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Mauritius since the last glacial: environmental and climatic reconstruction of the last 38 000 years from Kanaka Crater

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ABSTRACT: A 10 m long peat core from the Kanaka Crater (20° 25' S, 57° 31' E), located at 560 m elevation in Mauritius, was analyzed for microfossils. Eight radiocarbon ages show the pollen record reflects environmental and climatic change of the last ca. 38 cal ka BP. The record shows that the island was continuously covered by forest with *Erica* heath (*Philippia*) in the uplands. Cyperaceous reedswamp with *Pandanus* trees was abundant in the coastal lowlands as well as locally in the waterlogged crater. The record shows changes in climatic humidity (wet from 38.0 to 22.7 cal ka BP, drier from 22.7 to 10.6 cal ka BP, and wetter again from 10.6 cal ka BP to recent) as the main response to climate change. A high turnover in montane forest species is evidenced at 22.7 cal ka BP and at the start of the Holocene. The limited altitudinal ranges in the mountains of Mauritius (maximum altitude 828 m), and changing humidity being more important than changing temperature, suggests that in response to climate change a reassortment in taxonomic composition of montane forests might be equally important as displacement of forest types to new altitudinal intervals. We found weak impact of the latitudinal migration of the Intertropical Convergence Zone and data suggest that the Indian Ocean Dipole is a more important driver for climatic change in the southwest Indian Ocean. Copyright © 2011 John Wiley & Sons, Ltd.

KEYWORDS: Mauritius; Kanaka Crater; pollen analysis; Indian Ocean Dipole; climate change.

Introduction: oceanic island systems and climate change

Climate change may trigger individual plant taxa to migrate to new areas where plant-specific ecological ranges are within the range of climate variability. Plant communities and higher-ranked vegetation belts often include many taxa with similar ecological ranges, causing floristic discontinuities in the composition of the forests along climatological gradients, temperature, humidity and atmospheric CO₂ pressure in particular. Therefore, in the past, climate change resulted in a concerted migration of main vegetation types. Climate change-driven altitudinal shifts of main vegetation belts on East African mountains (e.g. Hedberg, 1951, 1964; Coetzee, 1967; van Zinderen Bakker and Coetzee, 1988) were further specified, for example, for Mount Kilimanjaro (Hemp, 2005, 2006), Mount Kenya (Street-Perrott *et al.*, 2007) and Madagascar (Gasse and Van Campo, 1998). In tropical lowlands vegetation change is more related to changes in annual precipitation, seasonality, and in coastal areas the distance to the seashore (Zinke *et al.*, 2003; Hoelzmann *et al.*, 2004; Kröpelin *et al.*, 2008). Also, records of past precipitation and palaeohydrology of East African lakes (Johnson *et al.*, 2000; Barker *et al.*, 2004) show the response of climate change on local and regional ecosystems. However, some records hardly show evidence of changing plant composition across periods of major global climate change (Mumbi *et al.*, 2008) and this seems best explained by the dampening effect of the Indian Ocean hot water pool (Marchant *et al.*, 2006).

Small oceanic islands do not allow plant taxa to migrate significantly in order to balance the ecological requirements to

changing climatic conditions. With sea-level stands lowered by ~120 m during the Last Glacial Maximum (LGM) (Yokoyama *et al.*, 2000; Lambeck and Chappell, 2001) the modern surface of Mauritius of 1865 km² increased ~20%. Under all conditions Mauritius had a very limited surface, hardly allowing individual plant taxa and higher-ranked plant associations to migrate. Humid riverine gallery forests may function as a relatively stable stock of plant diversity which offers shelter to plant taxa during a variety of climatological conditions (Hannah *et al.*, 2008).

Endemic island species evolved in isolation from continental species, often in the absence of large herbivores and predators (Biber, 2002). Endemic species are therefore vulnerable to exotic species introduced by humans. Extinctions caused by colonization have occurred on many islands (Burney, 1997; Whittaker and Fernández-Palacios, 2007) and are well documented. Understanding causality and mechanisms of these historic extinctions can broaden the understanding of prehistoric extinctions (Diamond, 1984).

Undisturbed lake sediments and peat deposits enable reconstruction of past vegetational and climatic change. Records of environmental change in Mauritius may provide a frame that can be used to better understand how in a small island a high level of diversity is conserved across environmental changes from glacial to interglacial conditions. In addition, a reconstruction of the vegetation from the period just before humans arrived shows a document of the natural vegetation and may help as a blueprint for conservation and restoration activities.

Here we present the first study of the environmental history of Mauritius. We selected the 10 m long peat core from Kanaka Crater to show a pollen-based document of vegetation change and inferred past climatic conditions. We aimed to assess levels

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of past environmental change across the LGM and we make first comparisons with pollen-based records of environmental change from Madagascar and East Africa. This paper paves the way for ongoing studies in Mauritius from other craters as well as from coastal lowland sites. This will allow us to arrive at a later moment at a regional synthesis of Late Pleistocene environmental change and hints for driving mechanisms involved.

Setting

Geology and geography

Mauritius, together with the islands Réunion and Rodrigues, form the archipelago of the Mascarene Islands. Mauritius has a volcanic origin, and is located in the southwest Indian Ocean between latitude $19^{\circ} 50'$ and $20^{\circ} 51'$ S and longitude $57^{\circ} 18'$ and $57^{\circ} 48'$ E (Fig. 1). It was formed between 7.8 and 6.8 million years ago (McDougall and Chamalaun, 1969) from a volcanic hotspot currently located off the southeast coast of Réunion. Volcanic activity on Mauritius lasted until 25 cal ka BP (Camoïn *et al.*, 2004). The highest peak on Mauritius is located in the southwest at 828 m altitude.

Kanaka Crater lies in the southern mountains at 560 m altitude. It reflects a well-formed cone with a diameter of 300 m at the top (Fig. 2). The age of the cone and the most recent period of volcanic activity are unknown. The centre of the crater is occupied by a mire without open water.

Climate

In tropical areas climatic conditions are determined by the position of the Intertropical Convergence Zone (ITCZ). The

position relates to the latitude of maximum solar insolation. On an annual timescale the seasonal shift of the sun drives the ITCZ northward during the Northern Hemisphere summer and southward during the Southern Hemisphere summer. As a result, the patterns of the tropical monsoon system are driven by solar insolation (Kutzbach, 1981). On orbital timescales climate change in tropical areas is most influenced by the Earth's precessional cycle (Pokras and Mix, 1987; Cruz *et al.*, 2005) with a frequency band between 19 and 23 ka. The maximum values of solar insolation and as a consequence the belt with maximum precipitation migrates between 20° N and 20° S. Higher insolation values would result in stronger summer monsoons, whereas lower insolation values would result in weaker monsoons (Kutzbach, 1981; Ruddiman, 2006). Thus Mauritius is expected to experience a climatic extreme every half precession cycle at 10 ka distance in time.

Another important driver of climate is the Indian Ocean Dipole (IOD), a system of independent ocean circulation in the Indian Ocean (Marchant *et al.*, 2006). The IOD causes anomalous sea surface temperature (SST) variability – with high SSTs in the western Indian Ocean and low SSTs in the eastern Indian Ocean – which has an impact on regional atmospheric circulation and rainfall (Saji *et al.*, 1999). In the Eastern Arc Mountains in Tanzania, moist air derived from the Indian Ocean has resulted in relative ecosystem stability across the LGM (Mumbi *et al.*, 2008). The influence of the IOD interferes with the potential impact of precessional-driven climate change and may provide a regional specific response.

Vegetation

The flora of Mauritius has a high degree of endemism, with 39.5% of the flowering plant species endemic to Mauritius and 21.7% endemic to the Mascarene Islands (Baider *et al.*, 2010). Mauritius was almost entirely forested before human colonization, which started in AD 1638. After human colonization, ecosystems became rapidly degraded and destroyed. Today only remnants of native vegetation covering some 2% of the island surface can be found (Baider *et al.*, 2010), but all vegetation remnants have been invaded by exotics (Lorence and Sussman, 1986).

Native vegetation types comprise seven major categories, mostly determined by altitude and annual precipitation: coastal areas, palm savanna, lowland forest, lower montane forest, moist forest, montane forest and azonal uplands (Vaughan and Wiehe, 1937; Florens and Baider, pers. comm.) (Table 1). Coastal areas comprise ecosystems such as mangroves, coraline sand dunes and coastal wetlands. Palm savannas grow under natural conditions in the coastal plains on the driest leeward areas of the island (Safford, 1997). The palm savannas in Mauritius have been completely replaced by cultivations of sugar cane (Vaughan and Wiehe, 1937). Round Island, a small island some 10 km north of the mainland of Mauritius, was connected to the mainland during last glacial lower sea-level stands; here some palm savannas have been left. Under wetter conditions palm savannas would have been succeeded by lowland forest. The lowland forests were also quickly destroyed after human colonization and no longer occur in Mauritius (Vaughan and Wiehe, 1937). Lower montane forest prevails in areas under influence of a rain shadow. Higher up on the slopes, up to the highest areas of Mauritius, moist forest is growing. Montane forest grows in the wettest parts of the slopes and the uplands. The uplands record the highest amounts of rainfall. Several vegetation types, such as *Pandanus* marsh, *Sideroxylon* thicket and *Erica* heath, are clustered under the category azonal upland vegetation.

Figure 1. Location of the Mascarene Islands in the Indian Ocean and elevation map of Mauritius. The location of sites mentioned in the text (Kanaka Crater, Tatos) and Port Louis, the capital of Mauritius, are shown. This figure is available in colour online at wileyonlinelibrary.com.

Figure 2. (A) Schematic drawing of the floor of the Kanaka crater. 'a' indicates contours of the peat surface; the area between contours 'a' and 'b' indicates shrub vegetation on the peat surface and 'c' indicates the contour of the present crater floor. (B) Peat and sediment thickness of the Kanaka mire. (C) Photograph taken from the rim on the southeast corner of the crater (photo by G. W. van der Plas). Indicated by an arrow is the coring site and indicated by an 'f' is the fern patch, and 'a', 'b' and 'c' indicate the contours of the crater floor. This figure is available in colour online at wileyonlinelibrary.com.

Materials and methods

In the Kanaka Crater the 10 m long Kanaka-1 core was collected in July 2008 with a Russian corer (Fig. 2). The sediments were continuous except for a small gap from 418 to 428 cm core depth. The infill thickness of the crater basin (Fig. 2) was measured in August 2010 with a 5 mm diameter fibreglass rod with extension rods of 95 cm length. To establish a chronological framework 11 ^{14}C dates were obtained from bulk samples. Calibration was done with the CALIB 6.0 software (Stuiver and Reimer, 1993), using the IntCal09 calibration curve (Reimer *et al.*, 2009). For pollen analysis, a sample volume of 1–1.5 cm³ was taken at 10 cm intervals along the core. Prior to processing, one tablet with exotic *Lycopodium* spores was added to a known sample volume to allow the calculation of pollen concentration values. All samples were

prepared using standard pretreatment techniques including sodium pyrophosphate, acetolysis and heavy liquid separation by a bromoform–ethanol mixture, specific gravity 2 (Faegri and Iversen, 1989). Pollen residues were mounted in glycerine gelatine and analysed with a Leitz microscope at 400 $\times$ magnification. About 400 pollen grains were counted for the pollen sum. Identification, where possible, was based on pollen morphological literature from East Africa (Caratini and Guinet, 1974; Bonnefille and Rioulet, 1980) and in particular the pollen morphological documentation published by H. Straka and co-workers between 1964 and 1989 in the series 'Palynologia Madagassica et Mascarenica' (listed in Hooghiemstra and Van Geel, 1998). We also used the African Pollen Database (<http://medias3.mediasfrance.org/apd/accueil.htm>) for identifications and have asked several African pollen experts for help with determination. All pollen grains were included in the pollen

Table 1. Categories of native vegetation according to differences in altitude (m), annual precipitation (mm) and characterizing taxa.

Characterizing taxa	
Coastal areas (altitude 0–50 m and rainfall 800–1500 mm a ⁻¹)	<i>Rhizophora</i> , <i>Bruguiera</i> (Rhizophoraceae), <i>Canavalia</i> (Fabaceae), <i>Lycium mascarense</i> (Solanaceae), <i>Acrostichum</i> (Pteridaceae), <i>Sesuvium ayresii</i> (Aizoaceae), <i>Zoysia matrella</i> , <i>Lepturus repens</i> (Poaceae), <i>Ipomoea</i> (Convolvulaceae), <i>Typha domingensis</i> (Typhaceae), <i>Atriplex</i> (Amaranthaceae)
Palm savanna (altitude 0–150 m and rainfall 800–1200 mm a ⁻¹)	<i>Latania</i> , <i>Hyophorbe lagenicaulis</i> (Arecaceae), <i>Lomatophyllum tormentorii</i> (Asphodelaceae), <i>Pandanus vandermeeschii</i> (Pandaceae), <i>Dracaena concinna</i> (Asparagaceae), <i>Ficus</i> (Moraceae), <i>Chrysopogon argutus</i> , <i>Cymbopogon caesius</i> (Poaceae)
Lowland forest (altitude 50–350 m and rainfall 1200–1600 mm a ⁻¹)	<i>Diospyros</i> (Ebenaceae), <i>Foetidia</i> (Lecythidaceae), <i>Cassine</i> (Celastraceae), <i>Erythroxylum</i> (Erythroxylaceae), <i>Protium obtusifolium</i> (Burseraceae), <i>Mimusops peiolaris</i> (Sapotaceae), <i>Eugenia</i> (Myrtaceae), <i>Terminalia bentzoe</i> (Combretaceae), <i>Ixora</i> , <i>Fernelia</i> , <i>Buxifolia</i> , <i>Coffea</i> (Rubiaceae)
Lower montane forest (altitude 200–550 m and rainfall 1600–2000 mm a ⁻¹)	<i>Warneckea trinervis</i> (Melastomataceae), <i>Syzygium</i> , <i>Eugenia</i> (Myrtaceae), <i>Mimusops</i> , <i>Labourdannasia</i> (Sapotaceae), <i>Diospyros</i> (Ebenaceae), <i>Ixora</i> , <i>Pyrostria</i> (Rubiaceae), <i>Protium obtusifolium</i> (Burseraceae), <i>Olea lancea</i> (Oleaceae), <i>Grangeria borbonica</i> (Chrysobalanaceae)
Moist forest (altitude 400–850 m and rainfall 2000–2600 mm a ⁻¹)	<i>Eugenia</i> , <i>Syzygium</i> (Myrtaceae), <i>Nuxia verticillata</i> (Stilbaceae), <i>Sideroxylon</i> , <i>Mimusops maxima</i> (Sapotaceae), <i>Erythrospermum</i> (Achariaceae), <i>Tabernaemontana</i> (Apocynaceae), <i>Aphloia</i> (Aphloiaceae), <i>Cassine</i> (Celastraceae), <i>Canarium</i> (Burseraceae), <i>Gaertnera</i> , <i>Chassalia</i> (Rubiaceae), <i>Pilea</i> (Urticaceae), <i>Cyathea</i> (Cyatheaceae), <i>Cnestis glabra</i> (Connaraceae), <i>Harungana madagascariensis</i> (Clusiaceae), <i>Clematis mauritiana</i> (Ranunculaceae), various ferns
Montane forest (altitude 500–850 m and rainfall 2600–3800 mm a ⁻¹)	<i>Syzygium</i> (Myrtaceae), <i>Nuxia verticillata</i> (Stilbaceae), <i>Pandanus</i> (Pandaceae), <i>Cyathea</i> (Cyatheaceae), <i>Weinmannia</i> (Cunoniaceae), <i>Pilea</i> (Urticaceae), <i>Tambourissa/Monimia</i> (Monimiaceae), <i>Calophyllum</i> (Clusiaceae), <i>Roussea simplex</i> (Roussaceae), various ferns
Azonal uplands (altitude 550–700 m and rainfall 3000–3200 mm a ⁻¹)	<i>Pandanus marsh</i> <i>Pandanus</i> (Pandaceae), <i>Machaerina</i> (Cyperaceae), <i>Calophyllum</i> (Clusiaceae), <i>Cyathea</i> (Cyatheaceae) <i>Sideroxylon thicket</i> <i>Sideroxylon</i> (Sapotaceae), <i>Dictyosperma</i> , <i>Acanthophoenix</i> , <i>Hyophorbe vaughanii</i> (Arecaceae), <i>Syzygium</i> (Myrtaceae), <i>Antirrhoea</i> , <i>Gaertnera</i> (Rubiaceae) <i>Erica heath</i> <i>Erica</i> (previously named <i>Philippia</i>) (Ericaceae), <i>Phillica</i> (Rhamnaceae), <i>Psiadia</i> , <i>Helichrysum</i> (Asteraceae)

Table 2. List of identified pollen and spore types and suggestions for link to plants. Taxa have been grouped according to their distributions and ecological affinities.

Pollen taxon	Plant taxon	Group
<i>Acalypha</i>		MF
<i>Allophylus</i>		MF
<i>Artemisia</i>	<i>A. cf. afra</i>	LF
Asteraceae	<i>cf. Helichrysum</i>	UH
<i>Clematis</i> type		MF
<i>Cyathea</i>		MF
<i>cf. Cycadaceae</i>	<i>Cycas</i>	LF
Cyperaceae		UM
<i>Dodonaea</i>		LF
<i>Dracaena</i> type		MF
<i>Erica</i>		UH
<i>Eugenia</i> type		MF
Euphorbiaceae		MF
<i>Filicium decipiens</i> type		MF
<i>Hydrocotyle</i> type	<i>cf. Gastonia</i>	LF
Leguminosae		LF
<i>Lycopodium</i>		MF
Malvaceae	<i>Trochetia blackburniana</i>	LMF
Melastomataceae		MF
<i>Molinaea</i>		MF
<i>Nuxia</i>		MF
Onagraceae	<i>Ludwigia</i>	LF
<i>Pandanus</i>		UM
<i>Pilea</i> type		MF
<i>Plantago</i>		LF
Poaceae		LF
<i>cf. Psiloxylon</i>		MF
<i>Pteris</i>		MF
<i>Rorippa insularis</i> type		LMF
Sapotaceae	<i>Sideroxylon, Mimusops, Labourdonnaisia</i>	MF
<i>Syzygium</i> type		MF
Urticaceae/Moraceae		MF
<i>Weinmannia</i>	<i>W. mauritiana, W. tinctoria</i>	MF

MF, Montane forest; LF, Lowland forest; UH, Upland heath; UM, Upland marsh; LMF, Lower montane forest.

sum, with the exception of known aquatic taxa, fern spores, fungal spores and non-pollen palynomorphs. After the pollen sum was reached, the remaining part of the microscope slide was examined at 250× magnification for new rare pollen and spore types and the presence of charcoal particles. Pollen diagrams were plotted with TILIA 1.5.12 (Grimm, 1993, 2004) software. Zonation was based on CONISS analysis, included in the TILIA program. All pollen and spore types and non-pollen palynomorphs were documented and numbered. Identified plant taxa (Table 2) were categorized into ecological groups with the botanical expertise of Vincent Florens and Claudia Baider. Ecological information from Rouillard and Guého (1999) was also used.

Results

Lithology and chronology

The 10 m long core consisted of homogeneous peat, mainly consisting of rootlets and sparsely of wood fragments. Eleven accelerator mass spectrometry radiocarbon dates were obtained from bulk material (Table 3). The samples at 443 cm and 996 cm depth cause an inversion in the age vs. depth relationship. This points to contamination of the samples and these dates have been rejected to produce the age model.

The sample at 695 cm depth shows too old an age and also has been rejected. Accumulation rates increased between 14 and 10 cal ka BP (Fig. 3) from approximately 60 to 20 a cm⁻¹. Additional inspection of the core did not indicate a change in peat growth. The best explanation for the net increase in the production of plant biomass could be wetter conditions after 11 cal ka BP. Accepting a linear accumulation rate between dated samples and accepting the top as recent, the age of the boundaries between pollen zones was calculated.

Zonation and description

Based on the CONISS analysis and regional vegetation change, six pollen zones could be recognized: zones KAN1-1 to KAN1-6. The sum of ecological groups, pollen sum values and CONISS dendrogram (Fig. 4) and the individual records of all taxa and unidentified types (Fig. 5) form the basis of the environmental reconstruction. The distinction between moist forest and montane forest is not evident from the actual level of pollen identifications and both forest types have been grouped into the montane forest biome.

Pollen zone KAN1-1 (1000–835 cm core interval; 17 samples)

Pandanus dominates the pollen spectra, but proportions are decreasing. Montane forest consists of *Pilea*, *Cyathea*, *Nuxia* and *Weinmannia*. The proportion of montane forest increases in this zone due to increasing values of *Pilea* and *Nuxia*. Low percentages of *Erica* and Asteraceae are recorded. Lower montane forest consists of *Rorippa insularis* and Malvaceae. Lowland forest is represented by *cf. Cycadaceae*, *Artemisia cf. afra*, *Hydrocotyle* type, *Dodonaea* and Poaceae. Tree fern *Cyathea* increases in this zone. *Lycopodium*, *Pteris* and monolete fern spores occur at low percentages. *Cercophora* and other unknown fungal spore types are present at the beginning of this zone. Charcoal particles are present in most of the samples.

Pollen zone KAN1-2 (835–755 cm core interval; eight samples)

The proportion of *Pandanus* decreases. Montane forest values are high. *Pilea*, *Nuxia*, *Weinmannia*, *Syzygium* and *cf. Syzygium* are more abundant than in the previous zone. Fungal spores are absent, with the exception of unknown T.mau-A.

Pollen zone KAN1-3 (755–455 cm core interval; 30 samples)

Proportions of *Pandanus* are high, while proportions of montane forest are low. *Pilea*, *Cyathea*, *Nuxia* and *Weinmannia* show lower values. *Dracaena* type, *Syzygium* and *cf. Syzygium* increase slightly at the end of the zone. *Erica* and Asteraceae show higher percentages. Malvaceae are almost absent in this zone. *Artemisia* shows higher percentages. *Dodonaea* appears again for a short interval. Fungal spores are present, including *Cercophora* and *Ustilina*. Microscopic charcoal is present in many samples.

Pollen zone KAN1-4 (455–375 cm core interval; seven samples)

Percentages of *Pandanus* decrease rapidly. Montane forest increases with high percentages of *Eugenia* and *Dracaena* type. Higher percentages are also recorded for *cf. Psiloxylon*, *Weinmannia*, Euphorbiaceae T.mau-172 and T.mau-8, *Molinaea* and *Allophylus*. *Erica* shows very low proportions and Asteraceae have disappeared. In the lower montane forest *Rorippa* disappears. From the lowland forest *cf. Cycadaceae*

Table 3. List of radiocarbon dates and sample-specific data, obtained from bulk material

Depth (cm)	Laboratory number	^{14}C a BP	$\delta^{13}\text{C}$	Cal a BP (1 σ)	Area (%) [†]	Cal a BP (2 σ)	Area (%) [†]	Age (a) in graph
45	GrA-47151	2 025 $\pm$ 35	-27.72	1926–2 004 2 026–2 036	0.929 0.071	1 892–2 063 2 085–2 107	0.964 0.036	1 978
195	GrA-42501	4 925 $\pm$ 40	-28.16	5 601–5 662 5 692–5 707	0.864 0.136	5 593–5 729	1.000	5 661
295	GrA-47152	6 310 $\pm$ 40	-27.39	7 174–7 221 7 235–7 270	0.541 0.459	7 163–7 317	1.000	7 240
395	GrA-42502	8 105 $\pm$ 45	-25.53	8 997–9 090	1.000	8 794–8 827 8 869–8 881 8 902–8 907 8 977–9 142 9 171–9 250	0.020 0.007 0.002 0.913 0.058	9 060
443	GrA-47154	*7 955 $\pm$ 45	-26.74	8 721–8 798 8 803–8 806 8 826–8 870 8 880–8 977	0.339 0.016 0.201 0.444	8 647–8 987	1.000	8 817
457	GrA-47155	9 040 $\pm$ 50	-27.65	10 190–10 239	1.000	9 943–9 989 10 015–10 021 10 042–10 059 10 146–10 287	0.030 0.002 0.009 0.958	10 217
595	GrA-47160	12 050 $\pm$ 60	-26.68	13 819–13 974	1.000	13 750–14 055	1.000	13 903
695	GrA-42504	*20 010 $\pm$ 90	-25.57	23 733–24 117	1.000	23 520–24 287	1.000	23 904
768	GrA-47161	20 730 $\pm$ 90	-27.04	24 537–24 881	1.000	24 430–25 019	1.000	24 725
945	GrA-47162	29 000 $\pm$ 170	-26.54	33 231–33 982	1.000	33 109–34 470	1.000	33 790
996	GrA-42505	*9 260 $\pm$ 50	-25.55	10 299–10 321 10 343–10 351 10 375–10 517	0.099 0.037 0.864	10 275–10 569	1.000	10 422

*Rejected dates. [†]Area (%) under probability distribution.

decreases and *Artemisia* disappears. Unknown monocotyledon (monocot) T.mau-101b decreases, while T.mau-137, T.mau-131, T.mau-127 and T.mau-54c increase. *Cyathea*, *Lycopodium* and monolet fern spores show higher percentages.

Pollen zone KAN1-5 (375–65 cm core interval; 31 samples)

Pandanus percentages slowly increase. *Pilea* shows a peak. *Weinmannia*, *Nuxia*, *Acalypha*, *Psiloxylon*, *Molinia*, *Syzy-*

gium, cf. *Syzygium* and *Eugenia* decline or disappear. Sapotaceae, Urticaceae/Moraceae and *Allophylus* increase. All lower montane forest taxa disappear. Monolet fern spores slowly increase. Fungal spores are present again, but only at certain depths and not continuous throughout the zone.

Pollen zone KAN1-6 (65–0 cm core interval; seven samples)

Pandanus percentages are high. High percentages are recorded for *Eugenia*, *Weinmannia*, *Acalypha* and Urticaceae/Moraceae. Melastomataceae, Cyperaceae, Poaceae, Onagraceae, Asteraceae, *Weinmannia*, monolet fern spores and the algal colony *Botryococcus* show a peak at 1 cm core depth.

Figure 3. Depth–age relationship of the sediments in core Kanaka-1. Solid diamonds reflect accepted dates and open diamonds reflect rejected radiocarbon dates at 996 cm, 695 cm and 443 cm core depth (see text). The dotted line shows two intervals with different peat accumulation rates. Error bars indicate the age range after calibration of the ^{14}C samples.

Environmental reconstruction

Period 1: ca. 38 to ca. 27.5 cal ka BP (zone KAN1-1)

The sediments consist of peat, with some woody fragments and small roots indicating that a low energetic regime prevailed in the crater. The slopes around the crater were covered by forest, as was the case until recently. Wood fragments are expected to originate from fallen trees that concentrate at the borders of the mire. Therefore large wood fragments are absent in more central parts of the mire. Peat was mainly formed by Cyperaceae, as is the case today.

There are many endemic *Pandanus* species in Mauritius that grow either in marshy conditions or in montane forest, which would have found many suitable places to occur in the Kanaka Crater. *Pandanus* would grow in dense populations on the crater floor around the edge of the mire. Native *Pandanus* alive today are found on the inside slope of the crater (Florens and

Figure 4. Pollen percentage diagram of core Kanaka-1 showing age, depth, lithology, downcore changes of the pollen concentration, proportions of main ecological groups, non-pollen palynomorphs, presence of charcoal, pollen zones, pollen sum values and the CONISS cluster dendrogram. This figure is available in colour online at wileyonlinelibrary.com.

Baider, pers. obs.). Before the destruction by humans *Pandanus* was probably abundant in these forests. *Pandanus* could also be found in the coastal plains (in particular, *Pandanus vandermeeschii*) as part of the palm savannas (Vaughan and Wiehe, 1937). However, these savannas were predominantly present on the leeward side of the island (north and northwest), where today's rainfall values may reach only 800 mm a⁻¹. Coastal areas upwind to Kanaka, given the main prevailing southeast

Figure 5. Pollen percentage diagram of core Kanaka-1 showing age, depth, downcore changes of all identified taxa, selected unknown pollen and spore types and pollen zones. This figure is available in colour online at wileyonlinelibrary.com.

trade winds, are much wetter ($1400\text{--}2000\text{ mm a}^{-1}$) and palm savanna would probably not have occurred there (Florens and Baider, pers. comm.).

Erica heathlands, at present day occurring in the uplands on immature, highly laterized and almost unweathered soils (Vaughan and Wiehe, 1937), could probably be found on the rim of the crater. Although the uplands receive high rainfall, the *Erica* heathlands have adapted to the xeromorphic conditions set by the substrate.

Montane forest was dominated by *Pilea* and *Nuxia*, with tree fern *Cyathea* growing in abundance. *Pilea* are typical small herbs growing in the deep shade of mature forests. The proportion of forest was low during this period, possibly indicating relatively dry climatic conditions. This interpretation is supported by the presence of fungal spores at the beginning of the period, which points to decomposition of exposed peat under dry conditions, and the presence of charcoal. The relatively abundant *Rorippa insularis* during this interval probably grew in the lowland forest along rivers and in other places where water was present.

Period 2: ca. 27.5 to ca. 22.7 cal ka BP (zone KAN1-2)

Montane forest quickly expanded, possibly replacing *Erica* heathlands. Humid conditions probably prevailed during this time interval. Fungal spores are no longer present, possibly pointing to higher water levels in the crater, and charcoal is not recorded.

Period 3: ca. 22.7 to ca. 10.6 cal ka BP (zone KAN1-3)

Erica heathlands expanded. *Pilea*, *Cyathea*, *Nuxia* and *Weinmannia* were the most important taxa of the montane forest, but its share decreased during this period. The *Pandanus*-dominated marshes expanded and probably replaced montane forest. There is a change towards a more open landscape with less forest, indicating that cooler and drier conditions prevailed. At the end of this period there is an increase of *Syzygium*, which indicates wetter conditions. The vegetation during the Lateglacial (between ca. 15 and ca. 11.5 cal ka BP) remained relatively stable up to the start of the Holocene.

Period 4: ca. 10.6 to ca. 9 cal ka BP (zone KAN1-4)

The share of Cyperaceae increased in the peat-forming vegetation in the crater, suggesting more humid conditions. An increase of *Cyathea* and *Lycopodium*, as well as other ferns, shows that climatic conditions became more humid again. Montane forest expanded and *Eugenia* was now the dominant tree together with *Dracaena*. In Mauritius *Eugenia* is typically associated with drier places. However, a considerable number of species also occur in montane forest, where they can become dominant (Florens and Baider, pers. comm.). Taking into account the previous comment that dry vegetation types would probably not have grown in the vicinity of the crater, *Eugenia* most likely became an important component of the montane forest around the crater. *Eugenia* took advantage of changing environmental conditions at the beginning of the Holocene and rapidly replaced other taxa such as *Syzygium* and *Nuxia*. This change in forest composition is also shown by the increase of *Weinmannia*, *Psiloxylon*, Euphorbiaceae T.mau-8, *Allophylus* and *Molinia*, as well as the increase and decline of unidentified monocots. Possible identifications for these unknown monocots could be palm genera that occur in

montane forest such as *Acanthophoenix*, *Dictyosperma*, *Hyophorbe* and *Tectiphiala*. *Pandanus* decreased rapidly. *Erica* disappeared during this interval from the record, possibly due to expansion of montane forest.

Period 5: ca. 9 to ca. 2.5 cal ka BP (zone KAN1-5)

Peat continued to accumulate and Cyperaceae were dominant in this vegetation. After the brief transitional phase with *Eugenia* dominating the montane forest, Sapotaceae increased and became an important forest element, together with *Pilea*, which remained abundant. *Eugenia*, *Weinmannia*, *Psiloxylon* and *Nuxia* declined rapidly or disappeared, evidencing that the forest composition changed substantially. Elements of the Sapotaceae family typically contain late successional species often associated with shady mature forests (Florens and Baider, pers. comm.). In these montane forests Sapotaceae can be dominant and develop into tall trees with an 'umbrella' crown that typically form a closed canopy with deep shade underneath. These conditions are suitable for many *Pilea* species, but not suitable for *Weinmannia*, *Psiloxylon* and *Nuxia*, which all require a substantially light environment to germinate (Florens and Baider, pers. comm.).

Cyathea ferns were still abundant in the forest and other unidentified ferns remained abundant as well, indicating that humid conditions prevailed throughout the Holocene. During this period *Pandanus* marsh started to increase slowly.

Period 6: ca. 2.5 cal ka to recent (zone KAN1-6)

Peat continued to accumulate in the crater. At the end of this period the share of Cyperaceae increased and algal colonies of *Botryococcus* appeared for the first time. We tentatively interpret this change as human impact on the peat surface rather than presence of open water in the Kanaka Crater. *Pandanus* remained abundant. *Eugenia* and *Weinmannia* increased during this period. Both trees became abundant at the Lateglacial to Holocene transition as well as in this period where human impact is expected. Therefore it may be indicative of forest turnover and disturbances. Trees belonging to the Sapotaceae family were still an important part of the montane forest; the forest composition of the previous period continued. The abundance of Melastomataceae increased rapidly, probably reflecting shrubs and herbs introduced during the 19th century. The melastomataceous species *Osbeckia octandra*, introduced before 1836, currently grows abundantly at the edge of the mire. During this period the variety of pollen types increased, which reflects a combination of natural and introduced vegetation. However, shortly after colonization large parts of the natural vegetation were quickly removed and replaced by crops of mainly sugar cane. The increase of Poaceae supports the interpretation that the landscape lost much of its forest.

Discussion

Early Holocene zonation

Initially the CONISS analysis identified the transition from zone KAN3 to KAN2 at 265 cm depth. Inspection of the pollen diagram and additional CONISS analyses revealed that this zonation was primarily caused by changes in the *Pandanus* and *Pilea* records. These taxa rather represent vegetation change of local importance on the crater floor and surrounding crater slopes. We assess the boundary between the end of the brief period of dominance of *Eugenia* and the start of the Sapotaceae

record, located at 375 cm depth, of more importance in terms of montane forest succession and regional environmental change.

Vegetation reconstruction

Logging in the crater area started in 1895 (Cheke, 1987). The natural forests at the Kanaka Crater became degraded and destroyed by the end of the 19th century. Exotic trees were planted during the late 1930s. The last pockets of degraded forests were destroyed in the 1970s, and nowadays native species can only be seen in isolation (Cheke, 1987).

Under natural conditions *Pandanus* marsh must have been growing along the borders of the mire. We have not found macro-remains of *Pandanus* reflecting the central location of the coring site.

In absence of the risk that the growing peat body was disrupted by the weight of the water mass a very thick sequence of peat was able to accumulate in the Kanaka Crater. We measured 19.8 m of peat and soft sediments (Fig. 2B). The peat-producing vegetation consisted mainly of cyperaceous vegetation. During coring in 2008 we also found some patches with *Sphagnum*, but *Sphagnum* spores have not been found in the fossil record. In contrast, *Botryococcus* was found in the latest part of the fossil record, but no open water was encountered in the crater. Both *Sphagnum* and *Botryococcus* may reflect introduced taxa.

On the crater wall and in the surrounding uplands around the crater montane forest could be found. *Erica* heathland probably found its natural habitat on the volcano and on the higher mountain ridges. According to Vaughan and Wiehe (1937) *Erica* can be found on 'an immature, highly laterized, almost unweathered soil'; in many places soil is even absent and shrubs root in the fissures between lava slabs. In a natural succession heath is replaced by *Sideroxylon* thicket, which is considered a vegetation type that in the succession precedes a forest. Unfortunately, Sapotaceae have not yet been identified in this study beyond the family level. The increase of the Sapotaceae recorded during the Holocene, after the heath disappeared, may be indicative of expanding *Sideroxylon* thickets. However, representatives of the Sapotaceae may also be found in the *Pandanus* marshes (*Sideroxylon*) and in wet montane forest (*Sideroxylon*, *Mimusops*). *Acalypha* can be abundant in the *Sideroxylon* thickets (Vaughan and Wiehe, 1941) and its presence increased significantly during the last 2500 years (period 6), making it likely this vegetation type occurred at least for 2000 years. Lower montane forest and lowland forest are hardly represented in the pollen record, which suggests these biomes were not present in the direct surroundings. Most probably these vegetation types grew on the leeward side of the island, where rainfall is lower.

Although the pollen flora of the Mascarene Islands was intensively studied by H. Straka and co-workers and published between 1964 and 1989 in the series 'Palynologia Madagassica et Mascarenica' (see Hooghiemstra and Van Geel, 1998), the quality of these pollen atlases is not always sufficient to arrive at robust identifications. Help with determination of several experts on African pollen resulted in additional identifications. The group of unknown pollen and spore taxa left in the pollen record is limited.

Two important changes in the vegetation composition can be easily identified. The first turnover in plant taxa occurred at ca. 22.7 cal ka BP at the transition from zones KAN2 to KAN3, when proportions of *Pilea*, *Cyathea*, *Nuxia* and *Weinmannia* changed substantially. The abundance of montane forest declined, while *Pandanus* and heathland increased. The second turnover in plant taxa occurred at the transition from the last glacial to the Holocene at ca. 10.6 cal ka BP. This is the

transition from zone KAN3 to KAN4, which is characterized by a disappearance or decline of *Erica*, Cycadaceae, *Artemisia*, *Syzygium*, *Nuxia* and *Pteris*, an increase of *Weinmannia*, and an appearance of *Eugenia*, *Dracaena*, *Psiloxylon*, Euphorbiaceae T.mau-8, *Lycopodium*, *Cyathea*, *Allophyllus* and *Molinia*. The presence of *Artemisia* during the last glacial is a significant observation, since *Artemisia* is not recorded at the present day in Mauritius. Pollen analysis of additional cores is needed to verify whether *Artemisia* had disappeared from the flora of Mauritius at the beginning of the Holocene. *Eugenia* increased ca. 10.6 and ca. 2.5 cal ka BP when vegetation is undergoing change. This suggests *Eugenia* is characteristic of dynamic environments and has a small window of opportunity in changes at longer timescales. When *Eugenia* increased after 10.6 cal ka BP, *Syzygium* and *Nuxia* disappeared, probably because *Eugenia* has a better competitive position. After 9.0 cal ka BP *Eugenia* and *Weinmannia* disappeared and were replaced by Sapotaceae. At the end of period 6 a suite of new pollen types appear in the record, strongly suggesting that introductions of exotic plant species by colonists are documented here.

Climate reconstruction

Based on the first pollen evidence the climate history of Mauritius can be divided into three distinct periods. A relatively humid period can be inferred from ca. 38 to ca. 23 cal ka BP, which is in support of conclusions from Lake Titivakely in Madagascar (Gasse and Van Campo, 1998). From ca. 23 to ca. 11 cal ka BP climate was drier. Our pollen record suggests a remarkable climatic stability throughout this period (pollen zone KAN3), which contrasts with the Titivakely record. At the start of the Holocene there was a regional expansion of montane forest and conditions in the crater became moister, as is evidenced by more fern vegetation – all together indicative of wetter climatic conditions. Orbital induced changes in the monsoon strength account for a large part of long-term climatic changes in tropical Africa (Gasse, 2000). At 20° S we may expect, with a time lag to the driving precession cycle, once in a ca. 23 ka period driest climatic conditions (i.e. around 30 and 10 cal ka BP) and with half a cycle offset wettest climatic conditions (i.e. around 20 cal ka BP and present day). In our pollen record this 23 ka precessional cycle is not clearly recognized. The expansion of *Pandanus* after 9.0 cal ka BP can be taken as evidence of increasing precipitation and reflecting the migration of the ITCZ towards its current southern position. In lowland sites increasing moisture may also be attributed to the rising sea-level stands but Kanaka Crater is expected to be little influenced. Based on the present record we conclude that in the case that precession is a main driver of climate change in Mauritius we have found little evidence of this driver. The dampening effect on climate change of the IOD seems important. Continuous supply of Indian Ocean-derived moisture may mask periods of a minimum summer insolation, resulting in wetter environmental conditions than expected (Mumbi *et al.*, 2008). Other studies in the western Indian Ocean area showed the impact of precession on vegetation and climate (e.g. Gasse and Van Campo, 1998). The small size of Mauritius makes this island in particular prone to the effects of the IOD, compared to the much bigger landmasses of Madagascar and the East African mainland. Montane forest was continuously present throughout the last 30 ka and there is no evidence that it experienced a period of major climate-induced stress. Therefore, this first record of vegetation dynamics suggests that there is no need for refugia to explain how wet biomes survived potentially dry climatic intervals, and the other way around.

Conclusions

This study is a first document of the vegetation and climate history of Mauritius since the last ice age. The sediment infill of Kanaka Crater has proven to be a high-quality archive of microfossils reflecting past environmental change. The pollen-based record shows that the island was continuously covered by forests of various types. The period 38.0–27.5 cal ka BP shows montane forest with *Pilea*, *Cyathea*, *Nuxia*, *Syzygium* and *Weinmannia*. Montane forest and *Erica* heath (*Philippia*) occurred in the uplands. In the crater cyperaceous reedswamp produced the organic material that dominates the sediment infill. *Pandanus* marsh grew around the borders of the mire. In the period 27.5–22.7 cal ka BP montane forest expanded. The period 22.7–10.6 cal ka BP shows a lower abundance of montane forest, while *Pandanus* marsh and *Erica* heath expanded. During the Lateglacial vegetation was relatively stable. The period 10.6–9.0 cal ka BP shows in the montane forest a significant turnover of taxa, with *Eugenia* becoming a dominant component of the forest. *Erica* heath disappeared. During the period 9.0–2.5 cal ka BP trees of the Sapotaceae family became important in the montane forest, while *Eugenia* became rare. The period of the last 2.5 ka shows an increase in proportions of *Weinmannia* and *Eugenia*. Close to recent times signals of human impact are found, with increased amounts of Poaceae and introduced melastomataceous species.

Changes in climatic humidity were the most important environmental changes, with wet conditions from 38.0 to 22.7 cal ka BP, drier conditions from 22.7 to 10.6 cal ka BP, and wetter conditions again from 10.6 cal ka BP to recent. Among the six distinct periods recognized, the transition from the Lateglacial to the Holocene showed the highest levels of species turnover. The limited altitudinal ranges in the mountains of Mauritius (maximum altitude 828 m), and changing humidity being more important than changing temperature, suggest that, in response to climate change, a reassortment in taxonomic composition of montane forests might be equally important as displacement of forest types to new altitudinal intervals. We found that changes in orbital insolation related to the latitudinal migration of the ITCZ had a weak impact on vegetation change. Data suggest that changing atmospheric moisture is more important than changing temperature, which hints to the IOD as an important driver of climate change in the southwest Indian Ocean.

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Abbreviations. IOD, Indian Ocean Dipole; ITCZ, Intertropical Convergence Zone; LGM, Last Glacial Maximum; SST, sea surface temperature

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