Short Paper

Ancient charcoal as a natural archive for paleofire regime and vegetation change in the Mayumbe, Democratic Republic of the Congo

Wannes Hubau [a,b,*], Jan Van den Bulcke [a], Peter Kitin [b], Florias Mees [c], Geert Baert [d], Dirk Verschuren [e], Laurent Nsenga [a,b], Joris Van Acker [a], Hans Beeckman [b]

[a] Ghent University, Department of Forest and Water Management, Laboratory for Wood Technology, Coupure Links 653, B-9000 Gent, Belgium
[b] Royal Museum for Central Africa, Laboratory for Wood Biology, Leuvensesteenweg 13, B-3080 Tervuren, Belgium
[c] Royal Museum for Central Africa, Department of Geology and Mineralogy, Leuvensesteenweg 13, B-3080 Tervuren, Belgium
[d] University College Ghent, Department of Plant Production, Schoonmeersstraat 52, B-9000 Gent, Belgium
[e] Ghent University, Department of Biology, Limnology Unit, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium

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ABSTRACT

Charcoal was sampled in four soil profiles at the Mayumbe forest boundary (DRC). Five fire events were recorded and 44 charcoal types were identified. One stratified profile yielded charcoal assemblages around 530 cal yr BP and >43.5 cal ka BP in age. The oldest assemblage precedes the period of recorded anthropogenic burning, illustrating occasional long-term absence of fire but also natural wildfire occurrences within tropical rainforest. No other charcoal assemblages older than 2500 cal yr BP were recorded, perhaps due to bioturbation and colluvial reworking. The recorded paleofires were possibly associated with short-lived climate anomalies. Progressively dry climatic conditions since ca. 4000 cal yr BP onward did not promote paleofire occurrence until increasing seasonality affected vegetation at the end of the third millennium BP, as illustrated by a fire occurring in mature rainforest that persisted until around 2050 cal yr BP. During a drought episode coinciding with the 'Medieval Climate Anomaly', mature rainforest was locally replaced by woodland savanna. Charcoal remains from pioneer forest indicate that fire hampered forest regeneration after climatic drought episodes. The presence of pottery shards and oil-palm endocarps associated with two relatively recent paleofires suggests that the effects of climate variability were amplified by human activities.

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Introduction

Combined reconstruction of past climate variability and ecosystem dynamics increases our understanding of ecosystem response to current and future climate change (e.g., Willis and Birks, 2006). Substantial work in temperate and arid regions of the northern hemisphere contrasts with the significant knowledge gaps that continue to exist for many tropical regions, particularly Central Africa (e.g., Leal, 2001; Emery-Barbier and Thiébault, 2005; Tchouto et al., 2009; Théry-Parisot et al., 2010; Maley et al., 2012; Neumann et al., 2012b). A well-known concept in tropical paleoecology and biogeography is that of the Central African forest refuges, which are submountainous, fluviatile or coastal regions enjoying rather moist (micro-) climate conditions thought to protect rainforests during dry climate anomalies (Maley, 1996, 2004; Sosef, 1996; Maley

and Brenac, 1998; Leal, 2001, 2004). Yet paleoecological reconstructions suggest that rainforest and other Central African ecosystems show a remarkably high sensitivity to natural climate changes such as prolonged drought or increased seasonality (e.g., Maley, 1996, 2001, 2004; Ngomanda et al., 2007, 2009a,b). Also, human activity cannot be overlooked when discussing climate and vegetation changes during the last three millennia, when agriculture and iron smelting were introduced in Central Africa, even though before the last millennium human impact on Central African forests was probably marginal (e.g., Maley, 1996, 2004; Brncic et al., 2007; Maley et al., 2012; Neumann et al., 2012b).

The most important source of evidence for the climate and vegetation history of Central Africa is lake-sediment records (e.g., Russell and Johnson, 2005, 2007; Stager et al., 2009) and the fossil pollen they contain (e.g., Maley, 1996, 2004; Maley and Brenac, 1998; Brncic et al., 2007; Hessler et al., 2010). These studies provide high-resolution temporal records from a select few locations with undisturbed lacustrine sedimentation, but do not offer great spatial detail. In contrast, macrocharcoal fragments can be found in terrestrial soils of any type of vegetation, reflecting local paleofire regimes. Also, the analysis of soil charcoal from profiles in natural environments (pedoanthracology) is not influenced by the effects of fuelwood selection strategies, as observed in charcoal analysis from archeological sites (archeoanthracology) (Di Pasquale et

* Corresponding author at: Ghent University, Department of Forest and Water Management, Laboratory for Wood Technology, Coupure Links 653, B-9000 Gent, Belgium. Tel.: +32 9 264 61 23; fax: +32 9 264 90 92.
E-mail addresses: wannes.hubau@ugent.be, w.hubau@leeds.ac.uk (W. Hubau), jan.vandenbulcke@ugent.be (J. Van den Bulcke), kitin@wisc.edu (P. Kitin), florias.mees@africamuseum.be (F. Mees), geert.baert@hogent.be (G. Baert), Dirk.verschuren@ugent.be (D. Verschuren), lnsenga@yahoo.fr (L. Nsenga), joris.vanacker@ugent.be (J. Van Acker), hans.beeckman@africamuseum.be (H. Beeckman).

al., 2008; Théry-Parisot et al., 2010). Pedoanthracology has proven to be a useful tool for reconstructing Holocene paleofire regimes in natural environments, especially in the forest-boundary of submountainous regions (Carcaillet and Thinon, 1996; Carcaillet et al., 1997; Di Pasquale et al., 2008). Additionally, soil charcoal analysis can reveal the past presence of woody plant taxa that are only rarely detected in pollen assemblages (Elenga et al., 2000; Lebamba et al., 2009). As a result, pedoanthracology is highly complementary with palynology for reconstruction of past vegetation dynamics (Emery-Barbier and Thiébault, 2005; Théry-Parisot et al., 2010; Hubau et al., 2012).

Hitherto, only a handful of studies on soil charcoal in Central Africa included the identification of charred wood remains, due to the high species richness of the area and lack of a scientifically sound identification procedure (e.g., Schwartz et al., 1990; Hart et al., 1996). Recently, Hubau et al. (2012) developed a transparent identification protocol that can allow a taxonomically more precise identification than generally obtained by pollen analysis. The main objective of the present study is to contribute to knowledge of Central African paleofire and vegetation history by applying this protocol to soil charcoal assemblages from an area of the Congolese rainforest that is expected to be sensitive to climate change. We selected a non-archeological study site (the Luki Reserve) at the southern end of the Mayumbe hills in the Democratic Republic of the Congo, (DRC), which are thought to have served as a submountainous forest refuge during late Pleistocene and Holocene episodes of climate deterioration (e.g., Maley, 1996, 2004; Sosef, 1996). Dry or more seasonal climate conditions result in forest regression and fragmentation, particularly at forest boundaries. However, little is known about patterns of past forest fragmentation in Central Africa at the local scale (e.g., Tchouto et al., 2009) and about the role of fire, which even in tropical rainforests is one of the most important causes of forest destruction (Cochrane et al., 1999; Cochrane, 2003). Therefore, specific research questions for the present study are: (1) what was the temporal and spatial occurrences of fire in the southern Mayumbe? (2) How consistent are anthracological reconstructions with known paleoclimate history? (3) Were paleofires only caused by climatic anomalies or also by humans?

Material and methods

Study area

The Lower Guinean rainforest is separated from the West African rainforests by the Dahomey Gap in Togo and Benin and from the eastern part of the rainforest by the swamps of the Ubangi and Congo Rivers (Leal, 2004). The Mayumbe is a chain of forested hills stretching along the Atlantic Ocean from Gabon down to the Luki reserve, which is located in the Bas-Congo province of the DRC, between 05 45.00′S and 05 70.00′S and between 13 05.00′E and 13 30.00′E (Fig. 1). With the establishment of the Luki reserve in 1937, its forests, soils and possible charcoal archives have been safeguarded from intense anthropogenic disturbance. As part of the 'Man and Biosphere' (MAB) program of UNESCO, a tripartite conservation zonation was applied, including a fully protected 'central zone', which contains an important relict of the semi-evergreen subequatorial Guinean rainforest that once covered the entire Mayumbe hills (e.g., Donis, 1948; Lebrun and Gilbert, 1954). However, its position at the southernmost edge of the Mayumbe forest (Fig. 1A) makes this forest relict vulnerable to climate change, involving natural forest fragmentation. As such, the Luki reserve is highly suitable for paleobotanical research.

Charcoal sampling and profile description

Four pedoanthracological profiles were excavated in the Luki reserve (Fig. 1). One profile was located in the peripheral UH48 stand (Couralet, 2010; Hubau et al., 2012) and three in the central zone (CZ1, CZ2, CZ3) of mature rainforest (Fig. 1B). All profiles were only

a few kilometers apart and located at elevations ranging from 180 to 460 m (Fig. 1D). Soil charcoal sampling was conducted as described by Hubau et al. (2012). For each profile a relatively flat area was chosen, avoiding steep slopes to minimize the effects of erosion or colluvial sedimentation (see Fig. 1D, including information on relief). Furthermore, all sampling sites were well-drained and located outside former agricultural fields (see Carcaillet and Thinon, 1996). Figure 1C presents a distribution map of soil types in the Luki reserve based on the soil map of Bas-Congo presented by Van Ranst et al. (2010).

Next, exploratory holes were drilled with an Edelmann auger, down to 1 m. A pedoanthracological profile of 100 cm × 150 cm surface area was excavated on a spot where prospection yielded charcoal and where the soil was relatively dry and penetrable. All profiles were excavated down to a depth of 140 cm. Deeper charcoal layers were detected and sampled by augering in the bottom of the profile pit. Charcoal fragments (largest dimension > 2 mm) were carefully collected by hand, and sorted per depth interval of 20 cm. Specific anthracomass was calculated as described by Carcaillet and Thinon (1996). Thin sections were prepared from undisturbed soil samples, following polyester impregnation using standard procedures (Murphy, 1986) and micromorphological features were described applying polarization microscopy, using the concepts and terminology of Stoops (2003). These features reveal variations in texture and possible bioturbation.

Charcoal description, identification and radiocarbon dating

For each profile interval, up to 50 charcoal fragments were analyzed using reflected light microscopy (RLM) following Hubau et al. (2012). All charcoal fragments were grouped into charcoal types, of which each type generally represents one species. Next, a large fragment of each charcoal type was mounted on a stub for scanning electron microscopy (SEM). Using SEM images, charcoal types were described applying the numbered anatomical features used for the on-line InsideWood database (IAWA Committee, 1989; InsideWood, 2011; Wheeler, 2011; Hubau et al., 2012). This produces two strings of numbered features. The first string represents primary features that are easily visible, while the second string represents secondary features that are variable or unclear. Finally, all charcoal types were identified applying the Central African identification protocol described by Hubau et al. (2012).

Soil features and distribution of charcoal types within the profile revealed possible profile stratification. One charcoal fragment from each stratigraphic interval was selected for AMS ^{14}C measurement at the Poznán Radiocarbon Laboratory (Poland) or Beta Analytic (Florida, USA). In case of ambiguous stratification patterns, two or three charcoal fragments from different intervals were selected. Calibration was performed with the OxCal v4.1.5 software (r:5) (Bronk Ramsey, 2009) using the SHCal04 calibration curve (McCormac et al., 2004).

Evaluation of identification reliability

The final result of the charcoal identification protocol is the association of each charcoal type with a small group of woody plant species, ranked according to their resemblance with the charcoal type anatomy (Hubau et al., 2012). Specifically, a 5-point ranking system was used, whereby 5 points were attributed in the case of perfect agreement between charcoal anatomy and woody species anatomy. Finally, the charcoal type received a 9-character label composed of the three first letters of respectively family, genus and species name of one of the best ranked species (Hubau et al., 2012). All identifications were evaluated according to two different reliability criteria. Criterion A concerns the phytosociological similarity of the retained species, with a good score if all highest ranked species have similar habitat preferences and a bad score if the highest ranked species occur in different vegetation types. Criterion B is based on the number of highest ranked species and their anatomy rank, with a high score for good resemblance between charcoal and
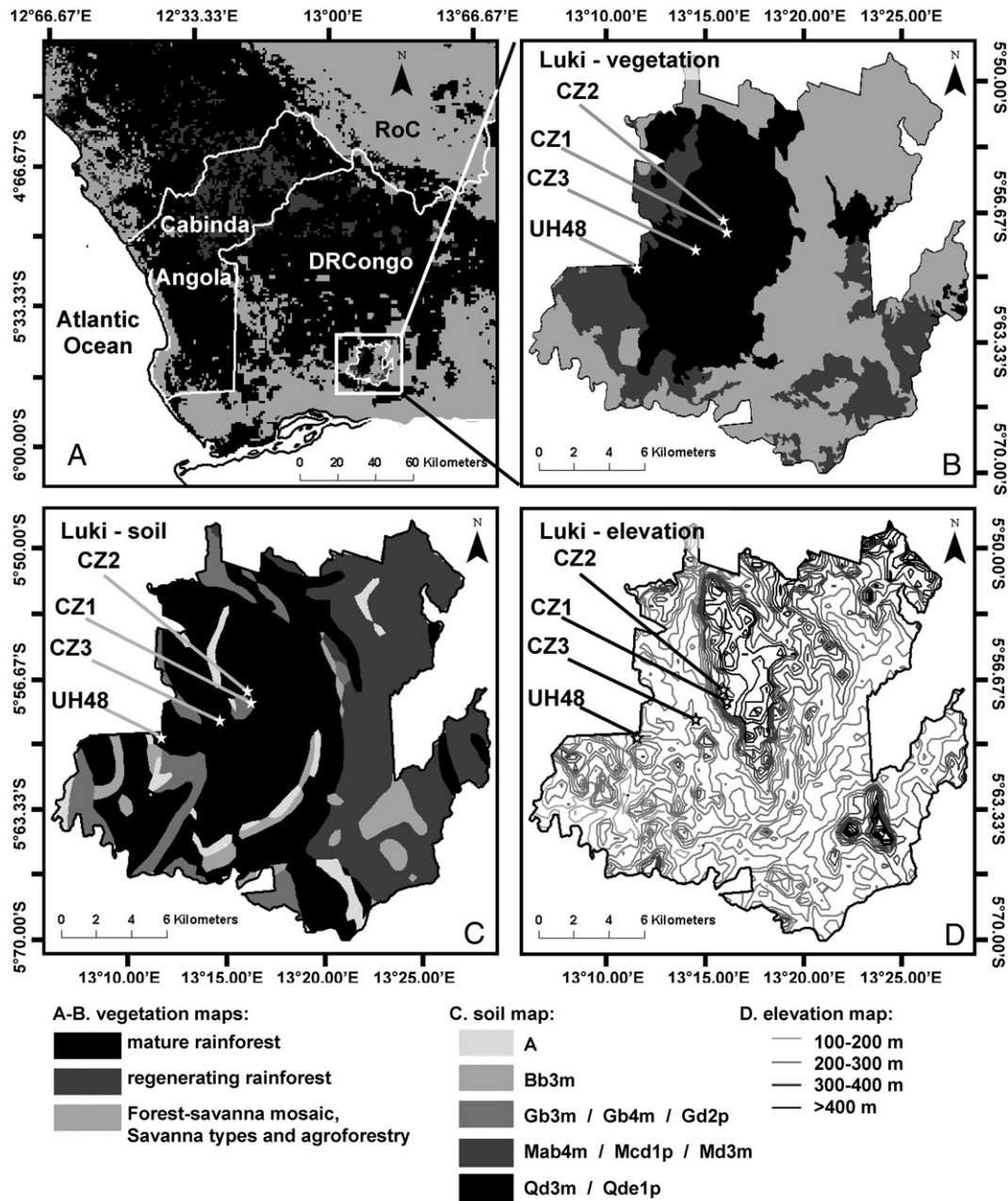
Figure 1. A. Location of the Luki reserve on the currently fragmented southernmost Mayumbe forest boundary, Democratic Republic of Congo (map derived from Mayaux et al., 1997). B. Vegetation map of the Luki reserve. All four studied soil profiles are located in relict stands of mature rainforest, although the direct surroundings are heavily fragmented and regenerating forest patches are not far away. C. Soil types in the Luki reserve (after Van Ranst et al., 2010). Type Gb3m (profile CZ1) — soil derived from gneiss, with advanced ABtC profile development (Acrisol; WRB, 2006), typically reddish, highly weathered, well-drained, with sandy clay texture, often limited below by gravel at 50–100 cm depth. Type Qd3m (profiles CZ2, CZ3 and UH48) — soil derived from quartzite, with advanced ABtC development (Acrisol; WRB, 2006), typically yellowish, highly weathered, well drained, with sandy clay-loam to sandy loam texture, often limited below by gravel at 50–100 cm depth. Type A (close to profile UH48) — deep alluvial soil, with ABwC profile development, imperfectly to moderately drained (Gleysol; WRB, 2006), with sandy loam texture, generally not limited by gravel until at least 100 cm depth. D. Elevation map of the Luki reserve. Profiles CZ1 and CZ2 are excavated on the relatively flat central hillcrest known as Ndiondio. Profiles CZ3 and UH48 are excavated on lower terrain, far enough from steep slopes to avoid severe erosion or colluvial deposition.

reference wood anatomy. Using these two criteria, the charcoal types were given a reliability rank ranging from 1 to 6.

Results

Profile description

Table 1 lists the uncalibrated and calibrated ages for all dated fragments. Figure 1C shows the distribution of soil types in the Luki reserve, derived from the soil map of the Bas-Congo province (Van Ranst et al., 2010), in which parent material composition is used at the highest taxonomic level. A description of the dominant soil type at each profile is given in the caption of Figure 1. Soils of the Luki area are Humic Acrisols in the WRB system and Kandiustalfs or Kandiustults in the USDA system (Baert, 1995), characterized by Bt horizon development (Van Ranst et al., 2010). Our field and soil thin section observations are largely compatible with this characterization. Figures 2 and 3 show soil profile descriptions, soil types, specific anthracomass and charcoal identification results.

Table 1
Conventional radiocarbon ages and calibrated ages.

Profile	Depth [cm]	Lab no	14C age [14C BP]	Calibrated age intervals [cal BP]		Probability [%]	
UH48	30–40	Poz-33055	2055 ± 30	2043 BP – 1872 BP		95.4 %	95.4 %
				1991 BP – 1922 BP		60.1 %	68.2 %
				1911 BP – 1900 BP		8.1 %	
UH48	80–90	Poz-39110	2205 ± 30	2308 BP – 2308 BP		28.9 %	95.4 %
				2209 BP – 2036 BP		62.4 %	
				2030 BP – 2004 BP		4.1 %	
				2300 BP – 2250 BP		22.5 %	68.2 %
				2177 BP – 2174 BP		1.0 %	
				2160 BP – 2098 BP		33.2 %	
				2091 BP – 2062 BP		11.6 %	
UH48	120–130	Poz-39109	2140 ± 35	2154 BP – 1946 BP		95.4 %	95.4 %
				2114 BP – 2078 BP		22.3 %	68.2 %
				2071 BP – 2000 BP		45.9 %	
CZI	40–60	Poz-33051	1770 ± 30	1704 BP – 1544 BP		95.4 %	95.4 %
				1691 BP – 1655 BP		24.7 %	68.2 %
				1628 BP – 1566 BP		43.5 %	
CZI	120–140	Poz-33052	1790 ± 30	1811 BP – 1753 BP		6.8 %	95.4 %
				1742 BP – 1532 BP		88.6 %	
				1706 BP – 1594 BP		60.8 %	68.2 %
				1584 BP – 1569 BP		7.4 %	
CZ2	60–80	Poz-33054	555 ± 30	554 BP – 504 BP		95.4 %	95.4 %
				544 BP – 515 BP		68.2 %	68.2 %
CZ3	20–40	Beta-314122	580 ± 30	626 BP – 607 BP		8.0 %	95.4 %
				561 BP – 510 BP		87.4 %	
				554 BP – 523 BP		68.2 %	68.2 %
CZ3	60–80	Beta-314123	>43500	–		–	

Shaded portions indicate 99.4% probability intervals.

Anthracomass, profile stratification and bioturbation

The numbers presented in Figures 2 and 3 are the first attempt to quantify anthracomass in Lower Guinean primary rainforest soils, as previous authors (e.g., Dechamps et al., 1988; Schwartz et al., 1990; van Gemerden et al., 2003) only present charcoal assemblage composition. Specific anthracomass of most 20-cm intervals is less than 25 ppm. Only profile UH48 contains intervals with a much higher specific anthracomass at 30–40 and 40–50 cm depths of 121 and 184 ppm, respectively. These values are comparable to those in soil profiles in the French Alps, where only two intervals yielded more than 20 ppm, with a maximum of 124 ppm (Carcaillet and Thinon, 1996). Pedoanthracological profiles in the Andes yielded a maximum of 300 ppm (Di Pasquale et al., 2008).

In profile CZ3, rock fragments are abundant below 40 cm depth and a clear contrast exists between an upper, organic A/AB horizon (0–40 cm) and a lower, argillic 2Bt horizon (40–80 cm). Moreover, two distinct specific anthracomass peaks (22 and 26 ppm) are separated by a charcoal-poor interval (40–60 cm; 3 ppm), reflecting stratification (e.g., Carcaillet et al., 1997; Di Pasquale et al., 2008). The charcoal assemblage in the A/AB horizon is dated to between 626 and 510 cal yr BP whereas that in the 2Bt horizon is older than 43.5 cal ka BP (Fig. 3, Table 1). Charcoal types occurring in the A/AB horizon do not occur in the 2Bt horizon, except for a few fragments that have probably been transported due to bioturbation, as indicated by the occurrence of channels, passage features and zones with a pellet structure in thin sections (Fig. 3). All other identifiable charcoal fragments in the 2Bt horizon have a weathered and brittle appearance and all belong to only one charcoal type (CAE GUI SPP).

In contrast to profile CZ3, profiles CZ1, CZ2 and UH48 do not exhibit a lithological discontinuity or significant clay illuviation. Still, in all three profiles the distribution of charcoal fragments displays peaking specific anthracomass values at the top of the profile, followed by a nearly charcoal-free layer and a secondary anthracomass peak lower down (Figs. 2, 3). This lower peak is weak in profiles CZ2 and UH48, but significant in profile CZ1 at 120–140 cm depth. Yet, fragments from this lower anthracomass peak belong to charcoal types that also occur in the surface interval and their radiocarbon ages are similar (Fig. 2, Table 1). Hence, profile CZ1 is not stratified and the local soil charcoal assemblage

probably originated from only one paleofire event, which occurred between 1704 and 1544 cal yr BP (Table 1). Likewise, profiles UH48 and CZ2 are not stratified and their charcoal assemblages originate from fire events that occurred between 2308 and 1872 cal yr BP at the UH48 site and between 554 and 504 cal yr BP at the CZ2 site (Figs. 2, 3).

The charcoal fragments in profiles CZ1, CZ2 and UH48 are scattered over a depth interval of 140 cm, although at each location they were formed during a single event. This could be explained by strong bioturbation, as evidenced by the occurrence of channels, passage features and zones with a pellet or granular microstructure (Figs. 2, 3). Ants and termites are abundant in semi-deciduous rainforest and can severely disturb stratified profiles and even archeological layers (e.g., Cahen and Moeyersons, 1977; McBrearty, 1990; Théry-Parisot et al., 2010). In profile CZ3, a horizon with a large number of rock fragments below 40 cm depth impeded bioturbation. This may have contributed to the preservation of two separate intervals with distinct charcoal assemblages, including one that is ancient (>43.5 cal ka BP). Besides bioturbation, micromorphological features also provide evidence for some colluvial deposition, even though sampling sites were chosen on relatively flat areas. Examples are the presence of chert fragments (CZ1, CZ2) and ironstone fragments (CZ2, UH48), relatively low grain angularity (UH48) and good sorting (UH48) (for terminology and interpretation, see Stoops, 2003; Stoops et al., 2010).

Since charcoal assemblages can be distributed over a thickness of more than 140 cm over a span of 600 yr (e.g., profile CZ2, Fig. 2), redistribution of charcoal fragments by bioturbation and colluvial deposition must be a rather fast process. Older charcoal assemblages could be present below 140 cm depth at the CZ1, CZ2 and UH48 sites, but if these would be spread over a large depth interval then specific anthracomass would be low, also diminishing the chance to find charcoal. Spreading of charcoal fragments over large soil volumes could also explain why none of the additional samples (140–180 cm) taken below the bottom of the profiles contain charcoal fragments (Figs. 2, 3).

Charcoal assemblage composition

Analysis of a total of 935 charcoal fragments yielded 44 charcoal types (see Supplementary Tables 1 and 2 for the complete inventory of all retained species names and their ecology, light requirements, morphology and geographical distribution area). The distributions of charcoal types within each soil profile is presented in Figures 2 and 3, including an attribution for each recovered charcoal type to one particular type of vegetation (gray shades). Specifically, some charcoal types originate from typical primary rainforest taxa, others mainly from regenerating forest taxa and others from prominent pioneer taxa. Some taxa have a large ecological tolerance, occurring in mature evergreen rainforest, in the forest–savanna transition zone and even in the seasonally variable climate conditions of woodland savanna (Figs. 2, 3).

Charcoal identifications for profile UH48 were presented earlier (Hubau et al., 2012), but one previously unidentified monocotyledon taxon has now been identified as a *Dracaena* species (Fig. 3, Supplementary Table 2). Charred endocarp remains of oil palm drupes (*Elaeis guineensis*) were found in all four profiles, most abundantly in profiles UH48 and CZ3 (upper intervals). Besides these endocarps, only charcoal type PHY ANT SPP occurs in more than one profile. Eight charcoal types remain unidentifiable, although they are clearly derived from mature woody species and different from all identified charcoal types. Furthermore, 11 unidentified charcoal types are derived from juvenile wood, fruit, bark or unidentified charred tissue (Figs. 2, 3). These fragments can be derived from some of the same woody species as the identified charcoal fragments.

Identification reliability

Table 2 presents the highest anatomy rank, the number of highest ranked species and the name of one of the highest ranked species for

Figure 2. Radiocarbon dates, soil profile characteristics, specific anthracomass and charcoal types recovered from sites CZ1 and CZ2. For every charcoal type, a representative species name and identification reliability evaluation is presented in Table 2.
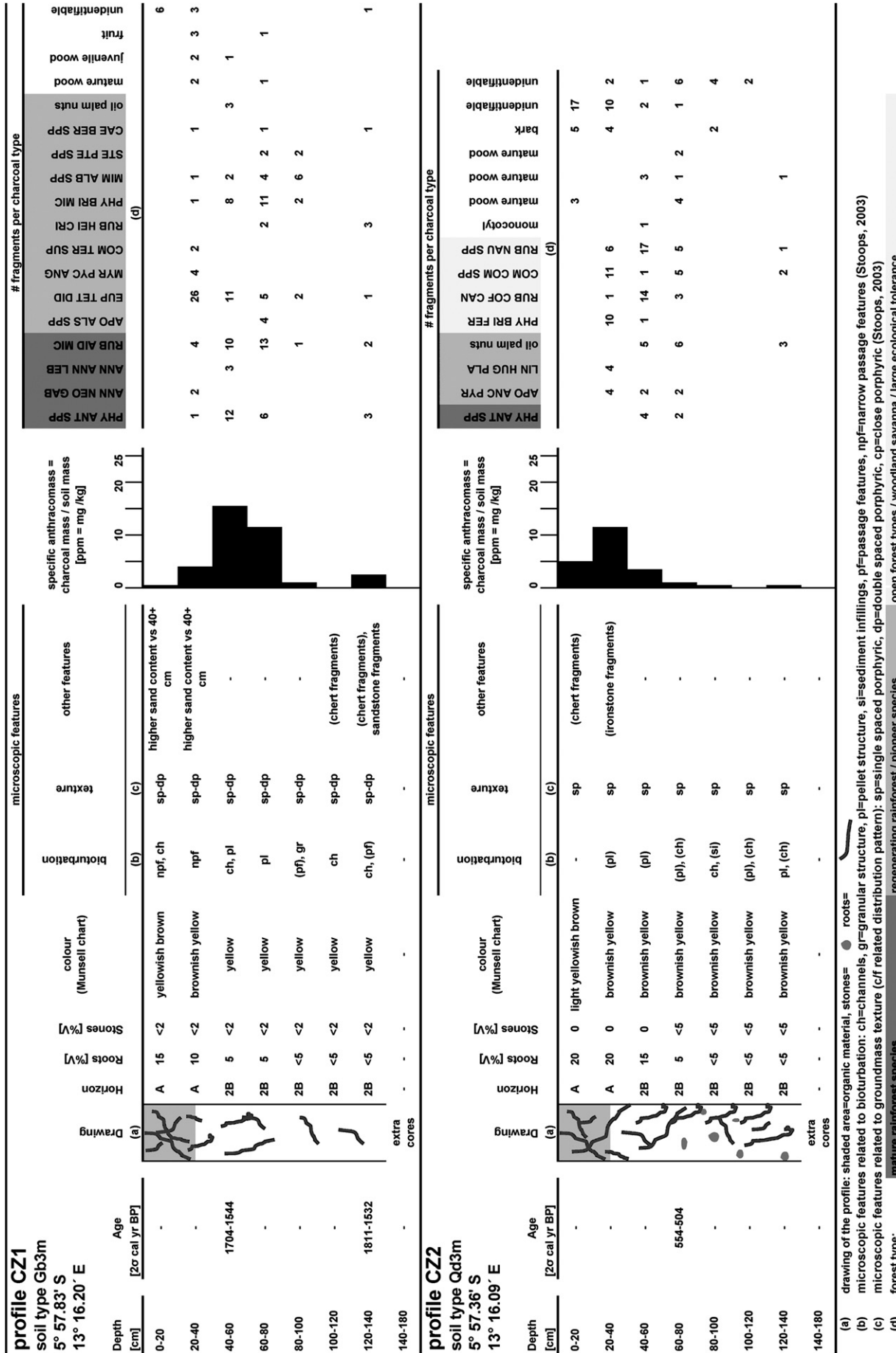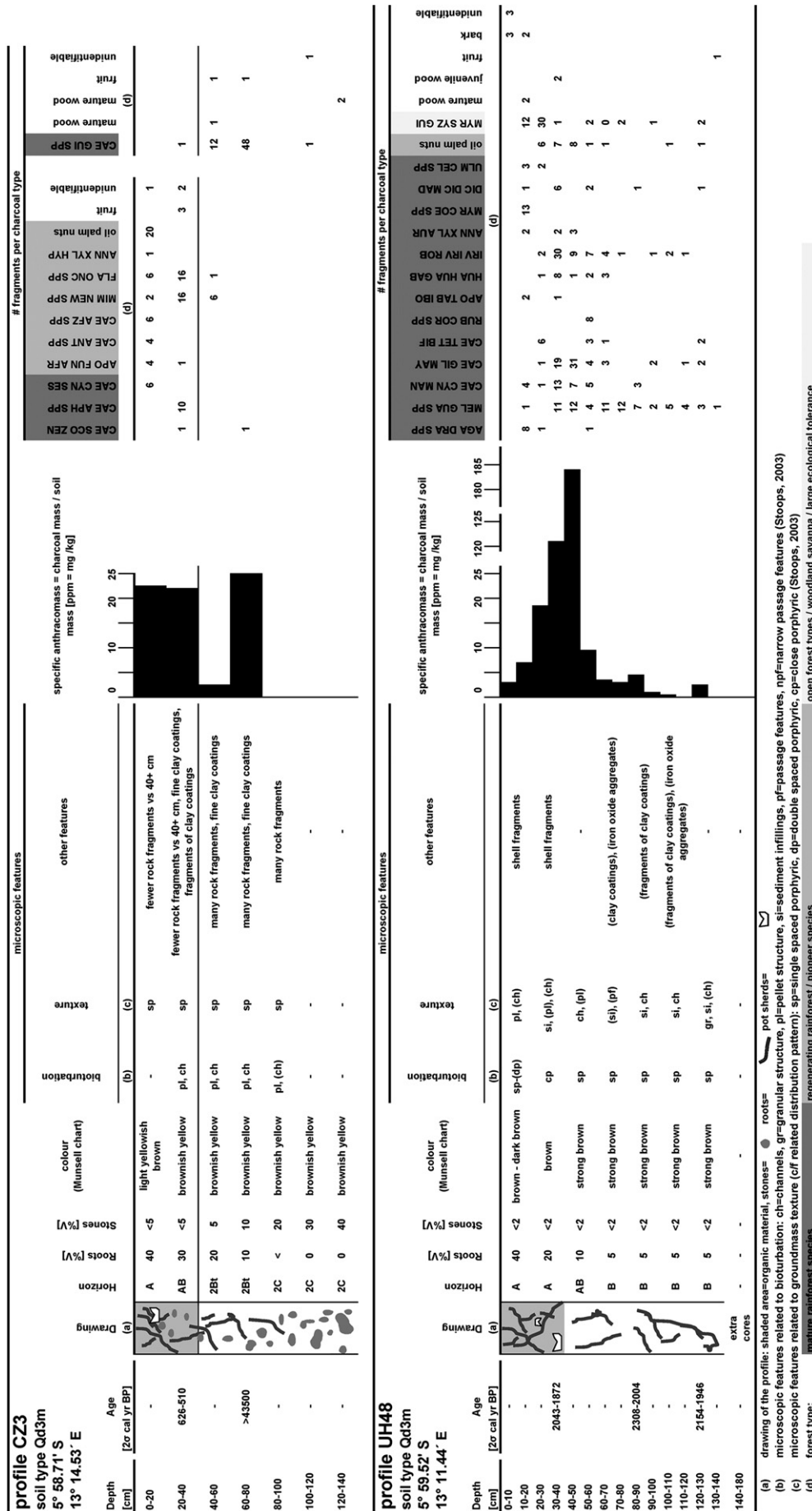
Figure 3. Radiocarbon dates, soil profile characteristics, specific anthracomass and charcoal types recovered from sites CZ3 and UH48. For every charcoal type, a representative species name and identification reliability evaluation is presented in Table 2.

Table 2
Representative species name and evaluation of identification reliability for each identified charcoal type presented in Figs. 2 and 3. The highest anatomy rank, the number of highest ranked species, and ecology of the highest ranked species are indicated.

Charcoal type	Profile	Family	Representative species	Highest anatomy rank (/5)	# Highest ranked species	Mature rainforest species	Regenerating forest species	Poineer	Woodland savanna species	Large ecological tolerance	Phytosociological similarity A	Woody species resemblance B	Reliability rank
APO ALS SPP	CZ1	Apocynaceae	cfr. Alstonia boonei De Wild.	5	2	a	a	p	a	a	+	+++	1
APO ANC PYR	CZ2	Apocynaceae	cfr. Ancylobothrys pyriformis Pierre	5	1	a	p	a	a	a	+	+++	1
APO FUN AFR	CZ3	Apocynaceae	cfr. Funtumia africana (Benth.) Stapf	5	2	a	a	p	a	a	+	+++	1
CAE ANT SPP	CZ2	Caesalpinioideae	cfr. Anthonotha pynaertii (De Wild.) Exell & Hillc.	5	2	a	p	a	a	a	+	+++	1
CAE SCO ZEN	CZ3	Caesalpinioideae	cfr. Scorodophloeus zenkeri Harms	5	1	p	a	a	a	a	+	+++	1
EUP TET DID	CZ1	Euphorbiaceae	cfr. Tetrorchidium didymostemon (8aill.) Pax & K. Hoffm.	5	1	a	a	p	a	a	+	+++	1
LIN HUG PLA	CZ2	Linaceae	cfr. Hugonia platysepala Welw. ex Oliv.	5	1	a	p	a	a	a	+	+++	1
PHY ANT SPP	CZ1	Phyllantaceae	cfr. Antidesma rufescens Tul.	5	2	p	a	a	a	a	+	+++	1
PHY ANT SPP	CZ2	Phyllantaceae	cfr. Antidesma rufescens Tul.	5	2	p	a	a	a	a	+	+++	1
AGA DRA SPP	UH48	Agavaceae	cfr. Dracaena arborea (Willd.) Link	5	5	p	a	a	a	a	+	++	1
CAE AFZ SPP	CZ3	Caesalpinioideae	cfr. Afzelia bella Harms	5	6	a	p	a	a	a	+	++	1
CAE GUI SPP	CZ3	Caesalpinioideae	cfr. Guibourtia demeusei (Harms) J. Leonard	5	5	a	p	a	a	a	+	++	1
MYR PYC ANG	CZ1	Myristicaceae	cfr. Pycnanthus angolensis (Welw.) Exell	5	3	a	a	p	a	a	+	++	1
ANN NEO GAB	CZ1	Annonaceae	cfr. Neostenanthera gabonensis (Engl. & Diels) Exell	4	1	p	a	a	a	a	+	+	2
CAE CYN MAN	UH48	Caesalpinioideae	cfr. Cynometra mannii Oliv.	4	1	p	a	a	a	a	+	+	2
COM TER SUP	CZ1	Combretaceae	cfr. Terminalia superba Engl. & Diels	4	1	a	a	p	a	a	+	+	2
MEL GUA SPP	UH48	Meliaceae	cfr. Guarea cedrata (A. Chev.) Pellegr.	4	2	p	a	a	a	a	+	+	2
MIM NEW SPP	CZ3	Mimosoideae	cfr. Newtonia glandulifera (Pellegr.) Gilbert & Boutique	4	2	a	p	a	a	a	+	+	2
RUB HEI CRI	CZ1	Rubiaceae	cfr. Heinsia crinita (Afzel.) G. Taylor	4	2	a	p	a	a	a	+	+	2
ANN ANN LEB	CZ1	Annonaceae	cfr. Annickia lebrunii (Robyns & Ghesq.) Sellen & Maas	4	5	p	a	a	a	a	+	–	2
CAE APH SPP	CZ3	Caesalpinioideae	cfr. Aphanocalyx microphyllus (Harms) Wieringa	4	4	p	a	a	a	a	+	–	2
CAE GIL MAY	UH48	Caesalpinioideae	cfr. Gilbertiodendron mayombense (Pellegr.) J. Leonard	4	4	p	a	a	a	a	+	–	2
CAE TET BIF	UH48	Caesalpinioideae	cfr. Tetraberlinia bifoliolata (Harms) Hauman	4	3	p	a	a	a	a	+	–	2
MYR SYZ GUI	UH48	Myrtaceae	cfr. Syzygium guineense (Willd.) DC.	4	4	a	a	a	a	p	+	–	2
PHY BRI FER	CZ2	Phyllantaceae	cfr. Bridelia ferruginea Benth.	4	3	a	a	a	p	a	+	–	2
RUB COF CAN	CZ2	Rubiaceae	cfr. Coffea canephora Pierre ex A. Froehner	4	6	a	a	a	a	p	+	–	2
RUB COR SPP	UH48	Rubiaceae	cfr. Corynanthe paniculata Welw.	4	7	p	a	a	a	a	+	–	2
APO TAB IBO	UH48	Apocynaceae	cfr. Tabernanthe iboga Baill.	3	3	p	a	a	a	a	+	—	3
PHY BRI MIC	CZ1	Phyllantaceae	cfr. Bridelia micrantha (Hochst.) Baill.	3	2	a	a	p	a	a	+	—	3
ANN XYL HYP	CZ3	Annonaceae	cfr. Xylopia hypolampra Mildbr.	5	4	p	p	a	a	a	–	++	4
CAE CYN SES	CZ3	Caesalpinioideae	cfr. Cynometra sessiliflora Harms	5	4	p	p	a	a	a	–	++	4
FLA ONC SPP	CZ3	Flacourtiaceae	cfr. Oncoba mannii Oliv.	5	4	p	p	a	a	a	–	++	4
MIM ALB SPP	CZ1	Mimosoideae	cfr. Albizia ferruginea (Guill. & Perr.) Benth.	5	5	p	p	a	a	a	–	++	4
HUA HUA GAB	UH48	Huaceae	cfr. Hua gabonii Pierre ex De Wild.	4	2	p	a	a	a	a	–	+	5
IRV IRV ROB	UH48	Irvingiaceae	cfr. Irvingia rabur Mildbr.	4	2	p	a	a	a	a	–	+	5
ANN XYL AUR	UH48	Annonaceae	cfr. Xylopia aurantiiodora De Wild. & T. Durand	4	5	p	a	a	a	p	–	–	5
CAE BER SPP	CZ1	Caesalpinioideae	cfr. Berlinia bracteosa Benth.	4	5	a	p	a	p	a	–	–	5
COM COM SPP	CZ2	Combretaceae	cfr. Combretum mortehanii De Wild. & Exell	4	11	p	a	a	p	a	–	–	5
MYR COE SPP	UH48	Myristicaceae	cfr. Coelocaryon botryoides Vermoesen	4	4	p	a	a	a	a	–	–	5
RUB AID MIC	CZ1	Rubiaceae	cfr. Aidia micrantha (K. Schum.) Bullock ex F. White	4	7	p	a	a	p	a	–	–	5
RUB NAU SPP	CZ2	Rubiaceae	cfr. Nauclea diderrichii (De Wild.) Merr.	4	5	p	a	a	p	a	–	–	5
STE PTE SPP	CZ1	Sterculiaceae	cfr. Pterygota macrocarpa K. Schum.	4	10	p	p	a	a	a	–	–	5
DIC DIC MAD	UH48	Dichapetalaceae	cfr. Dichapetalum madagascariense Poir.	3	2	p	a	a	a	p	–	—	6
ULM CEL SPP	UH48	Ulmaceae	cfr. Celtis mildbraedii Engl.	3	6	p	a	a	a	p	–	—	6

Reliability evaluation criteria:

			UH48	CZ1	CZ2	CZ3	ALL	UH48	CZ1	CZ2	CZ3	ALL
					# species					% species		
A	phytosociological similarity of highest ranked species											
+		similar habitat preferences	8	9	5	7	29	57	69	71	70	67
–		different habitat preferences	6	4	2	3	15	43	31	29	30	33
B	woody species resemblance											
+++		almost perfect resemblance with only one or two species (highest anatomy rank = 5/5)	0	3	3	3	9	0	23	43	30	24
++		almost perfect resemblance with more than two species (highest anatomy rank = 5-5)	1	2	0	5	8	7	15	0	50	18
+		good resemblance with only one or two species (highest anatomy rank = 4/5)	4	3	0	1	8	29	23	0	10	15
–		good resemblance with more than two species (highest anatomy rank = 4/5)	6	4	4	1	15	43	31	57	10	35
—		only moderate resemblance with one or more species (highest anatomy rank ≤ 3/5)	3	1	0	0	4	21	8	0	0	7
Reliability rank:			1	4	0	0	4					
1	phytosociological similarity (crit. A)	& almost perfect resemblance (criterion B)	1	4	3	5	13	7	31	43	50	33
2	phytosociological similarity	& very good resemblance	6	4	2	2	14	43	31	29	20	31
3	phytosociological similarity	& only moderate resemblance	1	1	0	0	2	7	8	0	0	4
4	phytosociological ambiguity	& almost perfect resemblance	0	1	0	3	4	0	8	0	30	9
5	phytosociological ambiguity	& very good resemblance	4	3	2	0	9	29	23	29	0	20
6	phytosociological ambiguity	& only moderate resemblance	2	0	0	0	2	14	0	0	0	4
		Total:	14	13	7	10	44	100	100	100	100	100
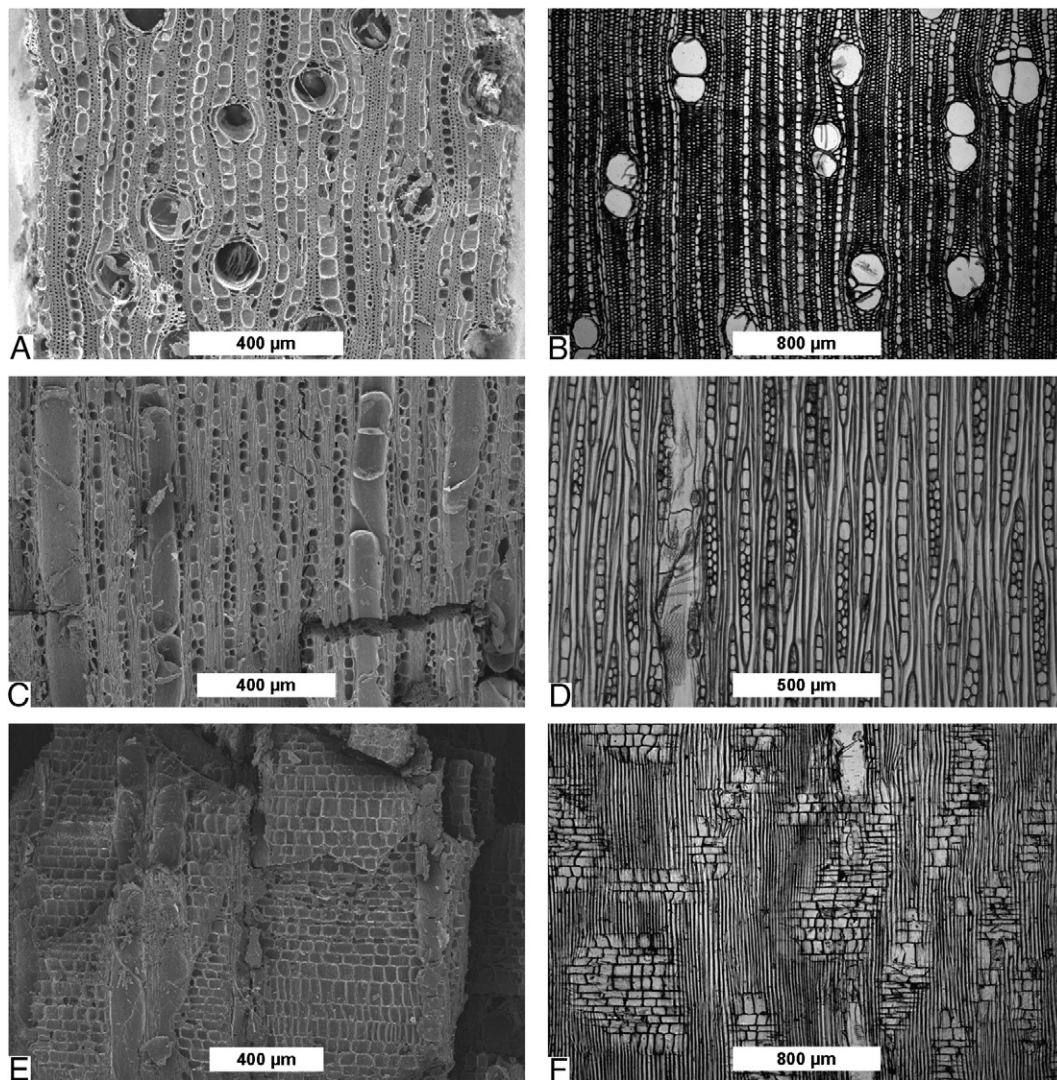
Figure 4. Left: Scanning Electron Micrographs (SEM) of charcoal type MYR PYC ANG; Right: Transmitted Light Micrographs (TLM) of a reference wood sample of *Pycnanthus angolensis* (Welw.) Exell (Tw 29820) (Myristicaceae). A–B: Transversal direction; C–D: Tangential direction; E–F: Radial direction.

each of the 44 identified charcoal types, along with the vegetation types in which the highest ranked species occur, and an identification reliability score based on our two evaluation criteria (see Material and methods section). In cases where only one species is ranked highest, our identification excludes any possible confusion regarding the ecology of the charcoal type (e.g., APO ANC PYR, EUP TET DID, LIN HUG PLA). However, for most charcoal types, several species receive the highest rank, with a maximum of 11 species (COM COM SPP). Sometimes, the highest ranked species had different phytosociological characteristics, complicating paleoecological interpretation of the charcoal type. In such cases, the charcoal type received a negative (−) score for evaluation criterion A. Evaluation criterion B specifies how well the charcoal type resembles reference material of the highest ranked species. Based on both criteria together, each charcoal type received an identification reliability rank.

Overall, 64% (27 types) of our identifications are highly reliable (ranks 1 or 2) because their highest ranked species do not have ambiguous phytosociological characteristics and resemble the charcoal type's anatomy almost perfectly or at least very well (Table 2). Identifications are especially reliable in profiles CZ2 and CZ3 (71% and 70% respectively), followed by profile CZ1 (62%) and finally profile UH48 (50%). As an illustration of a reliable identification, Figure 4 presents SEM images of charcoal type MYR PYC ANG from profile CZ1

together with transmitted light images of a reference wood sample of *Pycnanthus angolensis*, a prominent pioneer species. Only two charcoal types have highest ranked species that resemble the charcoal anatomy only moderately, although they are phytosociologically unambiguous (rank 3, APO TAB IBO and PHY BRI MIC). Finally, 33% (15 types) of all identifications are not reliable (ranks 4, 5 or 6) because their highest ranked species occur in different forest types, complicating proper ecological interpretation. As an example, some of the 11 highest ranked species of charcoal type COM COM SPP (*Combretum* spp.) occur in mature rainforest, whereas others are typical woodland savanna species (Table 2 and Supplementary Table 1).

Discussion

Temporal aspects of the paleofire regime in the Luki reserve

Natural fires in moist evergreen rainforest environments are generally rather rare because high air humidity reduces combustibility (Scott, 2000). The long period without recorded charcoal formation at the CZ3 site, spanning more than 43 ka (Fig. 3), appears to suggests that local paleofires did not occur on this site during the consecutive climate variations of the late Pleistocene and Holocene (e.g., Maley
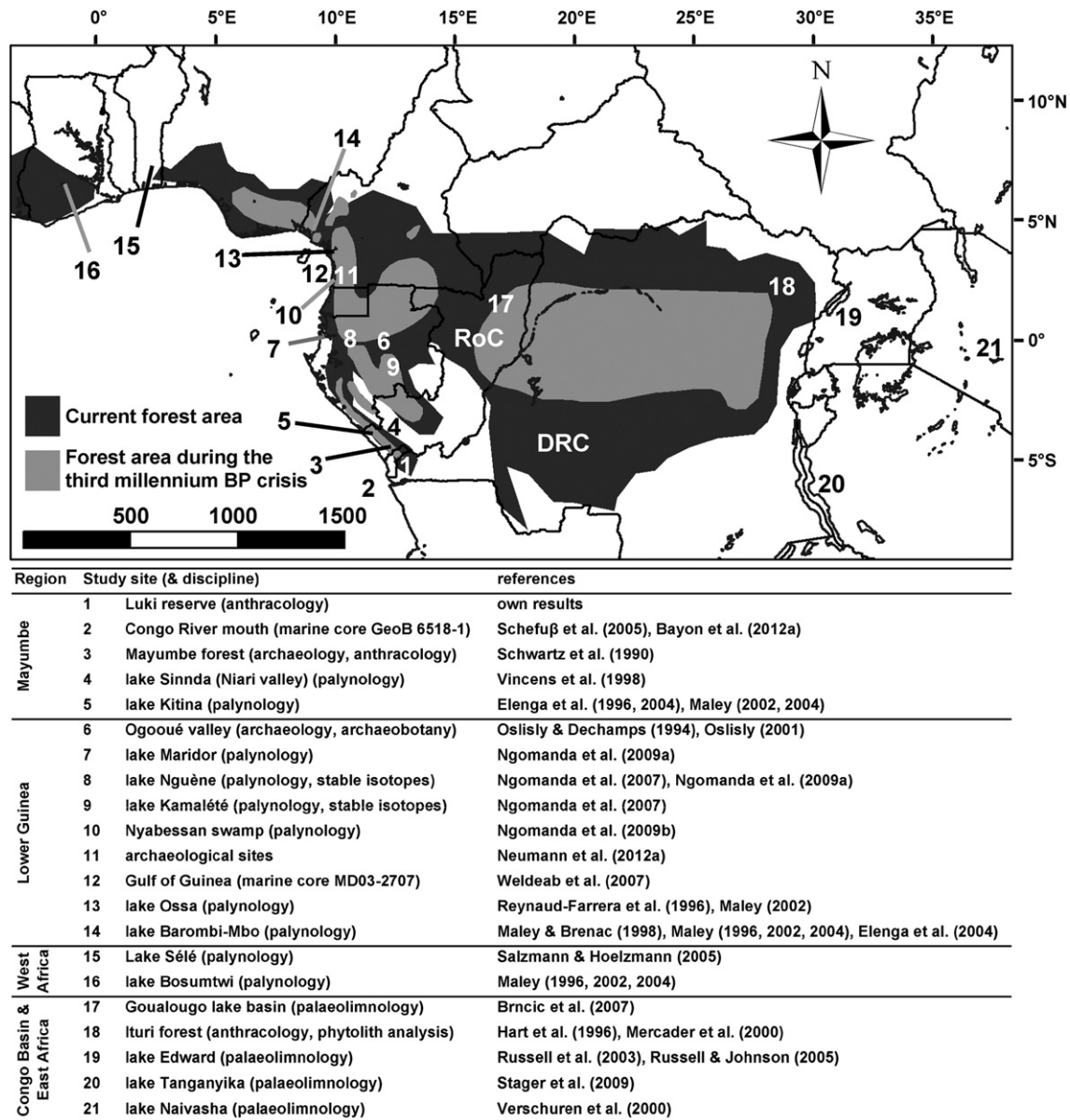
Figure 5. Geographical distribution of published paleoenvironmental records throughout equatorial Africa in relation to the Luki reserve (site 1), with indication of the type of source data and main references. The current distribution of rainforest is based on Mayaux et al. (1997) and forest area during the third millennium BP is adapted from Maley (2004).

and Brenac, 1998), implying possible long-term absence of fire in the Central African rainforest, even at forest boundaries (Fig. 1).

On the other hand, it is possible that the CZ3 profile does not represent a continuous paleoenvironmental archive. Specifically, temporal gaps in the macrocharcoal record may be due to a scarcity of woody plants combined with limited soil accumulation and profile development during dry episodes of the last glacial cycle (e.g., Dupont et al., 2000), when fires were probably more common in Central Africa (e.g., Bird and Cali, 1998). The absence of charcoal can also be a result of unrecognized severe soil erosion truncating the profile. Furthermore, presence of charcoal fragments from a *Guibourtia demeusei* stand older than 43.5 cal ka BP implies that naturally induced fires occurred during a period when the locality was covered with rainforest. Based on current understanding of Congo Basin vegetation history at this time scale, this charcoal may date from the (later phases of) MIS 5, i.e. older than ca. 75 ka, unless episodes of rapid climate change during Dansgaard–Oeschger cycles and Heinrich

stadials in MIS 3–4 allowed short-lived development of local rainforest, perhaps disturbed by fire (cf. Daniau et al., 2010). The charcoal assemblages of all other recorded paleofires in our Luki profiles are a testimony of fire within the rainforest (Figs. 2, 3, Table 2). Most probably this occurred in areas of fragmented forests where fires in dry and open savanna patches can burn forest edges and small forest patches, thus creating more fire-prone open spaces (Cochrane et al., 1999; Cochrane, 2003).

In paleoecological studies of the African rainforest, periods of inferred forest fragmentation are often attributed to the occurrence of arid climate anomalies (Vincens et al., 1998; Maley, 2001, 2002; Cochrane, 2003). On late-Quaternary time scales, Central African precipitation regimes are mainly controlled by the influence of northern high-latitude glaciation on the Atlantic Meridional Overturning Circulation (AMOC), reflected in differences in sea surface temperature (= ΔSST) between the tropics and the subtropics (Schefuß et al., 2005). High ΔSST is associated with stronger Southern Hemisphere trade winds hampering the

Region:	Lower Guinea - southern Mayumbe				Lower Guinea			Dahomey Gap	Congo Basin	East Africa		
Sites:	Luki reserve	Congo River mouth	Lake Sinnda	Lake Kitina	archaeological sites	Lakes Nguène and Kamalété	Lakes Ossa, Barombi Mbo and Bosumtwi, Nyabessan swamp, core MD03-2707	Lake Sélé		Lake Edward	Lake Tanganyika	Lake Naivasha
Site nr.:	1	2	4	5	3, 6, 11	7, 8, 9	10, 12, 13, 14, 16	15	17, 18	19	20	21
Ref.:	own results	Schefuß et al. (2005)	Vincens et al. (1998)	Elenga et al. (1996, 2004); Maley (2002, 2004)	Oslisly & Dechamps (1994), Schwartz et al. (1990) Oslisly (2001), Neumann et al., (2012a, 2012b)	Ngomanda et al. (2007, 2009a)	Reynaud-Farrera et al. (1996), Maley & Brenac (1998), Maley (1996, 2002, 2004), Ngomanda et al. (2009b), Weldeab et al. (2007)	Salzmann & Hoelzmann (2005)	Hart et al. (1996), Brncic et al. (2007)	Russell et al. (2003), Russell & Johnson (2005, 2007)	Stager et al. (2009)	Verschuren et al. (2000)

Time scale: 0 – 4000 cal yr BP

Luki reserve (1):
- fire, pioneers, woodland savanna (human activity)
- fire, pioneer taxa; no human activity
- fire, persisting semi-deciduous taxa (human activity)

Congo River mouth (2):
- weak ΔSST drop, wetting trend
- peaking ΔSST
- sharp ΔSST rise, aridification
- weak ΔSST drop, wetting trend
- peaking ΔSST
- sharp ΔSST rise, aridification
- weak ΔSST drop, wetting trend
- peaking ΔSST
- sharp ΔSST rise, aridification
- stable ΔSST, relatively wet

Lake Sinnda (4):
- brief drought (LIA), little impact
- return to wet
- forest regeneration hampered by anthropogenic grassland burning
- aridity lasts
- grasslands remain
- weak forest recovery
- anthropogenic grassland burning
- severe aridity, grasslands
- onset of aridity, semi-deciduous taxa, forest fragmentation

Lake Kitina (5):
- return to wet
- forest regeneration
- severe aridity, grasslands, human little impact
- onset of aridity, semi-deciduous taxa, heliophilous taxa

archaeological sites (3, 6, 11):
- Late Iron Age
- charcoal layers ~shifting cultivation
- Early Iron Age, fast spread of metallurgy down to the Mayumbe
- increased seasonality favoured cultivation of *Pennisetum glaucum*; arrival of iron smelting
- Neolithic, several pottery traditions
- cultural movement within Lower Guinea
- human-induced fires hampered forest recolonisation
- wave of Bantu migration following ridge lines running north-south through the forest

Lakes Nguène and Kamalété (7, 8, 9):
- wet-dry cycles (MCA), shade-intolerant taxa, rainforest disturbance
- return to wet
- forest recovery, increase in pioneers, semi-deciduous taxa
- increasing human activity
- 2nd forest breakdown centre of the rainforest, forest mosaic, Gramineae and pioneers, limited human impact
- severe aridity
- onset of aridity
- 1st forest breakdown periphery of rainforest, semi-deciduous species, heliophilous species

Lakes Ossa, Barombi Mbo and Bosumtwi, Nyabessan swamp, core MD03-2707 (10, 12, 13, 14, 16):
- return to wet, forest-savanna mosaics persist
- dry period, weak forest contraction
- forest disturbance, increase in oil palm
- return to wet
- non-synchronous forest re-invasion pioneers, Gramineae
- increasing SST, increased seasonality, cumuliform clouds, Gramineae and pioneers, bantu migration
- lowest SST, hyperarid in Sahel
- continuing drop of SST
- weakening West African monsoon, increasing aridity (dominating dry season)
- stratiform clouds

Lake Sélé (15):
- return to dry, open savanna
- return to wet
- forest-savanna mosaics
- pioneers
- natural spread of *E. guineensis*
- human impact overestimated
- dry
- formation of savanna corridor DAHOMEY GAP

Congo Basin (17, 18):
- 5 fire events
- 2 fire events
- 14 fire events, frequent small fires, increased anthropogenic burning
- 2 fire events
- onset of frequent forest fires (storms)
- 1 fire event, severe drought, persisting rainforest
- 2 fire events, onset of aridity

Lake Edward (19):
- wetter conditions
- major drought
- LIA
- wetter conditions
- major drought, MCA
- wetter conditions
- major drought
- Dark Ages
- return to wet
- increasing aridity
- variability of Indian monsoon

Lake Tanganyika (20):
- very wet
- dry (Spörer)
- very wet
- major drought
- very wet
- very wet
- increasingly wet
- widespread aridity

Lake Naivasha (21):
- dry
- wet (Maunder)
- dry
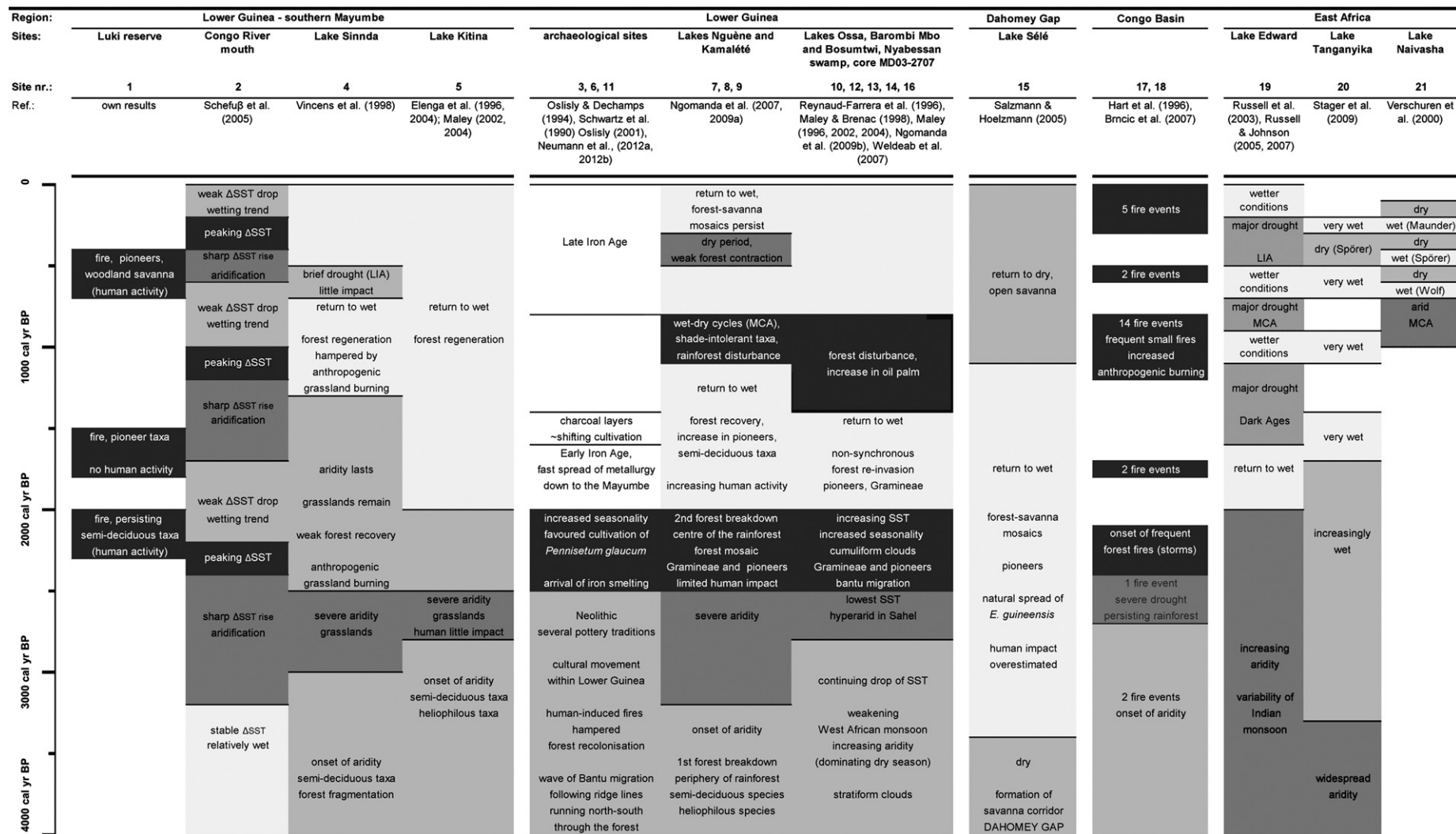- wet (Spörer)
- dry
- wet (Wolf)
- arid
- MCA

Figure 6. Summary of the main findings resulting from paleorecords reconstructed for the Mayumbe, the Lower Guinea, the Dahomey Gap, the Congo Basin and East Africa. Black fillings represent major disturbance periods. Dark gray indicates severe aridity, light gray indicates moderate aridity and very light gray indicates wet periods. Study site locations are presented in Fig. 5.

flow of moist air from the Atlantic Ocean into Central Africa, thus provoking relative aridity on the continent. Examples are MIS3 and MIS4, the last glacial maximum (LGM or MIS2), the Younger Dryas and the 8.2 ka event (Maley, 1996; Maley and Brenac, 1998; Alley and Ágústsdóttir, 2005; Schefuß et al., 2005). The steep rise in ΔSST starting around 3000 cal yr BP, a trend that continues to the present (Schefuß et al., 2005), is consistent with the increased abundance of fire events recorded within the last 3000 years in the Ituri forest (Hart et al., 1996) and the Luki reserve (Table 1, Figs. 2, 3). Specifically, the paleofire dated to between 2300 and 1900 cal yr BP at UH48 is broadly coeval with a reconstructed peak in ΔSST around 2300 cal yr BP. Also, the fire events at CZ2 and CZ3 dated to 600–500 years ago broadly coincide with a period of increasing ΔSST (Schefuß et al., 2005). Lack of recorded paleofires that presumably must have occurred during other inferred arid episodes in the recent past, such as around 1200–1000 cal yr BP (Schefuß et al., 2005), may be explained by a temporary setback of woody vegetation interrupting soil accumulation, and thus an absence of traces archived in the pedoanthracological record. Lack of recorded fire events in Luki or Ituri dating from older periods of known climatic drought (e.g., the Younger Dryas) can be explained both by this process and by rapid burial and scattering of charcoal assemblages by bioturbation as outlined above.

Species composition of the charcoal assemblages

Charcoal type richness as a reflection of forest species richness

The minimum species richness of the charcoal assemblages recovered from the Luki reserve, expressed as the sum of the identified types and of the unidentified types originating from mature wood, is on average 13 species per 1.5 m^2 (12 in CZ2, 10 in CZ3, 15 in CZ1, 16 in UH48). This is more than 10% of the 81 to 127 tree species per ha reported to occur in Central African natural rainforest stands (van Gemerden et al., 2003; Worbes et al., 2003). This suggests that the charcoal assemblages originated from species-rich forest types, rather than from species-poor savanna types.

However, these forest inventories must be considered a minimum estimate of true woody plant diversity, since they are usually limited to trees with breast-height diameters exceeding 10 cm (Worbes et al., 2003). Tree species dispersing seeds via wind, water or animals can produce off-site progeny. Also, the local soil seed bank can produce seedlings and young trees of species that are temporarily lacking from the site (cf. Daïnou et al., 2011).

On the other hand, species richness recorded in pedoanthracological profiles may also underestimate true charcoal diversity because some charcoal types can escape burial due to post-depositional processes such as horizontal transport by wind or water or by physical weathering severely fragmenting the charcoal particles (e.g., Théry-Parisot et al., 2010). Also, trees are not always completely charcoalified and they do not always fall down after the fire (Scott, 2000). Finally, given the relatively small sample size, uncommon tree species with a small share in the basal area are probably underrepresented in charcoal assemblages compared to dominant species. For example, only two charcoal types were clearly derived from liana species (APO ANC PYR, LIN HUG PLA; see Fig. 2) although tropical forests typically have a great diversity of lianas (Schnitzer and Bongers, 2002).

Diversity of burned forest types

Nearly all charcoal fragments in the oldest charcoal assemblage (>43.5 cal ka BP; profile CZ3) were derived from only one species, and probably from the same individual (Fig. 3). *Guibourtia* species are large (>20 m) trees typical of old-growth evergreen and semi-deciduous primary rainforest (Burkill, 1985; Leal, 2004; African Plants Database, 2011).

The fire event dated to between 2308 and 1872 cal yr BP in the UH48 stand undoubtedly burned a patch of mature rainforest. Thirteen out of 15 identified charcoal types yielded prominent indicators of mature

rainforest among the highest ranked species (Fig. 3). Examples are *Gilbertiodendron* species (CAE GIL MAY), *Guarea* species (MEL GUA SPP) and *Tetraberlinia bifoliolata* (CAE TET BIF) (Lebrun and Gilbert, 1954; Leal, 2004) (Fig. 3, Table 2). *Coelocaryon* species (MYR COE SPP) are also important indicators of old primary rainforest in the Luki reserve (Donis, 1948). Endocarps of the pioneer palm *E. guineensis* found in the UH48 assemblage were probably introduced by humans, given the presence of pottery fragments (Fig. 3).

The charcoal assemblage dated to 1704–1544 cal yr BP in profile CZ1 is dominated by charcoal types yielding prominent pioneers such APO ALS SPP (cf. *Alstonia* spp.), MYR PYC ANG (cf. *P. angolensis*) and COM TER SUP (cf. *Terminalia superba*) (Fig. 2, Table 2). These often occupy small patches within the rainforest but they sometimes also occur in large, nearly monodominant stands within old evergreen rainforest, indicating former disturbance at the landscape scale (Donis, 1948; Lebrun and Gilbert, 1954; Protabase, 2012). They are widely distributed and sometimes very abundant. Also, *Heinsia crinita* (RUB HEI CRI), *Pterygota* species (STE PTE SPP), *Tetrorchidium didymostemon* (EUP TET DID) and *Albizia* species (MIM ALB SPP) are significant indicators for regenerating forest (Table 2).

The CZ2 assemblage (554–504 cal yr BP) clearly indicates an open vegetation type. *Bridelia ferruginea* (PHY BRI FER) is common in the grasslands neighboring the Luki reserve, although it also occurs near forest edges (Donis, 1948; Lebrun and Gilbert, 1954; Vincens et al., 1998; African Plants Database, 2011). Second, in contrast to all other charcoal assemblages it includes two liana taxa, APO ANC PYR (cf. *Ancylobotrys pyriformis*) and LIN HUG PLA (cf. *Hugonia platysepala*). Lianas are favored by disturbance and they are relatively more abundant in forest gaps than under closed canopy (e.g., Schnitzer and Bongers, 2002). Finally, some of the highest ranked species for charcoal types COM COM SPP and RUB NAU SPP occur in woodland savanna, whereas others occur in mature rainforest (Fig. 2, Table 2). Although identification results clearly indicate a more open vegetation type, the relatively high species richness of the CZ2 assemblage (12 species per 1.5 m^2) indicates that it was probably dry deciduous forest or dry woodland rather than a savanna.

The upper charcoal assemblage of profile CZ3, dated to 626–510 cal yr BP, is dominated by prominent pioneer and secondary forest taxa such as APO FUN AFR (cf. *Funtumia africana*), CAE ANT SPP (cf. *Anthonotha* spp.) and CAE AFZ SPP (cf. *Afzelia* spp.) (Fig. 3, Table 2). However, the assemblage also includes two types belonging to prominent mature rainforest taxa (CAE CYN SES and CAE APH SPP) (Lebrun and Gilbert, 1954; Leal, 2004; Protabase, 2012). Although fast-growing pioneer species recruit easily in forest gaps and are initially more abundant and more successful than more slowly regenerating mature forest species (Protabase, 2012), it is possible that the latter resprouted from a cut- or broken-off stub after natural or human-induced disturbance (Mwavu and Witkowski, 2008), or recruited occasionally from the seedling bank or from the local soil seed bank (Daïnou et al., 2011).

Consistency with regional paleoclimate history

Figure 5 shows the distribution of existing paleobotanical and paleoclimatological records, with which the results of this study can be compared. The main patterns of regional climate and vegetation dynamics spanning the last 4000 years are summarized in Figure 6, grouped by geographical area and arranged according to distance from the study area. The records closest to the Luki reserve are those of Lake Kitina in the southern Mayumbe forest (Elenga et al., 1996, 2004; Maley, 2002, 2004), Lake Sinnda in the grasslands of the Mayumbe rainshadow area (Vincens et al., 1998), and from a marine site near the mouth of the Congo River (Schefuß et al., 2005). However, most information is derived from sites within the Lower Guinea farther north (Fig. 5). We also considered high-resolution paleolimnological records from Eastern Africa that give a detailed view of late Holocene climate variability.

i. Third millennium BP rainforest crisis

Two successive phases of late Holocene rainforest breakdown are documented extensively in the literature, as outlined in Figure 6. Since the Luki reserve is located on the southernmost edge of the Central African rainforest (Figs. 1, 5), one might expect that these events had impacted its forest considerably. The first phase occurred between 4000 and 2500 cal yr BP, when lowering SST in the Gulf of Guinea (Weldeab et al., 2007) is associated with a more arid climate in the Lower Guinea forest region. Although nearly all selected sites in Central and East Africa record increasing drought during this period, it impacted only on the boundaries of the Central African rainforest complex (Fig. 6; Vincens et al., 1998; Elenga et al., 2004; Salzmann and Hoelzmann, 2005; Ngomanda et al., 2009a,b; Maley et al., 2012). However, a complete absence of charcoal from between 4000 and 2500 cal yr BP in the Luki assemblages suggests that increasing aridity did not cause severe rainforest breakdown through fire at the study site (Figs. 2, 3). Indeed, the closed-canopy rainforest is remarkably resistant to drought because the canopy is able to trap transpired moisture, thus maintaining humidity levels and hampering combustion (Cochrane, 2003). Also, in the Ituri forest of eastern Congo (Fig. 5), only two of 28 paleofires date from this period (Hart et al., 1996).

The second phase of forest breakdown occurred between 2500 and 2000 cal yr BP, when rising sea-surface temperatures (Weldeab et al., 2007) resulted in a generally warmer and wetter climate, with pronounced seasonality. The wet season was characterized by the formation of large cumuliform clouds and the occurrence of torrential rains (Maley, 2002, 2004). Increasing ΔSST between the tropical and subtropical ocean (Schefuß et al., 2005) resulted in a strengthening of the trade winds, causing a long and pronounced dry season (Maley and Brenac, 1998; Elenga et al., 2004; Maley, 2004; Ngomanda et al., 2009a,b; Neumann et al., 2012a,b). Palynological studies show that this severe climate shift almost completely eradicated mature rainforest in certain regions of the Lower Guinea (Maley, 2002). Yet, the UH48 charcoal assemblage (Fig. 2) clearly indicates that despite the occurrence of fire, mature semi-deciduous rainforest persisted until the end of this severe breakdown phase, even at the forest boundary (Figs. 1, 5).

Given strong climate seasonality, windfalls during storms may have contributed to open up the rainforest canopy, creating additional gaps vulnerable to drought and fire (e.g., Maley, 2002; Ngomanda et al., 2009b). True rainforest trees generally have thinner protective bark layers and are thus easily destroyed by fires occurring in nearby forest gaps (Cochrane et al., 1999; Cochrane, 2003; Broadbent et al., 2008). As such, the combined effect of gap formation during wet seasons and severe drought with recurring fire during dry seasons may eventually have destroyed large blocks of contiguous forest. The occurrence of a paleofire within a mature rainforest stand at the UH 48 site indicates that forest destruction was still ongoing by the end of the third millennium BP. At that time the site was probably located at a forest edge or in a small mature rainforest patch within a matrix of fire-prone open vegetation. Increasing paleofire occurrence from 2200 cal yr BP onwards has also been reported for the Ituri forest (Fig. 6; Hart et al., 1996).

ii. Forest recovery after the third millennium BP rainforest crisis

After 2000 cal yr BP, the Lower Guinean climate returned to wet and relatively stable conditions (e.g., Maley, 2002, 2004; Ngomanda et al., 2007, 2009a,b). Decreasing Gramineae and increasing abundance of pioneer trees in pollen records indicate successful forest regeneration (Elenga et al., 1996; Maley, 1996, 2002, 2004; Reynaud-Farrera et al., 1996; Maley and Brenac, 1998; Elenga et al., 2004; Ngomanda et al., 2009a; Neumann et al., 2012b; see also Fig. 6). Likewise, the CZ1 charcoal assemblage dated to this period is dominated by pioneer species (Fig. 2, Table 2). This fire event occurred at least three centuries after the rainforest crisis, indicating that forest recovery was most likely a slow process. Recurring fire in scattered patches of savanna still affected regenerating forest patches, killing the most vulnerable tree species

(e.g., Broadbent et al., 2008). In the southern portion of the Lower Guinea, the combustibility of open vegetation probably remained high due to continuing drought until at least 1300 cal yr BP, as reported for the surroundings of Lake Sinnda (Fig. 6; Vincens et al., 1998). Indeed, steep ΔSST rises alternating with only weak ΔSST drops during the last 3000 years suggest that aridification continued (Schefuß et al., 2005). Yet, the increasing abundance of pollen from pioneer species on several sites indicate that forest re-establishment was eventually successful (e.g., Fig. 2; Maley, 2002).

iii. Medieval climate anomaly and Little Ice Age

Although manifestation of the Northern Hemisphere 'Medieval Climate Anomaly' (MCA, 1100–700 cal yr BP) and 'Little Ice Age' (LIA, 650–100 cal yr BP) in various tropical regions is under debate, many authors use this terminology as reference chronozones for tropical climate anomalies during these broad time periods (e.g., Vincens et al., 1998; Verschuren et al., 2000; Ngomanda et al., 2007; Russell and Johnson, 2007; Verschuren and Charman, 2008; Stager et al., 2009). One pattern that appears to be widespread across intertropical Africa is a switch towards wetter climatic conditions coincident with the MCA–LIA transition 700–650 cal yr BP (Verschuren and Charman, 2008). In eastern equatorial Africa the MCA-equivalent period was mostly dry (Verschuren et al., 2000; Russell et al., 2003; Stager et al., 2009), whereas close to the Atlantic coast in the Lower Guinea, the MCA appears to be characterized by fluctuating wet–dry conditions (Vincens et al., 1998; Schefuß et al., 2005; Ngomanda et al., 2007). Allowing for some dating mismatch between the available records, the start of the LIA-equivalent period is most often marked by the return of a more consistently wet climate in tropical Africa. However, after ca. 500–450 cal yr BP these wet conditions reversed to more or less pronounced aridity throughout western and central equatorial Africa, from near the Atlantic coast (Ngomanda et al., 2007) to the western shoulder of the East African plateau (Russell and Johnson, 2007). Persisting until ca. 200–150 cal yr BP, this prolonged drought coincides with coldest LIA temperatures in Western Europe (Verschuren and Charman, 2008). Only easternmost equatorial Africa, i.e., the portion of the continent situated beyond Atlantic Ocean influence, enjoyed relatively wet conditions throughout the LIA-equivalent period, and even there they were occasionally interrupted by decade-long dry spells (Verschuren et al., 2000, 2009; Tierney et al., 2013).

Earlier studies detailing vegetation dynamics during the broad MCA–LIA time interval in the Lower Guinea documented an increase in shade-intolerant trees under fluctuating wet–dry conditions during the MCA (Ngomanda et al., 2007), and forest disturbance with increasing oil palm abundance between 1400 and 800 cal yr BP (Reynaud-Farrera et al., 1996; Maley, 2002). In the Dahomey Gap, dry conditions and forest retreat started from 1100 cal yr BP and continued until the present (Salzmann and Hoelzmann, 2005). In the Ituri forest of eastern Congo, the entire period from 1300 to 800 cal yr BP is marked by an unusually high number of fire events (Hart et al., 1996). Likewise, the replacement of mature rainforest by woodland savanna at the CZ2 site (Fig. 2) shows that the MCA was undoubtedly a period of significant forest fragmentation in the Luki reserve. Due to recurrent fire, this open vegetation persisted into the early LIA-equivalent period. This diverse evidence for MCA drought on the continent is associated with a pronounced rise in tropical Atlantic ΔSST between 1200 and 1000 cal yr BP (Fig. 6; Schefuß et al., 2005).

Wetter conditions on land starting at the MCA–LIA transition promoted forest regeneration, as illustrated by the occurrence of pioneer trees around 600 cal yr BP in the Luki reserve (CZ3, Fig. 3) and in the pollen record of Lake Sinnda (Figs. 5, 6, Vincens et al., 1998). However, the fragmented Ituri forest structure remained vulnerable to fire, as evidenced by two fire events during this period (Hart et al., 1996). The CZ2 and CZ3 fire events both occurred between 630 and 500 cal yr BP, likewise during the wet early phase of the LIA (Fig. 6).

Wildfires or shifting cultivation?

Charcoal fragments found in soils of natural environments are sometimes a priori interpreted as witnesses of past slash-and-burn activity (van Gemerden et al., 2003). However, fire is also the major cause of natural vegetation disturbance, even in moist rainforests. Lightning is the most important initiator of wildfires and more successfully so in canopy gaps during episodes of climatic drought (Hart et al., 1996; Cochrane et al., 1999; Scott, 2000; Cochrane, 2003). The ancient charcoal in the deepest layer of profile CZ3 most likely formed during such a natural forest wildfire. While there are indications for the presence of Stone-Age human communities in the Lower Guinea before 43.5 cal ka BP (Oslisly, 2001), there is no evidence for wildfires having been ignited by humans in the Lower Guinea before the introduction of agriculture with the arrival of Bantu-speaking people around 2500 cal yr BP. Even then, evidence for actual farming activities remains scarce until about 1000 cal yr BP (Fig. 6; Neumann et al., 2012b). The early migrants were probably hunter-gatherers in the first place, and the crops they introduced from the subtropics (e.g., *Pennisetum glaucum*) needed a distinct dry season, which became more problematic after the third millennium BP rainforest crisis as climate returned to less seasonal conditions (Fig. 6; Neumann et al., 2012a,b). Moreover, humans confined their activities to natural forest gaps and preferred cutting softer pioneer trees rather than harder trees in the mature rainforest (Ngomanda et al., 2009b; Neumann et al., 2012a).

The charcoal assemblage of the UH48 profile dated to between 2300 and 1900 cal yr BP may represent a human-set fire in the context of shifting cultivation within or at the edge of a mature rainforest patch. Evidence in this direction includes the few small pottery shards recovered from the 20–40 cm interval of the profile, and charred endocarps of *E. guineensis* mixed with the charcoal of other taxa throughout the profile (Fig. 3). The traditional human consumption of *E. guineensis* is well-documented (Maley and Chepstow-Lusty, 2001; Neumann et al., 2012a). Furthermore, one charcoal type in the UH48 assemblage is identified as *Tabernanthe iboga* (APO TAB IBO), a well-known medico-magic plant commonly used during initiation ceremonies in the Lower Guinea (e.g., Akendengue et al., 2005; Banzouzi et al., 2008; Protabase, 2012). The presence of both pottery shards and oil palm endocarp fragments in the 0–20 cm interval of profile CZ3 (Fig. 3, 626–510 cal yr BP), suggests that this may have been a shifting cultivation site as well, although at both sites these few pottery shards may well be of younger origin than the charcoal fragments, since the distribution of charcoal and artifacts in soil is not always equally affected by post-depositional processes (Cahen and Moeyersons, 1977). The paleofire events recorded at CZ1 and CZ2 are almost certainly real wildfires. No artifacts were found in either profiles and the presence of a few charred oil palm endocarps can be explained by the fact that both paleofires burned patches of regenerating forest, the natural habitat of *E. guineensis*.

Conclusion

Four soil profiles from the Luki reserve in the southern Mayumbe forest of DRC yielded five distinct charcoal assemblages. One of the four profiles yielded charcoal from around 530 cal yr BP and a deeper charcoal layer of >43.5 cal ka BP, i.e., well beyond the period of recorded anthropogenic burning in this region. This result indicates that both natural wildfire occurrence and long-term absence of fire are possible in tropical rainforest. The increasing SST gradient between tropics and subtropics during the late Holocene caused increasing aridity in the southern Mayumbe since at least 4000 cal yr BP. However it appears to have promoted paleofire occurrence only from the end of the third millennium BP when temporarily enhanced seasonality caused severe forest fragmentation.

Persistence of mature rainforest (e.g., *Gilbertiodendron* species, *T. bifoliolata*) until the end of the third millennium BP rainforest crisis (2308–1872 cal yr BP), may illustrate the resilience of Central African rainforest against drought, even at the forest edge. Forest regeneration following this rainforest crisis was a slow process, as illustrated by our documentation of a paleofire dated to 1704–1544 cal yr BP, burning a pioneer forest stand (e.g., *P. angolensis*, *Alstonia* species). A more recent paleofire (626–510 cal yr BP) burned an open woodland savanna patch (e.g., *B. ferruginea*) and a stand of pioneer forest (e.g., *F. africana*, *Afzelia*) during the relatively wet period immediately following the MCA (1100–700 cal yr BP), indicating that the local MCA-equivalent period was probably a significant drought event in Central Africa and that forest regeneration was ongoing around 600 cal yr BP.

The documented Luki reserve fire event dated to before 43.5 cal ka BP was almost certainly a natural wildfire ignited by lightning. In contrast, pottery shards and oil palm endocarps associated with the paleofire dated to 2308–1872 cal yr BP and one of the two post-MCA paleofires suggests that these may have been set by humans practicing shifting cultivation. As shifting cultivation by Bantu migrants was initially only a marginal activity practised preferably in regenerating forest, the anthropogenic nature of most fires from that time is far from certain. Temporary natural climatic drought was probably the main driving force for paleofire occurrence, vegetation change and human migrations in the Central African forest. During the last millennium, shifting cultivation by a growing human population increasingly amplified the destructive effects of natural climate anomalies by slowing down forest regeneration in fire-prone areas.

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References

African Plants Database, 2011. African Plants Database Version 3.3.3, Conservatoire et Jardin botaniques de la Ville de Genève and South African National Biodiversity Institute, Pretoria. Published on the internet [accessed 10th January 2011–26th July 2011], from http://www.ville-ge.ch/musinfo/bd/cjb/africa/.

Akendengue, B., Lemamy, G.J., Bourobou Bourobou, H., Laurens, A., 2005. Bioactive natural compounds from medico-magic plants of bantu area. Studies in Natural Products Chemistry 32, 803–820.

Alley, R.B., Ágústsdóttir, A.M., 2005. The 8k event: cause and consequences of a major Holocene abrupt climate change. Quaternary Science Reviews 24, 1123–1149.

Baert, G., 1995. Properties and Chemical Management Aspects of Soils on Different Parent Rocks in the Lower Zaire. PhD Dissertation Ghent University (318 pp.).

Banzouzi, J.T., Makambila Koubemba, M.C., Prost, A., Mbatchi, B., Abena, A.A., 2008. Survey of analgesic plants used by tradipractitioners in Congo Brazzaville. International Journal of Botany 4, 176–185.

Bird, M.I., Cali, J.A., 1998. A million-year record of fire in sub-Saharan Africa. Nature 394, 767–769.

Brncic, T.M., Willis, K.J., Harris, D.J., Washington, R., 2007. Culture or climate? The relative influences of past processes on the composition of the lowland Congo rainforest. Philosophical Transactions of the Royal Society 362, 229–242.

Broadbent, E.N., Asner, G.P., Keller, M., Knapp, D.E., Oliveira, P.J.C., Silva, J.N., 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. Biological Conservation 141, 1745–1757.

Bronk Ramsey, C., 2009. Bayesian analysis of radiocarbon dates. Radiocarbon 51, 337–360.

Burkill, H.M., 1985. 1st edition. The Useful Plants of West Tropical Africa, 6. Royal Botanic Gardens, Kew.

Cahen, D., Moeyersons, J., 1977. Subsurface movements of stone artefacts and their implications for the prehistory of Central Africa. Nature 266, 812–815.

Carcaillet, C., Thinon, M., 1996. Pedoanthracological contribution to the study of the evolution of the upper treeline in the Maurienne Valley (North French Alps): methodology and preliminary data. Review of Palaeobotany and Palynology 91, 399–416.

Carcaillet, C., Barakat, H.N., Panaïotis, C., Loisel, R., 1997. Fire and late-Holocene expansion of *Quercus ilex* and *Pinus pinaster* on Corsica. Journal of Vegetation Science 8, 85–94.

Cochrane, M.A., 2003. Fire science for rainforests. Nature 421, 913–919.

Cochrane, M.A., Alencar, A., Schulze, M.D., Souza Jr., C.M., Nepstad, D.C., Lefebvre, P., Davidson, E.A., 1999. Positive feedbacks in the fire dynamic of closed canopy tropical forests. Science 284, 1832–1834.

Couralet, C., 2010. Community dynamics, phenology and growth of tropical trees in the rain forest reserve of Luki, Democratic Republic of Congo. PhD Thesis Faculty of Bioscience Engineering.Ghent University (173 pp.).

Daïnou, K., Bauduin, A., Bourland, N., Gillet, J.-F., Fétéké, F., Doucet, J.-L., 2011. Soil seed bank characteristics in Cameroonian rainforests and implications for post-logging forest recovery. Ecological Engineering 37, 1499–1506.

Daniau, A.-L., Harrison, S.P., Bartlein, P.J., 2010. Fire regimes during the Last Glacial. Quaternary Science Reviews 29, 2918–2930.

Dechamps, R., Lanfranchi, R., Le Cocq, A., Schwartz, D., 1988. Reconstruction d'environnements quaternaires par l'étude de macrorestes vegetaux (Pays Bateke, R.P. du Congo). Palaeogeography, Palaeoclimatology, Palaeoecology 66, 33–44.

Di Pasquale, G., Marziano, M., Impagliazzo, S., Lubritto, C., De Natale, A., Bader, M.Y., 2008. The Holocene tree line in the northern Andes (Ecuador): first evidence from soil charcoal. Palaeogeography, Palaeoclimatology, Palaeoecology 259, 17–34.

Donis, C., 1948. Essai d'économie forestière au Mayumbe. Publications de l'Institut National pour l'Etude Agronomique du Congo Belge (INEAC), Bruxelles, Belgique. Série scientifique 37 (92 pp.).

Dupont, L.M., Jahns, S., Marret, F., Ning, S., 2000. Vegetation change in equatorial West Africa: time-slices for the last 150 ka. Palaeogeography, Palaeoclimatology, Palaeoecology 155, 95–122.

Elenga, H., Schwartz, D., Vincens, A., Bertaux, J., de Namur, C., Martin, L., Wirrmann, D., Servant, M., 1996. Diagramme pollinique holocène du lac Kitina (Congo): mise en évidence de changements paléobotaniques et paléoclimatiques dans le massif forestier du Mayombe. Rendered Accounts of the Academy of Sciences, Paris, Series II 322, 749–755.

Elenga, H., de Namur, C., Vincens, A., Roux, M., Schwartz, D., 2000. Use of plots to define pollen-vegetation relationships in densely forested ecosystems of tropical Africa. Review of Palaeobotany and Palynology 112, 79–96.

Elenga, H., Maley, J., Vincens, A., Farrera, I., 2004. Palaeoenvironments, palaeoclimates and landscape development in Atlantic Equatorial Africa: a review of key sites covering the last 25 kyrs. In: Battarbee, R.W., Gasse, F., Stickley, C.E. (Eds.), Past Climate Variability through Europe and Africa. Kluwer Academic Publishers, The Netherlands, pp. 181–198.

Emery-Barbier, A., Thiébault, S., 2005. Preliminary conclusions on the Late Glacial vegetation in south-west Anatolia (Turkey): the complementary nature of palynological and anthracological approaches. Journal of Archaeological Science 32, 1232–1251.

Hart, T.B., Hart, J.A., Dechamps, R., Fournier, M., Ataholo, M., 1996. Changes in forest composition over the last 4000 years in the Ituri basin, Zaire. In: van der Maesen, L.J.G., van der Burgt, X.M., van Medenbach de Rooy, J.M. (Eds.), The Biodiversity of African Plants. Kluwer Academic Publishers, The Netherlands, pp. 545–563.

Hessler, I., Dupont, L., Bonnefille, R., Behling, H., González, C., Helmens, K.F., Hooghiemstra, H., Lebamba, J., Ledru, M.-P., Lézine, A.-M., Maley, J., Marret, F., Vincens, A., 2010. Millennial-scale changes in vegetation records from tropical Africa and South America during the Last Glacial. Quaternary Science Reviews 29, 2882–2899.

Hubau, W., Van den Bulcke, J., Mees, F., Van Acker, J., Beeckman, H., 2012. Charcoal identification in species-rich biomes: a protocol for Central Africa optimised for the Mayumbe forest. Review of Palaeobotany and Palynology 171, 164–178.

IAWA Committee, 1989. IAWA list of microscopic features for hardwood identification. IAWA Bulletin 10, 219–332.

InsideWood, 2011. The InsideWood Working Group (IWG), 2004–onwards. Published on the Internet [accessed 11th July 2011, 14:30 GMT], from http://insidewood.lib.ncsu.edu/search.

Leal, M.E., 2001. Microrefugia, small scale ice age forest remnants. Systematics and Geography of Plants 71, 1073–1077.

Leal, M.E., 2004. The African Rain Forest During the Last Glacial Maximum, An Archipelago of Forests in a Sea of Grass. PhD Thesis Wageningen University, Wageningen (96 pp.).

Lebamba, J., Ngomanda, A., Vincens, A., Jolly, D., Favier, C., Elenga, H., Bentaleb, I., 2009. Central African biomes and forest succession stages derived from modern pollen data and functional plant types. Climate of the Past 5, 403–429.

Lebrun, J., Gilbert, G., 1954. Une classification écologique des forêts du Congo. Publications de l'Institut National pour l'Etude Agronomique du Congo Belge (INEAC), Bruxelles, Belgique. Série scientifique 63 (89 pp.).

Maley, J., 1996. Le cadre paléoenvironnemental des refuges forestiers africains: quelques données et hypothèses. In: van der Maesen, L.J.G., van der Burgt, X.M., van Medenbach de Rooy, J.M. (Eds.), The Biodiversity of African plants. Kluwer Academic Publishers, The Netherlands, pp. 519–535.

Maley, J., 2001. The impact of arid phases on the African rain forest through geological history. In: Weber, W., White, L.J.T., Vedder, A., Naughton-Treves, L. (Eds.), African Rain Forest Ecology and Conservation, An Interdisciplinary Perspective. Yale University Press, New Haven, pp. 68–87.

Maley, J., 2002. A catastrophic destruction of african forests about 2500 years ago still exerts a major influence on present vegetation formations. IDS Bulletin 33, 13–30.

Maley, J., 2004. Les variations de la végétation et des paléoenvironnements du domaine forestier africain au cours du Quaternaire récent. In: Renault-Miskovsky, J., Semah, A.M. (Eds.), Guide de la préhistoire mondiale. Artcom'/Errance, Paris, pp. 143–178.

Maley, J., Brenac, P., 1998. Vegetation dynamics, palaeoenvironments and climatic changes in the forests of western Cameroon during the last 28,000 years B.P. Review of Palaeobotany and Palynology 99, 157–187.

Maley, J., Chepstow-Lusty, A., 2001. *Elaeis guineensis* Jacq. (oil palm) fluctuations in central Africa during the late Holocene: climate or human driving forces for this pioneering species? Vegetation History and Archaeobotany 10, 117–120.

Maley, J., Giresse, P., Doumenge, C., Favier, C., 2012. Comment on "Intensifying weathering and land use in Iron Age Central Africa". Science 337, 1040-d.

Mayaux, P., Janodet, E., Blair-Myers, C., Legeay-Janvier, P., 1997. Vegetation map of central Africa at 1:5 000 000. Trees series D: Thematic outputs, 1 (8 pp.).

McBrearty, S., 1990. Consider the humble termite: termites as agents of post-depositional disturbance at African archaeological sites. Journal of Archaeological Science 17, 111–143.

McCormac, F.G., Hogg, A.G., Blackwell, P.G., Buck, C.E., Higham, T.F.G., Reimer, P.J., 2004. SHCal04 Southern Hemisphere calibration, 0–11.0 cal kyr BP. Radiocarbon 46, 1087–1092.

Murphy, C.P., 1986. Thin Section Preparation of Soils and Sediments. AB Academic Publishers, Berkhamsted, U.K.(149 pp.).

Mwavu, E.N., Witkowski, E.T.F., 2008. Sprouting of woody species following cutting and tree-fall in a lowland semi-deciduous tropical rainforest, North-Western Uganda. Forest Ecology and Management 255, 982–992.

Neumann, K., Bostoen, K., Höhn, A., Kahlheber, S., Ngomanda, A., Tchiengué, B., 2012a. First farmers in the Central African rainforest: a view from southern Cameroon. Quaternary International 249, 53–62.

Neumann, K., Eggert, M.K.H., Oslisly, R., Clist, B., Denham, T., de Maret, P., Ozainne, S., Hildebrand, E., Bostoen, K., Salzmann, U., Scwartz, D., Eichhorn, B., Tchiengué, B., Höhn, A., 2012b. Comment on "Intensifying weathering and land use in Iron Age Central Africa". Science 337, 1040-c.

Ngomanda, A., Jolly, D., Bentaleb, I., Chepstow-Lusty, A., Makaya, M., Maley, J., Fontugne, M., Oslisly, R., Rabenkogo, N., 2007. Lowland rainforest response to hydrological changes during the last 1500 years in Gabon, Western Equatorial Africa. Quaternary Research 67, 411–425.

Ngomanda, A., Chepstow-Lusty, A., Makaya, M., Favier, C., Schevin, P., Maley, J., Fontugne, M., Oslisly, R., Jolly, D., 2009a. Western equatorial African forest-savanna mosaics: a legacy of late Holocene climatic change? Climate of the Past 5, 647–659.

Ngomanda, A., Neumann, K., Schweizer, A., Maley, J., 2009b. Seasonality change and the third millennium BP rainforest crisis in southern Cameroon (Central Africa). Quaternary Research 71, 307–318.

Oslisly, R., 2001. The history of human settlement in the Middle Ogooué Valley (Gabon): implications for the environment. In: Weber, W., White, L.J.T., Vedder, A., Naughton-Treves, L. (Eds.), African Rain Forest Ecology and Conservation, An Interdisciplinary Perspective. Yale University Press, New Haven, pp. 101–118.

Protabase, 2012. Plant Resources of Tropical Africa. Published on the Internet [accessed February–March 2012], from http://database.prota.org/search.htm.

Reynaud-Farrera, I., Maley, J., Wirrmann, D., 1996. Végétation et climat dans les forêts du sud-ouest Cameroun depuis 4770 ans BP. Analyse pollinique des sédiments du lac Ossa. Rendered Accounts of the Academy of Sciences, Series II 232, 403–410.

Russell, J.M., Johnson, T.C., 2005. A high-resolution geochemical record from Lake Edward, Uganda Congo and the timing and causes of tropical African drought during the late Holocene. Quaternary Science Reviews 24, 1375–1389.

Russell, J.M., Johnson, T.C., 2007. Little Ice Age drought in equatorial Africa: intertropical convergence zone migrations and El Niño–Southern Oscillation variability. Geology 35, 21–24.

Russell, J.M., Johnson, T.C., Kelts, K.R., Laerdal, T., Talbot, M.R., 2003. An 11 000-year lithostratigraphic and paleohydrologic record from Equatorial Africa: Lake Edward, Uganda–Congo. Palaeogeography, Palaeoclimatology, Palaeoecology 193, 25–49.

Salzmann, U., Hoelzmann, P., 2005. The Holocene history of the Dahomey Gap: a climatic induced fragmentation of the West African Rainforest. The Holocene 15, 190–199.

Schefuß, E., Schouten, S., Schneider, R.R., 2005. Climatic controls on central African hydrology during the past 20,000 years. Nature 437, 1003–1006.

Schnitzer, F.A., Bongers, F., 2002. The ecology of lianas and their role in forests. Trends in Ecology & Evolution 17, 223–230.

Schwartz, D., de Foresta, H., Dechamps, R., Lanfranchi, R., 1990. Découverte d'un premier site de l'âge du fer ancien (2110 B.P.) dans le Mayombe congolais. Implications paléobotaniques et pédologiques. Rendered Accounts of the Academy of Sciences, Paris, Series II 310, 1293–1298.

Scott, A.C., 2000. The Pre-Quaternary history of fire. Palaeogeography, Palaeoclimatology, Palaeoecology 164, 281–329.

Sosef, M.S.M., 1996. Begonias and African rain forest refuges: general aspects and recent progress. In: van der Maesen, L.J.G., van der Burgt, X.M., van Medenbach de Rooy, J.M. (Eds.), The Biodiversity of African plants. Kluwer Academic Publishers, The Netherlands, pp. 602–611.

Stager, C., Cocquyt, J.C., Bonnefille, R., Weyhenmeyer, C., Bowerman, N., 2009. A late Holocene palaeoclimatic history of Lake Tanganyika, East Africa. Quaternary Research 72, 47–56.

Stoops, G., 2003. Guidelines for Analysis and Description of Soil and Regolith Thin Sections. Soil Science Society of America, Madison, WI (184 pp.).

Stoops, G., Marcelino, V., Mees, F., 2010. Interpretation of Micromorphological Features of Soils and Regoliths. Elsevier (752 pp.).

Tchouto, M.G.P., de Wilde, J.J.F.E., de Boer, W.F., van der Maesen, L.J.G., Cleef, A.M., 2009. Bio-indicator species and Central African rain forest refuges in the Campo-Ma'an area, Cameroon. Systematics and Biodiversity 7, 21–31.

Théry-Parisot, I., Chabal, L., Chrzavzez, J., 2010. Anthracology and taphonomy, from wood gathering to charcoal analysis. A review of the taphonomic processes modifying charcoal assemblages, in archaeological contexts. Palaeogeography, Palaeoclimatology, Palaeoecology 291, 142–153.

Tierney, J.E., Smerdon, J.E., Anchukaitis, K.J., Seager, D., 2013. Multidecadal variability in East African hydroclimate controlled by the Indian Ocean. Nature 493, 389–392.

van Gemerden, B.S., Olff, H., Parren, M.P.E., Bongers, F., 2003. The pristine rain forest? Remnants of historical human impacts on current tree species composition and diversity. Journal of Biogeography 30, 1381–1390.

Van Ranst, E., Baert, G., Ngongo, M., Mafuka, P., 2010. Carte pédologique de la province du Bas-Congo et ville de Kinshasa, échelle 1:500.000. UGent, Hogent, UNILU, UNIKIN. 9789491114625.

Verschuren, D., Charman, D.J., 2008. Latitudinal linkages in late Holocene moisture-balance variation. In: Battarbee, R.W., Binney, H.A. (Eds.), Natural Climate Variability and Global Warming: A Holocene Perspective. Wiley-Blackwell, United Kingdom, pp. 189–231.

Verschuren, D., Laird, K.R., Cumming, B.F., 2000. Rainfall and drought in equatorial east Africa during the past 1100 years. Nature 403, 410–414.

Verschuren, D., Sinninghe Damsté, J.S., Moernaut, J., Kristen, I., Blaauw, M., Fagot, M., Haug, G.H., 2009. CHALLACEA project members, 2009. Half-precessional dynamics of monsoon rainfall near the East African Equator. Nature 462, 637–641.

Vincens, A., Schwartz, D., Bertaux, J., Elenga, H., de Namur, C., 1998. Late Holocene climatic changes in Western Equatorial Africa inferred from pollen from Lake Sinnda, Southern Congo. Quaternary Research 50, 34–45.

Weldeab, S., Lea, D.W., Schneider, R.R., Andersen, N., 2007. 155,000 years of West African monsoon and ocean thermal evolution. Science 316, 1303–1307.

Wheeler, E.A., 2011. InsideWood — a web resource for hardwood anatomy. IAWA Bulletin 32, 199–211.

Willis, K.J., Birks, H.J.B., 2006. What is natural? The need for a long-term perspective in biodiversity conservation. Science 314, 1261–1265.

Worbes, M., Staschel, R., Roloff, A., Junk, W.J., 2003. Tree ring analysis reveals age structure, dynamics and wood production of a natural forest stand in Cameroon. Forest Ecology and Management 173, 105–123.

WRB, 2006. World reference base for soil resources 2006. IUSS Working Group. World Soil Resources Reports, 103. FAO, Rome.