Palaeogeography, Palaeoclimatology, Palaeoecology (Global and Planetary Change Section), 97 (1992) 241–247
Elsevier Science Publishers B.V., Amsterdam

Development of grasslands and savannas in East Africa during the Neogene

T.E. Cerling

Department of Geology and Geophysics, University of Utah, Salt Lake City, Utah 84112, USA

(Received July 29, 1991; revised and accepted October 8, 1991)

ABSTRACT

Cerling, T.E., 1992. Development of grasslands and savannas in East Africa during the Neogene. Palaeogeography, Palaeoclimatology, Palaeoecology (Global and Planetary Change Section), 97: 241–247.

The development of savanna-type grasslands is a relatively recent phenomena in East Africa. The stable carbon isotopic composition of paleosol carbonates from fossil localities in East Africa show that C_4 vegetation was present by about 8–9 Ma but made up only a relatively small proportion of the total biomass. Although the proportion of C_4 vegetation increased in the Pliocene and Pleistocene there is no evidence for the development of virtually pure C_4 grasslands, as is characterized by tropical grasslands today, until Middle Pleistocene times. This has important implications concerning the evolution of mammals in Africa, including hominids.

Introduction

The stable carbon isotopic composition of modern soil carbonate and paleosol carbonate is an indicator of the proportion of C_4 photosynthesis in modern and ancient ecosystems (Cerling, 1984; Cerling et al., 1989; Quade et al., 1989a,b). The isotopic composition of C_3 plants, which are predominantly trees, shrubs, and cool season grasses ranges between about -23 to $-29‰$ (Deines, 1980; Ehleringer, 1988) and averages about $-26‰$ for pre-industrial (*ca.* pre-1850) conditions (Marino and McElroy, 1991). (The isotopic composition is reported in the permil (‰) notation where $\delta^{13}C = \{[(^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{standard} - 1\} \times 1000$ where the standard is the isotopic reference standard PDB. Oxygen isotopic values are calculated in an analogous manner where the standard is PDB for carbonates and SMOW for water.) C_4 plants are predominantly tropical (warm growing season) grasses and have a $\delta^{13}C$ values of about $-12‰$ (Deines, 1980; Marino and McElroy, 1991). The carbon isotopic composition of modern soil carbonate is enriched relative to soil respired CO_2 by 14–17‰ because of diffusion and isotopic equilibrium fractionation effects (Cerling, 1984, 1991; Cerling et al., 1989). Soil carbonate formed in the presence of a pure C_3 ecosystem has a $\delta^{13}C$ value of -10 to $-12‰$ compared to about $+2‰$ for soil carbonate formed under a pure C_4 vegetation (Cerling, 1984; Cerling et al., 1989). For $P(CO_2)$ values less than about 700 ppmV, which have been present since at least the middle Miocene, the above relationship is a valid analogy based on theoretical grounds (Cerling, 1991).

The term savanna is a useful one for describing open tropical vegetation, although it encompasses a wide range of vegetation types and has different meanings on different continents (Pratt et al., 1966; Sarmiento, 1984; Cole, 1986). Savannas are tropical ecosystems dominated by grasses and sedges, have strong seasonal development

Correspondence to: T.E. Cerling, Department of Geology and Geophysics, University of Utah, Salt Lake City, Utah 84112, USA

related to water stress, and may include woody species that do not form a continuous cover (Sarmiento, 1984). This definition includes the low and intermediate elevation ($< ca.$ 2500 m) grasslands with virtually no tree cover, and wooded (or bushed) grassland with up to 20% tree cover (Pratt et al., 1966). It excludes montane meadows and wetland ecosystems (boglands and swamps), both of which have abundant grasses. It also excludes closed canopy forest or woodland ecosystems. The dwarf shrub grassland of Pratt et al. (1966) is an open environment of the semi-arid regions of East Africa with a significant cover of grasses and is similar in many ways to the bushed grassland of Pratt et al. (1966) in the context of this paper.

Savannas grasses are predominantly C_4 grasses (Cole, 1986). The grasses that dominate East African savannas and semi-arid environments, such as *Andropogon, Aristida, Cenchrus, Chloris, Cymbopogon, Cynodon, Digitaria, Eragrostis, Eriochloa, Loudetia, Pennisetum, Setaria, Sporobolus*, and *Themida* (Vesey-Fitzgerald, 1973), are all C_4 grasses (Smith, 1982). In addition, most of the *Panicum* grasses of tropical Africa are C_4 grasses. C_4 grasses are found in forested settings only where the canopy is broken. C_3 grasses in Africa include montane and meadow grasses at relatively high altitudes (*Poa, Festuca*), and some grasses of wet bottomlands at low altitudes (*Phragmites, Typha, Oryza*); bamboo and primitive members of the Festuceae family, are C_3 grasses which can live in closed canopy tropical forests (Vesey-Fitzgerald, 1973). Virtually all trees and many shrubs use the C_3 photosynthetic pathway. However, many desert and semi-desert shrubs, including *Aloe, Euphorbia, Portulaca, Sanseveria*, use the C_4 pathway or the CAM pathway (Smith, 1982). CAM plants have carbon isotopic values intermediate between C_3 and C_4 plants.

Results and discussion

It is possible to use carbon isotopes to study the development of C_4 vegetation in paleoecosystems of East Africa. Savanna grasslands, wooded grasslands, and the dwarf shrub grasslands in East Africa have a significant amount of C_4 vegetation (Fig. 1), predominantly grasses. Modern soil carbonate from East Africa formed in these environments have $\delta^{13}C$ values from about -3 to $+1‰$ (Table 1) with the more positive values being from grassland soils. Soil carbonates formed under vegetation dominated by C_3 plants have $\delta^{13}C$ values from about -10 to $-12‰$. Soil carbonates are well preserved in the geologic record and can be used to reconstruct paleoecology (Quade et al., 1989a; Cerling and Hay, 1986; Cerling et al., 1988). Paleosols from many of the important fossil hominid localities of East Africa span the interval from about 16 Ma to the present and have been analyzed as part of this study. Ages and the stratigraphic context of Olduvai Gorge (Hay, 1976; Cerling and Hay, 1986), Laetoli (Hay, 1987; Curtis and Drake, 1987), the Turkana Basin (Cerling and Brown, 1982; McDougal, 1985; Brown et al., 1985; Brown and Feible, 1986; Cerling et al., 1988; Boshetto, 1988), the Baringo Basin (Hill et al., 1985, 1986),

TABLE 1

Stable carbon and oxygen isotopic composition of modern soil carbonates from savanna environments in East Africa. Standard deviation is for multiple analyses on different soils from the same locality.

Region	Elevation [a]	Vegetation type [b]	$\delta^{13}C$	$\delta^{18}O$
Koobi Fora, Kenya	350	dwarf shrub grassland	-2.7 ± 0.8	3.4 ± 1.2
Olduvai, Tanzania	1550	grassland	0.5 ± 0.5	0.3 ± 0.5
Laetoli, Tanzania	1800	wooded grassland	-3.2 ± 0.3	-1.7 ± 0.2
Nguu, Kenya	1050	wooded grassland	-2.9 ± 0.5	-3.3 ± 0.2
Baringo, Kenya	1600	wooded grassland	-1.3	-2.0
Simbi, Kenya	1800	wooded grassland	-1.2	-2.9

[a] approximate elevation in meters.
[b] using the classification of Pratt et al. (1966).

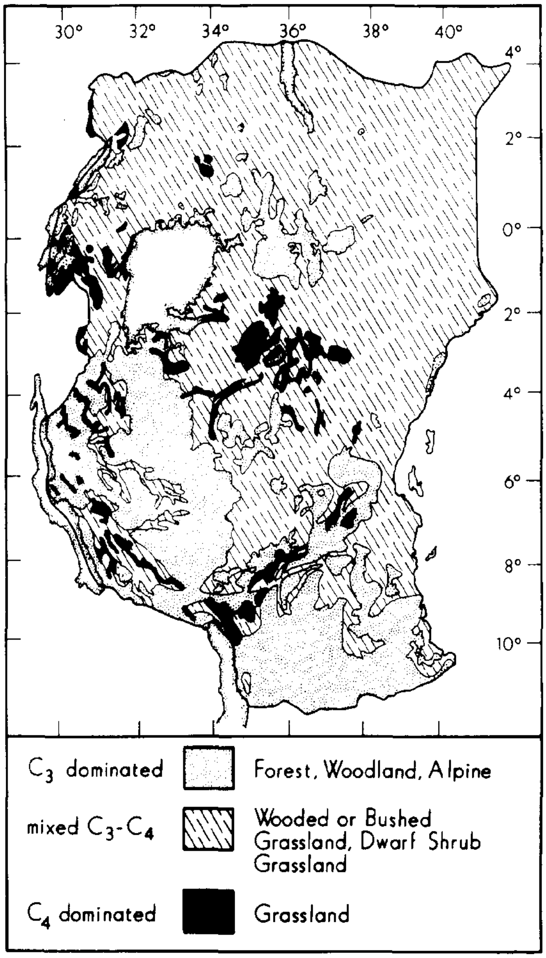

Fig. 1. Location map showing the modern distribution of vegetation types in East Africa. Vegetation distribution modified from Lind and Morrison (1974) and includes the vegetation types: grassland (dominantly C_4), desert shrub grassland and wooded grassland (mixed C_3/C_4), and forest and woodland (dominantly C_3).

Olorgesailie (Bye et al., 1987; Deino and Potts, 1990), and Fort Ternan (Shipman et al., 1981; Retallack et al., 1990; Cerling et al., 1991) have been previously described.

Paleosol carbonate in these sections is present as nodules and as rhizoliths in paleosol horizons. Paleosols were recognized by the presence of leached and bioturbated zones, and often showing evidence of clay cutans or development of color differentiation. Organic A-horizons were extremely rare. Leaching of carbonates from the upper parts of the soil often could not be used as a criteria of identification of these paleosols because of the lack of carbonate in the parent material of many of the paleosols; this was especially true when trachytic ash made up the parent material.

The carbon isotopic composition of carbonate from the paleosols shows an increase in the proportion of C_4 biomass present in the local ecosystem from the middle Miocene to the present (Fig. 2). Paleosols containing pedogenic carbonate older than about 10 Ma are uncommon and are found at Fort Ternan and near Lothidok in the Turkana Basin (Fig. 3). They have $\delta^{13}C$ values between -10 and -13‰, except for one very negative sample (*ca.* -15‰). These middle Miocene samples suggest that the local ecosystems were completely dominated by C_3 plants. The extremely negative values for paleosol carbonates from Fort Ternan are slightly more negative than modern soil carbonates formed under pure C_3 vegetation. Because co-existing paleosol organic carbon is also quite negative in the Fort Ternan paleosols it is likely that the soil formed under closed or nearly closed canopy conditions (Cerling et al., 1991) because under such conditions organic matter become quite depleted in ^{13}C (van der Merwe and Medina, 1989). The Fort Ternan site has been variously interpreted as representing environments ranging from forest to grassland (Shipman et al., 1981; Retallack et al., 1990; Cerling et al, 1991; Kappelman, 1991). This interpretation contrasts sharply with that of Retallack et al. (1990), who interpret the Fort Teman paleosols to indicate savanna grassland based on paleosol micromorphology.

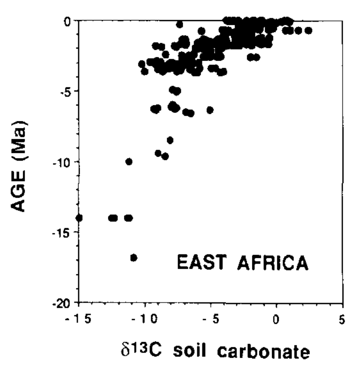

Fig. 2. Stable carbon isotopic composition of paleosol carbonate from East African fossil localities.

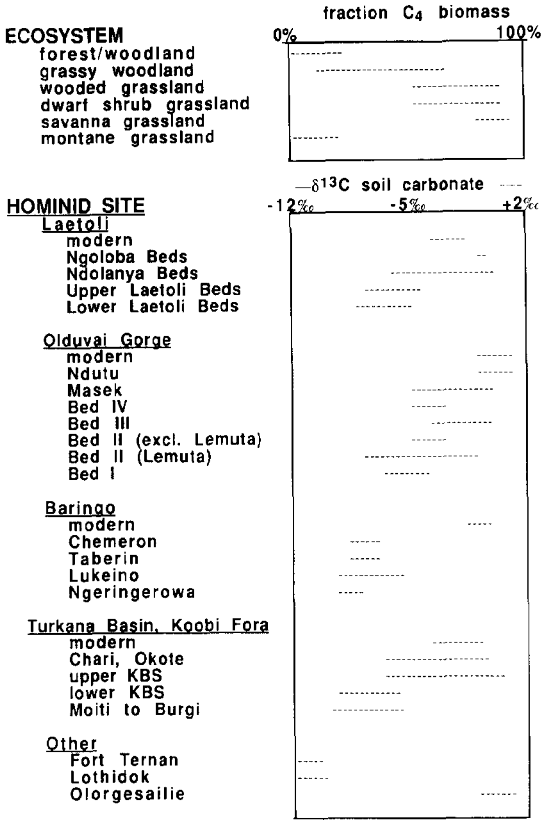

Fig. 3. Estimated C_4 biomass for modern East African ecosystems and fossil localities based on the carbon isotopic composition of paleosol carbonates. Summaries of the data for Olduvai Gorge, Koobi Fora, and Fort Ternan are found in Cerling and Hay (1986), Cerling et al. (1988), and Cerling et al. (1991), respectively. Data from Laetoli and the Baringo Basin, first presented here, are discussed in the text.

The oldest $\delta^{13}C$ values significantly more positive than $-10‰$ are from the Baringo Basin, indicating that C_4 plants were present by about 9.4 Ma. From about 9.4 to about 1.8 Ma $\delta^{13}C$ values for paleosol carbonates range from about -10 to $-5‰$, indicating that C_4 plants were an important part of the local ecosystem although they made up less than about 50% of the total photosynthesized biomass. This was true in both the Baringo and Turkana Basins, and at Laetoli (Fig. 3). Only one paleosol in the 9.4–1.8 Ma interval has $\delta^{13}C$ values significantly more positive than this: the striped calcrete from the Upper Ndolanya Beds at Laetoli has $\delta^{13}C$ of about $-1.5‰$ indicating a brief approach to a C_4 dominated ecosystem. The presence of C_4 biomass implies that the local ecosystems were open, but the relatively ^{13}C depleted carbonates indicate a vegetation more like a grassy woodland or grassy bushland for all of these localities.

At about 1.7 Ma there is a dramatic increase in the abundance of C_4 biomass in both the Turkana Basin and in Olduvai-Laetoli region, indicating C_4 abundances on the order of 60–80%. Although the stratigraphic position and relative ages of the paleosols within each sequence is well known, there are not yet precise correlations between the two sedimentary sequences so that I cannot say with certainty if the the increase in C_4 biomass was synchronous in the two regions, which are more than 1000 km apart. However, in both sequences the most ^{13}C enriched paleosol carbonates older than 1.4 Ma are about 1.7 Ma in age and the abundance of C_4 biomass as indicated by the ^{13}C content of paleosol carbonates decreased from the peak at 1.7 Ma to slightly lower values between 1.6 and 1.4 Ma.

After 1.4 Ma, the best record of the fraction of C_4 biomass comes from the Olduvai sediments. The Olduvai sequence provides evidence for high C_4 biomass at about 1.2 Ma, at about 0.6 Ma, and from 0.2 Ma to the present. The modern soil carbonates at Laetoli, Olduvai, and in the Turkana and Baringo Basins are the same as, or are more enriched in, ^{13}C than paleosol carbonates indicating that the modern ecologic setting is as rich, or richer, in C_4 biomass than has been found in the fossil record from these localities (Fig. 3). Prior to about 1.7 Ma ago none of these fossil localities had more than about 50% C_4 biomass present and while they may have been a somewhat open environment, were nothing like the grasslands or wooded grasslands of East Africa today. C_4 plants first became briefly dominant about 1.7 Ma ago and again at about 1.2 Ma, but only in the last 0.6 Ma have they consistently made up more than 50% of the biomass. This indicates that it is likely that the modern C_4 grasslands of East Africa are a relatively recent phenomena. The history of grassland development in East Africa contrasts sharply with that in Pakistan where there is evidence for continuous C_4 grasslands for the last 6 Ma (Quade et al. 1989a).

The oxygen isotopic composition of modern soil carbonate is well correlated with the isotopic composition of local meteoric water (Cerling, 1984), implying that the isotopic composition of soil carbonate is linked to local climatic conditions. In general, the most positive $\delta^{18}O$ values for precipitation are from hot and dry regions, while more negative values are associated with cooler and/or moister conditions. The bulk $\delta^{18}O$ value for modern atmospheric moisture is about $-9‰$ relative to SMOW. Soil moisture is determined by local infiltrating water and therefore it is to be expected that the isotopic composition is well correlated with the isotopic composition of local meteoric water. I believe that it is a mistake to apply the modern $\delta^{18}O$ versus local temperature relationship (Gat, 1980; Yurtsever and Gat, 1981) to the past because changes in global temperature and circulation patterns could significantly alter such patterns. However, the general trends for the isotopic composition of meteoric waters in the past were probably similar to those observed today.

The oxygen isotopic composition of paleosol carbonate from East Africa implies that some of the changes in ecology were related to climatic change, but that not all climatic change events resulted in the change in the fraction of C_4 biomass. When all of the sites are considered together, they show that the most ^{18}O depleted soil carbonates are found in sediments older than 6.5 Ma (Fig. 4). Unfortunately, I was not able to analyze any paleosols in the interval from 6.5 to about 8.5 Ma which is the interval where an important shift in the $\delta^{18}O$ of paleosol carbonates was found in Pakistan (Quade et al., 1989a).It is tempting to speculate that the shift in $\delta^{18}O$ in East Africa that occurred between 6.5 and 8.5 Ma was related to the shift observed on the Indian subcontinent at 8.0 Ma. The detailed record of $\delta^{18}O$ of paleosol carbonate from the Turkana Basin shows important positive excursions of ^{18}O at about 3.4 and 3.1 Ma (Cerling et al., 1988) which are not accompanied by shifts in the $\delta^{13}C$ value of paleosol carbonate. The $\delta^{18}O$ values for paleosol carbonates dramatically increases in the Turkana Basin at about 1.8 Ma, about 0.1 Ma before a dramatic increase in the $\delta^{13}C$ values, implying a significant change in the isotopic composition of soil water (and presumably soil moisture) prior to a major change in ecology that took place at about 1.7 Ma as documented by the shift in the $\delta^{13}C$ of paleosol carbonate. At Olduvai Gorge, the change in both $\delta^{18}O$ and $\delta^{13}C$ appear to be synchronous in time at about 1.7 Ma but there are only a few samples of paleosol carbonate in the period from 1.8 to 2.3 Ma.

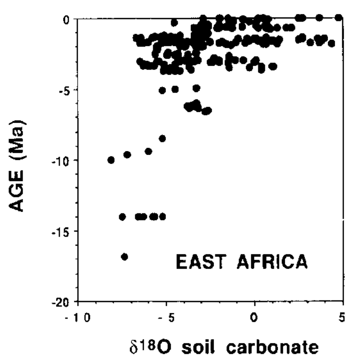

Fig. 4. Stable oxygen isotopic composition of paleosol carbonate from East African fossil localities.

At Olduvai, Baringo, Laetoli, and in the Turkana Basin, the $\delta^{18}O$ for modern soil carbonate is as positive, or more positive than for paleosol carbonates. This implies that the modern conditions for all three localities are probably as hot and dry as has been found in the geologic record.

The paleosol carbon isotopic of vegetation change in East Africa is independent from other methods for estimating paleo-ecologic conditions. However, it confirms the general trends of previous studies although it often differs in detail with respect to the interpretation of individual sites. Based on pollen analysis, Bonnefille (1984) interpreted East African vegetation to have been dominated by closed canopy forest in early Miocene, dry adapted forest and perhaps savanna in the Mid-Miocene, with the development of wooded grasslands and grasslands in the Pliocene and Pleistocene. Van Couvering (1980), using faunal analysis, notes a similar trend. Differences in interpretation are mainly in quantifying the importance of grasses in the local ecosystems. Bonnefille (1984) interprets Olduvai Beds I and II to be wooded grassland, whereas this analysis would imply that C_4 grasses made up 30–60% of the local biomass which would be more compatible with a grassy woodland or grassy shrubland (except during the Lemuta Member which briefly approached wooded grassland or dwarf shrub grassland conditions). Laetoli has been interpreted to be a wooded grassland similar to modern conditions today at Laetoli (Andrews, 1989); the stable carbon isotope approach would suggest that Laetoli was more wooded than today, which is in agreement with some (but not all) faunal arguments (Andrews, 1989). Fort Ternan has been variously interpreted to be everything between wooded grassland and forest (Shipman et al., 1981; Retallack et al., 1990; Cerling et al. 1991; Kappelman, 1991); the stable isotopic results are compatible with a forest or woodland interpretation. For most of the localities, the differences between these results are generally that the carbon isotopic results tends to favor less C_4 biomass than the other methods and hence less grass, assuming that all grasses are C_4 grasses.

Using the stable carbon isotopic composition of paleosol carbonate for paleoecologic studies differs from other methods of paleoecologic reconstruction. The carbon isotopic record integrates the proportion of carbon fixed annually by the two photosynthetic pathways, and it integrates this proportion over the lifetime of the soil. Furthermore, it distinguishes only between the C_3 photosynthetic pathway and the C_4 photosynthetic pathway. C_3 grasses, which today are found in the forest understory or in cool season growing conditions, are not distinguishable from other C_3 plants such as trees and shrubs. C_4 grasses are well adapted to heat and moisture stress and to low $P(CO_2)$ conditions (Elheringer, 1991). It is not known if extensive C_3 grasslands could have existed under higher atmospheric $P(CO_2)$ conditions. However, it is known that atmospheric $P(CO_2)$ has been similar to that today for the last 20 Ma (Cerling 1991). Therefore it is unlikely that the sites with a low proportion of C_4 biomass could have been long-lived grasslands.

There has been considerable speculation that evolution of African mammals, including hominids, in the Neogene was driven by ecologic changes, especially the development of grasslands and an open habitat (Vrba, 1985; Hill, 1987; Hill and Ward, 1988). These results suggest that the development of C_4 grasslands, which are so important in the modern East African landscape, was later than has been often supposed.

Conclusions

The carbon isotopic composition of paleosol carbonates from many of the important hominid localities in East Africa show that there has been a gradual increase in the proportion of biomass using the C_4 photosynthetic pathway over the last 10 Ma. This most likely indicates a replacement of woodland with progressively more C_4 grasses or other C_4 plants, although there is no evidence for a relatively pure C_4 grassland until about 1 Ma. These results suggest that the Serengeti-type grassland may be a relatively recent phenomena in East Africa. Oxygen isotopes in paleosol carbonates also indicate a gradual trend from the Miocene to the modern, and may indicate that the region was getting gradually drier through this time interval.

Acknowledgements

I thank B. Bochetto, F.H. Brown, B. Bye, R.L. Hay, A. Hill, J. Kingston, M.D. Leakey, R.E. Leakey, J. Quade, G.J. Retallack, and Y. Wang for assistance in the field and laboratory and for discussions. The NSF funded this work.

References

Andrews, P.J., 1989. Paleoecology of Laetoli. J. Hum. Evol., 18: 173–181.

Bochetto, H.B., 1988. Geology of the Lothidok Range. Thesis. Univ. Utah, Salt Lake City (unpublished).

Bonnefille, R., 1984. Cenozoic vegetation and environments of early hominids in East Africa. In: R.O. Whyte (Editor), The Evolution of the East Asian Environment. 2. *Palaeobotany, Palaeozoology, and Palaeonathropology*. Univ. Hong Kong, pp. 579–612.

Bonnefille, R. and Riollet, G., 1987. In: M.D. Leakey and J.M. Harris (Editors), *Laetoli: A Pliocene Site in Northern Tanzania*. Clarendon Press, Oxford, pp. 52–61.

Brown, F.H. and Feibel, C.S., 1986. Revision of lithostratigraphic nomenclature in the Koobi Fora region, Kenya. J. Geol. Soc. London, 143: 297–310.

Brown, F.H., McDougall, I., Davis, T. and Maier, R., 1985.

An integrated Plio-Pleistocene chronology for the Turkana Basin. In: E. Delson (Editor), *Ancestors: The Hard Evidence*. Liss, New York, pp. 82–90.

Bye, B.A., Brown, F.H., Cerling, T.E. and McDougall, I., 1987. Increased age estimate for the Lower Paleolithic hominid site at Olorgesailie, Kenya. Nature, 329: 237–239.

Cerling, T.E., 1984. The stable isotopic composition of modern soil carbonate and its relationship to climate. Earth Planet. Sci. Lett., 71: 229–240.

Cerling, T.E., 1991. Carbon dioxide in the atmosphere: evidence from Cenozoic and Mesozoic paleosols. Am. J. Sci., 291, 377–400.

Cerling, T.E. and Brown, F.H., 1982. Tuffaceous marker horizons in the Koobi Fora region and the lower Omo Valley. Nature, 299: 216–221.

Cerling, T.E. and Hay, R.L., 1986. An isotopic study of paleosol carbonates from Olduvai Gorge. Quat. Res., 25: 63–78.

Cerling, T.E., Bowman, J.R. and O'Neil, J.R., 1988. An isotopic study of a fluvial–lacustrine sequence: the Plio-Pleistocene Koobi Fora Formation, East Africa. Palaeogeogr., Palaeoclimatol., Palaeoecol., 63: 335–356.

Cerling, T.E., Quade, J., Wang, Y. and Bowman, J.R., 1989. Carbon isotopes in soils and paleosols as paleoecologic indicators. Nature, 341: 138–139.

Cerling, T.E., Quade, J., Ambrose, S.H. and Sikes, N., 1991. Fossil soils, grasses, and carbon isotopes from Fort Ternan: grassland or woodland? J. Hum. Evol., 21: 295–306.

Cole, M.M., 1986. *The Savannas: Biogeography and Geobotany*. Academic Press, London, 438 pp.

Deines, P., 1980. The isotopic composition of reduced organic carbon. In: P. Fritz and J.C. Fontes (Editors), *Handbook of Environmental Geochemistry. 1. The Terrestrial Environment*. Elsevier, Amsterdam, pp. 329–406.

Deino, A. and Potts, R., 1990. Single crystal dating of the Olorgesailie Formation, southern Kenya Rift. J. Geophys. Res., 95: 8453–8470.

Drake, R. and Curtis, G.H., 1987. K–Ar geochronology of the Laetoli fossil localities. In: M.D. Leakey and J.M. Harris (Editors), *Laetoli: A Pliocene Site in Northern Tanzania*, Clarendon Press, Oxford, pp. 48–52.

Ehleringer, J.R., 1988. Carbon isotope ratios and physiological processes in aridland plants. In: P.W. Rundel, J.R. Ehleringer and K.A. Nagy (Editors), *Applications of Stable Isotopic Ratios to Ecological Research*. Springer, New York, NY, pp. 41–54.

Ehleringer, J.R., Sage, R.F., Flanagan, L.B. and Pearcy, R.W., 1991. Climate change and the evolution of C_4 photosynthesis. Trends Ecol. Evol., 6: 95–99.

Gat, J.R., 1980. The isotopes of hydrogen and oxygen in precipitation. In: P. Fritz and J.C. Fontes (Editors), *Handbook of Environmental Geochemistry. 1. The Terrestrial Environment*. Elsevier, Amsterdam, pp. 21–47.

Hays, R.L., 1976. *Geology of the Olduvai Gorge*. Univ. Calif. Press, Berkeley, 203 pp.

Hay, R.L., 1987. Geology of the Laetoli area. In: M.D. Leakey and J.M. Harris (Editors), *Laetoli: A Pliocene Site in Northern Tanzania*. Clarendon Press, Oxford, pp. 23–47.

Hill, A., 1987. Causes of perceived faunal change in the later Neogene of East Africa. J. Hum. Evol., 16: 583–596.

Hill, A. and Ward, S., 1988. Origin of the Hominidae: The record of large hominoid evolution between 14 My and 4 My. Yearbook Phys. Anthropol., 31: 49–83.

Hill, A., Drake, R., Tauxe, L., Monaghan, M., Barry, J.C., Behrensmeyer, A.K., Curtis, G., Fine Jacobs, B., Jacobs, L., Johnson, N. and Pilbeam, D., 1985. Neogene paleontology and geochronology of the Baringo Basin. J. Human Evol., 14: 759–773.

Hill, A., Curtis, G.H. and Drake, R.E., 1986, Sedimentary stratigraphy of the Tugen Hills, Baringo District, Kenya. In: L.E. Frostick, R. Renaut, I. Reid, and J.-J. Tiercelin (Editors), *Sedimentation in the African Rift System*. Blackwell, Oxford, pp. 285–295.

Kappelman, J., 1991. The paleoenvironment of *Kenyapithecus* at Fort Ternan. J. Hum. Evol., 20: 95–129.

Lind, E.M. and Morrison, M.E.S., 1974. *East African Vegetation*. Longman, London. 257 pp.

Marino, B.D. and McElroy, M.B., 1991. Isotopic composition of atmospheric CO_2 inferred from carbon in C_4 plant cellulose. Nature, 349: 127–131.

McDougall, I., 1985. K–Ar and $^{40}Ar/^{39}Ar$ dating of the hominid-bearing Plio-Pleistocene sequence of Koobi Fora, Lake Turkana, northern Kenya. Geol. Soc. Am. Bull., 96: 159–175.

Quade, J., Cerling, T.E. and Bowman, J.R., 1989a. Development of Asian monsoon revealed by marked ecological shift during the latest Miocene in northern Pakistan. Nature, 342: 163–166.

Quade, J., Cerling, T.E. and Bowman, J.R., 1989b. Systematic variations in the stable carbon and oxygen isotopic composition of pedogenic carbonate along elevation transects in the southern Great Basin, USA. Geol. Soc. Am. Bull., 101: 464–475.

Pratt, D.J., Greenway, P.J. and Gwynne, M.D., 1966. A classification of East African rangeland with an appendix on terminology. J. Appl. Ecol., 3: 369–382.

Retallack, G.J., Dugas, D.P. and Bestland, E.A., 1990. Fossil soils and grasses of a Middle Miocene East African grassland. Science, 247: 1325–1328.

Sarmiento, G., 1984. *The Ecology of Neotropical Savannas*, Harvard Univ. Press, Cambridge, MA, 235 pp.

Shipman, P., Walker, A., Van Couvering, J.A., Hooker, P.J. and Miller, J.A., 1981. The Fort Ternan hominoid site, Kenya: geology, age, taphonomy, and paleoecology. J. Hum Evol., 10: 49–72.

Smith, B.N., 1982. General characteristics of terrestrial plants (agronomic and forests)—C3, C4, and crassulacean acid metabolism plants. In: A. Mitsui and C.C. Black (Editors), *CRC Handbook of Biosolar Resources*. CRC Press, Boca Raton, pp. 99–118.

Van Couvering, J.A.H., 1980. Community evolution in East African during the late Cenozoic. In: A.K. Behrensmeyer and A.P. Hill (Editors), *Fossils in the Making*, Univ. Chicago Press, Chicago, pp. 273–298.

Van der Merwe, N.J. and Medina, E., 1989. Photosynthesis and $^{13}/^{12}C$ ratios in Amazonian rain forests. Geochim. Cosmochim. Acta, 53, 1091–1094.

Vesey-Fitzgerald, D.F., 1973. *East African Grasslands*. East African Publ. House, Nairobi.

Vrba, E.S., 1985. Ecological and adaptive changes associated with early hominid evolution. In: E. Delson (Editor), *Ancestors: The Hard Evidence*, A.R. Liss, New York, NY, pp. 63–71.

Yurtsever, Y. and Gat, J.R., 1981. Atmospheric waters. In: J.R. Gat and R. Gonfiantini (Editors), *Stable Isotope Hydrology*. IAEA Tech. Rep. Ser., 210: 103–142.