Are modern savannas degraded forests ? - A Holocene pollen record from the Sudanian vegetation zone of NE Nigeria

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Abstract. A pollen record from a crater lake (Lake Tilla, 10°23'N, 12°08'E, c. 700 m asl) in the Sudanian zone of northeast Nigeria provides evidence for the persistence of woodland savanna throughout the Holocene. Wetter conditions from c. 10,000 B.P. to c. 6800 B.P. enabled the establishment of a dense Guinean savanna, though the occurrence and rapid spread of the montane element *Olea hochstetteri* indicates cool climatic conditions prior to c. 8800 B.P. Patches of closed dry forest may have existed, but never completely displaced the savanna vegetation. Grass fires were frequent throughout the Holocene and were probably important in promoting the open character of the vegetation. From c. 6800 B.P. onwards a gradual floristic change from a Guinean to a Sudano-Guinean savanna and a lowering of lake levels point to drier environmental conditions, which intensified around 3700 B.P. Human impact might have caused increasing sedimentation rates from c. 2500 B.P. onwards. The pollen diagram of Lake Tilla reflects a history of the savanna which appears to have been primarily controlled by climatic changes. The lack of unambiguous pollen indicators might be the reason why human activities remain palynologically hidden even for the late Holocene.

Key words: West Africa – Vegetation history – Climatic change – Savanna – Pollen analysis

Introduction

The modern Sudanian savanna of West Africa is a cultural landscape that has been strongly shaped by humans. Its history and origin is subject of controversy. The role of human impact has been emphasised by numerous botanists who suggest that a closed dry forest is the natural vegetation of the Sudanian zone, for example Aubreville (1949), Chevallier (1951) and Keay 1949). The hypothesis of the anthropogenic origin of the southern savannas was recently supported by Anhuf (1997), Guinko (1985), Hahn-Hadjali (1998) and Neumann and Müller-Haude (1999), who investigated isolated dry for-

est stands in Burkina Faso and The Ivory Coast. According to Anhuf and Frankenberg (1991) these forests formerly covered the northern Guinean and Sudanian zone up to the modern southern Sahel before its degradation by human activities to savanna and open woodlands (*forêt claire*). Frequent fires, mainly of anthropogenic origin, are stressed as a major factor being responsible for the opening of the forests. Assessments of vegetational development in fire-protected areas have demonstrated the rapid recolonisation of savanna by forests (Charter and Keay 1960; Swaine 1992). In contrast, Keay (1959a) notes that fire protection of *Isoberlinia* woodlands in the northern Guinea zone of Nigeria has little effect on floristic composition. The grass cover was never eliminated over wide areas and thus these vegetation types should not be regarded as derived savannas. A mosaic of savanna and forests is also considered to be the natural vegetation of the Sudanian and northern Guinean zones by Sanford and Isichei (1986) and Schnell (1976). Natural fires and large herbivore populations may have been responsible for the opening of vegetation long before human presence (Schnell 1976, Walter 1979). However, some problems are caused by the differing use of the terms "savanna", "woodland" and "forest". In this paper, following the "Yangambi Classification" (CSA 1956), woodland and savanna will be grouped and separated from the dry forest in which a continuous grass stratum is absent.

The discussion on the origin and history of the Sudanian savanna has mainly been based on floristic assessments of present vegetation. Recently, paleoecological information on the mid and late Holocene vegetation has been provided by macrofossils (charcoal) from an archaeological site in southeast Burkina Faso, which indicates a mosaic of dry forests and savanna around 7000 B.P. (Neumann and Ballouche 1992, K. Neumann, personal communication). Although the charcoal record gives no information on long term vegetational changes during the early and mid Holocene, it can be noted that the vegetation remained Sudanian. There is no evidence for the presence of taxa of more southerly origin, as has been recorded for the West African Sahel and Sahara (for example Hooghiemstra 1988; Lezine 1989; Maley

1981; Neumann 1989; Salzmann and Waller 1998; Schulz 1994). From 2700 B.P. onwards, the dry forest was gradually replaced by highly diversified savannas which Ballouche (1998) and Neumann and Ballouche (1992) attribute to increasing human activity. However, the relative importance of human impact and late Holocene climate as an agent of vegetational change is controversial and has also been discussed for the West African rain forest zone (for example Elenga et al. 1994; Maley 1991; Maley and Brenac 1998; Reynaud-Farrera et al. 1996; Schulz and Pomel 1992; Sowunmi 1999).

Whereas the Holocene vegetation history of the Sahel and the West African rain forest has at least partially been described by pollen records, long term paleoecological information on the Sudanian zone is still very scarce. This paper presents palynological results from a sediment core taken from Lake Tilla situated in the Sudanian zone of northeast Nigeria (10°23'N, 12°08'E). The 9 m pollen record provides information on vegetational history over the last c. 11,500 ^{14}C years B.P.

Site description

Lake Tilla is a crater lake (maar) situated about 10 km south-west of the town of Biu on a volcanic basalt plateau (Biu Plateau) of Pliocene and Quaternary age (Grant et al. 1972) (Fig. 1). Mean annual rainfall in Biu is about 1000 mm/a (1940-1962) with a wet season (May-October) of about 160 days (Tuley 1972). According to White (1983) the vegetation of the Biu Plateau can be characterised as undifferentiated woodland of the Sudanian zone, whereas Keay (1959b) attributes this region to the northern Guinea zone. De Leeuw and Tuley (1972) describe the vegetation of the plateau as consisting of *Acacia hockkii* savanna and degraded *Terminalia/ Combretum* shrubland with a high portion of *Isoberlinia*. In fact *I. doka* shrubs can be found in large numbers as fallow regrowth, sometimes forming uniform stands. Other characteristic woody taxa of this region, which are also abundant near the crater lake include *Lannea* spp., *Cassia* spp., *Combretum* spp., *Ficus* spp., *Ziziphus* spp. and *Boswellia dalziellii*. Closed dry forests are rarely found on the plateau. Intensive farming has established an open park savanna with only few isolated trees.

Lake Tilla is the largest lake of the Biu Plateau with a basal diameter of c. 700 m. Located at an altitude of 690 m asl the crater has the shape of an elongated bowl with a flat bottom. The inside walls are partly composed of massive columnar-jointed basalt and overlying tephra rings, with fragments derived from the older underlying rocks, both basalt and granite (Turner 1978). The lake is mainly fed by groundwater and shows no visible inlet or outlet. During the wet season the lake is fringed by a dense herbaceous vegetation with taxa of the families Poaceae (such as *Hyparrhenia rudis, Pennisetum subangustum, Andropogon gayanus*), Asteraceae (including *Acanthospermum hispidum, Vernonia kotschyana*), Amaranthaceae (such as *Amaranthus spinosus*) and Fabaceae (*Indigofera* spp., *Alysicarpus* spp.). Since the early 1970s the lake has regularly dried out towards the end of the dry season. An assessment in June 1933 indicated a maximum water depth of 5.20 m with a mean of 4.30 m (Davies 1954-56). At that time the lake was famous for its crocodile population.

Methods

Test cores were taken from several craters on the Biu Plateau (Dutsin Miringa, Dutsin Maldau, Gaa Tilla, Kwa Tilla, Lake Tilla). Only sediment samples from Lake Tilla contained well preserved pollen. The core presented (LT 97-1) was taken in the central and deepest part of the lake during the dry season using a modified Livingstone piston corer. Pollen samples were taken and analysed every 10 cm and prepared with HF and acetolysis following standard methods (Fægri and Iversen 1989). *Lycopodium* tablets were used to enable the calculation of pollen concentration (Stockmarr 1971). Pollen percentages are based on the arboreal and non-arboreal land pollen sum (TLP), from which the aquatic taxa (such as *Typha, Nymphaea*) and spores are excluded. The total pollen count generally exceeds 750 grains. However, due to the dominance of Poaceae in the upper layers (late Holocene), more than 1000 grains had to be counted there. Pollen grains were identified with the help of modern reference material held at the University of Frankfurt and literature (such as Bonnefille and Riollet 1980; Caratini and Guinet 1974; Maley 1970; Sowunmi 1973, 1995; Ybert 1979). Nomenclature follows that of Cronquist (1981) for families and the *Flora of west tropical Africa* (Hutchinson and Dalziel 1954-1972) for generic and specific names. For an assessment of fire frequency and intensity, microscopic charcoal particles were counted following the method of Clark (1982). The diagram was drawn using the TILIA/ TILIA*GRAPH software package (Grimm 1990). Pollen zones were delimited numerically by stratigraphically constrained cluster analysis using the computer program CONISS (Grimm 1987).
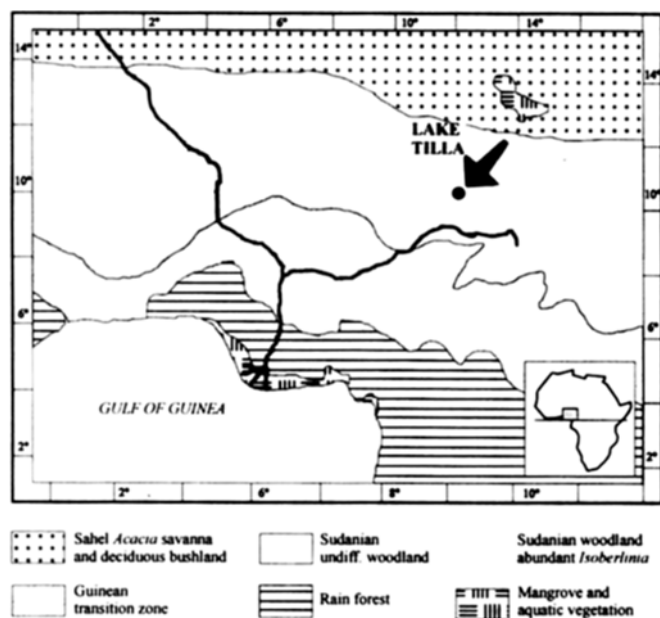

Sahel *Acacia* savanna and deciduous bushland

Guinean transition zone

Sudanian undiff. woodland

Rain forest

Sudanian woodland abundant *Isoberlinia*

Mangrove and aquatic vegetation

Fig. 1. Location map and vegetation zones (after White 1983)

Biu Plateau

AP ──────── NAP ──────────

Azadirachta indica
Myrtceae cf.Eucalyptus
Casuarina
Acacia
Balanites
Capparidaceae undiff.
Capparis
Salvadora
Ziziphus
Burkea africana
Butyrospermum
Caesalpiniaceae undiff.
Cassia
Combretaceae
Dichrostachys cinerea
Entada
Ficus
Khaya
Isoberlinia
Lannea/Sclerocarya
Maytenus
Mimosa pigra
Mitragyna
Parkia
Pterocarpus
Ampelidaceae undiff.
Clematis
Poaceae
Cyperaceae
Acanthaceae
Amaranthaceae/Chenopod.
Asteroideae
Centaurea
Lactuceae
Fabaceae undiff.
Lamiaceae
Rubiaceae undiff.
Borreria
Mitracarpus scaber
Sapindaceae
Tribulus
Monocotyledonae undiff.
Commelinaceae
Liliaceae
Typha
Nymphaea
Pteropsida (monolet)
Pteropsida (trilet)
unknown
Indet.
TLP

Nr.1 Lake Tilla, (PT) 10°32′N, 12°07′E — 421

NR.2 Ga - Tilla (SFS) 10°32′N, 12°08′E — 611

NR.3 Kwa Tilla (SFS) 10°31′N, 12°07′E — 712

Nr.4 Dutsin Maldau (SFS) 10°42′N, 12°06′E — 520

Nr.5 region Kwaya Bura (MPT), 140 km, 4 days — 656

20 40 60 80 100   20 40   20

+ < 1% TLP

Analyst: Ulrich Salzmann

SFS = surface samples / MPT = mobile pollen trap
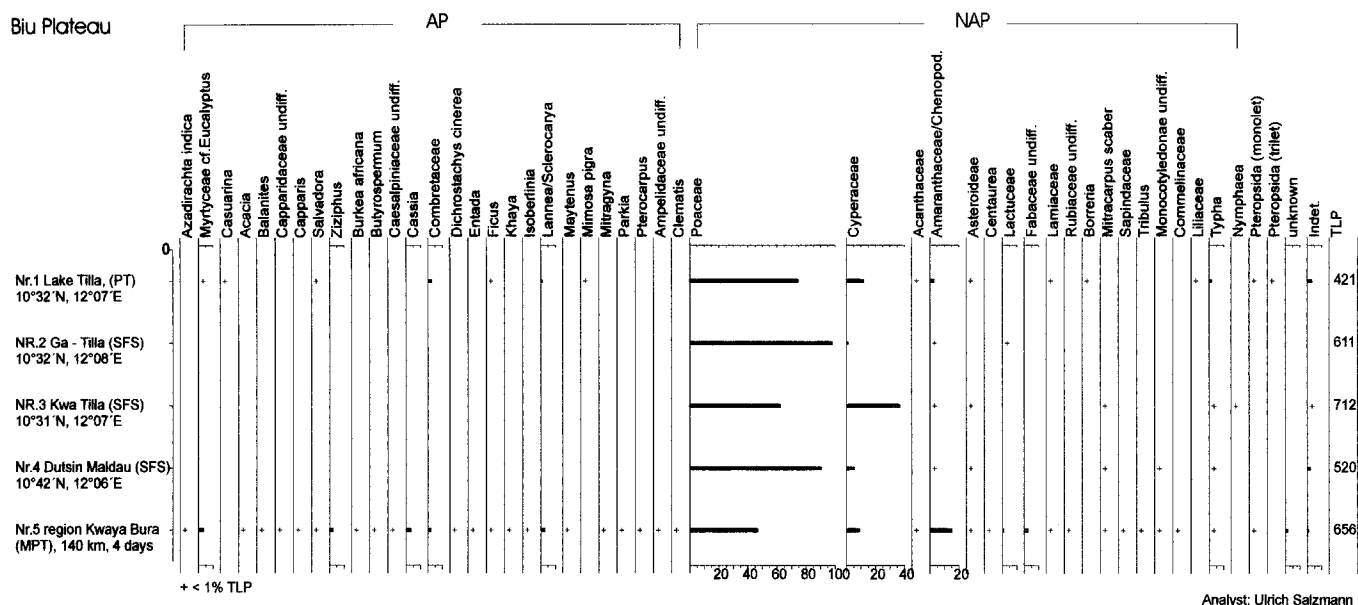
Fig. 2. Modern pollen rain from the Biu Plateau

Results

Modern pollen rain

The modern pollen rain of the Biu Plateau was assessed using surface samples, which were prepared in the same manner as the fossil material. As most of the surface samples showed poor pollen preservation, mobile pollen filters, which were impregnated with silicon oil (after Cour 1974) were additionally employed. Sample Nr.1 (Fig. 2) was taken with a pollen trap which was attached to the rear bumper of a vehicle, while it travelled across the dry lake floor of Lake Tilla over a distance of about 3 km. Sample Nr. 5 (Fig. 2) represents the seasonal pollen precipitation around the lake, which was measured with a mobile pollen trap attached to the roof of the vehicle for about four days in March.

The modern pollen spectra of the Biu Plateau are dominated by Poaceae (grasses) and Cyperaceae (sedges) which generally exceed 95% (Fig. 2). High Cyperaceae values were recorded in sample Nr. 1 and Nr. 3, which were taken in the vicinity of the semi-permanent lakes Tilla and Kwa Tilla. All spectra of the surface samples are dominated by the local pollen rain of grasses and herbs which grow right next to the sampling sites, whereas the regional woody vegetation is very under-represented. In contrast, the pollen rain measured with mobile pollen traps gives a more characteristic picture of the main woody vegetation of the surrounding open savanna. Sudanian and Sahelian elements (Combretaceae, Lannea/Sclerocarya, Salvadora) as well as the neophytes (plants introduced from elsewhere) Azadirachta indica, Casuarina and Eucalyptus are regularly present at low percentages. The neophytes seem to be the only unambiguous indicators of human activity. Ruderal taxa (such as Mitracarpus scaber, Borreria spp.) as well as cultivated trees (such as Butyrospermum paradoxum, Parkia biglobosa) occur only sporadically in the pollen spectra. Isoberlinia doka, which can be found in abundance on the plateau as fallow regrowth, is also heavily under-represented, most probably as a result of zoogamous (animal-pollinated) pollen dispersal. However, irrespective of the collection method used, all spectra represent the local or regional pollen rain. There is no evidence for long distance transport, either from the Guinean savanna (for example Lophira lanceolata, Uapaca togoensis) to the south, or from the neighbouring montane regions of the Jos Plateau or Mandara mountains (for example Olea hochstetteri syn. O. capensis).

Sediments and dating

The estimated time scale of the profile is based on a total of 12 accelerator mass spectrometer (AMS) radiocarbon dates from organic matter (Table 1). Three ^{14}C dates were obtained from a parallel sediment core (LT95-4) which was taken closer to the edge of the lake, about 80 m from coring site LT97-1. Pollen samples taken from the parallel core were counted at approximately 40 cm intervals to enable correlation of the radiocarbon dates between the cores.

Apart from the upper 41 cm, which consisted of dry greyish calcareous silt, the first 816 cm of core LT97-1 comprised a relatively uniform black lake mud with a high water content. At the bottom, between 830 and 900 cm, the black mud became more solid and showed interbedded greyish silt layers with sand. The sediment accumulation curve of profile LT 97-1 (Fig. 3) shows a rela-

Table 1. Radiocarbon dates (cal. B.P. after Stuiver and Reimer 1993)

Profile	Lab. code	uncal B.P. (± 1σ)	cal B.P. (± 1σ)	Depth of sample (cm)	Correlated depth LT 97-1
LT 97-1	UtC-7278	633 ± 36	650 - 554	23.5 - 24.5 cm	-
LT 97-1	UtC-6461	1146 ± 30	1066 - 986	51.0 - 52.0 cm	-
LT 95-4	UtC-5167	1536 ± 34	1416 - 1354	82.0 - 83.0 cm	120 cm
LT 97-1	UtC-7280	1863 ± 40	1860 - 1721	199.0 - 200.0 cm	-
LT 97-1	UtC-6460	2315 ± 48	2349 - 2320	313.0 - 314.0 cm	-
LT 95-4	UtC-4316	3188 ± 37	3459 - 3363	289.0 - 290.0 cm	390 cm
LT 97-1	UtC-6462	4034 ± 48	4537 - 4418	451.0 - 452.0 cm	-
LT 97-1	UtC-6464	5492 ± 46	6306 - 6218	551.0 - 552.0 cm	-
LT 97-1	UtC-7279	8210 ± 60	9251 - 8996	679.0 - 680.0 cm	-
LT 97-1	UtC-6463	9700 ± 60	10,974 - 10,728	797.0 - 798.0 cm	-
LT 95-4	UtC-4206	10,295 ± 59	12,227 - 11,902	777.0 - 778.0 cm	815 cm
LT 97-1	UtC-6459	11,120 ± 110	13,150 - 12,915	889.0 - 890.0. cm	-

tively constant sedimentation rate between c. 11,200 cal B.P and c. 2300 cal B.P., which is followed by a rapid increase in sedimentation between c. 2300 cal B.P. and c. 1100 cal B.P.

The pollen record

About 154 fossil pollen and spore taxa could be identified (Table 2). Trees and shrubs were phytogeographically grouped following the work of Aubreville (1950) Keay (1959b), De Leeuw and Tuley (1972), Schnell (1976) and White (1983). Three major groups are distinguished: Sahelian, Sudanian and Guinean. Apart from the late Pleistocene samples, pollen preservation was excellent throughout the profile and concentrations generally exceeded 70,000 grains/cm. Counts of microscopic charcoal particles were high throughout the profile. Their percentages remain relatively constant. Frequent grass fires might have been responsible as charred particles of grass epidermis regularly occur. Three local pollen assemblage zones can be recognised (Figs. 4,5):

LT-1 (893-805 cm). Poaceae, Cyperaceae, *Typha*, Amaranthaceae/Chenopodiaceae, Lactuceae zone. A zone characterised by high values of Poaceae (>80%),
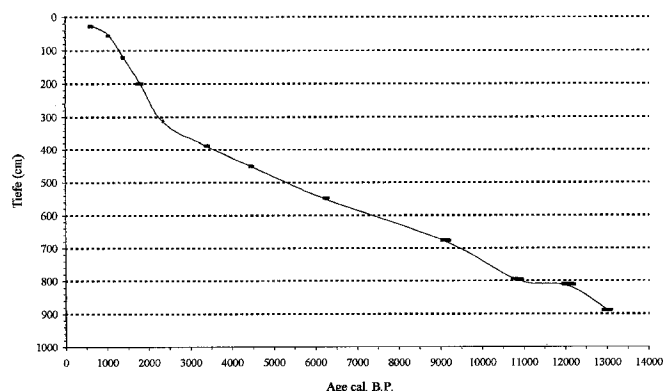

Fig. 3. Sediment accumulation rates based on linear interpolation of calibrated ^{14}C dates (calibration after Stuiver and Reimer 1993)

Table 2. List of pollen taxa arranged in phytogeographic groups

LAKE TILLA

LONG DISTANCE

Artemisia	Asteraceae
Ephedra	Ephedraceae
Ericaceae	
Olea	Oleaceae
Pinus	Pinaceae
Podocarpus	Podocarpaceae

TREES AND SHRUBS

Sahelian (incl. Saharo-Sahelian)

Acacia	Mimosaceae
Balanites	Zygophyllaceae
Capparidaceae undiff.	
Chrozophora	Euphorbiaceae
Commiphora	Burseraceae
Hyphaene/Borassus	Arecaceae
Maerua	Capparidaceae
Salvadora	Salvadoraceae
Ziziphus	Rhamnaceae

Sudanian (incl. Sudano-Sahelian)

Adansonia digitata	Bombacaceae
Allophylus	Sapindaceae
Annonaceae	*Lophira*
Anacardiaceae undiff.	
Bombax	Bombacaceae
Bridelia	Euphorbiaceae
Boswellia	Burseraceae
Burkea africana	Caesalpiniaceae
Butyrospermum paradoxum	Sapotaceae
Caesalpiniaceae undiff.	
Cassia	Caesalpiniaceae
Celtis	Ulmaceae
Celastraceae undiff.	
Cochlospermum	Cochlospermaceae
Combretaceae	
Cordia	Boraginaceae
Crossopterix febrifuga	Rubiaceae

Croton	Euphorbiaceae
Detarium	Caesalpiniaceae
Diospyros	Ebenaceae
Entada	Mimosaceae
Erythrina	Fabaceae
Ficus	Moraceae
Grewia	Tiliaceae
Isoberlinia	Caesalpiniaceae
Khaya	Meliaceae
Lannea/Sclerocarya	Anacardiaceae
Mitragyna	Rubiaceae
Nauclea	Rubiaceae
Parkia	Mimosaceae
Piliostigma	Caesalpiniaceae
Prosopis	Mimosaceae
Pterocarpus	Fabaceae
Rhus	Anacardiaceae
Securinega virosa	Euphorbiaceae
Sterculia	Sterculiaceae
Strychnos	Loganiaceae
Tapinanthus	Loranthaceae
Vitex	Verbenaceae
Ximenia americana	Olacaceae

Guinean (incl. Sudano-Guinean)

cf. Adina	Rubiaceae
Afraegle	Rutaceae
Afzelia cf. africana	Caesalpiniaceae
Alchornea	Euphorbiaceae
Antidesma	Euphorbiaceae
Apocynaceae	
Araliaceae undiff.	
Arecaceae undiff.	
Blighia	Sapindaceae
Cola cf. cordifolia	Sterculiaceae
Cussonia	Araliaceae
cf. Dialium	Caesalpiniaceae
Dombeya cf. buetnerii	Sterculiaceae
Elaeis guineenis	Arecaceae
Hymenocardia	Euphorbiaceae
Irvingiaceae	
Ixora	Rubiaceae
Lophira	Ochnaceae
Macaranga	Euphorbiaceae
Mallotus	Euphorbiaceae
Manilkara	Sapotaceae
Moraceae undiff.	
Morelia senegalensis	Rubiaceae
Monotes kerstingii	Dipterocarpaceae
Olea hochstetteri	Oleaceae
Phoenix cf. reclinata	Arecaceae
Raphia	Arecaceae
Salix cf. ledermanii	Salicaceae
Syzygium	Myrtaceae
Trema guineensis	Ulmaceae
Uapaca	Euphorbiaceae

WOODY CLIMBERS

Passifloraceae cf. Adenia	Passifloraceae
Paullinia pinnata	Sapindaceae
Ampelidaceae undiff.	
Cissampelos cf. mucronata	Menispermaceae
Cissus	Vitaceae
Clematis	Ranunculaceae
Menispermaceae undiff.	

Mussaenda	Rubiaceae
cf. Tacazzea spiculata	Periplocaceae
Thunbergia	Acanthaceae

HERBS

Poaceae	
Cyperaceae	
Acanthaceae undiff.	
Blepharis	Acanthaceae
Justicia	Acanthaceae
Amaranthaceae/Chenopodiaceae	
Apiaceae	
Asteroideae	
Centaurea	Asteraceae
Lactuceae	
Vernonia	Asteraceae
Boraginaceae undiff.	
Heliotropium	Boraginaceae
Brassicaceae	
Caryophyllaceae undiff.	
Polycarpaea	Caryophyllaceae
Corchorus	Tiliaceae
Cucurbitaceae	
Cucumis	Cucurbitaceae
Convolvulaceae undiff.	
Ipomoea	Convolvulaceae
Euphorbiaceae undiff.	
Acalypha cf. crenata	Euphorbiaceae
Phyllanthus undiff.	Euphorbiaceae
Indigofera	Fabaceae
Lamiaceae	
Lobelia	Campanulaceae
Lythraceae	
Malvaceae	
Talinum	Portulacaceae
Polygonaceae undiff.	
Rubiaceae undiff.	
Borreria	Rubiaceae
Kohautia	Rubiaceae
Mitracarpus scaber	Rubiaceae
Rutaceae	
Sapindaceae	
cf. Scrophulariaceae	
Solanum	
Thymeleaceae	
Urticaceae	
cf. Clerodendron	Verbenaceae
Monocotyledonae undiff.	
Commelinaceae	
Liliaceae	

AQUATICS

Typha	Typhaceae
Hygrophila	Acanthaceae
Nymphaea	Nymphaeaceae
Polygonum cf. senegalense	Polygonaceae

SPORES

Pteropsida (monolete)
Pteropsida (trilete)

UNKNOWN

INDETERMINATE

Cyperaceae (max. 17%) and *Typha* (1-6% TLP+Aq). In the lower part of this zone the number of taxa is remarkably low (<15), and *Olea hochstetteri* and *Cussonia* are the only woody taxa present. *Amaranthaceae / Chenopodiaceae* and Pteropsida (trilete) attain high frequencies (1-6% TLP + Pteropsida). An abrupt increase in Lactuceae can be recognised between 880 - 860 cm whilst arboreal taxa and Pteropsida are absent. Above 840 cm a number of tree taxa occur for the first time (such as Combretaceae, *Uapaca*, *Lannea/Sclerocarya*).

LT-2 (805-430 cm). Poaceae, *Uapaca*, *Olea hochstetteri*, Cyperaceae, Combretaceae, *Hymenocardia* zone. High tree pollen percentages are recorded consisting mainly of Sudanian and Guinean elements, though Poaceae remains the dominant taxon (>52%). Cyperaceae are consistently present (5-14 %). Fluctuations in the representation of woody taxa have been used to define four subzones.

LT-2a (805-710 cm). Poaceae, *Olea hochstetteri*, Cyperaceae, Combretaceae, *Alchornea, Uapaca* subzone. High percentages of *O. hochstetteri* (max. 15%) characterise this subzone. *Uapaca* values sharply increase towards the top (max. 13%) and there is a corresponding decline in Poaceae to a minimum of 52%. A large number of woody taxa (trees, shrubs and climbers) are consistently present with Combretaceae and *Alchornea* being most prominent (max. 2-3%). The aquatic *Typha* decreases at the start of this zone and then occurs, like most of the herbs, only sporadically. Pteropsida values of a maximum 3% TLP+Pteropsida are recorded.

LT-2b (710-630 cm). Poaceae, *Uapaca*, Cyperaceae, *Hymenocardia*, Combretaceae, *Cussonia*, *Alchornea*, *Burkea africana* subzone. A large number of taxa (max. 49) and high tree pollen percentages are recorded. Poaceae frequencies are relatively low, although they remain greater than 52%. Cyperaceae values are generally lower than in the preceding zone, while *Uapaca* percentages exceed 12%. Other Sudanian and Guinean tree taxa (such as Combretaceae, *Cussonia*, *Burkea africana*, *Ixora*, *Alchornea*), climbers and Pteropsida occur consistently with high values.

LT-2c (630-495 cm). Poaceae, *Uapaca*, Cyperaceae, *Hymenocardia*, Combretaceae subzone. A subzone distinguished by a fall in the number of taxa recorded and lower percentages for woody taxa including *O. hochstetteri*, *Cussonia*, *Alchornea* and *Burkea africana* values for which drop below 1%. Pteropsida, climbers and Asteroideae also occur at lower frequencies. *Monotes kerstingii* is consistently represented in the upper part of this subzone.

LT-2d (495-430 cm). Poaceae, Cyperaceae, *Uapaca*, Combretaceae subzone. *Uapaca* values decline to 1% and a corresponding increase occurs in Poaceae to a maximum of 81%. A number of Guinean trees present in preceding subzones are absent (such as *Mallotus*,

Lophira alata, *Ixora*), whereas *Isoberlinia* is constantly present for the first time. A slight increase in aquatics (*Typha*, *Nymphaea*) is recorded.

LT-3 (430-0 cm). Poaceae, Cyperaceae, Combretaceae, Amaranthaceae/Chenopodiaceae, Asteroideae zone. A zone characterised by low tree pollen taxa values (<12%) and high Poaceae (max. 90%) frequencies. Guinean trees only occur sporadically, while Sudanian and Sahelian elements are more consistently present. Amaranthaceae/Chenopodiaceae and Asteroideae percentages generally exceed 1%. The number of herbaceous taxa recorded is higher than in the previous zone. Cyperaceae and *Typha* are constantly present, with higher percentages at the bottom and particularly at the top of the zone. Four subzones can be defined:

LT-3a (430-332 cm). Poaceae, Cyperaceae, *Celtis*, Combretaceae, *Lannea/Sclerocarya* subzone. The Sudanian taxa Combretaceae, *Celtis* and *Lannea/Sclerocarya* are the dominant trees and shrubs. *Isoberlinia* and *Securinega virosa* occur consistently and Sahelian trees such as *Acacia* and *Hyphaene/Borassus* are present. The representation of *Uapaca*, *Olea hochstetteri* and *Alchornea* becomes sporadic. The herbaceous taxa *Acalypha* cf. *crenata*, Amaranthaceae/Chenopodiaceae, Asteroideae, *Mitracarpus scaber* and the aquatic *Typha* are regularly recorded.

LT-3b (332-195 cm). Poaceae, Cyperaceae, Amaranthaceae/Chenopodiaceae, Asteroideae, Combretaceae subzone. Tree pollen percentages fall below 5% and Poaceae values rise above 85%. Combretaceae and *Celtis* are the only trees which regularly occur at frequencies exceeding 1%.

LT-3c (195-20 cm). Poaceae, Cyperaceae, *Typha*, Amaranthaceae/Chenopodiaceae, Asteroideae, Combretaceae subzone. Tree pollen values slightly exceed those of the preceding subzone. A number of Sahelian taxa are consistently present, for example *Balanites*, *Commiphora*, *Acacia*, and *Hyphaene/Borassus*). Cyperaceae (max. 14%), Amaranthaceae/Chenopodiaceae (max. 3%) and Asteroideae (max. 4%) values rise. High frequencies of *Typha* (max. 8%) are recorded at the bottom and top of this subzone.

LT-3d (20-0 cm). Poaceae, *Typha*, Cyperaceae subzone. A subzone characterised by high *Typha* values (max. 35%) and a subsequent increase in Cyperaceae (max. 37%). The herbs *Mitracarpus scaber* and Lactuceae attain slightly higher values than in the preceding zone. Combretaceae, *Hymenocardia*, *Lannea/Sclerocarya*, *Celtis* and *Crossopterix febrifuga* are the dominant tree taxa.

Fig. 4. Simplified pollen diagram from Lake Tilla: Main taxa (^{14}C dates from parallel core LT95-1 in parentheses)

LAKE TILLA (LT97-1)

Analyst: Ulrich Salzmann
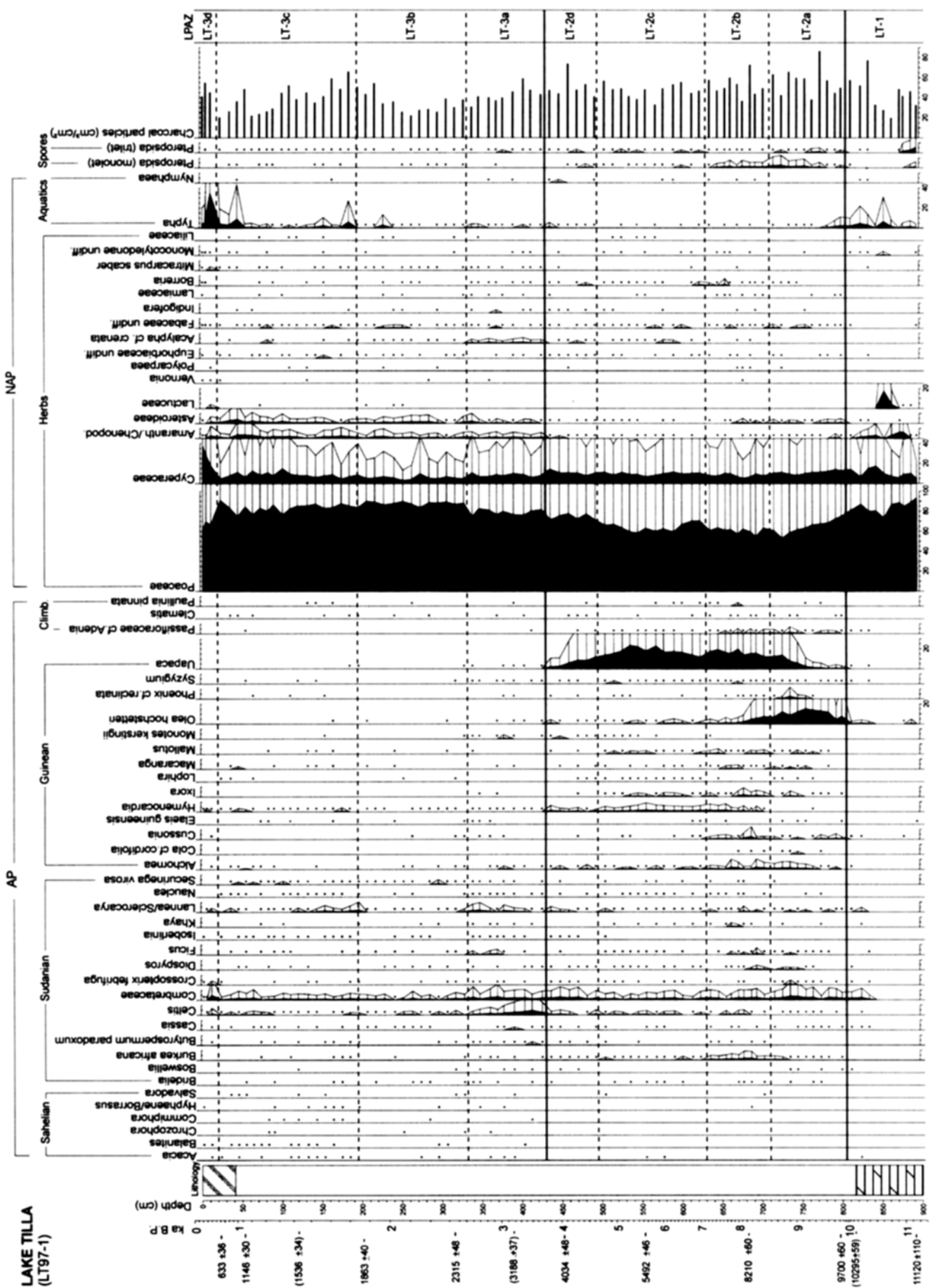
Interpretation

Late Pleistocene (c. 11,200-10,000 B.P.) Zone: LT-1

For the late Pleistocene (c. 11,200-10,000 B.P.) the pollen diagram provides evidence for the presence of open grassland with a scarce tree cover (notably *Olea hochstetteri*) on the Biu Plateau. Low lake levels are indicated by high *Typha* and Cyperaceae pollen values. As with the modern vegetation, Amaranthaceae and Lactuceae appear to have been abundant in the fringing vegetation. Fluctuating lake levels between c. 11,000-10,200 B.P. are indicated by sandy sediment layers and variable pollen percentages for taxa fringing the lake. Drier climatic conditions may have caused the temporary drying-out of the lake. Pollen is poorly preserved over this period which hampers detailed reconstruction of the regional vegetation. From c. 10,200 B.P. onwards a decline in the representation of pollen from the fringing vegetation and an increase in tree taxa suggest the onset of wetter conditions.

Early Holocene (10,000-8000 B.P.) Zone: LT-2a

A wetter climate and rising lake levels at the beginning of the Holocene are indicated by the decreasing percentages of emergent aquatics and the continuous deposition of the black organic lake muds. Increasing tree pollen percentages document the establishment of a diverse Guinean savanna initially dominated by *Olea hochstetteri*.

The modern distribution of *O. hochstetteri* in West Africa is restricted to mountainous regions, generally above 800-1300 m asl, with low temperatures and frequent fogs (Aubreville 1950; Knapp 1973; Maley and Livingstone 1983; Maley and Brenac 1998). This species is absent from the Biu Plateau today, with the nearest population about 240 km to the west on the Jos Plateau above 1400 m asl (White 1983) and about 160 km to the east on the Mandara mountains above 1300 m asl (Letouzey 1968, 1985). High percentages of *O. hochstetteri* in the early Holocene pollen spectra (max. 15%) preclude long distance transportation and clearly indicate the past presence of this species on the Biu Plateau. A wetter climate accompanied by low temperatures during the early Holocene is not only indicated by the dominance of *O. hochstetteri*, but also by increasing percentages of hygrophilous (water-requiring) Pteropsida and the palm *Phoenix reclinata*, which is today widely distributed in Afro-mountainous regions (Letouzey 1985). However the montane vegetation on the Biu Plateau appears to have remained in a transitional stage and never became fully established. Increasing percentages of *Lophira*, *Cussonia*, *Crossopterix febrifuga* and *Uapaca* in particular indicate the simultaneous development of a Guinean "lowland" savanna, which displaced the montane elements after c. 8800 B.P. A slight increase in temperature and evaporation, as well as stronger seasonality, may have been responsible for this vegetation change. Nevertheless, the relatively broad ecological amplitude of *O. hochstetteri* (White 1978) appears to have enabled this species to remain on the Biu Plateau until c. 3500 B.P. as indicated by its continuous presence at Lake Tilla through the mid Holocene.

Mid Holocene vegetation history (c. 8000-3800 B.P.) Zone: LT-2b, LT-2c, LT-2d

At the beginning of the mid Holocene a dense, highly diversified Guinean savanna woodland became established on the Biu Plateau. The highest tree pollen percentages, concentrations and the greatest number of taxa in the Lake Tilla diagram are recorded in subzone LT-2b. Although the spread of woody taxa is likely to have increased the tree cover density, savanna vegetation appears to have remained in most areas. The pollen spectra also contain a number of tree taxa which are characteristic of a Guinean or Sudano-Guinean savanna and which generally do not grow within forests, such as *Lophira*, *Cussonia*, *Burkea africana* and *Monotes kerstingii*). That patches of closed dry forests, with, for example, *Anogeissus*, *Lannea*, *Allophyllus* and woody climbers occurred within the savanna woodland cannot be completely discounted, though the high Poaceae pollen percentages show that a closed grassland vegetation layer covered most areas. Assessments of modern pollen rain in dry forest areas in Burkina Faso and Togo (Lezine and Edorh 1991; Neumann and Ballouche 1992) have shown that in these vegetation formations Poaceae pollen percentages fall below 50%.

Detailed reconstruction of the structure and physiognomy of the mid-Holocene savannas is made difficult by the under-representation of the mostly zoogamous trees in the pollen spectra. In addition, the separation and reconstruction of regional and local vegetation is hampered by the wide range of potential habitats for a number of Sudanian and Guinean taxa such as *Alchornea*, *Uapaca* and *Syzygium* which can be part of a savanna as well as a dense forest fringing the former lake. The high frequencies of *Uapaca* in the mid Holocene spectra probably reflect the establishment of a dense gallery forest with climbers around the lake in which *Ixora*, *Alchornea*, *Macaranga* and *Ficus* also regularly occurred.

A probable modern analogue of the Guinean savannas which appear to have covered the Biu Plateau at the beginning of the mid-Holocene can be found about 350 km to the south at the forest/savanna boundary where the annual rainfall generally exceeds 1200 mm (Clayton 1958; Jones 1963; Keay 1952; Killick 1959). Characteristic species include *Lophira lanceolata*, *Cussonia barteri*, *Uapaca togoensis*, *Burkea africana*, *Crossopterix febrifuga*, *Hymenocardia acida*, *Khaya senegalensis*, *Anogeissus leiocarpus* and *Ixora bauchiensis* (Adjanohoun and Ake Assi 1967; Knapp 1973; White 1983). Keay (1959 a,b) has called this formation a "Southern Guinean Savannah" which can be distinguished from the "Northern Guinean Savannah" (= Sudano-Guinean) by the lack of the trees *Monotes kerstingii* and *Isoberlinia doka*.

From c. 6800 B.P. onwards a decline in tree pollen percentages particularly *Cussonia*, *Burkea africana*, *Alchornea* and woody climbers, as well as the slight decrease in pollen concentrations, point to a gradual vegetational change, which was presumably accompanied by a reduction of tree cover. The occurrence of *Monotes kerstingii* from c. 5800 B.P. onwards, followed by
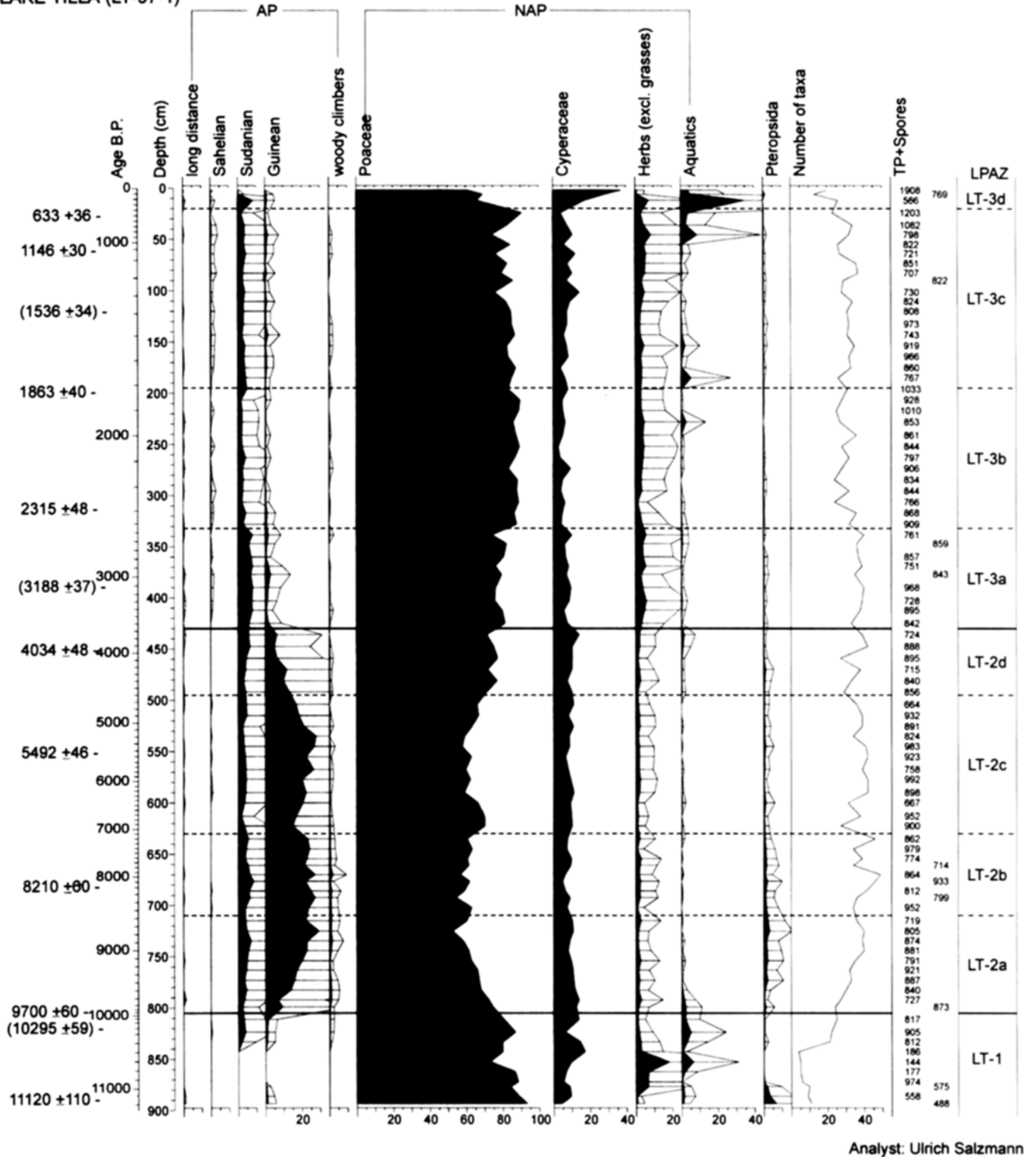
Fig. 5. Lake Tilla: Phytogeographic groups, number of taxa and total pollen sum (^{14}C dates from parallel core LT95-1 in parentheses)

Isoberlinia at c. 4800 B.P. indicates a floristic change from a Guinean savanna to a drier Sudano-Guinean savanna. This trend towards arid conditions appears to have intensified at the end of the mid Holocene. From 4800 B.P. (LT-2d) and particularly after 3800 B.P.

(LT-3a) many of the Guinean taxa appear only sporadically whereas Poaceae frequencies increase. The decline in *Uapaca* coincides with the slight increase in *Typha* which point to lower lake levels and a decline in the fringing swamp forest.

Late Holocene vegetation history (post c. 3800 B.P.)
Zone: LT-3a, LT-3b, LT-3c, LT-3d

By the beginning of the late Holocene a southern Sudanian savanna was established on the Biu Plateau with a floristic affinity that seems to have closely resembled that present today. After 3800 B.P. Guinean taxa occur only sporadically, whereas Sudanian and Sahelian elements become more abundant. Increasing percentages of *Celtis* cf. *integrifolia* and *Ficus* point to the establishment of a Sudanian open fringing forest, which replaced the former Guinean swamp forest with *Uapaca*. As is the case today, *Typha* and numerous herbs (Amaranthaceae/Chenopodiaceae, Asteroideae, *Acalypha crenata* and *Mitracarpus scaber*) colonised the seasonally flooded shoreline around the shrinking lake.

Whereas the vegetational changes between 6800-2500 B.P. can clearly be attributed to a gradual shift towards drier conditions, the overall decline of trees and shrubs associated with increasing sedimentation rates after 2500 B.P. cannot be explained by changing climatic conditions alone (Fig. 3). The corresponding spectra (LT-3b) neither show a distinct increase in fringing vegetation indicating lower lake levels, nor do they point to a floristic change towards a drier Sahelo-Sudanian savanna with an increase of Sahelian taxa. Furthermore it is questionable whether a thinning of tree cover density would enable such an increase in slope erosion, as the dense undisturbed grass cover generally provides sufficient soil protection to prevent it. Therefore it seems to be likely that human activities are responsible for the change in sedimentation. As a result of the preceding climatic deterioration, the lake may have become an important water reservoir for early pastoralists during the dry season. The grazing and trampling of cattle might have partly destroyed the protective grass cover on the slopes, as happens today. The decline in tree pollen percentages in subzone LT-3b is difficult to interpret as it may either reflect clearing of woodland by human activities or may have simply been caused by fluvial input of grass pollen together with the eroded soil material.

After c. 1800 B.P. (LT-3c) increasing percentages of *Typha*, Asteroideae and Amaranthaceae/Chenopodiaceae indicate a further lowering of lake level. The corresponding rise in tree pollen such as *Lannea/Sclerocarya*, Combretaceae and *Celtis* reflects the establishment of Sudanian savanna woodland around the edge of the former lake floor (which persisted until today) rather than a return to wetter conditions. The abrupt increase in *Typha* and Cyperaceae in the uppermost layers (LT-3d) documents the relatively recent silting up of the lake.

The increase in sedimentation rate after 2800 B.P. provides the strongest evidence of human impact. Other indicators are difficult to find. The charcoal curve, which might be expected to furnish information on early human activity, remains surprisingly low. Increasing frequencies of herbaceous taxa are probably the result of lower lake levels rather than indicating the spread of ruderal plants promoted by agro-pastoral activities. Another indicator of human impact could be an increase in records of trees of potential economic use. *Balanites aegyptiaca* and *Acacia albida* are valuable fodder trees

(Maydell 1983) and fruit dispersal might have been enhanced by domesticated animals. However, ecologically these species are very flexible and it might also indicate drier conditions. *Butyrospermum parkii* (shea-butter tree) is one of the most prominent economic trees of the Sudanian zone, though it appears not to have played an important role on the Biu Plateau.

Fire activity

The relatively unchanging quantities of charcoal particles in the sediments of Lake Tilla point to surprisingly constant fire frequencies and intensities on the Biu Plateau throughout the Holocene. A slight increase is only evident in the late Holocene spectra together with high *Typha* percentages, and in the samples covering the early Holocene wetter period. These fluctuations can be attributed to an increase in biomass of either the fringing vegetation or the surrounding savanna. High percentages of charred particles of grass epidermis indicate regular savanna fires. Although it cannot be excluded that human activity might have started fires long before the beginning of the Holocene, it should be stressed that the frequency remains remarkably constant even into the late Holocene. As human activity expanded, a corresponding increase in the frequency of fire would be expected. The consistency of the charcoal curve throughout the Holocene points to the importance of natural fires in maintaining woodland savanna ecosystems.

Discussion

Palaeoenvironmental and climatic changes

At Lake Tilla a period of fluctuating water levels suggests the development of wetter, but unstable, climatic conditions at the end of the late Pleistocene. The dry phase noted between c. 11,000 and 10,200 B.P. has also been recorded at several other sites in tropical Africa and can be attributed to the global climatic change of the Younger Dryas period (for example Bonnefille et al. 1992; Gasse et al. 1990; Maley and Brenac 1998; Salzmann and Waller 1998; Talbot et al. 1984). During the late Pleistocene the Biu Plateau around Lake Tilla was covered by an open grass savanna in which the presence of the montane element *O. hochstetteri* suggests cool climatic conditions. Given a wet adiabatic lapse rate of 0.6°C per 100 m, the spread of *O. hochstetteri* from the neighbouring Jos Plateau (presently at 1300 m asl) and Mandara mountains, to the Biu Plateau (ca. 800 m asl) would indicate a temperature about 3°C lower than today. A similar estimate has also been given for several other sites in tropical Africa (such as Bonnefille et al. 1992; Maley and Brenac 1998; Maley and Livingstone 1983).

A rise in lake level and the increase in Guinean tree taxa at c. 10.000 B.P. indicate an abrupt climatic change to wetter conditions which is recorded at nearly all West African palaeoecological sites at the beginning of the Holocene. With high frequencies of *O. hochstetteri* at the early Holocene, the pollen diagram of Lake Tilla shows striking similarities to that of Lake Bosumtwi situated in the rain forest zone of Ghana (Maley 1991;

Maley and Livingstone 1983). Here, the lowering of montane vegetation to about 400 m asl until about 8500 B.P is interpreted as being an indicator of low temperatures coupled with an increase of stratiform cloud cover and frequent fog. A similar conclusion can be drawn from the Lake Tilla diagram. *O. hochstetteri*, which is described by White (1978) as an "ecological transgressor" from upland to lowland regions, remained on the Biu Plateau presumably as residual vegetation until the beginning of the late Holocene. However, the relatively broad ecological amplitude of this species also suggests that caution should be exercised drawing detailed climatic conclusions in particular for the time period 9500-8500 B.P. The Guinean lowland savanna which prevailed during the early Holocene with the montane *O. hochstetteri* has no modern analogue at this latitude. The rapid spreading of this species around 9000 B.P. may simply have been caused by the high number of sites available for colonisation, and consequent pre-emption of them (making the habitats unavailable to other taxa).

Between 8500-6800 B.P. a swamp forest vegetation with Guinean affinities with, for example, *Uapaca*, *Alchornea* and *Macaranga* became established around the lake, whereas the formerly open savanna on the plateau was replaced by a dense Guinean savanna with *Cussonia*, *Uapaca* and *Hymenocardia*. Patches of closed dry forests may have occurred but never completely displaced the savanna vegetation. In floristic composition the mid Holocene vegetation closely corresponds to that of the modern Guinean savanna, which can be found in Nigeria about 350 km south of the Biu Plateau (Jones 1963; Keay 1959 a,b). Hence, the pollen spectra seem to support the assumption of a latitudinal shift of vegetation zones in response to fluctuating climatic changes (for example, Dupont and Agwu 1992; Hooghiemstra 1988; Lezine 1989). Similar vegetational trends could also be found in early and mid Holocene pollen sequences at Sahelian sites in Senegal (Lezine 1987, 1989) and the Manga Grasslands in northeast Nigeria (Salzmann 1996; Salzmann and Waller 1998). As with the Manga Grasslands, which are situated about 300 km north of Lake Tilla, maximum tree and shrub pollen values and the largest number of taxa are recorded during the early and mid Holocene suggesting wet conditions. Whereas at both sites in northeast Nigeria the pollen spectra clearly indicate the persistence of savannas throughout the Holocene, an increase in Guinean tree taxa in the pollen spectra from the Senegal is interpreted as a shift of mesophilous forests up to 16°N from about 9000 to 7000 B.P. (Lezine 1988). A mid Holocene wet period is also indicated by pollen records from Tjeri (Lake Chad), where a maximum northward extension of Sahelian vegetation was recorded between 7500-5000 B.P. (Maley 1981). About this time Lake Chad may have reached its highest level (Servant and Servant-Vildary 1980; Thiemeyer 1992).

From c. 6800 B.P. onwards, the pollen diagram from Lake Tilla points to a progressive vegetation change from a dense Guinean savanna to a more open Sudanian savanna, implying drier climatic conditions. Around 3700 B.P. a distinct change in the vegetation fringing the former lake and the occurrence of Sahelian taxa point to

the intensification of these conditions, which finally led to the establishment of a savanna closely resembling the modern vegetation. Major vegetational changes are recorded at nearly all West African palaeoecological sites at the beginning of the late Holocene (for example, Ballouche and Neumann 1995; Lezine 1989; Maley 1981, 1991; Sowunmi 1981; Kadomura and Kiyonaga 1994; Reynaud-Farrera et al. 1996). Again, the changes recorded at Lake Tilla closely correspond to developments occurring at the Sahelian zone of northeastern Nigeria (Holmes et al. 1997; Salzmann and Waller 1998). In the Manga Grasslands climatic deterioration from c. 5000 B.P. onwards is indicated by a gradual decline in the representation of many of the swamp forest elements. An abrupt biostratigraphical and sedimentological change at c. 3300 B.P. is interpreted as the major shift towards drier climatic conditions, which resulted in the establishment of the modern Sahelian vegetation. The results also broadly conform with investigations from the Lake Chad basin, though here aridification from c. 5000 B.P. onwards was interrupted by a late Holocene lacustrine phase between 3500-3000 B.P. (Maley 1981; Servant and Servant-Vildary 1980). After a subsequent distinct dry phase the return to wetter conditions during the last two millennia is indicated by rising lake levels and the renewed spread of forest in the Cameroon-Congo rain forest block (for example Elenga et al. 1994; Maley and Brenac 1998; Vincens et al. 1998). However, neither Lake Tilla nor the palynological and palaeolimnological results from the Manga Grasslands (Holmes et al. 1997; Salzmann and Waller 1998) give evidence for such fluctuations in climate during the late Holocene. In both regions continuous aridification is recorded from c. 6000/5000 B.P. onwards, which intensified around 3800-3300 B.P and finally resulted in the drying-out of many of the lakes.

While major climatic changes are evident for the late Holocene, it is highly likely that at the same time human activity increased. For the Lake Chad basin, archaeological excavations provide evidence for the introduction of pastoralism and ceramics around 4000 B.P. and the domestication of *Pennisetum* from at least 3000 B.P. onwards (Breunig et al. 1996; Klee and Zach 1999). Metalworking might have followed only several hundred years later and was practised on the Jos Plateau (Nigeria) by around 2500 B.P. (Calvocoressi and David 1979). Evidence of human activity in pollen diagrams is problematic due to the absence of unambiguous indicators. The modern pollen spectra of Lake Tilla indicate an open savanna but give no evidence for agricultural or pastoral activities. Increasing percentages of herbaceous taxa (notably weeds), trees of potential economic use and charcoal layers were considered by Ballouche and Neumann (1995), Kadomura and Kiyonaga (1994), Schulz (1994) and Sowunmi (1999) to demonstrate the importance of human activity in the late Holocene. Nevertheless, none of these indicators of human activities could be detected at Lake Tilla. The increase in herbs can confidently be related to the lowering of lake level, and the occurrence of trees with a potential economic use and charcoal particles remain relatively constant even in subrecent samples. As with the Manga Grass-

lands diagrams, the Lake Tilla sequence demonstrates the difficulties of detecting human activity in the savanna zone rather than implying that such activity was absent (Waller and Salzmann 1999).

The increase in sedimentation rates after 2500 B.P. is the only evidence to support the assumption that human impact increased during the late Holocene. As the pollen diagram provides no indication of a simultaneous lowering of lake level or a further floristic change towards a drier Sahelo-Sudanian savanna, the rise in erosion may reflect increasing human impact rather than an abrupt climatic change. However, the change in sediment accumulation coincides with vegetational changes which have been recorded at several sites in the West African rain forest zone (for example Elenga et al. 1994; Reynaud-Farrera et al. 1996) and are attributed by Van Geel et al. (1996) to a global climatic change around 2650 B.P. A significant change in geomorphody-namic processes between c. 3000-2000 B.P. is also indicated by fluvial terraces in west Cameroon and Nigeria which contain charcoal and numerous ceramics (for example Brunk 1992; Rohdenburg 1978; Van Noten and De Ploey 1977, Zeese 1991). As is the case of the latter fluvial terraces, it cannot be completely discounted that a further climatic change was responsible for the thinning of vegetation cover and increasing erosion rates at Lake Tilla as well. Thus, there is no unambiguous proof of increasing human activity around 3000-2000 B.P. in this region.

What caused the Sudanian savanna to form?

The discussion of the origin of savannas is directly related to the question as to which environmental conditions control the coexistence of the opposing life forms grasses and trees, and how far savannas represent a stable equilibrium. Walter (1979) postulated that the competition for the limited resource water is a key factor which restricts the distribution of natural savannas as a stable climatic climax to regions with an annual rainfall of 300-500 mm. Experiments in protected savanna areas (such as Charter and Keay 1960; Swaine 1992) and investigations on isolated forest stands in the Sudanian zone (for example Anhuf 1997; Guinko 1985; Hahn-Hadjali 1998; Kéré 1998; Neumann and Müller-Haude 1999) seem to support the assumption that the present precipitation in the southern savannas is sufficient to allow the establishment of dense forests. Grazing by wildlife or domestic animals, edaphic factors as well as natural and human induced fires have been advocated as additional key determinants maintaining the open savanna vegetation (for example Bourliere 1983; Cole 1986; Lawson 1986; Schnell 1976). The recent environmental changes which take place under the pressure of increasing land use and droughts have focussed the discussion on the role of human disturbance as a major agent. Numerous ecologists postulate that modern Sudanian and Guinean savannas are mostly the result of degradation of closed forests - a process which might have started during the mid and late Holocene (for example, Anhuf 1997; Anhuf and Frankenberg 1991; Guinko 1985; Chevalier 1951).

The hypothesis of the human origin of Sudanian savanna has to be questioned in the light of the new evidence provided by the Lake Tilla pollen diagram, which clearly demonstrates the stability of savanna formations throughout the Holocene. Changes in vegetation appear to have been mainly controlled by climate, although increasing precipitation rates during the early and mid Holocene did not result in the displacement of savanna by forest. Similar conclusions have been drawn from pollen records from the savannas and grasslands of the southern hemisphere near 10°S, which have also demonstrated the persistence of grassland and savannas throughout the late Quaternary (Livingstone 1971; Meadows 1984; Vincens 1989). Of particular interest are the results from the Miombo woodland of Zambia (Livingstone 1971; Vincens 1989), which is floristically closely related to the Sudanian *Isoberlinia*-savanna of the northern hemisphere (for example, White 1983). From the persistence of Miombo savanna Livingstone (1971) concluded that vegetational changes caused by an alteration in precipitation of about 50% from the present mean level would not be great enough to be palynologically recognisable. On the Biu Plateau, in contrast, changes in floristic composition seem to be closely linked to climatic trends, although the reconstruction of climatic induced changes in structure (notably tree cover density) remains problematic. The northward shift of Guinean savannas c. 9000 B.P. suggests that the zonal limits and floristic assemblages of the southern Sudanian and Guinean savannas may have already existed at the beginning of the Holocene and are not the result of recent anthropogenic degradation of forests. This coincides with the zonal classification of Keay (1959 a,b) who separated the "climatic" savannas of the northern and southern Guinea zone from the southern "derived savanna zone", which truly is the result of forest degradation.

What environmental factors other than climate could have maintained the savanna around Lake Tilla? Edaphic factors seem to have played only a minor role, as the soils of the Biu Plateau provide enough nutrients to support intensive agriculture, although they are generally weakly developed (Kparmwang et al. 1998). In addition, botanical investigations in Burkina Faso have shown that less developed soils which are poor in nutrients do not always hamper the establishment of forests (Hahn-Hadjali 1998; Neumann and Müller-Haude 1999). The isolated dry forest stands can frequently be found on shallow lateritic soils which are unsuitable for agriculture.

Of particular interest is the charcoal curve for Lake Tilla, which points to a surprisingly continuous fire history. Fires have often been mentioned as a major contributory cause in the development of savanna (for example Brookman-Ammisah et al. 1980; Charter and Keay 1960; Swaine 1992). Natural fires, most frequently caused by lightning at the beginning of the rainy season, are an elementary constituent of the savanna ecosystem (for example Goldammer 1990; Bond and Van Wilgen 1996). Nevertheless, the early presence of humans in west Cameroon is demonstrated by 30000 year old archaeological finds at the Shum Laka cave (de Maret et al. 1995), so that the impact of fires on the savanna

caused by early people cannot be completely discounted. Today natural fires are only of minor importance on the Biu Plateau as intensive grazing of herds and frequent burning by humans greatly reduces the amount of dead biomass at the end of the dry season. In contrast to natural fires, fires caused by people are generally characterised by high frequencies and low intensities (Van Wilgen et al. 1990). The change in fire regime, which could be expected to have occurred during the last millennia, does not seem to have affected the amount of charred particles in the Lake Tilla core. As the charcoal particle curve reflects both the intensity and frequency of fires in the source area (Singh et al. 1981), an overlapping of both parameters might be the reason why this change remained palaeoecologically silent. An additional important factor which might have influenced the ecological balance between grasses and trees long before human arrival is the impact of wild herbivores, notably elephants (for example Cumming 1982; Schnell 1976). Unfortunately their significance in the Holocene can hardly be determined by pollen analysis. Nevertheless, as with natural fires their importance certainly declined with increasing human impact.

The Lake Tilla profile suggests that climatic change and fire were major agents which controlled the physiognomy and structure of the savanna throughout the Holocene. Herbivory and human activities might have been of additional importance. Today agricultural and pastoral activities are clearly the major factors which shape the savannas of West Africa. As previously noted, unambiguous indicators of human activity are not available and hence no conclusion can be drawn from the Lake Tilla pollen diagram at what date the transformation to the modern park savanna by humans started. The scarcity of comparable sites available for the southern Sudanian zone hinders the reconstruction of Holocene vegetational and climatic trends on a subcontinental scale. However, the new results give no evidence that a closed dry or semi-deciduous forest was the natural vegetation - an assumption which is strongly linked with the old view of succession and stable climatic climax of Clements (1916). The pollen spectra of Lake Tilla rather support the idea that savannas are vegetation systems which do not have a cause, "but rather develop in response to a cluster of interacting factors" (Sanford and Isichei 1986, p. 105).

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