

Culture or climate? The relative influences of past processes on the composition of the lowland Congo rainforest

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This paper presents the results from a palaeoecological study to establish the impact of prehistoric human activity and climate change on the vegetation and soils of the Goualougo area of the Nouabalé-Ndoki National Park, in the Republic of Congo (Congo–Brazzaville). This is a region that is known from previous work (through evidence of pottery, furnaces and charcoal layers beneath the present day rainforest vegetation) to have had prehistoric settlement dating back to at least 2000 calibrated years before present. In addition, there is climatic evidence to suggest that significant variations in precipitation have occurred in central Africa over the last few millennia. Presently, the region is covered in uninhabited moist semi-evergreen rainforest. Key research questions addressed in this paper include the extent to which the present-day composition of rainforest in this region is as a result of processes of the past (climate change and/or human activity), and the resilience of the rainforest to these perturbations.

Statistical analyses of pollen, microscopic charcoal and geochemical data are used to determine the relationship over time between vegetation dynamics and climate change, anthropogenic burning and metal smelting. Significant changes in forest composition are linked to burning and climate change but not metallurgy. The strongest influence on the present day composition appears to be related to the increased anthropogenic burning that started approximately 1000 years ago. Results from this study are discussed in terms of their implications for the present and future management of this globally important forested region.

Keywords: Central Equatorial Africa; prehistoric human impact; palaeoecology; metallurgy; burning; climate change

1. INTRODUCTION

The Central Equatorial African lowland rainforests are under increasing threat from direct and indirect human impacts, including commercial logging, mining and conversion to farmland. It is estimated that up to 41% of this globally important forest block may be lost or severely fragmented in the next 50 years (Justice & Zhang 2001). In addition to direct forest loss, changing global climate also poses a risk for future forest structure through drought induced tree mortality and increased susceptibility to fire (Condit *et al.* 1996; Nepstad *et al.* 1999, 2004; Williamson *et al.* 2000).

Previous palaeoecological work in Atlantic Equatorial Africa and southern Congo–Brazzaville has concentrated on forest responses to climatic trends (Elenga *et al.* 2005). These studies broadly indicate that the forests have experienced dramatic changes over the last four millennia, sometimes with permanent forest loss. These changes are thought to be related to variations in rainfall patterns, perhaps driven by changes in sea

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surface temperature (SST) (Maley 1989). However, the impacts of such climate anomalies on the vegetation history of the central Congo forest block, as opposed to the current forest margins, have thus far not been subjected to scrutiny. Furthermore, the potential impact of prehistoric humans is often overlooked in interpretations of central African palaeoecological data (Willis *et al.* 2004).

Archaeological studies have indicated that prehistoric humans using pottery, iron, agriculture and animal husbandry have occupied wide areas of central Africa during the last 2000–4000 years (for a review see Oslisly 2001, White 2001). Multiple sites of pottery and iron artefacts have been discovered along the Congo river and its tributaries dating from 2300 years before present (BP) (Eggert 1993). The extensive lowland forests in northern Congo–Brazzaville therefore provide the ideal location to determine the past impacts of people and climate on rainforests.

Key questions for the present and future management of these forests therefore include: How resilient are forests in the central Congo basin to climatic fluctuations and human impact? What were the relative influences of culture and climate on past composition of the lowland

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Congo rainforest? Under future climate scenarios and increasing human impact, will species composition and diversity be affected? How much of what we see presently is a result of processes of the past (e.g. burning and climate change)? In order to address these questions, it is crucial that a longer term perspective on forest dynamics is obtained. One such record can be acquired through palaeoecological research, using fossil pollen to reconstruct past vegetation dynamics.

This paper presents the results of a palaeoecological study that examines the vegetation history of currently undisturbed lowland tropical forest in the Ndoki river area of the Congo basin. The overall aim of the study was to determine the relative influence of culture and climate on past and present forest composition.

In reconstructing both climate and anthropogenic drivers of vegetation change in palaeo-records, it is important to utilize lines of evidence for these that are independent from the pollen data itself. It is only by having such evidence that circularity (e.g. in using pollen to reconstruct climate and then using this inferred climate as a predictor of vegetation change) can be avoided in the line of argument. In this study, we therefore attempted to find independent lines of evidence for climate change and human activity against which to compare vegetation history.

This paper is therefore structured as follows. First it reviews the potential influences on current and past forest composition in the Congo basin, that is, variations in climate and previous human activities. Secondly, it presents and discusses the independent proxies developed in this study to reconstruct past climate and assess prehistoric human impact for the Goualougo study area. Thirdly, fossil pollen records obtained from the study area are compared with these independent proxies in order to determine the response of rainforest taxa to climate and prehistoric human impact and to understand their relative importance in shaping present day rainforest.

2. FACTORS INFLUENCING THE CENTRAL EQUATORIAL AFRICAN FORESTS (a) *Climate*

Climatically, Central Equatorial Africa is the third most extensive region of deep convection after the West Pacific warm pool region and Amazonia (Todd & Washington 2004). The primary driver of the general circulation in this region is tropospheric heating, which is achieved mainly through condensation of water vapour in deep convective clouds. In contrast, temperature has a very weak latitudinal gradient in the tropics, especially at the surface, and it is precipitation that shows the greatest variability.

Remarkably, few studies have attempted to characterize either the processes that determine rainfall over Central Equatorial Africa (e.g. Laing & Fritsch 1993), or the nature of variability at longer time-scales. Several studies have noted a positive association between rainfall over Central Equatorial African and tropical southern Atlantic SSTs (Hirst & Hastenrath 1983; Nicholson & Entekhabi 1987; Camberlin *et al.* 2001). Idealized climate model experiments forced with equatorial Atlantic SSTs show significant positive anomalies over the Central Equatorial African region of up to 40 mm month⁻¹ in response to the modest adjustments in SST (Todd & Washington 2004). Recent work has also documented a strong teleconnection between Central Equatorial African rainfall (and Congo River discharge) and the large-scale circulation over the North Atlantic (Todd & Washington 2004). In particular, these indicate a strong negative correlation with the North Atlantic Oscillation Index; positive rainfall anomalies over Central Equatorial Africa are related to cooler SSTs in the Atlantic region (Sutton & Allen 1997).

How do changes in precipitation affect tropical rainforest? Experiments carried out in the Brazilian Amazon show that trees subject to drought exhibit various adaptations to short-term water loss (i.e. an El Niño event). Trees may experience leaf shedding and a decrease in production of new leaves, leading to a loss of leaf area (Nepstad et al. 2002). Lower leaf area facilitates drying of the leaf litter layer, increasing the rate of fire spread (Nepstad et al. 2004). Although rainforests can exhibit resilience to drought due to the ability to tap deep water sources (Jipp et al. 1998), continued water deficit can lead to increased tree mortality, creating gaps in the forest cover (Williamson et al. 2000). This provides opportunities for lightdemanding secondary species to colonize the forest under a short-term drought scenario. However, observations from permanent plots in Panamá suggest that light-demanding species also suffer increased mortality during droughts (Condit et al. 1995), thus severe droughts may lead to the loss of forest cover.

Long-term, high-resolution pollen records from rainforests of Atlantic Equatorial Africa demonstrate fluctuations between mature and secondary forest taxa during the last 4000 years that may have been caused by changes in precipitation. For example, a sedimentary sequence covering the last 1325 years from Lake Kamalété in central Gabon shows an increase in the percentage of some pioneer species and a decrease in mature forest species from approximately 1240 to 450 calibrated years (cal. yr) BP hypothesized to be related to a decrease in the regional balance of available moisture (Ngomanda et al. 2005). At a site in southwestern Cameroon, pollen evidence from a sedimentary sequence at Lake Ossa indicates that the basin contained closed forest from 4770 to 2700 BP, when pioneer tree species increased in abundance. At approximately 1300 BP and after 600 BP mature forest species increased again, though not to the same percentages as prior to 2700 BP (Reynaud-Farrera et al. 1996). Diatom data from the same sequence indicates a major increase in allochthonous windblown diatoms from the Sahara after 2700 BP due to intensification of the dry season and/or of northern trade winds over West Africa, suggesting that the opening of the forest may be related to decreased precipitation (Nguetsop et al. 2004). Near Lake Ossa at Barombi Mbo, situated in evergreen rainforest in SW Cameroon, a similar trend of increasing percentages of pioneer species and a decrease in mature forest species after approximately 3000 BP is seen in the pollen record (Maley & Brenac 1998). Vegetation of Barombi Mbo may have opened up as a response to the same

decrease in precipitation reconstructed for Lake Ossa at that time. It is currently unknown however, whether Central Equatorial Africa experienced similar climatic conditions as those in Atlantic Equatorial Africa, or if the lowland Congo basin forest composition responded to climate change with changes in forest composition.

(b) Prehistoric human activities

Although structurally many central African rainforests appear pristine, studies have shown that some forests overlie extensive evidence of prehistoric clearance in the form of pottery, charcoal and palm nut layers, or even iron furnaces (White & Oates 1999). Close examination of the regeneration requirements of mature trees in such areas reveals that many species are likely to have only regenerated following large-scale disturbance (van Gemerden *et al.* 2003). Thus, the composition of modern day forests may still reflect past human activities.

In Central Equatorial Africa, the patterns of prehistoric human activity are difficult to discern due to a paucity of research sites, particularly in forested areas. However, from regional archaeological studies, a relative chronology of the technological and political changes that have impacted the region can be constructed. Cultural developments in Central Africa followed a very different trajectory from European and Asian prehistoric models. In Central Africa, there is little archaeological evidence of early farming communities (Neolithic), and thus there appears to have been a direct transition from the Late Stone Age into the Iron Age, referred to as the 'Stone to Metal Age' (Casey 2005).

Early native food resources that may have been staples include yams (*Dioscorea*) and the oleaginous nuts of oil palm (*Elaeis guineensis*) and *Canarium schweinfurthii* (Lavachery 2001). Oil palm fossils are often found in association with human artefacts (Stahl 1993; White & Oates 1999) and it is hypothesized to have been an important food for pre-agricultural and agricultural groups living in West Africa (Sowunmi 1985). However, oil palm has been the subject of much debate as to whether large increases seen in several palynological records after 3500 BP are natural expansions, or related to human activities (Sowunmi 1999, Maley & Chepstow-Lusty 2001).

The discovery of direct evidence for banana cultivation and husbandry of goats and/or sheep in the rainforest area of Cameroon at 800 BC indicated the antiquity of the transfer of farming practices and cultivars across the Congo basin (Mbida et al. 2000). Bananas and plantains are crops of Asian origin, thought to have been introduced to the African continent via the east coast and diffused from the Upper Nile region to Central and West Africa (Vansina 1990). The end of the first millennium AD has been estimated for the arrival of other Asian crops such as citrus, cocoyams, aubergines and sugarcane. Different farming methods were required for these new crops. Whereas bananas and oil palm grew well in forest soils and required only modest clearance of the forest, these new crops required more intensive clearing and burning preparation for planting, thus shifting cultivation probably expanded during this time (Vansina 1990). There is no direct evidence for prehistoric agriculture in the Sangha river region, but abundant fossil oil palm nuts have been found in nearby streams and dated from 2300 to 900 BP with most nuts dating to approximately 1700 BP (Fay 1997), indicating that for over a millennium this forest had been sufficiently open so as to allow oil palm to proliferate.

Metallurgy may have also been an important driver of forest change. The balance of archaeological data not only suggests that iron smelting was developed independently (probably more than once) in Central Africa as early as 3000–4000 years ago (Bocoum 2004; Maes-Diop 2004), but also that, unlike in the Asian/ European model, copper smelting was not necessarily a precursor to the development of iron smelting (Childs & Herbert 2005). This may be attributable to the ubiquity of iron ore across Central Africa and the relative scarcity of copper ore, particularly in West Africa. Copper ores occur more frequently south of the rainforest belt, in southern Congo, DRC and Zambia, and copper from such indigenous sources and from North Africa was traded extensively throughout the region. It is estimated that during the last 3000 years, over 50 000 tons of copper and brass were brought into central Africa, superseding iron as the currency of choice within the Congo basin in the nineteenth century (Childs & Herbert 2005).

The ecological impact of smelting may have been enormous. Reconstructions of iron smelting activities in Yatenga, Burkina Faso for example have demonstrated that reduction of a batch of iron ore over a 4–5 days process could require more than 900 kg of charcoal (Martinelli 2004). Goucher (1981) suggests that in the forest–savannah transition zone, iron smelting may have led to local deforestation. The strong iron smelting tradition in central Africa continued until the twentieth century when cheap European imports of scrap iron undermined local production, although local environmental degradation may have also had a role in the decline of indigenous smelting (Childs & Herbert 2005).

The Sangha river region today has low population densities and almost unbroken forest cover up to the savannah ecotone. Archaeological evidence for human activities around the coring site is scarce, but various opportunistic pottery finds along the Sangha river and its tributaries (including designated typologies Pikunda, 110 BC-120 AD; Likwala, 92 BC-124 AD; Munda, 353 BC-448 AD; and nearby Ndakan potsherds from approximately 350 BC-1750 AD) indicate that the area was probably continuously populated from 2300 BP to the present day (Eggert 1993; Brncic 2003). Iron smelting sites are found in the savannahs north of the Goualougo area as early as 800 BC and at the forest margin by the first centuries AD (Lanfranchi et al. 1998; Zangato 1999). Iron smelting appears on the lower Sangha river from 353 BC (Eggert 1993), indicating the pervasiveness and long existence of iron smelting technology in the area.

3. STUDY SITE AND METHODOLOGIES

The site used for palaeoecological analysis in this study is a small lake basin (100 m diameter) located in the middle of mixed species *terra firma* forest (2.164° N, 16.509° E) in the northern Congo–Brazzaville near a

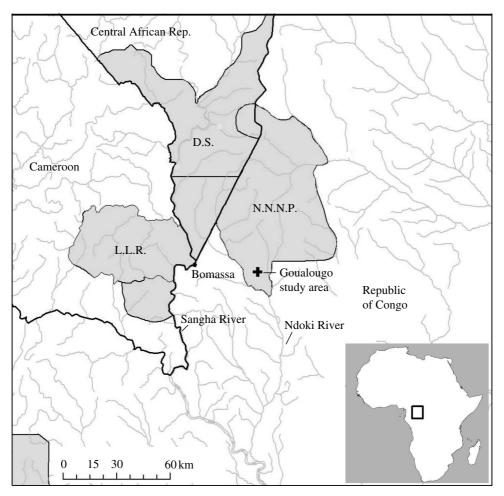


Figure 1. Map showing the location of the Goualougo study area. National Parks and Reserves are abbreviated as follows: N. N. N. P. (Nouabalé-Ndoki National Park), D. S. (Dzanga-Sangha Dense Forest Reserve) and L. L. R. (Lake Lobéké Reserve).

tributary of the Ndoki river (figure 1). It is situated in the vegetation zone of mixed moist semi-evergreen rainforest in Central Equatorial Africa (White 1983). The predominant vegetation is 'mixed species *terra firma* forest' described in detail for the adjacent Dzanga-Sangha reserve by Harris (2002). Other distinct vegetation types include monodominant *Gilbertiodendron dewevrei* forest, seasonally flooded forest and open swamp forest. Rainfall in the region is approximately 1500–1600 mm yr⁻¹ (regional measurements summarized in Harris 2002).

Sediments were extracted from the Goualougo lake using a modified Livingston piston corer (Wright 1967). A sedimentary sequence approximately 68 cm in length was collected from this basin. Chronology of the core was determined by AMS ¹⁴C dating (Poznań Radiocarbon Laboratory, Poland) and ²¹⁰Pb dating (*Ortec* Coaxial Well Photon Detector in the Oxford Long-term Ecology Laboratory).

Sub-sampling of the sedimentary sequence was carried out for pollen, geochemical and microscopic charcoal analyses.

(a) Pollen analysis

Sample preparation for pollen analysis was carried out following standard protocols (Bennett & Willis 2001). Identification of pollen grains involved comparison of fossil pollen to reference material held at the Oxford Long-term Ecology Laboratory and reference publications (Maley 1970; Caratini & Guinet 1974; Satabié 1974; Ybert 1979; Bonnefille & Riollet 1980; Salard-Cheboldaeff 1981, 1983, 1984; Sowunmi 1995, 1973). A minimum of 350 pollen and spore grains was counted per sample in order to ensure a statistically significant sample size (Bennett & Willis 2001).

(b) Charcoal analysis

Fire history surrounding the coring site was reconstructed through measurement of microscopic charcoal concentration in the sedimentary sequence. Slides for microscopic charcoal analysis were the same as those employed for pollen analysis, and charcoal was quantified using particle counts in relation to *Lycopodium* counts to give charcoal concentration in particles cm⁻³ (Whitlock & Larsen 2001; Tinner & Hu 2003). Ten scans were done across a slide at $400 \times$ magnification. A minimum of 30 *Lycopodium* was counted for each depth.

(c) Geochemical analyses

Traces of geochemical elements in lake sediments were used to detect both processes occurring outside of the basin catchment (e.g. input from wind-blown sediment) and those occurring within the catchment (e.g. changes in the soils surrounding the basin; Engstrom & Wright 1984, Boyle 2001). In addition, concentrations of trace elements revealing possible metallurgical activities were measured (Boyle 2001). In order to distinguish potential metallurgical dust from natural trace element contribution, the ratio of potential smelting minerals to titanium was calculated. Titanium has been used in other studies as a background reference for soil and sediment due to the resistance of Ti-bearing minerals to chemical weathering (Weiss et al. 2002). The geochemical elemental concentrations in the sedimentary sequence were measured at 2 cm intervals using a bulk sediment digestion technique (Bengtsson & Enell 1986) followed by plasma spectrometry. Aluminium and zinc were measured using ICP-AES due to their high concentration in the sediment (Perkin Elmer Optima 3300RL Inductively Coupled Plasma-Atomic Emission Spectrometer—operated by the Department of Geology, Royal Holloway, University of London). All other elements presented were measured using ICP-MS (Agilent 7500c—Inductively Coupled Plasma-Mass Spectrometer-operated by the NERC ICP-MS Facility, School of Earth Sciences and Geography, Kingston University).

(d) Data handling

Calibration of radiocarbon dates was performed using PalCal software (Weninger *et al.* 2002). The ²¹⁰Pb chronology of the top of the core was calculated using the constant rate of supply (CRS) model (Appleby 2001). Extrapolated and interpolated ages for the rest of the sequence were estimated using an age–depth model calculated from cubic spline interpolation in PSIMPOLL (Bennett & Heegaard 2006).

The pollen data were converted to pollen percentage data. This involved expressing the value for each pollen type counted in a sample as a percentage of the sum of all the pollen excluding Cyperaceae and Pteridophytes. The resulting pollen percentage data were plotted in a pollen diagram against age using the plotting program PSIMPOLL (Bennett 2005). The same program also enabled the plotting of the microfossil charcoal and geochemistry results. In order to determine where the main changes in vegetation occurred, the pollen percentage diagram was split into zones using optimal splitting by information content in the PSIMPOLL program (Birks & Gordon 1985). The number of zones used is the greatest number for which the splitting is statistically significant.

In order to view quantitatively any trends in the geochemical dataset independent of those related to depth, principal components analysis (PCA) of the geochemical dataset and microscopic charcoal concentration was undertaken using the programme CANOCO (ter Braak & Smilauer 2002).

Canonical correspondence analysis (CCA) in CANOCO (ter Braak & Smilauer 2002) was used to identify the environmental variables correlated most significantly to the pollen data. This direct ordination method gives an indication of where the optimum for a taxon occurs along a particular environmental gradient. If an environmental variable gives a large dispersion between taxa, then that variable can be assumed to explain the species distribution well.

In order to decide which variables to include in the canonical ordination model, Monte Carlo permutation tests were used (forward selection, ter Braak & Smilauer 2002). Only the variables that had a

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correlation with the pollen data significantly higher than what could have occurred by chance were included in the model. The significance of the variables is calculated on the basis of the supplementary explanatory power they have, once the effect of the variables already included in the model has already been accounted for. An ordination biplot was used to display the results of the CCA. Taxa are distributed on axes that are constrained by environmental data. The optimum of a taxon along the environmental gradient can be found by projecting a perpendicular line from the taxon to the environmental arrow. Taxa that are near the tip of an arrow are highly correlated with above average values for that environmental variable.

4. RECONSTRUCTED EVIDENCE FOR CLIMATE CHANGE IN CENTRAL EQUATORIAL AFRICA OVER THE PAST 3300 YEARS

In order to reconstruct past climate of Central Equatorial Africa through independent proxies we used two lines of evidence, examination of reconstructed SST obtained from Atlantic Ocean cores and geochemical analysis of the Goualougo sedimentary sequence.

Present day climate models suggest that fluctuations in SST had an influence on precipitation in Central Equatorial Africa (and in particular the lowland Congo basin; see above). By assuming that the contemporary links between SST (North and tropical Southern Atlantic) and the precipitation in Central Equatorial Africa were also in existence earlier in the millennium, some indication of past precipitation regimes may be gained from reconstructed SST. There are two notable ocean records with reconstructed SSTs for the interval of interest (i.e. 0-3300 cal. yr BP) from West Africa (ODP 659, deMenocal et al. 2000) and the western North Atlantic (Bermuda Rise, Keigwin 1996). Despite the distance between these two cores, reconstructions of SST from these cores using foraminiferal evidence reveals a number of similarities in predicted variability in the SST. Most notably, they record cooler SSTs corresponding to the Little Ice Age in NW Europe (between approx. 100 and 600 years ago) and warmer SSTs corresponding to the Medieval Warm Period (between 600 and 1200 years ago; figure 2a). Other fluctuations evident are cooler SSTs between 1200-2000 and 2800-3000 cal. yr BP interspersed by intervals of warmer SST between 2000-2800 and 3000–3400 cal. yr BP.

Thus, did increased SSTs result in lower precipitation over Central Equatorial Africa and lower SSTs result in higher precipitation? Results from the geochemical analyses of the Goualougo core provide some of the first evidence that was indeed the case. There is a clear pattern of fluctuations in the geochemical elements of inorganic minerals including Al, Cr, Fe, Ti and Mg (figure 2b, not all elements shown). The apparent synchrony of changes in quantities of these elements is statistically confirmed by PCA, which reveals a tight cluster of elements that is distinct from Mn, K and P (figure 3). The elements Mn, P and K most probably represent a signal of the stability of soils surround the basin throughout the

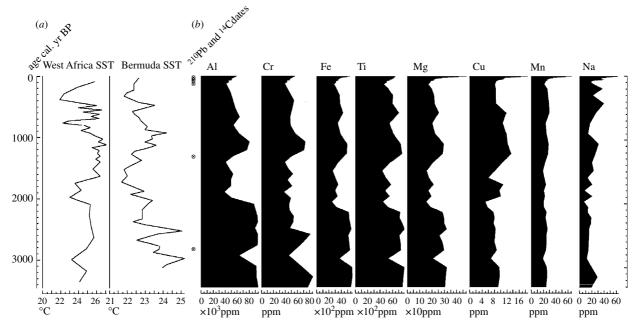


Figure 2. (*a*) Ocean records with reconstructed SSTs redrawn from 0–3300 cal. yr BP is from West Africa (ODP 659, deMenocal *et al.* 2000) to the western North Atlantic (Bermuda Rise, Keigwin 1996). (*b*) Results of geochemical analysis (this study). A subset of the measured elements is shown in the diagram.

3300 years covered in this record, as previous work has demonstrated that these elements are abundant in moist semi-evergreen tropical forest (Veenendaal *et al.* 1996). In contrast, fluctuations in the inorganic minerals (Al, Ti, etc.) probably represent an atmospheric dust signal related to climate.

The interpretation that these inorganic minerals indicate a dust signal is based on three lines of evidence. First, if they represented erosion of the topsoil surrounding the basin or local flooding of the catchment, then we would expect to see similar patterns also in the Mn, K and P-which are not apparent. Second, the composition of these elements is similar to dust input identified in both contemporary and palaeo-studies. A similar combination of elements interpreted as atmospheric mineral dust has been found in various sedimentary cores including terrestrial peat sequences of SE Asia (Weiss et al. 2002). A clear palaeo-dust signal from the West African Sahel has also been detected in a sedimentary sequence in northeastern Nigeria (Street-Perrott et al. 2000). The elemental composition of the 'dust signal' from the Goualougo vanga core is also very similar (in particular the high levels of Al, Fe and Ti) to present day aeolian dust collected off NW Africa (Stuut et al. 2005). Third, the peaks in the 'dust signal' show a close correlation to SSTs, in particular the Bermuda sequence whereby an increase in SST corresponds to an increase in these elements (figure 2), suggesting (as occurs presently) that the drier the climate, the greater the dust transport.

The most likely modern sources for dust deposited in the Congo basin are the Bodele depression in Chad and lesser studied sources to the east in southern Sudan. Based on 20 years of 6 hourly particle trajectories driven by contemporary three-dimensional winds from the Bodele depression, Washington *et al.* (2006) have shown that the main transport pathway from the Bodele depression occurs in a southwesterly direction before the dust is transported from east to west in the African Easterly Jet (AEJ) at an altitude of

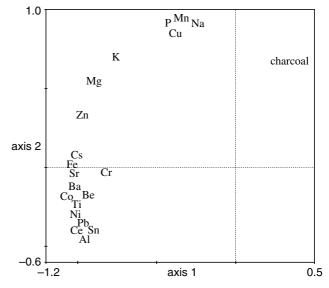


Figure 3. PCA ordination diagram (axes 1 and 2) of inorganic elements and microscopic charcoal measured in the Goualougo core.

approximately 3 km over the Sahel. While the Congo basin is not within the core transport pathway dust, particles can easily reach the basin within 5 days. Such events are more common in the boreal winter when the AEJ is more weakly developed and the tropical convection at its most southerly location over the southern African subcontinent (Washington *et al.* 2006). It is also clear from the contemporary dust cycle that wet deposition quickly clears the atmosphere of dust when tropical convection is expanded close to source regions. During dry conditions, without wet deposition, dust is easily transported over thousands of kilometres in the tropical northeasterlies.

From the geochemical record of Goualougo core, it is therefore apparent that over the past 3300 years the climate around the study region has fluctuated between a number of intervals of high dust input interspersed by intervals of low dust input. Given the present day links between dust transport and precipitation, and also evidence from the reconstructed SSTs, the geochemical evidence from the Goualougo indicates that dry intervals occurred at approximately 0–100, 700–800, 900–1200, 2000–2800 and 3000–3300 BP with the intervening periods probably considerably wetter than present day. These results provide an important climatic framework in which to view the vegetation dynamics represented in the pollen record from the Goualougo core and establish what influence climate variability has had on composition of the rainforest vegetation over time.

5. RECONSTRUCTED EVIDENCE FOR PREHISTORIC HUMAN ACTIVITIES

In order to gauge human activities near the Goualougo site that may have influenced past forest composition, we looked for evidence of anthropogenic burning and metallurgical practices in the Goualougo sedimentary sequence. Fire occurrence was determined from microfossil charcoal counts, while detection of metallurgical practices was obtained by measuring concentrations of the trace elements Cu and Fe. Results indicate evidence for anthropogenic burning and copper working.

From approximately 1200 cal. yr BP to the present, microscopic charcoal record shows a major increase in burning in the Goualougo area (figure 4). Results from a PCA show that microscopic charcoal abundance is negatively correlated with the dust signal and is therefore not a signal of fires associated with low rainfall (figure 3). In fact, the peak in charcoal concentrations occurs after 600 BP during increased rainfall related to the Little Ice Age (see above). Furthermore, there are no reports of wild fires occurring in lowland Central African forests under current environmental conditions. Occasional fires from lightning strikes have been reported to consume individual trees (Tutin et al. 1996), but such fires are unlikely to spread through the surrounding forest. Therefore the increase in burning over the last 1200 years, and particularly from 100 to 600 years ago when precipitation was higher, is almost certainly due to local human impacts.

An increase in copper deposition above background levels after 2000 BP as indicated by the Cu : Ti ratio in figure 4 suggests that Cu smelting or forging may have been an important activity in the region. This hypothesis must be tested further, given that there has been no archaeological evidence of Cu mining or working yet reported for the Sangha river region. However, geochemical analysis of early Roman sites in the United Kingdom showed that non-ferrous metalworking took place, despite the absence of metal detritus or artefacts (Cook *et al.* 2005). Such a study highlights the possibility that trade in Cu objects or Cu working may have taken place in the Goualougo area, and that future archaeological investigations may yet unearth further evidence of this.

Despite the considerable archaeological evidence for iron smelting in the Sangha river region from around

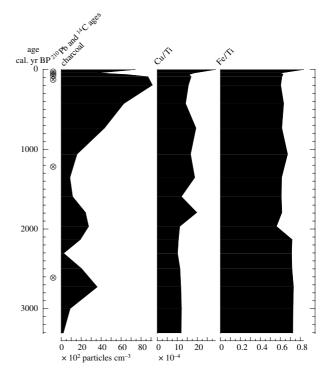
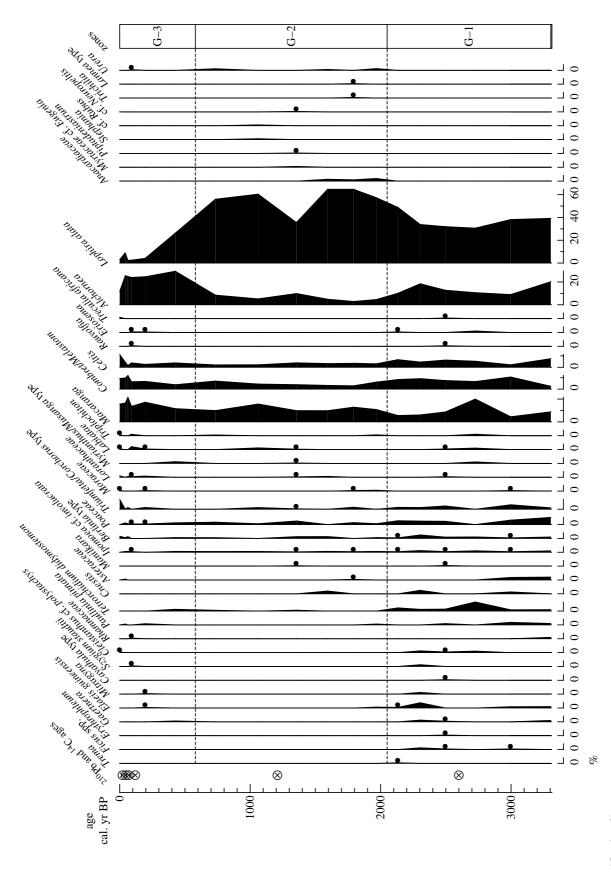


Figure 4. Microscopic charcoal concentration, Cu/Ti ratio and Fe/Ti ratio plotted against age for the Goualougo sedimentary sequence.

2300 years ago (see above), at no point in time do the geochemical data indicate a relative increase of atmospheric Fe in Goualougo as shown in the ratio of Fe : Ti (figure 4). One possible explanation is that Fe particles from smelting could not be detected above the high background levels of Fe already in the soil and atmospheric dust. Alternatively, there may have been no iron smelting sites in the direct vicinity of Goualougo.

6. EVIDENCE FOR VEGETATION CHANGE IN LOWLAND CONGO RAINFOREST AND THE RELATIVE INFLUENCES OF CULTURE AND CLIMATE ON ITS PAST COMPOSITION

Long-term changes in the forest composition at the Goualougo site were detected in the pollen record. As shown in the pollen diagram in figure 5, some pollen taxa representative of moist semi-deciduous lowland forest, such as Macaranga sp., Celtis sp. and Combretaceae/Melastomataceae, are present at similar abundances throughout the core, indicating the persistence of lowland semi-evergreen rainforest during the period in question. However, zonation of the diagram reveals three statistically significant zones that indicate distinct changes in forest composition. Zone G-1, which extends from the base of the core at 3300-2000 cal. yr BP, shows high levels of Trilete spores, as well as the highest levels throughout the core of herbs, shrubs and light-demanding tree species such as Tetrorchidium didimostemon, Alchornea sp., E. guineensis, Paullinia pinnata, Triumfetta/Corchorus and Poaceae. Zone G-2, extending from approximately 2000-600 cal. yr BP shows a very large increase in the percentage of Lophira alata pollen. There is an increase in mixed forest trees, including Anacardiaceae and



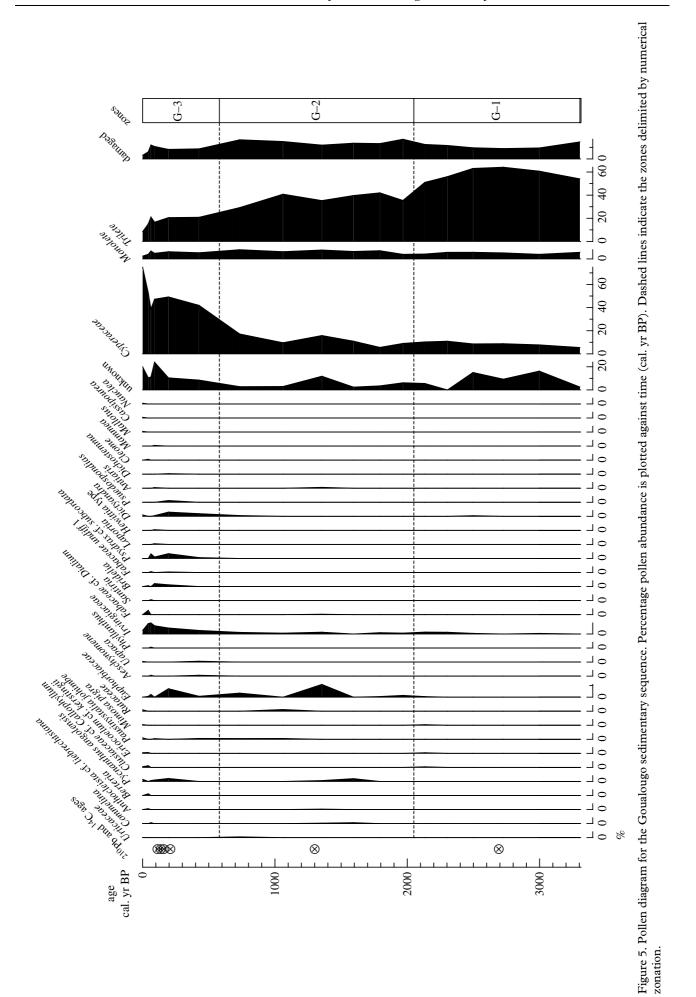




Figure 6. CCA ordination diagram (axes 1 and 2) of pollen taxa and microscopic charcoal, Al and Mn. Axes 1 and 2 explain 23.3 and 12.8% of the total variability, respectively. Taxa names are abbreviated from the pollen diagram in figure 5. For clarity, not all pollen taxa are shown.

Moraceae, while many of the light-demanding taxa that were abundant in Zone G-1 decline. Zone G-3, from 600 cal. yr BP to the present, shows some shrubs and trees peaking to some of their highest levels of pollen abundance, including *Alchornea* sp., *Dictyandra* sp., Irvingiaceae and *Psydrax cf. subcordatum*. At this time Trilete spores reach their lowest percentages, while the abundance of Cyperaceae pollen increases dramatically.

CCA was used to correlate these observed changes in vegetation with changes in climate (dust signal) and human impacts (burning and Cu smelting) in order to determine the relative impact of these drivers on specific taxa. The forward selection procedure by Monte Carlo permutations of the geochemical and microscopic charcoal data resulted in charcoal, Al and Mn being selected to enter the CCA (these were variables that had a statistically significant correlation with the pollen data). The vegetation–environment biplot is shown in figure 6. For clarity not all pollen taxa are shown. The first axis of the CCA biplot represents 23.3% of the variance in the pollen data (axis 1, significant at p=0.0410). This axis is most closely correlated with microscopic charcoal concentration whereas axis 2 is correlated with the dust signal, represented by Al. The first and second axes together explain 36.1% of the variance in the pollen data. The CCA diagram clearly shows that individual forest taxa have responded to both climate change and human impacts in different ways over the last three millennia. In the next three sections, we discuss the response of individual forest taxa to each of these impacts.

(a) Anthropogenic activities: burning

What effects did the increase in burning after 1000 cal. BP have on forest structure in the Goualougo region? Among the common pioneer trees that have shown increases during the last 1000 years are *Bridelia*, *Psydrax*, *Dictyandra* and *Rauvolfia*. The latter in particular is known to thrive in burnt forest (Hawthorne 1995). Also associated with increased burning are taxa that are nonpioneer light demanders which prefer secondary forest. For example, *Pycnanthus* regenerates well in disturbed forest, and part of its later increase may be as a result of burning (Hawthorne 1995). *Nauclea diderichii*, also an important rare timber species with pioneer ecology, only appears recently in the diagram. It is known to recruit more readily in fallow fields and large gaps (Hawthorne 1995; van Gemerden *et al.* 2003) and therefore may have increased in abundance due to recent burning.

The bark of *Pausinystalia* species is widely used for medicinal purposes in Central Africa. Although *Pausinystalia* is a mature forest tree, it maintains a steady presence in the pollen record from 1100 cal. BP to the present day and is associated with increased burning. While it may benefit from forest openings, owing to its medicinal value, it is also likely to have been protected from felling and retained in cleared sites.

Triplochiton scleroxylon is a widespread and important timber species in West Africa, but has a patchy distribution in the northwest of the Congo basin. It is thought that its low abundance may be due to an inability to invade forests on poor soils except where there is sufficient disturbance (Hall & Bada 1979). This is confirmed in the CCA biplot which shows *Triplochiton* correlated with higher concentrations of microscopic charcoal. Its presence in the pollen record during periods of increased burning is likely to be due to human disturbance creating areas suitable for its colonization. In closed forests in the Sangha river area there is practically no regeneration of *Triplochiton* currently (Harris 1998, personal observation).

An important tree family for humans is Irvingiaceae, which also appears to be correlated with the charcoal record, increasing in abundance during the last 800 years. Fruits from some species of this family are an important food source for forest dwellers. Although some Irvingiaceae are light demanding, they do not necessarily regenerate well with burning (Hawthorne 1995). Given their importance as a food species, they may have been protected around village sites as with *Pausinystalia*.

Have any species been lost due to past human activities? This does not seem to be the case for this area, perhaps because human densities were low enough that their activities created gaps for more light demanding species to establish in an otherwise dense forest. Only a few taxa seem to have decreased in abundance with the increase in burning. These are mainly other pioneer taxa such as *L. alata, Cnestis* and Poaceae, and for some of them the decrease appears to be related to increased moisture. It is difficult to say with certainty however, that no species have suffered from human activity, as the pollen record does not represent a complete inventory of species.

(b) Climate

The regional climate appears to have had a significant impact on local forest composition as shown by the correlation of the second CCA axis with Al concentration (with increasing values of Al representing the geochemical proxy for drier climate). However, despite evidence for drier intervals lasting hundreds of years, the low percentages of Poaceae pollen throughout the core indicate that the Goualougo forest was not encroached by savannah in the last 3300 years. Many taxa were more abundant during dry intervals, mainly light-demanding taxa such as *T. didimostemon*, *Erythrophleum*, *Trema*, *Gaertnera* and *E. guineensis*.

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Pycnanthus angolensis is a pioneer tree commonly found in disturbed forests, and indeed its distribution along the first axis of the CCA biplot indicates that it responds positively to anthropogenic disturbance. A more important factor for its occurrence in the fossil record may be the increase in moisture after 2000 BP and from 100–600 cal. yr BP. Ecological data for this tree indicates that, although it occurs in dry forest, it is very drought sensitive as a seedling, and this may explain why it was only present in the pollen record during wetter intervals (Hawthorne 1995).

Our pollen data indicate that E. guineensis abundance at this site is more correlated with dry intervals than with any increase in human activity. After 2000 cal. yr BP, E. guineensis pollen disappears from the pollen record except for reappearance ca 200 years ago. This is in contrast with the record of fossil E. guineensis nuts, which peaked in abundance in the area around 1700 BP (Fay 1997) and correspond to a predominantly wetter climate in the region. One explanation for the lack of pollen at this time is that *Elaeis* was not growing around the sedimentary basin during this time and that its pollen is not well dispersed. Both records agree, however, that the present day oil palm had decreased in abundance and was not being actively planted in the area. Kretsinger & Zana (1999) noted colonial records indicating that palm oil was actually imported and sold to inhabitants of the upper Sangha area in the early twentieth century. Intense tribal conflicts and population movements before and during the colonial period may have contributed to this decrease (Kretsinger & Zana 1999), as well increased moisture availability and a closing of forest gaps which were suitable for colonization (Maley & Chepstow-Lusty 2001).

The shift to a wetter climate after 2000 cal. BP, signified by the reduction of dust elements in the core, led to a corresponding shift in forest composition to more mature forest taxa. Those forest taxa that were able to expand during wet periods were primarily in the families Anacardiaceae, Clusiaceae, Moraceae and Urticaceae. Several pioneer trees appear to be more dependent on moisture than on disturbance, as evidenced by *Anthocleista* and *L. alata*.

Lophira alata is a widespread species common in semi-evergreen and evergreen forest (Veenendaal et al. 1996). Its dramatic expansion beginning just before 2000 BP coincides with an increase in moisture. Lophira does not show a corresponding decrease with a return of drier conditions between 900 and 1200 cal. BP, however, and it may have benefited initially from increased human activities.

(c) Anthropogenic activities: smelting

Copper concentration was not chosen in the forward variable selection for the CCA indicating that there was little explanatory power for changes in forest composition. The increase of both Cu and microscopic charcoal towards the top of the core suggests that Cu working may be related to the increase in burning in the area. However, copper forging alone may have had no direct impact on the vegetation due to the limited need of fuel wood for forging as opposed to smelting.

7. CONCLUSIONS

This study presents multi-proxy palaeoecological data covering the last 3300 years from a sedimentary sequence collected from lowland semi-evergreen forest in the Congo basin. Measurements of inorganic geochemistry, microscopic charcoal and pollen analysis were performed in order to determine the relative impacts of long-term climate change and human impacts on Central African forest. The results from this study address key questions for understanding the long-term ecology and dynamics of this critically important forest block. These questions concern:

- Forest resilience. Our data indicate that Central Equatorial Africa has been very resistant to past climatic and disturbance events. Moist semievergreen forest taxa persisted throughout the last 3300 years with no sign of savannah expansion, despite extensive periods of reduced (and increased) moisture compared with today and evidence for increased anthropogenic fires over the last 1000 years.
- The influence of culture on past forest composition. Prehistoric burning had a larger impact on species composition in the past than climate changes in the Goualougo study area. Such disturbance seemed to increase opportunities for light demanding tree taxa without resulting in degradation to a savannah landscape. However, it is impossible to determine conclusively whether other species that did not appear in our pollen record were adversely affected by past human activities.
- The influence of climate on past forest composition. Although the area around Goualougo remained forested during the last 3300 years, there was an identifiable impact of past climate change on forest composition. The increase of several pioneer tree taxa was associated with drier periods, notably *E. guineensis*, *Tetrorchidium* sp., and *Erythrophleum* sp. Conversely, during wetter intervals, a few pioneer taxa decreased in relative abundance, and may have been succeeded by species such as *L. alata* and mature forest species in the families Urticaceae, Moraceae and Clusiaceae.
- The relative influence of culture and climate on current forest composition. The effects of both past climate changes and anthropogenic activity are still evident in the Goualougo forest today. Many light-demanding or late secondary species growing in this forest are likely to have established under disturbance conditions such as relatively recent burning and may still be in a process of succession perhaps after abandonment of villages. We speculate that Marantaceae patches found around this park may be the indicators of such sites of previous human occupation; throughout the area, charcoal is easily found in the soil underneath forest cover (T. Brncic & D. Harris 2000, 2003, personal observation). In addition to recent changes in anthropogenic impacts, many of the older trees in the forest established in a period of higher rainfall than today and these taxa may decline in abundance if they fail to regenerate under current rainfall patterns.
- Future climate and human impacts. The trees commonly exploited by timber companies that have been identified in this study, L. alata, T. scleroxylon,

N. diderichii, Erythrophleum suaveolens and *P. angolensis*, have different long-term patterns of relative abundance and different responses to climate and anthropogenic disturbance. Although the forests of this region have demonstrated resilience to disturbances of the past, the impact of mechanized logging may have no historical analogue given that its rate is much more rapid than traditional slash and burn agriculture. Furthermore, the highest levels of prehistoric burning did not occur in conjunction with drier climates in the past. If in future, forest clearance and burning occur during prolonged dry periods, the species composition of the forest may suffer more severe changes than those seen in the last 3300 years.

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REFERENCES

- Appleby, P. G. 2001 Chronostratigraphic techniques in recent sediments. In *Tracking environmental change using lake sediments*, vol. 1 (eds W. M. Last *et al.*), pp. 171–203. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Bengtsson, L. & Enell, M. 1986 Chemical analysis. In Handbook of holocene palaeoecology and palaeohydrology (eds B. E. Berglund), pp. 423–451. Chichester, UK: Wiley.
- Bennett, K. D. 2005 Psimpoll. http://www.kv.geo.uu.se. Quaternary Geology Program, Uppsala University, Sweden.
- Bennett, K. D. & Heegaard, E. 2006 Estimation of age-depth relationships. In *Tracking environmental change using lake* sediments, vol. 4 (eds H. J. B. Birks et al.) Data handling and statistical techniques. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Bennett, K. D. & Willis, K. J. 2001 Pollen. In Tracking environmental change using lake sediments, vol. 3 (eds J. P. Smol et al.) Terrestrial, algal, and siliceous indicators, pp. 5–30. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Birks, H. J. B. & Gordon, A. D. 1985 Numerical methods in quaternary pollen analysis. London, UK: Academic Press.
- Bocoum, H. 2004 Iron metallurgy in Africa: a heritage and a resource for development. In *The origins of iron metallurgy in Africa* (ed. H. Bocoum). Paris, France: UNESCO.
- Bonnefille, R. & Riollet, G. 1980 Pollens des Savannes d'Afrique Orientale. Paris, France: CNRS.
- Boyle, J. F. 2001 Inorganic geochemical methods in palaeolimnology. In *Tracking environmental change using lake sediments*, vol. 2 (eds W. M. Last *et al.*), pp. 83–141. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Brncic, T. 2003 Ecology and patch dynamics of Megaphrynium macrostachyum (Marantaceae) in the rain forest of Central African Republic. D.Phil. thesis, Oxford University, Oxford, UK.
- Camberlin, P., Janicot, S. & Poccard, I. 2001 Seasonality and atmospheric dynamics of the teleconnection between African rainfall and tropical sea-surface temperature:

Atlantic vs. ENSO. Int. J. Climatol. 21, 973–1005. (doi:10. 1002/joc.673)

- Caratini, C. & Guinet, P. (eds) 1974 *Pollen et spores d'Afrique tropicale.* Talence, France: Centre d'Etudes de Geographie Tropicale.
- Casey, J. 2005 Holocene occupations of the forest and savanna. In *African archaeology* (ed. A. B. Stahl), pp. 225–248. Oxford, UK: Blackwell Publishing.
- Childs, S. T. & Herbert, E. W. 2005 Metallurgy and its consequences. In *African archaeology* (ed. A. B. Stahl). Oxford, UK: Blackwell Publishing.
- Condit, R., Hubbell, S. P. & Foster, R. B. 1995 Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecol. Monogr.* 65, 419–439. (doi:10.2307/2963497)
- Condit, R., Hubbell, S. P. & Foster, R. B. 1996 Assessing the response of plant functional types to climatic change in tropical forests. *J. Veg. Sci.* 7, 405–416. (doi:10.2307/ 3236284)
- Cook, S. R., Clarke, A. S. & Fulford, M. G. 2005 Soil geochemistry and detection of early Roman precious metal and copper alloy working at the Roman town of Calleva Atrebatum (Silchester, Hampshire, UK). J. Archaeol. Sci. 32, 805–812. (doi:10.1016/j.jas.2005.01.006)
- deMenocal, P., Ortiz, J., Guilderson, T. & Sarnthein, M. 2000 Coherent high- and low-latitude climate variability during the holocene warm period. *Science* 288, 2198–2202. (doi:10.1126/science.288.5474.2198)
- Eggert, M. K. H. 1993 Central Africa and the archaeology of the equatorial rainforest: reflections on some major topics. In *The archaeology of Africa: food, metals, towns* (eds T. Shaw *et al.*). London, UK: Routledge.
- Elenga, H., Maley, J., Vincens, A. & Farrera, I. 2005 Palaeoenvironments, palaeoclimates and landscape development in Atlantic Equatorial Africa: a review of key sites covering the last 25 kyr. In *Past climate variablility through Europe and Africa* (eds R. W. Battarbee *et al.*). Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Engstrom, D. R. & Wright, H. E. 1984 Chemical stratigraphy of lake sediments as a record of environmental change. In *Lake sediments and environmental history* (eds E. Y. Haworth *et al.*), pp. 11–68. Leicester, UK: Leicester University Press.
- Fay, J. M. 1997 The ecology, social organization, populations, habitat and history of the western lowland gorilla (Gorilla gorilla gorilla Savage and Wyman 1847). Ph.D. thesis, Washington University.
- Goucher, C. L. 1981 Iron is iron till it is rust—trade and ecology in the decline of West-African iron-smelting. *J. Afr. Hist.* 22, 179–189.
- Hall, J. B. & Bada, S. O. 1979 The distribution and ecology of Obeche (*Triplochiton Scleroxylon*). *J. Ecol.* 67, 543–564. (doi:10.2307/2259111)
- Harris, D. 2002 The vascular plants of the Dzanga-Sangha Reserve, Central African Republic. *Scripta Botanica Belgica [Monographic series]* 1–286.
- Hawthorne, W. 1995 *Ecological profiles of Ghanaian forest trees, tropical forestry papers.* Abingdon, UK: Nuffield Press.
- Hirst, A. C. & Hastenrath, S. 1983 Atmosphere–ocean mechanisms of climate anomalies in the Angola–tropical Atlantic sector. *J. Phys. Oceanogr.* 13, 1146–1157. (doi:10. 1175/1520-0485(1983)013<1146:AOMOCA>2.0.CO;2)
- Jipp, P. H., Nepstad, D. C., Cassel, D. K. & De Carvalho, C. R. 1998 Deep soil moisture storage and transpiration in forests and pastures of seasonally-dry Amazonia. *Clim. Change* **39**, 395–412. (doi: 10.1023/A:1005308930871)
- Justice, C. &, Zhang Q. 2001 Seeing the future now— Simulating forest changes in the Congo Basin. In *Congo Basin Information Series*. Biodiversity Support Program— CARPE.

- Keigwin, L. D. 1996 The little ice age and medieval warm period in the Sargasso Sea. *Science* **274**, 1503–1508. (doi:10.1126/science.274.5292.1503)
- Kretsinger, A. & Zana, H. 1999 Souvenirs de Bayanga 1890–1960. Bangui, Central African Republic: Projet Dzanga-Sangha.
- Laing, A. G. & Fritsch, J. M. 1993 Mesoscale convective complexes in Africa. *Mon. Weather Rev.* **121**, 2254–2263. (doi:10.1175/1520-0493(1993)121<2254:MCCIA>2. 0.CO;2)
- Lanfranchi, R., Ndanga, J. & Zana, H. 1998 New carbon 14C datings of iron metallurgy in the Central African dense forest. In *Resource use in the Trinational Sangha river region* of Equatorial Africa: histories, knowledge forms, and institutions, vol. 102 (eds H. E. Eves et al.), pp. 41–50. New Haven, CT: Yale School of Forestry & Environmental Studies.
- Lavachery, P. 2001 The Holocene archaeological sequence of Shum Laka Rock Shelter (Grasslands Western Cameroon). *Afr. Archaeol. Rev.* 18, 213–247. (doi:10.1023/ A:1013114008855)
- Maes-Diop, L.-M. 2004 Assessment of the dating of ancient relics of ironworking in Africa: main lessons. In *The origins of iron metallurgy in Africa* (ed. H. Bocoum). Paris, France: UNESCO.
- Maley, J. 1970 Contributions à l'étude du Bassin tchadien: atlas de pollens du Tchad. *Bull. Jard. Bot. Nat. Belg.* 40, 29–48.
- Maley, J. 1989 Late Quaternary climatic changes in the African rain forest; forest refugia and the major role of sea-surface temperature variations. In *Paleoclimatology* and paleometeorology; modern and past patterns of global atmospheric transport, vol. 282 (eds M. Leinen et al.), pp. 585–616. Dordrecht-Boston International, The Netherlands: D. Reidel Publishing Company.
- 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. *Rev. Palaeobot. Palynol.* 99, 157–187. (doi:10.1016/S0034-6667(97)00047-X)
- 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? Veg. Hist. Archaeobot. 10, 117–120. (doi:10.1007/PL00006920)
- Martinelli, B. 2004 On the threshold of intensive metallurgy: the choice of slow combustion in the Niger River Bend (Burkino Faso and Mali). In *The origins of iron metallurgy in Africa* (ed. H. Bocoum). Paris, France: UNESCO.
- Mbida, C. M., Van Neer, W., Doutrelepont, H. & Vrydaghs, L. 2000 Evidence for banana cultivation and animal husbandry during the first millennium BC in the forest of southern Cameroon. J. Archaeol. Sci. 27, 151–162. (doi:10.1006/jasc.1999.0447)
- Nepstad, D. C. *et al.* 1999 Large-scale impoverishment of Amazonian forests by logging and fire. *Nature* **398**, 505–508. (doi:10.1038/19066)
- Nepstad, D. C. *et al.* 2002 The effects of partial throughfall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon forest. *J. Geophys. Res.* 107, 8085. (doi:10.1029/2001JD000360)
- Nepstad, D., Lefebvre, P., Lopes da Silva, U., Tomasella, J., Schlesinger, P., Solórzano, L., Moutinho, P., Ray, D. & Benito, J. G. 2004 Amazon drought and its implications for forest flammability and tree growth: a basin-wide analysis. *Global Change Biol.* **10**, 704–717. (doi:10.1111/ j.1529-8817.2003.00772.x)
- Ngomanda, A., Chepstow-Lusty, A., Makaya, M., Schevin, P. & Maley, J. 2005 Vegetation changes during the past 1300 years in western equatorial Africa: a high-resolution

pollen record from Lake Kamalete, Lope Reserve, Central Gabon. *Holocene* **15**, 1021–1031. (doi:10.1191/0959 683605hl875ra)

- Nguetsop, V. F., Servant-Vildary, S. & Servant, M. 2004 Late Holocene climatic changes in west Africa, a high resolution diatom record from equatorial Cameroon. *Quat. Sci. Rev.* 23, 591–609. (doi:10.1016/j.quascirev. 2003.10.007)
- Nicholson, S. E. & Entekhabi, D. 1987 Rainfall variability in equatorial and southern Africa: relationships with sea surface temperatures along the southwestern coast of Africa. J. Appl. Meteorol. 26, 561–578. (doi:10.1175/1520-0450(1987)026<0561:RVIEAS>2.0.CO;2)
- Oslisly, R. 2001 The history of human settlement in the Middle Ogooué Valley (Gabon): implications for the environment. In *African rain forest ecology and conservation* (eds W. Weber *et al.*).
- Reynaud-Farrera, I., Maley, J. & Wirrman, D. 1996 Végétation et climat dans les forêts du Sud-Ouest Cameroun depuis 4770 ans BP: analyse pollinique des sédiments du Lac Ossa. Comptes Rendus de l'Academie de Sciences Serié IIa: Sciences de la Terre et des Planetes 322, 749-758.
- Salard-Cheboldaeff, M. 1981 Palynologie Camerounaise II: Grains de pollen de la forêt littorale de basse altitude. *106e Congres National des Sociétés Savantes* **106**, 125–136.
- Salard-Cheboldaeff, M. 1983 Palynologie Camerounaise. III: Grains de pollen de la forêt dense humide de basse et moyenne altitude. 108e Congres National des Sociétés Savantes, Grenoble 108, 117–129.
- Salard-Cheboldaeff, M. 1984 Palynologie Camerounaise. V: Grains de pollen de la forêt dense humide semicaducifoliée de moyenne altitude. 109e Congres National des Sociétés Savantes, 19–35. (fasc. II)
- Satabié, B. 1974 Contribution de la palynologie à l'étude des Irvingiacées d'Afrique Tropicale. *Adansonia* 14, 277–289.
- Sowunmi, M. A. 1973 Pollen grains of Nigerian plants; 1, Woody species. Grana 13, 145–186.
- Sowunmi, M. A. 1985 The beginnings of agriculture in West Africa: botanical evidence. *Curr. Anthropol.* 26, 127–129. (doi:10.1086/203234)
- Sowunmi, M. 1995 Pollen of Nigerian plants. II. Woody species. Grana. 34, 120–141.
- Sowunmi, M. A. 1999 The significance of the oil palm (*Elaeis guineensis* Jacq.) in the late Holocene environments of West and west central Africa: a further consideration. *Veg. Hist. Archaeobot.* 8, 199–210. (doi:10.1007/BF02342720)
- Stahl, A. B. 1993 Intensification in the west African Late Stone Age: a view from central Ghana. In *The archaeology* of Africa: food, metals, towns (eds T. Shaw et al.). London, UK: Routledge.
- Street-Perrott, F. A. et al. 2000 Drought and dust deposition in the West African Sahel: a 5500-year record from Kajemarum Oasis, northeastern Nigeria. The Holocene 10, 293–302. (doi:10.1191/095968300678141274)
- Stuut, J.-B., Zabel, M., Ratmeyer, V., Helmke, P. & Schefuss, E. 2005 Provenance of present-day eolian dust collected off NW Africa. J. Geophys. Res. Lett. 110, D04202. (doi:10. 1029/2004JD005161)
- Sutton, R. T. & Allen, M. R. 1997 Decadal predictability of North Atlantic sea surface temperature and climate. *Nature* 388, 563–567. (doi:10.1038/41523)
- ter Braak, C. J. F. & Smilauer, P. 2002 CANOCO reference manual and CanoDraw for windows user's guide. Ithaca, NY: Microcomputer Power.
- Tinner, W. & Hu, F. S. 2003 Size parameters, size-class distribution and area-number relationship of microscopic charcoal: relevance for fire reconstruction. *The Holocene* 13, 499–505. (doi:10.1191/0959683603hl615rp)

- Todd, M. C. & Washington, R. 2004 Climate variability in central equatorial Africa: influence from the Atlantic sector. *Geophys. Res. Lett.* **31**, L23202. (doi:10.1029/ 2004GL020975)
- Tutin, C. E. G., White, L. J. T. & Mackanga Missandzou, A. 1996 Lightning strike burns large forest tree in the Lopé Reserve, Gabon. *Global Ecol. Biogeogr. Lett.* 5, 36–41. (doi:10.2307/2997469)
- 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. *J. Biogeogr.* **30**, 1381–1390. (doi:10.1046/j.1365-2699.2003.00937.x)
- Vansina, J. 1990 Paths in the rainforests. London, UK: James Currey Ltd.
- Veenendaal, E. M. 1996 Responses of West African forest tree seedlings to irradiance and soil fertility. *Funct. Ecol.* 10, 501–511. (doi:10.2307/2389943)
- Washington, R. et al. 2006 Links between topography, wind, deflation, lakes and dust: the case of the Bodele Depression, Chad. Geophys. Res. Lett. 33, L09401. (doi:10.1029/2006GL025827)
- Weiss, D., Shotyk, W., Rieley, J., Page, S., Gloor, M., Reese, S. & Martinez-Cortizas, A. 2002 The geochemistry of major and selected trace elements in a forested peat bog, Kalimantan, SE Asia, and its implications for past atmospheric dust deposition. *Ceochimica et Cosmochimica Acta* 66, 2307–2323. (doi:10.1016/S0016-7037(02) 00834-7)
- Weninger, B., Jöris, O., & Danzeglocke, U. 2002 Cologne radiocarbon calibration & palaeoclimate research package (CALPAL). Universität zu Köln, Institut für Ur- und Frühgeschichte, Radiocarbon Laboratory, Köln, http:// www.calpal.de/.
- White, F. 1983 The Guineo–Congolian regional centre of endemism. The vegetation of Africa: a descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa. Paris, France: UNESCO.
- White, L. J. T. 2001 The African rain forest. Climate and vegetation. In *African rain forest ecology and conservation* (eds W. Weber *et al.*), pp. 3–29. London, UK: Yale University Press.
- White, L. J. T. & Oates, J. F. 1999 New data on the history of the plateau forest of Okomu, southern Nigeria: an insight into how human disturbance has shaped the African rain forest. *Global Ecol. Biogeogr.* 8, 355–361. (doi:10.1046/ j.1365-2699.1999.00149.x)
- Whitlock, C. & Larsen, C. 2001 Charcoal as a fire proxy. In Tracking environemntal change using lake sediments, vol. 3 (eds J. P. Smol et al.). Terrestrial, algal, and siliceous indicators, pp. 75–97. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Williamson, G. B., Laurance, W. F., Oliveira, A. A., Delamônica, P., Gascon, C., Lovejoy, T. E. & Pohl, L. 2000 Amazonian tree mortality during the 1997 El Nino drought. *Conserv. Biol.* 14, 1538–1542. (doi:10.1046/ j.1523-1739.2000.99298.x)
- Willis, K. J., Gillson, L. & Brncic, T. M. 2004 How "virgin" is virgin rainforest? *Science* **304**, 402–403. (doi:10.1126/ science.1093991)
- Wright Jr, H. E. 1967 A square-rod piston sampler for lake sediments. J. Sediment. Petrol. 37, 976.
- Ybert, J.-P. 1979 Atlas des pollens de Côte d'Ivoire. *Initiations Documents Techniques O.R.S. T.O.M.* **40**, 1–40.
- Zangato, M. E. 1999 Sociétés Préhistoriques et Mégalithes dans le Nord-Ouest de la République Centrafricaine. *African archaeology*, vol. 46, p. 223. Cambridge, UK: BAR.