



Research papers

Diversity and ecology of tropical African fungal spores from a 25,000-year palaeoenvironmental record in southeastern Kenya

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ARTICLE INFO

Article history:

Received 14 July 2010

Received in revised form 17 December 2010

Accepted 3 January 2011

Available online 7 January 2011

Keywords:

non-pollen palynomorphs

fungal spores

Lake Challa

Kenya

Late-Glacial

Holocene

ABSTRACT

Fossil fungal spores and other non-pollen palynomorphs (NPPs) are powerful environmental proxies in European palaeoecological and archaeological contexts. However, their application on other continents, and particularly in the tropics, is hampered by uncertain equivalence with morphologically similar taxa in Europe, and incomplete knowledge of their ecology in the new local contexts. Here we use fossil NPP assemblages in a 25,000-year sediment record from Lake Challa, a steep-sided crater lake near Mt. Kilimanjaro in southeastern Kenya, to assess NPP diversity in a tropical-African context and the equivalence of African taxa with their European counterparts. We recovered a total of 65 well-defined NPP types, of which 61 are fungal spores, and 42 could be linked to known taxa. We provide diagnoses and illustrations of 61 recovered taxa, 58 of which have not been documented before.

Using the Challa pollen record of past regional vegetation dynamics and two independent proxies of past temperature and rainfall, we also assessed the association of individual fungal taxa with particular species and biomes of tropical-African vegetation, and with the history of regional climate change. We often found strong correspondence between the stratigraphic distribution of individual fungal spore taxa and the occurrence of specific vegetation types. Changing climate conditions appear to have had a strong impact on the ability of fungi to play a role in the decomposition of dead plants. For fungal spore assemblages, the most prominent change in regional palaeoenvironments over the past 25,000 years occurred at the start of the wet early Holocene, following Younger Dryas drought. *Epicoccum purpurascens* is common in the Glacial and Late-Glacial parts of the sequence, but shows a strong decline during the early Holocene. *Coniochaeta* cf. *ligniaria* occurs throughout the record but shows dramatic fluctuations that appear to relate to major changes in humidity. Correlation between fungal abundance and humidity is also observed in taxa for which the Challa region provided suitable habitat from ca. 16,500 cal.yr BP (e.g., *Curvularia*) or from the Late-Glacial to Holocene transition (e.g., *Tetraploa aristata*, *Dictyoarthrinium* cf. *sacchari*, cf. *Byssothecium*, types HdV-1032 and HdV-1033, cf. *Alternaria*, cf. *Brachysporium*, cf. *Helminthosporium*, *Spegazzinia tessartha* and cf. *Lasiodiplodia theobromae*). Many of these taxa did not occur, or were rare, during both wet and dry phases of the Glacial period, suggesting an additional temperature effect on their occurrence in tropical African environments. A possibly dominant role of temperature is revealed in the stratigraphic distribution of *Acrodictys*, which appears at the onset of deglacial climate warming ca. 17,500 cal.yr BP and remains common throughout both wet and dry phases of the Holocene. Spores of the dung-inhabiting fungus *Sporormiella* occur throughout the 25,000-year record without notable fluctuations, suggesting little changes in the overall population density of large herbivores in the region.

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1. Introduction

The palaeoecological potential of fungal remains is not yet fully explored. Many palynologists do not present or discuss the remains of fungi and other non-pollen palynomorphs (NPPs) that are

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commonly found in pollen preparations. However, palaeomycological information can be very useful, especially in studies of peat, lake and soil deposits (van Geel, 1978, 1986, 2001; van Geel et al., 1981, 1989; Gill et al., 2009; Feeser and O'Connell, 2010; Kramer et al., 2010; Montoya et al., 2010; Mudie et al., 2010) and in archaeological contexts (van Geel et al., 2003; Zong et al., 2007; Cugny et al., 2010; Gauthier et al., 2010; McAndrews and Turton, 2010). Agricultural societies and domesticated animals have created a range of new habitats for fungi. Consequently the mycoflora of settlement sites and the surrounding cropland, pastures and hay meadows reflects these land-use and land-cover changes with different fungal assemblages relative to the original, undisturbed natural ecosystems. Up to now, the large majority of fungal and other NPP 'Types' have been recorded in European peat and lake deposits (for an overview of the palaeo-mycological literature see van Geel and Aptroot, 2006). In general the remains of fossil fungi in Quaternary deposits are almost exclusively ascospores, conidia and chlamydoconidia produced by Ascomycetes (including their anamorphs). Most of them are thick-walled and highly melanized (dark-pigmented). Many thin-walled spores, which disperse better and commonly occur in samples of atmospheric dust, either do not preserve in lake and peat sediments or are not recognizable after the chemical treatment used to prepare pollen samples for microscopic analysis.

The use of fossil fungal spores to enhance palaeoenvironmental studies has been particularly limited in equatorial Africa, where an initial attempt to analyse fungal spores in lake sediments was conducted by Wolf (1966, 1967). Jarzen and Elsik (1986) studied fungal palynomorphs from recently deposited river sediments in Zambia. They described, illustrated and classified fungal palynomorphs with form-generic names according to the system proposed by Elsik (1976), and could refer some of the fungal palynomorphs to extant taxa. The only actuo-mycological studies in Kenya were conducted by Caretta et al. (1998, 1999). One recent application of fungal spore palaeoecology has been carried out at the Munsa archaeological site in Uganda (Lejju et al., 2006). Spores of *Kretzschmaria* (syn. *Ustilina*), a mild parasite causing soft-rot of wood on several tree species (van Geel and Andersen, 1988) indicated that the mid-Holocene landscape at Munsa was relatively forested. Presence of ascospores of the obligatory dung fungus *Sporormiella*, together with the less stenotopic dung fungi *Cercophora* and *Sordaria* type suggested that large herbivores inhabited the Munsa area at that time (Lejju et al., 2005). Given the age of the sediments and the absence of archaeological evidence for pastoralism in western Uganda prior to ca. 3000 BP, this dung was probably produced by wild herbivores such as elephants. Fungal spores from later periods at Munsa were attributed to domesticated livestock (Lejju et al., 2005).

To stimulate more widespread application of NPP palaeoecology in tropical African contexts, we studied fungal spores and selected other NPPs in the 25,000-year sediment record of Lake Challa in southeastern Kenya. Our primary objectives are to 1) assess the overall taxonomic diversity of East African NPPs, and 2) to use the stratigraphic turnover of fungal taxa during the major climate and environmental changes marking the Glacial-to-Holocene transition as a guide to their potential as ecological indicators. We compare the NPP record with selected pollen curves of common African trees and herbs, and with independent proxies of regional climate (temperature and rainfall) history to study relationships that might elucidate habitat requirements of individual NPP taxa. This paper does not concern the ecosystem shifts and climatic interpretation of the pollen record itself, as this will be presented in a separate publication. Instead we focus on documenting and describing the main types of fungal spores and some other NPPs, and on evaluating the potential of fossil NPP assemblages to contribute to multi-proxy reconstructions of past environmental change in tropical Africa.

2. Material and methods

2.1. Study site and material

Lake Challa (3° 19' S, 37° 42' E) is a 4.2 km², ca. 94 m deep crater lake, filling a steep-sided volcanic caldera at 840 m elevation immediately southeast of Mt. Kilimanjaro (Fig. 1). In this equatorial location, twice-yearly passage of the Intertropical Convergence Zone over the adjacent western Indian Ocean creates a bimodal rainfall pattern, with southeasterly monsoon winds bringing 'long rains' from March to mid-May and northeasterly monsoon winds bringing 'short rains' from late October through December. The local climate is tropical semi-arid, with monthly mean daytime temperatures ranging from 26 °C in July–August to 30 °C in February–March. Total annual rainfall is ca. 565 mm year⁻¹ and surface evaporation ca. 1735 mm year⁻¹, resulting in a negative water balance for Lake Challa (Payne, 1990). The lake is maintained by shallow groundwater originating from rainfall falling higher up the slope of Mt. Kilimanjaro. Rainfall in East Africa is spatially modified by the dissected topography of the plateau, and inter-annually by cyclic fluctuations in sea surface temperature linked to the Indian Ocean Dipole and the El Niño Southern Oscillation (Marchant et al., 2006).

Today Lake Challa is surrounded by a landscape of mostly open bush and grass savanna with scattered woodland trees and shrubs, and strips of moist riverine forest in (seasonally dry) stream gullies (White, 1983); the northern and western outer slopes of the Challa caldera are covered with dry colline savanna forest of *Acalypha fruticosa* and *Acacia* species (Hemp, 2006; Fig. 1c). The inner caldera slopes are covered by a narrow strip of evergreen riverine forest on rock-fall along the shoreline, a dry 'succulent' forest with *Commiphora baluensis*, *Haplocoelum foliolosum* and *Euphorbia bussei* on steep middle slopes, and open grassland with scattered trees and shrubs on gentle higher slopes below the rim.

In 2005 three parallel piston cores of 20–22 m length were recovered from a mid-lake location (3° 19.05' S, 37° 41.88' E). Following cross-correlation of overlapping core sections these together form a 21.65-m long composite sequence of mostly finely laminated organic muds. Excision of five turbidite horizons yielded a single 20.82-m long sequence of continuous deepwater sedimentation (Verschuren et al., 2009). Lake Challa's spatially uniform sedimentation and relatively stable physical limnology over the past 25,000 years (Moernaut et al., 2010) accumulated a climate archive with high temporal resolution and virtually unprecedented radiometric (²¹⁰Pb, ¹⁴C) age control (see the supplementary online information of Verschuren et al., 2009). Age indications in the present paper are given in calendar years BP (Before Present), with Present being 1950 AD.

2.2. Laboratory procedures

Sediment samples of 1 ml volume extracted for microfossil analysis were boiled in 10% Na-pyrophosphate, dehydrated with 96% acetic acid and treated with an acetolysis mixture of one part H₂SO₄ to nine parts acetic anhydride. The samples were heated in this mixture to 100 °C for ca. 10 min in a water bath. Sample tubes were then cooled, centrifuged and washed with distilled water, and centrifuged again in 96% ethanol. The separation of organic material from sand and clay was accomplished in a heavy liquid (bromoform-ethanol mixture, specific gravity 2). The samples were finally washed in 96% alcohol, centrifuged, put in glycerine and stored overnight in an oven at 40 °C before being mounted on microscope slides for identification and counting. Following the methodology initiated by van Geel (1972, 1978), 'Type' numbers were assigned to each type of non-pollen microfossil with characteristic morphology. Their coded designation of origin HdV stands for Hugo de Vries-Laboratory, University of Amsterdam. Using mycological literature, in many cases

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