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Invited review

Quaternary forest associations in lowland tropical West Africa☆

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ABSTRACT

Terrestrial fossil pollen records are frequently used to reveal the response of vegetation to changes in both regional and global climate. Here we present a fossil pollen record from sediment cores extracted from Lake Bosumtwi (West Africa). This record covers the last *c.* 520 thousand years (ka) and represents the longest terrestrial pollen record from Africa published to date. The fossil pollen assemblages reveal dynamic vegetation change which can be broadly characterized as indicative of shifts between savannah and forest. Savannah formations are heavily dominated by grass (Poaceae) pollen (>55%) typically associated with Cyperaceae, Chenopodiaceae–Amaranthaceae and Caryophyllaceae. Forest formations are palynologically more diverse than the savannah, with the key taxa occurring in multiple forest zones being Moraceae, *Celtis*, *Uapaca*, *Macaranga* and *Trema*. The fossil pollen data indicate that over the last *c.* 520 ka the vegetation of lowland tropical West Africa has mainly been savannah; however six periods of forest expansion are evident which most likely correspond to global interglacial periods. A comparison of the forest assemblage composition within each interglacial suggests that the Holocene (11–0 ka) forest occurred under the wettest climate, while the forest which occurred at the time of Marine Isotope Stage 7 probably occurred under the driest climate.

1. Introduction

Today West Africa contains highly diverse grasslands and forests (Myers et al., 2000) which play an important role in the global carbon cycle (Lewis et al., 2009) and climate systems (Wang and Eltahir, 2000). The distribution and composition of tropical West African vegetation is strongly linked to the prevailing climate (Holdridge et al., 1971). However, over the coming decades regional climate models suggest that temperatures will increase and precipitation regimes, such as the West African Monsoon, will alter (Christensen et al., 2007). The response of vegetation to the projected climate change remains uncertain. One way in which we can improve our understanding of the relationship between vegetation and climate is to examine fossil vegetation records which span periods of global climate change of a comparable magnitude.

The most recent period of time which spans a similar magnitude climate fluctuation to those projected for the future is the last glacial–interglacial transition; *c.* 21–10 thousand years (ka) ago (Jolly et al., 1998; Annan and Hargreaves, 2013). At the last glacial–interglacial transition, West African terrestrial records of past vegetation change, indicate the expansion of forests into previously savannah dominated regions (Maley, 1991; Elenga et al., 1994; Maley and Brenac, 1998). Continuously deposited sediments recovered from offshore West African marine locations in the Gulf of Guinea (*e.g.* Dupont and Agwu, 1992; Dupont et al., 1998; Jahns et al., 1998) and the tropical Atlantic (*e.g.* Dupont et al., 1989; Lézine and Casanova, 1991), indicate that the pattern of forest expansion occurred repeatedly and coincident with periods of warmer global climate during the latter half of the Quaternary period (Dupont, 2011), *i.e.* forests were more extensive in West Africa during interglacial periods. However, interpretation of the composition of specific vegetation associations from marine fossil pollen records is inherently difficult due to: (i) wide pollen source areas (river and wind bourn input), (ii) complex oceanic transport pathways, including offshore water currents (Dupont et al., 2000), and (iii) low pollen concentrations within the sediments (*e.g.* Frédoux, 1994). Consequently, marine pollen records are representative of a large, but not accurately defined source area.

In this paper we present the first fossil pollen data from the landmark Lake Bosumtwi sediment core to provide an overview of tropical West African vegetation change during the last *c.* 520 ka. We focus this study on exploring the palynological (floristic)

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composition of six past forest stages. Based upon correlation of the Bosumtwi forest (BF) stages with fossil pollen records from the marine (*e.g.* Dupont et al., 1989; Dupont and Agwu, 1992; Frédoux, 1994; Dupont and Weinelt, 1996; Dupont et al., 1998; Jahns et al., 1998), and in line with independent age estimates (Koeberl et al., 1997; Jourdan et al., 2009; Shanahan et al., 2012, 2013) we interpret the six forest zones as most likely equivalent to the last six interglacial periods (Marine Isotope Stages [MIS] 13, 11, 9, 7, 5e and 1). The past forest assemblages are then related to the modern day vegetation of West Africa. To place the Lake Bosumtwi findings in a broader context we go on to synthesise previously published fossil pollen work from tropical West Africa into regional vegetation maps. The 'time-slice' past vegetation maps produced are used to discuss West African continental-scale changes in vegetation distribution.

2. Setting: tropical West Africa

2.1. Modern vegetation

Seven vegetation biomes have been recognised in tropical West Africa: (i) Deserts and Xeric Shrublands, (ii) Tropical and Subtropical Grasslands, Savannas and Shrublands, (iii) Tropical and Subtropical Dry Broadleaf Forests, (iv) Tropical and Subtropical Moist Broadleaf Forests, (v) Flooded Grasslands and Savannas, (vi) Montane Grasslands and Shrublands, and (vii) Mangroves (Fig. 1; White, 1983; Olson et al., 2001). The two most extensive biomes in tropical West Africa are the 'Tropical and Subtropical Grasslands, Savannas and Shrublands' and the 'Tropical and Subtropical Moist Broadleaf Forests' with a further two, 'Montane Grasslands and Shrublands' and 'Mangroves' limited to small areas at high altitude and along the coast respectively (Fig. 1). These four biomes have been sub-divided into fourteen 'ecoregions' that have characteristic vegetation associations which are, in turn, related to the prevailing climate conditions (Table 1; Olson et al., 2001).

2.2. Prevailing climate

Temperature and precipitation in tropical West Africa vary along an approximately north-south gradient (36–24 °C, and <600–6000 mm/yr). The Intertropical Convergence Zone (ITCZ), the tropical rainbelt and the West African Monsoon govern the climate in West Africa. The tropical rainbelt lies *c.* 1000 km (or 10°) south of the surface ITCZ (Nicholson, 2009). During boreal summer, an increase in northern hemisphere summer (June–August) insolation results in a northward shift in the ITCZ and the development of an area of low pressure over North Africa. Differential pressure brings moisture eastwards from the Atlantic Ocean to western Africa (SW monsoon). In boreal winter, the opposite occurs, with the ITCZ displaced southwards. Dry, aerosol-rich, continental January trade winds from the NE dominate over West Africa in the winter months (December–February).

2.3. Lake Bosumtwi

2.3.1. Physical setting and hydrology

Lake Bosumtwi (6°30'N, 1°25'W) occupies a 1.08 ± 0.04 Myr (Koeberl et al., 1997; Jourdan et al., 2009) meteorite impact crater in metamorphosed rocks belonging to the Precambrian-age Birimian Supergroup (Koeberl et al., 2007). The impact crater has a diameter of *c.* 11 km with a crater rim which varies in elevation from 210 to 460 m above sea level (asl). Since the time of impact *c.* 294 m of sediment has accumulated in the centre of the basin (Koeberl et al., 2005). The sedimentary deposits within the lake have originated

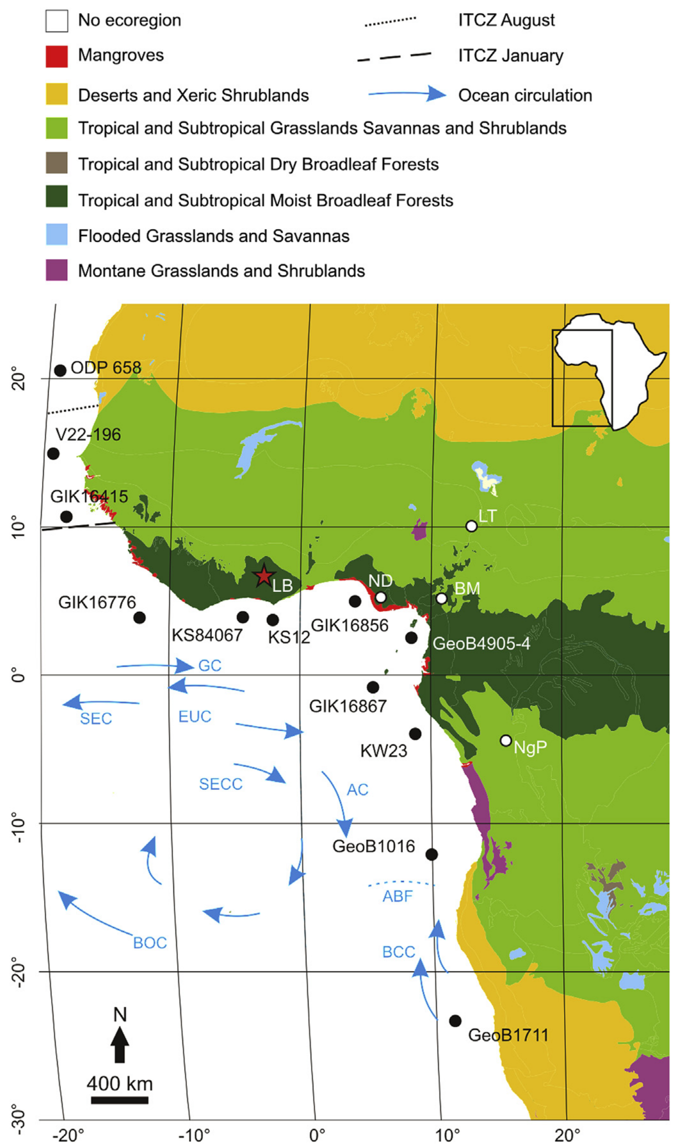

Fig. 1. Map of the modern vegetation biomes of West Africa (White, 1983; Olson et al., 2001) with climatological and oceanographic characteristics as well as the location of Lake Bosumtwi and other records relevant to this study (Table 2). LB = Lake Bosumtwi; LT = Lake Tilla; ND = Niger Delta; BM = Barombi Mbo; NgP = Ngamakala Pond; GC = Guinea Current; SEC = South Equatorial Current; EUC = Equatorial Undercurrent; SECC = South Equatorial Counter-Current; AC = Angola Current; BOC = Benguela Ocean Current; BCC = Benguela Coastal Current; ABF = Angola-Benguela-Front. Oceanographic surface currents from Dupont et al. (2000). Note ITCZ does not extend over land.

from erosion of the inside of the crater wall, vegetation within the crater, long distance aeolian transport and biological and evaporative processes within the lake.

Today, Lake Bosumtwi is 8.5 km in diameter (52 km^2) with the lake floor at 21 m asl at its deepest point and with a present day lake surface elevation of 97 m asl (thus *c.* 74 m water depth). Lake Bosumtwi is hydrologically isolated from the regional aquifer by the bedrock and the crater walls. The lake is highly stratified, with an anoxic hypolimnion beneath 15–18 m water depth, resulting in anoxic sedimentation with thinly laminated varves (Peck et al., 2004). The closed hydrology of Lake Bosumtwi makes the lake level extremely sensitive to changes in precipitation, cloudiness and temperature (Shanahan et al., 2006).