

# Middle- to late-Holocene moisture changes in the desert of northwest Namibia derived from fossil hyrax dung pollen

Graciela Gil-Romera,<sup>1\*</sup> Louis Scott,<sup>2</sup> Eugène Marais<sup>3</sup> and George A. Brook<sup>4</sup>

(<sup>1</sup>Department of Biology (Botany), Universidad Autónoma de Madrid, Campus de Cantoblanco, 28049 Madrid, Spain; <sup>2</sup>Department of Plant Sciences, University of the Free State, P.O. Box 331, 9300 Bloemfontein, South Africa; <sup>3</sup>National Museum of Namibia, P.O. Box 1203, Windhoek, Namibia; <sup>4</sup>Department of Geography, University of Georgia, Athens GA 30602, USA)

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**Abstract:** New pollen results and radiocarbon dating from fossil hyrax middens derived from the edge of the northern Namib Desert address the shortage of continental palaeobotanical evidence in arid Namibia by providing evidence for the environmental conditions during the mid to late Holocene in the region. The results obtained reflect long-term stability in the area throughout most of the sequence. Higher than modern moisture availability is suggested between *c.* 6 and 1 ka BP by the increased abundance of Poaceae, Cyperaceae or Chenopodiaceae, which respond rapidly by flowering after modest quantities of rainfall. Around 1 ka and recently arid conditions seem to have prevailed, with a decrease in Poaceae and an increase in Acanthaceae. Other palaeoecological evidence from the local and regional surroundings that focused on fluvial deposits, marine palynology and mineralogy confirms this mid-Holocene increase in more effective rainfall.

**Key words:** Palynology, vegetation history, palaeoenvironments, arid environments, Namib Desert, Namibia, hyrax dung, Holocene.

## Introduction

Virtually no palaeobotanical information is available from the arid areas of the world as organic material is rarely preserved in the absence of anaerobic environments such as swamps or lakes. It is, however, important to understand the environmental history of arid zones since desertification and degradation of the soils in dry, semi-arid and subhumid zones threatens 40% of the Earth's surface, which is inhabited by 37% of the world's population (United Nations Convention to Combat Desertification, <http://www.unccd.int/>, last accessed September 2006; Thomas *et al.*, 2005). Humans and their technologies had an erratic effect on the environment and the climate during the last millennium, and it is not clear how it will be affected in future. Palaeoenvironmental research in climate sensitive regions, such as the desert edge, permits us to find possible past analogue scenarios for the climatic change that currently affects these areas.

In Namibia, and especially in the Namib Desert, diverse records of palaeoenvironmental conditions have been studied to explore the origins, dynamics and past evolution of the climatic system (van Zinderen Bakker, 1972, 1975, 1998; Tyson, 1986; Deacon and Lancaster, 1988; Vogel, 1989; Heine, 1998, 2005; Scott and Lee-Thorp, 2005). However, most studies have examined the hyper-arid environment of the Central and Southern Namib so that the history in Northern Namib is even more poorly understood.

Fossil pollen evidence from continental Namibia is very rare since suitable basins for its preservation are scarce (Scott *et al.*, 1991, 2004; Scott, 1996). Thus, pollen analysis in peat bogs or other water bodies is virtually impossible and different pollen sources must be explored (Horowitz, 1992). The pollen-analytical potential of different herbivorous mammal middens (*Procapra*, *Petromus*, *Meles*) has been shown to be a powerful tool in palaeoenvironmental studies in arid Africa (Pons and Quezel, 1958; Scott and Bousman, 1990; Scott and Cooremans, 1992; Scott, 1996; Carrión *et al.*, 1997b; Scott and Vogel, 2000; Pearson and Betancourt, 2002; Scott *et al.*, 2004).

\*Author for correspondence (e-mail: [graciela.gil@uam.es](mailto:graciela.gil@uam.es))

Hyraxes (*Procavia*) are small herbivorous mammals from a wide range of habitats throughout the whole African continent (Skinner and Smithers, 1990). These animals normally occupy rock shelters, also along the Great Escarpment in Namibia. They usually do not forage more than 500 m away from their refuges to avoid falling prey to their natural enemies, raptors and large cats. The hyrax's food sources include a great variety of plant parts such as flowers, fruits, leaves and grass shoots, although diet composition depends on the season (Sale, 1965; Hoeck, 1975; Lensing, 1978; Fourie and Perrin, 1989). They are generally not very selective, especially in those places with scant vegetation. Hyraxes are mainly browsers because of their ability to climb, although they are functional grazers when grass is available (Fourie and Perrin, 1989). They can tolerate long periods without water because their highly efficient kidneys concentrate urine, excrete carbonates and produce a dense substance, which crystallized is called *hyraceum* (Rübsamen *et al.*, 1982).

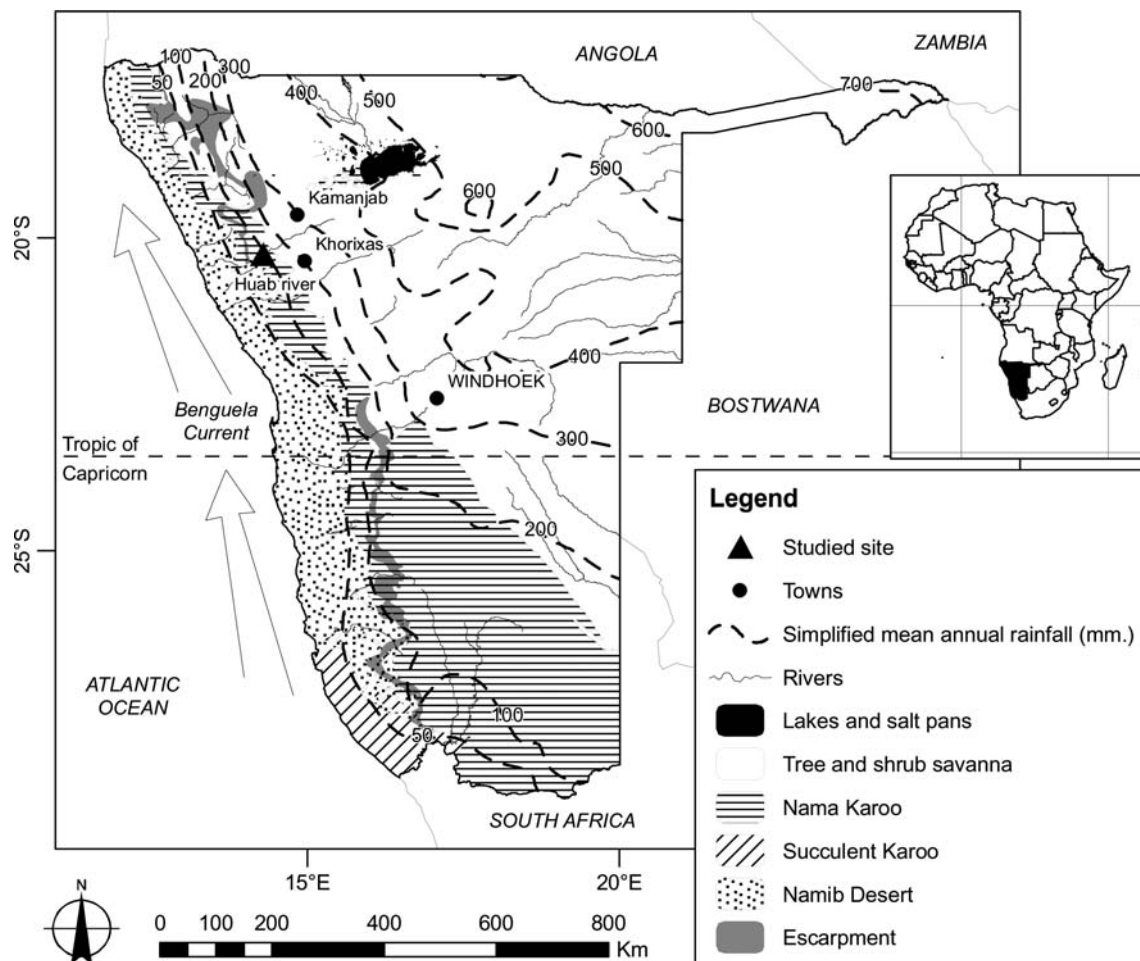
Groups of hyraxes always use fixed latrines over a long period of time for urinating and defecating, often in certain protected shelters under overhanging rocks. Semi-spherical faecal pellets are successively accumulated and embedded in quick-drying urine (*hyraceum*) often forming nearly horizontal middens that are stratigraphically coherent, although sometimes vertical flows of *hyraceum* also occur. Apart from masticated plant material in the pellets, *hyraceum* (see Figure 2B) encloses and preserves high concentrations of microfossils, principally pollen and spores, which are airborne or derived either accidentally or purposefully through hyrax diets (Scott and Bousman, 1990; Carrión *et al.*, 1997a). This dietary input is a very interesting

feature because, apart from ever-present wind-pollinated pollen, it probably also includes a reasonable proportion of insect-pollinated pollen (Carrión, 2002). Moreover, entomophilous taxa are abundant in deserts where pollination is ensured in this way, in an area where low plant densities do not guarantee wind pollination (Horowitz, 1992). The pollen-trapping quality of the urine and dung allows the preservation of a regional pollen signal over time.

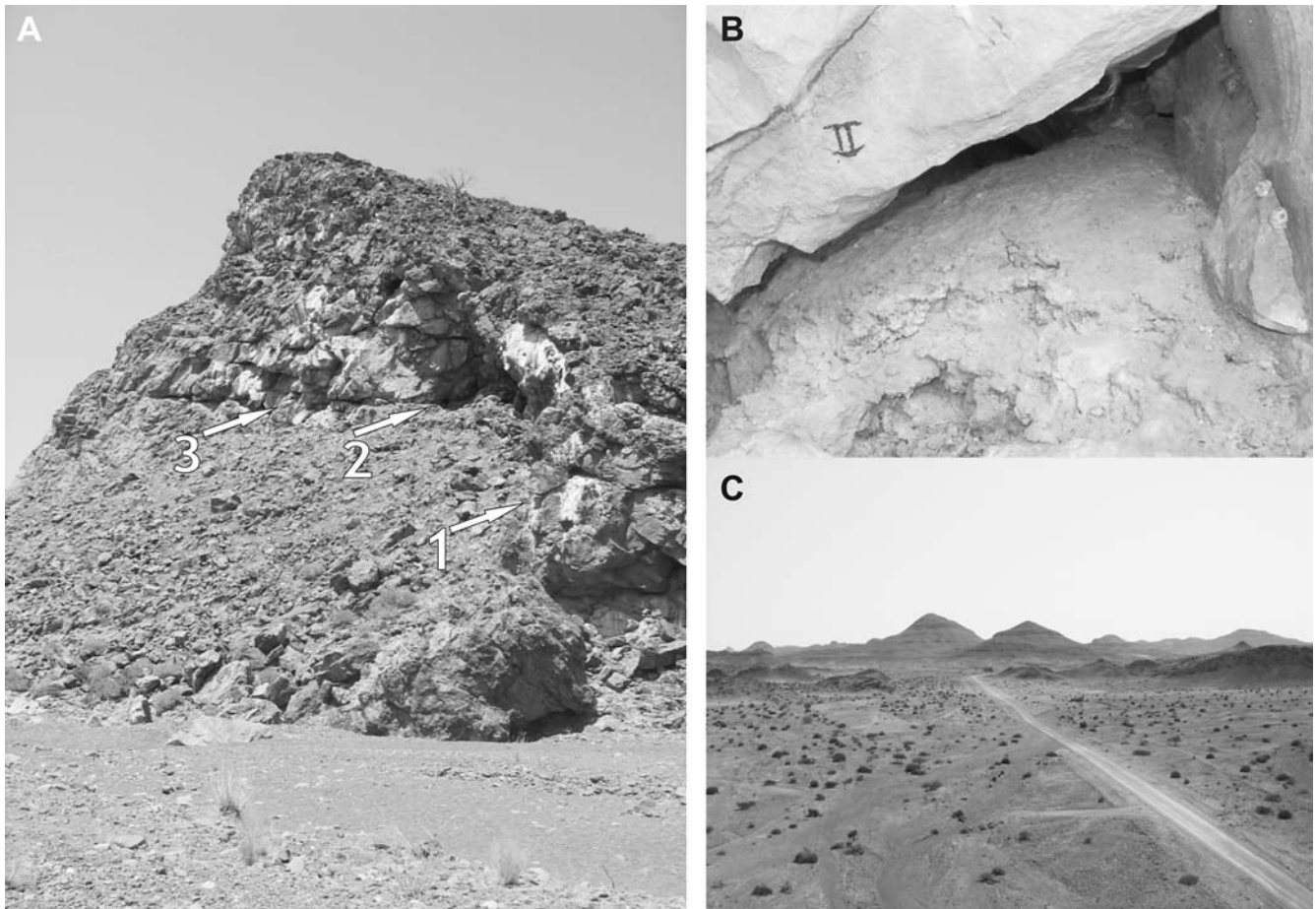
We present a new middle-Holocene hyrax midden pollen record from northwestern Namibia in order to develop a better palaeoenvironmental understanding of this arid zone. The pollen samples were recovered from seven hyrax middens (*Procavia welwitschia*) near Vrede, in the Huab River valley, around 100 km inland from the coast in the Damaraland region (Figure 1). The pollen sequence provides a well-dated middle- to late-Holocene record of vegetation dynamics in the study area over the last 6000 years and gives evidence for past environmental change in northern Namibia.

## Regional setting and vegetation

The Vrede hyrax midden sites ( $20^{\circ}19'49''$  S  $14^{\circ}10'11''$  E) are at 540 m above sea level at the base of the northwestern escarpment. The middens are located in an outcrop of dolomitic limestone, schists and calcareous silicate rocks of the Karibib Formation of the Damara Orogen (Miller, 1983; Schneider, 2004). Rocks at the dung shelters are encrusted in white urine precipitate while the middens are light brown in colour at this locality (Figure 2A,B), in contrast with dark



**Figure 1** Map of Namibia showing the study area, rainfall isohyets, vegetation biomes and the Great Escarpment. Kamanjab and Khorixas are the nearest meteorological stations



**Figure 2** (A) Hillslope where the samples were recovered. The arrows point to different shelters where middens were recovered. 1, middens I to III; 2, middens IV and V; 3 middens VI and VII. (B) Close-up of one of the latrines (midden II, samples 18–21 and 39–41). *Hyraceum* is the whitish substance that cements the midden. (C) General view of the landscape around the site. (Photos G. Gil-Romera)

brown glossy hyraceum and stained rocks we have often encountered at other slightly more moist localities. Samples were extracted from shallow shelters along a cliff in the north-facing slope of a hill next to the C39 road from Khorixas to the Skeleton Coast (see Figure 2C). The base of the outcrop is on the edge of a small, unnamed tributary of the Huab River.

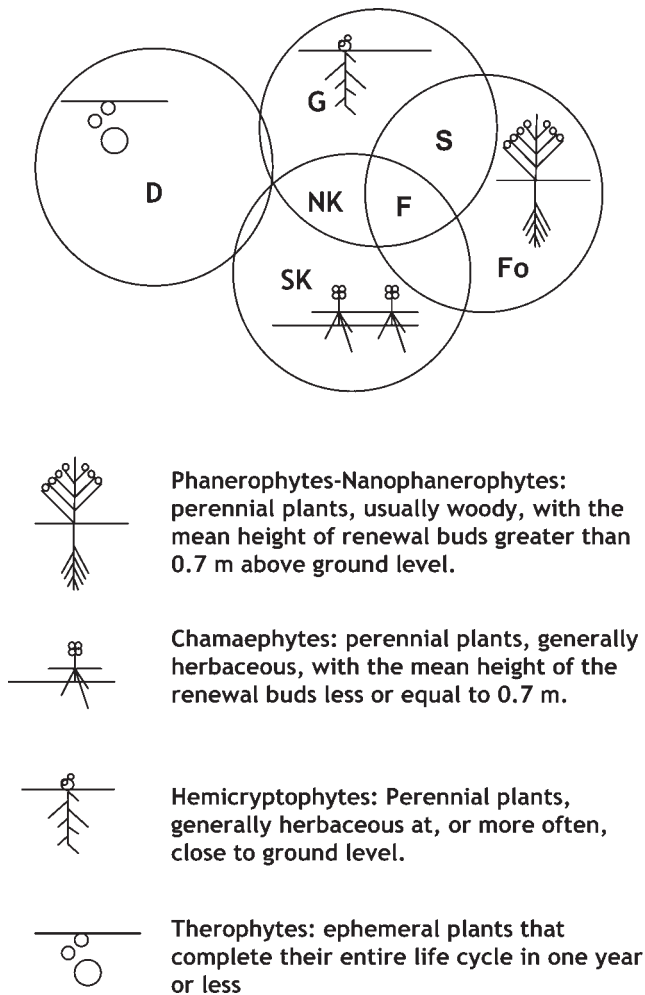
The locality is in the Nama-Karoo Biome (Irish, 1994; Rutherford and Westfall, 1994), effectively representing a transition between the Coastal Desert Biome to the west and the Savanna Biome of the interior. Raunkiaer's life forms (Raunkiaer, 1934) has been applied by Rutherford and Westfall (1994) and Rutherford (1997) to characterize the Southern African biomes. Figure 3 summarizes these forms and their appearance in different biomes. The Nama-Karoo vegetation from the study area includes a plant community dominated by namely chamaephytes and hemicryptophytes, though the transitional nature of this formation allows for the presence of therophytes or phanerophytes.

Ecotone areas are effective monitors of global climate change and especially useful in the exploration of past climatic change scenarios as they are often more sensitive to climatic variation than the main bodies of adjacent ecosystems, which have greater inertia and stability (Di Castri *et al.*, 1988; Neilson, 1993; Noble, 1993). The relationship between ecotone dynamics and climatic change is, however, complicated by the individualistic response of species, their interaction, as well as the time-lag of vegetative development (Liu *et al.*, 2001). Additional levels of complexity are imposed at the site because of its location within the foothills of the northwestern escarpment and the associated topographical effects on local

climate, as well as the complex geology of the surrounding area and its influence on local soils. Basement granites of the Kamanjab Inlier, a limestone-dolomite succession of the Damaran metamorphic belt, and early Cretaceous basalts and quartz latites of the Etendeka Formation occur within the tributary catchment area upstream from the site (Miller, 1983).

In arid areas, the most important environmental factors controlling successful plant germination and subsequent establishment are the amount of rainfall, the spatial and temporal distribution of rainfall and soil moisture availability. The closest meteorological stations are at Khorixas and Kamanjab, with annual rainfall averages of 216 mm and 309 mm, respectively. This rainfall occurs mostly during the summer months (Figure 4). Since both of these stations are more than 100 km inland on the interior African plateau, the annual rainfall at the study site is significantly lower than that suggested by the available meteorological information. Prevailing onshore winds may carry advective fog, which develops at night over the cold coastal current, as far inland as the base of the escarpment. Such occurrences are too infrequent and temporal to contribute significantly to the available moisture at the site.

Northern Namibian rainfall generally occurs when an equatorial trough forms over the western interior of Southern Africa during the austral summer (Tyson, 1986), triggering the advection of tropical humid air masses carried by the southwards migration of the Inter-Tropical Convergence Zone (ITCZ). Aridity in Namibia is a consequence of a high-pressure system dominating the climate of Southern Africa

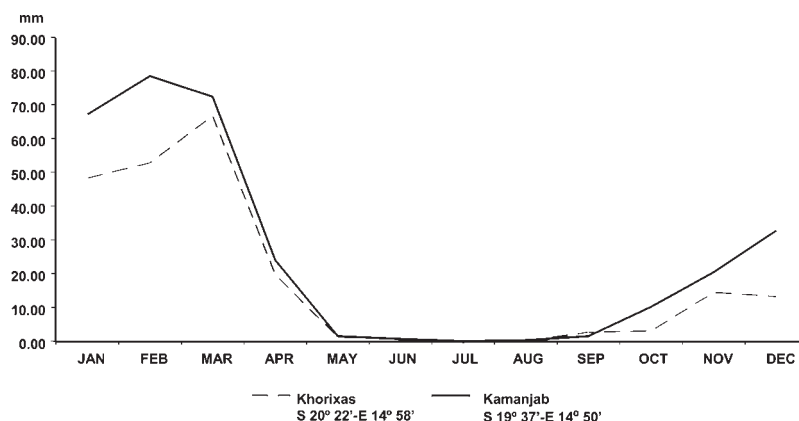


**Figure 3** Raunkiaer's life forms (Raunkiaer, 1934) in relation with the different southern African biomes. D, desert; G, grassland; NK, Nama-Karoo; SK, succulent Karoo; S, savanna; F, fynbos; Fo, forest (modified from Rutherford, 1997)

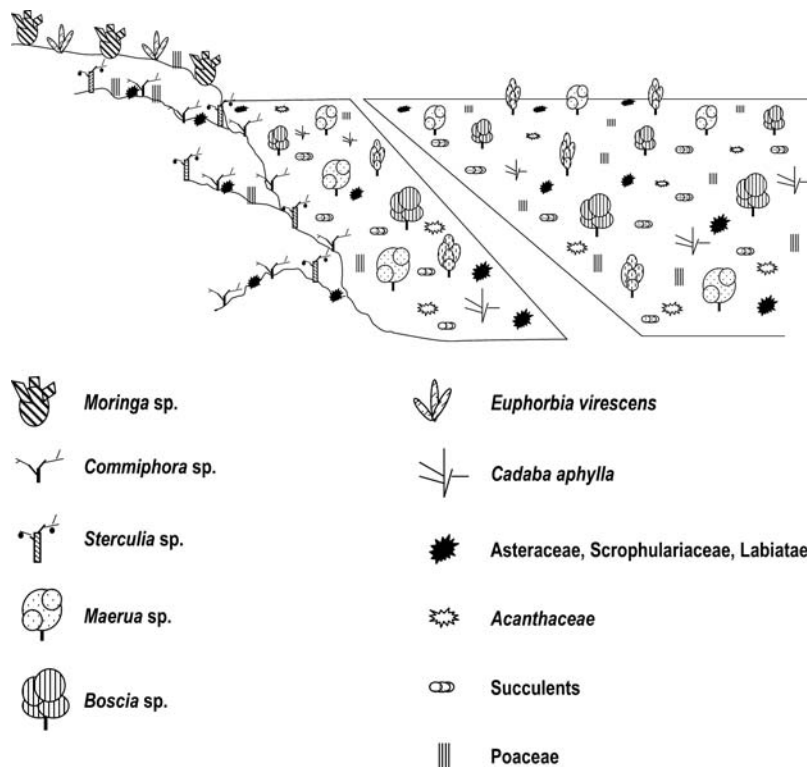
during the austral winter (July) as well as a semi-permanent coastal high-pressure ridge associated with Benguela Current upwelling and related cold water in the South Atlantic Ocean along the African west coast. The South Atlantic Anticyclone causes persistent subsidence and divergent wind-flow while the low offshore temperatures give rise to reduced oceanic evaporation and minimal precipitation along the coast and adjacent interior (van Zinderen Bakker, 1975; Tyson, 1986; Deacon and Lancaster, 1988). Only rarely does the maritime humid air, coming from the Indian Ocean, reach the western-

most part of the country because of the inhibiting effect of the high-pressure system along the Atlantic coast. Rare summer-time incursions of the warm Angolan current along the northern Namibian coastline and reduced upwelling intensity may allow an influx of moist tropical air from the north (Nicholson and Entekhabi, 1987). When this happens it provides an additional source of moisture for this region, especially along the escarpment foothills. The combined effect of two climatic systems, the high-pressure system and the Benguela current to the west, and the tropical moisture from the north and east, causes a pronounced precipitation gradient from west to east.

The availability of edaphic moisture (a factor that relates to soil depth) is relevant to the vegetation in different habitats in the study area (Figure 5). The shallow, superficial soils on the hills permit rapid runoff; therefore the life forms found on the hillsides are mainly composed of phanerophytes and chamaephytes with strong root systems, such as *Commiphora* sp., *Sterculia* sp., *Moringa ovalifolia* as well as stands of *Euphorbia virescens*. In addition, Acanthaceae (mainly *Justicia* sp. and *Blepharis* sp.), Asteraceae, Scrophulariaceae and Lamiaceae can be found in some places with deeper soil. Seasonal occurrence of hemicryptophytes and therophytes can be expected, especially after rain when therophyte seeds can germinate and hemicryptophytes may develop root systems to survive ensuing dry periods (Breckle, 2002). Examples of such physiognomic types are different species of Poaceae, eg, *Stipagrostis uniplumis* (the dominant grass) or the widespread *Tribulus terrestris* (Zygophyllaceae). The edaphic effect is more pronounced on the plains surrounding the hills where, despite the absence of running water, the silts and sands of the soils retain moisture for longer periods. This allows for the presence of Capparaeae trees such as *Boscia albitrunca*, *Maerua schinzii* or other taxa such as *Salvadora persica*. Some chamaephytes of Aizoaceae-type appear in the deeper soil areas, as well as more abundant perennial and annual grasses. Further south in the main Huab River valley, where permanent subsurface water availability and occasional seasonal flood events are the norm, the floristic diversity is greater and the plant composition consists of a riverine assemblage. Current riverine taxa include: *Tamarix usneoides*, *Datura stramonium* (Cucurbitaceae), *Salsola* sp., *Sarcocornia* sp. (Chenopodiaceae) and Cyperaceae. Obviously, the tree concentration also increases closer to the river, with a greater profusion of *Acacia*, *Salvadora* and *Colophospermum mopane* in and along the riverbed. No Combretaceae was observed near the study site, though *Combretum imberbe* and *Terminalia prunioides* are present in the main Huab River valley.



**Figure 4** Mean rainfall average curves at the closest meteorological stations. Data provided by Namibian Meteorological Service



**Figure 5** Schematic showing the main floristic features in the area and their topographical distribution

## Materials and methods

Dung midden sections were sampled from seven shallow rock shelters (I–VII, Figure 2A and B). Some thin layers (*c.* 1–2 cm thick) were processed as individual samples while thicker sections were subsampled in the laboratory along vertical profiles (Figure 6). Where possible, samples with a thickness of approximately 1 cm were taken, cleaned and processed. Pollen was extracted from each sample by using KOH digestion, acetolysis treatment, mineral separation through floatation in  $ZnCl_2$  (*c.* 2 g/ml) solution and washing with HF (Faegri and Iversen, 1989; Scott and Bousman, 1990). Microscopic analysis of residues, mounted in glycerine jelly, produced pollen counts of at least 250 per sample. Pollen concentrations were estimated by means of the exotic spore method (Stockmarr, 1972) using *Lycopodium*. Charcoal area was estimated counting charcoal fragments bigger than 75  $\mu m$  and using the linear regression explained in Tinner and Hu (2003). Eventually 41 samples from seven different middens were analysed, as well as four modern samples consisting of fresh hyrax dung. Nine radiometric dates were provided by the Quaternary Dating Research Unit, CSIR, Pretoria (QUADRU, Pta-numbers) and three AMS by Groningen Accelerator, The Netherlands (GrA-numbers). Additional samples are currently being dated. The samples were calibrated using the radiocarbon calibration program (CALP) for Southern Hemisphere measurements provided by QUADRU.

Percentages and concentrations in the pollen diagram were displayed using the software Tilia 2.0 and TGView (Grimm, 1991). Proportions were calculated on the basis of the pollen sum, which includes the taxa under tree, shrub and herb groups. Spores and Cyperaceae percentages form part of the total pollen sum, which includes the totals of all taxa.

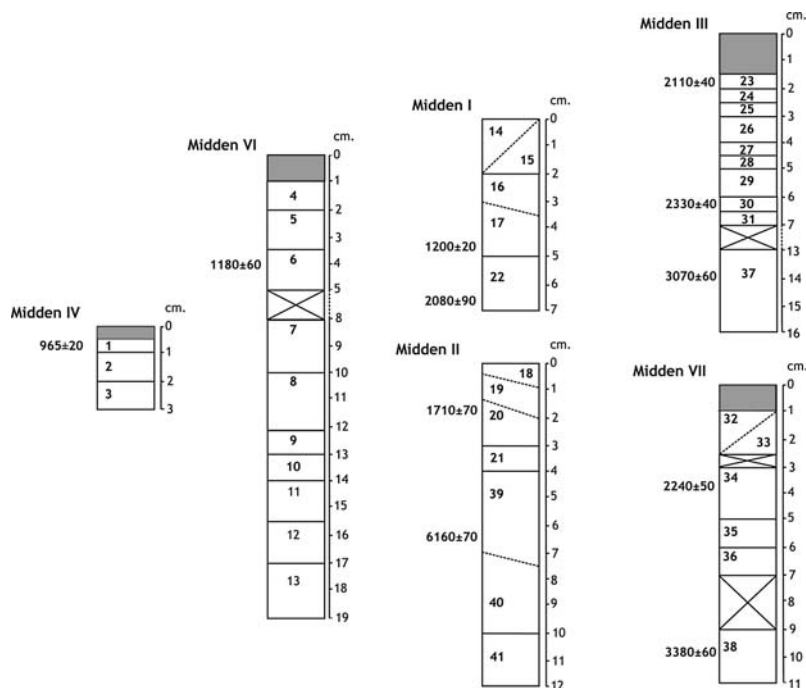
Different multivariate ordination methods were used to portray and evaluate pollen variations. Non-metric Multi-

dimensional Scaling (NMDS) was initially applied, since the variables do not fit into a normal distribution. However, NMDS computes dissimilarity matrixes, which produced a very unequal grouping in the indirect gradient analysis. Detrended Correspondence Analysis (DCA) yielded similar results to Principal Component Analysis (PCA), which was eventually employed given that it demands less data transformation (as DCA does with first axis segmentation and rescaling). Additionally, factor scores can be plotted for each observation in our chronological sequence.

## Results

The radiocarbon dates reveal that the middens represent a vegetation history for the site over the last 6000 years (Table 1). The  $\delta^{13}C$  (‰ PDB) values do not show notable fluctuations to infer real changes on the  $C_3$ – $C_4$  plant composition. In connection with sediment stratigraphy, continuous sediment accumulation cannot be assumed for several reasons, eg, a lack of chronological control in some key samples including the lower-most part of midden VI, varying time resolution and pollen concentration between middens, unconformities within and also time gaps between middens, inherent but difficult to detect variability in every dung unit, and gaps between samples resulting from discrete sampling intervals. However, because of limited current knowledge about taphonomy of pollen in dung (Carrion, 2002; Scott *et al.*, 2003) we will refer to samples as a whole while bearing in mind the limitations mentioned. On this basis centennial resolution could be considered within most of the middens, except for the oldest samples, where a gap of more than three millennia is observed.

The different samples are presented schematically in Figure 6 to show their stratigraphical context in a chronological sequence. Pollen in the modern samples (Figure 7), numbers M1 to M4, reflect roughly the same vegetation although the uneven proportions in Labiatae, Euphorbiaceae



**Figure 6** Middens studied, where the thickness of samples, uncalibrated radiocarbon dating and their stratigraphical context are detailed. Arabic numbers correspond to samples analysed within every midden; shaded portions correspond to material that was removed and the crossed areas represent material that was not processed. Broken lines in middens represent non-linear sampling

and Capparaceae suggest some local variation. Depositional effects can also explain the differences in the total pollen concentration.

In general, the fossil-sequence is characterized by the constant presence of a small group of prominent taxa, with minor variations. These pollen spectra consist of Poaceae, *Tribulus*, Acanthaceae – including the *Blepharis*, *Petalidium*, *Justicia-Monechma* and *Ruellia* types – and *Commiphora* (Scott, 1982). Centennial fluctuations reveal a gradual decrease in the presence of Poaceae and *Commiphora*, while Acanthaceae appears prolific in the modern surface samples. Some trees are of specific interest because they are not currently found in the area, such as *Rhus*, *Kirkia*, *Spirostachys*, *Dombeya* or *Dodonaea* – the latter is a non-indigenous plant (Curtis and Mannheimer, 2005). The tree–shrub–herb pollen ratio, corresponding roughly with phanero-, chamae-, hemicypto- and therophyte life forms, suggests minor vegetation change during the mid Holocene.

The Nama-Karoo Biome is represented through the regular co-dominance of shrubs, herbs and a generally low proportion of trees. The latter becomes more noticeable in fresh dung samples, suggesting that the current environment has a relatively higher tree ratio in relation to other plants, but not necessarily that trees were more frequent.

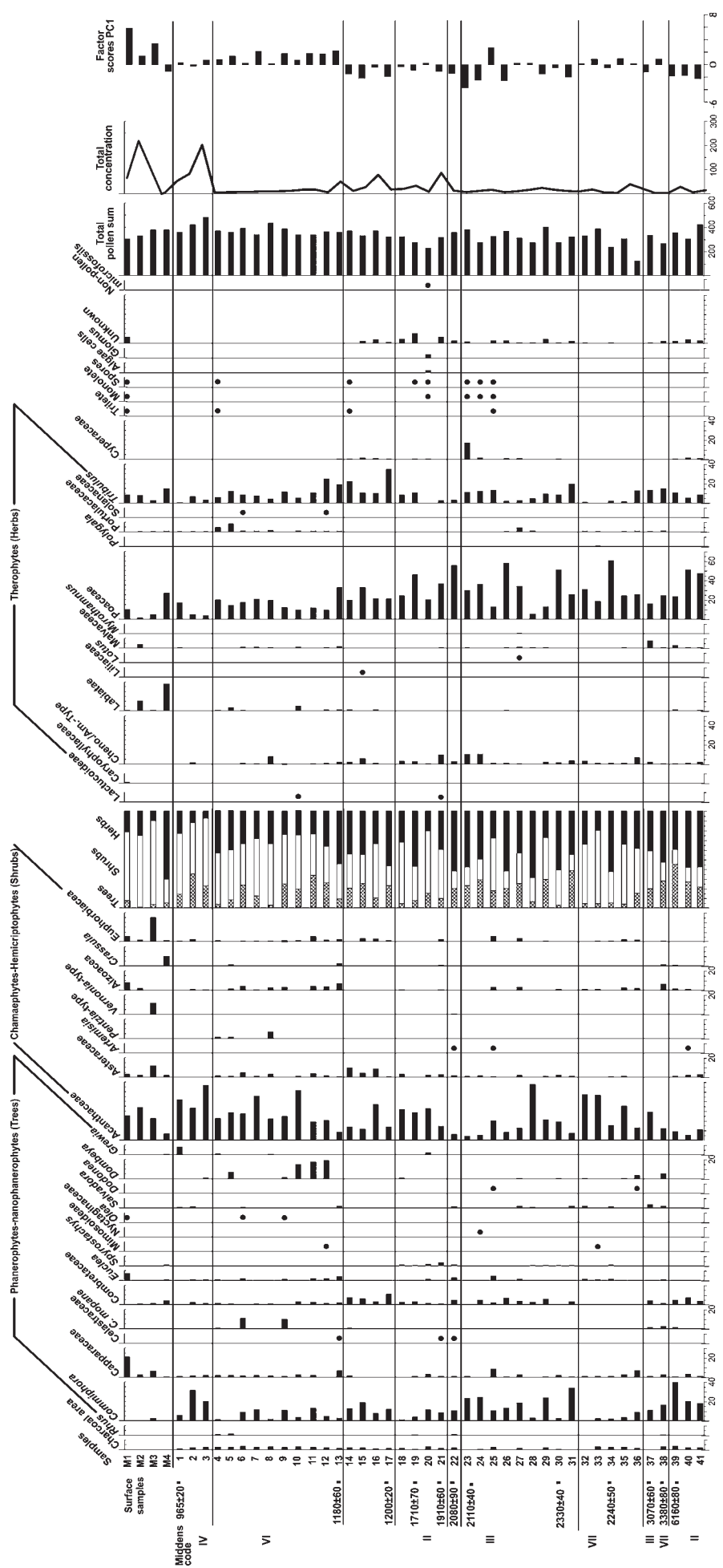
The first principal (PC1) component in the PCA explains around 17% of the variance (Figure 8). The variability of PC1 in modern samples seems to cover the total variability in the fossil samples; nevertheless fresh pellets may reflect seasonal variation while the fossil samples represent averaged pollen input over several decades or centuries. Thus the modern pollen spectra could be reflecting seasonal signals rather than wide environmental differences. Taxa correlating positively with PC1 include Acanthaceae, Asteraceae, Capparaceae (probably mainly *Boscia* and *Maerua*) and *Colophospermum mopane*, as well as some succulents such as Aizoaceae-type and Euphorbiaceae. A large number of taxa are negatively corre-

**Table 1** Radiocarbon dates and isotopes ratios from the Huab river (northwestern Namibia)

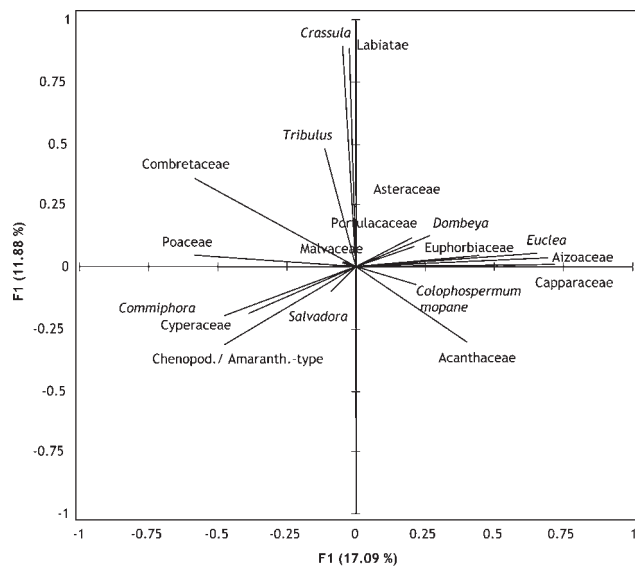
Lab no. <sup>a</sup>	Sample designation	Midden number	$\delta^{13}\text{C}$ (‰PDB)	Radiocarbon age, yr BP	Calibrated ages
Pta-8630	4034	IV	– 24.2	965 ± 20	AD 1040–1159
GrA-20769	4040	VI	– 25.5	1180 ± 60	AD 811–847
Pta-8876	4027.2	I	– 24.7	1200 ± 20	AD 870–895
Pta-8S78	4028.5	II	– 24.7	1710 ± 20	AD 382–409
Pta-8879	4028.6	II	– 24.6	1910 ± 60	AD 72–228
Pta-8645	4026	I	– 25.7	2080 ± 90	173 BC–AD 60
GrA-22030	4032.3	III	– 19.6	2210 ± 40	353–299 BC
Pta-8883	4045.2	VII	– 25.6	2240 ± 50	370–186 BC
GrA-22031	4032.12	III	– 20.9	2330 ± 40	394–370 BC
Pta-8888	4044.2	VII	– 24.3	3030 ± 50	1298–1130 BC
Pta-8649	4033	III	– 24.3	3070 ± 60	1298–1130 BC
Pta-8645	4029	II	– 22.2	6160 ± 80	5212–4813 BC

<sup>a</sup>Pta-, QUADRU at Pretoria, <sup>14</sup>C dating; GrA-, Groningen, AMS dating. Calibrated age range shown with an error of  $\pm 1\sigma$ . Calibration curve used is Southern Hemisphere INTCAL (1998) obtained from Northern Hemisphere 98, adjusted by 40 years except for the last century where it is based on actual South African tree ring measurements (Vogel *et al.*, 1993).

Vrede, near Huab river, NW Namibia  
 20° 19' 49" S / 14° 10' 11",  
 527 m.a.s.l.



**Figure 7** Pollen diagram for Vrede sediments with the PCI factor scores on the left. Roman numbers refer to the different middens sampled and Arabic numbers to the samples analysed (see Figure 6). Histogram bars represent percentages of every taxa on the basis of pollen sum except for charcoal area which is measured in mm<sup>2</sup>/cm<sup>3</sup>; dots mean presences below 0.5%. Total concentration is measured in number of pollen grains/grams × 10<sup>3</sup>



**Figure 8** Selected taxa plotted after factors one and two of principal component analysis

lated, including Poaceae and Cyperaceae, and also taxa adapted to living either in extremely arid circumstances or having a great tolerance to a wide range of habitats, such as *Commiphora*, *Tribulus* and Combretaceae. *Salvadora*, which occurs predominantly along the dry riverbeds of west-flowing streams in Namibia (Curtis and Mannheimer, 2005), has neutral PC1 loadings.

The second principal component (PC2), accounting for *c.* 12% of the variance, is not discussed here because it reflects a complex assemblage in which environmental parameters are difficult to identify.

Keeping in mind that the section from *c.* 6000 yr BP to around 1100 yr BP involves a gap in the record of 3000 years, PC1 factor values for available parts of this section (Figure 7, far right) have a negative trend, suggesting that the ratio of Poaceae, Combretaceae, *Tribulus*, *Commiphora*, Chenopodiaceae and Amaranthaceae during the intervals covered were higher in relation to Acanthaceae, *Euclea*, Capparaceae and succulent elements such as *Euphorbia* and Aizoaceae-type. The factor values change to positive scores *c.* 1000 yr BP and in the modern samples representing present climatic conditions and vegetation assemblages. We note, however, that the last millennium is not continuously covered by our record.

## Discussion

The arid and semi-arid regions of Namibia are subject to unpredictable fluctuations of the biotic system, which are directly related to the quantity and spatial distribution of rainfall (Sullivan, 1996). Environmental variability is an inherent feature of desert ecosystems, which in the long-term produces its own stability with a high degree of resilience (Sullivan, 1996; Sullivan and Konstant, 1997). In this context, with reference to our results, it can be assumed that the floristic landscape in the study area has an intrinsic low quantitative stability whilst maintaining the same qualitative relationships. For instance, there is a constant fluctuation in the phanero-, chamae- and hemicryptophyte ratio, though the average physiognomic composition seems to fit the Nama-Karoo Biome in general terms. The fact that the site is situated in an ecotone must be considered since the narrow belt of Nama-

Karoo at this latitude is sandwiched between the Desert and the Savanna Biomes, thus the logical assumption is that the recorded variability is not exclusive to either of these biomes. In the absence of major climatic changes during the middle to late Holocene, related changes in the life-form composition would therefore mean a switch towards one of those biomes, but without fitting solely in either.

Climatic interpretation based on the observed fluctuations of individual taxa is problematic since the percentage change in each taxon could be ascribed to local or seasonal variations in rainfall rather than to regional climatic trends. However, the recorded chronology allows us to infer decadal or centennial climatic trends that are highly resolved in most samples. The PCA yields a complex combination of taxa in PC1, suggesting a suite of floristic elements that respond by flowering rapidly to a small increase in water availability.

Thus increased spectral presence of Poaceae and Cyperaceae, as reflected in negative PC1 values, would mean local increases in rainfall. Grasses, in particular, flower very rapidly after rain. The absence of constant moisture around the rocky outcrop precludes the presence of Cyperaceae at the present time, though this taxon is abundant in the Huab River valley to the south where underground water is forced upwards by the underlying geology. The possibility of a long-distance input of pollen into the fossil sequence from the river cannot be excluded, although the pollen may indicate the past presence of Cyperaceae in the tributary at the base of the outcrop.

The other taxa with negative correlations are those that are extremely well adapted to a wide range of habitats; eg, species in the genus *Commiphora* are trees whose modern distribution is wide although they are predominantly found in the Nama-Karoo ecotone between the Savanna and the Desert, with its preferred habitat on hill slopes (Curtis and Mannheimer, 2005). The Combretaceae family, characterized in the area by *Combretum imberbe* and *Terminalia prunioides*, has comparable behaviour although it prefers less exposed locations. The former genus is generally found in plains, dry riverbeds and the latter on hill slopes. The flowering period for both groups of trees seems to be rain-dependent (Curtis and Mannheimer, 2005) with a maximum flower production, on average, between November and January. Since the meteorological data (Figure 3) indicate that precipitation is most likely between November and March, it provides supporting evidence for rain-dependent flowering. However, interannual flower production is likely to be opportunistic with respect to the season in view of the aridity of this region. We contend that the therophytes, represented by Chenopodiaceae and Amaranthaceae pollen (Cheno/Am-type) and *Tribulus*, have similar flowering strategies by rapidly reacting to rainfall events or by relying on underground moisture. In addition, *Tribulus* is a ruderal plant, growing in highly eroded or disturbed soils, thus, its presence might be due to anthropogenic influences, eg, livestock grazing.

Although the natural distribution patterns of taxa that cluster on the negative and positive sides of the PC1 axis do not indicate a clear moisture gradient, they might represent different physiological responses in terms of drought endurance and independence of flowering to rainfall. It seems likely that flowering in the positive group may be unrelated to the rainfall season of the area. Aizoaceae, Capparaceae, Euphorbiaceae, etc., are less rain-dependent forms that can last through drier conditions, eg, Capparaceae such as *Boscia albitrunca*, *B. foetida*, *Maerua schinzii*, *M. parviflora* and *Cadaba aphylla*, which flower in September and October. Other taxa, such as Acanthaceae are very well adapted to

exceptionally arid environments, producing flowers even under drought conditions. Moreover, the sequence of Acanthaceae pollen is negatively related to Poaceae, with a Pearson's  $R$  of  $-0.46$  ( $p < 0.05$ ).

We therefore interpret PC1 as a moisture availability factor, with negative correlations implying slightly increased rainfall and positive correlations slightly decreased rainfall. Consequently, we propose that the fossil middens were accumulated during a more stable period of wet spells between 6 and 1 ka, i.e. reduced interannual variability. A notable decrease in the abundance of Poaceae pollen, as well as in the percentages of tree spectra, characterizes the available records in the last 1000 years (including the modern samples). Since we recorded no radical change in the vegetation composition, the intra-seasonal frequency and annual amount of rainfall during the last 1000 years was probably not much greater than at present.

Apart from changes in the rainfall pattern, different environmental factors could have been shaping the landscape as well. As suggested above, the erratic behaviour of some taxa could be attributed to anthropogenic effects, such as grazing, eg. the recent decrease in Poaceae and the increment in *Tribulus* since *c.* 1200 yr BP. There is some archaeological evidence showing an early human presence at different localities of Northwestern Namibia (Jacobsohn, 1995; Kinahan, 2001; Albrecht *et al.*, 2001; Lenssen-Erz and Vogelsang, 2005). The transition from hunter-gatherer societies to herders in northern Namibia has been largely discussed (Lenssen-Erz and Vogelsang, 2005) although general agreement places this change 2000 years ago. This supports human activities in our studied area. However, that change was not a profound transformation, but rather comprised the occasional presence of some sheep brought by nomadic groups that did not apparently impact markedly on the Nama-Karoo dynamics. Moreover, as explained above, the interannual rainfall variability coefficient in the Namib edge is so high – around 30% (Bollig and Schulte, 1999) – that even if degradation occurred as result of overgrazing, it can be easily conflated with vegetation changes caused by the lack of rain (Bollig and Schulte, 1999). In conclusion, although human presence cannot be discounted, the plant variation might not be attributed to their actions, even in view of the aridifying effect of grazing activities.

On the other hand, possible climatic mechanisms for an increase in rainfall frequency in the mid Holocene are difficult to identify, as our record is not continuous. However, relatively minor shifts in atmospheric circulation patterns, eg. in the ITCZ or Congo Air Boundary (Tyson, 1986), in ocean currents or sea surface temperature (SST), or in the precessional cycle may have played a role.

In terms of rainfall seasonality, it is likely that this area remained in the summer rainfall zone, as variations in the vegetation composition do not indicate major changes in rainfall seasonality. A slight increase in the succulent elements is observed in the modern samples, while Asteraceae percentages remained constant through the whole series. Thus higher numbers of Aizoaceae, Euphorbiaceae or Crassulaceae in the modern samples cannot be due to winter rain as the study area currently receives only summer rainfall (Figure 3). The postulated middle-Holocene increase in rainfall is therefore not likely to reflect an increase in winter rain, as it was not accompanied by an increase in succulent pollen types.

Currently, tropical easterlies or easterly waves reinforce long-term wet spells over the summer rainfall area of Southern Africa (Tyson, 1986). Short-term wet periods seem to be associated with a quasi-stationary surface trough in the

westerly zone affecting the west coast of Southern Africa (Tyson, 1986). More reliable rainfall for our recorded phases between *c.* 6000 and 1000 yr BP may therefore be ascribed to a strengthening in the easterlies or lasting low pressures in the western interior of the subcontinent.

The available proxy data for northwest Namibia are exceptionally heterogeneous and show that various environments reacted very differently to weak climatic fluctuations. However, a spatially coherent picture of wetter conditions during the Holocene hypsithermal is emerging. Palaeoenvironment studies in northwestern Namibia (Kaokoland and Damaraland) have mainly focused on geological features such as fluvial deposits (Rust and Vogel, 1988; Brunotte and Sander, 2000; Eitel *et al.*, 2005) and marine palynology and mineralogy (van Zinderen Bakker, 1984; Gingele, 1996; Shi *et al.*, 1998, 2000; Dupont *et al.*, 2004). Despite the lack of synchronicity in the different sequences, some of them confirm wetter conditions in the mid Holocene between *c.* 8000 and 4000 yr BP.

The work of Rust and Vogel (1988), Vogel (1989) and Srivastava *et al.* (2004) on the landforms of the Hoanib, Hoarusib and Khumib rivers shows wetter conditions with erosion activity between 8000 and 1000 yr BP, followed by an increase in aridity towards present conditions. Brunotte and Sander (2000) describe a loess accumulation in different basins of Kaokoland (Omungunda, Opuwo and Okaoraore) during the last three millennia, which seems to correspond with an increase in moisture and fluvial activity during the transition between the mid and later Holocene. Eitel *et al.* (2005), in their study on the Aamspoort Silt terrace of the Hoanib basin, conclude that there was decreased rainfall in northern Namibia during the last 1000 years.

Pollen in marine core GeoB 1023, off the northern Namibian-South Angolan coast, near the Cunene river mouth (17°09'S 11°01'E) shows an increase of Poaceae and a decrease in desert and semi-desert taxa between 6.3 and 4.8 ka cal. BP (Shi *et al.*, 1998; Dupont *et al.*, 2004). Although north of our study site, these findings seem to confirm humid conditions in the middle Holocene. In these studies the grass spectra fluctuate from 5000 BP with an eventual decrease in the last 1000 years. A Holocene marine clay mineral record, also from the mouth of the Cunene River (Gingele, 1996), indicates a maximum fluvial signal between 6 and 5 ka. This could be the result of a wet period at that time. However, the same study points to less fluvial activity during the last 4000 years. The GeoB 1023 core also indicates a rapid drop in alkenone-derived sea surface temperatures to present values over the past 1000 years (Dupont *et al.*, 2004), while similar decreases in SSTs during the late Holocene have also been recorded in marine cores from the Walvis Bay area further to the south (Kirst *et al.*, 1999). Since increased rainfall over the southwestern African interior is associated with higher Benguela SSTs (Nicholson and Entekhabi, 1987; Kirst *et al.*, 1999), this may have contributed to more reliable rainfall at our study site.

In a wider regional framework in Namibia, other studies provide additional evidence of a mid-Holocene wetter period in the desert and the hinterland. To relate our results with these studies can be difficult, since the observed palaeoecological patterns may be due to very different causes. Changes in the ratios of gecko and gerbil microfaunal remains from fossil owl pellets in the Mirabib shelter, in the Central Namib Desert (Brain and Brain, 1977) show that this particularly arid site could have been wetter than the present during the period *c.* 7000–6000 yr BP. It further shows an increase in arid

conditions in the upper part of the sequence, though no  $^{14}\text{C}$  ages are available between 5190 and 400 yr BP.

In the Kuiseb River valley, rapid deposition of the Homeb silts occurred at *c.* 15 and 6 ka, suggesting increased river flow at these times (Srivastava *et al.*, 2006). Moreover, high numbers of grass pollen in hyrax dung found in the same valley suggest fluctuating moisture conditions during the last *c.* 2000 years, with dry spells *c.* 1000 yr BP and at present (Scott, 1996). Pollen studies of spring deposits in Windhoek, central Namibia, and sediments in Lake Otjikoto, a sinkhole in northern Namibia (Scott *et al.*, 1991), respectively, indicate a moist and warm phase of climate between *c.* 7000 and 6000 yr BP, and more moisture before 3500 yr BP. Relative dryness after 3500 yr BP is seen in the sinkhole, although a temporary wet phase occurred before 1000 BP.

Excess air in the Stampriet artesian aquifer in the western Kalahari (Stute and Talma, 1997) may point to rapid recharge at *c.* 6000 yr BP. This indicates a transition from a drier to a wetter climate with increased dissolution of trapped air bubbles in the groundwater. Finally, Heine (2005) gives a palaeoclimatic synthesis for the Holocene in Namibia, employing various kinds of dated archives. He concludes that despite the general Holocene climatic stability in Namibia, fluctuating but progressively drier conditions have occurred. Included in the fluctuations is more rainfall during the 'Little Ice Age', as recorded in valleys of the northern Namib.

Other palaeoclimatic evidence of palaeoenvironmental conditions during the Holocene transition in Southern Africa are summarized in Partridge *et al.* (1990), Scott (1993) and Scott and Lee-Thorp (2005). Various types of evidence suggest relatively wet conditions in the northern part of the subcontinent during the mid Holocene, between 7000 and 5000 yr BP. In a palaeoenvironmental review of Southern Africa for the last 3000 years, Tyson (1986) concludes that the general pattern seems to indicate that conditions were wetter than the present for this period. There is general agreement that the mid-Holocene period was wetter in Southern Africa from *c.* 6000 to 4000 yr BP. However, the precise duration of this wetter period remains unclear, as some records to the east in the subcontinent show dryness by *c.* 5000 yr BP (Scott and Lee-Thorp, 2005).

## Conclusions

The fossil pollen record recovered from seven fossil hyrax middens in the Vrede outcrop in northwest Namibia, suggests long-term stability in the Nama-Karoo Biome during the recorded intervals of the last 6000 years. The different dating resolutions of dung deposits, together with the complex stratigraphical context of middens, make it difficult to evaluate trends. However, clear patterns appeared in the vegetation dynamics. Plant composition and its relative abundance have remained nearly constant although a generally wet period, with more frequent and probably heavier summer rains, is indicated for the available sections between *c.* 6 and 1 ka BP. Nevertheless, the extreme climatic variability, the complexity of floral physiological adaptations to aridity and non-equilibrium of floral responses to the amount and distribution of rainfall, makes the interpretation of the pollen fluctuations difficult in terms of climatic change. The apparent mid-Holocene increase in effective rainfall is reflected in the flourishing of plants that can respond quickly to low amounts of precipitation (Poaceae, *Tribulus*, Chenopodiaceae, Cyperaceae, etc.) and it is supported by other local, regional and subcontinental data. Human presence might have shaped this landscape to some

extent, although it seems an unlikely explanation for the vegetation change.

This study provides further confirmation of the value of hyrax middens as a source of terrestrial fossil pollen in arid environments.

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