous 30% decrease in mean annual rainfall, which is in broad agreement with the concomitant lake level declines in the East African region. Using a similar method, Vincens et al. (1993) gave an estimated temperature drop of $4.2 \pm 3.6^{\circ}\text{C}$ and a mean precipitation drop of 15% (with a large deviation) for Lake Tanganyika. Livingstone (1971) noted that the pollen assemblages covering this period generally reflect lower precipitation or a more uneven seasonal distribution in rainfall; thus the large deviations from the mean precipitation values calculated by Bonnefille et al. (1990) and Vincens et al. (1993) might reflect uneven seasonal distribution of rainfall.

3.4.3. 14 000 to 10 000 yr BP

Some of the pollen curves of the Cherangani Hills indicate that the cold climate was coming to an end at about 12 400 yr BP (Coetzee 1967). Kendall (1969) observed from a palynological study of a core taken from Pilkington Bay, Lake Victoria, that prior to 12 000 yr BP, forest was either absent or of small extent in the area. The terminal phase of the last glaciation at Lake Bogoria (14 680 to 12 050 yr BP) was characterised by an abundance of herbaceous taxa, e.g. Gramineae, Cyperaceae, Compositae, and *Typha*, and to a much lesser extent, the tree pollen *Podocarpus*, *Juniperus*, *Myrica*, *Olea*, *Phoenix* (wild date palm) *Celtis*, *Allophylus* and *Macaranga*, amongst others; tree pollen became progressively much more abundant and diversified, with *Prunus africana*, *Stoebe kilimandscharica*, *Hagenia abyssinica* and *Schrebera alata* being found exclusively within this zone (Vincens 1986). In Sacred Lake, sedimentological evidence indicates that the period of maximum aridity occurred just before

13 500 yr BP, at a time when there was a change from C₄-dominated to a C₃-dominated vegetation community (Olago 1995, Olago et al. 1999); this is supported by the occurrence, after 14 050 yr BP, in Sacred Lake of maximum *Artemisia* pollen values, which indicate an accentuation of dry conditions, and increases in *Cliffortia* and, later, *Hagenia* pollen could indicate a slight climatic amelioration (Coetzee 1967). Small *Celtis* pollen maxima (currently found on the plateau and lower altitudes in the forests of Mt. Kenya) may indicate moister conditions in the lowlands at ca 12 300 yr BP. Street-Perrott & Perrott (1993) noted that the Sacred Lake pollen assemblages between 14 000 and 10 000 yr BP are presently climatically indistinguishable, although they observe slightly higher values of *Artemisia* and moister montane forest tree species, e.g. *Hagenia*, and a decline in *Podocarpus*. Increases in humidity after 11 600 yr BP at Lake Rutundu are indicated by low counts of *Artemisia* pollen and increasing *Hagenia* pollen (Coetzee 1967). Highest values of Ericaceae between 10 800 and 10 300 yr BP at Lake Rutundu coincide with reduced Gramineae and montane forest zone elements (*Hagenia*, *Podocarpus*, etc.) in Sacred Lake, and a definite increase in temperature is recorded at ca 10 300 yr BP by the dominant Ericaceous zone pollen (Coetzee 1967). A temperature increase is inferred in the Burundi Highlands between 15 000 and 13 000 yr BP (Roche & Bikwemu 1989, Bonnefille et al. 1990). This period also coincides with the maximum extension of grassland in the region, and with the lowest tree diversity and the noticeable occurrence of *Artemisia* (Bonnefille & Riollet 1988). Stable carbon isotope data show expansion of C₄ grasslands in this area (Aucour & Hillaire-Marcel 1993, Aucour et al. 1994). A slight climatic amelioration, marked by some expansion of montane forest at ca 14 000 yr BP, is also observed around Muchoya and Ahakagyezi Swamps in the Rukiga Highlands (Taylor 1990). In the region of Congo, the forest underwent major expansion from ca 12 000 yr BP (Giresse & Lanfranchi 1984).

The period 12 400 to 10 000 yr BP marked a time of climatic transition, with rising temperatures and an increasingly moist climate; details remain unclear, and there were probably large climatic fluctuations such as a brief return to arid conditions just prior to 10 000 yr BP (Coetzee 1967, Flenley 1979a,b, Hamilton 1982). Progressive humidity is observed during the terminal Pleistocene in Lake Abiyata (Lézine 1982). In the Mt. Elgon area the forest began to spread and diversify due to a moistening climate, culminating in the establishment of mesic montane forest by 9000 yr BP (Hamilton 1987). At ca 12 000 yr BP forest appeared in the Pilkington Bay (Lake Victoria) area, and declined shortly at ca 10 000 yr BP (Kendall 1969). Around Lake Bogoria, there was a decline in Gramineae and Cyper-

aceae, while Pteridophytes and arboreal pollen increased; the latter included the Combretaceae, *Phoenix*, *Podocarpus*, *Olea* and *Macaranga*, while *Juniperus* and *Myrica* became rare (Vincens 1986). At this time, the Lake Naivasha region was characterised by an *Olea-Podocarpus* assemblage, with *Myrica*, *Rapanea*, *Celtis*, *Pygeum*, and *Artemisia* (Maitima 1991), indicating a succession of forest vegetation, and suggesting a wet climate (Maitima 1988). Although the continued occurrence of *Anthospermum*, *Artemisia* and *Stoebe* pollen between 13 800 and 11 000 yr BP indicates that the Ericaceous belt vegetation was still present around Muchoya, the abundance of *Hagenia* and Urticaceae pollen from ca 12 000 yr BP, and the contemporaneous establishment of *Hagenia*-dominated woodland around Ahakagyezi, indicates an expansion of moist forest types and an altitudinal elevation of vegetation belts resulting from temperature and precipitation increases (Taylor 1990). Further increases in temperature are indicated in the Muchoya and Ahakagyezi pollen spectra at ca 11 100 and 10 600 yr BP, when moist lower montane forests became established at the sites (Taylor 1990). At Muchoya Swamp in southwest Uganda, *Hagenia* forest was re-established at ca 11 000 yr BP (Morrison 1968). The δ¹³C data show an increase in C₃ plants (Aucour & Hillaire-Marcel 1993, Aucour et al. 1994). Open forest began to be established at 12 000 yr BP around the north basin of Lake Tanganyika, achieving its maximum development and diversity at about 10 000 yr BP, while the forests and the Afroalpine belt vegetation regressed considerably, attaining, by 10 000 yr BP, a position close to that observed today (Vincens 1989a). Around the south basin of Lake Tanganyika, montane forest communities abruptly retreated at 12 000 yr BP, whereas the Zambezi woodlands greatly expanded and diversified (Vincens 1989b). These changes occur within the context of a climatic amelioration, primarily related to temperature increases (Vincens 1989a,b).

3.4.4. 10 000 to 0 yr BP

From 10 000 to 4000 yr BP, climatic changes are evidenced by major alterations in plant communities. In Sacred Lake, forest pollen types become exceedingly dominant from 10 560 to ca 6000 yr BP, and marked declines in Ericaceous zone pollen occur (Coetzee 1967, van Zinderen Bakker & Coetzee 1972). A pollen spectrum from the Galana Boi Beds of the northeast Lake Turkana basin is characterised by montane forest and thicket taxa not found in modern pollen; these pollen are thought to have been transported to the lake by rivers originating in the Ethiopian Highlands, suggesting both increased runoff and an extension of the

highland forests (Owen et al. 1982). This, coupled with the high percentage of Pteridophytes, suggests increased rainfall over the catchment (Owen et al. 1982). The local elements are dominated by herbaceous pollen, notably Gramineae and Compositae, and arboreal forms are uncommon (Owen et al. 1982). However, the occurrence of more humid vegetation types near the lake (compared to present vegetation) suggest an increase in rainfall, measuring at least 200 mm yr⁻¹ above the modern average (Vincens 1989c). During the early Holocene at Cherangani, the lowest part of the Ericaceous belt, with *Stoebe* dominant, became established. The Lake Naivasha pollen sequence shows that the vegetation established at ca 12 070 yr BP persisted until ca 6500 yr BP (Maitima 1991). At ca 6500 yr BP tree taxa such as *Rapanea* and *Pygeum* disappeared from the Lake Naivasha pollen record, while *Podocarpus* and *Olea* became more abundant, and *Alchemilla* appeared in the record, with higher percentages of Chenoams and *Amaranthus*, indicating that dry conditions were initiated at this time (Maitima 1991). At Pilkington Bay, the forest returned after a short decline at ca 10 000 yr BP, and there was a shift from evergreen to semi-deciduous forest between 7000 and 6000 yr BP (Kendall 1969). From 6000 to 5000 yr BP, there is a pronounced resurgence of the *Hagenia* pollen curve in Sacred Lake (van Zinderen Bakker & Coetze 1972); the increase in *Hagenia* pollen values and the decrease in Gramineae suggest that forest was moving up the mountain as conditions became warmer and wetter (Street-Perrott & Perrott 1993).

In Kashiru, an important extension of montane forest occurred between ca 10 000 and ca 5000 yr BP (Roche & Bikwemu 1989). Morrison (1968) recorded a shift from moist montane *Hagenia* forest to a mixed montane or bamboo forest in Muchoya Swamp at ca 6000 yr BP, marked by a sharp decline in *Hagenia* and a sharp increase in Ericaceae, and explained this change as being possibly due to human influence, as interpreted in the nearby Butongo Swamp (M. E. S. Morrison unpubl. data), where *Polyscias* (and *Olea*) succeeds *Hagenia* abruptly, and *Polyscias fulva* (a well-known tree of secondary succession with a short life span of 40 yr or less) persists through 9 m of lake sediment. However, the Butongo sequence was not radiocarbon dated. Around the north basin of Lake Tanganyika, an increase in rainfall is inferred at 10 000 yr BP from the pollen spectrum and is supported by a great increase in fern pollen, transported also by rivers and streams (Vincens 1989a). This wet and warm phase characterised a major part of the Holocene around the northern basin of Lake Tanganyika (Vincens 1989a).

By the middle Holocene, climatic conditions in the Turkana region had become more comparable with

those at present, based on the pollen assemblages, which are dominated by Gramineae, with rare arboreal taxa (Owen et al. 1982). From the Lake Baringo site, increases in *Podocarpus*, *Juniperus* and *Olea* and the development of *Acacia* and *Dodonea* are observed at ca 4500 yr BP and from 2500 yr BP to the present, while those characteristic of high altitude forest, such as *Hagenia abyssinica*, *Hypericum*, *Stoebe*, and Eriaceae no longer occur (Vincens 1986). There are no indications of lowland forest in the Lake Naivasha region after ca 4000 yr BP (high values of the relatively high-export pollen types *Podocarpus* and *Olea* are recorded in the pollen sequence and are thought to be far travelled), and the climate was hot and dry (Maitima 1991). Perrott (1982a,b) observed that a sharp increase in *Podocarpus* pollen (which signifies the onset of drier conditions), dated at ca 3720 yr BP at Kimilili Lake (Mt. Elgon), correlates to that observed from the Hobley Valley mire of Mount Kenya (4265 m a.s.l.). From 5000 to 3285 yr BP, pollen of montane forest species become dominant at Sacred Lake, and *Hagenia* pollen is almost absent; warm, wet conditions, marked by pollen of wetter montane forest, e.g. *Afrocrania*, *Prunus* and *Neoboutonia* (Street-Perrott & Perrott 1993), reached a maximum at about 4000 yr BP (van Zinderen Bakker & Coetze 1972). The sharp rise in *Podocarpus* pollen shortly after 4000 yr BP (Street-Perrott & Perrott 1993) correlates with a similar rise in the Hohnel Valley mire, marking the onset of drier conditions (Perrott 1982b). From 3285 yr BP to present, very high values of *Podocarpus* and other montane forest elements (e.g. *Olea*, *Macaranga*, *Pygeum*, *Neoboutonia*, *Galiniera* and *Celtis*) indicate the development of the Dry Montane Rain Forest (Coetze 1967, Street-Perrott & Perrott 1993). From ca 4620 yr BP much higher humidities are recorded on Mount Kilimanjaro, during which time the forest at the Cherangani site reached its maximum (Coetze 1967). This has been explained by a temperature rise which caused the clouds to be formed at a higher altitude than at present (Coetze 1967). Hamilton et al. (1986) note increases in *Podocarpus*, *Olea* and *Syzygium* pollen at Ahakagezi Swamp between 3500 and 3600 yr BP. However, Taylor (1990) observed that expansions of dry forest taxa around Ahakagezi and Muchoya occurred after ca 3900 and 3400 yr BP respectively. In Kashiru Swamp, a significant extension of Gramineae and Eriaceae, accompanied by a decline of all forest elements except *Podocarpus*, *Maytenus* and *Hypericum*, occurred (Roche & Bikwemu 1989). Roche & Bikwemu (1989) noted a cold and dry period centred around 2500 yr BP in the Kashiru area. In the region of Congo, a slight trend towards aridity is evident from 3000 yr BP south of the equator (Giresse & Lanfranchi 1984). From 2500 yr BP a progressive degradation of the

arboreal cover and a concomitant development of Gramineae is observed in the north basin of Lake Tanganyika and is related to an increasingly dry climate and possibly to human interference (Vincens 1989a). However, traces of cultures or plantations are seen only in the surface sediments of the cores, where rare pollen such as *Elaeis guineensis* (wild oil palm) occurs (Vincens 1989a).

3.5. Southern Africa

Floristic Zones XI, XII, XIII, XIV. Climate south of 15° S is subtropical and semi-arid. Summer rainfall is greatest in the north and east in association with subtropical convection in close proximity to warm sea surface temperatures. The southwest Cape region experiences a Mediterranean-type climate with winter rain during May to July and summer drought from November to January due to influence of westerly air streams.

3.5.1. >22 000 yr BP

In general, scarcity of radiocarbon dates and uncertain age determinations only allow questionable inferences to be made on vegetation history of the period before 25 000 yr BP (Scott 1990). No single detailed palaeovegetation record exists for the whole Quaternary, but shorter pollen profiles show marked shifts in modern phytoclimata in response to glacial-interglacial changes in climate (Scott et al. 1997). More specifically, the vegetation changes in southern Africa comprised wide shifts in biome composition and boundaries, attributed to orbitally related fluctuations in temperature, precipitation and seasonal distribution patterns of moisture (Scott et al. 1997). The 190 000 yr pollen sequence from the Tswaing Crater (the Pretoria Saltpan), although discontinuous in places (15 000 to 21 000, 25 000 to 31 000 and 80 000 to 150 000 yr BP), is the longest Quaternary sequence from South Africa (Scott 1999). The record shows marked cycles of vegetation change in South Africa's savannah biome, with pollen types ranging between *Podocarpus* forest pollen, warm woodland savannah elements, dry savannah elements and cool or temperate shrubland (fynbos) elements (Scott 1999). The pollen data from the Tswaing Crater have been compared with that of the nearby Wonderkrater sequence (Scott 1999) and the following climatic inferences made: 2 moderately warm and 2 cool phases occurred between 190 000 and 150 000 yr BP; between ca 80 000 and ca 33 000 yr BP, 3 warm pulses, relative to the generally cooler conditions from 33 000 to 11 000 yr BP, are recorded.

3.5.2. 22 000 to 14 000 yr BP

Large areas around the south Tanganyika basin (773 m a.s.l.) were occupied by dry montane forest vegetation (*Podocarpus*, *Olea*, *Juniperus* and *Eriaceae*, today located above 1600 m) from 25 000 to 12 000 yr BP, and the Zambezi woodlands were greatly reduced, with *Brachystegia* and some Euphorbiaceae as the main arboreal components, suggesting cool and dry climatic conditions (Vincens 1989b). In Lake Ishiba Ngandu, Zambia, a pollen record (Livingstone 1971) shows that the vegetation was characterised by grassland with Ericaceous elements, and some montane forest genera like *Podocarpus*, *Olea* and *Myrica*. Further south in the Wonderkrater sequence of northern Transvaal, a cold phase with an estimated temperature drop of 5 to 6°C is inferred to have occurred sometime between 25 000 and 11 000 yr BP (Scott 1990). The cold phase is associated with relatively humid climates, except for the coldest period, which corresponds with a dry spell (Scott 1990). In the upland grasslands of the eastern Orange Free State, more fynbos and swamps occurred under wet conditions at ca 23 000 yr BP, followed by slightly drier conditions between 22 600 and 20 000 yr BP, then considerably drier and cooler climates from ca 20 000 to 18 000 yr BP (Scott 1990). In general, pollen evidence for this period shows that a considerable depression of vegetation belts occurred, displacing upland grasslands and shrublands to areas presently occupied by tropical savannah (Scott 1984, 1990).

3.5.3. 14 000 to 10 000 yr BP

In general, temperatures ameliorated and precipitation increased from about 14 000 yr BP in southern Africa (Scott et al. 1997). Montane forest communities around the south Tanganyika basin abruptly retreated at 12 000 yr BP, whereas the Zambezi woodlands greatly expanded and diversified (Vincens 1989b). These changes occur within the context of a climatic amelioration, primarily related to temperature increases (Vincens 1989a,b). Diatom analysis of a 40 000 yr record from Lake Chesi, Zambia, indicates that maximum shrinkage and chemical concentration of the lake occurred between 15 000 and 13 000 yr BP (Stager 1988). In the Transvaal bushveld, tropical savannah elements began increasing from 11 000 yr BP (Scott 1990). There is no clear evidence of cooling in the pollen records of South Africa for the period 11 000 to 10 000 yr BP (the Younger Dryas), although oceanic cooling probably occurred off the coast of South Africa (Scott et al. 1995). The available data suggest that the Younger Dryas had no distinct counterpart in the inte-

rior of southern Africa, or at least that an effect was not large enough to show up in the fossil pollen record (Scott et al. 1995).

3.5.4. 10 000 to 0 yr BP

Rainfall declined markedly in the early Holocene, but by 7000 yr BP, the biomes of southern Africa began to reflect modern conditions (Scott et al. 1997). Sediments from areas north of 28° S show prominent tropical woodland pollen, indicating that the period between 7000 and 6500 yr BP was associated with optimal temperatures during the Holocene (Scott 1993). Generally, the advent of moister conditions in southern Africa during the early to mid-Holocene is recorded earlier (7500 to 6500 yr BP) in the north at ca 26° S than around 31° S (5000 yr BP), and this is provisionally associated with a relative shift in seasonality from a predominance of all-season precipitation to a greater proportion of summer rainfall (Scott 1993). The increase in tropical savannah elements in the Transvaal bushveld, from 11 000 yr BP through to 6500 yr BP, suggests a gradual warming and drying (Scott 1990). A return to wetter conditions is marked by increasing prominence of Combretaceae and other broad-leaved savannah elements before 6500 yr BP, and related patterns of change have been found in the southern Kalahari (Scott 1990). The Namib desert was more grassy at ca 6500 yr BP, and moister conditions at that time are supported by pollen data from hyrax middens from the Kuiseb river (Scott et al. 1997).

Holocene vegetation at Lake Ishiba Ngandu consisted of grassland with tropical woodland elements (Livingstone 1971). Lake Cheshi, Zambia, levels were exceptionally high between 8000 and 4000 yr BP (Stager 1988). Grassland has been the dominant vegetation on the Nyika plateau, Malawi, for the past 4500 yr, reflecting the contemporary vegetation pattern of small patches of montane forest in a sea of montane grassland (Meadows 1984). The driest part of the Holocene in southern Africa seems to have been the early Holocene. Particularly cool intervals in southern Africa occurred around 2800, 1600 and 300 yr BP (Little Ice Age) (Lindesay 1998). Human impact on vegetation is recorded from about 1500 yr BP (Scott et al. 1997).

4. SUMMARY: TEMPORAL PROFILE OF VEGETATION CHANGE IN AFRICA

Most vegetation records in Africa do not extend beyond 30 000 yr BP, except for a few from the humid tropics, such as Sacred Lake, Mount Kenya (Coetzee

1967, Street-Perrott et al. 1997, Olago et al. 1999), and Muchoya Swamp, Rukiga Highlands (Taylor 1990). Excluding the finer details unique to each site or region, there are broad generalisations that can be made for the period 30 000 yr BP to present.

From 30 000 to 22 000 yr BP, correlation of vegetation changes throughout the continent is not clear-cut; however, most sites are interpreted as having been cooler and less humid than at present. Highland vegetation was depressed to lower altitudes relative to their positions today, and grasslands became more widespread while lowland forests became increasingly fragmented in the humid tropics. These changes are primarily attributed to lower temperatures related to progressive global cooling. The last glacial maximum (LGM) period from 22 000 to 14 000 yr BP marks a time of high coherency in vegetation change throughout the African continent. This period, generally the coolest and most arid, marked the maximum depression and fragmentation of high altitude vegetation, maximum fragmentation of lowland forests, maximum extension of grasslands in the humid tropics, and maximum extension of the subtropical deserts. The period from 14 000 to 10 000 yr BP is viewed as a time of climatic amelioration, with rising temperatures and higher humidity. Depressed highland vegetation moved back up in altitude, lowland forests expanded, grasslands retreated, desert and semi-arid areas receded in spatial extent, etc. The record of these responses, however, are not well synchronised across the continent and are largely dependent on regional factors such as topography and aspect, and on the altitude and latitudes of the sites investigated. The maximum expression of humid vegetation types was manifested during the early Holocene, between 10 000 and 8000 yr BP, except in southern Africa, where it took place a little later. Drier conditions set in at about 4000 yr BP in equatorial and northern Africa, and vegetation types and distribution established at that time remain so today.

The palaeovegetation changes in Africa have been attributed largely to changes in temperature, and secondarily to changes in precipitation. However, uncertainties still exist. For example, it has been noted that the estimates of tropical sea surface temperatures by CLIMAP (1981) and temperatures derived from adjacent land areas during the LGM are inconsistent (2°C vs 4 to 7°C respectively) (Rind & Peteet 1985, Guilderson et al. 1994). The lower limits of the estimated temperature changes derived for East Africa recently using pollen transfer functions (e.g. Bonnefille et al. 1990, Vincens et al. 1993), however, do overlap with the upper limits of the CLIMAP (1981) temperature estimates, within the limits of uncertainty. Polar ice cores have, in addition, provided evidence of large

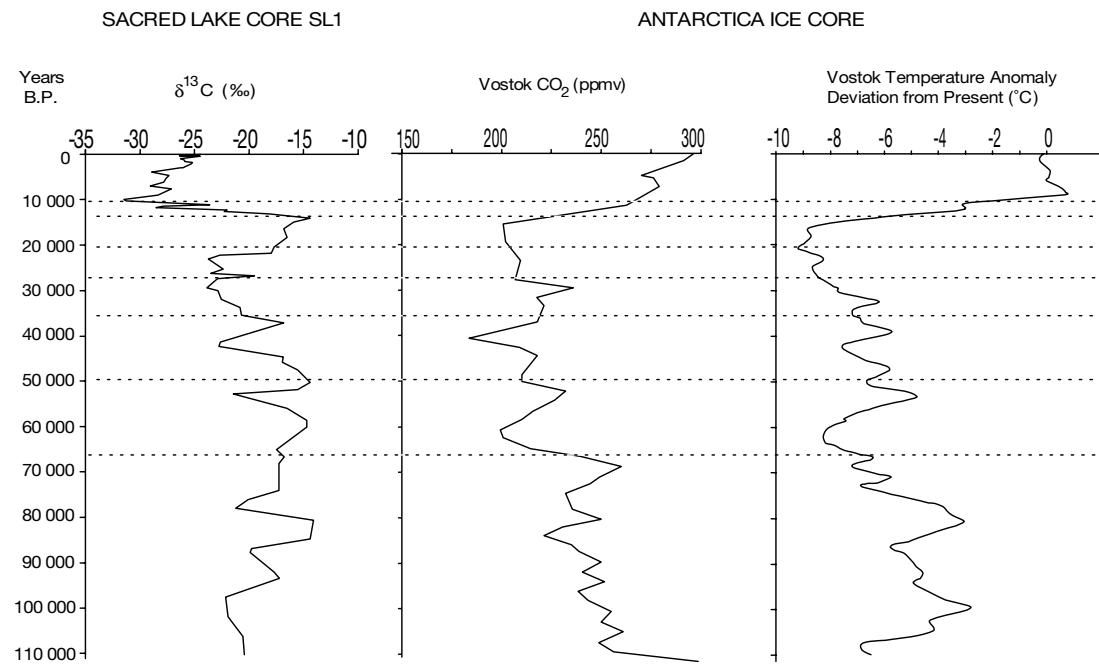


Fig. 6. Sacred Lake stable carbon isotope record versus Vostok ice core record

changes in the concentrations of the atmospheric greenhouse gases CO_2 and CH_4 through geological time (Delmas et al. 1980, Stauffer et al. 1984, Barnola et al. 1987, Chappellaz et al. 1990, Jouzel et al. 1993) extending back to 250 000 yr ago in the case of the Vostok ice core (Jouzel et al. 1993). The gases vary in phase, and correlate well with temperature changes (Jouzel et al. 1993). Changes in the concentrations of these gases provide a strong climate feedback mechanism: Lorius et al. (1990) and Chappellaz et al. (1990) estimated that ca 50% of the Vostok temperature change over the last climate cycle may be accounted for by contributions from CO_2 and CH_4 (with a feedback factor of 3.5 owing to changes in atmospheric water vapour, clouds, and snow and ice cover) while most of the other 50% may be accounted for by the growth and decay of northern hemisphere ice sheets. Palaeoclimate modelling experiments (COHMAP Members 1988) also suggest that the changes in atmospheric CO_2 and CH_4 concentrations are sufficient to drive large variations in summer monsoon rainfall in the low latitude regions.

Fig. 6 shows the similarity of the bulk stable isotope values of the Sacred Lake profile and the Vostok ice core CO_2 and temperature profiles. An elaborate explanation, arguing for changes in atmospheric CO_2 contents as being the primary driver of vegetation change in the tropics, and not temperature as previously supposed, has been advanced, arising from re-

sults obtained on bulk and compound-specific analysis of organic sediments from Sacred Lake and other supporting lines of evidence (Olago 1995, Huang et al. 1995, Street-Perrott et al. 1997, Olago et al. 1999). Periods of low precipitation/aridity tend to accentuate the effect of lower atmospheric CO_2 (Olago 1995, Olago et al. 1999). These data suggest that temperature estimates for the last glacial maximum in the tropics are most probably too high, and that the role of precipitation changes in influencing vegetation dynamics is enhanced by low atmospheric CO_2 concentrations. These conclusions are supported by results from a process based vegetation model simulating the response of montane vegetation in Kashiru, East Africa, to changes in atmospheric CO_2 concentration and climate (Jolly & Haxeltine 1997). On a longer time scale, the vegetation changes on Mount Kenya respond to the precessional cycle: the 23 000 yr cycle is attributed largely to precessionally driven changes in atmospheric CO_2 concentrations (Olago et al. 2000). Higher precessional harmonics are also evident: the 11 500 yr cycle (indicated by both mineral magnetics and $\delta^{13}\text{C}$ trends) is related to the twice yearly passage of the sun across equatorial sites (Short et al. 1991), and thus reflects the effect of the seasonality of rainfall (twice yearly) on Mount Kenya (Olago et al. 2000). The data underline the importance of long-term orbital forcing and its impact on tropical vegetation through cyclic modulation of atmospheric trace gases and precipitation.

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