

**Climatic sensitivity of
East African savanna
woodland**

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Sensitivity of the grassland-forest ecotone in East African open woodland savannah to historical rainfall variation

I. Ssemmanda¹, V. Gelorini², and D. Verschuren²

¹Department of Geology, Makerere University, P.O. Box 7062, Kampala, Uganda

²Limnology Unit, Department of Biology, Ghent University, K.L. Ledeganckstraat 35, 9000 Gent, Belgium

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Correspondence to: D. Verschuren (dirk.verschuren@ugent.be)

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Abstract

Fossil pollen records provide key insight into the sensitivity of terrestrial ecosystems to climate change at longer time scales. However, tracing vegetation response to relatively modest historical climate fluctuations is often complicated by the overriding signature of anthropogenic landscape disturbance. Here we use high-resolution pollen data from a ~200 year lake-sediment record in open woodland savannah of Queen Elisabeth National Park (southwestern Uganda) to assess the sensitivity of the tropical lowland grassland-forest ecotone to historical fluctuations in annual rainfall on the order of 10% lasting several decades. Specifically we trace vegetation response to three episodes of increased regional rainfall dated to the 1820s–1830s, ca. 1865–1890 and from 1962 to around 2000. During inferred wetter episodes we find increases in the relative pollen abundance from trees and shrubs of moist semi-deciduous forest (*Allophylus*, *Macaranga*, *Celtis*, *Alchornea*), riparian forest (*Phoenix reclinata*) and savannah woodland (*Myrica*, *Acalypha*, Combretaceae/Melostomataceae) as well as local savannah taxa (*Acacia*, *Rhus* type *vulgaris*, *Ficus*), together creating strong temporary reductions in Poaceae pollen (to 45–55% of the terrestrial pollen sum). During intervening dry episodes, most notably the period ca. 1920–1962, Poaceae pollen attained values of 65–75%, and dryland herbs such as *Commelina*, *Justicia* type *odora* and Chenopodiaceae expanded at the expense of Asteraceae, *Solanum*-type, *Swertia usumbarensis*-type, and (modestly so) Urticaceae. Noting that the overall diversity of arboreal taxa remained high but their combined abundance low, we conclude that the landscape surrounding Lake Chibwera has been an open woodland savannah throughout the past 200 years, with historical rainfall variation exerting modest effects on local tree cover (mostly the abundance of *Acacia* and *Ficus*) and the prevalence of damp soil areas promoting *Phoenix reclinata*. The strong apparent expansion of true forest trees during wet episodes can be explained partly by enhanced pollen influx via upland streams. Pollen from exotic trees and other cultural indicators

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appears from the 1970s onwards, but their combined influence fails to mask the region's natural vegetation dynamics.

1 Introduction

For East Africa and most other tropical regions where written history extends only to the late-19th century, concrete information on past climate-driven and human-induced landscape dynamics can only be gleaned from natural paleo-environmental archives preserved in lake and bog deposits. Unfortunately, many pollen-based reconstructions of past vegetation change that supposedly indicate early anthropogenic deforestation in East Africa are ambiguous, partly because traditional paleoecological indicators do not unambiguously separate between natural and anthropogenic effects on vegetation with, and partly because of a longstanding bias against the possibility of significant climate-driven vegetation change within the last few millennia (Verschuren, 2004).

Over the past decade, paleoclimate reconstructions with appropriate time resolution have documented strong late-Holocene moisture-balance variation in both eastern and western regions of the East African Plateau (Verschuren et al., 2000; Verschuren, 2001; Stager et al., 2005; Russell and Johnson, 2005, 2007; Russell et al., 2007). Consequently, socio-economic and conservation implications of modern-day human impact on East Africa's ecosystems must now be evaluated against the reference background of a continuously changing, inherently unstable physical environment. Parallel reconstruction of climate (Verschuren et al., 2000) and vegetation history (Lamb et al., 2003) in the central Kenya Rift Valley over the past 1000 years, extracted from one and the same well-dated sediment record, indicated that at least in semi-arid eastern portions of the East African Plateau, climate-driven moisture-balance fluctuation at decade-to-century time scales may have caused marked shifts in terrestrial vegetation ecotones; significant anthropogenic forest clearance there seems to have started only in the 17th century AD, after the introduction of maize by Arab merchants. Archaeological and linguistic data from regions north and west of Lake

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Victoria (Reid, 2000; Robertshaw and Taylor, 2000; Killick, 2009; de Filippo et al., 2012) suggest that (sub)humid western areas of the East African Plateau experienced human landscape modification for a substantially longer period of time. Unfortunately, ambiguity in the pollen records of past vegetation history and/or dating mismatches with the separate proxy records of past climate change have so far hampered efforts to distinguish more clearly climatic and human influences on vegetation history in this region (e.g., Marchant and Taylor, 1998; Taylor et al., 1999; Ssemmanda et al., 2005; Ryves et al., 2011). As a result, it remains difficult to estimate the magnitude of climatic moisture-balance variation responsible for a certain vegetation change inferred from fossil pollen, and to translate pollen assemblage changes into reconstructions of past vegetation change across the landscape. An integrated and quantitative paleoecological approach, including region-specific calibration of paleovegetation proxies (e.g., Vincens et al., 2006; Gelorini et al., 2012b) and their historical validation (e.g., Gelorini et al., 2012a), will be key to a more robust discrimination of vegetation responses to climate change and (pre-) historical human impact.

In this study, we investigate fossil pollen (and fern spore) assemblages in a ~200 year high-resolution lake-sediment record from pristine open woodland savannah in southwestern Uganda to assess the sensitivity of the East African lowland grassland-forest ecotone to historical, decade-scale trends in annual rainfall. Specifically we trace regional vegetation response to three episodes of increased rainfall dated to the 1820s–1830s, ca. 1865–1890 and from 1962 to around 2000. Over the nearby Lake Victoria basin, the most recent of these episodes represented a positive rainfall anomaly on the order of 10% from the long-term mean (Nicholson and Yin, 2001). Analyses of sedimentological characteristics (Bessemis et al., 2008) and non-pollen palynomorphs (Gelorini et al., 2012a) from this same record had demonstrated the local occurrence of dry/wet climate cycles which matched the timing of regional climate variability reconstructed from longer lake records nearby (Stager et al., 2005; Russell et al., 2007). In addition, we analysed the modern pollen spectra from surface-sediment samples in eight other small lakes bridging the regional

natural landscape around Lake Chibwera is a wooded grassland, composed mainly of the grasses *Themeda triandra*, *Imperata cylindrica* and *Cymbopogon nardus* with dispersed *Acacia gerrardii*, *Acacia siberiana*, *Capparis tomentosa* and *Ficus* sp. Bush thickets (evergreen bushland; White, 1983) of *Capparis tomentosa* and *Euphorbia candelabrum* trees shelter *Jasmina* sp. and *Ipomoea* sp.; *Sporolobus pyramidalis* is a common grass. Riparian forest in nearby Kyambura Gorge and along the ravines of ephemeral streams include trees such as *Cynometra* sp. and *Diospyros abyssinica*, and the palm *Phoenix reclinata* in wet open-canopy areas (Krueger and Johnson, 1996; FAO, 2005; Kirabo et al., 2011).

2.2 Regional climate, vegetation and land use

The climate of southwestern Uganda is classified as tropical sub-humid, with a bimodal seasonal rainfall regime peaking in March–May and October–December. Rainfall patterns are strongly driven by monsoonal winds from the Indian Ocean, modulated by the north-south passage of the Intertropical Convergence Zone (ITCZ) across the equator, and associated west–east movement of the Congo Air Boundary (CAB) separating Indian Ocean and Atlantic moisture sources (Nicholson, 1996; Mutai and Ward, 2000). Depending on local topography, mean annual rainfall varies between ~ 800 and 1300 mm yr⁻¹, reaching around 900 mm yr⁻¹ on the Rift Valley floor near Lake Chibwera, and mean annual evaporation varies from ca. 1600 to 1900 mm yr⁻¹ (Bessemis et al., 2008). As indicated by historical gauge measurements and water-level reconstructions from Lake Victoria (Piper et al., 1986; Nicholson and Yin, 2001; Stager et al., 2005), regional rainfall has fluctuated substantially in the past ~ 200 years, with periods of relative drought (e.g., in the late 18th/early 19th century and AD ~ 1920–1962) alternating with episodes of wetter conditions (e.g., ~ 1865–1885 and ~ 1962–2000; Fig. 2).

Modern-day vegetation on the uplands of the Rift Valley escarpment east of our study area is identified as Lake Victoria Regional Mosaic (White, 1983), which is a forest/savannah mosaic with remnants of evergreen or semi-deciduous forest

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(specifically the Kasyoha-Kitomi Forest Reserve), and savanna woodland with trees such as *Acacia*, *Combretum* and *Euphorbia*. Here, persistence of the understory grass layer (mainly *Pennisetum purpureum* and *Themeda triandra*) depends on regular burning, either natural or (increasingly) anthropogenic. Demographic pressure has significantly reduced Uganda's natural forests and bushlands (Andrua, 2002); except for national parks, forest and wildlife reserves, most landscapes in the crater lake-districts are now strongly impacted by agricultural activity (cropland and plantations), in our study area to within 2 km of Lake Chibwera (Fig. 1). The region's remaining fragments of evergreen forest are characterized by *Parinari excelsa*, *Strombosia scheffleri*, *Drypetes gerrardii* and *Carapa grandiflora*. In the semi-deciduous forests (such as Maramagambo forest in QENP, to the south-west of Lake Chibwera), *Maesopsis eminii*, *Olea welwitschii*, *Sapium ellipticum* and *Phyllanthus discoideus* characterize the colonizing stage, followed by a succession of mainly *Khaya anthotheca*, *Entandrophragma* ssp. and *Cynometra alexandri*, and climax vegetation composed of *Cynometra alexandri* with *Celtis* ssp. and *Strychnos mitis* (Langdale-Brown, 1964; Vincens et al., 1997; Kirabo et al., 2011). Montane rainforest (e.g., *Podocarpus milandjianus*, *Rapanea melanophloeos*, *Prunus africana*) and Afroalpine vegetation (Ericaceae) is mostly restricted to the Rwenzori Mountains (Vincens et al., 1997), over 50 km to the northwest of Lake Chibwera.

3 Material and methods

3.1 Sediment sampling, lithology and chronology

Sediment core CHIB02-1P (0–117 cm) was recovered in two sections from the deepest part of Lake Chibwera, using a rod-operated single-drive piston corer (Wright, 1980). The unconsolidated uppermost sediments (~ 25–30 cm) were extruded upright in 1 cm increments with a fixed-interval sectioning device (Verschuren, 1993), and transferred to Whirl-Pack bags. The deeper, more consolidated sediments were retained intact

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in the original core tubes (Bessemis et al., 2008). Due to depletion of uppermost mud following previous analyses, we extended the Chibwera sequence upward 9 cm (now totaling 126 cm), using the overlapping UWITEC gravity core CHIB08-1G collected at the same GPS position (Gelorini et al., 2012a). The cores were cross-correlated using data of bulk sediment composition (based on loss-on-ignition, LOI) and magnetic susceptibility, and the depths of lithostratigraphical transitions defined by Bessemis et al. (2008) adjusted accordingly. The chronological framework is based on combined ^{210}Pb and ^{137}Cs dating, supplemented by two AMS ^{14}C dates on terrestrial plant macrofossils, calibrated using CALIB 5.0 (Stuiver et al., 2005); see Bessemis et al. (2008) for details.

The extended composite sequence of Lake Chibwera consists of four lithostratigraphic units (Fig. 4). Unit 1 (126–121 cm) is composed of dry but organic clays with few large plant fragments, representing a poorly defined pre-19th century lacustrine phase (Bessemis et al., 2008). It is overlain by a horizon of dry clay (Unit 2, 121–112 cm) with modest organic content (11–16%), marking the lake's complete desiccation (but likely seasonal flooding) during a prolonged episode of extreme regional drought in the late 18th to early 19th century (Verschuren, 2004; Bessemis et al., 2008). This desiccation horizon is overlain by a section of moist, organic peaty clay with abundant coarse plant fragments (Unit 3, 112–101 cm), representing the early to mid-19th century phase of gradual lake filling, characterized by a shallow-water environment with submerged macrophytes and swampy riparian zone. It is followed by soft organic clays (Unit 4, 101–0 cm), reflecting the true lacustrine phase with mostly higher lake level which has prevailed from the 1860s until today (Bessemis et al., 2008).

The relationship between fossil pollen assemblages and actual vegetation cover across the grassland-forest ecotone of southwestern Uganda was calibrated using modern-day pollen spectra from nine surface-sediment samples recovered from Lake Chibwera and eight neighbouring crater lakes. Seven of these lakes are located inside the protected area of QENP, and span the vegetation gradient from open grass savannah (Kikorongo and Kitagata, both north of Kazinga Channel) to open

savannah woodland (Chibwera) or bushland (Bagusa, immediately south of Lake George) to moist semi-deciduous forest (Kacuba, Kyasanduka and Nyamusingire, all in Maramagambo forest) (Fig. 1). The two other lakes (Kanyamukali and Katinda) were originally located near the woodland-forest border but are now strongly impacted by land clearance and agricultural activity.

3.2 Pollen analysis

From the Chibwera sediment sequence, in total 33 samples of 1 mL volume were extracted for pollen analysis, mostly from 1 cm increments at 4 cm intervals (except for two 3 cm increments in the uncompacted upper 10 cm). In all other lakes, pollen was extracted from homogenized samples of the upper 3–5 cm of uncompacted surface muds, which according to ^{210}Pb -dating results (Russell et al., 2007; Bessems et al., 2008) on longer sequences from four of these lakes (Chibwera, Katinda, Kanyamukali, Kitagata) have accumulated in the last four to ten years. Following standard procedures (Faegri et al., 1989), the samples were treated with warm 10% KOH, warm 10% Na pyrophosphate, 96% acetic acid, an acetolysis mixture of 1 : 9 H_2SO_4 and acetic anhydride boiled to 100 °C for 10', and finally 96% ethanol. A bromoformethanol mixture with specific gravity 2.0 was used to separate pollen grains from heavier mineral sediment components. The microfossil extracts were then put in glycerine, dried overnight in an oven at 40 °C and finally mounted on microscope slides.

Pollen (and fern/moss spore) nomenclature and identifications in this study are based on the African Pollen Database (APD) (for details: <http://medias.obs-mip.fr/apd>; Vincens et al., 2007). In most samples at least 500 terrestrial pollen grains were counted (range 275–1313; mean 638). If Poaceae pollen counts were too low to ensure a solid percent abundance estimate, counting continued until ideally at least 300 Poaceae pollen grains were encountered. Abundances of individual pollen and spore taxa are expressed as percentages of the non-local pollen sum (i.e., excluding (semi-) aquatic taxa such as the Cyperaceae, and ferns and mosses); the results were plotted using TILIA 1.7.16 (Grimm, 2011). Pollen assemblage zones

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abundance in our surface-sediment samples is likely inversely proportional to distance from its nearest important pollen source in farmlands to the east, southeast or north of the study area.

The case of *Eucalyptus* highlights the mosaic distribution of natural and impacted vegetation types in our study area at the spatial scale of individual sites' relevant pollen source area, resulting in "mixed" pollen assemblages (Vincens et al., 2006). This also explains the presence of typical savannah trees (*Acacia*, *Maerua*, *Euclea*) in our pollen spectra from inside Maramagambo forest; although park vegetation immediately surrounding all three lakes may be relatively pristine, farmland or degraded forest occurs to within a few km of these sites (Fig. 1). The percent Poaceae pollen recorded at our three forest sites nevertheless remains markedly lower than at our open savannah woodland sites (Fig. 3). Similarly, the presence of *Acalypha* (here most likely the low-stature woodland shrubs *A. fruticosa* and *A. indica*), *Phoenix reclinata*-type and *Celtis* in pollen spectra from pristine grass savannah sites can be considered "contamination" from more densely wooded savannah and/or strips of riverine forest nearby, or from more distant semi-deciduous forest. Nevertheless, the percent grass pollen recorded at the true grass savannah sites remains markedly higher than at wooded savannah sites (Fig. 3).

The apparent over-representation of Poaceae at our three forest sites is consistent with the results of Duffin and Bunting (2008), who in the mosaic vegetation of a southern African savanna found that local grasses produced about twice as much pollen as the arboreal taxa. Nevertheless, in our study region the summed pollen percentage of true forest trees increases from 5.1–13.8% in grass and woodland savannah sites to 12.5–20.9% at the three sites inside semi-deciduous Maramagambo forest. Pollen from *Podocarpus* and *Prunus africana*-type originate from Afromontane vegetation on the Ruwenzori Mountains, at least 30 km away. Also the modest amount of Ericaceae pollen recovered at our reference lakes likely originates in the Rwenzori, although the occurrence of short-stature Ericaceae on the local Rift Valley escarpment cannot be excluded (Henry Osmaston, personal communication). Pollen from *Olea*

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about 1860 onwards (Unit 4). In the temporal sequence of pollen assemblages, three successive phases can be discerned. At the base of this subzone marked decreases of Poaceae (to 55–60%), Asteraceae, Chenopodiaceae and *Achyranthes-type aspera* are compensated by a temporary expansion of *Acacia* and *Rhus* type *vulgaris*, along with the herbs *Polygonum senegalense*-type and *Solanum*-type. *Myrica* and the Urticaceae record similarly rapid but more long-term increases. Shortly thereafter the summed abundance and diversity of woodland tree taxa increases strongly, most notably by *Acalypha* and *Phoenix reclinata*-type but also *Ficus*, *Myrica*, *Celtis*, *Flueggea virosa*, *Euclea*, *Baphia*-type and a representative of the Combretaceae/Melastomataceae. Together with the robust presence of Urticaceae, this diversification of tree taxa and reduction in Poaceae suggests wetter climatic conditions promoting the development of a type of savannah woodland not unlike the vegetation surrounding Lake Chibwera today (compare with Fig. 3). The strong reductions in Cyperaceae (to 25%), *Typha domingensis*-type and undifferentiated fern and moss spores reflect lake filling, in which emergent aquatic vegetation retreated to a more or less narrow belt along the shoreline. However, in the upper half of this subzone (dated between 1850 and 1895), Poaceae pollen abundance increases again to 70–80%, along with a renewed increase of Chenopodiaceae, and appearances of other dryland herbs such as *Commelina-type forskalaei*, *Tarenna-type graveolens* and *Justicia-type odora*. Expansion of these taxa is mostly at the cost of *Acalypha*, but also of *Ficus*, *Myrica*, *Euclea* and *Baphia*-type along with *Solanum*-type herbs. The simultaneous increase in Cyperaceae pollen (peaking at 35%) suggests an expansion of the littoral sedge swamp and thus a lowering of lake level, but this is not clearly recorded in the lithostratigraphy.

Pollen assemblages of sub-zone Chib-2b (84–67 cm, ca. 1895–1925) are characterised by a strong decline in Poaceae pollen to its lowest level (45%) of the entire sequence, accompanied by strong rises in woodland trees such as *Acalypha*, *Phoenix reclinata*-type, *Celtis*, *Flueggea virosa* and *Euclea*, but also true forest trees such as *Allophylus*, *Macaranga*-type and *Dodonaea viscosa*-type. Also

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Alchornea, mostly rare before, is now consistently present. Among the herbaceous taxa, the Urticaceae do well but also Asteraceae, *Cyatula*-type *orthocantha*, *Solanum*-type, *Swertia usambarensis*-type and *Tarenna*-type *graveolens*; in contrast, Chenopodiaceae disappear almost completely. Within the group of aquatic taxa, Cyperaceae retreats from its earlier maximum, although not in synchrony with the reduction in Poaceae. Overall this pollen sub-zone suggests the presence of savannah woodland with greater tree cover than today, and more damp soil habitat promoting *Phoenix reclinata*. The increases in *Allophylus* and *Macaranga*-type trees suggest a simultaneous expansion of nearby evergreen and moist semi-deciduous forest, all indicative of climatic conditions significantly wetter than today.

Sub-zone Chib-3a (67–31 cm, ca. 1925–1970) is characterized by the strong rebound of Poaceae pollen to 70–75%, whereas woodland trees such as *Myrica*, *Celtis*, *Flueggia virosa*, *Acalypha* and *Phoenix reclinata*-type, as well as all forest trees, experience modest to strong reductions. Among the herbaceous taxa, Asteraceae and *Cyatula*-type *orthocantha* of the Amaranthaceae almost disappear, and also the presence of Urticaceae is less robust than throughout Zone Chib-2. The Chenopodiaceae again expand in synchrony with the Poaceae, supplemented by *Commelina*-types *benghalensis* and *forskalaiei*, and *Justicia*-type *odora* (the latter for the first time consistently present). The Cyperaceae initially maintain their starting value of ca. 20%, but then somewhat unexpectedly fall to values of ca. 10% in the upper half of this sub-zone. Overall, this pollen sub-zone documents the return of a more negative climatic moisture balance, and the resulting decline of tree cover in the savannah woodland surrounding Lake Chibwera.

The three pollen assemblages defining Sub-zone Chib-3b (31–21 cm, ca. 1970 to the late 1980s) are broadly similar to those of Chib-3a, except for increases in *Allophylus*, *Myrica*, *Celtis*, the Urticaceae and *Tarenna*-type *graveolens*, a robust re-appearance of *Alchornea*, and the (near-) disappearance of Chenopodiaceae, *Commelina*-type *benghalensis* and *Justicia*-type *odora*. These species responses suggest the return of a wetter climate, however the percent abundances of *Acalypha*

50%) and reductions in, amongst others, *Celtis*, *Acalypha*, *Macaranga*, *Allophylus*, Combretaceae/Melastomataceae, and *Swertia usambarensis*. Woodland taxa such as *Phoenix*, *Euclea* and *Alchornea* remain stable, creating uncertainty as to whether increasing Poaceae pollen actually reflects vegetation response to a new trend of climatic drying. The recent reductions in influx of *Allophylus* and *Celtis* pollen may also result from human encroachment into the Kasyoha-Kitomi forest. The only robust indication in the Chibwera pollen record of a recent drying trend is the doubling of Cyperaceae pollen in sub-zone Chib-4b compared to Chib-4a, which we interpret to reflect expansion of the local sedge swamp, and thus a lowered lake level.

5 Discussion

5.1 Pollen-assemblage signatures of vegetation response to climate change

Alternating opposite trends in the percent abundances of grass (Poaceae) pollen and some arboreal taxa, particularly *Acalypha* and *Phoenix reclinata*-type, in the Lake Chibwera record define a historical sequence of six distinct episodes of climate-driven vegetation change in the past ~ 250 years. To a large extent, stratigraphic zone boundaries determined by numerical clustering of successive pollen assemblages (Fig. 4: CONISS zones Chib-1 to Chib-4b) coincide with the levels where shifts (increases/decreases) in the Poaceae percentage curve become apparent.

Three episodes of inferred dry climatic conditions (late 18th century to ca. 1820, ca. 1850–1880, ca. 1920–1980; red shading in Fig. 4) are characterized by high (> 70%) or rising percentages of Poaceae pollen, and solid occurrences of herbaceous taxa such as the Chenopodiaceae, *Justicia*-type *odora*, and *Commelina*-types *benghalensis* and *forskalaiei*. Chenopodiaceae pollen is commonly used as indicator of vegetation disturbance by humans (e.g., Taylor et al., 2005; Drescher-Schneider et al., 2007). However, chenopods also occur naturally in African grasslands visited by large wild herbivores (Gelorini and Verschuren, 2012). Peak Chenopodiaceae abundances (up

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to 3 %) in pollen zone Chib-1 (126–115 cm) indicate that these plants expanded on and around the seasonally flooded Chibwera lake bed during the late 18th-century drought, possibly benefiting from soil disturbance caused by large mammals.

The three inferred wet phases (ca. 1820–1850, ca. 1880–1920, ca. 1980–2004) are characterized by low (45–50 %) or decreasing percentages of Poaceae pollen, and at least modest increases in savannah trees and shrubs (*Acacia*, *Rhus* type *vulgaris*) and herbs such as Asteraceae, Urticaceae, *Solanum* and *Swertia usumbarensis*-type. Also taxa of denser woodland and shrub savannah (*Acalypha*, *Myrica*, *Combretum*), riparian forest (*Phoenix reclinata*-type) and moist or semi-deciduous forest (*Celtis*, *Macaranga*-type, *Alchornea*, *Allophylus*) show a repeated positive response during these episodes. Clear peaks in (otherwise rare) Ericaceae pollen during the latter two of these periods supports our earlier suggestion that this is pollen may originate from low-elevation heather species occurring along the Rift Valley escarpment, rather than the distant Afroalpine zone in the Rwenzori. The strongest responses (i.e., with greatest impact on the relative abundance of Poaceae) occur in *Acalypha* and *Phoenix reclinata*-type. Some savanna and woodland trees, such as *Euclea* and *Flueggea virosa*, resemble the latter two taxa by expanding strongly at the end of the lake drystand ca. AD 1820, but then show fairly stable (*Flueggea*) or gradually increasing (*Euclea*) abundances over the following 200 years. Trends in Asteraceae are mostly opposite to those in Poaceae, except that both peak during the late 18th-century drought. Even allowing for some promotion of Asteraceae by intensifying human activity along park boundaries since the 1980s (Fig. 4: zone Chib-4a), it appears that in this open woodland savannah, Asteraceae tend to benefit from increased moisture while also having taken advantage of new habitat created by a lake drystand.

The inferred alternation of wet and dry episodes in the Chibwera region over the past ~ 250 years is consistent with historical data and independent lake-based reconstructions of East African climate change within recent centuries (Verschuren, 2004). Severe late-18th century drought (lasting until AD 1815–1820) followed by high rainfall in the 1820s has now been documented as a cycle of desiccation and refilling in

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shallow lake basins throughout equatorial East Africa (e.g., Verschuren, 1999; Russell et al., 2007; Bessems et al., 2008). Compilation of historical records indicates that the region's climate was again relatively dry from the 1830s to the early 1850s (Nicholson and Yin, 2001). Lake Victoria is said to have risen rather steadily in the first decades after its discovery in 1858, until reaching its highest documented level in 1878. This was followed by a rapid decline in the 1880s, and relative stabilization around its present-day level from the 1890s until 1961–1962, when exceptional rainfall caused high Nile discharge and lake transgressions across East Africa (Flohn, 1987). Notwithstanding intermittent dry years in the 1970s and 1980s, this somewhat more positive regional moisture balance has been maintained for four decades; only within the last decade has Lake Victoria regressed to levels approaching its pre-1961 mean (Fig. 2). Also the level of Lake Chibwera fell 0.6 m between our field campaigns in July 2001 and August 2008; the accompanying expansion of riparian wetland likely explains the more substantial presence of Cyperaceae pollen in the uppermost cored sediments (zone Chib-4b). The lake-level reconstruction for Lake Victoria by Stager et al. (2005), which is based on the percent abundance of shallow-water diatoms in the sediment record of one of its peripheral bays, confirms that in the late 18th and earliest 19th centuries, also Lake Victoria stood lower than at any time since then (Fig. 2).

Strong congruence of the temporal pattern of pollen-inferred vegetation change around Lake Chibwera with this history of regional climate change suggests a causal relationship. However, the exact timing of reconstructed vegetation changes appears somewhat delayed relative to the improving or deteriorating moisture balance which is likely to have caused them (compare Fig. 4 with Fig. 2). The discrepancy can be attributed partly to dating uncertainty in the Chibwera sediment record (see Bessems et al., 2008). Still, the late 20th-century vegetation response likely caused by the improved moisture balance which started in the early 1960s is recorded in sediments dated to the 1970s and up to around 1980 (the Chib-3b/Chib-4a zone boundary), i.e. well above the robust ^{137}Cs marker horizon of peak atomic bomb testing in 1964 (at 36 cm; Fig. 5). Taxa such as *Allophylus*, *Myrica*, *Rhus* type *vulgaris*, *Celtis*, *Alchornea*

and Urticaceae expanded rapidly (already at the base of zone Chib-3b), followed by *Solanum*-type and *Swertia*-type, and finally by *Acalypha* and *Phoenix reclinata*-type; it is the latter which drive much of the recorded decline in Poaceae pollen.

5.2 Sources of pollen in Lake Chibwera sediments

Lake Chibwera occupies a low-rimmed maar crater basin, situated in an open grass-dominated landscape grading into woodland and forest occupying the uplands which flank the Rift Valley to the north and south. As a result, both today and in the past Lake Chibwera has captured pollen from a variety of biomes: Afromontane forest, closed-canopy lowland evergreen and semi-deciduous forests, open-canopy savannah woodland and grass and shrub savannah. The pollen record of vegetation change recorded in Lake Chibwera sediments therefore reflects vegetation response to climate variability both in the immediately surrounding landscape (excluding truly local (semi-) aquatic vegetation) and at a broader regional scale (cf. Jackson, 1990; Sugita, 2013). Discerning between them is facilitated by comparisons with the composition of pollen spectra deposited at reference sites today (Mathias and Giesecke, 2014). In this study, these are distributed across the regional forest-grassland ecotone which in turn reflects a (largely topographic) gradient in climatic moisture balance. Also the relevant pollen source areas of each reference site, which for “medium-sized” lakes in these (semi-) open forests, woodlands and grasslands are on the order of 600–900 m in diameter (Duffin and Bunting, 2008; Sugita, 2013), all encompass multiple types of vegetation, resulting in mixed assemblages (cf. Sect. 4.1). Nevertheless, systematic differences in the percent abundance of characteristic taxa associated with each biome help to assess the magnitude of vegetation change which occurred at Lake Chibwera in the last ~ 250 years.

The largest fraction of pollen in both modern-day and fossil assemblages preserved in the sediments of small and medium-sized lakes originates from vegetation in their near surroundings (Jacobson and Bradshaw, 1981; Broström et al., 2004; Duffin and Bunting, 2004), and are delivered to the lakes either by wind, precipitation or local

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surface run-off (Moore et al., 1991). This includes the typically airborne pollen of Poaceae, *Euclea*, Capparidaceae species, *Flueggea virosa*, *Rhus* type *vulgaris* and other taxa common to the local SAVA biome, and of some trees in the forest of Kyambura gorge ~ 5 km to the west. Pollen of Afromontane *Podocarpus* and *Prunus africana*-type must be advected exclusively by wind, from the Ruwenzori mountains. An unknown but sizable fraction of pollen from *Celtis*, *Macaranga*, *Allophylus* and *Dodonaea viscosa*-type, which grow in either pristine or degraded fragments of moist and semi-deciduous forest on the eastern Rift Valley flank, reaches Lake Chibwera by surface inflow via the Mbanga stream and Lake Kyanwiga. This may also be the case for Cupressaceae and *Eucalyptus*, plantations of which now partly replace this forest. In the case of Cupressaceae, however, an alternative pollen source are cypress trees planted in the 1980s at a camping site in the direct vicinity of Lake Chibwera (Gelorini et al., 2012a). Advection by wind from intact forest further to the east (Kasyoha-Kitomi) or south (Maramagambo) likely contributes a lesser fraction of the forest-tree pollen reaching Lake Chibwera, considering that the distance to these sources mostly exceeds 10 km.

The principal source of *Phoenix reclinata*-type and *Acalypha* pollen, the two taxa showing the strongest response to climate-driven moisture-balance change in the Chibwera record, is uncertain. *Phoenix reclinata* is a characteristic component of local stands of riparian forest, hence stream inflow from distant stands is potentially a major contributor. However, riparian forest also occurs in shallow ravines traversing the savannah to the north and west of Lake Chibwera (Fig. 1), and it occupies sizable areas of damp soil in dry crater basins immediately to the south and east. Thus, increasing abundance of *Phoenix reclinata*-type pollen may reflect a true expansion of riparian forest and damp soil habitat in the near vicinity of Lake Chibwera, with deposition of wind-dispersed pollen. Similarly, stream inflow is a likely source of pollen from *Acalypha* herbs and shrubs growing along distant forest margins, but *Acalypha fruticosa* is a shrub of dry woodlands and shrub savanna (Hemp, 2006), such as now occurs to the north of Lake Chibwera towards Lake George (Fig. 1). Crucially, for both

Acalypha and *Phoenix*, the fraction of pollen contributed by stream inflow may vary together with climatic moisture balance, such that the effective size of Lake Chibwera's pollen source area for these taxa cannot be assumed constant through time. A wetter climate is likely to both promote populations near Lake Chibwera and enhance the input of pollen from more distant (potentially stable) stands.

5.3 Vegetation history of open woodland savannah in the Rift Valley of western Uganda

Throughout the ~250 year time window represented by the studied sediment sequence, Lake Chibwera has been situated in vegetation of plant functional type tr3+g belonging to the SAVA biome (Vincens et al., 2006). This is indicated by the continuously high (variable, but always > 45 %) percentages of Poaceae pollen, the low combined percentage of trees and shrubs with a Sudanian (White, 1983) phytogeographical affinity such as *Euclea*, *Maerua* and *Acacia*, and the consistent presence of dryland herbs belonging to the Amaranthaceae, Chenopodiaceae and Commelinaceae. Dry phases in the Chibwera pollen record display higher Poaceae percentages (maxima of 75–80 %) than recorded in the modern-day samples from our two grass savannah sites, in which they account for ca. 63–67 % of the pollen sum. This implies that during historically dry episodes within the past ~200 years, treeless grassland was more extensive in the landscape around Lake Chibwera than is the case today at QENP sites located more centrally in the dry Rift Valley between lakes Edward and George (Fig. 1). Even less woodland trees and shrubs were present during the late-18th century drought when Lake Chibwera stood dry, but Poaceae pollen did not attain higher percentage values because of peak contributions from herbs (Asteraceae, *Achyranthes*, chenopods) growing on and around the dry lake bed.

In the pollen assemblage of the earliest wet episode, dated to the mid-19th century, Poaceae drops to percentage values of ca. 55 %, equivalent to those of Lake Chibwera and other open woodland savannah sites within QENP today. The two other recognized wet episodes, dated to the late 19th-early 20th century and the last decades of the

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20th century, display grass pollen values that are substantially lower still (45–50%), approaching that of our reference sites located in protected semi-deciduous forest. It is doubtful that during these wet periods the entire landscape around Chibwera developed high tree cover, or that regional forest cover contracted during dry periods.

5 Excluding *Acalypha* and *Phoenix reclinata*-type, the combined abundance of forest tree taxa remains rather low, and many taxa are found only occasionally. Together, this implies a distant location of the moist and semi-deciduous forests from which taxa such as *Macaranga*, *Celtis*, *Olea capensis*-type, *Allophylus*, *Holoptelea grandis*,
10 *Myrsine africana*, *Cassia*-type, *Embelia* and *Diospyros* originate, throughout the period represented by this record. More limited stream discharge from the eastern escarpment during dry episodes further reduced the visibility of these taxa in the Chibwera pollen assemblages. The comparatively higher percent abundances and strong apparent climate response of *Acalypha* and *Phoenix reclinata* indicate that
15 multi-decadal variation in climatic moisture balance caused significant changes in the regional prevalence of savannah woodland/bushland and riparian forest stands, beyond what can be explained by changes in stream input.

6 Conclusions

Combination of a high-resolution pollen record with modern pollen-assemblage data from reference sites spanning the modern-day regional vegetation ecotone permitted tracing local vegetation response to (multi-)decadal climatic moisture-balance variation in a natural savannah landscape of western Uganda. We find that the landscape surrounding Lake Chibwera in Queen Elisabeth National Park has been an open woodland savannah throughout the past 200 years, with historical rainfall variability exerting relatively modest effects on local tree cover (mostly the abundance of *Acacia*
20 and *Ficus*) and the prevalence of damp soil areas (reflected in the abundance of *Phoenix*). Enhanced pollen influx via upland streams seems to be responsible for the strong apparent expansion of true forest trees during wet episodes. Hence, isolation of
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the truly local vegetation response will require palynological investigation of a savanna site with similarly continuous deposition but limited hydrological sensitivity compared to Lake Chibwera. On the positive side, the (site-specific) influence of pollen from exotic trees and other cultural indicators fails to mask the region's natural vegetation dynamics.

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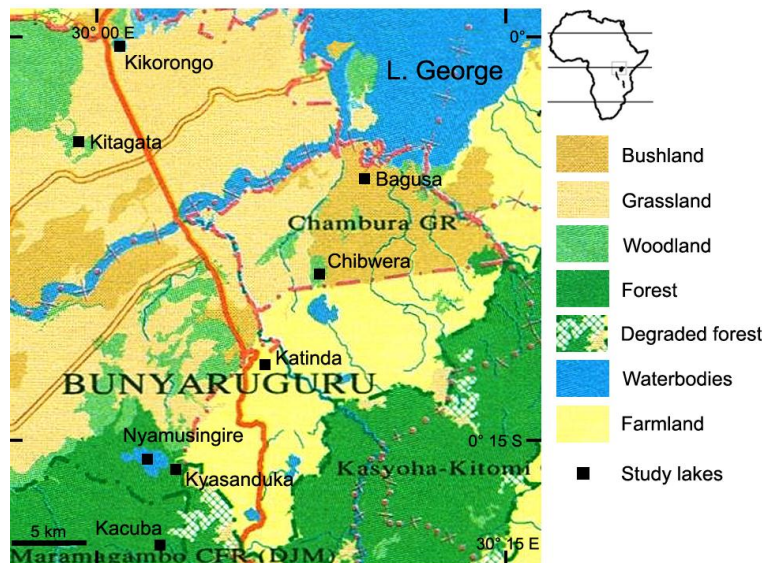


Fig. 1. Map of modern-day vegetation distribution in the Bunyaruguru area of southwestern Uganda (equatorial East Africa, cf. inset map), showing the locations of Lake Chibwera and eight pollen reference sites within and near Queen Elisabeth National Park (red dash-stippled line is the park boundary). Modified from the National Biomass Study (1996) map of Uganda land cover stratification.

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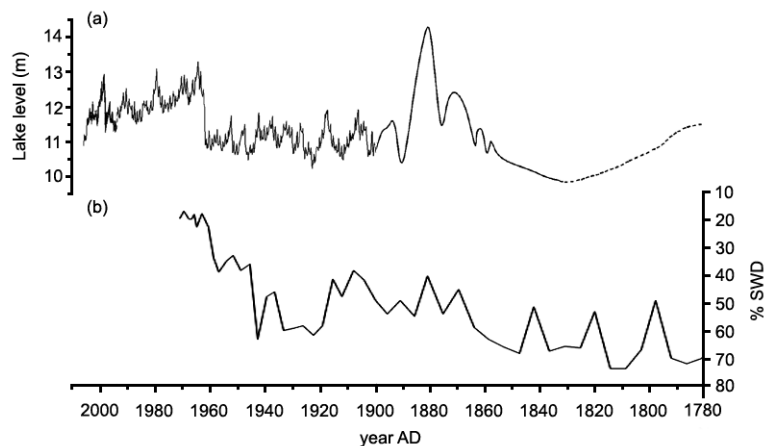


Fig. 2. Moisture-balance variability in Uganda during the past ~200 years, inferred from **(a)** historical reports and Lake Victoria water-level gauge data (since 1896) at Jinja (modified after Nicholson and Yin, 2001), and **(b)** percent shallow-water diatom species (% SWD) in fossil diatom assemblages from a peripheral bay of Lake Victoria (Stager et al., 2005).

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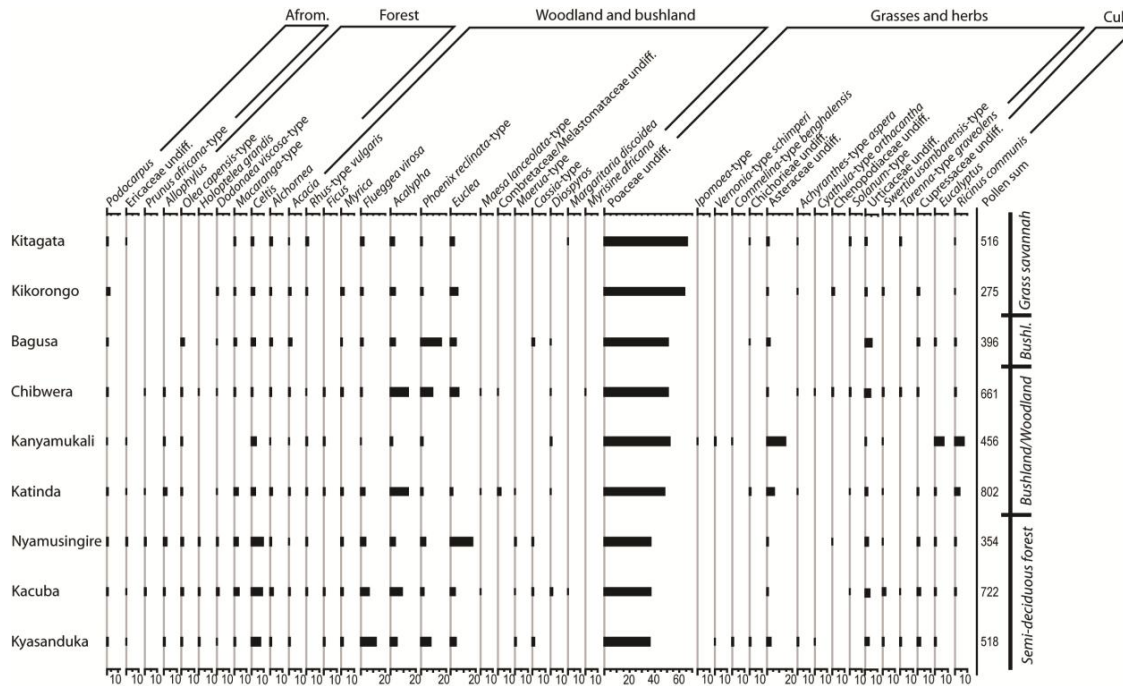


Fig. 3. Percentage abundances of selected terrestrial pollen taxa recovered from surficial bottom sediment of nine reference lakes in the Bunyaruguru area. The selection is identical to that shown in Fig. 4, except for seven types (*Baphia* type, *Embelia* type, *Hymenodictyon*-type *floribundum*, *Sericostachys*-type *scandens*, *Polygonum senegalense*-type, *Commelina*-type *forskalaiei* and *Justicia*-type *odora*) not found in these surface-sediment samples. Sites are ordered from top to bottom according to their position along the regional grassland-forest gradient.

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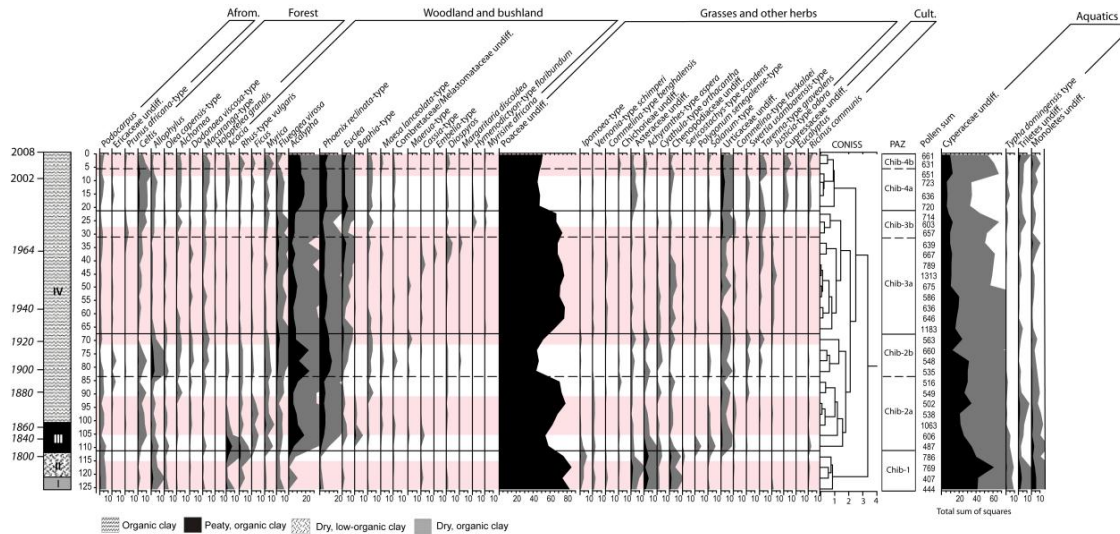


Fig. 4. Stratigraphic distribution and zonation of pollen taxa with minimum overall abundance of 0.5 % in the studied sediment sequence from Lake Chibwera. Taxon abundances are expressed as percentages of the terrestrial pollen sum (black, with $\times 5$ exaggeration curves in grey). The chronology is based on ^{210}Pb , ^{137}Cs and AMS ^{14}C dating (Bessemers et al., 2008). Dry phases (cf. Fig. 2) are highlighted by pink shading. PAZ: Pollen Assemblage Zones.

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