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Vegetation Evolution in the Mountains of Cameroon During the Last 20 000 Years: Pollen Analysis of Lake Bambili Sediments

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1. Introduction

Tropical rainforests are the most biologically diverse ecosystems on the planet (Puig, 2001). In the highlands and mountains of western Cameroon (Central Atlantic Africa), a set of plateaus and mountains that contain large forested areas, this diversity is now subject to significant human pressure due to a large population engaged in agriculture and ranching. Momo Solefack (2009) shows that between 1978 and 2001 deforestation in Oku was 579 ha / year, with a annual rate of 4% increase. In addition to anthropogenic impacts, climate change plays a major role in influencing the distribution and composition of ecosystems (Walther et al., 2002; Thomas et al., 2004; Schröter et al., 2005; Thuiller et al., 2006).

The Bamenda Highlands have a particular forest characterized by the presence of one of the few African gymnosperms, *Podocarpus latifolius*. This species migrated from East to West Africa through Angola and then colonized the high mountains of Cameroon. It is currently restricted to altitudes above 1800 m, in the areas of Mount Oku and Kupé (Letouzey, 1968). Pollen data of Central Atlantic Africa have shown that this *Podocarpus* forest was once significantly more extensive than today during the last climatic cycle, especially during the last ice age (Dupont et al., 2000; Elenga and Vincens, 1990; Maley and Livingstone, 1983). At this time, *Podocarpus* was present at low and mid altitudes mixed with the dense Guineo-Congolian forest. The expansion of *Podocarpus* into these areas did not end until very recently, about 3000 years ago (Vincens et al., 2010). Such a distribution, involving the recent migration of the species to higher altitudes (White, 1993), suggests that such forests are likely refugia. This chapter, based on a sedimentary sequence of 14 m taken at Lake Bambili covering the last 20,000 years, presents the first palynological data from altitude in this region. Preliminary analysis of data from Bambili has been presented by Assi-Kaudjhis et al. (2008). The aim of this paper is to study the development and evolution of mountain forest in Cameroon over this interval.

2. Location, climate, and vegetation of bambili

Lake Bambili (05°56'11.9 N, 10°14'31.6 E, 2273 m asl) is a crater lake that lies in the volcanic zone of Cameroon (Figures 2 and 3) in the Bamenda Highlands and Bamboutos Mountains.

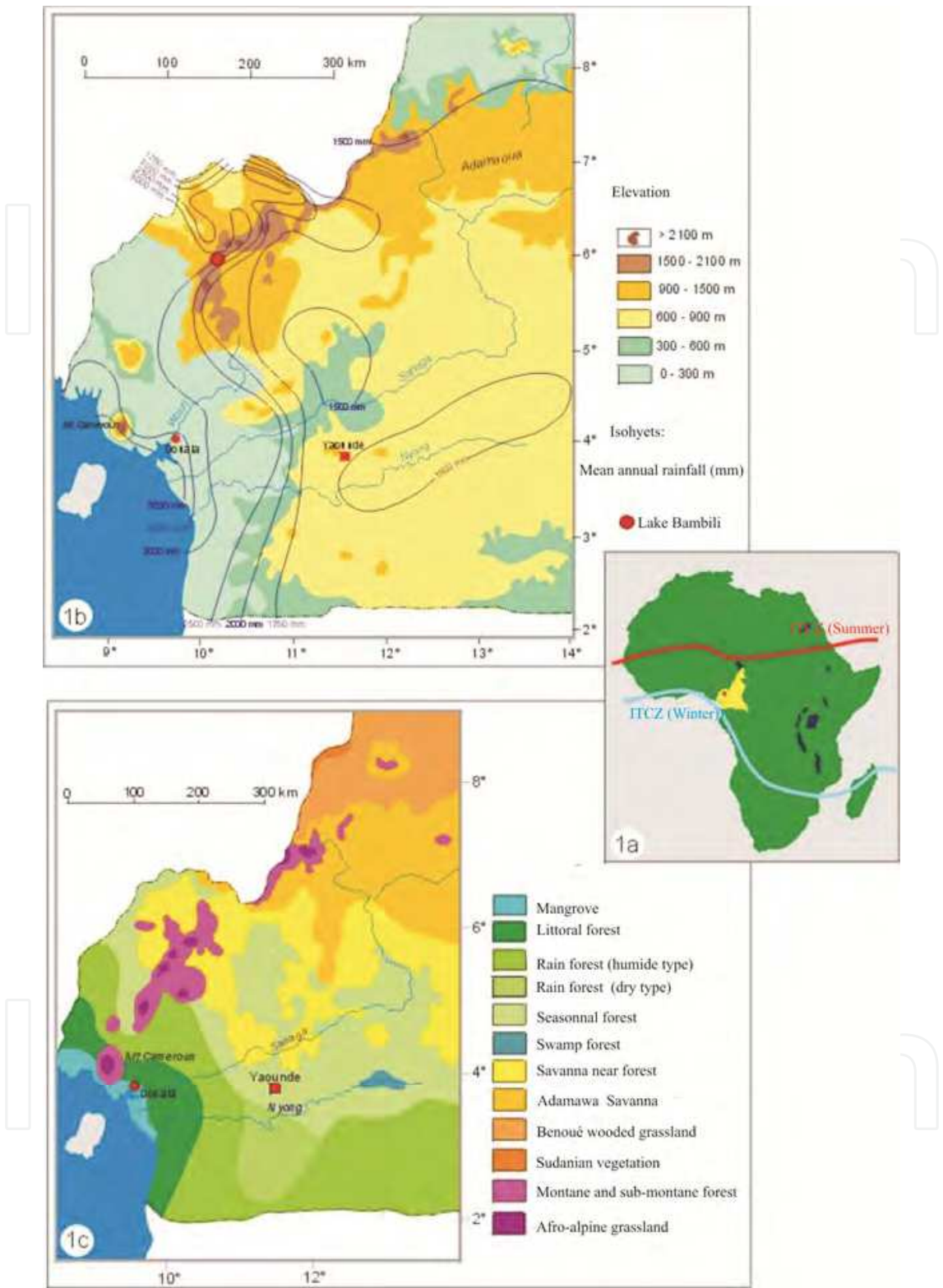


Fig. 1. Presentation of the study site (in Assi-kaudjhis et al., 2008).
1a: Location of Lake Bambili, Cameroon; red line: ITCZ boreal summer; blue line: boreal winter ITCZ.
1b: Topography and rainfall in the study area.
1c: Phytogeography of the study area (Letouzey, 1968).

In northeastern Bambili, Mount Oku rises to 3011 m asl, the second highest peak in the country after Mount Cameroon (4070 m asl). The lake is part of a complex formed by two adjacent craters separated by about 45 m in altitude. The highest crater today is a swamp that discharges water into the crater below. The lower crater contains a lake of about 3 m depth. The lower crater contains a lake of about 3m depth with a single outlet to the northeast. The lake margin is narrow, consisting of a strip of herbaceous sub-aquatic vegetation, such as Cyperaceae and ferns, growing on peat-rich soil.



Fig. 2. The crater lake Bambili (05 ° 56'11.9 N, 10 ° 14'31.6 E, 2273 m asl). The red dot indicates the core location in the lower crater lake and the yellow dot is the second core location in the swamp of the second upper crater.

Centrally located in the Guineo-Congolian region, Cameroon has a relatively humid climate due to the location of the country to the Gulf of Guinea (Suchel, 1988) which is responsible for the long rainy season over 4 / 5 of the country (western and southern regions) and slightly drier tropical climates in the north of the Adamawa plateaus. The seasonal alternation of southwesterly moisture flux and northerly dry winds, called the Alizé, creates a wet season from March to October and a more variable drier period during the rest of the year. The influence of altitude and distance from the coast result in lower precipitation in Bambili than Douala (2280 mm in Bamenda at 1370 m asl and 2107 mm in Bafoussam at 1411 m asl) and lower average temperatures (19°C to 20°C in Bamenda and Bafoussam against 26°C in Douala). Dry season precipitation from November to February is below 50 mm (Web LocClim, FAO, 2002). During the rainy season, precipitation is as high as 400 mm per month with temperatures fluctuating between 18.1 and 21.2°C.

Cameroon vegetation (Figures 3a and 3b) was described by Letouzey (1968, 1985) and White (1983). It is divided by latitude and altitude. At Bambili, aquatic vegetation grows in bands at the lake margin in the area of permanent open water: after *Nymphaea* sp. (Nymphaeaceae) on the edge of open water is a belt of Cyperaceae, ferns and aquatic plants, then, on the dry ground appear species of Poaceae.



Fig. 3a. Satellite Photo of crater lake Bambili (05°56'11 .9 N, 10°14'31 .6 E, 2273m asl).The dashed line connecting Bambili to Lake Oku is 36.5 km. Dark Red = forest; Light red = mosaic of fallow and degraded forest; Dark Blue = marshland; Black = open water; White = bare soil.

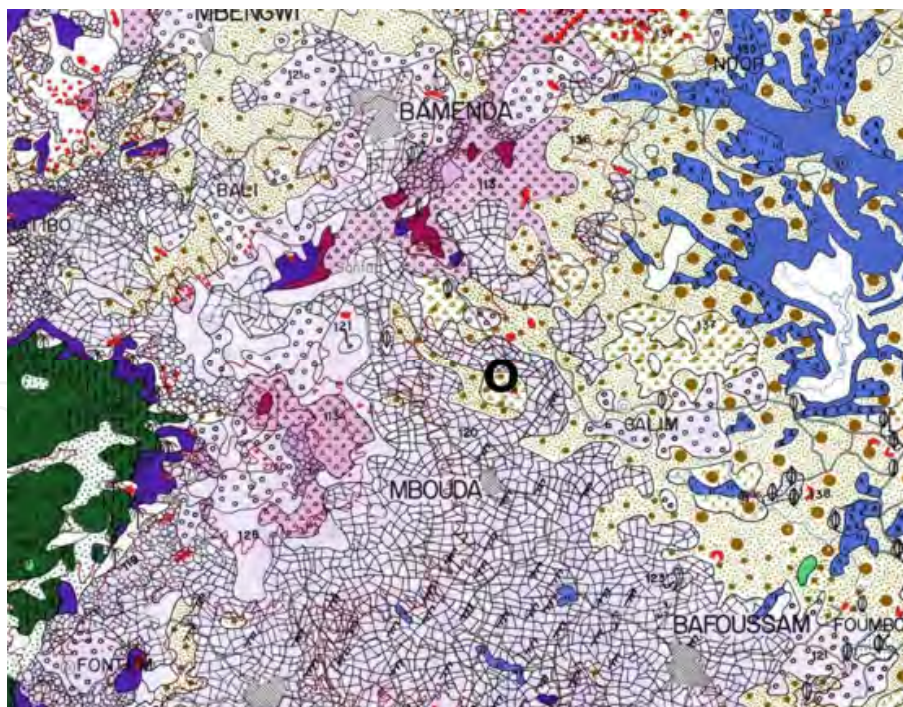


Fig. 3b. Vegetation map of the Bambili region (Letouzey, 1985) Green = moist forests; Light pink = fallow; Red = montane forest; Violet = submontane forest; Blue = marshland; Yellow = edge of the montane forest; Light yellow = savanna. Black circle indicates the location of Lake Bambili.

In general, the distribution of the plant communities of Cameroon at altitude is as follows:

Above 2400 m asl: afro-alpine
<i>Alchemilla fisheri</i> subsp. <i>camerunensis</i> (Rosaceae)
<i>Agrostis mannii</i> (Poaceae)
<i>Veronica mannii</i> (Asteraceae)...
From 2400 to 1600 m asl: montane forest
<i>Podocarpus latifolius</i> (Podocarpaceae)
<i>Rapanea melanophloeos</i> (Myrsinaceae)
<i>Olea capensis</i> (Oleaceae), <i>Hypericum</i> sp. (Ulmaceae)
<i>Nuxia congestata</i> (Loganiaceae)
<i>Embelia</i> sp. (Myrsinaceae), <i>Celtis</i> (Ulmaceae)
<i>Clematis simensis</i> (Ranunculaceae)
<i>Hypericum</i> sp. (Hypericaceae)
<i>Syzygium staudtii</i> (Myrtaceae)
<i>Gnidia glauca</i> (Thymelaeaceae)
<i>Schefflera abyssinica</i> , <i>S. mannii</i> (Araliaceae)
<i>Arundinaria alpina</i> (Poaceae)
From 1600 to 800 m asl: sub-montane forest (boundary between Guineo-Congolian and Afro-montane regions)
<i>Olea hochstetteri</i> (Oleaceae)
<i>Schefflera abyssinica</i> (Araliaceae)
<i>Microglossia densiflora</i> (Asteraceae)
<i>Maytenus undata</i> (Celastraceae)
<i>Hypericum revolutum</i> (Hypericaceae)
<i>Prunus africana</i> (Rosaceae)
<i>Alchemilla fischeri</i> (Rosaceae)...
Combined with elements of semi-deciduous rain forest
<i>Polyscias fulva</i> (Araliaceae)
<i>Santiria trimera</i> (Burseraceae)
<i>Bridelia speciosa</i> (Euphorbiaceae)
<i>Uapaca</i> sp. (Euphorbiaceae)
<i>Leonardoxa africana</i> (Caesalpiniaceae)
<i>Celtis africana</i> (Ulmanceae)
<i>Anthocleista</i> (Loganiaceae)...
Savannas and herbaceous layer
<i>Annona senegalensis</i> (Annonaceae)
<i>Bridelia ferruginea</i> (Euphorbiaceae)
<i>Cussonia djalonensis</i> (Araliaceae)
<i>Terminalia avicennioides</i> (Combretaceae)
<i>Vernonia turbinata</i> (Compositae)
<i>Hymenocardia acida</i> (Euphorbiaceae)

The organization of vegetation, based on Letouzey's studies (1968). But now, it is a theory, as environmental conditions have deteriorated (Table I). Thus, analysis of satellite images of

1998 and 2003 show that the forest cover around Bambili has deteriorated sharply in recent decades (Assi-Kaudjhis, 2011).

	1988	%	2003	%
Savanna, grassland and crops	3676.17	13.3	11615.65	42.03
Residential areas and bare soil	2196.79	7.95	4 766.18	17.25
Forest	3660.14	13.23	2472.65	8.95
Degraded forest	18086.1	65.40	8754.07	31.66
Lakes	31.81	0.12	29.31	0.11

Table I. Area (ha) of different units of land between 1988 and 2003.

3. Materials and methods

Two cores of 13.5 m and 14.01 m were taken a few meters apart at Lake Bambili in February 2007 and January 2010, respectively (Figure 4). The cores were taken using a Russian manual corer (Jowsey, 1966) in sections of 60 cm in length. The two sedimentary sequences were combined into a single sequence on the basis of benchmark levels identified in each, the depth (mcd) was calculated. The cores were sampled every 5 to 10 cm for pollen analysis.



Fig. 4. Coring on Lake Bambili using the Russian manual corer.

Overall, the sediments are composed of organic material and clay. From 0 to 635 cm, organic rich brown peat dominates becoming more compact and darker towards the base. Between 635 and 657 cm, sediments are mostly organic rich with centimeter-sized nodules of gray-green clay. Finally, 657 cm to the base of the sequence is an organic-rich compact black clay. A charcoal layer is observed at 1355 cm.

Laboratory number	Depth (cm) of the sample	Nature of the sample	Radiocarbon age BP			cal age-	cal age+	Average age (years cal BP)
SacA 8485	199-200	peats	1125	±	30	980	1037	1008.5
SacA 8486	299-300	peats	1745	±	30	1615	1704	1659.5
SacA 8487	399-400	peats	2170	±	30	2124	2301	2212.5
SacA 8488	499-500	peats	2315	±	30	2329	2352	2340.5
SacA 8489	599-600	peats	2485	±	30	2491	2707	2599
SacA 8490	699-700	peats	3175	±	30	3370	3442	3406
SacA 8491	799-800	peats	5515	±	30	6284	6318	6301
SacA 8492	899-900	peats	7255	±	35	8014	8156	8085
SacA 8493	999-1000	peats	8160	±	45	9015	9135	9075
SacA 8494	1099-1100	peats	10050	±	45	11404	11705	11554.5
SacA 8495	1198-1199	peats	11560	±	50	13323	13439	13381
SacA 10870	1248-1249	peats	12550	±	50	14605	14946	14775.5
SacA 10872	1348-1349	peats	14330	±	60	16950	17387	17168.5
Laboratory number	Depth (cm) of the sample	Nature of the sample	Radiocarbon age BP			cal age-	cal age+	Average age (years cal BP)
BB01-2010	1325	peats	14150	±	60	17032	17405	17218.5
BB01-2010	1355	charcoal	15020	±	60	18062	18505	18283.5
BB01-2010	1377	peats	15840	±	70	18840	19258	19049
BB01-2010	1410	peats	16910	±	70	19962	20256	20109

Table II. Radiocarbon dates and age model of the two cores taken in 2007 and 2010 at Bambili.

Seventeen AMS dates were performed, which show a continuous deposition for the last 20,000 years with a sedimentation rate ranging from 0.208 cm per year between 0 and 650 cm and 0.05 cm per year from 650 cm to the base (Table II). Radiocarbon measurements were calibrated using the CALIB software version 5.0. (Stuiver et al., 2005). The samples for pollen analysis were chemically treated with hydrochloric acid (HCl) and hydrofluoric acid (HF) according to the conventional method described by Faegri and Iverson (1975) preceded by a sieving at 250 microns to remove coarse particles. Treatment was terminated by filtration at 5 microns.

A total of 141 samples were analyzed with an average time resolution of 146 years. Counts ranged from 303 to 1500 pollen grains according to the richness of each sample, and 203 pollen taxa were identified. Data are presented as a diagram drawn on the basis of percentages calculated on a sum excluding aquatic plants and ferns.

The CONISS program used in the Tilia program (Grimm, 1987) was employed for the subdivision of the pollen diagram in zones. Analysis of palynological richness (Birks and Line, 1992), in order to estimate biodiversity, was performed with the software PSIMPOLL (<http://www.chrono.qub.ac.uk/psimpoll/psimpoll.html>).

4. Results

The microflora (Table III) consists of 119 taxa of trees, lianas and palms, together with 36 herbaceous taxa and 32 undifferentiated taxa, which correspond to plants that may be trees or herbs. Finally, 10 taxa correspond to aquatics plants, 4 to ferns and one to a plant parasite.

Family	Taxon	Habit	AA	FM	FSM	FSD	FDH	SAV	STP
LOGANIACEAE	Nuxia-type	A	X	X	X				
POLYGALACEAE	Polygala-type	AL	X	X	X			X	
ROSACEAE	Rubus	AL	X	X	X				
ROSACEAE	Rosaceae undiff.	I	X	X	X				
SOLANACEAE	Solanum-type	I	X	X	X				
URTICACEAE	Urticaceae undiff.	I	X	X	X				
BALSAMINACEAE	Impatiens	N	X	X	X	X			
RANUNCULACEAE	Thalictrum	N	X	X	X				
ERICACEAE	Ericaceae undiff.	A	X	X					
ERICACEAE	Erica-type	A	X	X					
MYRICACEAE	Myrica	A	X	X					
MYRSINACEAE	Rapanea	A	X	X					
RANUNCULACEAE	Ranunculaceae undiff.	A	X	X					
THYMELAEACEAE	Gnidia-type	A	X	X					
MYRSINACEAE	Maesa	AL	X	X				X	
GENTIANACEAE	Gentianaceae undiff.	I	X	X			X		
HYPERICACEAE	Hypericum	I	X	X					
ROSACEAE	Alchemilla	N	X	X					
ACANTHACEAE	Isoglossa	N	X	X					
CRASSULACEAE	Crassula	N	X	X					
DIPSACACEAE	Dipsacaceae undiff.	N	X	X					
LOBELIACEAE	Lobelia	N	X	X					
RUBIACEAE	Galium-type	N	X	X					
POLYGONACEAE	Rumex	N	X		X				
MYRSINACEAE	Myrsine-type africana	A	X						
ASTERACEAE	Artemisia	I	X						X
RUBIACEAE	Anthospermum	I	X						
LAMIACEAE	Leucas-type	N	X					X	
PRIMULACEAE	Anagallis	N	X					X	
EUPHORBIACEAE	Flueggea	A		X	X	X	X	X	
SALICACEAE	Salix	A		X					
ACANTHACEAE	Mellera-type	I		X					
ARALIACEAE	Araliaceae undiff.	A		X	X	X		X	
ARALIACEAE	Polyscias	A		X	X	X		X	

Family	Taxon	Habit	FM	FSM	FSD	FDH	SAV	STP
BURSERACEAE	Santiria-type	A	X	X	X	X		
COMBRETACEAE	Combretaceae/Melastomataceae undiff.	A	X	X	X	X	X	
HYPERICACEAE	Harungana	A	X	X	X		X	
MELIACEAE	Carapa-type procera	A	X	X	X	X		
MELIACEAE	Entandrophragma-type	A	X	X	X	X		
MELIACEAE	Meliaceae undiff	A	X	X	X	X	X	
MORACEAE	Ficus	A	X	X	X	X	X	
MORACEAE	Trilepisium-type madagascariensis	A	X	X	X	X		
MYRSINACEAE	Embelia-type	A	X	X	X	X		
MYRTACEAE	Syzygium-type	A	X	X	X	X	X	
RUBIACEAE	Pavetta	A	X	X	X			
RUBIACEAE	Psydrax-type	A	X	X	X			
RUTACEAE	Zanthoxylum-type	A	X	X	X	X	X	
SAPINDACEAE	Allophylus	A	X	X	X	X	X	
STERCULIACEAE	Dombeya-type	A	X	X	X			
ULMACEAE	Celtis	A	X	X	X	X	X	
ULMACEAE	Celtis/Trema	A	X	X	X		X	
ARALIACEAE	Schefflera	A	X	X				
HYPERICACEAE	Psorospermum	A	X	X			X	
OLEACEAE	Olea capensis	A	X	X				
RUBIACEAE	Keetia-type cornelia	A	X	X				
SAPOTACEAE	Sapotaceae undiff.	A	X	X			X	
SIMAROUBACEAE	Brucea	A	X	X				
OLEACEAE	Olea europaea-type	A	X	X				
DILLENiaceae	Tetracera	AL	X	X	X	X	X	
APOCYNACEAE	Landolphia-type	AL	X	X		X		
ACANTHACEAE	Justicia-type	I	X	X	X			
APOCYNACEAE	Apocynaceae undiff.	I	X	X	X	X	X	X
FABACEAE	Dolichos-type	I	X	X	X			
URTICACEAE	Laportea-type	N	X	X	X			
ACANTHACEAE	Hypoestes-type	N	X	X	X		X	
AMARANTHACEAE	Achyranthes-type	N	X	X			X	
RUBIACEAE	Spermacoce-type	N	X	X				
BEGONIACEAE	Begonia	N andNL	X	X	X			
PALMAE	Phoenix	PA	X	X	X			
LORANTHACEAE	Tapinanthus-type	Par	X	X				
ANACARDIACEAE	Lannea-type	A	X		X		X	
CELASTRACEAE	Celastraceae undiff.	A	X		X	X	X	
IRVINGIACEAE	Irvingia-type	A	X		X	X		
RUTACEAE	Clausena anisata	A	X		X		X	
EUPHORBIACEAE	Phyllanthus-type	A	X		X		X	
AQUIFOLIACEAE	Ilex mitis	A	X					

Family	Taxon	Habit	FM	FSM	FSD	FDH	SAV	STP
CELASTRACEAE	Maytenus	A	X				X	
PODOCARPACEAE	Podocarpus	A	X					
RHAMNACEAE	Rhamnus-type	A	X					
ROSACEAE	Prunus	A	X					
FLACOURTIACEAE	Flacourtia	A	X					
CELASTRACEAE	Cassine	AL	X		X	X		
MIMOSACEAE	Acacia	AL	X				X	X
MENISPERMACEAE	Cissampelos-type	AL	X				X	
FABACEAE	Indigofera	I	X		X		X	
RANUNCULACEAE	Clematis-type	L	X		X			
FABACEAE	Eriosema-type	N	X		X	X	X	
AMARANTHACEAE	Celosia argentea-type	N	X				X	
FABACEAE	Lotus-type	N	X					
GENTIANACEAE	Sebaea	N	X			X		
GENTIANACEAE	Swertia abyssinica-type	N	X					
GESNERIACEAE	Streptocarpus	N	X					
EUPHORBIACEAE	Alchornea	A		X	X	X	X	
EUPHORBIACEAE	Antidesma-type	A		X	X	X	X	
EUPHORBIACEAE	Uapaca	A		X	X	X	X	
LOGANIACEAE	Anthocleista	A		X	X	X	X	
ANACARDIACEAE	Pseudospondias-type	A		X	X			
ANACARDIACEAE	Sorindeia-type	A		X	X		X	
EUPHORBIACEAE	Macaranga-type	A		X	X			
EUPHORBIACEAE	Margaritaria discoidea	A		X	X		X	
MELIANTHACEAE	Bersama	A		X	X		X	
MIMOSACEAE	Entada-type	A		X	X		X	
MORACEAE	Myrianthus-type	A		X	X		X	
RUBIACEAE	Ixora-type	A		X	X			
STERCULIACEAE	Sterculia-type	A		X	X		X	
EUPHORBIACEAE	Croton-type	A		X	X		X	
CAESALPINIACEAE	Leonardoxa-type africana	A		X		X		
EUPHORBIACEAE	Bridelia-type	A		X		X	X	
EUPHORBIACEAE	Erythrococca-type3	A		X			X	
FABACEAE	Baphia-type	AL		X	X	X		
RUBIACEAE	Tarenna-type	AL		X				
CAPPARIDACEAE	Capparidaceae undiff.	I		X	X		X	X
EUPHORBIACEAE	Acalypha	I		X	X			
STERCULIACEAE	Pterygota	N		X	X			
MENISPERMACEAE	Stephania-type abyssinica	NL		X				
OCHNACEAE	Campylospermum	A		X				
MALPIGHIACEAE	Acridocarpus	AL		X				

Family	Taxon	Habit	FSD	FDH	SAV	STP
EUPHORBIACEAE	Drypetes-type	A	X	X		
EUPHORBIACEAE	Tetrorchidium	A	X	X		
MELIACEAE	Khaya-type	A	X	X	X	
MIMOSACEAE	Pentaclethra macrophylla	A	X	X		
MORACEAE	Antiaris-type toxicaria	A	X	X	X	
MYRISTICACEAE	Pycnanthus	A	X	X		
OLACACEAE	Strombosia	A	X	X		
RUBIACEAE	Bertiera	A	X	X		
RUBIACEAE	Pausinystalia-type	A	X	X		
ANACARDIACEAE	Rhus-type	A	X		X	
ARALIACEAE	Cussonia	A	X		X	
BALANITACEAE	Balanites	A	X		X	
CONNARACEAE	Cnestis-type	A	X		X	
DICHAPETALACEAE	Tapura fischeri-type	A	X			
EUPHORBIACEAE	Mallotus-type	A	X			
HYMENO-CARDIACEAE	Hymenocardia	A	X		X	
OCHNACEAE	Lophira	A	X		X	
OLEACEAE	Schrebera	A	X			
RUBIACEAE	Morelia-type senegalensis	A	X		X	
RUTACEAE	Teclea-type	A	X			
SAPINDACEAE	Aphania-type senegalensis	A	X		X	
SAPINDACEAE	Blighia	A	X			
SAPINDACEAE	Lecaniodiscus/ Aphania senegalensis	A	X			
ULMACEAE	Holoptelea grandis	A	X		X	
CAESALPINIACEAE	Cassia-type	I	X		X	
TILIACEAE	Triumfetta-type	I	X		X	
SAPINDACEAE	Sapindaceae undiff.	AL	X	X		
OCHNACEAE	Sauvagesia erecta	N	X			
ANISOPHYLLEACEAE	Anopyxis klaineana	A	X			
CAESALPINIACEAE	Crudia-type	A		X		
EUPHORBIACEAE	Klaineanthus gaboniae	A		X		
EUPHORBIACEAE	Thecacoris-type	A		X		
RUBIACEAE	Adenorandia-type kalbreyeri	A		X		
SAPINDACEAE	Aporrhiza	A		X		
OLACACEAE	Olacaceae undiff.	AL		X		
EUPHORBIACEAE	Cyathogyne	N		X		
BURSERACEAE	Commiphora	A			X	X
CAPPARIDACEAE	Crateva adansonii	A			X	X
MENISPERMACEAE	Cocculus	A			X	X
RUBIACEAE	Mitragyna-type inermis	A			X	X
CAPPARIDACEAE	Maerua-type	A			X	
CAPPARIDACEAE	Boscia-type	I			X	X
LAMIACEAE	Basilicum polystachyon/Hoslundia opposita	I			X	

Family	Taxon	Habit	SAV	STP
VERBENACEAE	Lippia-type	I	X	
AMARANTHACEAE/CHENOPODIACEAE	Amaranthaceae/Chenopodiaceae undiff.	N	X	X
RUBIACEAE	Mitracarpus villosus	N	X	X
STERCULIACEAE	Hermannia-type	N	X	X
LAMIACEAE	Leonotis-type	N	X	
AMARANTHACEAE	Aerva-type	N		X
PROTEACEAE	Faurea-type	A	X	
VITACEAE	Cissus	I	X	
COCHLOSPERMACEAE	Cochlospermum	I	X	X
SAPINDACEAE	Pappea capensis	A	X	
CAESALPINIACEAE	Parkinsonia aculeata-type	A	X	
ANACARDIACEAE	Anacardiaceae undiff.	A		
ACANTHACEAE	Acanthaceae undiff	I		
APIACEAE	Apiaceae undiff.	I		
ASTERACEAE	Asteraceae undiff.	I		
ASTERACEAE	Cichoriae undiff.	I		
EUPHORBIACEAE	Euphorbiaceae undiff.	I		
EUPHORBIACEAE	Euphorbia-type	I		
FABACEAE	Fabaceae undiff.	I		
LAMIACEAE	Lamiaceae undiff.	I		
RUBIACEAE	Rubiaceae undiff.	I		
SOLANACEAE	Solanaceae undiff.	I		
MONOCOTYLEDONAE	Monocotyledones	I		
BRASSICACEAE	Brassicaceae undiff.	N		
ASTERACEAE	Centaurea-type	N		
PLANTAGINACEAE	Plantago	N		
POACEAE	Poaceae undiff.	N		
EUPHORBIACEAE	Ricinus communis	N		
CYPERACEAE	Cyperaceae undiff.	Nq		
HALORRHAGACEAE	Lauremburgia tetrandra	Nq		
HYDROCHARITACEAE	Ottelia-type	Nq		
NYMPHAEACEAE	Nymphaea	Nq		
ONAGRACEAE	Ludwigia-type	Nq		
ONAGRACEAE	Onagraceae undiff.	Nq		
POLYGONACEAE	Polygonum senegalense-type	Nq		
POTAMOGETONACEAE	Potamogeton	Nq		
TYPHACEAE	Typha	Nq		
XYRIDACEAE	Xyris	Nq		
Monoletes smoothferns		Sp		
Monoletes ferns NL		Sp		
Triletes smooth ferns		Sp		
Triletes ferns NL		Sp		

Table III. List of pollen taxa determined at Bambili. Taxa are ranked according to membership of the corresponding plants to specific vegetation types: AA: Afro-montane;

FM: montane forest; FSM: sub-montane forest; SDF: semi-deciduous forest; FDH: rainforest ; SAV: savannah; STP: steppe. The plant habit is based on definitions of Vincens *et al.* (2007)
A: trees; AL: trees and / or lianas; PA: palm; Par: parasites; N: herbs; NL: herbaceous lianas; Nq: aquatic herbs; I: undifferentiated; Sp: fern.

The pollen diagram shows changes in tree taxa percentages between 10.56% (16,593 cal yrs BP) and 95.28% (7032 cal yrs BP) (Figure 4). A number of these taxa belong to the montane forests and mid-altitude dense forest, which are present in almost all samples analyzed. These include *Podocarpus*, *Schefflera*, *Alchornea*, *Celtis*, *Embelia*, *Maesa*, *Macaranga*-type, *Olea capensis*, *Ficus*, *Syzygium* and *Rapanea*. However, these percentages are highly variable: from 0.2 to 45.75%. Based on these changes as well as that of the appearance and disappearance of other characteristic taxa (*Aerva*, *Alchemilla*, *Artemisia*, *Farsetia*, *Hypericum*, *Ilex mitis*, *Gnidia*-type and *Myrica*), five pollen zones were distinguished for the sequence:

Zone I: 14.01 to 13.21 mcd (20,109-17,192 cal yrs BP)

This zone is characterized by high percentages of herbaceous plants including Poaceae undiff., which decreases from the base (75.68%) to the top (34.44%), and Asteraceae undiff. (30.29%). The tree percentages do not exceed 26.64%.

This zone also includes many taxa of trees and herbaceous plants that characterize today's open spaces, such as savannas and steppes, including *Lannea* (1.22%), *Commiphora* (0.44%) Capparidaceae undiff. (0.34%) and *Aerva*-type (6.15%). The afro-alpine meadow and tree line are also represented by a number of taxa: *Myrica* (16.99%), Ericaceae undiff. (3.09%), *Artemisia* (1.68%), *Maesa* (1.29%), *Gnidia*-type (0.93%) linked to montane elements, *Nuxia* (9.31%) *Rapanea* (1.25%), *Rubus* (2.37%), and *Carapa procera* (1.82%). The trees of the sub-montane forest and semi-deciduous forest are present in proportions not exceeding 2.5%. These are primarily *Antiaris*, *Antidesma*, *Lophira*, *Pausynistalia*, *Trilepisium madagascariensis*-type, and Sapindaceae undiff.

Based on the variations of the main taxa of this zone (Asteraceae, *Aerva*-type, *Anthospermum*, *Myrica*), two sub-areas were identified:

Subzone Ia: 14.01 to 13.63 mcd (20,109-18,589 cal yrs BP)

This subzone is characterized by the maximum percentages of Asteraceae undiff. (30.29%) at 13.495 mcd (19,049 cal yrs BP). The vegetation is dominated by herbaceous taxa and shrubs of the open savanna or forest edges: Amaranthaceae / Chenopodiaceae undiff. (2.30%), Asteraceae undiff. (30.29%), *Aerva*-type (2.63%), Solanaceae undiff. (3.13%), Lamiaceae undiff. (4.15%), *Achyranthes*-type (0.95%), *Lannea* (0.41%) *Boscia* (0.41%), *Crudia* (0.35%) and Urticaceae undiff. (0.74%).

Subzone Ib: 13.63 to 13.21 mcd (18,589-17,192 cal yrs BP)

All trees decreased from 32.89% to 12.84%, while herbaceous taxa increase from 44.40% to 80.41%. This sub-zone is characterized by the successive peaks, between 18,436 and 18,167 cal yrs BP, of herbaceous taxa of the subalpine vegetation type: *Anthospermum* (6.95%), followed at 17,640 cal BP by a first peak of *Olea capensis* (4%) and *Schefflera* (6.22%).

Zone II: 13.21 to 12.295 mcd (17,192-14,320 cal yrs BP)

This area is characterized by high values of Poaceae undiff. (68.58%) associated with *Aerva* at maximum values (6.15%). Asteraceae remains significant throughout the zone.

Other savanna and steppe taxa are also present: *Amaranthaceae* / *Chenopodiaceae* undiff (1.39%), *Commiphora* (0.48%), *Mitragyna inermis*-type (0.24%), *Faurea* (0.45%) *Crateva adansonii* (0.23%). Progressions of *Myrica*-type and *Aerva* determine two sub-zones:

Sub-zone IIa: 13.21 to 12.83 mcd (17,192-15,916 cal yrs BP)

In this sub-zone, the montane forest trees and afro-alpine meadow values remain small or decline sharply from the previous zone: *Podocarpus* (3.56%), *Myrica* (2.85%), *Schefflera* (2.49%), *Syzygium* (1.85%), *Olea capensis* (1.43%), *Embelia*-type (2.31%) and *Ericaceae* undiff. (1.1%) while only *Anthospermum* disappears.

Sub-zone IIb: 12.83 to 12.295 mcd (15,916-14,320 cal yrs BP)

This sub-zone is distinguished by very high values of *Myrica* between 15,496 and 14,320 cal yrs BP (16.99%). All trees increase (31.84%); however, this primarily montane taxa (30.94%; *Carapa* type *procea*, *Clausena anisata*, *Clematis*, *Embelia*, *Ilex mitis*, and *Lannea*), and sub-montane taxa (7.82%; *Macaranga*, *Bredelia*-type, *Croton*-type, *Erythrococca*). Most savanna and steppe components disappear, except for *Mitragyna inermis*-type, *Cohlospermum*, *Commiphora*, and *Crateva adansonii*, with percentages not exceeding 1%.

Zone III: 12.295 to 11.005 mcd (14,320-11,572 cal yrs BP)

This zone is marked by the drastic reduction of *Poaceae* undiff. percentages by more than 11.13% (minimum at 11,757 cal yrs BP). The percentages of all trees increase, especially *Schefflera* (19.07%) and *Podocarpus* (7.45%). This zone is also characterized by the final disappearance of *Myrica*, which is replaced by *Ilex mitis* (5.11%).

Between 14,200 and 13,602 cal yrs BP, tree percentages decreased significantly, especially *Schefflera* and *Podocarpus* which represent only 12.03% and 7.45%, respectively.

Zone IV: 11.005 to 6.80 mcd (11,572-3,252 cal yrs BP)

The increase in trees initiated in the previous zone continues in zone IV with percentages reaching the maximum value of 92%. Conversely, *Poaceae* undiff. disappears along with all elements of non-native steppe and savanna. The changing environment consists of two phases:

Subzone IVa: 11.005 to 9.205 mcd (11,572-8,252 cal yrs BP)

The disappearance of *Ilex mitis* precedes the maximum phase of forest expansion. The general increase of trees results in the appearance and / or expansion of a series of montane forest taxa: *Olea capensis* (15.61%), *Syzygium* (12.62%), *Maytenus* (4.36%), *Ficus* (6%), *Embelia* (3.40%), *Rubus* (5.38%), *Achyranthes*-type (1.38%), *Clematis* (1.84%), *Celtis* (4.34%) *Podocarpus* (32.13%) and *Schefflera* (36%). The sub-montane forest taxa are also increasing: *Alchornea* (7.36%), *Mallotus*-type (3.35%), *Macaranga*-type (3.88%), *Erythrococca*-type (2.07%), and *Streptocarpus* (4.15%).

Subzone IVb: 9.205 to 6.80 mcd (8,292-3,252 cal yrs BP)

This sub-zone is marked by the re-emergence of *Ilex mitis* (1.74% to 10.15%) and the irregular representation of different forest taxa, all trees ranging from 86.93% to 75.80%. Montane forest taxa, such as *Ericaceae* undiff. (1.32%), *Isoglossa* (0.23%), *Gnidia* (1.15%), *Maesa* (4.36%), *Rapanea* (3.48%) and *Nuxia*-type (1.75%), have relatively high percentages.

Zone V: 6.80 to 0 mcd (3,252 cal yrs BP-Present)

The pollen spectra of this area reveal a severely depleted forest with percentages of trees that represent only 39% on average. Many taxa completely disappear (*Indigofera*, *Blighia*, Sapindaceae undiff., *Brucea*, *Sauvagesia*, *Faurea*, *Salix*). Others remain present in significant percentages such as *Podocarpus* (up to 19.43%), *Olea capensis* (12.24%), *Schefflera* (45.25%), *Ilex mitis* (13.27%), Asteraceae undiff. (15.74%), and Ericaceae undiff. (4.45%). In addition, *Achyranthes* (1.53%) and *Laportea*-type (6.33%), both characteristic of degraded environments, along with *Gnidia* (6.08%), *Impatiens* (1.52%) and *Ricinus* (0, 60%) occur and progress in this area. The different variations of the percentages of major taxa suggest four sub-zones:

Subzone Va: 6.80 to 5.805 mcd (3,252-2,549 cal yrs BP)

There is a change in vegetation in this sub-zone marked by the loss of forest as percentages fall to 46% (*Alchornea* (1%), *Allophylus* (0.29%), *Antiaris* (0.30%), *Antidesma*-type (0.81%), *Carapa*-type *procea* (0.34%), *Celtis* (0.40%), *Clausena anisata* (0.67%), Combretaceae undiff. (0.30%), *Cussonia* (0.64%), *Drypetes* (0.29%), *Embelia* (0.30%), Ericaceae undiff. (0.39%), *Erythrococca*-type (0.34%), *Ficus* (0.30%), *Gnidia* (0.31%), *Podocarpus* (5.43%), *Olea capensis* (0.30%), and *Schefflera* (7.66 %)). Poaceae undiff., Asteraceae undiff., and ferns increase dramatically to 36.50%, 5.53% and 15.35%, respectively.

Subzone Vb: 5.805 to 1.905 mcd (2,549 -960 cal yrs BP)

Forest vegetation recovers but is impoverished and deteriorates very quickly at 960 cal yrs BP. This sub-zone also shows the importance of indicators for open environments: *Celtis* (11.84%), *Laportea* (6.33%), Solanaceae undiff. (2.59%), Poaceae undiff (48.95%), *Macaranga* (10.10%), Lamiaceae undiff. (2.17%), *Hypoestes*-type (2.55%), and *Clematis* (2.36%). The majority of the montane taxa cited in the previous sub-zone regress: *Podocarpus* (0.51%), *Maytenus* (0.28%), *Embelia*-type (0.42%), *Syzygium* (1.27%), *Schefflera* (0.84%), *Ilex mitis* (1.68%), *Antiaris* (0.76%), *Rapanea* (0.38%) and *Cussonia* (0.31%).

Subzone Vc: 1.905 to 0.605 mcd (960-266 cal yrs BP)

This subzone marks the minimum representation of trees in the Holocene with a percentage of 18%. Herbaceous plants increase, especially Poaceae undiff. (78%), Asteraceae undiff. (4.11%), Urticaceae (*Laportea*-type) (1%) and Solanaceae undiff. (5.80%). Forest elements such as *Olea capensis* (1.61%), *Podocarpus* (1.36%), *Maytenus* (0.4%), *Syzygium* (1.27%), and *Ficus* (0.34%) as well as afro-alpine elements such as Ericaceae undiff. (0.34%), *Hypericum* (0.40%), and *Isoglossa* (0.80%), are present in very small quantities.

Subzone Vd: 0.605 to 0 mcd (266 cal yrs BP-Present)

The top of this record is differentiated by the extreme poverty of the forest flora dominated by *Schefflera* (45%) and *Embellia* (11%), associated with *Syzygium* (7.07%), *Hypoestes*-type (4.04%), *Clematis* (2.26%), *Celtis* (3.80%), *Ilex mitis* (0.45%), *Cussonia* (3.61%), *Achornea* (4.22%), and *Macaranga*-type (1.1%). Poaceae undiff. remain at a high level and Solanaceae undiff. increases (5.5%).

5. Discussion: The evolution of vegetation cover

5.1 An open and degraded vegetation during the ice age

Forest cover

At Bambili, forest cover was extremely low during the late glacial period (18,000-23,000 cal yrs BP). The vegetation is dominated by herbaceous plants, as is the case in all West African sites regardless of altitude: the swamp Shum Laka (Kadomura, 1994) at 1200 m asl on the Bamenda plateau at Barombi Mbo at the foot of Mount Cameroon (Maley and Brenac, 1998) and Lake Bosumtwi, Ghana (Maley, 1987) located in low and mid altitudes. The pollen studies from the mountains of East Africa also reflect the general degradation of tropical forests during this period (Livingstone, 1967, Coetzee 1967, Hamilton, 1982). Three pollen sites located in southern hemisphere, however, show a different pattern. At Ngamakala, a forest sites in the southern Congo located 400 m asl, the environment, although degraded, remains forest during the glacial period until 13,000 yrs BP (Elenga et al., 1994). At Kisiga Rugaro, a forested part of the Eastern Arc Mountains shows a certain environmental stability during the whole glacial period (Mumbai et al. 2008). They note, however, that the herbaceous plants recorded their highest percentages between 19,000 and 14,000 cal yrs BP, which could correspond to drier and colder conditions than even the preceding LGM. Mumbai et al. (2008) suggest that the relative stability of ecosystems during the last ice age is due to the influence of the Indian Ocean that would have allowed the maintenance of a rain forest while the regional climate of East Africa was dry. At Lake Masoko (9°20'S, 33°45'E, 840 m asl), Vincens et al. (2006) also identify a uninterrupted development phase of semi-deciduous forest from 23,000 - 11,800 cal yrs BP.

The composition of local vegetation

The composition of pollen spectra of the Last Glacial Maximum (LGM) at Bambili shows a mixture of floristic elements representative of distinct stages: the sub-montane forest, the semi-deciduous forest (*Antiaris*, *Antidesma*, *Lophira*, *Pausynistalia*, *Trilepisium madagascariensis*-type, Sapindaceae undiff.), the montane forest (*Nuxia*, *Rapanea*, *Rubus*, *Carapa procea*, *Myrica*, *Gnidia*-type, *Maesa*, Ericaceae undiff.) and Afro-alpine (*Artemisia*, *Alchemilla*, *Anthospermum*, *Hypericum*, *Rumex*, *Isoglossa*). Herbaceous taxa dominate open areas or forest edges. Among these are: Poaceae undiff., Cyperaceae undiff., Amaranthaceae / Chenopodiaceae undiff., Asteraceae undiff., Lamiaceae undiff., *Achyranthes*-type and Urticaceae undiff. Among the arboreal taxa, montane forest taxa dominated; however, their percentages are very low.

Distant contributions

The LGM is characterized by the presence of savanna and steppe taxa such as *Aerva*-type, *Boscia*-type, Capparidaceae undiff., *Commiphora*, *Crataeva adansonii*, *Crudia*-type, *Lannea*-type and *Maerua*-type that show the importance of long-distance aeolian input, related to an increased flow of trade winds (Sarnthein et al., 1981) and possibly the extension of Sudan-Zambezian vegetation zones due to dry conditions. A layer of charcoal was observed at 1355 cm. Dating of this layer yielded an age of 18 283 cal yrs BP (15 020 ± 60 ¹⁴C BP) suggesting the importance of fire at this time in the environment near Lake Bambili.

5.2 The post-glacial forest colonization

Chronology of colonization forest

In the global post-glacial context, recolonization of forest is observed. At Bambili, this occurs in three distinct stages (Figure 5) interrupted by two phases of regression corresponding to the Heinrich event 1 (H1) and the Younger Dryas.

The first phase of colonization starts at 18,400 cal yrs BP with the appearance of *Anthospermum*. This taxon is noted by Livingstone (1967) as an important element of the first stage of colonization of lava fields in the region of the Virunga volcanoes in East Africa. In Cameroon, *Anthospermum camerounensis*, is a dwarf grass found in Afro-alpine vegetation types (Letouzey, 1968). This taxon is followed by a large increase of *Olea capensis* and *Schefflera*, forming a first phase of increase in trees. The increase of trees stops at 17 100 cal yrs BP, with the increase of *Aerva*-type, which indicates the strengthening of the boreal winter northeasterly wind flow from the Sahelian steppes and large fires are indicated by charcoal layers. This increase is contemporaneous with H1, the characteristics of climate on a global scale are drought (Mix et al., 2001; Kageyama et al., 2005; Timmermann and Menvielle, 2009).

Vegetation at Bambili remains relatively stable for about 1900 years when a second stage of forest colonization begins at 14,900 cal yrs BP. This stage is initiated by the appearance of *Myrica*, a fire-tolerant, sun-loving shrub common in clearings of the upper montane forests (Livingstone, 1967). This taxon is followed by another sun-loving species, *Ilex mitis*, and finally by *Olea capensis*, *Podocarpus* and *Schefflera*. This phase culminates in a very short period between 13,800 and 13,700 cal yrs BP, corresponding to the beginning of the warm Alleröd in high latitudes (Roberts et al., 1993, 2010). This increase of forest cover at Bambili is coeval with the start of the African Humid Period dated to 15,500 cal yrs BP by DeMenocal et al. (2000). This period was marked by increased flow of the Niger River (Lézine and Cazet, 2005) and the general rise in lake levels (Gasse, 2000; Shanahan et al., 2006). At Bambili, Stager and Anfang-Sutter (1999) found a positive P / E during this period. The presence of steppe taxa such as *Aerva* up to 11,700 cal yrs BP, however, shows that trade wind flow was still significant over this period. This is in contrast with the termination of Saharan dust transport to the ocean further north noted by DeMenocal et al. (2000).

Between 13,000 and 11,700 cal yrs BP, a second phase of forest decline is recorded. This phase does not correspond to the total destruction of the forest. It is characterized instead by a massive regression of *Schefflera*. All trees recorded a large decrease with the exception of *Podocarpus*, *Rapanea* and *Gnidia*-type. The permanence of steppe elements reflects the importance of continued northeasterly circulation. This phase corresponds to the YD (Younger Dryas) in the high latitudes (Roberts et al., 1993). As mentioned earlier, the YD is generally dry in tropical North Africa, reflected in the general lowering of lake levels (Gasse, 2000). This episode is marked by increased dust transport to the Atlantic recorded from the equator (Lézine et al., 1994) to the Saharan latitudes (DeMenocal et al., 2000). The YD signature on forest vegetation is however not very visible in the Ivory Coast as outlined Lézine and Le Thomas (1995). Despite evidence of increased sedimentological transport by the trade winds, the authors noted no major changes in the forest environment during this episode. The YD seems to be more clearly recorded in the vegetation surrounding lakes Barombi Mbo and Bosumtwi. Data from Barombi Mbo show an increase of spores (2 to over

15%), Poaceae (13 to 17%) and pioneers taxa such as *Trema*, *Macaranga*, *Mallotus* and *Alchornea* around 12,500 yrs BP (Maley and Brenac, 1998). At the same site, Lebamba et al. (2010) show, after ca 14,000 cal yrs BP, the decline of tropical rain forests and seasonal increases in savanna biomes. At Bosumtwi, there is an increase in grasses and sedges, while the tree taxa regress (Maley, 1991). From 11,500 cal yrs BP, *Schefflera* leads a new phase of forest expansion with a forest optimum dated between 10,000 and 8400 cal yrs BP. The development of the forest is gradual between 11,500 and 10,200 cal yrs BP and results in the expansion of montane taxa. Next, *Rubus*, *Rapanea*, *Embelia*-type and *Syzygium* appear in turn. The elements of the montane forest, in particular, *Schefflera*, *Podocarpus*, *Olea* and *Syzygium* rose steadily over this period. Submontane forest is also present through a number of taxa that appear sporadically, such as *Cussonia*, *Macaranga*-type, *Antiaris*-type *toxicaria*, and *Allophyllus*.

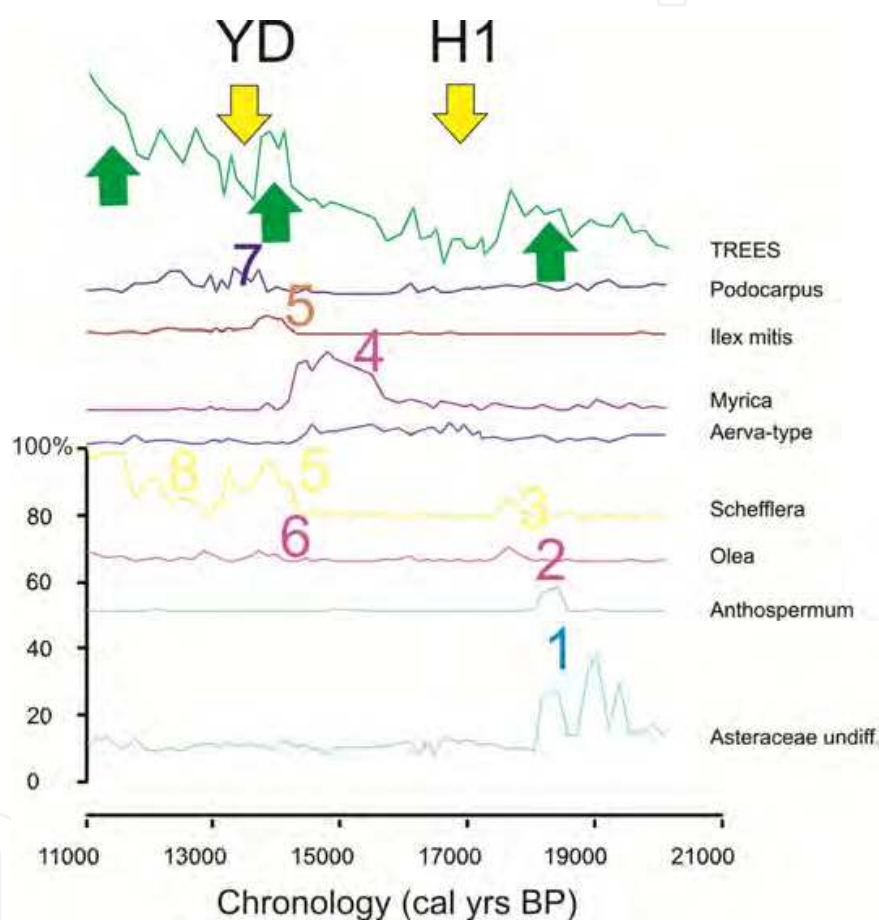


Fig. 5. Colonization of the postglacial forest. The curves are made from percentages of each taxon from 21,000 to 11,000 cal yrs BP. This colonization takes place in three phases forest interrupted by two regressions corresponding to H1 and the YD. It starts at 18,400 cal yrs BP with the appearance of *Anthospermum* (1) followed by *Olea capensis* (2) and *Schefflera* (3). The interruption to 17,100 cal yrs BP, marked by the increase of *Aerva*-type is correlated with H1. A second phase of forest colonization starts at 14,900 cal yrs BP with the appearance of *Myrica* (4) monitoring and *Ilex mitis* *Schefflera* (5), *Olea capensis* (6) and *Podocarpus* (7). Between 13,000 and 11,700 cal yrs BP, a second phase of regression is observed with decreasing forest trees. Then, from 11,500 cal yrs BP, *Schefflera* (8) opens the Holocene forest expansion phase.

Example of two major forest taxa: *Olea* and *Podocarpus*

Comparison of pollen data from sites Barombi Mbo, Tilla and Bambili shows that, since 20,000 years BP, some plants have moved from low to high altitudes. This is the case of *Olea* (Figure 6) which shows percentages up to 35%, during the glacial period at Barombi Mbo (Maley and Brenac, 1998), indicating the presence of the plant source at low altitude near the lake. Its percentage decreased drastically from 12,000 cal yrs BP. At this time, *Olea* appears at Tilla, 700 m north of the volcanic line in Cameroon (Salzmann et al., 2000) where it develops until it reaches 14%. It then extends to 2200 m asl at Bambili after 10,800 cal yrs BP where it remained until the end of the Holocene forest. This tree is still present in the mountains at the edge of montane forest and sub-montane, near the village of Oku. *Olea* is known to be a pioneer taxon, which explains its presence at the beginning of the forest recovery at Tilla, before the development of Euphorbiaceae (*Uapaca*) that characterize the forest in the Holocene. The behavior of *Olea* during the glacial-interglacial transition could be related to temperature changes. With rising temperatures after 12,000 years at low altitude, *Olea* migrates toward higher elevations to its current location.

Unlike the previous taxon, *Podocarpus* shows a similar pattern at both sites (Figure 7). It is not represented in the LGM sediments, and pollen percentages that reached Barombi Mbo are so low that it precludes the possibility of its presence at low altitude. At Bambili, it also reduced at this time. *Podocarpus* at Bambili increases from 10,000 cal yrs BP, then develops during two periods centered around 7560 cal yrs BP and 3360 cal yrs BP. It is interesting to note that these two peaks are also found at Barombi Mbo; however, here values are a full order of magnitude lower than at Bambili. This could support the hypothesis of two distinct phases of expansion of *Podocarpus* in altitude during the Holocene.

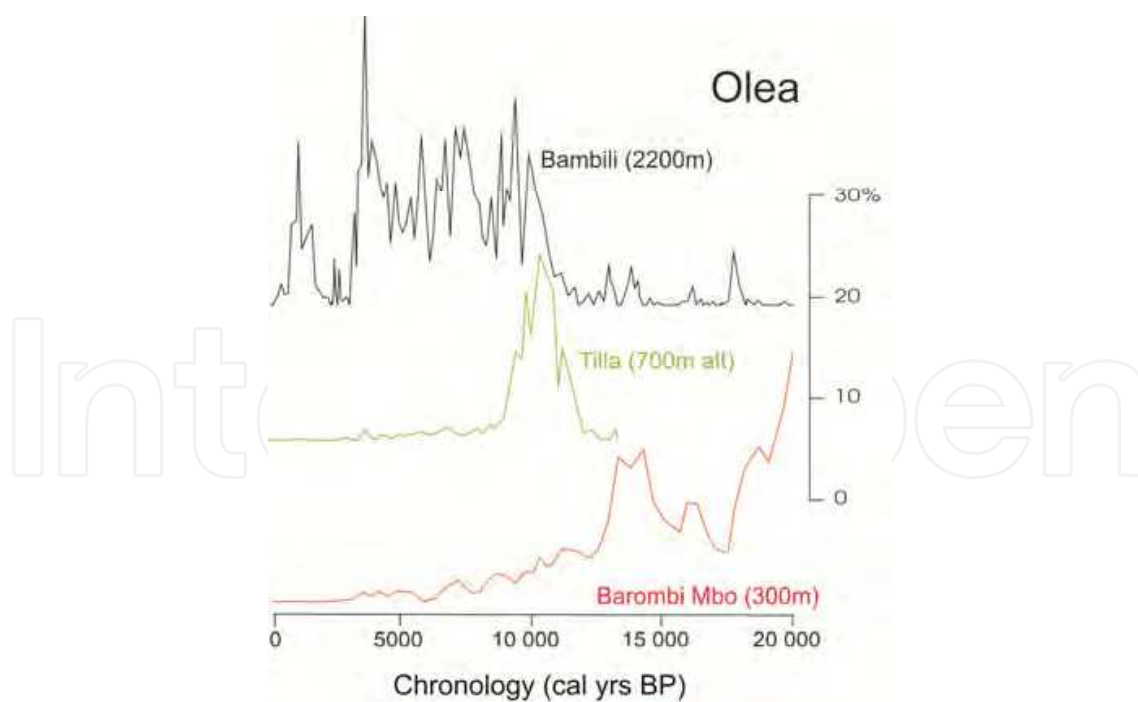


Fig. 6. The evolution of *Olea*-type at Bambili, Tilla and Barombi Mbo. During the Last Glacial Maximum, *Olea*-type has a significant presence in Barombi Mbo until 12,000 cal yrs BP. The presence is then recorded at Tilla between 12,000 and 11,800 cal yrs BP and at Bambili at 10,800 to 3300 cal yrs BP.

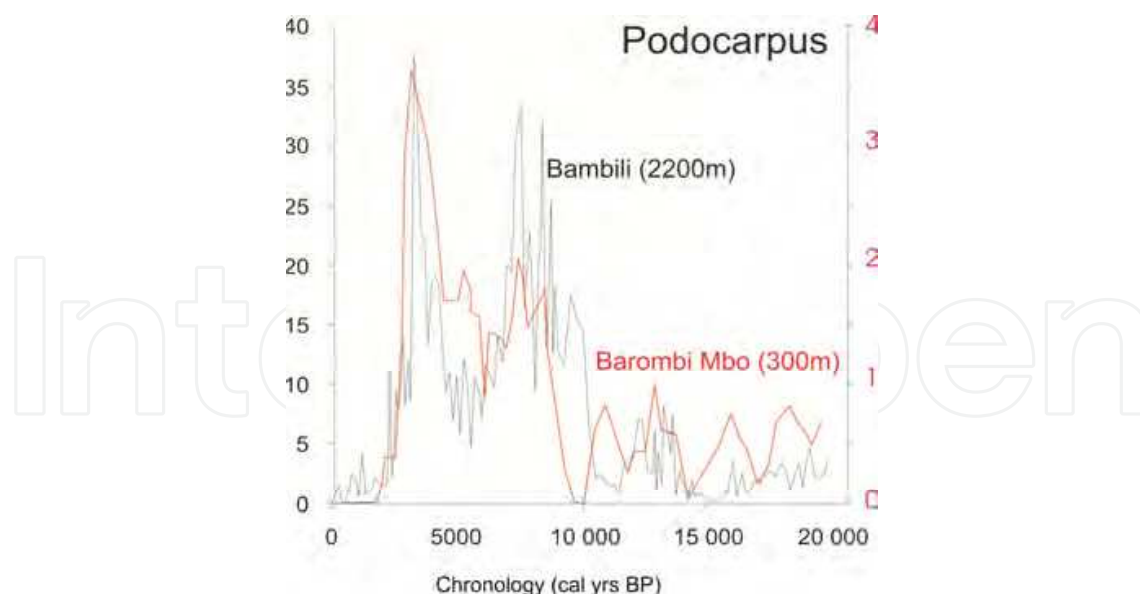


Fig. 7. The evolution of *Podocarpus* at Bambili and Barombi Mbo. The trend in *Podocarpus* expansion is similar between sites; however, the values are often an order of magnitude higher at Bambili.

The expansion of *Podocarpus* during the Holocene is also attested throughout Central Africa from the Atlantic site at 8 m asl at Ossa (Reynaud-Farrera, 1995; Reynaud-Farrera et al., 1996), as well as those of Mboandong at 130 m asl (Richards, 1986), Mbalang at 1100 m asl (Vincens et al., 2009), Njupi at 1108 m asl (Zogning et al., 1997), Bafounda at 1310 m asl (Tamura, 1990), and Shum Laka (W-10) at 1355 m asl (Kadomura, 1994).

5.3 The optimum forest of the early Holocene

The optimum forest at Bambili occurs between 10,000 and 8400 cal yrs BP and is characterized by the dominance of tree taxa at values from 80-92%. Of the 118 total tree taxa determined to Bambili, this period includes more than half (67 taxa), the majority belonging to the montane and semi-deciduous forests. These are mainly *Schefflera*, *Syzygium*, *Podocarpus*, *Olea capensis*, *Rapanea* for the montane forest and *Macaranga*, *Celtis*, *Cussonia*, *Antiaris* for semi-deciduous forest. Elements of the open areas have disappeared (*Leonotis*, *Leucas*, *Boscia*, *Aerva*) or decreased (*Impatiens*, *Achyranthes*, *Solanaceae undiff*, *Galium* / *Rubia*).

In tropical Africa during the early Holocene, the percentages of pollen from woody genera are high throughout the region, indicating the expansion of forests into higher latitudes and altitudes (Lézine, 2007). In West Africa, the marine records suggest that the Guineo-congolian forests were not separated by the savanna corridor that exists today in Togo and Benin, the "Dahomey Gap" (Dupont et al., 2000), which is confirmed by the analysis of lake sediments from Sele (Salzmann et al., 2000). Tropical plants migrated northwards along the rivers and lakes stretching across the Sahel and the Sahara (Watrén et al., 2009). The mangrove taxon *Rhizophora* also occupied many coastal areas northward to around 21°N (Lézine, 1997).

Bonnefille et al., (1995) noted also a reduction in forest cover during the LGM and a discontinuous forest colonization at Rusaka Swamp (3°26'S, 29°37'E, 2070 m asl). Many authors link the expansion of Guineo-congolian forest and mangrove with a reinforcement

of the Atlantic monsoon at the beginning of the Holocene (Marzin et Braconnot, 2009). Rainfall was significantly higher than today and seasonality was reduced as shown by the high lake levels (Gasse, 2000; Shanahan et al., 2006) and increased fluvial transport (Lézine and Cazet, 2005).

5.4 The destabilization of the forest in the mid-Holocene: The 8.2 event

The forest phase at Bambili is marked by a very short but indicated episode of regression which occurs at the time of the 8.2 event in the high latitudes (Von Grafenstein et al., 1998). It is reflected in the physiognomy of the forest by lower percentages of trees and the more or less pronounced decrease in values of some taxa. The most remarkable decreases are those of *Schefflera*, *Podocarpus*, *Rapanea*, and to a lesser extent those of *Olea capensis*, *Maesa*, *Syzygium*, *Ilex mitis*, *Nuxia*, and *Embelia*, all standard elements of the montane forest as well as those of *Cussonia*, *Alchornea*, and the submontane forest. This degradation could be caused by dry conditions as suggested by the lower lake levels at Lake Bosumtwi (Shanahan et al., 2006) related to the slowdown of the thermohaline circulation in the North Atlantic (Pissart, 2002).

5.5 The end of the Holocene forest at Bambili

After 8400 cal yrs BP, changes in taxa suggest some forest instability. This phase of disruption occurs gradually, leading to the brutal destruction of the forest at 3300 cal yrs BP. At this period, *Podocarpus* opposes *Schefflera*, *Syzygium* and *Alchornea*. Forest degradation begins at 4500 cal yrs BP, with the decline of *Schefflera* followed by that of *Olea capensis* at 3500 cal yrs BP and *Podocarpus* at 3300 cal yrs BP. The drastic reduction of montane forest elements at 3300 cal yrs BP probably favored soil erosion and sediment supply from the crater rim. The latter was then increased by the return of wet conditions during the early part of this interval after logging dated between 2500 and 1300 cal yrs BP.

At 3300 cal yrs BP, lower montane forest taxa values are partially offset by increases of *Syzygium*, *Maesa* and *Gnidia*-type, indicating the opening of the forest. This opening peaks at 2600 cal yrs BP with the increase of *Urticaceae* and *Poaceae* undiff. . The evolution of the vegetation was organized in two stages. Between 2500 and 1300 cal yrs BP, a small forest recovery takes place. Forest vegetation is dominated by *Ilex mitis* associated with *Schefflera* and to a lesser extent *Syzygium*, *Rapanea*, *Maesa*, *Nuxia*, and *Gnidia*-type. *Podocarpus* and *Olea capensis* are poorly represented. In the later part of this phase, the presence of sub-montane elements successively occurs such as *Macaranga*, *Celtis*, and *Lophira*. Finally, the Afro-montane elements (*Ericaceae* undiff., *Hypericum*, *Isoglossa*), with smaller percentages are generally better represented than in the high forest phase. This phase corresponds to wet period as suggested at Bambili by Stager and Anfang-Sutter (1999) who noted a P / E positive. The lake level rose during this period as reflected in the diatom assemblages; however, this could be artificially enhanced by the increased sediment transport from the lake margin. A humid climate is also noted in Ossa between 2700 and 1300 cal yrs BP by Nguetsop et al. (2004) confirming its regional character. At 960 cal yrs BP, the deep decline of *Schefflera*, partially offset by higher percentages of *Olea*, illustrates another phase of environmental degradation. The opening in the middle is highlighted by the dominance of *Poaceae* and *Urticaceae*. Between 960 cal yrs BP to the present, a marked upturn in forest is observed, with expansion of *Schefflera* (45%). The degradation of forest leads to a generalized fall in the majority of taxa, montane and submontane. The presence of *Asteraceae* undiff, *Ilex*

mitis, *Ficus*, *Embelia*-type, *Maesa*, *Rapanea*, *Sygyzium*, *Gnidia*-type, *Clematis*-type, *Nuxia*-type, *Hypoestes*-type, *Alchornea*, *Sapotaceae* undiff., *Solanaceae* undiff, however, *Celtis* reveals nature montane forest mixed with the semi-deciduous forest.

5.6 The impact of environmental change on biodiversity

Fluctuations in biodiversity, calculated using the method developed by Birks and Line (1992) (Figure 8), show four phases of maximum biodiversity that correspond to periods of transition or disturbance of the forest. These phases are centered around 18,000 cal yrs BP, 12,000 cal yrs BP, 6500 cal yrs BP and 1500 cal yrs BP. The highest values of the record occur during the post-glacial colonization of forest following the YD (ca 12,000 cal yrs BP) and at the end of the small logging period (ca 1000 cal yrs BP). During these periods, forest biodiversity is increased due to the internal forest dynamics incorporating the gradual disappearance and appearance of certain plants resulting in greater overall species richness. According to Birks and Line (1992), floristic richness is favored during phases of "intermediate" disruption. The ecosystem fragmentation associated with such disruption limits the domination of one single component as long as the disturbance is not sufficient to cause the complete disappearance of the ecosystem on a regional scale.

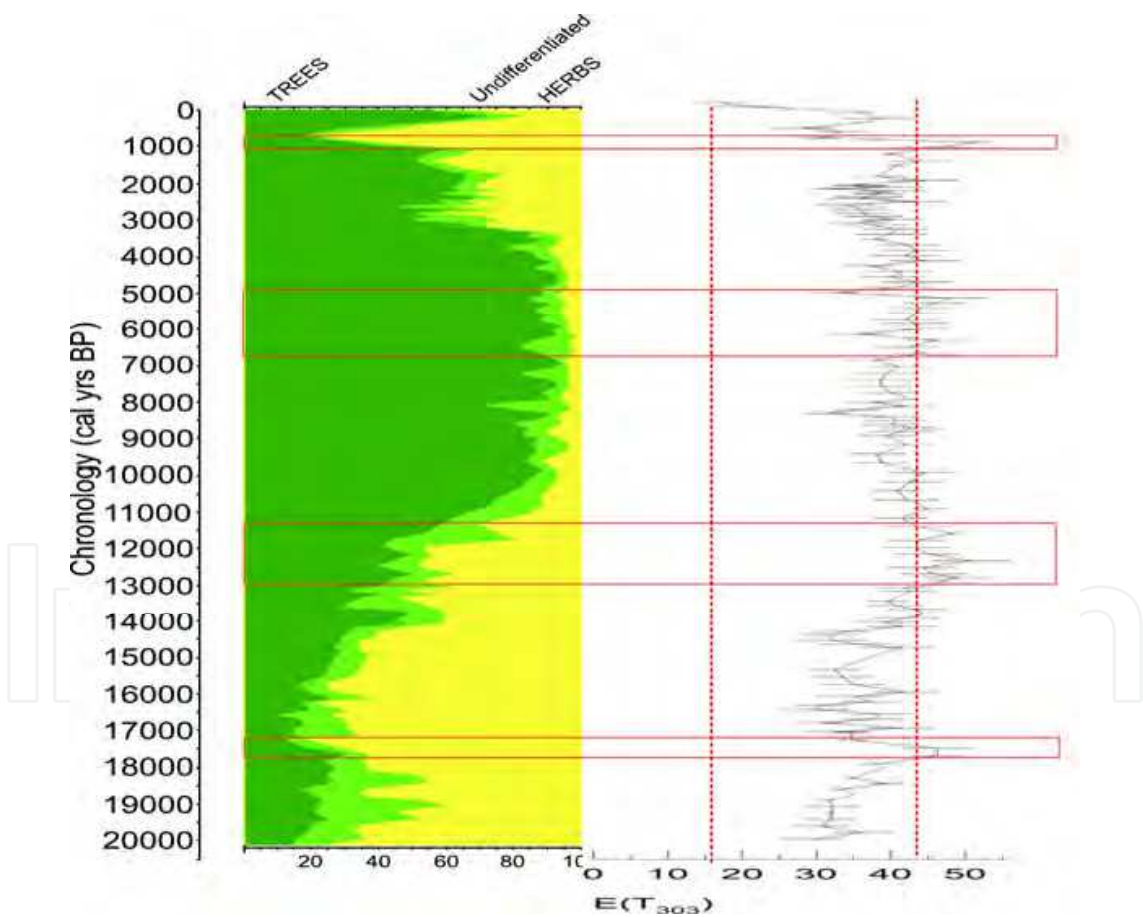


Fig. 8. Physiognomy of the vegetation and changes in biodiversity at Bambili. Left, Bambili diagram synthesis with the percentages of trees, herbs and undifferentiated. Right, rarefaction analysis showing Bambili biodiversity. Biodiversity is very high in the transition phases of the vegetation (red boxes). The dashed lines indicate the minimum of biodiversity (left line) and the value of average biodiversity (right line).

At Bambili, highest biodiversity does not follow forest stabilization, in contrast, biodiversity indices are generally low during these times. As shown in Figure 8, the current biodiversity surrounding Lake Bambili is the lowest in the last 20,000 years. This confirms the considerable impoverishment of the environment related to the recent deterioration of the forest environment undoubtedly amplified by the action of man, as evidenced by the comparative analysis of satellite photos from 1998 and 2003.

6. Conclusion

This palynological study of the paleoenvironments surrounding Bambili reveals the history of montane Central Atlantic Africa over the last 20,000 years. It also provides unique evidence on the response of Cameroon's mountain forests to climate change. During the LGM, a highly degraded forest formation was present around Bambili dominated by light-demanding components suggesting a dry environment. For the Holocene, the proportion of tree pollen shows continuous forest cover between 10,000 and 3300 yrs cal BP. The expansion of forest, very dynamic at the beginning of the Holocene, led to installation of a montane forest dominated by *Schefflera*, *Podocarpus* and *Olea* which responded individually to climate change. This forest lasted for much of the Holocene, then floristic composition changed. From this period, forest degrades very sharply during three centuries and the forest loses about 40% of its importance.

This is in agreement with the general context of equatorial forest evolution as a result of drier conditions of the end of the Holocene humid period. As emphasized by Birks Line (1992) "floristic richness is maximized by the disruption and fragmentation of the landscape when it reaches a level sufficient to prevent the domination of a single species and insufficient to cause the extinction of all components of the landscape. "The lowest percentages of trees on the top of the Bambili sequence dominated by a single taxon: *Schefflera*, indicates the disturbance of the landscape which reached a maximum level showing considerable impoverishment of the local flora. However, despite the effects of climate, intensified anthropogenic impacts have dramatically reduced forest biodiversity in recent decades. Continuation of such practices, associated largely with agriculture and ranching, in the future will likely lead to the disappearance of this ecosystem.

Palynological studies on other sites of Cameroon during LGM are needed to better assess the extent of *Podocarpus* forest.

7. Acknowledgements

This work was financed by IFORA and C3A. We thank for their contributions Anne-Marie Lézine, Emile Roche, Annie Vincens, Sarah Ivory, the LSCE and the palynology laboratory of the University of Liège.

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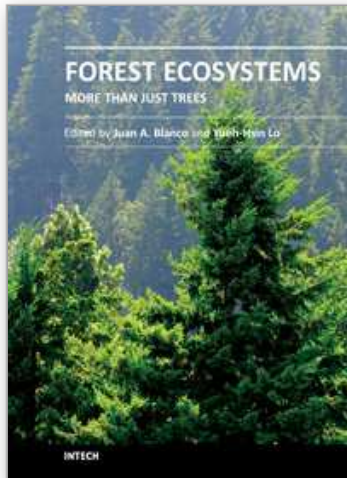
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Forest Ecosystems - More than Just Trees

Edited by Dr Juan A. Blanco

ISBN 978-953-51-0202-1

Hard cover, 464 pages

Publisher InTech

Published online 07, March, 2012

Published in print edition March, 2012

The common idea for many people is that forests are just a collection of trees. However, they are much more than that. They are a complex, functional system of interacting and often interdependent biological, physical, and chemical components, the biological part of which has evolved to perpetuate itself. This complexity produces combinations of climate, soils, trees and plant species unique to each site, resulting in hundreds of different forest types around the world. Logically, trees are an important component for the research in forest ecosystems, but the wide variety of other life forms and abiotic components in most forests means that other elements, such as wildlife or soil nutrients, should also be the focal point in ecological studies and management plans to be carried out in forest ecosystems. In this book, the readers can find the latest research related to forest ecosystems but with a different twist. The research described here is not just on trees and is focused on the other components, structures and functions that are usually overshadowed by the focus on trees, but are equally important to maintain the diversity, function and services provided by forests. The first section of this book explores the structure and biodiversity of forest ecosystems, whereas the second section reviews the research done on ecosystem structure and functioning. The third and last section explores the issues related to forest management as an ecosystem-level activity, all of them from the perspective of the other parts of a forest.

How to reference

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Chimène Assi-Kaudjhis (2012). Vegetation Evolution in the Mountains of Cameroon During the Last 20 000 Years: Pollen Analysis of Lake Bambili Sediments, Forest Ecosystems - More than Just Trees, Dr Juan A. Blanco (Ed.), ISBN: 978-953-51-0202-1, InTech, Available from: <http://www.intechopen.com/books/forest-ecosystems-more-than-just-trees/ecosystem-dynamics-and-biodiversity-of-the-cameroon-mountains-during-the-last-20-000-years-pollen-an>

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