

2025-02-01

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Elsevier

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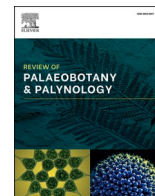
<https://doi.org/10.1016/j.revpalbo.2024.105240>

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Contents lists available at ScienceDirect

## Review of Palaeobotany and Palynology

journal homepage: [www.elsevier.com/locate/revpalbo](http://www.elsevier.com/locate/revpalbo)

## Multiporate Poaceae pollen grains observed in the recent fossil record from the Greater Serengeti Ecosystem and Lake Victoria region

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### ARTICLE INFO

#### Keywords:

Speke Gulf  
Grasses  
Grasslands  
Lake sediments  
Savannahs  
Paleoecology  
Palynology  
Microfossils

### ABSTRACT

The analysis of fossil pollen from sediments is used to understand past vegetation and land cover variability. The observations of multiporate Poaceae pollen from sediments have received little attention in the literature and causes and rates of occurrence have few estimates, and the rates observed in the sediments are much lower than estimates observed from modern plants in Asia. Pollen analysis of the uppermost sediments from Speke Gulf, Lake Victoria, eastern Africa, showed relative abundances of Poaceae between 65 and 75% during the past centuries. A total of 19 of the ~11,000 Poaceae pollen grains observed had conspicuous morphological variations and were documented. More consistent presence of abnormal grains occurred since the mid twentieth century, at the same time of increased anthropogenic environmental stressors. Multiporate pollen grains of Poaceae have been previously observed in Asia, South America, and northern Africa, predominantly in the Panicoideae subfamily. Morphological variations may present an added challenge for automated pollen identification techniques and descriptions of fossil pollen.

### 1. Introduction

Fossil pollen analysis provides information on long-term changes to vegetation patterns and insight into past human-environment interactions and land-use changes (Traverse, 2007; Schüler and Hemp, 2016; Daniau et al., 2019). Pollen analysis applied to modern plant specimens, melissopalynology, aerobiology and air quality provides information on a wide range of biological, ecological and anthropogenically-modified processes (Mercuri, 2015). The study of pollen has a century-long history with a large body of literature on pollen identification (Beug, 2004; Moore et al., 1991; Faegri et al., 1989; Birks and Berglund, 2018; Schüler and Hemp, 2016). The specialist literature specific to aberrant and abnormal pollen grains has received little attention and predominantly covers deeper geologic time scales

(Nowak et al., 2022; Vajda et al., 2023) or observations from modern plant specimens (Salgado-Labouriau and Rinaldi, 1990). Aberrant pollen grains have also been explored in environments of extreme environmental stress, such as, investigations of plants growing within highly impacted fallout areas around Chernobyl (Levkovskaya, 2012; Makarenko et al., 2024; Zub et al., 2024) and as analogue comparisons to past major environmental stressors interpreted from the fossil record (Foster and Afonin, 2005). The literature on abnormal pollen thus has received several avenues of interest, yet, publications are uncommon for the Holocene timespan and the topic has received limited attention (Table 1), in part, due to the challenge of disentangling the multiple processes that potentially influence the variable abundances of abnormal grains. This contrasts with studies of other aquatic indicators preserved in lake sediments, where assessments of the frequency of

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<https://doi.org/10.1016/j.revpalbo.2024.105240>

Received 6 October 2024; Received in revised form 13 November 2024; Accepted 14 November 2024

Available online 16 November 2024

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**Table 1**

Summarised example studies that presented multiporate Poaceae pollen grains identified in a literature review. Additional studies identified that are not summarised below include (Erdtman, 1944; Meo et al., 1988; Nazir et al., 2013; Radaeski, 2015).

Poaceae taxa known to produce multiporate pollen	Material	Geography	Reference
7 species	Plant specimens	Venezuelan mountains	Salgado-Labouriau and Rinaldi, 1990
3 species	Plant specimens	Central and South America	Zucol, 1998
<i>Paspalum</i> spp.	Plant specimens	China	Ma et al., 2001
2 species: <i>Leptochloa panicea</i> , <i>Schmidtia pappophoroides</i>	Plant specimens	China, Uganda	Liu et al., 2004
14 species	Plant specimens	China	Guohua et al., 2009
3 species of 65 investigated diporate	Plant specimens	Brazil	Radaeski et al., 2016
6 species of 95 investigated diporate	Plant specimens	Brazil	Radaeski et al., 2017
Fossil Poaceae grains	Holocene sediments	Brazil	Radaeski et al., 2017
5 species	Plant specimens	Brazil	Radaeski and Bauermann, 2018
10+ species	Plant specimens	Pakistan	Harun et al., 2022; Nazish and Althobaiti, 2022
Fossil Poaceae grains	Holocene coprolites	Libya	Mercuri et al., 2022
5 taxa	Plant specimens	Tibet in China	Gu et al., 2025
Fossil Poaceae grains	Late Holocene sediments	Lake Victoria, Tanzania	Core SPK7, this study

abnormalities have been used to study past changes in the frequency of mutations, e.g. as a consequence of increasing industrial pollution (Ilyashuk et al., 2003; Cattaneo et al., 2004). Several recent studies that observed Holocene occurrences of abnormal Poaceae pollen and that of other taxa have interpreted morphological anomalies as indicators of paleoenvironmental stress conditions, which range from climate variability to anthropogenic land use pressures (Radaeski et al., 2017; Mercuri et al., 2022; Gu et al., 2025).

Several factors contribute to the growth and dispersal of abnormal pollen grains including cold or hot temperature stresses (Satake and Hayase, 1970; Noskova et al., 2009; Santiago and Sharkey, 2019), nutrients, and ultraviolet stress (Murphy and Mitchell, 2013; Fijałkowska-Mader, 2020; Benca et al., 2022), and anthropogenic causes such as industrial metals in air pollution (Tretyakova and Noskova, 2004; Nayab and Alam, 2024). In Poaceae, the pollen grains typically have a relatively conspicuous monoporate morphology and are readily identifiable by analysts in palynological samples (Faegri et al., 1989). Higher taxonomic resolution and morphological groups is possible through microscopy analysis of the morphological features and morphometrics (Skvarla et al., 2003; Joly et al., 2007; Jan et al., 2015; Wei et al., 2023; Gu et al., 2025). Some Poaceae taxa are known to generate pollen grains with an atypical number of pores (Table 1) that are visible as apertures through the pollen grain surface that are apparent at optical microscopy, generally at 200–1000x magnification (Punt et al., 2007; Basak et al., 2023). Abnormalities in fossil Poaceae pollen have been occasionally reported in the recent fossil record of South America (Radaeski et al., 2017) and Saharan Africa (Rotunno et al., 2019; Mercuri et al., 2022). The presence of multiporate Poaceae grains may be an indicator of apomixis and asexual reproduction (Guohua et al., 2009; Mercuri et al., 2022). This is especially the case in species found in grass-dominated savannas in semi-arid regions (Brown and Emery, 1957) that

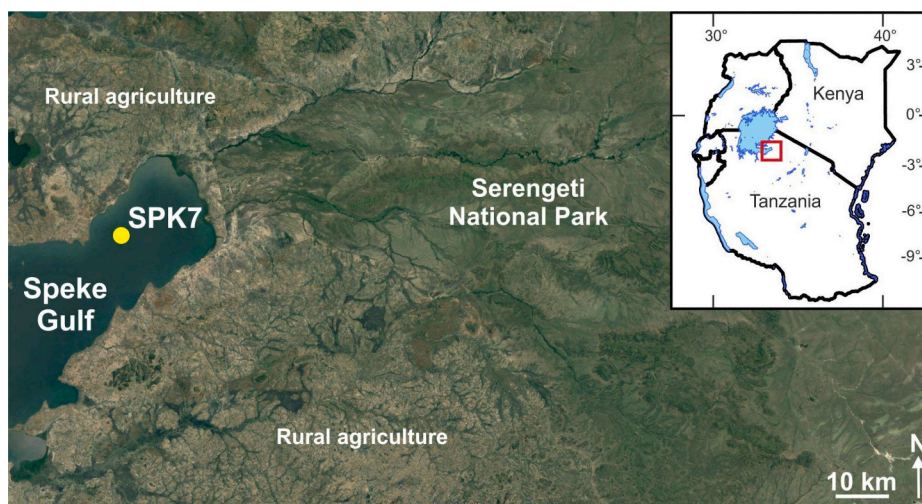
experience high disturbance pressures through grazing, trampling, fires and highly competitive reproduction potential by seed and germination pathways (Belsky, 1986; O'Connor and Pickett, 1992; Anderson et al., 2012). The prevalence of production and dispersal of aberrant pollen grains has very few estimates in tropical savannas and Poaceae are known to produce up to 20 million pollen per inflorescence (Prieto-Baena et al., 2003) leading to the pollen being preserved abundantly in sediments, soils and other depositional systems. Rates of abnormal pollen and spore production are of interest to assess past environmental stresses, adaptation, and anthropogenic impacts (Satake and Hayase, 1970; Ortiz et al., 2013; Mercuri et al., 2022; Nowak et al., 2022).

Such methods are particularly important in ecosystems characterised by high environmental variability. The Greater Serengeti Ecosystem of equatorial eastern Africa includes protected areas with large expanses of savannas. In previous pollen analysis of Lake Victoria sediments, Poaceae was relatively abundant ranging from 20 to 80% since 17,500 cal years BP until present time (Kendall, 1969; Temoltzin-Loranca et al., 2023a, 2023b). More widely, Poaceae dominate much of the wider landscape surrounding southeastern Lake Victoria as a main constituent of the herb layer in the various savanna mosaic Serengeti ecosystems. Grass cover is consumed by wild and domestic herbivory and during fires (Sinclair and Norton-Griffiths, 1979; Bond and Keeley, 2005; Shetler, 2007; Courtney Mustaphi et al., 2022). The Poaceae pollen production is unknown as there are no records of modern pollen production and no published data of pollen trap and deposition in the area (Julier et al., 2021). Many Poaceae taxa persist in the Serengeti, including introduced invasive taxa and crops (Anderson et al., 2015; Bukombe et al., 2021; Ngondya and Munishi, 2022), particularly maize, *Sorghum* and millet species (Mati et al., 2008; Sitati et al., 2024). There are also aquatic and semiaquatic Poaceae taxa at the lake shoreline, marginal and ephemeral wetlands, and riverine areas (LVBC, 2011). Here we report on the occurrences of multiporate Poaceae pollen grains in the very recent fossil record of the past two centuries observed in a sediment core collected from Lake Victoria.

## 2. Methods

### 2.1. Study area

Speke Gulf (1135 m asl) is a large, relatively flat and shallow (~10 m) embayment of Lake Victoria located in Tanzania (Fig. 1; Rach and Rosendahl, 1989; Scholz et al., 1990). The land uses and vegetation around the gulf consist of rural agriculture, livestock keeping and small urban settlements, marginal wetlands, shrublands and woody or grassy savannas (Awange and Ong'ang'a, 2006; Mugo et al., 2020), which includes large expanses of protected areas (Sinclair and Norton-Griffiths, 1979; Scoon, 2018). River inflows arrive from the woody and grassy savannas of the Greater Serengeti Ecosystem, as well as the shrubby and agricultural areas of Simiyu, Shinyanga, Mwanza, and southwestern Mara Regions (Sitati et al., 2024). The prevailing winds are diurnal and seasonal, varying between onshore and offshore. The modal predominance is easterly crossing the Serengeti Plains and woody savannas of western Serengeti. There are over 70 species of Poaceae in Serengeti and perennial grasses predominate plant richness and relative cover in the savannas (Anderson et al., 2007). A non-exhaustive literature review of descriptions and reports of multiporate pollen grains observed from plant specimens, pollen traps, and paleoecological studies found one taxon described from a plant specimen in Uganda that has a distribution range overlapping with our study region and that produced three-aperturate, non-annulate pollen from both perfect and imperfect florets on the upper and lower florets of the spikelet. (Poaceae: Pappophorae: *Schmidtia pappophoroides* Steud.; Liu et al., 2004) (Table 1) and the cereals and known hybrids (Mercuri et al., 2022).



**Fig. 1.** Inset map of equatorial eastern Africa (top right) and study area (red square) and general land cover with continuous savannah and woodlands in protected areas and mosaicked rural agriculture. The SPK7 sample collection location (yellow circle) in Speke Gulf, Lake Victoria, Tanzania. Basemap: Google Earth, 2023. <http://earth.google.com/web/> (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

## 2.2. Sediment core collection and laboratory analysis

On 13 July 2018, a 21.5 cm surface sediment core was collected from 9.5 m water depth near Bulamba Bay, Speke Gulf (SPK7; geographic coordinates 2.19195° S, 33.66975° E; 1135 m asl; WGS84; [Surveys and Mapping Division, 1976](#)). The core was collected with a gravity corer (6.6 cm internal diameter tubes; Pylonex AB, Umeå, Sweden) deployed from an anchored motorboat ([Renberg and Hansson, 2008](#); [Courtney-Mustaphi et al., 2021](#); [Scaini et al., 2024](#)). The core was vertically extruded by a threaded rod at 0.5 cm intervals into sterile plastic bags (Whirl-pak Nasco, Pleasant Prairie, WI, USA), transported, and refrigerated at 4 °C ([Verschuren, 1993](#); [Renberg and Hansson, 2008](#)).

Wet sediment subsamples of 1 cm<sup>3</sup> were contiguously extracted down core ( $n = 43$ ) for palynological preparation, which followed a sequence of chemical digestions using 10% HCl, 10% KOH, 40% HF, and acetolysis ([Erdtman, 1960](#); [Faegri et al., 1989](#)), H<sub>2</sub>O rinsed and centrifuged between steps, and sieved through a ceramic crucible mesh size of 500 µm ([Moore et al., 1991](#)). The digested residues were transferred to 85% glycerine with a safranin or fuchsine stain and mounted onto a microscope slide with a rectangular 22 × 32 mm coverslip. One tablet of *Lycopodium clavatum* spores was added to each sample prior to the chemical treatment to estimate microfossil concentrations ([Stockmar, 1971](#); batch number 1031 with  $n = 20,848$ ,  $1\sigma = 3457$  spores per tablet; University of Lund, manufactured in 2011). A small amount of the residue was stained and mounted onto a microscope slide. Pollen grains were counted under a Leica DM2500 LED illuminated optical microscope at 400x magnification. Total pollen counts ranged from 163 to 482 grains and averaged 368 grains ( $\sigma = \pm 95$ ), comparable with [Temoltzin-Loranca et al. \(2023a, 2023b\)](#). When a Poaceae pollen grain was observed that appeared to have two or more pore apertures, the grain was rolled by gently pressing the coverslip with a metal pick to observe the pore apertures and associated annulae to confirm if multiple pores were present and that it was not due to an optical aberration, a tear in the pollen, or small minerogenic clast attached to the surface. For photo documentation, multiporate Poaceae pollen grains were imaged with a Canon 90D EOS 35 mm digital camera.

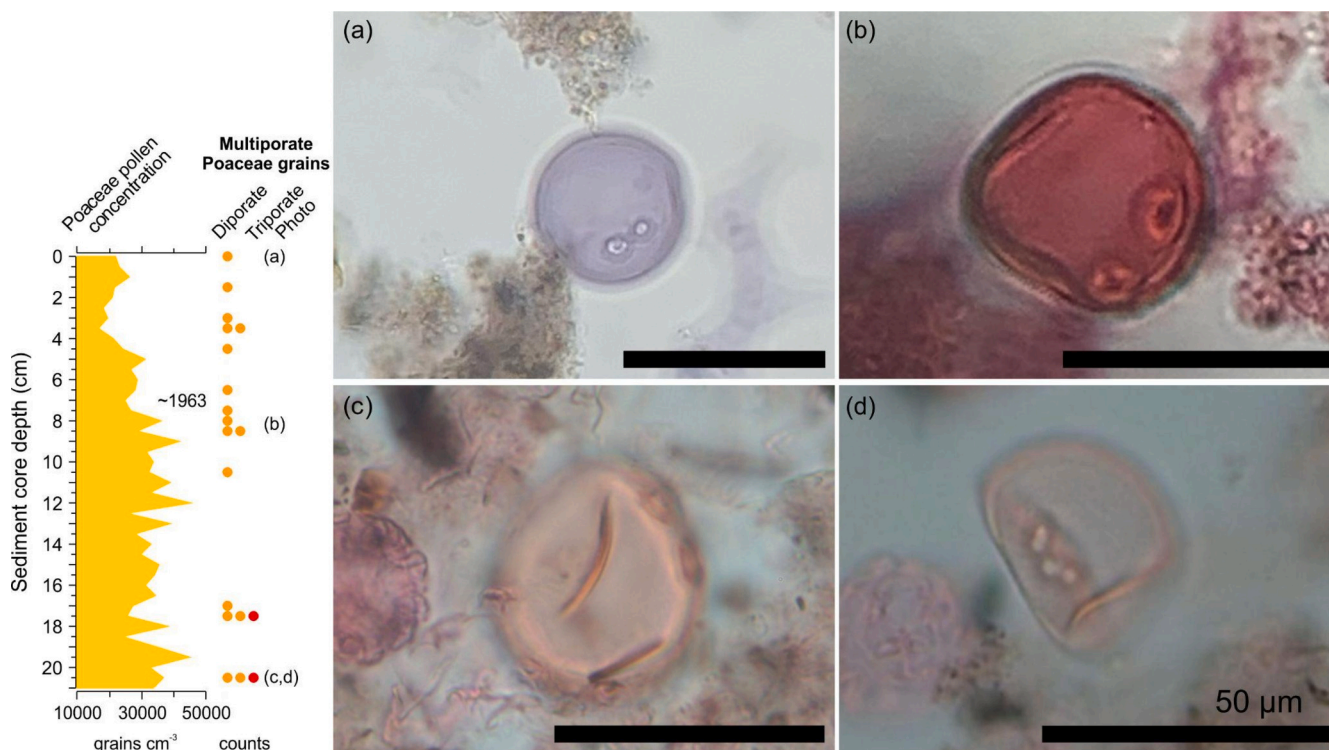
Gamma-ray spectrometry of lead-210 and caesium-137 radioisotopes suggest an intact sediment stratigraphy. A peak in caesium-137 counts was caused by the height of aboveground atomic explosive testing approximately 1963 Common Era (CE; [Appleby et al., 1986](#)) and was used to estimate the abnormal Poaceae pollen occurrence rate between 1963 and 2018 CE, when the age assessment has less uncertainty. Indicators of possible effect of industrial pollution in the environment

included total Hg, which is influenced by global atmospheric deposition ([Pacyna et al., 2010](#); [Streets et al., 2011, 2017](#); [Amos et al., 2013](#)) and point-source pollution from mining ([Bowell et al., 1995](#); [Dutton et al., 2019](#); [Seki et al., 2022](#)). To measure total Hg concentrations,  $1.0 \pm 0.3$  g of dry crushed sediments were loaded and combusted within Hg-free air and Hg concentrations were measured by atomic absorption spectrophotometry with a Direct Mercury Analyser (model DMA-80, Milestone GmbH, Heerbrugg, Switzerland) ([Glauser et al., 2022](#)) with an average recovery of 98%. Standard measurement procedures were performed by a quality control pre-sequence of three blank runs, one process blank (wheat flour) and three liquid primary reference standards (PRs; 50 mg of 100 ng g<sup>-1</sup> NIST-3133 in 1% BrCl) ([Wohlgemuth et al., 2020](#); [Wohlgemuth et al., 2022](#)).

## 3. Results

Poaceae pollen was observed in each sample and averaged 70% abundances and varied from 65 to 75% with a maximum concentration of 45,000 grains cm<sup>-3</sup> near the base of the sediment core and decreased to 18,000 at 3.0 cm depth, during the latter half of the twentieth century, before increasing slightly toward the core top ([Figs. 2 and 3](#); [Courtney Mustaphi et al., 2024](#)). For the analysed core, a total of 19 multiporate grains were observed amongst the 11,085 Poaceae grains observed (0.17%). When present, 1–3 multiporate grains were observed in the samples. Of the aberrant grains observed, 17 were diporate Poaceae pollen grains observed in 13 of 43 (30%) samples ([Fig. 2a–c](#)). Two triporate Poaceae-type grains were observed in the deeper samples at 17.5–18.0 and 20.5–21.0 cm ([Fig. 2d](#)) and the latter co-occurred in a sample that also contained diporate grains ([Fig. 2](#)). The upper half of the core and bottommost sediments of the core had diporate grains and 11.0–17.5 cm had no multiporate Poaceae grains ([Fig. 2](#)). The occurrence rate of morphological abnormal Poaceae grains since the 1963 caesium-137 peak gamma radiation between 6 and 8 cm depth was 0.21% of all Poaceae grains observed and yielded a calculated estimate of 0.11–0.15 abnormal grains per year (1963–2018 CE with age model  $1\sigma$  uncertainty range). Total mercury (Hg) of the sediments of core SPK7 increased during the early 1900s and remains at high levels to present. Hg is an indicator of anthropogenic pollution and land use pressures are useful as associative evidence of the increased population and resource pressure in the region of southeastern Lake Victoria.





**Fig. 2.** Stratigraphic plot of Poaceae pollen concentration and presence of multiporate Poaceae grains observed in the SPK7 sediment core (21.5 cm long). Diporate Poaceae pollen grain count (orange circles,  $n = 17$ ) and triporate grains (red circles,  $n = 2$ ). Date of peak caesium-137 measured through gamma-ray spectrometry (6–8 cm depth). Digital photographs of multiporate Poaceae grains observed in the uppermost sediments of Speke Gulf, Lake Victoria. a) Diporate Poaceae grain found at 0.0–0.5 cm surface sediments and stained with fuchsine. b) A diporate Poaceae grain with thick intine and exine and conspicuously protruding annulus around each pore found at 8.0–8.5 cm (older than 1963 CE) stained with Safranin. c) A diporate Poaceae grain and d) a triporate grain observed at 20.5–21.0 cm, lightly stained with Safranin. Approximate scale bar of 50  $\mu\text{m}$  (black rectangles). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

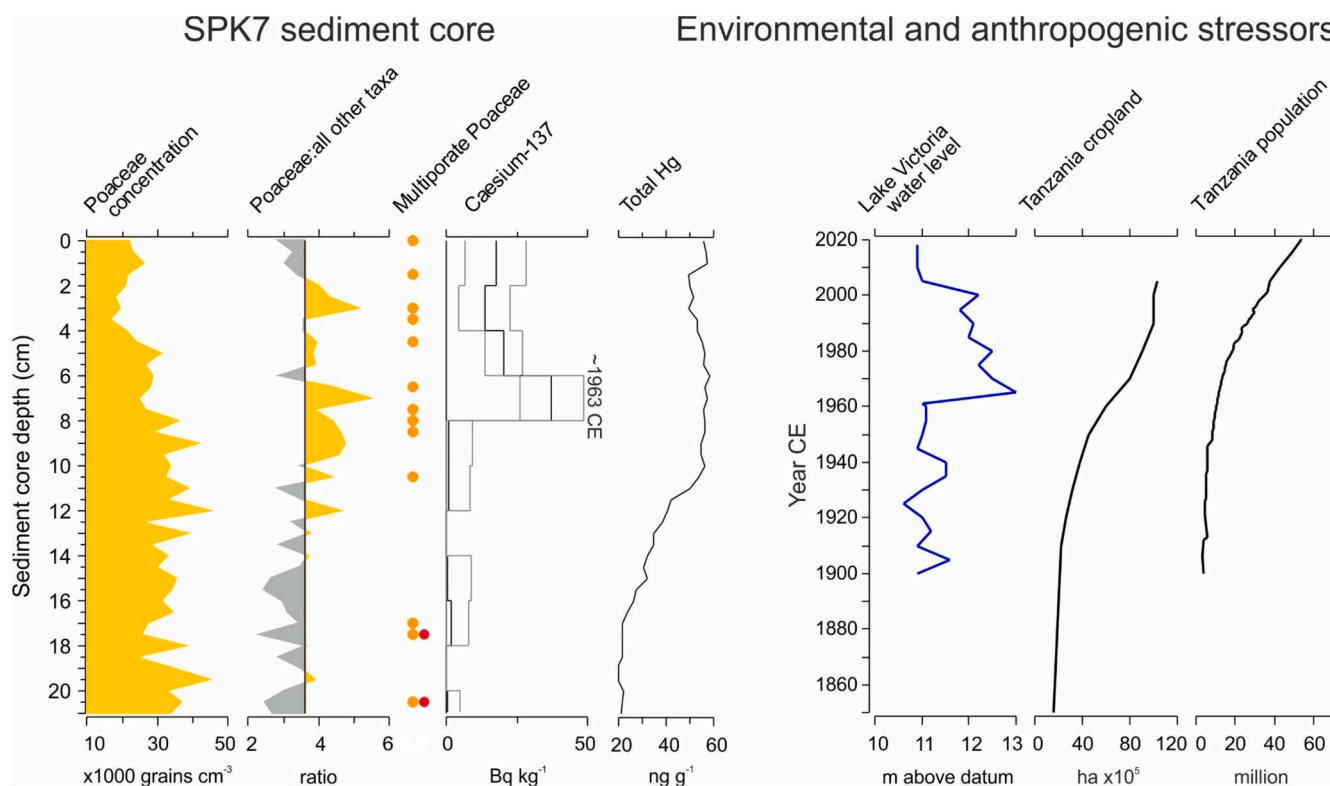
#### 4. Discussion

Multiporate Poaceae pollen grains were observed in the SPK7 sediment core that dated, predominantly in the uppermost half of the core (1900s CE) and the base (older than 1870 CE, based on the gamma-ray spectrometry; Fig. 3). No multiporate grains were observed from 11.0–17.5 cm, approximately dated to the nineteenth century. The multiple pores were often clustered together and the pore morphologies were qualitatively noted to vary slightly in morphology (Fig. 2a–c; see also comparable observations in Zucol, 1998; Radaeski et al., 2017). At SPK7, most often the pores appeared morphologically similar yet with one pore slightly smaller (Fig. 2a). Pollen spectra from savannah ecosystems have high Poaceae abundances (Gillson, 2006; Ekblom and Gillson, 2010; Ssemmanda et al., 2014; Colombaroli et al., 2018; Githumbi et al., 2018a, 2018b; Temoltzin-Loranca et al., 2023a) and this may increase the probability of observing abnormal pollen grains. Few records from Asian, African and South American grasslands, document pollen morphological variation of pore numbers on Poaceae grains (Salgado-Labouriau and Rinaldi, 1990; Guohua et al., 2009; Mercuri et al., 2022) and the Speke Gulf results extend observations in space to the eastern Africa region and also to the very recent fossil record of the past two centuries.

Poaceae pollen have been reported with multiple pores observed from modern plant specimens, Holocene lake sediments and archaeological contexts (Table 1). Plant survey observations have been reported from South America (Salgado-Labouriau and Rinaldi, 1990; Zucol, 1998; Radaeski et al., 2016, 2017; Radaeski and Bauermann, 2018), Asia (Ma et al., 2001; Guohua et al., 2009; Harun et al., 2022; Nazish and Althobaiti, 2022; Gu et al., 2025) and Africa (Liu et al., 2004). Multiporate Poaceae has also been observed in Holocene lake sediments from

South America (Radaeski et al., 2017) and Lake Van, Turkey (Lucia Wick, personal communication), and archaeological contexts in Saharan Africa (Mercuri et al., 2022). Multiporate pollen has been observed in Poaceae: Panicoideae (Guohua et al., 2009; Radaeski and Bauermann, 2018), with pore numbers varying from 1 to 6 amongst 14 investigated taxa, and relative occurrences of 3.5–37.3%. For some multiporate grain examples, the arrangement of the pores appeared clustered (Guohua et al., 2009), as was observed in the grains from Speke Gulf (Fig. 2a–d). The archaeobotanical analysis of Poaceae pollen associated with the Takarkori archaeological site, Libya, found a rate of multiporate grains of 0.1% (Mercuri et al., 2022), almost half the abundance found at SPK7.

The use of Poaceae species as food extends back to consumption of wild cereals and eventual seed sowing propagation, cropping, fodder and construction material, and pastoralism by the Late Stone Age (Lane, 2013; Mercuri et al., 2018; Prendergast, 2020). Use of domestic grasses accelerated in the region during the African Iron Age and associated material cultures have been found in study area (Hartwig, 1971; Lane, 2004; Shetler, 2007; Crowther et al., 2018). The land use and land cover changes around Speke Gulf have been significant over the past two centuries. In summary, defaunation from hunting pressures due to the global ivory trade likely impacted the wild herbivore grazing pressures in the region during the 1800s and the Rinderpest outbreaks of the late 1800s and early 1900s impacted both wild and domesticated gregarious mammalian herbivores as well as the local human populations (Sinclair and Norton-Griffiths, 1979; Shetler, 2007; Marchant et al., 2018). Changes to grazing pressures on savannahs could have cascading effects coupled with changing fire regimes and grassy and woody plant competition. Since the early phases of protected area gazettement and conservation, herbivore populations increased by mid-to-late 1900s to modern levels. Throughout the century, conversion from savannah and



**Fig. 3.** Stratigraphic plot of Poaceae pollen concentration (yellow silhouette), ratio of Poaceae to all other pollen counted (yellow:grey silhouette), and presence of multiporate Poaceae grains observed in the SPK7 sediment core (diporate grains show in orange circles and triporate grains in red). Total Hg of dry sediments in core SPK7 as an associative indicator of industrial pollution. Date of peak caesium-137 measured through gamma-ray spectrometry (black line) and  $1\sigma$  uncertainty of measurement (grey lines). Lake Victoria water level above the dam near Jinja, Uganda (blue line), and modelled estimate of cropland land use-land cover and population of Tanzania (black lines; Klein Goldewijk et al., 2011). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

brushland to small-scale agriculture has been observed across much of the region (Fig. 3; Mati et al., 2008; Klein Goldewijk et al., 2011; Probert et al., 2019; Veldhuis et al., 2019; Sitati et al., 2024).

The total mercury (Hg) of the sediments of core SPK7 are associative evidence of regional industrial activity that has increased during the 1900s (Fig. 3). There was a more consistent observation of pollen abnormalities in the upper half of the sediment core (~1900s) as a combination of increased indirect anthropogenic pressures to land use and land cover, damming of the Nile outflow of Lake Victoria, increased population and population density in Mwanza have all contributed to environmental stressors on some of the plant species in the region. Variability in the rates of pollen morphological abnormalities may potentially have an underestimated influence on the viability for pollination and the impacts on conservation and agriculture, both for crops and grazing. The predominance of abnormal Poaceae grains in the latter half of the twentieth century suggests the need for monitoring of modern pollen rain in the region and to investigate potential relationships between anthropogenic and environmental stressors on Poaceae.

The literature on palynological abnormalities focuses on modern plant specimens or deep geologic timescales leaving a substantial temporal gap that includes the Quaternary and Holocene. Some additional insight might be noteworthy from other palynological taxa that could be used to guide studies of Poaceae. Several morphological variations and abnormalities have been reported by observations through optical microscopy of pollen and spores of other taxa. Faegri et al. (1989) presented diporate pollen as a morphology and line drawn diagrams show spherical grains with antipodal pores, but was not explicitly linked to observations of Poaceae pollen (Faegri et al., 1989: pages 249 and 275) and briefly mention that “*Colchicum* is regularly, *Betula*, *Myriophyllum*, etc. are exceptionally diporate” (Faegri et al., 1989: page 275; and see

Vahdati et al., 2023). *Myriophyllum* has been reported to have variable numbers of pores that are asymmetrically clustered (Aiken, 1978), including diporate grains. Betulaceae: *Alnus* taxa have a variable number of pores (Vishnu-Mittre and Sharma, 1963; Leopold et al., 2012; May and Lacourse, 2012; Shayanmehr et al., 2015; Kizilpinar Temizer and Turkmen, 2016) and has been observed in extinct taxa (Reinink-Smith, 2010; Liu et al., 2014). Anecdotal observations of variable pore numbers have been reported from additional plant families, such as Cannabaceae, Moraceae, Acanthaceae, Urticaceae, and Juglandaceae (Whitehead, 1963; Radaeski et al., 2017). Abnormalities in pollen grains from Pinophyta have also been recorded, for example, *Pinus* grains of modern plants have been observed that have multi saccate morphologies (Wilson, 1965; Tretyakova and Noskova, 2004; Noskova et al., 2009) and have been anecdotally observed with trisaccate and multiple sacs from Holocene aged lake sediment cores from western and subarctic boreal Canada (author observations) and also in fossilised saccate pollen and spores as old as the Permian (Foster and Afonin, 2005; Benca et al., 2022). Several factors have been suggested for increased prevalence of abnormalities that are exogenous, environmental factors or anthropogenic stressors (Yablokov et al., 2009; Møller et al., 2016; Makarenko et al., 2024), and factors that are endogenous to populations (hybridisation, genetic and phenotypic variability).

In the fossil record, morphological abnormalities are likely to be the most conspicuous to observe visually and there has been less research on micro-deformities or other abnormalities. The taphonomic and observational bias toward conspicuous morphological abnormalities of pollen grains, such as a variable number of pores, produces some underestimation of the rate of all forms of deformity and abnormality. Other, less conspicuous abnormalities that are known to occur in modern specimens (Kolpakova et al., 2017) will be difficult to observe on fossil

material or require detailed description (Gu et al., 2025). Future work should investigate both modern and past rates of production of abnormal pollen morphologies, presence and prevalence amongst taxa (Chaturvedi et al., 1998; Perveen, 2006), and potential causal factors, such as genetics, diseases, competition, grazing pressures, nutrients, climate, fire and pollution. Detailed observations on comorbidity and occurrences of multiple abnormalities of modern Poaceae pollen grains would inform analysts of morphological clues that could potentially be observed in the fossil record. Observations may include (sub)fossil material, modern pollen, melissopalynology samples, experimental manipulation studies of plants, and comparative analysis between highly polluted and less polluted sites (Braga et al., 2023). The literature on pollen and spore abnormalities, anecdotal observations, and supplementary information (images and drawings) are highly dispersed. Malformations, morphological variations, and other abnormalities observed in (sub)fossil pollen grains should also be included as an attribute in pollen data and stored in data repositories and paleoecological databases (Goring et al., 2015; Williams et al., 2018; Birks et al., 2023) for multidisciplinary scientific use, outreach, and education (Flantua et al., 2023; Wilson, 2023). Efforts to increase the total pollen count analysed by human analysts and through the use of automated pollen identification systems will improve observations of morphological variations in Poaceae grains due to the relatively low frequencies. Automation may also provide more rapid morphometrics such as grain diameters, pore widths, and aperture sizes that could provide additional sources of evidence of morphological variations and spatiotemporal patterns in the paleoenvironmental record. The variety of morphological abnormalities of pollen grains also represents a unique additional challenge for communication amongst the research community (Joosten and de Klerk, 2002) and for automated identification techniques that are currently in development that may misidentify abnormal grains (France et al., 2000; Durand et al., 2024; von Allmen et al., 2024).

## 5. Conclusion

The recent sediments of the past few centuries from Speke Gulf, Lake Victoria, contained the first reported multiporate Poaceae pollen grains from Sub-Saharan Africa. There are several potential causes that may have led to the higher rates of malformations in this region, including exogenous factors such as climatic stresses, ultraviolet stress, and atmospheric pollutants during the past century. The increased anthropogenic pollution and land use pressures correlate with more consistent abnormal Poaceae pollen. However, aberrant pollen can also be produced by endogenous factors such as genetic and phenotypic variations within the grass taxa perhaps also linked to extreme climatic and other environmental stressors. These factors could be studied through experimentation and observational studies to further understand the causes and impacts of these malformations on the functioning of grasslands. The inclusion of morphological variants of pollen should be described and included in pollen data and spectra to add to our knowledge of occurrence and patterns for developing larger datasets for analysis.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

A data set to reproduce this study is available at Courtney Mustaphi et al., 2024 at <https://doi.org/10.7910/DVN/JGZTIK>, Harvard Dataverse

## Acknowledgements

We thank staff of Speke Bay Lodge, Lamadai, for logistical support and Willy Tinner and Erika Gobet for the use of the palynological laboratory at the Institute of Plant Sciences, University of Bern, Switzerland, by Fabian Rey. The gamma-ray spectrometry was undertaken by Samuel Muñoz at Northeastern University, USA, and the sediment mercury measurements were done by Lena Wohlgemuth at the University of Basel. We thank Lucia Wick, Oliver Heiri, Konrad Gajewski, Frank H. Neumann, Sally Archibald, and Mike Anderson for discussions of observations on aberrant pollen and grass ecology topics. CCM, RK and AS were supported through the 'Adaptation and Resilience to Climate Change (ARCC)' project awarded to PL, LM, AE and RM and administered by the Department of Archaeology and Ancient History, Uppsala University, Sweden, and The Nelson Mandela-African Institution of Science and Technology, NM-AIST, Arusha, Tanzania, under the Sustainability and Resilience - tackling climate and environmental changes programme funded through Swedish Research Council (Vetenskapsrådet), Sida and Formas (2016-06355); the Leverhulme Trust funded 'Uncovering the Variable Roles of Fire in Savannah Ecosystems' project (IN-2014-022) led by Colin Beale; and a travel grant from the Swiss Society for Quaternary Research (CH-QUAT 2019). SOB was supported by the Swiss National Science Foundation Ambizione grant (PZ00P2\_208687). Open access financing was provided through the University of Basel.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.revpalbo.2024.105240>.

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