Vegetation Response to Climatic Change in Central Rift Valley, Kenya

JOSEPH MWORIA MAITIMA

Department of Zoology, Duke University, Durham, North Carolina 27706, and Palynology Department, National Museums of Kenya, P.O. Box 40658 Nairobi, Kenya

Received September 6, 1988

Pollen analysis of a 15.5-m sediment core from Lake Naivasha, central Rift Valley of Kenya, reveals that the vegetation from before 20,290 to nearly 12,000 yr B.P. was dominated by open grasslands, indicating arid conditions. Within this period a moderately wetter climate existed between 17,000 and 15,000 yr B.P., shown by relatively slight increase in both the montane and lowland forest vegetation. From approximately 12,000 to 6500 yr B.P., a change toward more trees and forests started at lower altitudes around the basin of Lake Naivasha, and later in the higher montane regions. After 6000 yr B.P. a decline in forest and lowland trees opened the vegetation into more grasslands and by 4000 yr B.P. a vegetation similar to the present was attained and has persisted to the present. During this period shallow-water aquatic plants became abundant in Lake Naivasha.

INTRODUCTION

The climate of East Africa for the last 30,000 yr, includes a prolonged period of aridity and low temperatures indicated by low lake levels, reduced forests, and widespread grasslands, until about 13,000 yr B.P., possibly interrupted by a moist episode around 17,000 yr B.P. (Harvey, 1976; Livingstone, 1980). Since 13,000 yr ago, the climate became increasingly wet, reaching a climax in the ninth millennium B.P. (Bakker and Coetzee, 1969; Street and Grove, 1976). Gradual desiccation followed, often associated with temperature increases. Hamilton (1982) speculates that the glaciations he designates I and II may date to 18,000 and shortly before 11,500 yr B.P., respectively. From a core at about 3800 m in the summit region of Oldoinyo Lesatima in the Nyandarua Mountains, Perrott and Street-Perrott (1982) infer that glaciation occurred shortly before 12,200 yr B.P.

In the central Rift Valley of Kenya, a trend toward warmer and wetter conditions at approximately 12,500 yr B.P. coincided with deglaciation at higher altitudes (Hamilton, 1982). A short period of cooler and drier conditions occurred about 10,500–10,000 yr B.P. (Washbourn, 1975; Richardson, 1966). A return to warm moist conditions after 10,000 yr B.P. which probably lasted until 5600 yr B.P. or later (Butzer, *et al.*, 1972; Richardson and Richardson 1972), is indicated by a rise in lake levels. The three Rift Valley lakes in the area of the present study (Fig. 1) have been low and intermittent since that time; evidence suggests that maximal Holocene aridity occurred in these basins between 4000 and 3000 yr B.P. (Richardson and Richardson, 1972).

The evidence for these statements is drawn from four main sources: (1) geological and microfossil data on changes in lake levels in the Rift Valley (Richardson, 1966; Richardson and Dussinger, 1986; Washbourn, 1975); (2) pollen records largely from montane lake sediments of East Africa (Bakker, 1964; Coetzee, 1964; Livingstone, 1967, 1975); (3) documented changes in the altitude and distribution of perennial ice cover and analysis of glacial deposits in montane regions (Hastenrath, 1984; Mahaney, 1988; Osmaston, 1958, 1965); and (4) data obtained from the present distribu-

0033-5894/91 $3.00

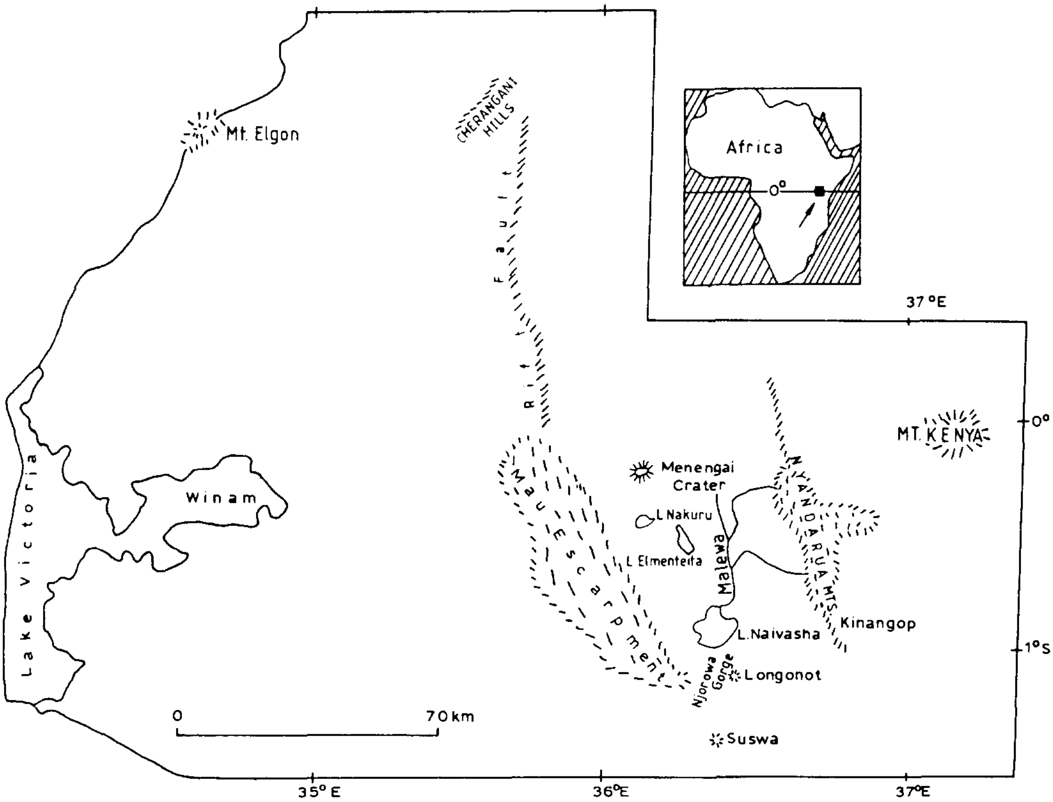

FIG. 1. Map showing the central Rift Valley of Kenya.

tion of the African flora (primarily forest) and fauna.

While much has been done, some general gaps exist. For example, most pollen assemblages come from montane environments and little is known about Quaternary changes in the woodland or grassland plant communities below an altitude of 2100 m, or the mixed *Olea* (olive)-*Tarchonanthus* (leleswa)-*Acacia* (mostly fever tree) communities of forest savanna ecotone of central Rift Valley between 2000 and 2300 m (Ambrose, 1984).

This paper presents results of a palynological analysis of a 15.5-m sediment core from Lake Naivasha (Fig. 1) in the central Rift Valley of Kenya. The core spans a little more than the last 20,000 years. The record is long enough to include the last glacial maximum in temperate latitudes and the switch to interglacial conditions at about 12,000 yr B.P. (Hamilton, 1982). The record also covers the period of maximum rainfall in East Africa at approximately 9000 to 5000 yr B.P., a time marked by high lake levels in lakes Naivasha, Nakuru, and Elmenteita.

STUDY AREA

The central Rift Valley of Kenya is an area of moderate altitude that resulted from formation of the rift. The area forms a catchment for the drainage from two extensive forest stands on both margins of the rift; the Nyandarua Mountains on the east rise to about 3960 m and Mau Escarpment on the west to above 3000 m. The catchment presently includes three lakes: Naivasha, Nakuru, and Elmenteita (Fig. 1).

Lake Naivasha located at 0° 45′S and 36° 20′E has an altitude of 1890 m. It has no outlet at present but is thought to have discharged during the middle Holocene through Njorowa Gorge to the south (Richardson and Richardson, 1972). Several rivers feed the lake from the north, where the Malewa River forms the main inlet (Fig. 1). The lake has an average depth of about 4 m; a maximum depth of 7.6 m was recorded in 1957. An area of about 120 km^2 and a shoreline of approximately 50 km were recorded in 1968 (Melack, 1979). Lake Naivasha receives drainage from higher parts of the valley floor in the Kinangop Plateau and also from the montane regions of the Nyandarua Mountains and the valley floor east of the lake. To the south, Mt. Longonot, Mt. Suswa (Fig. 1), and other smaller volcanoes form a barrier which is broken by Njorowa Gorge.

CLIMATE AND MODERN VEGETATION

Lake Naivasha lies within the range of the Intertropical Convergence Zone. Prevailing winds are from the east and northeast. Mt. Kenya and Mt. Nyandarua capture most of their rainfall from the monsoons and cast a significant rainshadow over the central rift, particularly over the Naivasha basin, the central part of which receives less than 500 mm of precipitation per year (Ambrose, 1984). The floor of the rift is mildly warm and dry, while the higher reaches of the escarpments are increasingly cold and wet. Rainfall and temperature, which are closely correlated with altitude, are altered by the rainshadow cast by the mountains east of the rift. In the central rift temperature decreases with altitude at a rate much faster than precipitation increases (Ambrose, 1984).

Where natural vegetation remains, the floor and the flanks of the central Rift Valley between about 1500 and 1890 m are characterized by open to densely wooded *Acacia* savanna grasslands, and annual rainfall is less than 600 mm. From 1980 to 2290 m, a mixed *Olea-Tarchonanthus-Acacia* bush becomes common at the montane forest–savanna ecotone, and rainfall is over 600 mm. A closed montane sclerophyll forest of *Juniperus* and *Podocarpus* extends from 2290 to 2600 m, with bamboo in wet areas above 2400 m; in this zone annual rainfall ranges from 800 to 1600 mm. Open moorland with stands of forest and bamboo occurs above 2600 m, where rainfall is over 1600 mm (Ambrose, 1984).

MATERIALS AND METHODS

Lake sediments analyzed in this study were subsamples of a 15.5-m-long core raised from the main portion of Lake Naivasha by J. L. Richardson and P. Waiswa in 1969–1970, using a modified Livingstone piston sampler (coring procedures described by Wright *et al.*, 1965) and shipped to Richardson's laboratory in Pennsylvania. Samples weighing about 0.5 g each, and collected at 20 cm intervals along the core, were processed following the procedure described by Faegri and Iversen (1975). The procedure involved treatment with 10% HCl, 5% KOH, acetolysis mixture (Erdtman, 1960) and HF (52% hydrofluoric acid) to remove carbonates, humic acids, cellulose, and silica, respectively. From every sample processed, three pollen slides were prepared for pollen count, each consisting of 30 μl of pollen residue embedded in liquid glycerin and a coverslip sealed at the edges with conformal coating. Pollen counts were made at 400× magnification using a Leitz Ortholux microscope with apochromatic objectives. Oil immersion at 900× and 950× magnification were used to identify unfamiliar pollen grains.

Identification of pollen grains was based on comparison with modern pollen and photographic collections in the laboratory of D. A. Livingstone at Duke University, reference to published pollen atlas (Bonnefille, 1971; Bonnefille and Riollet, 1980), and pollen-type descriptions (Heusser, 1971; Kingham, 1976; Ferguson and Strachan, 1982). At least 500 pollen grains were counted from each sample, except in a few samples where preservation was poor. Generally samples from levels with much sand and ash had very few or no pollen, resulting in gaps in the pollen diagram. Pollen grains were identified at various taxonomic levels. In most cases identification was made at generic level such as *Acalypha,* and in one case two pollen types belonging to one genus were identifiable, i.e., *Olea* fine reticulate and *Olea* wide reticulate. Several pollen types could be identified only at family level, e.g., in Compositae, and in one case pollen could be identified belonging to either Chenopodiaceae or Amaranthaceae (Cheno/Am.). A total of 87 pollen types were identified. Pollen counts were entered into a Radio Shack TRS-80 model II microcomputer using COREPLOT program (Tucker and Tucker, 1985). Using the coreplot, separate pollen diagrams were plotted based on terrestrial pollen sum and aquatic pollen sum.

Pollen deposition rates were calculated using the method described by Kendall (1968) in which the number of pollen grains counted in a known volume of pollen residue is used to calculate the total pollen contained in the sample processed and is then expressed as number of pollen grains deposited per square centimeter per year.

CHRONOLOGY

Five radiocarbon dates (Fig. 2) were obtained for the core from Teledyne Isotopes, Inc. by J. L. Richardson. The rate of sediment accumulation, calculated by dividing the length of the sediment accumulated by the number of years between ^{14}C dates, was

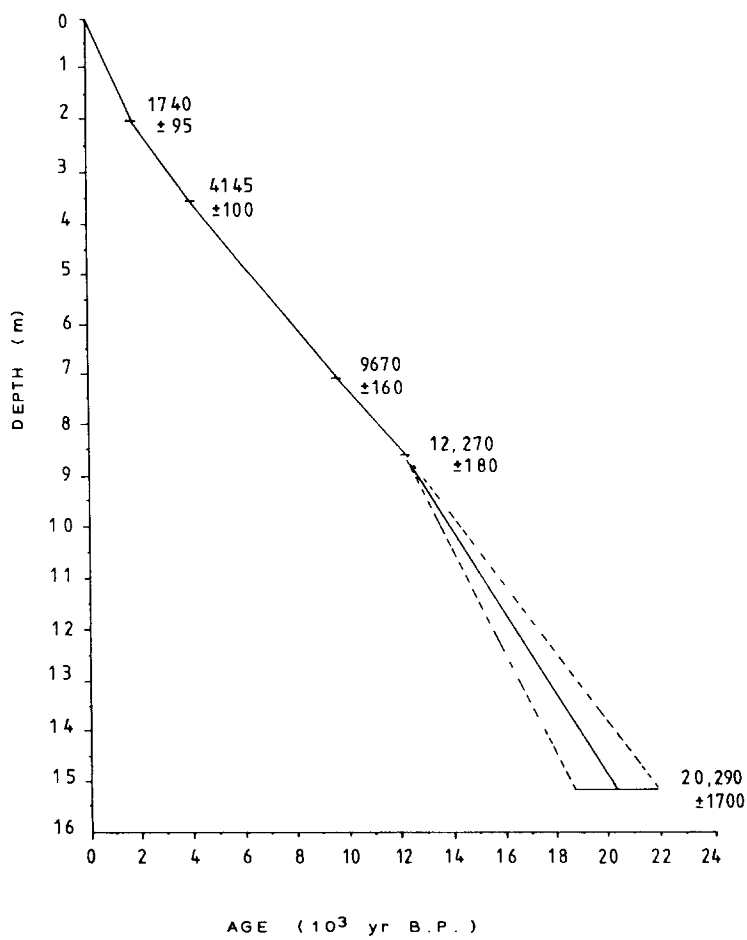

FIG. 2. Plot of ^{14}C dates vs depth in the Naivasha core.

nearly twice as high between 0 and 1740 yr B.P. (0.115 cm/yr) as between 1740 and 12,270 yr B.P. It was quite constant within the later time period. Between 1740 and 4145 yr B.P. the sedimentation rate was 0.062 cm/yr; between 4145 and 9670 yr B.P. its rate was 0.063 cm/yr and between 9670 and 12,270 B.P. the rate was over 25% higher (0.081 cm/yr). A diagram of the implied changes in sedimentation rates is shown in Figure 2 with the radiocarbon chronology.

POLLEN STRATIGRAPHY

From the 15.5-m core, 39 stratigraphic levels found to contain sufficient pollen were analyzed for their pollen taxa counts. A plot of relative percentages of 25 major terrestrial pollen taxa is presented in Figure 3. Relative percentages of pollen taxa in the aquatic pollen sum and pollen influx calculated as number of pollen grains deposited per year per cm^2 of sediment surface are shown in Figures 4 and 5, respectively.

The diagrams have been divided into two distinctive pollen zones (Zone I and Zone II); each zone was further divided into subzones (a, b, and c). Identification of zone and subzone boundaries was based entirely on pollen assemblages as they appear on the diagram. Although zonation was not based on the sedimentary stratigraphy, there appears to be a relationship between the pollen zone boundaries and the nature of sediment. At four out of five zone boundaries pollen preservation is poor; gaps in the pollen diagram are at levels where samples did not contain pollen. The pollen of *Sesbania* (Papilionaceae) show no significant stratigraphic changes in the entire core.

Zone I extending from a little before 20,290 to about 12,270 yr B.P., is characterized by high percentages of *Cheno/Am.*, *Compositae*, and *Anthospermum* (Rubiaceae). In this zone *Olea* (Olive) pollen, both fine and wide reticulate types, and *Podocarpus* pollen were low. Subzone Ia dating from before 20,290 to approximately 18,000 yr B.P. has an assemblage dominated by Gramineae, *Cheno/Am.*, *Chenopodium*, *Compositae*, and *Sesbania*. This assemblage has very low percentages of *Podocarpus* and *Olea* fine reticulate pollen; wide reticulate *Olea* is completely absent. Subzone Ib, from about 18,000 to 14,700 yr B.P., has an assemblage showing increase in pollen percentages for most taxa. *Anthospermum*, *Hagenia* (Rosaceae), *Vernonia* (Compositae), *Acalypha* (Euphorbiaceae), *Aeschynomene* (Papilionaceae), and *Celtis* (Ulmaceae) start to appear in the pollen sum, while *Podocarpus* and wide reticulate *Olea* show higher percentages. Toward the end of this period there is a sudden drop in both *Olea* pollen types, *Celtis*, Compositae, *Blepharis* (Acanthaceae), *Hagenia*, and *Anthospermum*. Subzone Ic, approximately 14,700 to 12,270 yr B.P., shows a reverse of the trend in the previous subzone Ib. A return to an assemblage more similar to that in Ia is observed. *Podocarpus* and *Olea* pollen fall to trace amounts, while *Celtis*, *Blepharis*, and *Anthospermum* disappear altogether.

Zone II representing 12,270 yr B.P. to present, is characterized by higher proportions of both wide and fine reticulate pollen types of *Olea* and *Podocarpus*. Subzone IIa, 12,270 to probably 6500 yr B.P., is dominated by fine reticulate *Olea* pollen, with relatively higher percentages of *Aeschynomene* (Ambach), *Artemisia*, *Celtis*, *Rapanea*, and the first and the only presence of *Pygeum* pollen. During this period Cyperaceae pollen shows relatively lower percentages. Subzone IIb, approximately 6500 to 4000 yr B.P., shows much higher proportions of *Podocarpus*, *Olea* fine and wide reticulate, and Liliaceae pollen types. It is within this period that *Nymphaea* and *Alchemilla* pollen appear in the record, and *Cheno/Am.*, *Amaranthus*, and *Chenopodium* rise to higher proportions after being nearly absent in the previous subzone. Subzone IIc, from 4000 yr B.P. to present, also contains abundant *Olea* and *Podocarpus*, but is distinguished from IIb

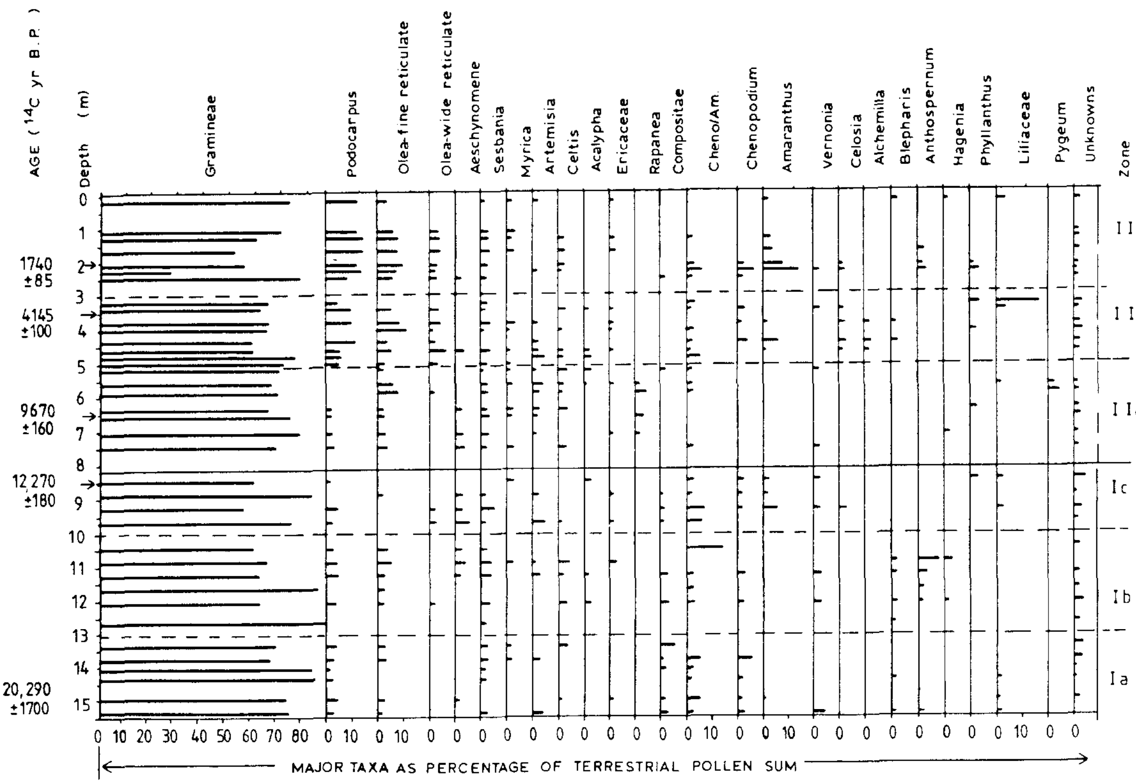

FIG. 3. Pollen diagram showing major terrestrial taxa of the Lake Naivasha core.

by higher percentages of *Cheno/Am.*, *Chenopodium, Amaranthus, Celtis, Phyllanthus,* and Nymphaea pollen, by reappearance of *Anthospermum* pollen, and by reduced proportions of all other pollen taxa.

INTERPRETATIONS

In both terrestrial and aquatic pollen sums (Figs. 3 and 4) the high percentages of Gramineae and Cyperaceae pollen, respectively, obscure the importance of other types. Unfortunately, both pollen types are not distinguishable beyond family level. *Sesbania* pollen show no stratigraphic changes in the entire core, probably due to river-transport and lake-shore contributions, because *Sesbania* species recorded in the Rift Valley are components of lake-shore, swamp, and riverine vegetation.

The stratigraphic boundary that separates zones I and II of the pollen diagram falls at about 12,270 yr B.P. The higher percentages of *Olea* and *Podocarpus* pollen in zone II distinguishes it from zone I. Zone II could therefore be characterized as an *Olea-Podocarpus* zone. Species of both *Podocarpus* and *Olea* are wind-pollinated and their pollen have a wide dispersal range. *Podocarpus* has such a wide dispersal range that Coetzee (1967) warns against interpreting proportions less than 20% in the pollen sum as an indication of a nearby *Podocarpus* forest. Three species, *Podocarpus gracilior* Pilger, *Podocarpus milanjianus* Rendle, and *Podocarpus usambarensis* Pilger, are now abundant in the highland forests above 2100 m, and have a discontinuous distribution below this altitude. On the other hand, two species of *Olea* (*Olea africana* Mill. and *Olea hochstetteri* Baker) are widespread in woody grasslands and drier upland forests. Comparing the proportions of *Olea* and *Podocarpus* pollen in both zones I and II does suggest a source much farther than present from before 20,290 to about 12,270 yr B.P. (zone I), implying a reduction in the extent of montane forest through a rise of

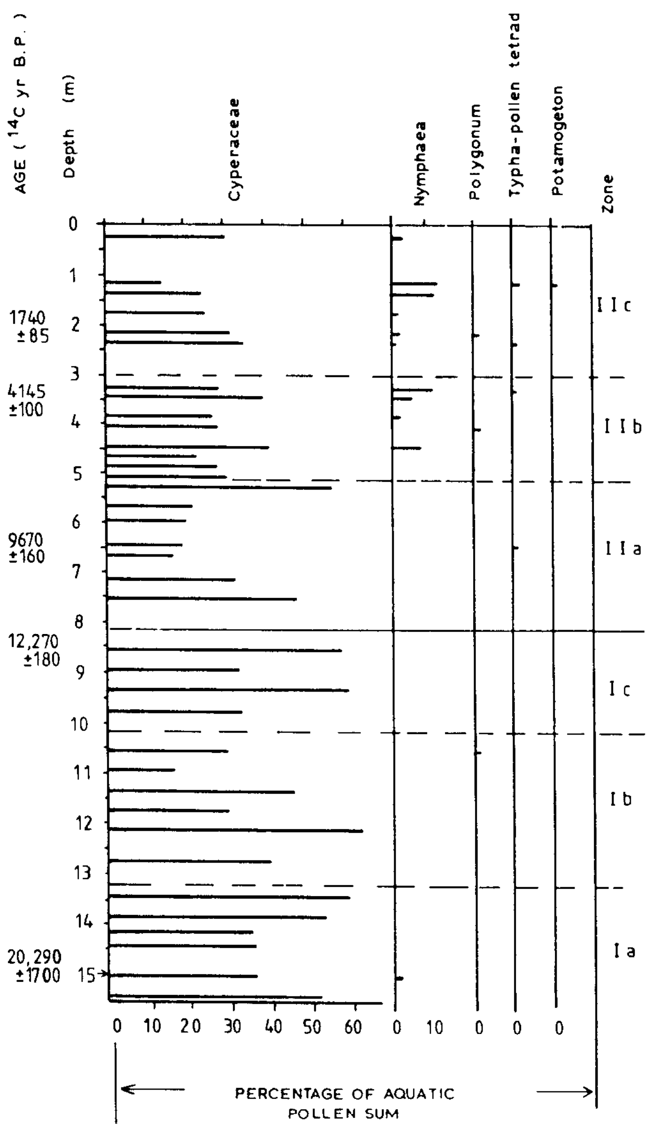

FIG. 4. Pollen diagram showing aquatic taxa of the Lake Naivasha core.

its lower margin to considerably higher altitudes. During this period, prominent terrestrial pollen types other than Gramineae were *Cheno/Am.*, Compositae, *Anthospermum,* and *Aeschynomene*. These taxa, except the Ambach which is a component of lake shore vegetation, are indicators of dry conditions (Coetzee, 1964, 1967; Kendall, 1969; Livingstone, 1971). High abundance of Ambach pollen, when accompanied by other indicators of dry conditions, may indicate exposed lake flats or shallow waters because all the modern species in the study area are found in water along lake margins, river banks, or in seasonal and permanent swamps. The relatively higher percentages of Cyperaceae pollen in zone I may have been due to local production in exposed lake margins and possibly a wider dispersal range because of a reduced tree canopy cover.

The prolonged period of aridity in zone I appears to have been interrupted by a short episode of moderately wet climate between

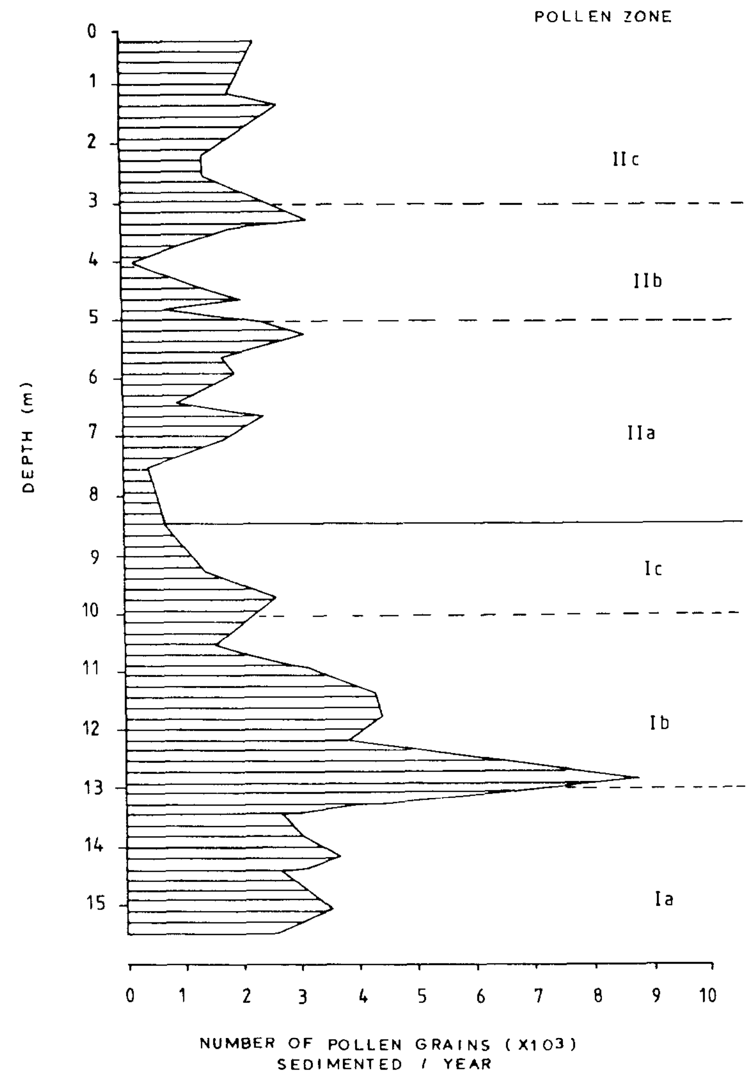

FIG. 5. Pollen deposition in Lake Naivasha.

approximately 17,000 and 15,000 yr B.P. represented in the diagram by subzone Ib. The slightly higher percentages of the forest taxa *Podocarpus, Olea, Celtis, Anthospermum,* and *Hagenia* compared to other subzones of zone I indicate a highland forest more widespread or closer to the Lake Naivasha basin. By comparison, the *Anthospermum* pollen type encountered in this study was similar to that of *Anthospermum herbaceum* L.f. in the pollen collection (Maitima, 1988), which is presently found in edgerows and short grass on the Nyandarua Mountains (Dale and Greenway, 1961). The higher percentages of *Anthospermum* pollen during this period, and the presence of *Hagenia* pollen, the only strictly montane type in Naivasha pollen record, confirms a moderate expansion of montane forest, possibly with its lower margin being closer to the floor of central Rift Valley. The relatively lower percentages of *Cheno/Am.* pollen during this wet phase could be due to a reduction in local production as higher lake levels reoccupied formerly exposed flats.

From 15,000 to 12,270 yr B.P. (subzone Ic) the pollen assemblage shows a return to dry conditions similar to those in subzone Ia. Pollen stratigraphy in subzone Ia is similar to that of subzone Ic in taxa composition except for the additional presence of *Artemisia* pollen in Ic, and lower proportions of *Podocarpus* and both fine and wide reticulate *Olea* pollen. *Artemisia* pollen was reported by Hamilton (1982), Kendall (1969), and Coetzee (1967) as an indicator of dry conditions. In the central Rift Valley of Kenya, *Artemisia afra* Willd. is found in the dry shrubby montane grasslands (Agnew, 1974). The decline of Ambach pollen, which increased in proportions during the wet phase of subzone Ib, was probably due to reduced lake margins, swamps, and rivers.

Subzone II begins at approximately 12,270 yr B.P. and extends to the present. This zone can be characterized as an *Olea-Podocarpus* pollen zone due to the abundance of these types in the stratigraphy. This zone starts with a pollen assemblage that displays an increase in forest vegetation, as shown in subzone IIa (12,270 to approximately 6500 yr B.P.) by the pollen of *Olea* (fine reticulate type), *Rapanea, Celtis, Myrica* (Myricaceae), *Pygeum* (Rosaceae), and *Artemisia.* The increase in *Myrica* and *Artemisia* pollen, which are indicators of dryness in the montane forest (Hamilton, 1982; Coetzee, 1967), indicates a dry forest in the Nyandarua Mountains. The pollen of *Rapanea* (Myrsinaceae) and *Pygeum* indicate a forest or more closed vegetation on the valley floor. *Rapanea pulchra* Gilg and Schellenb., *Rapanea rhododendroides* (Gilg) Mez, and *Pygeum africanum* Hk.f. are recorded by Dale and Greenway (1961) as common tree components in the forest of Nyandarua Mountains. During this period of subzone IIa, the pollen of *Cheno/Am., Amaranthus, Chenopodium,* and Cyperaceae are in relatively lower percentages, probably due to a reduction in local production as the exposed dry lake flats are covered by water. The pollen assemblage in subzone IIa indicates wet conditions.

At about 6500 yr B.P. *Podocarpus* pollen joined that of *Olea* in dominating the tree pollen record while other tree components like *Rapanea* and *Pygeum* disappear altogether. For the first time, pollen of *Alchemilla* (Rosaceae) appears in the record during this period. Despite the increase in *Podocarpus* and *Olea* pollen, this assemblage indicates dry conditions, due to the decline of all other tree taxa, especially those in the lowlands. *Alchemilla* pollen was reported by Coetzee (1967) to indicate warmer conditions at high altitudes when the pollen of other indicators of the same conditions and open vegetation are present. Higher percentages of *Cheno/Am., Amaranthus,* and *Chenopodium* indicate a dry period. *Nymphaea* (Nympheaceae) pollen which appears to be prominent in the aquatic pollen sum during this period, is an indication of low lake levels (Kendall, 1969) because it is a rooted aquatic plant. Liliaceae, mostly grassland herbs (Agnew, 1974), made a significant contribution to the terrestrial pollen sum during this period and could be interpreted as an indication of widespread grasslands. These observations therefore indicate a dry period between 6500 and 4000 yr B.P.

From 4000 yr B.P. to present (subzone IIc) there is no indication of a lowland forest. The highland forest was dry and much less abundant. Higher proportions of *Nymphaea* pollen and absence of *Aeschynomene* indicate reduced lake levels and more open lake shore vegetation. This assemblage suggests a dry and hotter climate than that of previous subzone IIb.

DISCUSSION

The paleoecology of East Africa is now broadly understood from the initial palynological investigations of Bakker (1964), Coetzee (1964, 1967), Livingstone (1962, 1967, 1971, 1975), Morrison (1968), and Kendall (1969) who have inferred that glacier retreat in East Africa was roughly coincident with that of Europe and Americas.

Butzer *et al.,* (1972) and Perrott and

Street-Perrott (1982) document changes in the levels of East African lakes. Lake Nakuru reached levels much lower than present until about 12,500 yr B.P., with a slightly higher stand between approximately 12,500 and 10,000 yr B.P. Richardson and Richardson (1972) report that Lake Naivasha discharged to the south through the present Njorowa Gorge prior to 5650 and 3040 yr B.P. There followed a sudden drop in water level to near dryness until 1000 yr B.P. when the lake attained the present level (Richardson and Dussinger, 1986). These changes in the level of Lake Naivasha have been determined by the analysis of diatoms and ostracode stratigraphies. Palynological data are useful in augmenting the limnological records in reconstructing the paleoecology and climatic changes of lake basins.

The pollen diagram from Lake Naivasha is largely dominated by grass pollen, which unfortunately cannot be differentiated beyond family level. The only information that can be obtained from grass pollen in this study is that relatively higher percentages indicate more open vegetation, and lower percentages with higher proportions of tree pollen may indicate a more closed vegetation. There is a high correlation between the vegetation changes reported in this study and the climatic patterns of the central Rift Valley described by other workers. The major vegetational change that separates zone I and zone II pollen assemblages falls at a time when lake levels in the central Rift Valley, and even Lake Victoria, rose significantly (Kendall, 1969; Richardson and Dussinger, 1986), montane vegetation records imply a shift to wetter conditions (Bakker, 1964; Coetzee, 1964; Livingstone, 1967), and glacial moraines were formed in the Nyandarua Mountains (Hastenrath, 1984; Hamilton, 1982; Perrott and Street-Perrott, 1982). Zone I of the Naivasha pollen record, interpreted as a dry period and possibly punctuated by a short moderately wet episode, corresponds to a period of reduced water level in Lake Naivasha (Richardson and Dussinger, 1986). The early to middle Holocene high lake levels correspond to the wetter period of subzone IIa in the pollen stratigraphy. Richardson and Richardson (1972) explain the higher altitude replacement of dry montane forest by moist tropical forest after 5600 yr B.P. to be due to temperature increase being greater than precipitation increase, leading to an increase in evapotranspiration rates at lower altitudes. Subzone IIb shows a trend to more open lowland vegetation and widespread moist highland forest.

The climatic changes observed by Kendall (1969) at Pilkington Bay in northern Lake Victoria basin correlate for most part with those of the central Rift Valley reported here. The Naivasha pollen diagram (Fig. 3), however, gives no evidence of a vegetation change about 10,000 yr B.P. that Kendall observed for Lake Victoria. There also is no evidence of a temperature change about this time in the pollen diagram from the Ruwenzori (Livingstone, 1967); while there were vegetation shifts on the Cherangani Hills, it is not clear whether they were due to fluctuations of temperature or moisture (Bakker, 1964). A similar correlation of the Naivasha pollen record can be made with the montane zones of Mount Kenya and Cherangani Hills (Coetzee, 1964; Bakker, 1964). Sediment discontinuity and inconsistency of radiocarbon chronology of the records from Lake Abiyata in Ethiopia (Lezine, 1982; Lezine and Bonnefille, 1982) make it difficult to compare the pollen stratigraphy from that area with the Naivasha record.

The Lake Naivasha pollen record has produced evidence of a brief wetter or moister period between about 17,000 and 15,000 yr B.P. (subzone Ib). A pollen diagram from Sacred Lake at 2440 m on Mt. Kenya was interpreted by Coetzee (1967) as indicating dry conditions due to a high incidence of *Artemisia* pollen in the corresponding zone T (Coetzee, 1967). Pollen records from Kaisungor Swamp at 2900 m on the Cherangani Hills (Bakker, 1964; Hamilton, 1982) and from Laboot Swamp at 2880 m on Mt. Elgon (Hamilton, 1982) indicate an arid climate during this period, whereas interpretations of diatom and ostracode assemblages from Lake Naivasha indicate relatively higher lake levels during this time. It is difficult to explain the climatic implications of the Naivasha pollen record, especially between 17,000 and 15,000 yr B.P., due to the lack of sufficient paleoecological data from lowland East Africa. More palynological data are needed from middle- and low-altitude localities to understand local vegetation shifts in response to climatic change, and to permit comparisons with the better-known patterns from montane areas.

Pollen influx rates show that more pollen was deposited during dry periods, which may have been due to a relative increase in grasses and more effective wind dispersal in the more open vegetation. The pattern of changes in pollen deposition are closely related to the observed pollen zonation. This similarity shows that the changes in pollen assemblages are due to changes in the vegetation and not to sedimentation processes.

In conclusion, the vegetation changes in Lake Naivasha basin show a period of aridity from before 20,290 to approximately 12,270 yr B.P., possibly interrupted by a short wetter interval at about 17,000 yr B.P. A wet phase from 12,270 to 6500 yr B.P. caused an expansion of forests, creating a woody vegetation around Lake Naivasha. A dry climate between 6500 and about 4000 yr B.P. reduced the forest and increased grasslands. Between 4000 yr B.P. and the present the climate has been hot and dry.

ACKNOWLEDGMENTS

Throughout this study I have received invaluable advice and assistance from D. A. Livingstone and D. A. Burney. D. A. Livingstone read the original manuscript and made many useful suggestions. I thank J. L. Richardson for allowing me to use subsamples from his core for this study. The work was supported by grants from Wenner-Gren Foundation, L.S.B. Leakey Foundation, and the Graduate school of Duke University. The study was done using facilities provided by the National Science Foundation in the Laboratory of D. A. Livingstone in the Department of Zoology, Duke University.

REFERENCES

Agnew, A. D. Q. (1974). "Upland Kenya Wildflowers, A Flora of Ferns and Herbaceous Flowering Plants of Upland Kenya." Oxford Univ. Press, London/New York.

Ambrose, A. S. (1984). "Holocene Environments and Human Adaptations in the Central Rift Valley, Kenya." Unpublished Ph.D. dissertation, University of California, Berkeley.

Bakker, E. M. van Z. (1964). A pollen diagram from equatorial Africa, Cherangani, Kenya. *Geologie en Mijnbouw* **43,** 123–128.

Bakker, E. M. van Z., and Coetzee, J. A. (1969). A re-appraisal of late Quaternary climatic evidence from tropical Africa. *Palaeoecology of Africa* **7,** 151–181.

Bonnefille, R. (1971). Atlas des pollens D'Ethiopie: Principales Especes des forets de montagne. *Pollen et Spores* **13**(1).

Bonnefille, R., and Riollet, G. (1980). "Pollens des savannes d'Afrique Orientale." Editions du centre National de la Recherche Scientifique.

Butzer, K. W., Isaac, G. L., Richardson, J. L., and Washbourn-Kamau, C. (1972). Radiocarbon dating of East African lake levels. *Science* **175,** 1069–1076.

Coetzee, J. A. (1964). Evidence for a considerable depression of the vegetation belts during the upper pleistocene on the East African Mountains. *Nature (London)* **204**(4958), 564–566.

Coetzee, J. A. (1967). Pollen analytical studies in East and Southern Africa. *Palaeoecology of Africa* **3,** 1–146.

Dale, I. R., and Greenway, P. J. (1961). Kenya Trees and shrubs. *Buchanans Estate.*

Erdtman, G. (1960). The acetolysis method. A revised description. *Svensk Botanisk Tidskrift* **54,** 561–564.

Faegri, K., and Iversen, J. (1975). "Textbook of Pollen Analysis," 3rd ed. Blackwell Oxford.

Ferguson, I. K., and Strachan, R. (1982). Pollen morphology and taxonomy of the tribe Indigofereae (Leguminosae: Papilionoideae). *Pollen et spores* **24**(2).

Hamilton, A. C. (1982). "Environmental History of East Africa: A Study of the Quaternary." Academic Press, London.

Harvey, T. J. (1976). "The Paleolimnology of Lake Mobutu Sese Seko, Uganda-Zaire: The Last 28,000 Years." Unpublished Ph.D. dissertation, Duke University.

Hastenrath, S. (1984). "The Glaciers of Equatorial East Africa." Reidel, Dordrecht.

Heusser, C. J. (1971). "Pollen and Spores of Chile." University of Arizona Press, Tucson, AZ.

Kendall, R. L. (1968). "An Ecological History of

Lake Victoria Basin." Unpublished Ph.D. dissertation, Duke University.

Kendall, R. L. (1969). An ecological history of Lake Victoria basin. *Ecological Monographs* **39**, 121–176.

Kingham, D. L. (1976). A study of the pollen morphology of tropical African and certain other Vernonia (Compositae). *Kew Bulletin* **3**, 9–26.

Lezine, A. M. (1982). Etude palynologique des sediments quaternaires du lac Abiyata (Ethiopie). *Paleoecology of Africa* **14**, 93–98.

Lezine, A. M., and Bonnefille, R. (1982). Holocene pollen diagram from a core in Lake Abiyata (Ethiopia, 7° 42′ North). *Pollen et Spores* **24**(3–4), 463–480.

Livingstone, D. A. (1962). Age of Deglaciation in the Ruwenzori Range, Uganda. *Nature (London)* **194**, 859–860.

Livingstone, D. A. (1967). Postglacial vegetation of Ruwenzori Mountains of equatorial Africa. *Ecological Monographs* **37**, 25–52.

Livingstone, D. A. (1971). A 22,000 year pollen record from the plateau of Zambia. *Limnology and Oceanography* **16**, 349–356.

Livingstone, D. A. (1975). Late Quaternary climatic change in Africa. *Annual Reviews of Ecology and Systematics* **6**, 249–280.

Livingstone, D. A. (1980). Environmental changes in the Nile headwaters. *In* "The Sahara and the Nile" (M. A. J. Williams and H. Faure, Eds.), pp. 339–359. A.A. Balkema, Rotterdam.

Mahaney, W. C. (1988). Holocene glaciers and paleoclimate of Mount Kenya and other East African Mountains. *Quaternary Science Reviews* **7**, 211–225.

Maitima, J. M. (1988). "History of Vegetation in the Central Rift Valley, Kenya." Unpublished M.A. thesis, Duke University.

Melack, J. M. (1979). Photosynthetic rates in four tropical African fresh waters. *Freshwater Biology* **9**, 555–571.

Morrison, M. E. S. (1968). Vegetation and climate in the uplands of southwestern Uganda during the late pleistocene period. *Journal of Ecology* **56**, 363–384.

Osmaston, H. A. (1958). "Pollen Analysis in the Study of the Past Vegetation and Climate of Ruwenzori and its Neighbourhood." Unpublished B.Sc. thesis, Oxford University.

Osmaston, H. A. (1965). "The Past and Present Climate and Vegetation of Ruwenzori and its Neighbourhood. "Unpublished Ph.D. thesis, Oxford University.

Perrott, R. A., and Street-Perrott, F. A. (1982). New evidence for a late Pleistocene wet phase in northern intertropical Africa. *Palaeoecology of Africa* **14**, 57–75.

Richardson, J. L. (1966). Changes in level of Lake Naivasha, Kenya, during postglacial times. *Nature (London)* **209**, 290–291.

Richardson, J. L., and Richardson, A. E. (1972). The history of an African Rift lake and its climatic implications. *Ecological Monographs* **42**, 499–534.

Richardson, J. L., and Dussinger, R. A. (1986). Paleolimnology of mid-elevation lakes in the Kenya Rift Valley. *Hydrobiologia* **143**, 167–174.

Street, F. A., and Grove, A. T. (1976). Environmental and climatic implications of late Quaternary lake-level fluctuations in Africa. *Nature (London)* **261**, 385–390.

Survey of Kenya (1970). "Atlas of Kenya." Government Printers, Nairobi.

Tucker, V. A., and Tucker, A. E. (1985). A microcomputer data management program for plotting pollen diagrams. *Pollen et Spores* **27**, 277–288.

Washbourn, C. K. (1975). Late Quaternary shorelines of Lake Naivasha, Kenya. *Azania* **10**, 77–92.

Wright, H. E., Livingstone, D. A., and Cushing, E. J. (1965). Coring devices for lake sediments, P. 4994-520. *In* "Handbook of Paleontological Techniques" (B. Kummel and D. Raup, Eds.). Freeman, San Francisco.