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ARTICLE *in* PALAEOGEOGRAPHY PALAEOCLIMATOLOGY PALAEOECOLOGY · OCTOBER 2004

Impact Factor: 2.75 · DOI: 10.1016/j.palaeo.2004.07.007

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Palaeogeography, Palaeoclimatology, Palaeoecology 213 (2004) 115–123
PALAEO
www.elsevier.com/locate/palaeo

Eocene dry climate and woodland vegetation in tropical Africa reconstructed from fossil leaves from northern Tanzania

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Received 10 September 2003; received in revised form 2 June 2004; accepted 6 July 2004

Abstract

Eocene vegetation and climate data from tropical latitudes are sparse despite special interest in the Eocene as the warmest epoch of the Cenozoic and an often-cited analogue for greenhouse Earth conditions. Tropical Africa is noteworthy for its shortage of Eocene fossils, which could serve as proxies for climate and reveal community structural evolution during the continent's geographic isolation. In this paper, we report paleobotanical remains from a middle Eocene crater lake at 12°S paleolatitude in north central Tanzania, which provide a plant community reconstruction indicating wooded, rather than forest, vegetation and precipitation estimates near modern (660 mm/year). The plant community was dominated by caesalpinioid legumes and was physiognomically comparable to modern miombo woodland. Paleoprecipitation estimates, the first for the Paleogene of Africa, are calculated from fossil leaf morphology using regression equations derived from modern low-latitude leaves and climate. Mean annual precipitation estimates are 643 ± 32 and 776 ± 39 mm/year, and wet months precipitation estimates (all months averaging ≥ 50 mm) are 630 ± 38 and 661 ± 38 mm. A slightly larger proportion of annual precipitation occurred in the dry months compared with today, which may indicate greater equability of precipitation in the Eocene.

Keywords: Eocene; Tanzania; Paleobotany; Paleoclimate; Paleogene; Africa

1. Introduction

Fossils and isotope records from middle and high latitudes indicate that the Eocene was the warmest epoch of the Cenozoic (Wolfe, 1994; Zachos et al., 2001; Wing, 2000). However, biota and climates at low latitudes during the Eocene are poorly understood, because data from the paleotropics are extremely rare (Morley, 2000; Greenwood and Wing, 1995). Tropical Africa specifically lacks data necessary to document the geographic extent, composition, and regional climate associated with rain forest or woodland ecosystems, which are widespread on the continent

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doi:10.1016/j.palaeo.2004.07.007

today. From what little is known, Africa was home to a largely endemic fauna and flora during its Paleogene isolation, but these are not well understood with respect to phylogenetic history or geographic distribution during the Eocene (Morley, 2000; Gunnell et al., 2003). In this paper, we report a middle Eocene flora from 12°S paleolatitude that will help to fill a large gap in Africa's biologic history and provides the first Paleogene climate estimates for the continent.

The Mahenge paleontological site (4°47′ 38″S; 34°15′ 28″E; Fig. 1), Singida District, Tanzania, consists of fossiliferous lacustrine deposits accumulated in a crater lake formed as the result of a kimberlite eruption (Mannard, 1962). Analysis of ^{206}Pb/^{238}Ur in kimberlite zircons dates the time of the eruption and formation of the crater at 45.83±0.17 Ma and provides a maximum age for lacustrine sedimentation, which would have begun soon after crater formation (Harrison et al., 2001). Excavations near the lake center produced plants, fish, insects, a bat, and a frog with stomach contents, most of which come from 75 cm of alternating carbonaceous shales and finely laminated mudstones near the base of a 3-m section (Fig. 2; Herendeen and Jacobs, 2000; Baez, 2000; Harrison et al., 2001; Murray, 2000, 2001; Murray and Budney, 2002). Selective preservation of small leaves near the lake center (Roth and Dilcher, 1978) is unlikely based on our observation that larger leaves appeared no more common near the lake margin.

Initial study of 70 fossil plant specimens collected in 1996 indicated a woodland environment (Herendeen and Jacobs, 2000), implying that precipitation at Mahenge was less than 1100 mm/year, the approximate minimum needed to support forest vegetation today. An additional 300 plant specimens were collected at Mahenge in 2000. Among the total collection are 19 to 21 leaf morphotypes, each assumed to represent a

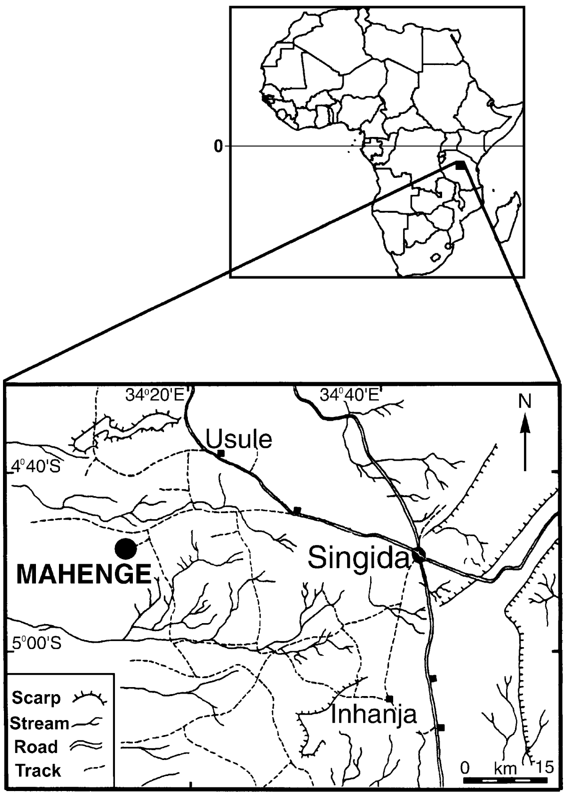


Fig. 1. Location of Mahenge, Singida District, north-central Tanzania.

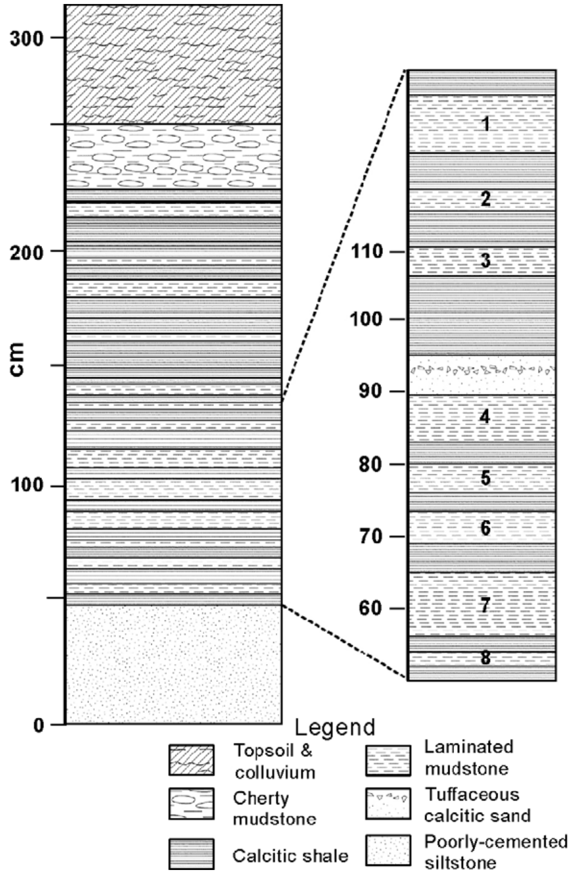


Fig. 2. Stratigraphic section.

Table 1
Regression equations used to estimate paleoprecipitation at Mahenge

Regression equations	Data from which equation was derived
Natural log of mean annual precipitation (MAP)	
(1) lnMAP (cm)=2.566+0.309(Mln$A$)[a], R^2=0.734, F=110.6, σ=<0.001	Tropical Africa and Bolivia (N=42; Gregory-Wodzicki, 2000; Jacobs, 1999, 2002)
(2) lnMAP<260 cm=2.167+.354(Mln$A$), R^2=0.709, F=187.8, σ=<0.001	Tropical Africa, Bolivia, and tropical to subtropical Western Hemisphere, including seven African samples (N=79; Gregory-Wodzicki, 2000; Jacobs, 1999, 2002; Wilf et al., 1998)
Natural log of wet months precipitation (Wet Ppn)[b]	
In Wet Ppn (cm)=2.07+0.367(Mln$A$), R^2=0.748, F=118.8, σ=<0.001	Tropical Africa and Bolivia (N=42) (Gregory-Wodzicki, 2000; Jacobs, 1999, 2002)

[a] Mln$A$ is the average leaf area of all dicot species calculated according to Wilf et al. (1998), where $M\ln A=\sum a_i p_i$, and a_i represents the seven means of the natural log areas of the size classes of Raunkiaer (1934) as modified by Webb (1959), and p_i represents the proportion of species in each of the size classes (see Table 2).

[b] Wet months precipitation is the total for all months having an average≥50 mm.

species, and each providing leaf morphological characters used to calculate precipitation estimates.

2. Methods and results

2.1. Paleoprecipitation estimates

Among woody dicots, characters of the leaf margin, surface area, apex, base, and shape are correlated with temperature and precipitation parameters at a regional scale (Raunkiaer, 1934; Webb, 1968; Dilcher, 1973; Hall and Swaine, 1981; Givnish, 1984; Wolfe, 1993; Wilf et al., 1998). These leaf–climate relationships are quantified using nonlinear or linear multivariate or univariate predictive models in which fossil leaves stand as proxies for past climate (Wolfe, 1993; Wilf et al., 1998; Jacobs, 1999; Gregory-Wodzicki, 2000). Univariate linear regression equations are used herein with data from Mahenge to estimate both mean annual and wet months precipitation, the total of all months having a mean of ≥50 mm. The equations derive from measurements of modern leaves and precipitation at latitudes between 25°N and 25°S in Africa, South America, and North America (Wilf et al., 1998; Jacobs, 1999, 2002; Gregory-Wodzicki, 2000). The independent predictor variable, Mln$A$, is calculated as follows: $M\ln A=\Sigma a_i p_i$, where a_i represents the means of the natural log areas of seven size classes and p_i is the proportion of species in each size class (Raunkiaer, 1934; Webb, 1959; Givnish, 1984; Wilf et al., 1998). Thus, Mln$A$ is weighted by the proportion of species in each size class. Two equations estimate the natural log of mean annual precipitation, one derived from 42 African and Bolivian assemblages (Table 1, Eq. (1)) and another using 79 modern leaf and climate assemblages from low-latitude Africa, South America, and North America (Jacobs, 2002) (Table 1, Eq. (2)). The African and Bolivian data have nearly identical regression lines and could be combined to

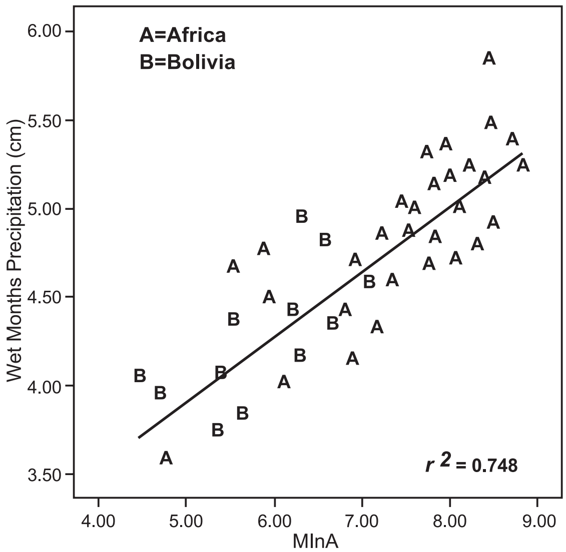


Fig. 3. Scatter plot of Mln$A$ and wet months precipitation (total for all months having an average≥50 mm). Mln$A$ and the regression model derived from these data are as defined in Table 1.

Table 2
Species leaf size data

Size class[a]	Size class ranges (cm^2)	p_i Size classes[b] all levels split (N=21)	p_i Size classes—all levels lumped (N=19)	p_i Size classes—level 7 split (N=12)	a_i[c]	Mln$A$[d] (a_ip_i)—split all levels (N=21)	Mln$A$ (a_ip_i)—lumped all levels (N=19)	Mln$A$ (a_ip_i)—split level 7 (N=12)
Leptophyll	≤0.25	0.10	0.11	0.08	2.12	0.20	0.22	0.18
Nanophyll	>0.25–2.25	0.24	0.16	0.25	4.32	1.03	0.68	1.08
Microphyll	2.25–20.25	0.62	0.68	0.58	6.51	4.03	4.45	3.80
Notophyll	20.25–45.00	0.05	0.05	0.08	8.01	0.39	0.42	0.67
Mesophyll	45.00–182.25	0.00	0.00	0.00	9.11	0.00	0.00	0.00
Macrophyll	182.25–1640.20	0.00	0.00	0.00	10.90	0.00	0.00	0.00
Megaphyll	>1640.20	0.00	0.00	0.00	13.10	0.00	0.00	0.00
					Σa_ip_i	5.65	5.78	5.72

Leaf morphotypes (assumed to be species) can be split into a maximum of 21 species or lumped into a minimum of 19 species.
[a] Size classes are those of Raunkiaer (1934) modified by Webb (1959).
[b] Relative proportions (p_i).
[c] Mean of the natural log area for each size class (a_i).
[d] Mln$A$ are calculated for both split and lumped classifications; Mln$A$ as defined for Table 1.

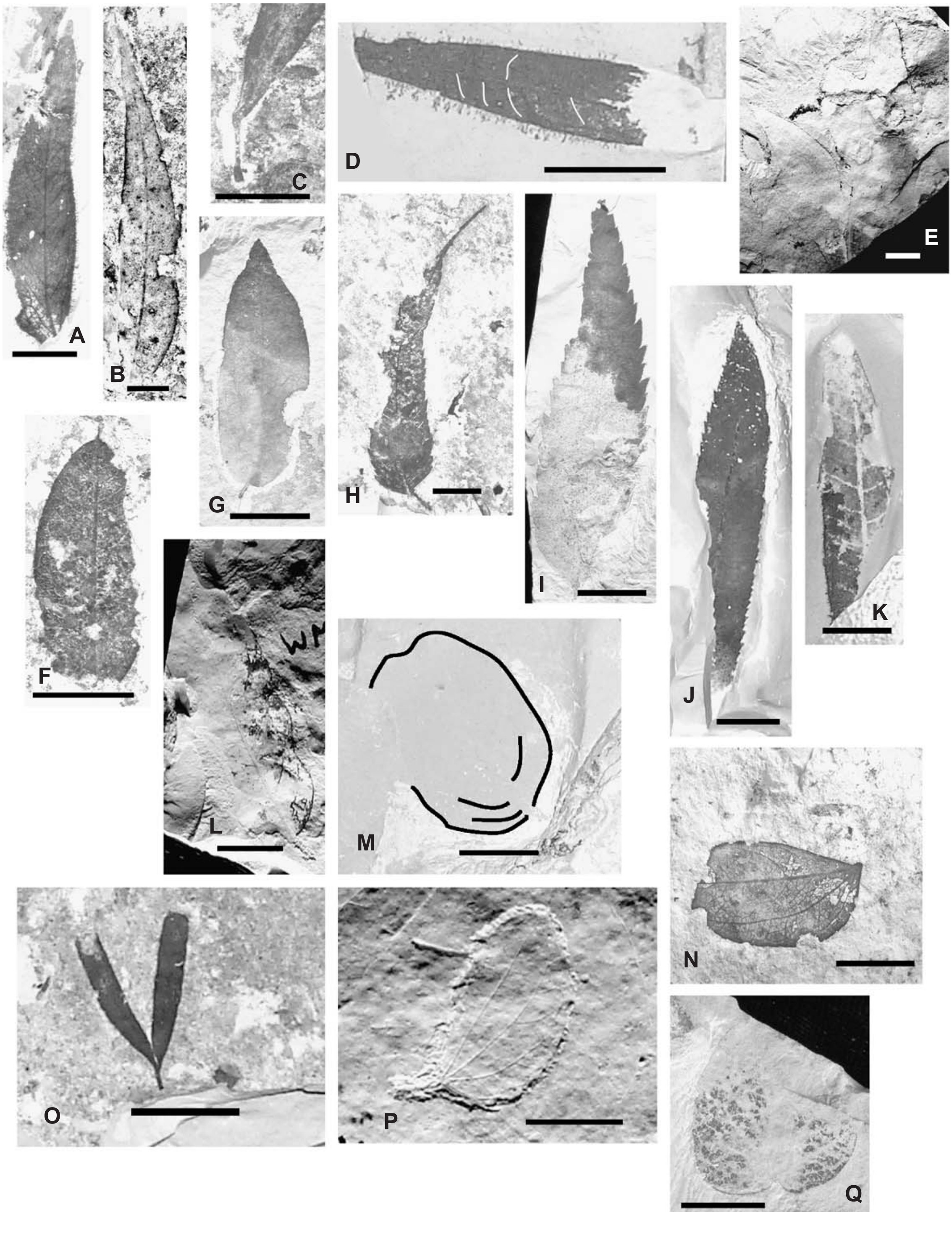
derive a regression equation for the wet months precipitation, which like mean annual precipitation is also correlated with leaf area (Fig. 3). Wet months precipitation data were not available from the remaining 37 low-latitude modern samples.

Leaf size was recorded for each species, and the relative proportion of species in each size class was determined for the Mahenge assemblage (Table 2). Because species richness affects relative proportion values and because some taxa at Mahenge are difficult to delineate, separate Mln$A$ values and precipitation estimates are given for split (21 species) or lumped (19 species) counts. Leaf morphotypes (species) are shown in Figs. 4 and 5).

Precipitation estimates are shown in Table 3 and Fig. 6. Estimates are calculated using fossil leaf data grouped from all stratigraphic levels and separately from the most fossil-rich level, level 7, which produced a subset of 12 species. The advantage of calculating precipitation estimates, combining data from all levels, is that it maximizes the number of specimens in the sample. However, lumping stratigraphic levels may introduce more than one plant community to the collection over the time of deposition. The errors for paleoprecipitation estimates for level 7 overlap with those for estimates derived from leaves found among all levels (Table 3). This demonstrates that there is no ecologically important difference between the climate signal derived from the single stratigraphic level vs. the signal derived from the combination of all levels in the lake.

Mean annual precipitation estimates at Mahenge range from a minimum of 643±32 to a maximum of 776±39 mm (depending on whether Eq. (1) or (2) is used), indicating that precipitation was near to the modern annual mean of 660 mm/year recorded for Singida. Wet months precipitation, estimated at 630±38 or 660±38 mm (for 21 or 19 species), is close to the modern wet months average of 595 mm. Dry months precipitation can be determined simply by calculating the difference between the mean annual precipitation and wet months precipitation estimates, provided that both are obtained from regression equations derived from the same data sets. Eq. (1), which predicts mean annual precipitation, is derived from the same data set as

Fig. 4. Leaf morphotypes (species). All scale bars=10 mm. A, MP 70 (Unkn.J); B, MP310a and C, MP300b (narrow cf. *Cynometra*); D, WM066 (oblanceolate Unkn); E, WM 231 (Compound Unkn.); F, MP38 (Unkn. N); G, MP257 (Unkn. M); H, Wm246 (Unkn. Y toothed); I, WM200 (bigtooth Unkn.); J, WM345 (fine-toothed Unkn. D); K, WM344 (cf.*Parinari*); L, WM238 (crenulate? margin); M, WM269 (emarginated Unkn. E); N, WM515 (Unkn. caesalpinioid f igured in Herendeen and Jacobs [2000]); O, WM507 (Unkn. legume); P, WM 180 (Unkn legume?); Q, MP16 (cf. *Bauhinia*). Morphotypes shown in O and P are omitted in lumped species counts.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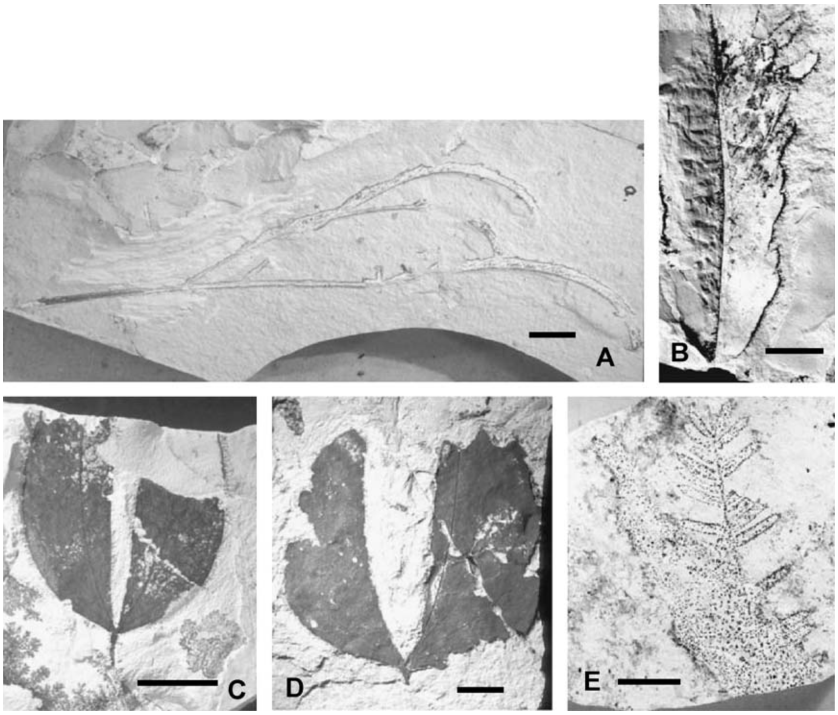

Fig. 5. Leaf morphotypes (species). All scale bars=10 mm. A, WM285, *Acacia mahengensis* (Herendeen and Jacobs, 2000); B, WM233 (Unkn. mimosoid); C, WM151, cf. *Cynometra* (Herendeen and Jacobs, 2000); D, WM277, *Aphanocalyx singidaensis* (Herendeen and Jacobs, 2000); E, WM003, Unkn. legume (Herendeen and Jacobs, 2000).

the predictive equation for wet months precipitation. The estimates indicate that 15% to 16% of the annual precipitation fell during the dry months. Today, an average total of only 65 mm, or about 10%, falls during 7 dry months. This difference is small, but could indicate that precipitation season-

Table 3
Mean annual and wet months precipitation estimates for Mahenge

Mahenge	MAP Eq. (1)[a] (mm)	MAP Eq. (2)[a] (mm)	Wet months Ppn (mm)	Dry months Ppn (mm)[b]
All levels—taxa split (*N*=21)	746±39[c]	643±32	630±38	116
All levels—taxa lumped (*N*=19)	776±39	676±32	661±38	115
Level 7 (*N*=12)	762±39	662±32	647±38	
Singida[d]	Modern MAP (mm)		Modern wet months (mm)	Modern dry months (mm)
	660		595	65

Modern data from Singida shown for comparison.

[a] Equations given in Table 1. Data are given in Table 2.

[b] The difference between mean annual precipitation calculated from Eq. (1) and the wet months precipitation.

[c] The standard error shown is the standard error of the predicted value, which takes into account the error for each new prediction (depending on the *X* values) and the error (σ^2) associated with the residuals (Neter et al., 1996; Snedecor and Cochran, 1989). Transformation of the error from the log scale was approximated by use of the following equation from Casella and Berger (1990): SE=SE(log*Y*)*exponent (observed value log*Y*).

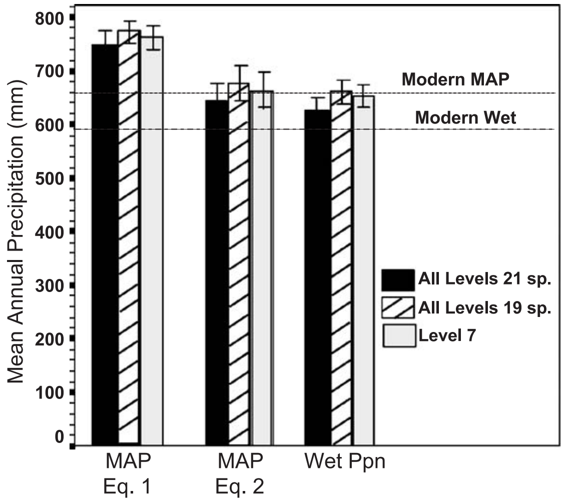

Fig. 6. Estimated mean annual precipitation (MAP) values for the Mahenge site. Eqs. (1) and (2) refer to those shown in Table 1. Data provided in Tables 2 and 3. Error bars are the standard error of the mean predicted value.

ality was less pronounced than today because middle Eocene dry months precipitation comprised a larger proportion of the annual total. Eocene paleogeography, including the absence of the Tibetan Plateau, which plays a large role in monsoon circulation patterns today, would contribute to these differences (Lockwood, 1985; Ruddiman and Kutzbach, 1989; Prell and Kutzbach, 1992; Zhisheng et al., 2001).

2.2. Vegetation reconstruction

One third of the species (7 of 21) at Mahenge are in the family Leguminosae, subfamilies Caesalpinioideae and Mimosoideae. About 65% of the classified leaves are caesalpinioid and include cf. *Cynometra*, *Aphanocalyx*, and two or three other unnamed taxa (Herendeen and Jacobs, 2000). Leaf morphological attributes (Table 2, Figs. 4 and 5) and precipitation estimates at Mahenge are consistent with a woodland vegetation structure (Table 3, Fig. 6). Although the species composition is different, at the subfamily level, the Mahenge assemblage is most comparable to miombo woodlands, which comprise a significant part of the vegetation cover in eastern Africa today and are dominated by a few small-leaved caesalpinioid legume genera.

3. Discussion

The low density of fossil sites across the tropical zone has failed to delineate the boundaries of rain forest and woodland communities resulting in conflicting large-scale vegetation reconstructions for the early to middle Eocene. These include continentwide rainforest to at least 15°S (Axelrod and Raven, 1978; Wolfe, 1985; Wing et al., 1995; Willis and McElwain, 2002) savanna woodland stretching from the Congo Basin to 35°S (Coetzee, 1993) and a mix of taxonomically unique wet forest and more open vegetation in the tropical latitudes (Morley, 2000). Support for some open vegetation and seasonally dry climate in the early to middle Eocene in Cameroon, Nigeria, and Egypt comes from palynological records that document moderate amounts of grass pollen and angiosperm richness (Van Hoeken-Klinkenberg, 1966; Kedves, 1971; Adegoke et al., 1978; Salard-Cheboldaeff, 1981; Jacobs et al., 1999), but this could be limited to wetland vegetation (Morley, 2000). Boureau et al. (1983) suggest woodland or savanna were present in the interior of northern Africa during the early to middle Eocene based on the occurrence of fossil wood related to living Combretaceae. Mahenge documents the presence of a woodland community not previously recorded from the Eocene (or Paleogene) of tropical Africa and indicates that rainforest vegetation, if present in the eastern part of the continent, would have been limited to somewhere north of 12°S, where a climate wetter than Mahenge could have been present.

3.1. Potential Influence of pCO_2 on leaf morphology and climate estimates

Estimates of atmospheric CO_2 concentration for the middle Eocene range from approximately equal to modern (Cerling, 1992; Pearson and Palmer, 1999) to as much as eight times higher (Berner and Kothavala, 2001). CO_2 provides the carbon necessary for plant growth, and numerous studies on the acclimatory and developmental effects of higher than modern atmospheric CO_2 concentration on leaves indicate that leaf response may be absent, limited, or temporary (Wolfe et al., 1998; Atkin et al., 1999; Pritchard et al., 1999). Leaves that respond to elevated CO_2 most often show an increase in thickness rather than surface area (Pritchard et al., 1999). However, if atmospheric CO_2 was elevated at 46 Ma and was accompanied by an increase in leaf size at Mahenge, then precipitation estimates for the site would be high and the environment would have been drier than estimated.

4. Conclusions

Fossil plants from Mahenge document woodland vegetation similar physiognomically to extant miombo woodlands at a paleolatitude of 12°S during the middle Eocene. The climate was as dry as today, but precipitation may have been more equably distributed. The assemblage does not resemble lowland tropical rain forest physiognomically or compositionally. Rain forests did not extend across the whole of tropical Africa during the middle Eocene, but, if present, were limited in the eastern region to areas north of 12°S paleolatitude.

Acknowledgements

We thank the Tanzanian Antiquities Unit, the National Museums of Tanzania, Dar es Salaam, and the Singida District Executive Director and his colleagues for their cooperation and support. We thank Gregg Gunnell, Jason Head, Beth Kowalski, Ferdinand Mizambwa, Charles Msuya, and Kent Newman for their collaborative support. We are grateful to the Manonga–Wembere project and Terry Harrison for their help and our introduction to Mahenge. Statistical advice from Rudy Guerra is gratefully acknowledged, but authors take responsibility for any errors. We thank Louis Jacobs, Kathleen Pig, Alisa Winkler, and Dale Winkler for their comments. We thank Aaron Pan for photography of plant fossils. This research was supported by National Science Foundation grant EAR-9909494 (BFJ).

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