CHAPTER 21

Modern pollen studies from tropical Africa and their use in palaeoecology

Adele C.M. Julier, Saúl Manzano, Estelle Razanatsoa & Andriantsilavo H.I. Razafimanantsoa

Plant Conservation Unit, University of Cape Town, Cape Town, South Africa

Esther Githumbi[1]

Department of Physical Geography and Ecosystem Science, Lund University, Lund, Sweden

Donna Hawthorne

School of Geography and Sustainable Development, Irvine Building, University of St Andrews, United Kingdom

Glory Oden

Department of Plant and Ecological Studies, University of Calabar, Calabar Nigeria

Lisa Schüler

Department of Palynology and Climate Dynamics, Albrecht-von-Haller Institute for Plant Sciences, Göttingen University, Göttingen, Germany

Monique Tossou

Department of Plant Biology, University of Abomey-Calavi, Benin

Jane Bunting

Department of Geography, Geology and Environment, Faculty of Science and Engineering, University of Hull, United Kingdom

ABSTRACT: Modern pollen studies are valuable for the calibration of pollen records and contribute to the understanding of past vegetation dynamics. Here, we present a qualitative review of available published and (where possible) unpublished modern pollen studies conducted in tropical Africa since pollen analysis emerged as a discipline in the early 20th century. At present,

[1]Other affiliation: *Department of Biology and Environmental Science, Linnaeus University, Kalmar, Sweden*

DOI 10.1201/9781003162766-21

modern pollen rain studies are geographically unevenly distributed across the continent. We found that most countries across tropical Africa have some modern pollen records, with East African countries being particularly well represented in both older and more recent literature. Many countries, arid regions and transitional phytochoria, however, require further study. This review is intended to guide palaeoecologists and palynologists embarking on new studies by bringing together the history of modern pollen studies conducted to date. Targeting new studies to areas where data are currently lacking will help to build a better understanding of modern pollen deposition on the continent. Moreover, we provide recommendations for designing studies so that their results can be used in quantitative modelling techniques for climate or vegetation reconstructions.

21.1 INTRODUCTION

Palaeoecological studies on sedimentary deposits use proxies such as pollen, charcoal, fungal spores and diatoms to reconstruct changes in past environments. These proxies can reveal crucial information about ecosystem responses to climate change, fire occurrence, herbivore activity, and impacts of humans on landscapes on centennial to millennial time scales (Gillson 2015). As such, palaeoecological data are hugely important in understanding the past dynamics of ecosystems and are increasingly being used to inform management decisions and restoration targets (Manzano *et al.* 2020). In order to interpret and validate records from the past, however, these proxies need to be calibrated.

Calibration most commonly takes the form of studies of modern systems; for instance, pollen from surface lake mud samples can be compared to the vegetational composition of the area around those lakes (Sugita 2007a, 2007b). These comparisons allow palaeoecologists to determine which plants produce lots of pollen grains relative to their vegetational abundance and which produce very little. Modern pollen datasets are increasingly being used to calibrate models of pollen dispersal and deposition, allowing for more quantitatively rigorous reconstructions of past vegetation to be developed (Fang *et al.* 2019).

In temperate regions, there has been an abundance of studies conducted on modern pollen rain (Davis *et al.* 2013), and these results have been used to calibrate models of pollen dispersal and deposition (Bunting and Middleton 2005; Jackson and Lyford 1999; Theuerkauf *et al.* 2016). These models have allowed increasing accuracy and precision of vegetation reconstructions, but often rely on extensive datasets, which are relatively rare in the tropics (Bonnefille *et al.* 2004; Gajewski *et al.* 2002; Vincens *et al.* 2006). Gajewski *et al.* is a particularly important work as it used 1170 modern pollen samples available at the time of publication to reconstruct climate across all major phytochoria and climatic zones (albeit with patchy coverage) in Africa. This demonstrates the importance and potential utility of modern pollen work in Africa, and highlights the need to target under-studied geographical regions and vegetation types.

Here, we present qualitative accounts of modern pollen work (published and unpublished, where available) conducted to date in tropical Africa with the aim of summarising key details from the studies, and highlighting those geographical regions and vegetation types that require further targeted work. This review will provide a useful starting point for researchers looking to ground their palaeoecological work in modern data, and will also highlight potential ways forward to improve our interpretations of African palaeoecological data.

21.2 METHODS AND TERMINOLOGY

The geographical extent of this study is the tropics of Africa, the region between 23.5° N and 23.5° S (Figure 1). This is due to the global importance of the tropical regions in terms of

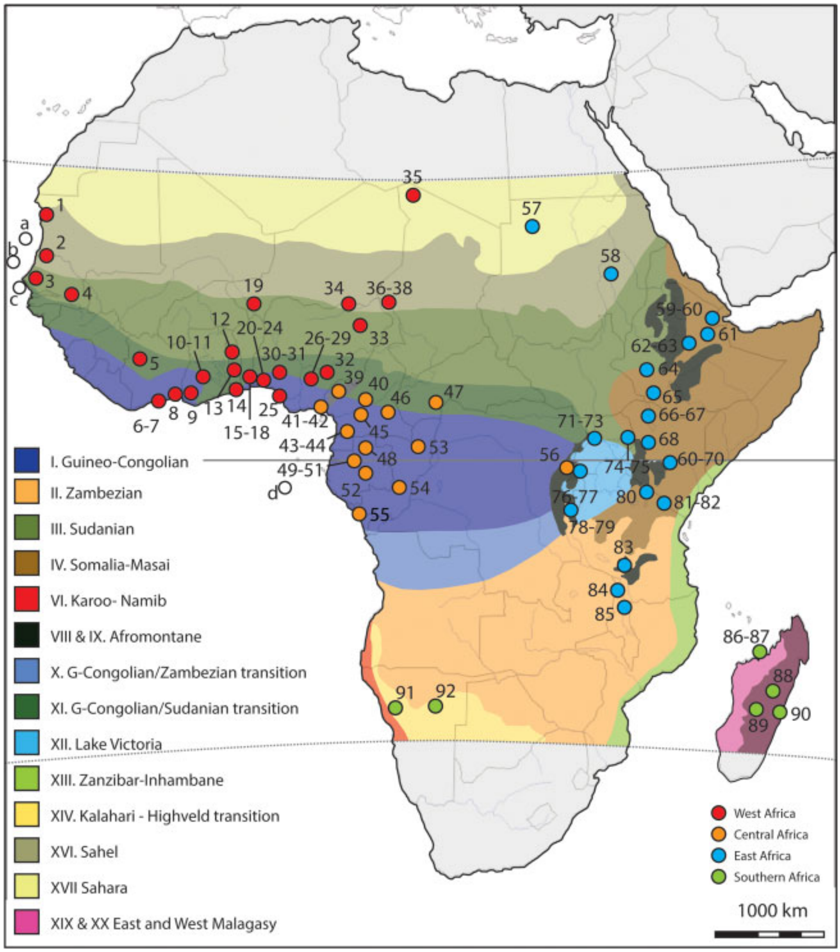

Figure 1. Map showing locations of modern pollen studies and phytochoria (White 1983). Numbers refer to studies in Table 2.

biodiversity and conservation status. Pollen studies were located by searching for country specific papers in, for example, Google Scholar, Microsoft Academic, ResearchGate and Web of Science, using terms such as '[country name] modern pollen' '[country] aeropalynology' and equivalent terms in French. References to unpublished theses were found in existing literature; Table 2 shows whether they are publicly available. Existing modern pollen rain studies from each country are summarised using vegetation type descriptions as they are reported in publications so that the studies retain their local relevance. We then use phytochoria as established by White (1983) (eg. Guineo-Congolian Regional Centre of Endemism) to group studies. We chose this approach to retain the diversity of vegetation classifications used in the studies, whilst also capturing continent-scale patterns.

For each of the reviewed papers, we identified (where possible) the methods used to collect the modern pollen data. Melissopalynological studies are excluded from this review as they are of limited relevance to palaeoecological studies. Sampling techniques vary in how closely they resemble the sediment records, the length of time over which they collect pollen, and which types of pollen they are biased towards collecting. There are a variety of methods used to collect modern pollen data in the tropics (see Jantz *et al.* 2013). For details of the specific methods, refer to the individual studies listed in Table 2. General terms used in this paper are defined as follows:

(i) Surface samples: A general term referring to samples from the uppermost sediment layer, typically soil, peat, lake or marine sediment.
(ii) Soil samples: Samples taken from an area from the top layer of soil (including leaf litter and humus), not from within a water body.
(iii) Core top samples: samples from the top of a sediment core that are assumed to be modern.
(iv) Pollen Traps: Artificial pollen traps come in a variety of formats (Bush, 1992; Gosling *et al.*, 2003; Tauber, 1967) and capture pollen over set periods of time.
(v) Moss/Lichen polsters: Samples of moss and/or lichen are harvested from the ground or trees.
(vi) Glycerol/Silicon oil slides: These are used to sample pollen over a very short period of time by catching grains directly onto a slide
(vii) Filters: Air filters can be used to trap pollen grains; mainly used in offshore sampling.

21.3 WEST AFRICA

West Africa has been the site of a large number of studies (Figure 1). Multiple studies have been carried out in Senegal, Côte d'Ivoire and Togo, (Edorh 1986; Lézine 1988; Ybert 1980), with studies covering the main vegetation types of that region. Nigeria has a large number of pollen rain studies, with many conducted for aeropalynological purposes. Several countries do not appear to have any published (or unpublished but cited elsewhere) modern pollen records, namely; Guinea, Guinea-Bissau, Sierra Leone, Liberia, Gambia, Mali, and Burkina Faso.

An extensive summary of modern pollen data for west Africa was compiled by Lézine *et al.* (2009), who compared modern pollen spectra to climate and vegetation. This work found that biomes are generally well represented by their pollen spectra, which capture the main components of the vegetation and can be used to reconstruct climatic parameters. The exceptions to this were tropical forest biomes, likely due to their high levels of entomophily, and human-impacted dry forest at the Sudanian-Sahelian ecotone.

Off-shore pollen studies have been conducted to complement work on marine cores in the Gulf of Guinea (Calleja *et al.* 1993; Caratini and Cour 1980; Dupont and Agwu 1991; Hooghiemstra *et al.* 1988; Melia 1984; Romero *et al.* 2003). Marine studies off West Africa are synthesised in Hooghiemstra *et al.* (2006) and in this review we focus on continental records.

21.3.1 Mauritania

Only five modern pollen samples have been recorded from Mauritania, (Lézine and Hooghiemstra 1990). These samples are soil samples and record high levels of Amaranthaceae and Brassicaceae pollen, reflecting the Saharan environment. Due to the dry environment, these samples likely represent a maximum of one year of pollen deposition, despite being collected from near to water sources.

21.3.2 Senegal

Modern pollen from soil and mud samples from Senegal was first studied by Lézine (1987) with the majority of samples published in later manuscripts (Lézine 1988; Lézine and Edorh 1991; Lézine and Hooghiemstra 1990). Samples were collected from Sudanian forests and demonstrated that pollen and vegetation from this zone are relatively well correlated (see also Togo). A strong

Sahelian influence was observed in the northernmost samples, typified by taxa such as *Acacia* and *Balanites*. In southern samples, Combretaceae represents the Sudanian vegetation type. Lake surface samples from Lake Guiers (Lézine 1988), demonstrated that the pollen record from the lake, which is located in the Sahelian zone but has a drainage basin extending across vegetation types, is dominated by relatively local taxa such as Poaceae, with a strong Sahelian element (7%) and less of a Sudanian element (2%).

21.3.3 Côte d'Ivoire

Work has been conducted terrestrially and in mangrove swamps in Côte d'Ivoire. Ybert (1975) covered the savannah-forest boundary using monthly sampled pollen traps across transects of forest to savannah. These revealed high levels of temporal variability in pollen rain, but showed that Poaceae dominated in the savannah sections (at percentages of >40%), along with Ulmaceae-Moraceae type and *Lippia multiflora* Moldenke. *Alchornea* was reported as being abundant across the transects. Fredoux (1978) presented modern samples from Mangrove swamps which showed low levels of *Rhizophora* and other species typical of Mangrove swamps, instead being dominated by dry land pollen types (Lézine 1997).

21.3.4 Ghana

Three modern pollen studies are currently known from Ghana. Maley (1983) included some modern surface samples in a preliminary study of Lake Bosumtwi (a site which went on to yield a *c*. 500,000 year record (Miller and Gosling 2014)). These surface samples were taken from small ponds and lakes in the semi-deciduous forest region of the country and showed high levels of *Musanga*, *Celtis* and *Triplochiton scleroxylon* pollen and low levels of Poaceae. These findings correlated with those of Julier *et al.* (2019) which showed consistently high levels of *Celtis* and *Triplochiton* in pollen trap samples from transects across 100 m by 100 m square vegetation monitoring plots, with traps placed every 20 m along the transect, near to Kumasi, also in the semi-deciduous vegetation type. Traps from a wet evergreen forest plot showed that variability in modern pollen rain was high. Unlike traps from the semi-deciduous plot, however, the wet evergreen traps demonstrated high spatial variability, with traps 20 m apart producing drastically different pollen spectra.

Trap data from the savannah-forest boundary in Ghana (Julier *et al.* 2017) showed that Poaceae abundances of >40% could be considered indicative of a savannah landscape. These two studies (Julier 2017; Julier 2019) were intended to inform palaeoecological interpretations, specifically of Lake Bosumtwi. The data gathered cover a range of vegetation types but lack temporal resolution, with the maximum number of sampled years being three for the forested ecosystems and one for the savannah transitional mosaic.

21.3.5 Togo

The first, and most extensive, study of modern pollen conducted in Togo was by Edorh (1986) who collected 125 soil and river surface samples from a range of vegetation types across Togo, encompassing forest and savannah. It was found that pollen broadly reflected vegetation, but at a local scale. Some of these samples were later published in Lézine and Edorh (1991), who demonstrate that some Sudanian vegetation types such as Combretaceae woodlands and *Isoberlina* woodlands are distinguishable on the basis of their pollen spectra. Anemophilous non-arboreal taxa frequently dominated the signal, and that samples may be biased towards local representation, meaning that a high spatial density of samples is necessary to reflect regional vegetation composition. The pollen spectra were also correlated successfully with rainfall, highlighting the difference between the Guinea-Congolian and Sudanian vegetation zones (Chalié *et al.* 1990).

A study of modern pollen from Mangroves in Togo (Edorh and Afidegnon 2008) demonstrated that the modern pollen spectra, on the whole, represented their parent vegetation types well and were able to distinguish between *Avicennia* and *Rhizophora* mangrove environments.

21.3.6 Bénin

The first known pollen rain study in Bénin is Tossou *et al.* (2012) which focuses on southern Bénin. Surface sediments were taken from the main plant formations: semi-deciduous dense humid forest, floodplain forest, mangrove, swampy forest, swampy meadow and plantation with *Acacia auriculiformis*. Pollen analysis of 38 soil samples identified a total of 126 pollen taxa from 65 families. The most abundant pollen taxa broadly reflect the different plant formations recorded, therefore suggesting that they could be used to reconstruct changes in landcover from palaeo-ecological data in Southern Bénin. A further study (Zanou *et al.* (2020)) focused on the modern pollen rain in the Lama classified forest (south Bénin) from surface sediments. This study allowed a comparison between the pollen content of the sediments and the botanical diversity of the formation. Pollen analysis of 50 sediment samples identified a total of 62 pollen taxa belonging to 31 families and 44 genera. The dominant taxa are Poaceae, *Cassia*, and Combretaceae. The index of similarity between the species inventoried and those contained in the sediments is greater than 50%. Aeropalynological work using traps has also been conducted in Bénin (Tchabi *et al.* 2017; Tossou *et al.* 2016), finding higher pollen content in the air with higher winds and temperature, but lower pollen content with high rainfall, and the most abundant pollen counts in the dry season (November to March).

21.3.7 Niger

The only known study from Niger is an aeropalynological study from Caratini and Frédoux (1988), which presents 27 pollen trap samples with pollen data presented as monthly values from a savannah area in Niamey, south Niger. Around 60% of the annual pollen rain was Poaceae, which peaked in August and September, the rainy season. Cyperaceae pollen was found to peak in October to December and Chenopodiaceae pollen peaked at 5% in December through January, the dry season.

21.3.8 Nigeria

In Nigeria, a large number of aeropalynological studies have been conducted (Abdulrahaman *et al.* 2015; Adekanmbi and Ogundipe 2010; Adeniyi *et al.* 2018; Adeonipekun *et al.* 2016; Agwu 2001 1986; Agwu and Osibe 1992; Alebiousu *et al.* 2018 2018; Ezikanyi *et al.* 2016; Ibigbami and Adeonipekun 2020; Njokuocha 2006). These studies all use some form of pollen trap (modified Tauber traps or 'Gbenga 2' aerofloral samplers) and are primarily for the study of allergenic particles in the atmosphere. They typically record results monthly, with time periods recorded varying from a few months (Abdulrahaman *et al.* 2015) to more than a year (Adeniyi *et al.* 2018). The studies generally found high pollen abundances in the wet season (aside from (Adeniyi *et al.* 2018) who found lower abundances of pollen in the wet season) and high abundances of Poaceae, regardless of their location and year of sampling. In some instances, forest elements such as *Celtis*, *Milicia*, and *Berlinia* are found, indicating long distance transport from forested areas (Ezikanyi *et al.* 2016; Njokuocha 2006). The studies are almost exclusively located in urban areas and are therefore of limited use for palaeoecological reconstructions. Modern pollen work on soil and trap samples from the north of Nigeria showed extremely high levels of Poaceae and Cyperaceae (>95%), but also that modern pollen assemblages primarily reflect their local vegetation, not long-distance transport (Salzmann 2000; Salzmann and Waller 1998).

21.3.9 Chad (including Lake Chad)

The first modern pollen study conducted in Chad was by Maley (1972) who took surface samples from Lake Chad and nearby areas. These results were reproduced as part of Maley's account of the palaeoecology of Lake Chad (Maley 1981). These samples demonstrated the importance of rivers in the long distance transport of pollen, but that the surface samples did capture vegetation changes from the area around the lake. Schulz (1976) also reported modern samples from Chad and compared these with 8000–9000 yr BP samples. The study showed relatively high levels of Poaceae pollen in both modern and fossil samples, but higher levels of montane pollen in the fossil samples. Ybert (1980) used pollen filters to capture pollen rain from November 1971 through December 1972. It was shown that Poaceae is the most abundant taxon, and peaks in September. Amaral *et al.* (2013) used modern sample data from Maley (1972) and other, previously unpublished work to perform biomisation, thereby assigning estimates of mean annual precipitation to time periods covered by a core from Lake Chad covering the period from 6700–500 yr BP.

21.4 CENTRAL AFRICA

In Central Africa, Cameroon, Gabon and the Republic of Congo contain the largest number of studies focusing on modern pollen-vegetation relationships (Elenga 1992; Elenga *et al.* 2000; Henga-Botsikabobe *et al.* 2020; Jolly *et al.* 1996; Lebamba *et al.* 2009; Reynaud-Farrera 1995; Tovar *et al.* 2019; Vincens *et al.* 2000). Other countries in the region lack records; the Central African Republic yields just one study (Aleman *et al.* 2012), the Democratic Republic of Congo has a single study spanning the Uganda-Congo border (Beuning and Russell 2004), and Equatorial Guinea has one study of marine surface pollen records, offshore in the Gulf of Guinea (Dupont and Agwu 1991).

21.4.1 Cameroon

Modern pollen studies in Cameroon are currently concentrated in the south and south-east of the country, and focus on pollen-vegetation relationships. Vincens *et al.* (2000) examine the pollen in soil and litter samples from 26 contiguous plots along a forest-savannah transect. They conclude that the two main ecosystems, forest and savannah, are clearly represented in the surface samples at the local scale, with few pollen grains found outside their producing communities. The density of the forest canopy largely inhibits regionally wind-dispersed pollen from entering the forest and in the savannah these values are typically <1% (Vincens *et al.* 2000).

A similar study by Lebamba *et al.* (2009) examines 24 surface samples from the southern Cameroon lowlands, in forest and savannah environments. They demonstrate that major vegetation types can be differentiated using modern pollen percentages, and a distinction made between secondary and mature forests and well drained and hygrophilous forest types, therefore the pollen analysis is a robust way of discriminating between the maturity, structure and composition of Central African forests. This is reinforced by a study of 50 surface samples from the forests and savannahs of southern Cameroon which defined distinct plant communities (Reynaud-Farrera (1995)). Verlhac *et al.* (2018) studied modern soil samples from across an elevational gradient in the Cameroon highlands and found that modern pollen assemblages reconstruct the upper and lower limits of the Afromontane forests well.

Vincens *et al.* (2000) note that there are individual taxa which can be misrepresented in the pollen spectra, including markers of the main community types (e.g. *Albizia* and *Rinorea*). The differences between the observed vegetation and the pollen analysed in surface samples is often a function of the production and dispersal of individual taxa. However, botanical survey methods, such as only recording trees of more than 10 cm in diameter at breast height (DBH) will also influence the record.

A number of modern pollen studies from Cameroon examine the transportation and dispersal of pollen throughout the Sanaga River Basin (Bengo 1996, 1992; Bengo *et al.* 2020) and off-shore in marine surface sediments on the continental shelf (Van Campo and Bengo 2004). Thirty-eight surface samples from the banks of the Sanaga River and twelve of its main tributaries were collected to characterize the origin of the pollen and its mode of transport to the continental shelf. Bengo *et al.* (2020) demonstrate that pollen analysed in the riverbank sediment clearly reflects the surrounding vegetation cover, and transport to the coast of the Gulf of Guinea is essentially through the drainage of large basins. Examining seventy-one modern samples from the continental shelf off the coast of Cameroon (Van Campo and Bengo 2004), they found a dominance of the mangrove pollen type *Rhizophora,* which is located along the shoreline, a high pollen producer and effectively transported by water. They also note the dominance of Poaceae and *Alchornea,* which likely arrive on the shelf by riverine transport from the grasslands of northern Cameroon and riverbanks and forest edges throughout the Sanaga Basin, respectively. Analysing modern surface samples along river basins therefore greatly supports the interpretation of source area of pollen captured in marine and off-shore sediments.

21.4.2 Central African Republic

There is a paucity of modern pollen studies in the Central African Republic. A single study by Aleman *et al.* (2012) investigates modern pollen (identified as arboreal and non-arboreal), phytoliths and stable carbon isotopes in 17 soil samples from a forest-savannah environment. Combining these results with field Leaf Area Index (LAI) measurements, they calibrate a multi-proxy model to reconstruct LAI in palaeo-sequences, providing a long-term estimate of tree cover. This approach provides a useful method for assessing past changes in vegetation cover, and transitions from forest to savannah and *vice versa*.

21.4.3 Equatorial Guinea

There is a lack of records from terrestrial Equatorial Guinea, however, one study exists which examines the distribution of pollen grains within the Gulf of Guinea and the influence of wind and water on pollen transport (Dupont and Agwu 1991), this study is reviewed in Hooghiemstra *et al.* (2006)

21.4.4 Gabon

Gabon has a number of studies incorporating modern pollen samples. An early study by Jolly *et al.* (1996) examined 16 surface soil samples from the rainforest of north-eastern Gabon to test pollen-vegetation relationships along a number of transects. They establish pollen markers for a number forest types, and explore the pollen production of individual taxa (e.g. *Alchornea* and *Macaranga*) which showed the largest pollen abundance. Ngomanda (2005) carried out research in the forests of Gabon, focusing on the past 5000 years, as part of a doctoral dissertation. Later publishing, with others, palynological data from two lake cores, the tops of which represent the modern pollen signal (Ngomanda *et al.* 2007).

Lebamba *et al.* (2009) analysed 57 surface soil and litter samples from the forests of north-eastern and south western Gabon. They demonstrated that major vegetation types can be differentiated by their modern pollen percentages, and distinctions made between different forest types (e.g. secondary and mature forests).

More recently in Gabon, Henga-Botsikabobe (2015) completed a doctoral dissertation examining surface samples and palaeo-cores from Lope National Park, to reconstruct the past forest composition and analyse its response to changing environmental conditions. Henga-Botsikabobe *et al.* (2020) then later published detailed results from 23 tropical marshes within the Lope National Park examining modern pollen-vegetation relationships. Surface samples were collected from 50 random points across each marsh environment and homogenised to obtain one representative sample per marsh. They found that the modern pollen signal is highly influenced by the local marsh vegetation and a very high diversity of forest taxa are recorded, making it possible to quantify changes between adjacent mature, secondary and pioneer forests. Low proportions of Poaceae were found in the surface samples, which is thought to be influenced by their mode of deposition. This challenges common interpretations, which use these proportions as a measure of savannah *vs*. forest. This is a unique study from an alternative depositional context and provides unique insights for interpreting modern samples and core sequences from marsh environments.

21.4.5 Republic of the Congo

Modern palynological studies in the Republic of Congo are concentrated in the South and South West of the country, within the Batéké Plateau and Mayombe massif regions and along the littoral coast. Elenga *et al.* (1994) examine two cores from a swamp in the Batéké Plateaux region of the Congo, within the Guineo-Congolian region (White 1983) to illuminate palynological evidence of past vegetation change. While this study does not focus on modern pollen-vegetation relationships, it utilises insights and results from a previous doctoral study by Elenga (1992) incorporating modern pollen rain from the same region. For example, Elenga *et al.* (1994) comment on the large local pollen production of Gramineae.

Elenga *et al.* (2000) later carry out a more focused study on the pollen-vegetation relationships in the same region. Palynological data was analysed from 12 sites, each comprising 20-30 surface subsamples and compared to forest inventory data. At the local scale, the modern pollen rain largely reflected the forest taxa observed, and due to the dense canopy, only a few grains originated from extra-local sources. There were variations in the pollen production of individual species and Elenga *et al.* (2000) found that certain species, which are characteristic of these forests, are found in low percentages in the surface samples, for instance, species in the families Caesalpiniaceae, Euphorbiaceae and Annonaceae. Equally, a number of taxa may be overrepresented in the pollen spectra due to high pollen productivity (e.g. *Treculia, Syzygium* and *Dacryodes*).

Tovar *et al.* (2019) examined 12 surface samples and a core sequence from a monodominant *Gilbertiodendron dewevrei* (De Wild.) J. Léonard forest in the northern Republic of Congo. The authors found that *Gilbertiodendron* represented between 3.8% and 6% of the pollen count in the surface samples from the monodominant forest patches. The most abundant taxa in these samples were *Lophira alata*-type and *Celtis* spp. No *Gilbertiodendron* pollen was found in samples outside the monodominant patches. These studies provide important insights into the pollen production and dispersal of key Congo Basin taxa which are important for many palaeoecological interpretations in the region.

While currently, modern pollen-vegetation studies are relatively scarce across the Congo Basin, the recent discovery of a large area of peatland in the Cuvette Centrale (Dargie *et al.* 2017) has sparked new research in the region. The peatland represents an important palaeoecological archive, which may holds insights into additional pollen-vegetation relationships in this alternative depositional context.

21.4.6 Democratic Republic of the Congo

There are no modern pollen studies solely within the Democratic Republic of Congo. A single palaeoecological study exists from the Lake Edward Basin, which spans the Ugandan-Congo border (Beuning and Russell 2004). This study examines a lacustrine core to reconstruct the climatic and vegetation history of the area, with reference to a number of modern pollen assemblages collected from crater lakes within Maramagambo forest reserve, on the Ugandan side of the border. While the authors found that the modern pollen assemblages contained taxa similar to those found in the basal metres of the Lake Edward Basin core, the percentages of Poaceae varied, indicating that the basal metres of the core were more similar to the pollen spectra of the semi-deciduous forest to the east of Lake Victoria, potentially representing a comparable modern environment.

21.5 EAST AFRICA

East Africa is where some of the continent's foundational modern pollen work was conducted (Coetzee 1967; Hedberg 1954; Livingstone 1967). An early review of modern pollen work conducted in the tropics included a summary of East African montane work (Flenley 1973). Several countries, however, do not appear to have any studies of modern pollen rain; Eritrea, Somalia and South Sudan. Laseski (1983) analysed 59 surface samples from Uganda, Rwanda, Tanzania, Zambia, Kenya and Tanzania. These samples were used to derive relationships between pollen and rainfall, and are included in analyses such as Gajewski *et al.* (2002) but the original thesis was not available for this review and is therefore not covered in detail here. Vincens (2006) analysed a large number (150) of modern pollen samples across seven phytogeographical regions. These are used in biomisation with a high level of success (82.6% of sites correctly assigned). These studies by Gajewski and Vincens demonstrate the usefulness and potential of accessible, broad-geographical and climatic analytical studies on modern pollen in the tropics.

21.5.1 Sudan

Eleven soil samples were analysed by Ghazali and Moore (1998) from an initial set of 30, the majority of which did not contain pollen. These were taken from desert, semi-desert, scrub and grassland ecosystems. Poaceae was, by far, the most abundant pollen type identified in the samples. Non-arboreal pollen dominated generally, which is a true reflection of the nature of the ecosystems sampled. A higher proportion of entomophilous pollen than might usually be expected was found in some samples, including *Acacia* pollen despite no *Acacia* trees being present within a 100 m radius of the sample site. Further work by Ghazali (2002) resulted in seven more samples (including one collected in a moving vehicle) from along a transect in the Nile Valley, encompassing mainly desert ecosystems. The assemblages from these samples were mostly dominated by anemophilous taxa such as Poaceae, although only 8 out of 40 pollen taxa identified were anemophilous. It was noted by the authors that, as in their previous study, a large number of samples of those originally collected did not contain pollen. This is likely due to the highly arid climate and sometimes alkaline soils of Sudan.

21.5.2 Djibouti

Three modern samples, from river sediment, lake surface mud, and soil, from desert sites in Djibouti are presented in Bonnefille *et al.* (1980). These samples are presented for comparison with the results from a core dated to 45,000 yr BP, although only three samples possessed high concentrations of pollen, likely due to arid climate conditions. The modern samples showed higher levels of Cyperaceae and forest taxa, but lower Poaceae than those from the core.

21.5.3 Ethiopia

Ethiopia has been the site of many studies of early hominin evolution, including some pollen work from site Fejej FJ-1 establishing palaeoecological histories for archaeological finds (Mohamed Umer *et al.* 2004).

Bonnefille *et al.* (1987) studied modern pollen samples from the Awash Basin from an elevational range of 500–3000 m asl and four vegetation types; subdesert steppe, riparian, evergreen bushland and montane forest. River and soil samples were taken and used to inform interpretations of the Hadar formation, from between 2.9–3.3 million years ago. These data are used to infer climate conditions during the evolution of early hominins. Another study from Bonnefille *et al.* (1993) found that modern pollen samples separated vegetation communities from different altitudes well, although due to high levels of entomophily, the taxonomic composition was not accurately reflected.

Recently, 20 modern pollen (and phytolith) samples from springs in Awash Valley have been published (Barboni *et al.* 2019) which allowed records from fossil springs to be interpreted. These spring environments are thought to be important environments for early hominins, as constant supplies of water in otherwise fluctuating or arid landscapes, therefore playing an important role in early hominin evolution and dispersal.

A large number of modern pollen samples from Ethiopia (with fewer samples from Kenya and Burundi) were included in studies that aimed to develop transfer functions to reconstruct rainfall (Bonnefille *et al.* 1992; Roeland *et al.* 1988) and temperature in fossil records. It was found that it is possible to reconstruct modern temperatures and precipitation with a high degree of accuracy based on the large and geographically widespread datasets used in the analyses.

21.5.4 Uganda

Hedberg (1954) sampled moss and lichen, predominantly from *Carex* bogs, within the Alpine and Ericaceous belts of the Ruwenzori Mountains in Uganda. It was found that, within the Alpine belt, pollen dispersal is predominantly local. Ericaceous pollen is found to be, although relatively local in its dispersal, a potentially useful indicator taxon. For other taxa, similar conclusions were drawn for these Ugandan samples as for those from Mount Kenya.

Osmaston (1958) conducted palaeoecological work in the same region as Hedberg (1954) and Livingstone (1967) took cores from Lakes Bujuku, Kitandra and Mahoma, whose top-most sediments can be considered surface samples. These core-top samples showed low levels of Poaceae, even in alpine belts, leading Livningstone dismiss Poaceae as an indicator of cooler alpine conditions in the past.

Hamilton (1972) analysed modern samples from Kigezi (largely samples from swamps) and Ruwenzori (various environments) and Mount Elgon (within the 'Montane Forest' and 'Ericaceous and Afroalpine' Belts). These samples demonstrated that, in general, transport of pollen to higher altitudes from low altitudes is more common than in the opposite direction. Flenley later hypothesised that this was due to wind directions generally being up slope in the day and downslope at night, and that pollen is generally released in the day (Flenley 1973). Hamilton used the modern samples to develop lists of pollen types by dispersal propensity, and from these lists made suggestions on the interpretation of pollen diagrams, including the fact that aquatic taxa and taxa that likely represent long distance transport are omitted from pollen sums.

Vincens *et al.* (1997) used modern data from previous studies, as well as including original data from surface samples from their own research and previously unpublished data to investigate pollen rain across a wide environmental and elevational gradient in Uganda. Their study encompassed multiple vegetation types including savannah, forest-savannah mosaic, montane forest, the Ericaceous belt and the alpine belt. They found that modern pollen rain can successfully separate different vegetation types but that characteristic plant taxa of certain ecosystems may be completely lacking from their pollen signals.

In their paper from Mubwindi Swamp, south-west Uganda, Marchant and Taylor (2000) present data of modern pollen spectra recovered from surface samples of sediment. Pollen types encountered were grouped into five categories, according to their level of representivity when compared with abundances of the same taxa in the sampled vegetation: under representative, moderately under representative, representative, moderately over representative, and over representative. The results of this research show that most of the dryland pollen incorporated into swamp sediments is produced by local plants close to the site of deposition. Generally, abundances of arboreal taxa such as *Alchornea*, *Anthocleista*, *Croton*, *Dombeya*, *Ilex*, Myrtaceae, *Newtonia*, *Polyscias*, *Prunus*, *Rapanea* and *Zanthoxylum* in the modern pollen appear to closely reflect the occurrence of their parent taxa within the surrounding vegetation. This close relationship between the representation of the parent taxa in dryland vegetation and the pollen percentage in surface samples allows the incorporation of these taxa in the nonlocal pollen sum (Marchant *et al.* 1997).

21.5.5 Kenya

Hedberg (1954) conducted the first modern pollen analyses for Kenya, using moss and lichen samples taken from the Teleki Valley, Mount Kenya. He also sampled ice from the peak of Mount Kenya for pollen, which was found to contain many pollen grains and spores, assumed to be from the preceding years to decades. *Podocarpus* was found to be abundant in the moss samples, demonstrating long-distance transport of 6-10 km. Samples from the Bamboo forest zone were found to contain little Poaceae pollen, which was attributed to Bamboo's irregular flowering and death after flowering. *Alchemilla* was found to be locally abundant, with poor dispersal. Hedberg also determined that it was not possible to determine *Senecio* forest from its pollen spectrum alone, as similar amounts of '*Compositae: Tubiflorae*' (the Asteraceae pollen type used that included *Senecio*) were found in samples from other vegetation types. Undifferentiated *Lobelia* pollen was found but was not considered to be of any use as an indicator taxon due to the occurrence in the area of various species of *Lobelia* with different environmental preferences. Coetzee (1967) also examined modern pollen samples from Mount Kenya, and drew similar conclusions to Hedberg (1954) around the abundance of *Podocarpus*. Rucina (2000) also notes over-abundance of *Podocarpus* from modern samples from the Aberdare Mountains, south-west of Mount Kenya. Hamilton (1972) noted that the analyses of Coetzee and Herberg possessed relatively low taxonomic resolution. This issue was somewhat addressed by Livingstone (1967) who worked from a better reference collection and published results including core-top samples from Uganda (see Uganda).

Modern pollen on Mount Elgon (which experiences different weather patterns on its southern and eastern flanks, with the southern receiving higher rainfall) was studied by Hamilton and Perrott (1980) who used both soil samples and pollen traps along two elevational transects. Of these transects, one was on the wetter southern side of the mountain, and the other was on the drier, eastern side. Due to their transects being elevational, a number of different vegetation types were sampled; Montane forest, Ericaceae thicket, High altitude grassland, *Alchemilla* scrub, Rocky ground communities, Mires, and agricultural land. Their findings indicated that Montane forest produced the most pollen, and that it was represented in other areas both up and downslope of its extent. Poaceae pollen abundances were found to reflect the local abundance of grasses in the vegetation. Many pollen taxa, including *Schefflera* and Amaranthaceae, were found to disperse very poorly and do not travel far from their parent plants, whereas some, such as *Acalypha*, Urticaceae, *Juniperus*-type and *Podocarpus*-type, demonstrated long-distance transport. Sediment samples taken nearly a decade apart (1967 and 1976) showed very similar pollen assemblages, leading the authors to conclude that surface samples represent longer-term modern pollen deposition well. Vincens (1984) investigated modern pollen from Lake Turkana and concluded that only 7% of pollen in the lake was aerially deposited.

A biome reconstruction using modern pollen data from East Africa used 40 sites from Northern Kenya (Vincens *et al.* 2006), the modern pollen rain was assigned into plant functional types then biomes. The study indicated that modern pollen rain correctly predicted modern vegetation types except in transition zones where the drier/more open vegetation type was predicted. This Vincens (2006) study includes the results and data from previous unpublished studies by the same author. A study running between 2014 and 2015 set up pollen traps in the Mau forest (around Nyabuiyabuyi swamp) and the Amboseli Park at Kimana, Ormakau and Isinet swamps. 30 pollen traps at each site (total 120) were left at each site for a period of 1 year (Githumbi 2017). During the recovery of the traps a year later only at Nyabuiyabuyi were 21 of the 30 traps recovered, at the other sites the recovery rate was less than 20%. The major cause of trap disappearance/selection was wildlife. Due to this, new initiatives in Amboseli are in progress where new traps are to be located in areas that can be continually monitored to ensure survival of the traps.

21.5.6 Burundi

Bonnefille and Riollet (1988) conducted a study of modern pollen as part of work on a core from Kashiru Swamp, in the Burundi highlands. They collected soil samples from a range of different altitudes in the Teza forest, between 2100 and 2500 m asl. These samples were taken across the montane forest-Ericaceous moorland transition, and reflected this vegetational change. Ericaceous pollen did not disperse far from its vegetation zone, and as altitude increased, a sharp decrease in arboreal pollen was observed. *Macaranga* pollen accounts for around 40% of the pollen from the montane forest samples, and the authors interpret this as a sign that these forests may have been previously disturbed. They also note that the trees that are characteristic of the forest (*Entandrophragma, Prunus, Chrysophyllum and Neoboutonia*) are extremely rare in the modern pollen spectra.

21.5.7 Tanzania

Modern pollen work in Tanzania was conducted by Vincens (1987) on Lake Natron. It was established that modern pollen assemblages recovered from the lake were relatively uniform across the lake except from where rivers emptied into the lake. Pollen assemblages from the lake surface samples captured the important vegetation types in the catchment basin, but not in a representative manner.

From a modern pollen-rain study along the elevational gradient on Kilimanjaro Schüler *et al.* (2014) show that it is crucial to establish a modern pollen-rain-vegetation relationship for the calibration and interpretation of a fossil pollen record from mountain sites across a gradient of alpine vegetation types including savannah, lower montane, middle montane and upper montane forest types. On Kilimanjaro, the authors analysed modern pollen-rain on plant family level to derive the elevational forest zone (lower, mid, and upper forest zone as per Hemp (2006)) of the surrounding vegetation. Climatic conditions of the study sites were further assessed and put into relation with pollen-rain and forest vegetation (Schüler 2013) which is important for the interpretation of palaeo-records. However, it was shown that the occurrence of plant families along the altitudinal gradient are differently represented in the modern pollen depending on their various reproduction factors. This can further be quantified as a transfer factor as introduced for montane forest taxa in south west Uganda by Marchant and Taylor (2000). The diversity trend captured in the modern pollen-rain on the elevational gradient on Mt Kilimanjaro reflects the plant diversity in the vegetation. However, Schüler *et al.* (2014) observed differences in the taxa richness as the pollen and fern spore dispersal seems to be strongly influenced by the regional wind patterns.

Ivory and Russell (2016) collected modern pollen samples from Lake Tanganyika, which showed consistently high levels of Poaceae pollen (>60% in all samples) and low levels (<6%) of forest taxa even when intact forest was present on the shoreline very close to the sampling site. They conclude that modern pollen assemblages in Lake Tanganyika do reflect, to some extent, the shoreline vegetation, and that depth is not a significant factor in the assemblage composition.

21.5.8 Malawi

Modern pollen samples in Malawi were collected by Meadows (1984), who used a combination of pollen traps and soil samples on the Nyika Plateau. Pollen traps placed at ground level and one metre height were compared and found to produce extremely similar assemblages. The author found that pollen trap and surface samples produced very similar pollen spectra, even with the amount of re-worked pollen being similar. Re-worked, in this instance, implied re-floated into the atmosphere. The three vegetation types investigated in the study, Dambo (shallow wetlands), Grassland and Forest were able to be distinguished by their pollen spectra. Some pollen taxa were found to be 'well-dispersed', including Ericaceae (in contrast to other studies from East Africa eg. (Hamilton 1972)), Poaceae and Cyperaceae. Further samples were collected and analysed from surface samples of Lake Malawi itself by DeBusk (1995, 1997), who found that high levels of mixing, and different inputs (e.g. wind versus riverine) led to a very coarse signal within the lake, from which it was not possible to distinguish distinct pollen assemblages corresponding to vegetation types on the shores.

21.6 SOUTHERN AFRICA

Within the tropics of Southern Africa, a relatively large number of studies have been carried out in some countries, including in Madagascar and South Africa. Angola, Botswana, Mozambique and Zimbabwe lack any modern pollen studies in their tropical regions.

21.6.1 Madagascar

Modern pollen samples from Madagascar mostly covered the sub-humid forest grassland mosaic of Central Highlands with little to no representation of the dry deciduous forest, savannah woodland, and the spiny thickets in the south western region. Early surface sample analysis for palaeoecological purposes was conducted by Burney (1988) based on 13 perennial lakes and bogs in the sub-humid forest grassland mosaic of Central Highlands. These wetlands were sampled directly, by pushing a vial into the surface of the bog using various devices, depending on the water depth and type of sediment (Burney 1988). Based on the rate between arboreal pollen (AP) and non-arboreal pollen (NAP) distinction of taxa associated with grasslands (with grass pollen ≥55%), forest/grassland mosaic (grass pollen between 22–38%), and montane shrub grassland (Ericaceae pollen ≥40%) were identified. The presence of Ericaceae-dominated montane shrub grasslands and the forest formations of the northern and eastern parts of the island were recorded. Along these, ecosystems such as riparian woodlands on the lakeshores, patches of montane were also represented as the case of the sample collected at Ankazominady in the central highlands. These findings enabled interpretations of palaeoecological work and established at least a qualitative distinction between Malagasy paleoenvironments in the region. However, Burney suggested the need for larger modern pollen datasets and the inclusion of more phytogeographic information combined with multivariate statistical methods for better interpretations.

Straka (1991) published 89 samples from mosses and surface sediments within which 60 samples were from Madagascar. Straka's samples represented seven vegetation types. The humid forest included seven samples with three samples in the littoral forests, three in the humid forest at low altitude, and one in the secondary forest called *Savoka*. However, most of the samples were collected in the subhumid forest in the Central Highlands with a total of 48 samples. The ericoid thickets were represented with four samples which were characterised by a high percentage of Ericaceae/Vaccinaceae (45–98%) with low diversity or with a moderate percentage of Ericaceae/Vaccinaceae combined with Asteraceae type Aster (30%). For all the samples analysed by Straka, only one from the Spiny thicket in the south of the island was collected. Yet, the pollen results presented taxa typical of this vegetation such as type Euphorbia (24,5%), type Acacia and they even found one pollen grain of an *Alluaudia ascendens* (Drake) Drake (Didiereaceae) and also a high percentage of Asteraceae (52%) (Straka 1991). Straka's analysis was however only qualitative and more advanced quantitative analysis are needed.

After almost three decades, seven samples from the top of sediment cores and surface samples were collected and analysed by Razafimanantsoa (2015) from the Northwest dry deciduous forest in Madagascar. These samples represented taxa from different soil types within the dry deciduous forest, but also the degraded dry forest and savannah ecosystems. Results showed the presence of high pollen rain concentration in the dry forest and savannah ecosystem compared to the degraded forest (Razafimanantsoa 2015). In the pollen results, the dry deciduous forest is characterised by *Commiphora* and *Dalbergia* as well as Rubiaceae type, while Poaceae and *Ziziphus* were abundant in the savannah. The degraded forest was on the other hand characterised by the abundance of *Eucalyptus* sp. These initial surface sample results by Burney (1988), Straka (1991) and Razafimanantsoa (2015) in addition to recently collected samples (fieldwork session in 2015, 2016 and 2019) from the succulent woodland, dry deciduous and sub-humid forest could form the basis to establish a reference based on the distribution of pollen and their representation in the various vegetation types in Madagascar.

Similar to these surface samples destined for palaeoecological interpretations, several investigations of pollen rain based on samples from spore Brutayert traps are important tools to help for the interpretation of past pollen record. Analysis of pollen samples from the Capital of Madagascar in the Central Highlands was first published as a thesis in the early 80' covering the period of 1979, 1980, 1981 (Rajeriarison 1983). This study found that the pollen in the region contains a high percentage of Poaceae which were interpreted by Straka (1991) to have reflected rice fields and savannah that are abundant in the region (Straka 1991).

21.6.2 Namibia

Namibian modern pollen has been recently studied by Tabares *et al.* (2018) who used soil surface samples to test the correspondence between vegetation and pollen in savannah ecosystems. They found that pollen is able to separate out distinct vegetation types such as *Acacia* woodland and open mixed woodland well, although overall species richness is not reflected well by pollen assemblages. Grazing pressure was found to be indicated by *Alternanthera*, *Tribulus*, and *Limeum* and the co-occurrence of *Dichrostachys*, *Phyllanthus* and *Crotalaria* is an indicator of environmental encroachment.

Hyrax dung middens, one of the few pollen records available from extreme arid environments such as the Namib desert, were investigated by Gil-Romera *et al.* (2006) and included four modern dung samples. These modern samples were found to be more widely variable than their fossilised equivalents, suggesting that they represented shorter time sampling periods than older dung extracted from middens.

21.7 SPATIAL SPREAD OF MODERN POLLEN STUDIES

The spatial distribution of modern pollen studies in tropical Africa is not even, with work being concentrated in certain areas and countries (Figure 1). Table 1 shows a breakdown of number

Table 1. Phytochoria and number of modern pollen studies that include samples from each Phytochoria (White 1983).

Phytochoria (White 1983)	Number of studies including samples from this region
I. Guineo-Congolian regional centre of endemism	39
II. Zambezian regional centre of endemism	5
III. Sudanian regional centre of endemism	16
IV. Somalia-Masai regional centre of endemism	14
VI. Karoo-Namib regional centre of endemism	2
VII. Mediterranean regional centre of endemism	1
VIII and IX. Afromontane archipelago-like regional centre of endemism and extreme floristic impoverishment	7
X. Guineo-Congolia/Zambezia regional transition zone.	0
XI. Guinea-Congolia/Sudania regional transition zone.	1
XII. Lake Victoria regional mosaic.	8
XIII. Zanzibar-Inhambane regional mosaic.	0
XIV. Kalahari-Highveld regional transition zone.	0
XVI. Sahel regional transition zone.	11
XVII. Sahara regional transition zone.	5
XIX and XX East and West Malagasy regional centres of endemism	4

of studies by Phytochoria, which demonstrates that within the tropical region of Africa, the Guineo-Congolian region is most represented, followed by the Sudanian region and the Sahel. These regions cover large areas of land, and are also important biologically, harbouring a very large number of species within multiple vegetation types. There are other comparably extensive phytochoria which are much less well represented. The Zambezian region, for instance, has very few studies but covers a large part of southern Africa. The Guineo-Congolian/Zambezian regional transition zone and the Kalahari-Highveld regional transition zone do not have any studies at all, and the Guinea-Congolia/Sudania regional transition zone has just one study.

It is also apparent, from Figure 1 (and Table 2) that large swathes of Africa have few to no studies, including much of central and central Southern Africa. Coastal regions are better represented than inland areas, and studies tend to be clustered in countries where foundational palaeoecological work had taken place, such as Uganda and Cameroon.

21.8 THE FUTURE OF MODERN POLLEN STUDIES IN AFRICA

21.8.1 Geographical and vegetation priority areas

Although the number of modern pollen rain studies in Africa has increased over the past few decades, many countries and vegetation types are still under-investigated (Figure 1). Some of these instances of under-representation, for instance in the Saharan region, are likely due to environmental factors like aridity, meaning that gathering modern pollen samples from soil is impractical and often unsuccessful. Any modern samples that are collected in the course of palaeoecological fieldwork will not necessarily coincide with flowering of ephemeral species that thrive in arid environments, potentially producing pollen that is dispersed rapidly and potentially

Table 2. Table showing studies consulted in this study including their number for Figure 1.

Number	Area	Reference	Data collection	Focus of the Study
	WEST AFRICA			
1	Mauritania	Romero *et al.* (2003)	Pollen traps	Palaeoecology
2	Senegal, Mauritania	Lézine and Hooghiemstra (1990)	Lake surface	Palaeoecology
3	Senegal, Mauritania, Ocean	Lézine and Hooghiemstra (1990)	Soil, river, marine mud surface samples	Palaeoecology
4	Senegal, Togo	Lézine and Edorh (1991)	Soil, river surface samples	Palaeoecology
-	Senegal, Mauritania	Lézine (1987)	Soil and river samples	Palaeoecology
5	Côte d'Ivoire	Ybert (1975)	Pollen traps	Palaeoecology
6	Côte d'Ivoire	Fredoux (1978)		
7	Côte d'Ivoire	Caratini *et al.* (1987)		Palaeoecology
8	Côte d'Ivoire, Chad	Ybert (1980)	Glycerine slides	Aeropalynology
9	Ghana	Julier *et al.* (2019)	Pollen traps	Palaeoecology
10	Ghana	Maley (1983)	Lake surface samples	
11	Ghana	Julier *et al.* (2017)	Pollen traps	Palaeoecology
12	Togo	Chalié *et al.* (1990)	Soil surface	
13	Togo	Edorh (1986)	Soil surface	Palaeoecology
14	Togo	Edorh and Afidegnon (2008)	Soil surface	Palaeoecology
15	Bénin	Zanou *et al.* (2020)	Soil surface	
16	Bénin	Tossou *et al.* (2012)	Soil surface	Palaeoecology
17	Bénin	Tchabi *et al.* (2017)	Pollen traps	Aeropalynology
18	Bénin	Tossou *et al.* (2016)	Pollen traps	Aeropalynology
19	Niger	Caratini (1988)	Pollen traps	Aeropalynology
20	Nigeria	Adeniyi *et al.* (2018)	Pollen traps	Aeropalynology

(continued)

Table 2. Continued.

Number	Area	Reference	Data collection	Focus of the Study
21	Nigeria	Adekanmbi and Ogundipe (2010)	Pollen traps	Aeropalynology
22	Nigeria	Ajikah *et al.* (2015)	Pollen traps	Aeropalynology
23	Nigeria	Ibigbami and Adeonipekun (2020)	Pollen traps	Aeropalynology
24	Nigeria	Adeonipekun *et al.* (2016)	Pollen traps	Aeropalynology
25	Nigeria	Agwu (2001)		Aeropalynology
26	Nigeria	Abdulrahaman *et al.* (2015)	Pollen traps	Aeropalynology
27	Nigeria	Ezikanyi *et al.* (2016)	Pollen traps	Aeropalynology
28	Nigeria	Agwu (1986)	Soil surface/ Water samples	Palaeoecology
29	Nigeria	Agwu and Osibe (1992)		Aeropalynology
30	Nigeria	Njokuocha (2006)	Pollen traps	Aeropalynology
31	Nigeria	Adekanmbi *et al.* (2018)	Pollen traps	Aeropalynology
32	Nigeria	Alebiosu *et al.* (2018)	Pollen traps	Aeropalynology
33	Nigeria	Salzmann (2000)	Pollen traps/ Soil surface	Palaeoecology
34	Nigeria	Salzmann and Waller (1998)	Pollen traps/ Soil surface	Palaeoecology
35	Chad	Schulz (1976)	Pollen traps	Palaeoecology
36	Chad	Maley (1972)	Soil surface	Palaeoecology
37	Chad	Amaral *et al.* (2013)	Soil surface	Palaeoecology
38	Chad	Maley (1981)	Soil surface	Palaeoecology
–	Various	Melia (1984)	Filters and Marine	Aerobiology, Palaeoecology
–	Various	Hooghiemstra (1988)	Littoral and marine surface	Palaeoecology
–	Various	Lézine *et al.* (2009)	Various	Palaeoecology
–	Multiple	Dupont (1991)	Marine surface	Palaeoecology
–	Ocean	Calleja *et al.* (1993)	Filters	Palaeoecology

(continued)

Table 2. Continued.

Number	Area	Reference	Data collection	Focus of the Study
a	Various	Lézine (1997)	Littoral and Marine	Palaeoecology
b	Various	Caratini and Cour (1980)	Filters with silicon oil	Aeropalynology, Palaeoecology
	CENTRAL AFRICA			
39	Cameroon	Verlhac *et al.* (2018)	Soil surface	Palaeoecology
40	Cameroon	Bengo (1992)		Palaeoecology
41	Cameroon	Van Campo (2004)	Soil surface	
42	Cameroon	Reynaud-Farrera (1995)	Marine surface	Palaeoecology Palynology
43	Cameroon	Lebamba *et al.* (2009)	Core top	Palaeoecology
44	Cameroon	Bengo (1996)	Soil surface	Palaeoecology, Palynology
45	Cameroon	Bengo *et al.* (2020)	Soil surface	Palynology, Hydrology
46	Cameroon	Vincens *et al.* (2000)		Modern pollen-vegetation relationships, Palynology
47	Central African Republic	Aleman *et al.* (2012)	Soil surface and superficial litter	Modern pollen-vegetation relationships, Palaeoecology
48	Gabon, Cameroon	Lebamba *et al.* (2009)	Soil surface	Palaeoecology, Palynology
49	Gabon	Ngomanda *et al.* (2007)	Soil surface and superficial litter	Palaeoecology, Palynology
50	Gabon	Henga-Botsikabobe (2015)	Soil surface	Modern pollen-vegetation relationships, Palaeoecology
51	Gabon	Henga-Botsikabobe *et al.* (2020)	Soil surface	Modern pollen-vegetation relationships, Palaeoecology, Palynology
52	Gabon	Jolly *et al.* (1996)	Soil surface	Modern pollen-vegetation relationships

(continued)

Table 2. Continued.

Number	Area	Reference	Data collection	Focus of the Study
-	Gabon	Ngomanda (2005)		
53	Republic of Congo	Tovar *et al.* (2019)	Soil surface	
54	Republic of Congo	Elenga (1992)	Surface samples	
55	Republic of Congo	Elenga *et al.* (2000)	Soil surface	Palaeoecology
56	Democratic Republic of Congo	Beuning *et al.* (2004)	Soil surface and core top	Palaeoecology
d	Marine, Gulf of Guinea	Dupont *et al.* (1998)	Soil surface and core top	Palaeoecology
	EAST AFRICA			
57	Sudan	El Ghazali (2002)	Soil surface	Palaeoecology
58	Sudan	El Ghazali and Moore (1998)	Soil surface	Palaeoecology
59	Djibouti	Bonnefille *et al.* (1980)	Soil surface	Palaeoecology
60	Ethiopia	Bonnefille (2004)	Soil surface	Archaeology
61	Ethiopia, Tanzania	Barboni *et al.* (2019)	Soil surface	Palaeoecology
62	Ethiopia	Bonnefille *et al.* (1987)	Soil surface	Palaeoecology
63	Ethiopia, Kenya, Burundi	Roeland *et al.* (1988)	Soil surface	Palaeoecology
64	Ethiopia	Bonnefille *et al.* (1993)	Soil surface	Palaeoecology
65	Ethiopia	Mohamed Umer *et al.* (2004)		Archaeology
66	Kenya	Vincens (1984)		Palaeoecology
67	Kenya	Vincens *et al.* (2006)		Palaeoecology
68	Kenya	Tiercelin *et al.* (1987)		
69	Kenya	Rucina (2000)	Soil surface/ Moss polster	Palaeoecology
70	Kenya, Tanzania	Coetzee (1967)		Palaeoecology
71	Uganda	Vincens *et al.* (1997)	Soil surface	Palaeoecology

(continued)

Table 2. Continued.

Number	Area	Reference	Data collection	Focus of the Study
72	Kenya, Uganda	Hedberg (1954)	Moss/Lichen polsters	Palaeoecology
73	Uganda	Hamilton (1972)	Soil surface	Palaeoecology
74	Uganda, Kenya	Hamilton and Perrott (1980)		Palaeoecology
75	Tanzania, Kenya, Uganda, Ethiopia, Somalia	Bonnefille *et al.* (1992)	Soil surface	Palaeoecology
76	Uganda	Marchant and Taylor (2000)	Soil surface	Palaeoecology
77	Uganda	Marchant *et al.* (1997)	Soil surface	
78	Tanzania	Schüler *et al.* (2014)	Pollen traps	Palaeoecology
79	Tanzania	Ivory and Russell (2016)	Soil surface	Palaeoecology
80	Tanzania	Vincens (1987)	Core top	Palaeoecology
81	Burundi	Bonnefille and Riollet (1988)	Soil surface	Palaeoecology
82	Tanzania	Schüler (2013)		
83	Tanzania	Vincens *et al.* (2006)	Surface samples	Palaeoecology
84	Malawi	Meadows (1984)	Soil surface, pollen trap, core top	Palaeoecology
85	Malawi	DeBusk (1997)	Lake surface	Palaeoecology
	SOUTHERN AFRICA			
86	Madagascar	Razafimanantsoa (2015)	Soil surface	Modern pollen-vegetation relationships
87	Madagascar	Ramavovololona (1986)	Pollen traps	Aeropalynology
88	Madagascar	Rajeriarison (1983)	Pollen traps	Aerobiology
89	Madagascar and Mascareings	Straka (1991)	Soil surface/ moss polster	Modern pollen-vegetation relationships
90	Madagascar	Burney (1988)	Soil surface	Palaeoecology
91	Namibia	Tabares *et al.* (2018)	Soil surface	Palaeoecology
92	Namibia	Gil-Romera *et al.* (2006)	Dung	Palaeoecology

* Note that publications that are inaccessible but whose existence is confirmed by citations, or their inclusion in revision works are in italics.

destroyed due to dryness and heat. This problem of aridity could be addressed by setting artificial pollen traps. Transitional zones between different phytochoria are also under-represented, possibly due to their relatively small geographical extent. These areas should, however, receive attention in future studies due to their potential value in developing understanding of vegetation responses to climate change over time. The transitions between phytochoria such as the Guineo-Congolian region, the Sudanian region, and the Sahel, for instance, are likely to have shifted in the past in response to climate drivers (Salzmann and Hoelzmann 2005; Watrin *et al.* 2007). The pollen assemblages at the boundaries of these phytochoria are, therefore, important for the interpretation of shifts observed in fossil pollen records such as that from Lake Bosumtwi (Miller *et al.* 2016) and marine cores (Dupont and Agwu 1992).

21.8.2 Methodological recommendations for pollen dispersal and deposition modelling

The goal of pollen analysis has since the earliest days of the discipline been the reconstruction of past landcover, but the relationship between pollen assemblage at a point and surrounding vegetation is not simple. There are three broad methods for using modern pollen and vegetation data to improve interpretation of sedimentary pollen records. The first method, biomisation, assigns pollen types to plant functional types, then using the plant functional type spectrum to assign a biome, on the assumption that biomes are persistent features of the vegetation (Jolly *et al.* 1998; Vincens *et al.* 2006). Biomisation results are used in the validation of vegetation models such as Dynamic Global Vegetation Models (Hély *et al.* 2006). The second method, the modern analogue technique, statistically matches fossil pollen assemblages to the nearest modern pollen assemblage, and the past environment then assumed to be the same as the present one (Peyron *et al.* 2006). The third method, pollen-vegetation relationship modelling, uses a model of pollen dispersal and deposition (pdd) to establish a relationship between landcover and pollen assemblage, then applies an inverse form of this to reconstruct past land cover (Duffin and Bunting 2008; Gillson and Duffin 2007; Sugita 2007a, 2007b).

Here, we focus on the pdd model and how studies of modern pollen rain in tropical Africa could improve its applicability and relevance. The pdd modelling approach to landcover reconstruction reconstructs the wider past landscape (Bunting and Middleton 2009; Sugita 2007a, 2007b), by assuming that the relationship between plant and pollen is constant over time. The technique has been developed extensively over the last decade and is becoming a valuable tool for investigations of patterns of and controls on land cover change, especially in the northern temperate zone (e.g. Marquer 2017; Li *et al.* 2020).

Challenges in extending the pdd approach (and the modern analogue approach) to the tropics are two-fold-collecting calibration datasets of modern pollen and associated vegetation data, and the development of appropriate pollen dispersal models. Identifying appropriate trapping techniques in tropical ecosystems can be difficult; many ecosystems lack natural pollen traps such as moss polsters, and some ecosystems are too arid or fire-impacted to allow multi-year trap placement and recovery, which has been shown to be advantageous in tropical systems (Haselhorst *et al.* 2020). Collecting vegetation data for comparison with the modern pollen data is also often a challenge (Bunting *et al.* 2013). Existing vegetation maps may not be at appropriate scale, woody plants may only be recorded above 10 cm DBH, which excludes some that may flower thereby contributing to the pollen signal, and vegetation surveys hampered by difficult terrain and incomplete or challenging taxonomy. Dispersal models often fail to incorporate zoophilous taxa, although reducing the number of taxa used in studies can go some way to solving this issue (Whitney *et al.* 2019).

Despite these challenges, research is underway in tropical and sub-tropical areas to develop means of applying the pdd modelling approach to reconstruction of land cover from pollen records. It has considerable potential in improving the integration of palaeoecology with ecology, archaeology and climate modelling (e.g. Harrison *et al.* (2020)), adding a long term perspective critical to meet socioecological challenges such as planning for climate change adaptation and mitigation.

This review can support the use of pdd modelling in African palynology by showing the range of data available across the continent. Existing pollen datasets can be identified in locations where it may be possible to extract suitable vegetation data from remote sensing and data collected for other purposes, and achieve initial model calibration for major habitats. We also hope to alert colleagues to the potential of modern pollen samples, and therefore encourage study design which can be used for model testing and calibration as well as for the analyst's primary purpose.

21.9 CONCLUSIONS

In this review, we have collated and described modern pollen work conducted in tropical Africa to date. We have provided country-scale summaries of the literature and identified potential areas for future work, including arid regions and transitional regions. If these areas are focussed on in forthcoming work, a more complete understanding of pollen-vegetation relationships in tropical Africa will be developed, which will in turn contribute to improved interpretations of fossil pollen records. Further, targeted modern pollen studies, designed with quantitative modelling approaches in mind will also allow more rigorous interpretations of pollen fossil records to be developed for Africa.

21.10 ACKNOWLEDGEMENTS

We would like to thank Dr. Anne-Marie Lézine and Prof. Henry Hooghiemstra for kindly sharing papers and information that greatly helped this review. Prof. Christelle Hély and an anonymous reviewer also provided helpful and detailed comments that significantly improved the work, for which we are extremely grateful. ACMJ acknowledges funding from the NRF African Origins Platform (117666). SM fromthe NRF Competitive Programme for Rated Researchers (118538). ER acknowledges The Southern African Science Service Centre for Climate Change and Adaptive Land Management (SASSCAL, 466418 c/c BIO1056) and the University Research Committee accredited (URC) from the University of Cape Town (2020). DH acknowledges funding by CongoPeat, a NERC Large Grant (NE/R016860/1) to Simon L. Lewis.

REFERENCES

Abdulrahaman, A.-A., Aruofor, O.S., Taofik, G., Kolawole, O.S., Olahan, G.S. and Oladele, F.A., 2015, Aeropalynological Investigation of the University of Ilorin, Ilorin, Nigeria. *Journal of Applied Sciences and Environmental Management* **19**, pp. 53–63, 10.4314/jasem.v19i1.7.

Adekanmbi, O., Ogundipe, O., 2010, Aeropalynological Studies of the Univesity of Lagos Campus, Nigeria. *Notulae Scientia Biologicae,* **2**, pp. 34–39, 10.15835/nsb245393.

Adeniyi, T., Olowokudejo, J.D. and Adeonipekun, P.A., 2018, Annual records of airbone pollen of Poaceae in five areas in Lagos, Nigeria. *Grana*, **57**, pp. 284–291, 10.1080/00173134.2017.1356865.

Adeonipekun, A.P., Agbalaya, A.E. and Adeniyi, T., 2016, Aeropalynology of Ayetoro-Itele, Ota Southwestern Nigeria: A preliminary study. In: *Human Palaeoecology in Africa: Essays in Honour of M. Adebisi Sowunmi*, edited by Oyelaran, P.A., Alabi, R.A. and Adeonipekun, P.A., pp. 130–155 (Ibadan: PAN and University of Ibadan Press).

Agwu, C.O.C., 2001, A study of Niger Delta environment through air-borne palynomorphs, Port Harcourt, Nigeria. *Palaeoecology of Africa*, **27**, pp. 191–205.

Agwu, C.O.C., 1986. History of climate and vegetation of east central Nigeria as deduced from pollen analysis: preliminary investigations. *Bulletin de liaison de l'Association Sénégalaise pour l'Etude du Quaternaire Africain* **76** pp. 5–8.

Agwu, C.O.C. and Osibe, E.E., 1992, Airborne palynomorphs of Nsukka during the months of Febuary-April, 1990. *Nigerian Journal of Botany,* **5**, pp. 177–185.

Alebiousu, O.S., Adekanmbi, O.H., Nodza, G.I. and Ogundipe, O.T., 2018, Aeropalynological study of two selected locations in North-Central Nigeria. *Aerobiologica*, **34**, pp. 187–202, 10.1007/s10453-017-9506-2.

Aleman, J., Leys, B., Apema, R., Bentaleb, I., Dubois, M.A., Lamba, B., Lebamba, J., Martin, C., Ngomanda, A., Truc, L., Yangakola, J.-M., Favier, C., Bremond, L. and Woods, K., 2012, Reconstructing savanna tree cover from pollen, phytoliths and stable carbon isotopes. *Journal of Vegetation Science* **23**, pp. 187–197, 10.1111/j.1654-1103.2011.01335.x.

Amaral, P.G.C., Vincens, A., Guiot, J., Buchet, G., Deschamps, P., Doumnang, J.-C. and Sylvestre, F., 2013, Palynological evidence for gradual vegetation and climate changes during the African Humid Period termination at 13° N from a Mega-Lake Chad sedimentary sequence. *Climate of the Past* **9**, pp. 223–241, 10.5194/cp-9-223-2013.

Barboni, D., Ashley, G.M., Bourel, B., Arráiz, H. and Mazur, J.-C., 2019, Springs, palm groves, and the record of early hominins in Africa. *Review of Palaeobotany and Palynology* **266**, pp. 23–41, 10.1016/j.revpalbo.2019.03.004.

Bengo, M.D., 1996, *La sédimentation pollinique dans le sud-Caméroun et sur la plateforme marine à l'époque actuelle et au Quaternaire récent?: études des paléoenvironnements*, PhD Thesis, Université de Montpellier 2.

Bengo, M.D., 1992, *Etude palynologique et statistique de quelques echantillons fluviatiles actuels du Bassin de la Sanaga*. D.E.A. Université de Montpellier 2.

Bengo, M.D., Elenga, H., Maley, J. and Giresse, P., 2020, Evidence of pollen transport by the Sanaga River on the Cameroon shelf. *Comptes Rendus. Géoscience,* **352**, pp. 59–72, 10.5802/crgeos.1.

Beuning, K.R.M. and Russell, J.M., 2004, Vegetation and sedimentation in the Lake Edward Basin, Uganda-Congo during the Late Pleistocene and early Holocene. *Journal of Paleolimnology* **32**, pp. 118, 10.1023/B:JOPL.0000025253.51135.c4.

Bonnefille, R., Buchet, G., Friis, I., Kelbessa, E. and Mohammed, M.U., 1993, Modern pollen rain on an altitudinal range of forests and woodlands in South West Africa. *Opera Botanica,* **121**, pp. 71–84.

Bonnefille, R., Chalié, F., Guiot, J. and Vincens, A., 1992, Quantitative estimates of full glacial temperatures in equatorial Africa from palynological data. *Climate Dynamics*, **6**, pp. 251–257, 10.1007/BF00193538.

Bonnefille, R., Gasse, F., Azema, C. and Denefle, M., 1980, Palynologie et interprétation palaéoclimatique de trois niveaux pléitocene supérieur d'un sondage du Lac Abhé (Afar, Territoire de Djibouti). *Mémoires du Muséum national d'Histoire naturelle,* B, **27** pp. 149–164.

Bonnefille, R., Potts, R., Chalié, F., Jolly, D. and Peyron, O., 2004, High-resolution vegetation and climate change associated with Pliocene Australopithecus afarensis. *Proceedings of the National Academy of Sciences of the United States of America* **101**, pp. 12125–12129, 10.1073/pnas.0401709101.

Bonnefille, R. and Riollet, G., 1988, The Kashiru Pollen Sequence (Burundi) Palaeoclimatic Implications for the Last 40,000 yr B.P. in Tropical Africa. *Quaternary Research*, **30**, pp. 19–35, 10.1016/0033-5894(88)90085-3.

Bonnefille, R., Vincens, A. and Buchet, G., 1987, Palynology, Stratigraphy and Palaeoenvironment of a Pliocene Hominid Site (2.9-3.3 M.Y.) at Hadar, Ethiopia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **60**, pp. 249–281, 10.1016/0031-0182(87)90035-6.

Bunting, M.J., Farrell, M., Broström, A., Hjelle, K.L., Mazier, F., Middleton, R., Nielsen, A.B., Rushton, E., Shaw, H. and Twiddle, C.L., 2013, Palynological perspectives on vegetation survey: A critical step for model-based reconstruction of Quaternary land cover. *Quaternary Science Reviews* **82**, pp. 41–55, 10.1016/j.quascirev.2013.10.006.

Bunting, M.J. and Middleton, D., 2005, Modelling pollen dispersal and deposition using HUMPOL software, including simulating windroses and irregular lakes. *Review of Palaeobotany and Palynology* **134**, pp. 185–196, 10.1016/j.revpalbo.2004.12.009.

Bunting, M.J. and Middleton, R., 2009, Equifinality and uncertainty in the interpretation of pollen data: the Multiple Scenario Approach to reconstruction of past vegetation mosaics. *The Holocene* **19**(5), pp. 799–803, 10.1177/0959683609105304.

Burney, D.A., 1988, Modern pollen spectra from Madagascar. *Palaeogeography, Palaeoclimatology, Palaeoecology* **66**, pp. 63–75, 10.1016/0031-0182(88)90081-8.

Calleja, M., Rossignol-Strick, M. and Duzer, D., 1993, Atmospheric pollen content off West Africa. *Review of Palaeobotany and Palynology*, **79**, pp 335–368, 10.1016/0034-6667(93)90029-T.

Caratini, C. and Frédoux, A., 1988, Caractérisation des aérosols désertiques à Niamey (Niger) par leur contenu pollinique. *Institut Français de Pondichéry, Travaux de la section scintifique et technique*, **25**, pp. 251–268.

Caratini, C. and Cour, P., 1980, Aéropalynologie en Atlantique Orientale au large e la Mauritanie, du Sénégal et de la Gambie. *Pollen et Spores* **22**, pp. 245–255.

Caratini, C., Tastet, J.-P., Tissot, C. and Fredoux, A., 1987, Sédimentation palynologique actuelle sur le plateau continental de Côte d'Ivoire. In *Palynologie et Milieux Tropicaux*, edited by Cambon, G., Richard, P. and Suc, J.P., Mémoires et Travaux de l'Institut de Montpellier, 17, pp. 69–100.

Chalié, F., Edorh, T.M., Bonnefille, R., Guiot, J. and Roeland, J.-C., 1990, Signal de la pluviosité dans les données polliniques actuelles du Togo. *Comptes rendus de l'Académie des Sciences, Paris*, 2, **311**, pp. 893–899.

Coetzee, J.A., 1967. Pollen analytical studies in East and Southern Africa. In Palaeoecology of Africa. *Palaeoecology of Africa*, **3**, pp. 11–46.

Dargie, G.C., Lewis, S.L., Lawson, I.T., Mitchard, E.T.A., Page, S.E., Bocko, Y.E. and Ifo, S.A., 2017, Age, extent and carbon storage of the central Congo Basin peatland complex. *Nature* **542** pp. 86–90, 10.1038/nature21048.

Davis, B.A.S., Zanon, M., Collins, P., Mauri, A., Bakker, J., Barboni, D., Barthelmes, A., Beaudouin, C., Bjune, A.E., Bozilova, E., Bradshaw, R.H.W., Brayshay, B.A., Brewer, S., Brugiapaglia, E., Bunting, J., Connor, S.E. de Beaulieu, J.-L., Edwards, K., Ejarque, A., Fall, P., Florenzano, A., Fyfe, R., Galop, D., Giardini, M., Giesecke, T., Grant, M.J., Guiot, Jöel, Jahns, S., Jankovská, V., Juggins, S., Kahrmann, M., Karpińska-Kołaczek, M., Kołaczek, P., Kühl, N., Kuneš, P., Lapteva, E.G., Leroy, S.A.G., Leydet, M., Guiot, José, Jahns, S., Jankovská, V., Juggins, S., Kahrmann, M., Karpiñska-Kołaczek, M., Kołaczek, P., Kühl, N., Kuneš, P., Lapteva, E.G., Leroy, S.A.G., Leydet, M., López Sáez, J.A., Masi, A., Matthias, I., Mazier, F., Meltsov, V., Mercuri, A.M., Miras, Y., Mitchell, F.J.G., Morris, J.L., Naughton, F., Nielsen, A.B., Novenko, E., Odgaard, B., Ortu, E., Overballe-Petersen, M.V., Pardoe, H.S., Peglar, S.M., Pidek, I.A., Sadori, L., Seppä, H., Severova, E., Shaw, H., Święta-Musznicka, J., Theuerkauf, M., Tonkov, S., Veski, S., van der Knaap, W.O., van Leeuwen, J.F.N., Woodbridge, J., Zimny, M. and Kaplan, J.O., 2013, The European Modern Pollen Database (EMPD) project. *Vegetation History and Archaeobotany,* **22**, pp. 521–530.

DeBusk, G.H., 1997, The distribution of pollen in the surface sediments of Lake Malawi, Africa, and the transport of pollen in large lakes. *Review of Palaeobotany and Palynology*, **97**, pp. 123–153, 10.1016/S0034-6667(96)00066-8.

Debusk, G.H.J., 1995, *Transport and stratigraphy of pollen in Lake Malawi, Africa*. PhD Thesis, Duke University.

Duffin, K.I. and Bunting, M.J., 2008, Relative pollen productivity and fall speed estimates for southern African savanna taxa. *Vegetation History and Archaeobotany* **17**, pp. 507–525, 10.1007/s00334-007-0101-2.

Dupont, L.M. and Agwu, C.O.C., 1992, Latitudinal shifts of forest and savanna in N. W. Africa during the Brunhes chron: further marine palynological results from site M 16415 (9° N 19° W). *Vegetation History and Archaeobotany* **1**, pp. 163–175, 10.1007/BF00191556.

Dupont, L.M. and Agwu, C.O.C., 1991, Environmental control of pollen grain distribution patterns in the Gulf of Guinea and offshore NW-Africa. *Geologische Rundschau* **80**, pp. 567–589, 10.1007/BF01803687.

Edorh, T.M., 1986, *Végétation et pluie pollinique actuelles au Togo*. PhD Thesis; Université d'Aix-Marseille 3.

Edorh, T.M. and Afidegnon, D., 2008, Représentation pollinique de la végétation actuelle des zones humides du Sud-Est du Togo. *Annales des Sciences Agronomiques* **10**, pp. 51–70.

El Ghazali, G.E.B., 2002, Modern Pollen spectra and contemporary Vegetation in South-eastern Sahara, Sudan. *Sudan Journal of Scientific Research,* 81.

El Ghazali, G.E.B. and Moore, P.D., 1998, Modern lowland pollen spectra and contemporary vegetation in the eastern Sahel Vegetation Zone, Sudan. *Review of Palaeobotany and Palynology* **99**, pp. 235–246, 10.1016/S0034-6667(97)00042-0.

Elenga, H., 1992, *Végétation et climat du Congo depuis 24 000 ans B. P: analyse palynologique de séquences sédimentaires du Pays Bateke et du littoral*. PhD Thesis, Université d'Aix-Marseille 3.

Elenga, H., de Namur, C., Vincens, A., Roux, M. and Schwartz, D., 2000, Use of plots to define pollen-vegetation relationships in densely forested ecosystems of Tropical Africa. *Review of Palaeobotany and Palynology* **112**, pp. 79–96, 10.1016/S0034-6667(00)00036-1.

Elenga, H., Schwartz, D. and Vincens, A., 1994, Pollen evidence of late Quaternary vegetation and inferred climate changes in Congo. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **109**, pp. 345–356, 10.1016/0031-0182(94)90184-8.

Ezikanyi, D.N., Nnamani, C.V. and Osayi, E.E., 2016, Relationship between Vegetation and Pollen Spectrum in South East Nigeria. *International Research Journal of Biological Sciences* **5**, pp. 57–66.

Fang, Y., Ma, C. and Bunting, M.J., 2019, Novel methods of estimating relative pollen productivity: A key parameter for reconstruction of past land cover from pollen records. *Progress in Physical Geography: Earth and Environment*, **43**, pp. 731–753, 10.1177/03091333198 61808.

Flenley, J.R., 1973, Use of modern pollen rain samples in the study of the vegetational history of tropical regions. *Symposium of the British Ecological Society* (Oxford: Blackwell).

Fredoux, A., 1978, *Pollens et spores d'espèces actuelles et quaternaires de région périlagunaires de Côte d'Ivoire*. PhD Thesis, Université de Montpellier 2.

Gajewski, K., Lézine, A.-M., Vincens, A., Delestan, A. and Sawada, M., 2002, Modern climate-vegetation-pollen relations in Africa and adjacent areas. *Quaternary Science Reviews* **21**, pp. 1611–1631, 10.1016/S0277-3791(01)00152-4.

Gillson, L., 2015, *Biodiversity, Conservation and Environmental Change: Using palaeoecology to manage dynamic landscapes in the Anthropocene* (Oxford University Press).

Gillson, L. and Duffin, K.I., 2007, Thresholds of potential concern as benchmarks in the management of African savannahs. *Philosophical Transactions of the Royal Society B: Biological Sciences* **362**, pp. 309–319, 10.1098/rstb.2006.1988.

Gil-Romera, G., Scott, L., Marais, E. and Brook, G.A., 2006, Middle-to late-Holocene moisture changes in the desert of northwest Namibia derived from fossil hyrax dung pollen. *The Holocene* **16**, pp. 1073–1084, 10.1177/0959683606069397.

Githumbi, E.N., 2017, *Holocene Environmental and Human Interactions in East Africa*. PhD Thesis, University of York.

Hamilton, A.C., 1972, The interpretation of pollen diagrams from highland Uganda. *Palaeoecology of Africa*, **7**, pp. 45–149.

Hamilton, A.C. and Perrott, R.A., 1980, Modem pollen deposition on a tropical African mountain. *Pollen et Spores* **22**, pp. 437–468.

Harrison, S.P., Gaillard, M.-J., Stocker, B.D., Vander Linden, M., Klein Goldewijk, K., Boles, O., Braconnot, P., Dawson, A., Fluet-Chouinard, E., Kaplan, J.O., Kastner, T., Pausata, F.S.R., Robinson, E., Whitehouse, N.J., Madella, M. and Morrison, K.D., 2020, Development and testing scenarios for implementing land use and land cover changes during the Holocene in Earth system model experiments. *Geoscientific Model Development,* **13**, pp. 805–824, 10.5194/gmd-13-805-2020.

Haselhorst, D.S., Moreno, J.E. and Punyasena, S.W., 2020, Assessing the influence of vegetation structure and phenological variability on pollen-vegetation relationships using a 15-year Neotropical pollen rain record. *Journal of Vegetation Science* **31**, pp. 606–615, 10.1111/jvs.12897.

Hedberg, O., 1954, A Pollen-Analytical Reconnaissance in Tropical East Africa. *Oikos* **5**, pp. 137–166, 10.2307/3565157.

Hély, C., Bremond, L., Alleaume, S., Smith, B., Sykes, M.T. and Guiot, J., 2006, Sensitivity of African biomes to changes in the precipitation regime. *Global Ecology and Biogeography* **15**, pp. 258–270, 10.1111/j.1466-8238.2006.00235.x.

Hemp, A., 2006, Continuum or zonation? Altitudinal gradients in the forest vegetation of Mt. Kilimanjaro. *Plant Ecology*, **184**, pp. 27–42, 10.1007/s11258-005-9049-4.

Henga-Botsikabobe, K..B., 2015, *Fonctionnement écologique et évolution des écosystèmes dans un contexte de mosaïque foret-savane et de présence humaine depuis 4000 BP au Parc National de la Lopé (Gabon)*. PhD Thesis, Paris.

Henga-Botsikabobe, K., Ngomanda, A., Oslisly, R., Favier, C., Muller, S.D. and Bremond, L., 2020. Modern pollen-vegetation relationships within tropical marshes of Lopé National Park (Central Gabon) *Review of Palaeobotany and Palynology* **275**, pp. 104–168, 10.1016/j.revpalbo.2020.104168.

Hooghiemstra, H., Lézine, A.-M., Leroy, S A.G., Dupont, L. and Marret, F., 2006, Late Quaternary palynology in marine sediments: A synthesis of the understanding of pollen distribution patterns in the NW African setting. *Quaternary International* **148**, pp. 29–44, 10.1016/j.quaint.2005.11.005.

Hooghiemstra, H., Maizels, J., Ward, R.G.W., Shackleton, N.J., West, R.G. and Bowen, D.Q., 1988, Palynological records from northwest African marine sediments: A general outline of the interpretation of the pollen signal. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences* **318**, pp. 431–449.

Ibigbami, T. and Adeonipekun, O., 2020, Comparative aeropalynology of two communities in Lagos State, southwestern Nigeria. *Notulae Scientia Biologicae* **12**, pp. 729740, 10.15835/nsb12310768.

Ivory, S.J. and Russell, J., 2016, Climate, herbivory, and fire controls on tropical African forest for the last 60ka. *Quaternary Science Reviews* **148**, pp. 101–114, 10.1016/j.quascirev.2016.07.015.

Jackson, S.T. and Lyford, M.E., 1999, Pollen Dispersal Models in Quaternary Plant Ecology: Assumptions, Parameters, and Prescriptions. *Botanical Review* **65**, pp. 39–75, 10.1007/BF02856557.

Jantz, N., Homeier, J., León-Yánez, S., Moscoso, A. and Behling, H., 2013, Trapping pollen in the tropics – Comparing modern pollen rain spectra of different pollen traps and surface samples across Andean vegetation zones. *Review of Palaeobotany and Palynology* **193**, pp. 57–69, 10.1016/j.revpalbo.2013.01.011.

Jolly, D., Bonnefille, R., Burcq, S. and Roux, M., 1996, Representation pollinique de la forêt dense humide du Gabon, tests statistiques. *Comptes rendus de l'Académie des Sciences, Paris, 2, A* **322**, pp. 63–70.

Jolly, D., Prentice, I.C., Bonnefille, R., Ballouche, A., Bengo, M., Brenac, P., Buchet, G., Burney, D., Cazet, J.-P., Cheddadi, R., Edorh, T., Elenga, H., Elmoutaki, S., Guiot, J., Laarif, F., Lamb, H., Lézine, A.-M., Maley, J., Mbenza M., Peyron, O., Reille, M., Reynaud-Farrera, I., Riollet, G., Ritchie, J.C., Roche, E., Scott, L., Ssemmanda, I., Straka, H., Umer, M., Van Campo, E., Vilimumbalo, S., Vincens, A.and Waller, M., 1998, Biome reconstruction from pollen and plant macrofossil data for Africa and the Arabian peninsula at 0 and 6000 years. *Journal of Biogeography* **25**, pp. 1007–1027, 10.1046/j.1365-2699.1998.00238.x.

Julier, A.C.M., Jardine, P.E., Adu-Bredu, S., Coe, A.L., Duah-Gyamfi, A., Fraser, W.T., Lomax, B.H., Malhi, Y., Moore, S., Owusu-Afriyie, K. and Gosling, W.D., 2017, The modern pollen-vegetation relationships of a tropical forest-savannah mosaic landscape, Ghana, West Africa. *Palynology,* **42**(3), pp. 1–15.

Julier, A.C.M., Jardine, P.E., Adu-Bredu, S., Coe, A.L., Fraser, W.T., Lomax, B.H., Malhi, Y., Moore, S. and Gosling, W.D., 2019, Variability in modern pollen rain from moist and wet tropical forest plots in Ghana, West Africa. *Grana* **58**, pp. 45–62, 10.1080/00173134.2018.1510027.

Laseski, R., 1983, *Modern pollen data and Holocene climate change in eastern Africa*. PhD Thesis, Brown University.

Lebamba, J., Ngomanda, A., Vincens, A., Jolly, D., Favier, C., Elenga, H. and Bentaleb, I., 2009, Central African biomes and forest succession stages derived from modern pollen data and plant functional types. *Climate of the Past* **5**, pp. 403–429, 10.5194/cp-5-403-2009.

Lézine, A.-M., 1997, Evolution of the West African mangrove during the Late Quaternary: A review. *Géographie physique et Quaternaire* **51**, pp. 405–414, 10.7202/033139ar.

Lézine, A.-M., 1988, New pollen data from the Sahel, Senegal. *Review of Palaeobotany and Palynology*, **55**, pp. 141–154, 10.1016/0034-6667(88)90082-6.

Lézine, A.-M., 1987, *Paléoenvironnements végétaux d'Afrique Nord-Tropicale depuis 12 000 B.P.: analyse pollinique de séries sédimentaires continentales (Sénégal-Mauritanie)*. PhD Thesis, Université Aix-Marseille 2.

Lézine, A.-M. and Edorh, T.M., 1991, Modern pollen deposition in West African Sudanian environments. *Review of Palaeobotany and Palynology* **67**, pp. 41–58, 10.1016/0034-6667(91)90015-U.

Lézine, A.-M. and Hooghiemstra, H., 1990, Land-sea comparisons during the last glacial-interglacial transition: pollen records from West Tropical Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* **79**, pp 313–331, 10.1016/0031-0182(90)90025-3.

Lézine, A.-M., Watrin, J., Vincens, A. and Hély, C., 2009, Are modern pollen data representative of West African vegetation? *Review of Palaeobotany and Palynology* **156**, pp. 265–276, 10.1016/j.revpalbo.2009.02.001.

Li, F., Gaillard, M.-J., Cao, X., Herzschuh, U., Sugita, S., Tarasov, P.E., Wagner, M., Xu, Q., Ni, J., Wang, W., Zhao, Y., An, C., Beusen, A.H.W., Chen, F., Feng, Z., Goldewijk, C.G.M.K., Huang, X., Li, Yuecong, Li, Yu, Liu, H., Sun, A., Yao, Y., Zheng, Z. and Jia, X., 2020, Towards quantification of Holocene anthropogenic land-cover change in temperate China: A review in the light of pollen-based REVEALS reconstructions of regional plant cover. *Earth-Science Reviews,* **203**, pp. 103–119, 10.1016/j.earscirev.2020.103119.

Livingstone, D.A., 1967, Postglacial Vegetation of the Ruwenzori Mountains in Equatorial Africa. *Ecological Monographs* **37**, pp. 25–52, 10.2307/1948481.

Maley, J., 1981, *Etudes Palynologiques dans le Bassin du Tchad et Paléoclimatologie de l'Afrique Nord-Tropicale de 30,000 ans a l'Epoque Actuelle* (Paris: ORSTOM).

Maley, J., 1972, La sedimentation pollinique actuelle dans la zone du Lac Tchad. *Pollen et Spores* **14**, pp. 263–397.

Manzano, S., Julier, A.C.M., Dirk-Forbes, C.J., Razafimanantsoa, A.H.I., Samuels, I., Petersen, H., Gell, P., Hoffman, M.T. and Gillson, L., 2020, Using the past to manage the future: the role of palaeoecological and long-term data in ecological restoration. *Restoration Ecology*, **28** 6, pp. 1335–1342, 10.1111/rec.13285.

Marchant, R. and Taylor, D., 2000, Pollen representivity of montane forest taxa in south-west Uganda. *New Phytologist* **146**, pp. 515525, 10.1046/j.1469-8137.2000.00662.x.

Marchant, R., Taylor, D. and Hamilton, A., 1997, Late Pleistocene and Holocene History at Mubwindi Swamp, Southwest Uganda. *Quaternary Research*, **47**, pp. 316–328, 10.1006/qres.1997.1887.

Marquer, L., Gaillard, M.-J., Sugita, S., Poska, A., Trondman, A.-K., Mazier, F., Nielsen, A.B., Fyfe, R.M., Jönsson, A.M., Smith, B., Kaplan, J.O., Alenius, T., Birks, H.J.B., Bjune, A.E., Christiansen, J., Dodson, J., Edwards, K.J., Giesecke, T., Herzschuh, U., Kangur, M., Koff, T., Latałowa, M., Lechterbeck, J., Olofsson, J. and Seppä, H., 2017, Quantifying the effects of land use and climate on Holocene vegetation in Europe. *Quaternary Science Reviews* **171**, pp. 20–37, 10.1016/j.quascirev.2017.07.001.

Meadows, M.E., 1984, Contemporary Pollen Spectra and Vegetation of the Nyika Plateau, Malawi. *Journal of Biogeography* **11**, pp. 223–233, 10.2307/2844641.

Melia, M.B., 1984, The distribution and relationship between palynomorphs in aerosols and deep-sea sediments off the coast of Northwest Africa. *Marine Geology* **58**, pp. 345–371, 10.1016/0025-3227(84)90208-1.

Miller, C.S. and Gosling, W.D., 2014, Quaternary forest associations in lowland tropical West Africa. *Quaternary Science Reviews* **84**, pp. 7–25, 10.1016/j.quascirev.2013.10.027.

Miller, C.S., Gosling, W.D., Kemp, D.B., Coe, A.L. and Gilmour, I., 2016, Drivers of ecosystem and climate change in tropical West Africa over the past ∼540 000 years. *Journal of Quaternary Science* **31**, pp. 671–677, 10.1002/jqs.2893.

Mohamed Umer, M., Kaniewski, D. and Renault-Miskovsky, J., 2004, Etude palynologique du site de Fejej FJ-1. In: *Les Sites Préhistoriques de La Région de Fejej, Sud-Omo, Ethiopie, Dans Leur Contexte Stratigraphique et Paléontologique*, editted by de Lumley, H. and Beyene, Y., pp. 173202, (Paris: Association Pour La Diffusion de La Pensée Française, Editions Recherche Sur Les Civilisations).

Ngomanda, A., 2005, *Dynamique des écosystèmes forestiers du Gabon au cours des cinq derniers millénaires*. PhD Thesis, Université de Montpellier 2.

Ngomanda, A., Jolly, D., Bentaleb, I., Chepstow-Lusty, A., Makaya, M., Maley, J., Fontugne, M., Oslisly, R. and Rabenkogo, N., 2007, Lowland rainforest response to hydrological changes during the last 1500 years in Gabon, Western Equatorial Africa. *Quaternary Research*, **67**, pp. 411–425, 10.1016/j.yqres.2007.01.006.

Njokuocha, R.C., 2006, Airborne pollen grains in Nsukka, Nigeria. *Grana* **45**, pp. 73–80, 10.1080/00173130600555797.

Osmaston, H.A., 1958, *Pollen analysis in the study of the past vegetation and climate of Ruwenzori and its neighbourhood*. BSc Thesis, University of Oxford.

Peyron, O., Jolly, D., Braconnot, P., Bonnefille, R., Guiot, J., Wirrmann, D. and Chalié, F., 2006. Quantitative reconstructions of annual rainfall in Africa 6000 years ago: Model-data comparison. *Journal of Geophysical Research: Atmospheres* **111**, 10.1029/2006JD007396.

Rajeriarison, C., 1983, Etude du contenu pollinique de l'atmosphere de la région d'Antananarivo (Madagascar): Bilan d'une année d'observations. *Pollen et Spores* **25**(1), pp. 75–90.

Razafimanantsoa, A.H.I., 2015, *Etude des pluies polliniques de la Région de Boeny et des autres formations végétales malgaches*. MS Thesis, Université d'Antananarivo.

Reynaud-Farrera, I., 1995, *Histoire des paléoenvironnements forestiers du sud-Cameroun à partir d'analyses palynologiques et statistiques de dépôts holocènes et actuels*. PhD Thesis, Universté de Montpellier 2.

Roeland, J.-C., Guiot, J. and Bonnefille, R., 1988, Pollen et reconstruction quantitative du climat. Validation des données d'Afrique orientale. *Comptes rendus de l'Académie des Sciences, Paris* **307**, pp. 1735–1740.

Romero, O.E., Dupont, L., Wyputta, U., Jahns, S. and Wefer, G., 2003, Temporal variability of fluxes of eolian-transported freshwater diatoms, phytoliths, and pollen grains off Cape Blanc as reflection of land-atmosphere-ocean interactions in northwest Africa. *Journal of Geophysical Research: Oceans* **108**(C5), 10.1029/2000JC000375.

Rucina, S.M., 2000, *Pollen vegetation relationships in the Aberdare Mountains, Kenya*. MS Thesis, University of Wales, Aberystwyth.

Salzmann, U., 2000, Are modern savannas degraded forests? – A Holocene pollen record from the Sudanian vegetation zone of NE Nigeria. *Vegetation History and Archaeobotany* **9**, pp. 1–15, 10.1007/BF01295010.

Salzmann, U. and Hoelzmann, P., 2005, The Dahomey Gap: an abrupt climatically induced rain forest fragmentation in West Africa during the late Holocene. *The Holocene* **15**, pp. 190–199, 10.1191/0959683605hl799rp.

Salzmann, U. and Waller, M., 1998, The Holocene vegetational history of the Nigerian Sahel based on multiple pollen profiles. *Review of Palaeobotany and Palynology* **100**, pp. 39–72, 10.1016/S0034-6667(97)00053-5.

Schüler, L., 2013, *Studies on late Quaternary environmental dynamics (vegetation, biodiversity, climate, fire and human impact) on Mt. Kilimanjaro, comparing the dry northern with the wet southern slopes*. PhD Thesis, Georg-August-Universität Göttingen.

Schüler, L., Hemp, A. and Behling, H., 2014, Relationship between vegetation and modern pollen-rain along an elevational gradient on Kilimanjaro, Tanzania. *The Holocene,* **24**, pp. 702–713, 10.1177/0959683614526939.

Schulz, E., 1976, Aktueller Pollenniederschlag in der zentralen Sahara und Interpretationsmoglichkeiten quartarer Pollenspektren. *Palaeoecology of Africa*, **9**, pp. 8–14.

Straka, H., 1991, Palynologia Madagassica et Mascarenica. 2nd partie. Echantillons de surface. *Akademie der Wissenschaften und der Litteratur* (Stuttgart: Franz Steiner Verlag).

Sugita, S., 2007a, Theory of quantitative reconstruction of vegetation I: pollen from large sites REVEALS regional vegetation composition. *The Holocene* **17**, pp. 229–241, 10.1177/0959683607075837.

Sugita, S., 2007b, Theory of quantitative reconstruction of vegetation II: all you need is LOVE. *The Holocene* **17**, pp. 243–257, 10.1177/0959683607075838.

Tabares, X., Mapani, B., Blaum, N. and Herzschuh, U., 2018, Composition and diversity of vegetation and pollen spectra along gradients of grazing intensity and precipitation in southern Africa. *Review of Palaeobotany and Palynology* **253**, pp. 88–100, 10.1016/j.revpalbo.2018.04.004.

Tchabi, F.L., Tossou, G.M., Akoegninou, A. and Trigo, M.M., 2017, Étude aéropalynologique de la commune d'Abomey-Calavi (Benin) au cours de la grande saison des pluies. *Revue Française d'Allergologie* **57**, pp. 308–316, 10.1016/j.reval.2017.03.004.

Theuerkauf, M., Couwenberg, J., Kuparinen, A. and Liebscher, V., 2016. A matter of dispersal: REVEALSinR introduces state-of-the-art dispersal models to quantitative vegetation reconstruction. *Vegetation History and Archaeobotany*, **25**, pp. 541–553, 10.1007/s00334-016-0572-0.

Tossou, G.M., Chabi, L.F., Akoègninou, A., Ballouche, A. and Akpagana, K., 2016, Analyse pollinique de l'atmosphère du campus d'Abomey-Calavi (Bénin). *Revue Française d'Allergologie* **56**, pp. 65–75, 10.1016/j.reval.2015.11.002.

Tossou, G.M., Yedomonhan, H.Y., Adomou, C.A., Akoegninou, A., Akpagana, K., 2012, Dépôt pollinique actuel et végétation du sud du Bénin. *International Journal of Biological and Chemical Sciences* **6**, pp. 1647–1668, 10.4314/ijbcs.v6i4.23.

Tovar, C., Harris, D.J., Breman, E., Brncic, T. and Willis, K.J., 2019, Tropical monodominant forest resilience to climate change in Central Africa: A Gilbertiodendron dewevrei forest pollen record over the past 2,700 years. *Journal of Vegetation Science* **30**, pp. 575–586, 10.1111/jvs.12746.

Van Campo, E. and Bengo, M.D., 2004, Mangrove palynology in recent marine sediments off Cameroon. *Marine Geology*, **208**, pp. 315–330, 10.1016/j.margeo.2004.04.014.

Verlhac, L., Izumi, K., Lézine, A.-M., Lemonnier, K., Buchet, G. and Achoundong, G., Tchiengué, B., 2018, Altitudinal distribution of pollen, plants and biomes in the Cameroon highlands. *Review of Palaeobotany and Palynology,* **259**, pp. 21–28, 10.1016/j.revpalbo.2018.09.011.

Vincens, A., 1987, Recent pollen sedimentation in Lake Natron, Tanzania: a model for the interpretation of fossil spectra in arid region. Sédimentation pollinique actuelle dans le lac Natron, Tanzanie?: un modèle pour l'interprétation de spectres fossiles en région aride. *Sciences Géologiques, bulletins et mémoires,* **40**, pp. 155–165, 10.3406/sgeol.1987.1757.

Vincens, A., 1984, Environnement végétal et sédimentation pollinique lacustre actuelle dans le bassin du lac Turkana (Kenya). *Revue de Paléobiologie*, **vs**, pp. 235–242.

Vincens, A., Bremond, L., Brewer, S., Buchet, G. and Dussouillez, P., 2006, Modern pollen-based biome reconstructions in East Africa expanded to southern Tanzania. *Review of Palaeobotany and Palynology* **140**, pp. 187–212, 10.1016/j.revpalbo.2006.04.003.

Vincens, A., Dubois, M.A., Guillet, B., Achoundong, G., Buchet, G., Kamgang Kabeyene Beyala, V., de Namur, C. and Riera, B., 2000, Pollen-rain-vegetation relationships along a forest-savanna transect in southeastern Cameroon. *Review of Palaeobotany and Palynology* **110**, pp. 191–208, 10.1016/S0034-6667(00)00009-9.

Vincens, A., Ssemmanda, I., Roux, M. and Jolly, D., 1997, Study of the modern pollen rain in Western Uganda with a numerical approach. *Review of Palaeobotany and Palynology* **96**, pp. 145–168, 10.1016/S0034-6667(96)00022-X.

Watrin, J., Lézine, A.-M., Gajewski, K., Vincens, A., 2007, Pollen-plant-climate relationships in sub-Saharan Africa. *Journal of Biogeography* **34**, pp. 489–499, 10.1111/j.1365-2699.2006.01626.x.

White, F., 1983, The vegetation of Africa. (Paris: UNESCO).

Whitney, B.S., Smallman, T.L., Mitchard, E.T., Carson, J.F., Mayle, F.E. and Bunting, M.J., 2019, Constraining pollen-based estimates of forest cover in the Amazon: A simulation approach. *The Holocene* **29**, pp. 262–270, 10.1177/0959683618810394.

Ybert, J.-P., 1980, Le contenu pollinique de l'atmosphère en Côte d'Ivoire et au Tchad. *Grana* **19**, pp. 31–46, 10.1080/00173138009424985.

Ybert, J.-P., 1975, Emissions polliniques actuelles dans la zone du contact forêt-savane en Côte d'Ivoire *Bulletin de la Société Botanique de France* **122**, pp. 251–268, 10.1080/00378941.1975.10835659.

Zanou, A.R.S., Tossa-Dognon, A.D., Batawila, K., Akoegninou, A. and Akpagana, K., 2020, Étude de la pluie pollinique de la forêt classée de la Lama. *Journal de la Recherche Scientifique de l'Université de Lomé (Togo)* **22**, pp. 63–76.