Drivers of ecosystem and climate change in tropical West Africa over the past \(~\text{540 000 years}\)

CHARLOTTE S. MILLER,† WILLIAM D. GOSLING,† DAVID B. KEMP,† ANGELA L. COE† and IAIN GILMOUR‡

1Department of the Environment, Earth and Ecosystems, The Open University, Milton Keynes MK7 6AA, UK
2Department of Physical Sciences, The Open University, Milton Keynes MK7 6AA, UK

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ABSTRACT: A paucity of empirical non-marine data means that uncertainty surrounds the impact of climate change on terrestrial ecosystems in tropical regions beyond the last glacial period. The sedimentary fill of the Bosumtwi impact crater (Ghana) provides the longest continuous Quaternary terrestrial archive of environmental change in West Africa, spanning the last \(~\text{1.08 million years}\). Here we explore the drivers of change in ecosystem and climate in tropical West Africa for the past \(~\text{540 000 years}\) using pollen analysis and the nitrogen isotope composition of bulk organic matter preserved in sediments from Lake Bosumtwi. Variations in grass pollen abundance (6–99%) indicate transitions between grassland and forest. Coeval variations in the nitrogen isotopic composition of organic matter indicate that intervals of grassland expansion coincided with minimum lake levels and low regional moisture availability. The observed changes responded to orbitally paced global climate variations on both glacial–interglacial and shorter timescales. Importantly, the magnitude of ecosystem change revealed by our data exceeds that previously determined from marine records, demonstrating for the first time the high sensitivity of tropical lowland ecosystems to Quaternary climate change.

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KEYWORDS: Lake Bosumtwi; nitrogen isotopes; orbital forcing; palynology; West Africa.

Introduction

Understanding the relationship between tropical ecosystems and climate in Africa is of critical importance because of the continent’s sensitivity to global climate change (IPCC, 2013), the region’s high ecological value (Myers et al., 2000) and its role in hominid evolution (deMenocal, 2004). Today, the highly biodiverse tropical West African region is regarded as being particularly vulnerable to impacts from a rapidly growing human population (Lambin et al., 2003), and naturally driven periodic multi-decadal drought (Shanahan et al., 2009). Furthermore, in West Africa, projected regional warming (1–1.5°C by 2099) threatens the stability of current ecosystems (IPCC, 2013). Little is known, however, about the resilience of the natural vegetation to such high-magnitude climate change.

Quaternary (last 2.6 million years, Ma) records of environmental change in West Africa can provide vital insights into how ecosystems may respond to future climate change because of the comparable magnitude of Quaternary temperature changes (Gosling and Holden, 2011) with those predicted in the coming years (IPCC, 2013). This task is inhibited, however, by an absence of terrestrial successions that reconstruct ecosystem dynamics at a regional scale on long time scales. Rather, marine successions have hitherto formed the basis of understanding Quaternary ecosystem change in West Africa beyond the past \(~\text{20 ka}\) (Dupont, 2011). The interpretation of marine records of terrestrial vegetation changes is compromised by uncertainties concerning: (i) wide pollen source areas (comprising both river and aeolian inputs) (Hooghiemstra et al., 2006), (ii) complex oceanic transport pathways, potentially involving offshore water currents (Hooghiemstra et al., 2006) and (iii) typically low pollen concentrations that may dampen the true variance of terrestrial vegetation change (Dupont, 2011).

The sedimentary fill of the Lake Bosumtwi impact crater (Ghana, West Africa; 6°30′N, 1°25′W; Fig. 1) has yielded the longest Quaternary terrestrial archive of African vegetation to date, spanning the last \(~\text{540 ka}\) (Miller and Gosling, 2014). The lake is an ideal site for investigating past vegetation and climatic change because it: (i) has been accumulating sediment for the last \(~\text{1.08 ± 0.04 Ma}\) (Jourdan et al., 2009), (ii) currently lies just \(~\text{400 km south of the savannah to deciduous woodland transition}\) (Fig. 1; Supplementary Fig. 52) (White, 1983), (iii) is hydrologically closed in terms of both surface and groundwater, and therefore lake level is highly sensitive to changes in moisture balance (Balbot and Johannsen, 1992), and (iv) lies within the seasonal migration path of the tropical rainbelt (Nicholson and Grist, 2001; Miller and Gosling, 2014). The large diameter of the Bosumtwi crater (6–11 km) (Koeberl et al., 2005) also means that the majority (>80%) of the pollen accumulating in the sediments throughout the period of deposition is likely to be derived from the regional landscape, following the model of Jacobson and Bradshaw (1981).

Methods

In 2004, 1833 m of sediment was cored from 14 separate drill holes from Lake Bosumtwi by the International Continental Drilling Program (Koeberl et al., 2005). In this study we have used core BOS04-5B (hereafter 5B), which was recovered from the deepest part of the lake (74 m) and yielded the longest sedimentary succession (295 m in length; Koeberl et al., 2005). To reconstruct past vegetation shifts and moisture balance changes we conducted pollen and nitrogen stable isotope (δ¹⁵N) analysis of organic matter on the upper 151 m of 5B (interval studied to date).

Fossil pollen samples (n = 217, at an average temporal resolution of c. 2.4 ka) from 5B were counted to a minimum of 300 terrestrial pollen grains using a Nikon eclipse 50i

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composition (preceded by centrifugation (10 min at 1500 r.p.m.) to prevent
residues was determined at approximately 1.24-m intervals
ments to calculate charcoal concentration values.
spore tablet to
Charcoal concentration values were calcu-
their angular structure, opacity and the presence of visible
fragments above 10
samples as counted for pollen and spore analysis. Charcoal
indicates that the Poaceae is not an aquatic species, but most
characteristic woody taxa (e.g. 



where \( R \) is the isotope-number ratio, \( N(15N)/N(14N) \), of the
two isotopes of nitrogen in specimen \( P \), and the equivalent
parameters follow for the international measurement standard
Air. The average \( \delta^{15}N \) of IAEA NO3 and the in-house urea
standard was 4.6 ± 0.12‰ (1σ) and −0.9 ± 0.12‰ (1σ),
respectively. The measured \( \delta^{15}N \) value for IAEA NO3 is
within uncertainty of certified published values (4.7 ± 0.2‰)
demonstrating the accuracy of our protocol. As a true
estimate of our precision, six aliquots of sample 52E-1 from
75–75.5 cm (140.6 m composite depth, c. 504.8 ka; Table S1)
were analysed, returning a standard deviation of 0.45‰ (1σ).
These samples were run on multiple days and consequently
represent the uncertainty of the reported \( \delta^{15}N \) of organic
residues from Lake Bosumtwi.

Chronological control within core 5B is provided by
radiocarbon back to ~47 ka and optically stimulated lumines-
cence (Shanahan et al., 2013b), and a basal Ar–Ar age for the
crater impact glass of 1.08 ± 0.04 Ma (Fig. S3). The age model
used for the pollen and nitrogen isotope data shown here was
derived by linear interpolation of age with depth through the
radiocarbon ages to ~47 ka, and then linear interpolation
from the oldest radiocarbon age to the basal Ar–Ar age.

Results and discussion
To characterize major ecosystem change (vegetation shifts)
around Lake Bosumtwi we examined the fossil pollen record
(Figs 2 and 3; Supplementary Table S2). Poaceae (grass
family) is the most common taxon in the pollen record of 5B,
but shows high variability in abundance through the core,
ranging from 0 to 99% of total terrestrial pollen content
(Fig. 3). Pollen concentration is high throughout the core
(average 35 300 grains cm\(^{-3}\)) except for 34–33 m, which is
effectively barren (90–1400 grains cm\(^{-3}\)). A positive correla-
tion (\( r = 0.67 \)) between Poaceae and charcoal concentration
indicates that the Poaceae is not an aquatic species, but most
likely a combustible species from the tropical and subtropical
grasslands, savannah and shrublands (Olson et al., 2001;
Fig. S1 and Table S2). DCA has been used to characterize the
main variance within the fossil pollen dataset (Figs 2 and 3).
The pollen taxa identified were classified into ecological
groups (phytchoria; Table S2). The weighting of pollen taxa
along DCA axis 1 is interpreted as characterizing shifts
between savannah (‘savannah’ phytchoria) and woody
species (from the ‘deciduous woodland–Sudano-Guinean
transition’ and the ‘tropical and subtropical moist broadleaf
forests’ phytchoria). Characteristic savannah taxa (e.g. Poa-
ceae, Caryophyllaceae, Amaranthaceae) are separated from
characteristic woody taxa (e.g. Fasertia, Alchornea, Celtis,
Macaranga; Table S2). As Poaceae is present also in the
deciduous woodland–Sudano-Guinean transition, the discus-
sion concerning grasslands and forests that follows will use
the vegetation classification of Olson et al. (2001), where
grasslands are ‘tropical and subtropical grasslands, savannah
and shrublands’ and forests are ‘subtropical moist broadleaf
forests’.

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Our data indicate the occurrence of several high-magnitude transitions between grassland and forest (Fig. 3A, B). Notably, between 96 and 58 m (~350–200 ka) there are high-frequency shifts between grassland and forest dominance, culminating in a remarkably stable interval of grassland dominance between 58 and 35 m (~200–130 ka, >80 % Poaceae). These large-scale shifts in vegetation indicate significant and rapid changes in environmental conditions around Lake Bosumtwi. Modern African vegetation associations indicate that typically grassland vegetation requires an average precipitation of <600–2000 mm a\(^{-1}\) and a dry season of 4–8 months. Conversely, forest vegetation requires precipitation ranging from 1000 to >10000 mm a\(^{-1}\) and a dry season of 0–5 months (Table S3; Olson et al., 2001; Miller and Gosling, 2014).

Evidence for pronounced environmental changes in the Lake Bosumtwi record is also provided by our \(\delta^{15}\)N data. \(\delta^{15}\)N values of terrestrial plant material recovered from Lake Bosumtwi range from 4.5 to 10.3‰ (Talbot and Johannessen, 1992; Shanahan et al., 2013a). In contrast, \(\delta^{15}\)N values of aquatic plants in Lake Bosumtwi are higher (12.8 ± 0.9‰) with a significant contribution from \(^{15}\)N-enriched dissolved nitrogen, produced via denitrification in anoxic bottom waters and upwelled seasonally into the mixed layer (Talbot and Johannessen, 1992; Shanahan et al., 2013a). In core 5B, \(\delta^{15}\)N values of organic matter range from +2 to +14‰ (Fig. 3C). The assimilation and cycling of nitrogen in lakes involves several dissolved inorganic nitrogen (DIN) species. However, in tropical African lakes, during times of stable water column stratification, low DIN concentrations result in an important shift in N cycling by favouring the dominance of cyanobacteria, capable of fixing molecular nitrogen (Talbot and Johannessen, 1992). Organic matter formed via this metabolic pathway typically has \(\delta^{15}\)N values around 0 ± 2‰, similar to that of atmospheric N. Limitation of DIN in Lake Bosumtwi has previously been interpreted as indicative of periods of stable water column stratification, promoted by high lake level (Talbot and Johannessen, 1992; for further information see SOM). Consequently, we interpret decreases in \(\delta^{15}\)N as indicative of increasing lake levels (Fig. 3C). Importantly, this inference is supported by the close correlation between intervals of low \(\delta^{15}\)N and forest vegetation expansion (Fig. 3), indicating a clear association between forest expansion and enhanced regional moisture availability.

The temporal pattern of vegetation and lake level change in the Bosumtwi record through the last ~540 ka suggests that major ecological and climate oscillations occurred in-phase with orbitally paced Antarctic temperature changes (Fig. 3). Specifically, through most of the Lake Bosumtwi record (notably between ~540 and ~350, and ~130 and 0 ka), oscillations in vegetation and lake-level occurred in-phase with ~100-ka-scale glacial-interglacial climate oscillations (Fig. 3). Spectral analysis of Poaceae abundance, DCA axis 1 and \(\delta^{15}\)N data support this observation, indicating high variance in these records at ~30-m (i.e. ~100-ka) periods (Fig. S4). This interpretation is intuitive as globally warmer interglacial intervals are associated with low grassland abundances from the region, whereas cooler glacial conditions are associated with high grassland abundances (Fig. 3A, B) (Dupont, 2011).

Similar evidence for an orbital control on fossil pollen abundance has been recognized from nearby marine sediment cores (Figs 1 and 4), further emphasizing the link between orbital-scale processes and tropical climate (deMenocal et al., 1993). In comparison with the Lake Bosumtwi record, however, these marine cores do not reveal the true extent of the regional impact of global climate change on West African tropical ecosystems (Fig. 4). Firstly, the inferred vegetation changes from the pollen data of marine cores are of lower magnitude and display only ambiguous correlation with global temperature (Fig. 4). Secondly, the marine records display predominantly gradual vegetation changes rather than the more rapid transitions observable in the Bosumtwi record (Fig. 4). This rapidity may of course be due to possible sedimentary breaks during periods of lake level low-stand; however, the only low-stand that has been identified from the sedimentology occurs between 135 and 75 ka (Scholz et al., 2007). The

Figure 2. Ordination of Lake Bosumtwi fossil pollen DCA taxon scores axis 1 vs. axis 2. Axis 1 represents most of the ecological variance (eigenvalue (EV) 0.44, axis 2 EV is 0.21). DCA was performed on all pollen/spore taxa reaching an abundance of >2 % of the pollen sum in at least one sample. In total, 43 pollen/spore taxa were included from 217 samples. Ecological groupings follow Table S2 (phytochoria). Note that the savannah species plotting positive on axis 1 is cf. Securinega, and although classified by Fréoud (1994) as savannah some species prefer moist soil. Poaceae is grouped into both the savannah and the deciduous woodland phytocorria.

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low-magnitude variability evident in the marine records is probably because marine pollen records are representative of a large, poorly constrained source area (Dupont, 2011). Additionally, the vegetation changes evident in the marine cores vary in both magnitude and timing (Fig. 4), and this could be attributable to latitudinal differences (Shanahan et al., 2015). Large-scale changes in global climate resulted in an expansion and contraction of the grassland, and thus a movement north or south of the grassland to forest transition (Dupont, 2011). Marine sites located near to this ‘transitional zone’ (Fig. 1) display a generally higher magnitude of vegetation change in the fossil pollen record (Fig. 4). Nevertheless, we must be careful in making these terrestrial–marine comparisons. The sediments of GIK16415 and GIK16776 were extremely poor in pollen, with pollen sums less than 300 grains, making the percentages somewhat unreliable. Removing all samples with low pollen sums (<50 grains) results in a sparse vegetation record.

Our study provides the first West African terrestrial data over multiple glacial–interglacial cycles to support the
hypothesis that high-latitude glaciations influenced low-latitude vegetation and climate (Maley and Livingstone, 1983), probably through concomitant fluctuations in Atlantic sea surface temperatures, which mediated the latitudinal displacement of the tropical rainbelt (Weldeab et al., 2007). Importantly, however, comparison of the Lake Bosumtwi record between 96 and 35 m, (~350–130 ka; Fig. 3A, B) with Antarctic climate (Fig. 3E) suggests high-latitude forcing of West African climate was weaker in this interval, with vegetation changes instead showing rapid fluctuations on shorter (millennial) timescales (Fig. 3A, B). Over this period (~350–130 ka) the strength of orbital precession reached a maximum (Fig. 3D), enhancing low-latitude seasonality and therefore the strength of the West African summer monsoon.

Figure 4. Comparison of Lake Bosumtwi core 5B Poaceae (grass) record with Poaceae records from nearby marine cores. Note that the Bosumtwi record is quantified as percentage abundance relative to total terrestrial pollen abundance. The marine core Poaceae datasets are calculated based on the sum of total pollen and spores and the data are from Pangaea. Locations of alphabetically labelled sites are shown in Fig. 1. Grey lines on each plot are the calculated 95% confidence intervals for pollen percentage data based on Maher (1972). Note the low variability in these marine records relative to the Lake Bosumtwi record.
During this interval the seasonal limit of the tropical rainbelt probably moved northward in response to strengthened insolation (Shanahan et al., 2015), which resulted in greater moisture delivery to North Africa during the summer (Larrasoaña et al., 2003), but lower rainfall to the south because of the longer summer dry season. This inference is supported by the generally low lake level throughout this interval at Lake Bosumtwi (Fig. 3C), and the broad coincidence between maximum precession amplitude and a long period of grassland stability (58–35 m). The Bosumtwi data indicate that the role of precession in controlling tropical climate (Clement et al., 2004) and vegetation is variable, and dependent upon the Earth’s precise orbital configuration.

The ~540-ka sedimentary record from Lake Bosumtwi, Ghana, provides two key new insights into the relationship between global climate and tropical ecosystems. First, regional-scale grassland–forest shifts are approximately twice as large as previously indicated from marine records (meaning we may have previously underestimated the scale of the vegetation shifts), and also include hitherto unrecognized millennial-scale variability. Second, these large-scale vegetation changes can be linked to changes in the global climate system driven by orbital precession, and that the sensitivity of the tropical ecosystem depends on the precise orbital configuration. These insights emphasize the susceptibility and sensitivity of West Africa to large-scale environmental changes, information that is of key importance for the accurate parameterization of climate models and the prediction of future ecosystem development.

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Supplementary Material

Figure S1. The relationship between charcoal and grass concentration, and the relationship between charcoal and total pollen concentration.

Figure S2. Map of present-day ecoregions of West Africa.

Figure S3. Relationship between sediment depth and age for the Lake Bosumtwi 5B sediment core.

Figure S4. Spectral analysis of fossil Poaceae pollen and δ15N from Lake Bosumtwi.

Table S1. δ15N sample replicate data.

Table S2. Fossil pollen taxa groupings.

Table S3. Modern vegetation of tropical West Africa.

Abbreviations. DCA, detrended correspondence analysis; DIN, dissolved inorganic nitrogen.

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