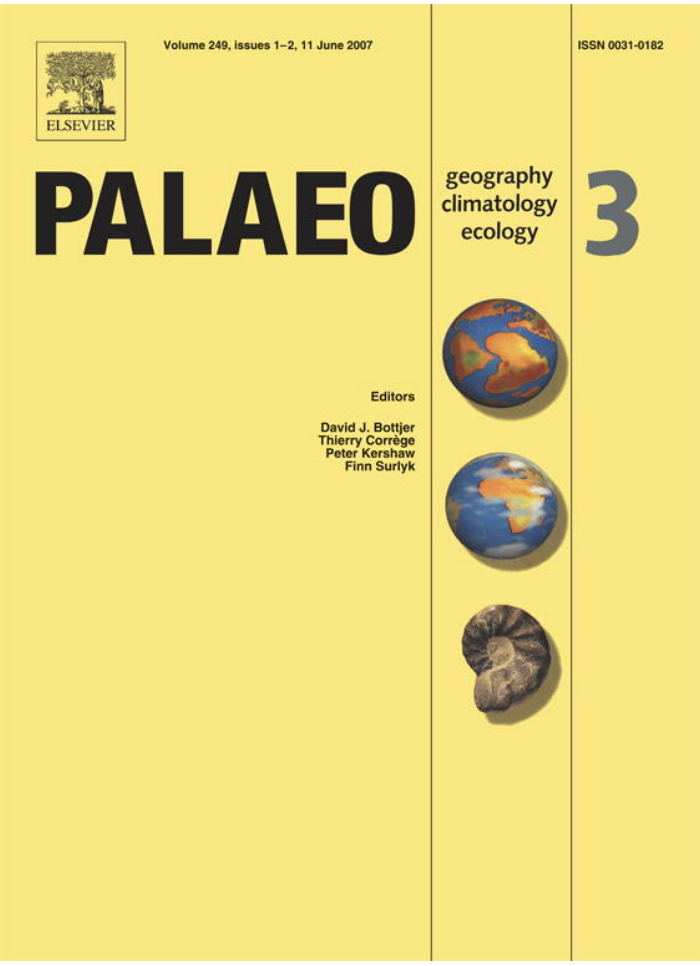

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Late Holocene environmental change in the northwestern Namib Desert margin: New fossil pollen evidence from hyrax middens

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Abstract

The lack of anoxic environments in arid lands makes well-preserved fossil pollen difficult to find. The scarcity of continental palaeobotanical data in tropical arid zones restricts the understanding of aridification processes in these endangered ecosystems. It is essential to improve the knowledge about their environmental histories during the Holocene, and therefore we attempt to investigate the causes and describe the patterns of vegetation change in northern Namibia. With that aim we analyzed pollen from fossil hyrax dung that accumulated over long periods of time by sampling stratigraphically coherent sequences in five radiocarbon-dated middens. The fossil hyrax middens were found in rock shelters on the eastern desert edge in the northwestern Kaokoveld, within the so-called Nama-Karoo biome. This is an ecotonal area between the Namib Desert and the Savanna biomes which reflects features from both systems and its life form composition largely depends on an erratic rainfall pattern. Thirty-three samples were analyzed for pollen and the pollen record reflects a non-continuous vegetation history over the last 5200 yr with a hiatus between ca. 4200 and 1690 yr BP. The pollen spectra reflect arid savanna vegetation with a marked increase in the tree/grass ratio from ca. 1300 cal yr BP. The most likely cause for this change is a decline in moisture that we relate to intrinsic savanna dynamics, with early pastoralism, megahervibore migration and changes in the hyrax diet playing a minor role.

Keywords: Namib Desert; Holocene; Palynology; Savanna dynamics; Nama-Karoo; Vegetation history; Hyrax middens

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1. Introduction

Hyperarid, arid or semiarid climates characterize a third of the land surface on Earth (Le Houérou, 1996). However, very little is known about palaeoenvironmental conditions in these areas. Understanding the current desertification processes, both natural and human related, requires research on the Holocene climates of these areas to discern the causes of past ecosystem fluctuations. Palaeobotanical vegetation analyses could facilitate interpretations about current vegetation transformation and its natural or anthropic determinants. This is especially relevant for land management or for identifying unique landscapes where endemicity or biogeographic features should be protected.

Several studies using different palaeo-archives have focused on the northern Namib Desert. They are either oceanic (Shi et al., 1998; Stuut et al., 2002), or continental

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records. The latter includes mainly sedimentological, pedological and geomorphological studies (Vogel and Rust, 1987; Vogel, 1989; Eitel et al., 2001; Stuut and Lamy, 2004; Eitel et al., 2004; Heine, 2004; Eitel et al., 2005; Srivastava et al., 2005; Thomas et al., 2005; Eitel et al., 2006). Palynological data are extremely limited and most studies have focused on the Central Namib (van Zinderen Bakker, 1984; van Zinderen Bakker and Müller, 1987; Scott et al., 1991; Scott, 1996; Shi et al., 1998; Shi et al., 2000; Shi et al., 2001; Dupont and Wyputta, 2003; Dupont et al., 2004; Scott et al., 2004; Gil Romera et al., 2006). However, all of these archives are sparse and lack synchroneity as some of them are poorly dated, though they confirm Holocene climate oscillations. In palaeoenvironmental terms, little is known about the northern part of the desert.

Fossil pollen is easily available in lacustrine or swampy deposits in humid or sub-humid areas. In these regions the abundance of vegetation and good preservation of pollen grains, due to the existence of submerged anaerobic environments, facilitate pollen extraction and identification. The erosive and permanently aerobic conditions in arid lands prevent the formation of suitable polleniferous sediments (Horowitz, 1992). Moreover, moderate pollen production and the dominance of insect-pollinated taxa limit pollen availability in general. An attempt to overcome the erosional and depositional limitations has led palynologists working in drylands to study biogenic deposits. In the arid lands of Southern Africa, herbivorous mammal dung has proven extremely valuable for fossil pollen studies (Scott, 1990; Scott and Bousman, 1990; Scott and Cooremans, 1992; Scott, 1994; Scott, 1996; Carrión et al., 1997a,b; Scott et al., 2005).

Fossil hyrax middens have been especially useful as a source of palynomorphs. During formation they trap local and regional pollen grains and in addition record changes in the pollen signal over time. The dung accumulations, embedded in quick-drying adhesive urine (*hyraceum*), represent pollen in hyrax diet and airborne pollen. They often represent long time intervals and therefore good pollen records. Hyraxes are widespread on the African continent, including the arid parts, as inhabitants of rock shelters. They are not very selective in their feeding habits, although they are preferentially grazers and occasionally browsers (Fourie and Perrin, 1989), and their foraging excursions do not normally exceed 500 m (Rübsamen et al., 1982). Unlike the rodent middens typical in North America and the Atacama desert (Jackson et al., 2005; Maldonado et al., 2005; Holmgren et al., 2006), hyraxes do not gather plant remains, so palaeobotanical sources are restricted mainly to fossil pollen and to rare, accidentally included, macrofossils from latrines. However, since these animals habitually defecate and urinate in distinct latrine areas over long periods of time (Scott and Bousman, 1990; Carrión et al., 1999) they usually build up stratigraphically coherent sequences, unlike the chaotic nest building of rodents. Sub-samples in individual heaps can give continuous fossil pollen fluctuations over certain intervals and a combination of different middens may produce longer sequences (Scott, 1996; Scott and Vogel, 2000; Scott and Woodborne, in press).

In this study, which is part of a continuing effort in northwestern Namibia, fossil latrines were sampled near Okandjombo (Kaokoveld), 95 km inland from the coast. The results of palynological analysis and their indications for vegetation change and its likely environmental causes are presented here.

2. General setting

The middens were found in shallow rock shelters (18° 15′ 46″ S; 12° 51′ 02″ E) weathered into heavily fractured quartzites of the Nosib Group of the Damara Orogen (Miller, 1983), near Okandjombo at 824 m altitude (Fig. 1). A fault-line, with a strike of 315°, cuts through the outcrop along an ephemeral streambed below the shelters that occur in deep cracks related to biotite schistosity and extensive jointing. The predominantly rocky hillsides have shallow acidic soils (0–20 cm) in pockets between cobbles and rocky outcrops, with deeper sand only occurring in the streambed.

Northern Namibia receives monsoonal summer rainfall, with a steep, eastward rainfall gradient from the coast to the interior, related to the predominant coastal aridity of the Namib Desert. The hyper-arid conditions are produced by a permanent but not stationary South Atlantic high-pressure cell along the Namib coast, reinforced by low humidity over the northward flowing cool Benguela upwelling current (Tyson, 1986). This forms a high-pressure gradient, with minimum evaporation, which prevents incursions of moist air from the east to penetrate further west to the coast. Weaker Benguela upwelling events, together with associated weakening of the coastal high-pressure inversion, allow moist Indian Ocean air masses to reach the western area of Namibia and produce rainfall over the Namib Desert.

In northern Namibia wet spells may also be induced by the southwards migration of the ITCZ during the summer (van Zinderen Bakker, 1975; Tyson, 1986; Nicholson and Entekhabi, 1987; Preston-Whyte and

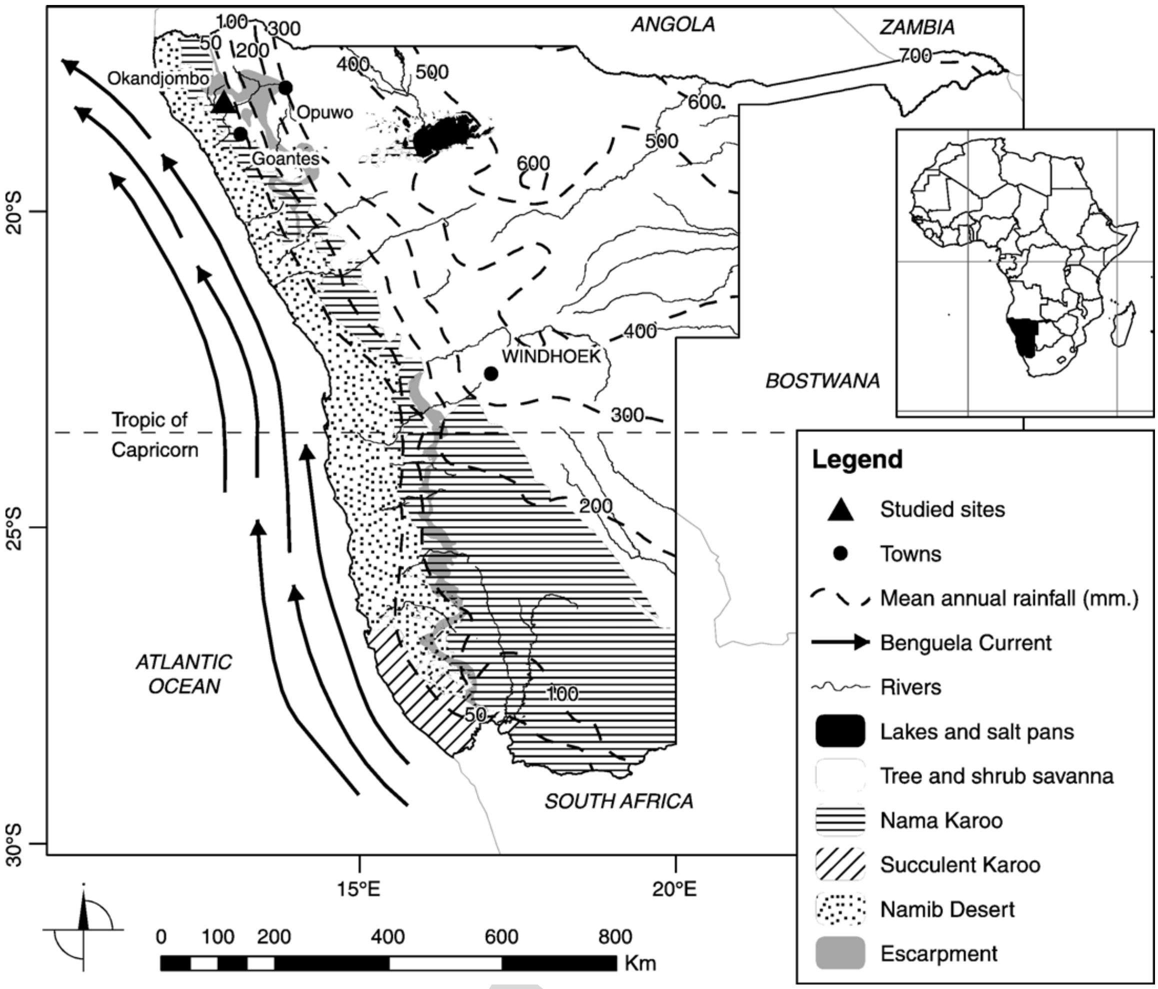

Fig. 1. Map of Namibia showing the study area, rainfall isohyets, vegetation biomes and the Great Escarpment. Goantes is the closest meteorological station (own elaboration after GIS data from Mendelsohn et al., 2002).

Tyson, 1988; Nicholson, 2000), particularly by fluctuations in the associated Congo Air Boundary (CAB). The CAB is the convergence area for the Atlantic and Indian Ocean air-streams and its position occasionally fluctuates southwestwards from southern Angola and Botswana to northern Namibia, resulting in an increase in precipitation (Tyson, 1986). The modern long-term wet spells in the northern Namib Desert are produced by negative anomalies in the pressure fields. The southwestwardly movement of the tropical rain-bearing systems (CAB and ITCZ) facilitates the formation of easterly waves and tropical lows over northern Namibia causing divergence fields to force tropical convection and latent heat release over that area. Short-term wet periods seem to be associated with a quasi-stationary surface trough in the westerly zone of Southern Africa (Tyson, 1986; Nicholson and Entekhabi, 1987; Preston-Whyte and Tyson, 1988; Nicholson, 2000).

Okandjombo is therefore affected by the easterly rain-bearing systems originating from the Indian Ocean and also by tropical rainfall when the CAB penetrates unusually far south. However, despite clear rainfall seasonality affecting the area, precipitation along the desert margin is highly unpredictable on temporal–spatial scales (Lancaster et al., 1984; Tyson, 1986; Günster, 1995; Jury and Engert, 1999; Hachfeld and Jürgens, 2000; du Plessis, 2001; Zeidler et al., 2002; Legget et al., 2003; Richters, 2005) and this strongly affects the ecosystem dynamics. We lack current climatic data from the study area because there is no meteorological station near Okandjombo and the nearest ones are either far to the interior or to the south (Fig. 1). The isohyets represented in Fig. 1 are after Mendelsohn et al. (2002), interpolated from rainfall data available in Namibia. Judging from these isohyets, the mean annual precipitation for Okandjombo would be less than 50 mm. The precipitation for the nearest comparable station at Goantes (18° 47′ S, 13° 07′ E; 40 mm/a; 1979–2000) fluctuates between 0 and 176 mm per yr (Fig. 2). No other reliable data is available from the region.

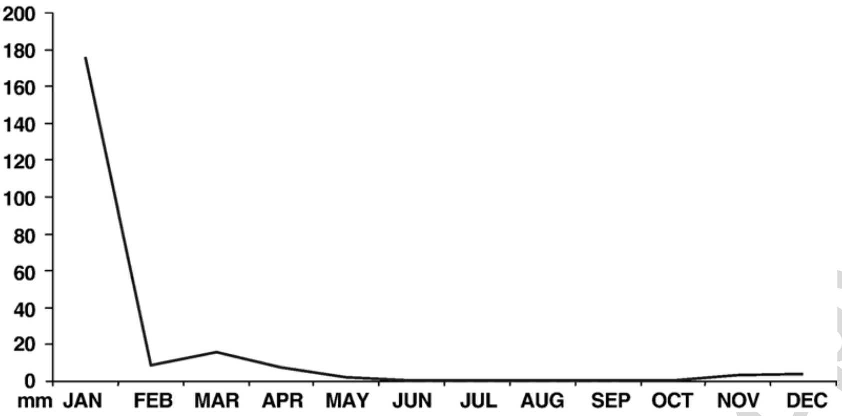

Fig. 2. Mean monthly rainfall curves for Goantes. Precipitation in mm for the period 1980–2000.

Okandjombo lies in the northern Nama-Karoo biome, which stretches between the Savanna and Desert biomes. It is a transitional zone, which is defined by the predominant plant life forms of mainly chamaephytes and hemicryptophytes (Irish, 1994; Rutherford and Westfall, 1994). Its transitional character implies overlapping features from the biomes nearby. As a result, savanna trees such as *Colophospermum mopane* (Caesalpinoideae), which is frost-intolerant with a high efficiency in water use (Scholes et al., 2002; Burke, 2006), or *Terminalia prunioides* and *Combretum imberbe* (both Combretaceae) are found in dry streambeds with thicker soils and less transpiration. Some other trees well adapted to aridity also occur such as *Maerua schinzii* and *Boscia albitrunca* (both Capparaceae), *Gymnosporia senegalensis* (Celastraceae), *Lyceum* sp. (Solanaceae), *Rhigozum brevispinosum* (Bignoniaceae), *Sesamothamnus guerichii* (Pedaliaceae) and succulents such as *Euphorbia* (Euphorbiaceae). Others like *Commiphora* sp. (Burseraceae), *Sterculia* sp. (Sterculiaceae) and *Moringa* sp. (Moringaceae) are able to grow on rocky slopes because their roots penetrate cracks in the bedrock to access water. *Salvadora persica* (Salvadoraceae) and *Euclea* (Ebenaceae) are very sparse phreatophytes along ephemeral channels. Amongst the chamaephytes some families like Labiatae, Scrophulariaceae and Acanthaceae are common, as well as the genus *Salsola* (Chenopodiaceae). The most frequently occurring perennial grass is *Stipagrostis uniplumis*, though other Poaceae supplement the hemicryptophyte and therophyte component.

Slope aspect may determine local plant distributions through its effect on evapotranspiration (Fig. 3). For example, on the north-facing slope where samples were collected, trees (micro-phanerophytes) are scattered with some Combretaceae and *Commiphora*, and there is a very low abundance of chamaephytes and therophytes. By contrast, the south facing slope has a denser tree cover and a different plant suite that includes more Capparaceae, Combretaceae, *Lycium* and relatively more annual and perennial grasses as well as more flowering shrubs (Labiatae, Scrophulariaceae and Acanthaceae). Independent of exposure to the sun, but related to soil depth, *Colophospermum mopane* and some isolated stands of *Salvadora* are predominantly found along the dry riverbed.

The transitional character at this site can be an especially useful feature as a small-scale proxy for continental-scale biogeographic patterns (Gosz, 1992). Broad-scale ecotones are more likely to be the result of regional climatic features, such as gradients of temperature and moisture, than of fine-scale features of the habitat (Gosz, 1992). Additionally, high diversity is expected as transitions between structurally contrasting systems would result in a combination of microhabitats with properties different from adjacent biomes, thus amplifying or attenuating some system processes (Neilson, 1993; Noble, 1993).

3. Methodology

A field survey was carried out to locate hyrax middens in rock shelters adjacent to the dry river channel and to record the vegetation in the area. Six middens were sampled and fresh pellets were collected in order to obtain present-day palynomorph spectra. Sampling of the dung accumulations was carried out following the individual stratigraphy of dung heaps as far as possible (see Fig. 4). Some middens were too thin for multiple samples to be taken. In these cases single samples were taken of the entire deposit.

Pollen was extracted from each sample by using KOH digestion, acetolysis treatment, mineral separation through floatation of organics on $ZnCl_2$ solution, and

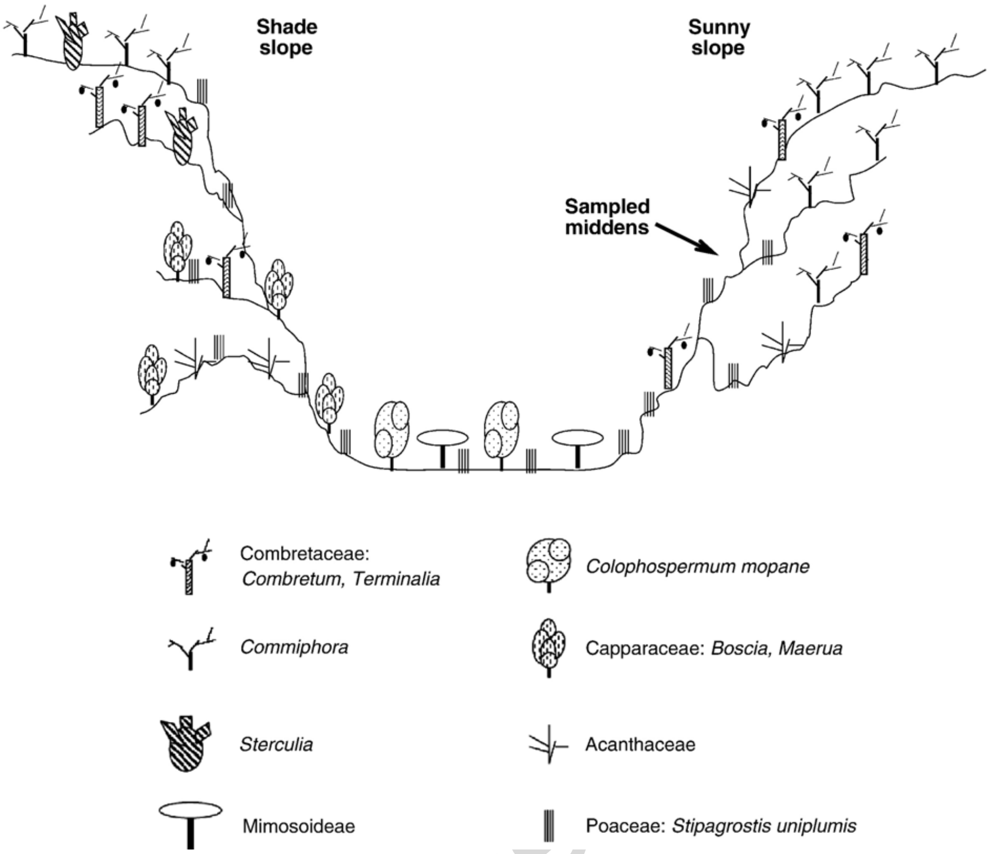

Fig. 3. Site schematic with the main floristic elements and their topographical distribution at the Okandjombo study site (18° 15′ S, 12° 51′ E).

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 in almost all the samples. Pollen concentrations were estimated by means of the exotic *Lycopodium* spore method (Stockmarr, 1973). Samples from four fossil middens on the north-facing slope were studied, as well as one sub-recent (modern but pre-1954) and four modern samples. Nine samples were dated by the radiometric or AMS radiocarbon technique at the Quaternary Dating Research Unit, CSIR, Pretoria, South Africa (QUADRU) and at the Center for Applied

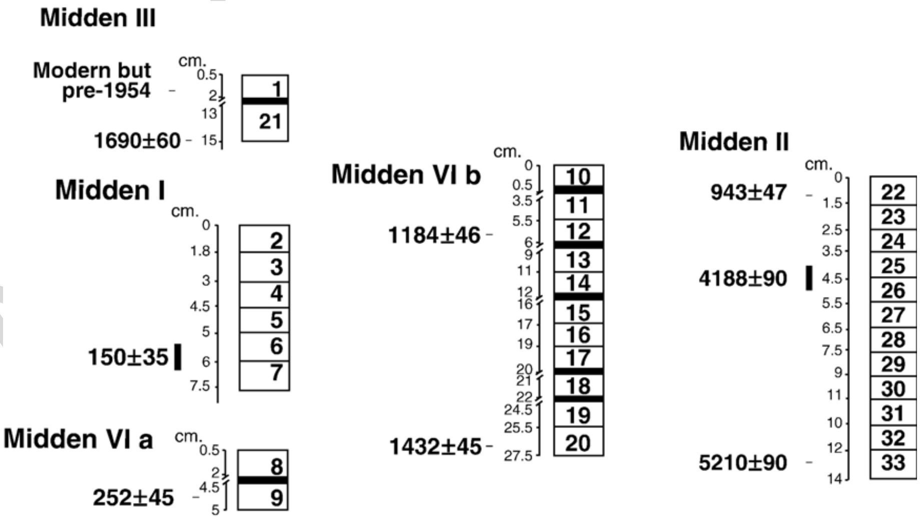

Fig. 4. Hyrax midden sequences (Roman numerals) with details on thickness of samples, uncalibrated radiocarbon dating and their stratigraphical context. Arabic numbers correspond to analyzed samples within every midden; black bands represent material that was not processed.

Isotope Studies of the University of Georgia, Athens, U.S.A. The ages were corrected to a δ13C of −25‰ PDB and calibrated using the Southern Hemisphere INTCAL (1998) curve included in the program CALP provided by QUADRU (Table 1). Charcoal areas were estimated counting charcoal fragments bigger than <75 μ and using the linear regression explained in Tinner and Sheng Hu (2003).

We experimented with different multivariate techniques were used in order to summarize, in a low-dimensional ordination, the plant community data. Detrended correspondence analysis (DCA) of a data matrix, which included total pollen values of all taxa and samples, was preferred given the absence of normality in our data distributions and the low variance obtained by them. DCA was computed using the software PAST (Hammer et al., 2001). In addition, a Pearson's correlation index was calculated to determine the relationships between different pollen spectra.

4. Results and interpretation

The studied middens record the vegetation change at the site from ca. 6000 cal yr BP to the present (Table 1). However, there are some important questions to consider when interpreting the observed differences in pollen spectra. First, we do not know exactly how much time, decades or centuries, each sample represents. Secondly, although we assume that each midden accumulated at a constant rate (estimated from two or more radiocarbon ages) in order to estimate the ages of undated samples, with limited dates we cannot prove that this was the case and that there were not hiatuses in accumulation or variable rates of accumulation. Besides, there exists an important time gap in the chronology obtained since there are no midden material dated between ca. 4200 and 1690 yr cal BP.

Given these constraints, we therefore focused on the broad temporal trends in the pollen spectra and not on detailed differences between them. Thus, in Fig. 4 the results for each midden are arranged in order of age with approximately centennial resolution between samples. Exceptions to this are Midden II, where the top sample (#22) belongs to the last millennium and the intermediate and bottom-most samples (25–26 and 33 respectively) are mid-Holocene (Fig. 4).

The hyrax dung samples were, in general, rich in pollen with an average concentration of 100×10^3 pollen grains per gram of sample.

The current vegetation appears to be well represented in fresh dung samples, MS1 to MS4 (modern sample 1 to 4), although there is some heterogeneity amongst them, possibly due to local effects. The unequal percentages of Combretaceae, *Colophospermum*, Poaceae or Acanthaceae can be attributed to different wind influences as the samples were obtained from different middens on opposite sides of the valley. Taxa variability in the modern samples is most likely attributable to seasonal effects, since these scats may record the environmental conditions at a particular point in time. By contrast, pollen in the fossil samples accumulated over much longer periods, resulting in integration of seasonal and even decadal changes in vegetation and therefore pollen characteristics.

The fossil record is characterized by the dominance of some trees as well as some herbs (Fig. 5). Indeed, the prominent proportions of pollen of *Colophospermum mopane*, Combretaceae, *Commiphora* and to some

Table 1
Radiocarbon dates and isotopes ratios from Okandjombo (northwestern Namibia)

ID samples	Lab numbers	Noncalibrated age ^{14}C yr BP (±1σ)	Calibrated age cal yr BP	Calibrated age Cal AC-BC	δ^{13}C
Oupembe III 4520.4 (1)	UGAMS R01056	Modern[a]	–	1683–1954 AD	−23.15
Orupembe I 4518.2 (6 and 7)	QUADRU Pta-9384	150±35	152	348(409)–438 AD	−24.4
Orupembe VIa 4524.3 (9)	UGAMS R01057	252±45	280	1650–1802 AD	−23.27
Orupembe VIb 4526 (11)	UGAMS R01058	1184±46	1200	869(893)–972 AD	−24.03
Orupembe VIb 4530 (20)	UGAMS R01059	1432±45	1445	662(653)–675 AD	−24.18
Orupembe II 4519.3 (22)	UGAMS R01054	943±47	1001	1037(1160) –1197 AD	−21.44
Orupembe III 4520 (21)	QUADRU Pta-9385	1690±60	1637	348(409)–438 AD	−23.8
Orupembe II 4519.17 (between 4519.6 and 4519.7) (25 and 26)	UGAMS R01055	4188±50	4240	2884–2579 BC	−21.80
Orupembe II 4519.14 (33)	QUADRU Pta-9387	5210±90	6126	4045–(3972) 3938 BC	−22.8

Calibrated age range shown with an error of ±1σ. QUADRU Pta.-: Quaternary Dating Research Unit, Pretoria, South Africa. UGAM R0: Centre for Applied Isotope Studies of the University of Georgia, Athens, U.S.A. Calibration was fitted to the Southern Hemisphere INTCAL (1998) curve included in the program CALP provided by QUADRU.

[a] Modern, but pre-1954.

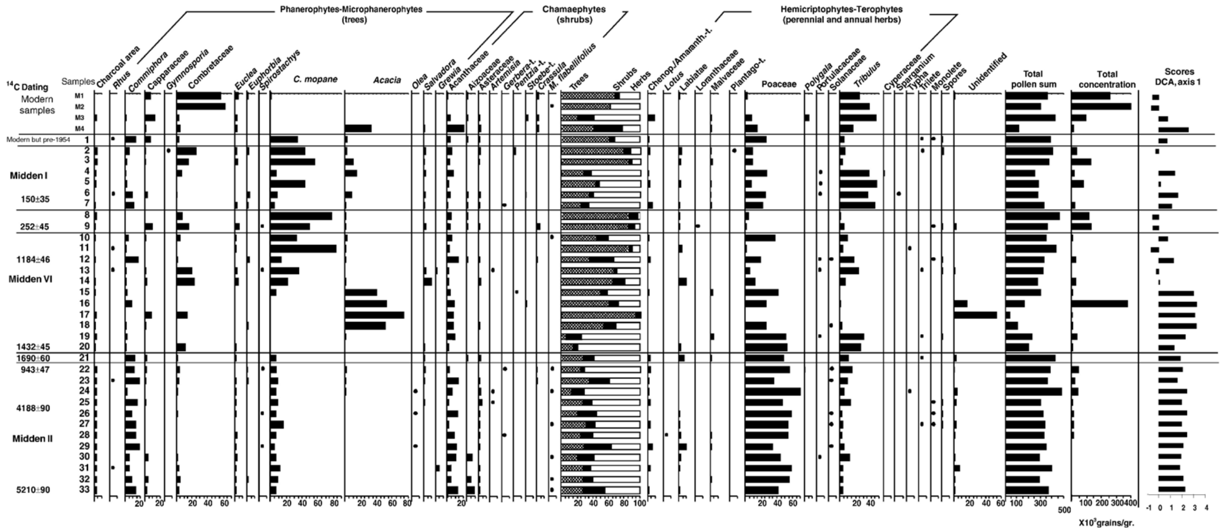

Fig. 5. Pollen diagram for Okandjombo hyrax middens with the DCA axis 1 factor scores on the right. Roman numerals refer to the different middens and Arabic numbers to the analyzed samples (see Fig. 3). Histogram bars represent the percentages of taxa as the total pollen sum except for the charcoal area, which is measured in mm^2/cm^3; dots indicate presences below 0.5%. Total concentration is measured as the number of pollen grains/gram × 10^3. The samples from Midden III were arranged chronologically instead of together.

Table 2
Pearson correlation matrix for some selected taxa

	Commiphora	*Colophospermum mopane*	Combretaceae	Poaceae	*Tribulus*
Commiphora	**1.00**	−0.21	**−0.35**	**0.55**	−0.15
Colophospermum mopane	−0.21	**1.00**	0.07	**−0.32**	−0.23
Combretaceae	**−0.35**	0.07	**1.00**	**−0.42**	0.23
Poaceae	**0.55**	**−0.32**	**−0.42**	**1.00**	−0.25
Tribulus	−0.15	−0.23	0.23	−0.25	**1.00**

Bold values are significantly different from 0 with a significance level α=0.05.

extent, *Acacia* and Capparaceae, together with Poaceae and *Tribulus*, nearly define the whole variation of the pollen spectra. The most noticeable oscillation is a steep increase in mopane trees and *Acacia* (Mimosoideae) from ca. 1300 cal yr BP onwards, while Poaceae decreases during this same period. This is quantitatively supported by the Pearson's correlation index values (Table 2). This shows a negative correlation between Combretaceae and *Commiphora,* and Combretaceae and Poaceae, whilst Poaceae and *Commiphora* seem to vary together. The major trend indicated by the pollen diagram is a progressive increase in the tree/grass pollen ratio during the last millennium (Fig. 5).

Floristically the tree layer was dominated by mopane trees until recently when Combretaceae and Capparaceae became more prominent. Chenopodiaceae (including Amaranthaceae pollen type), Asteraceae or Euphorbiaceae appear constantly in low percentages throughout the diagram, indicating a regular but scattered presence of these families.

The first DCA axis (Fig. 6, Table 3) seems to reflect the above-mentioned trend in the pollen diagram. This axis accounts nearly 40% of the observed variance and assigns lower values, including most of the arboreal taxa (*Colophospermum mopane*, Combretaceae, *Euclea*, *Salvadora*, Capparaceae) except *Acacia* (Mimosoideae),

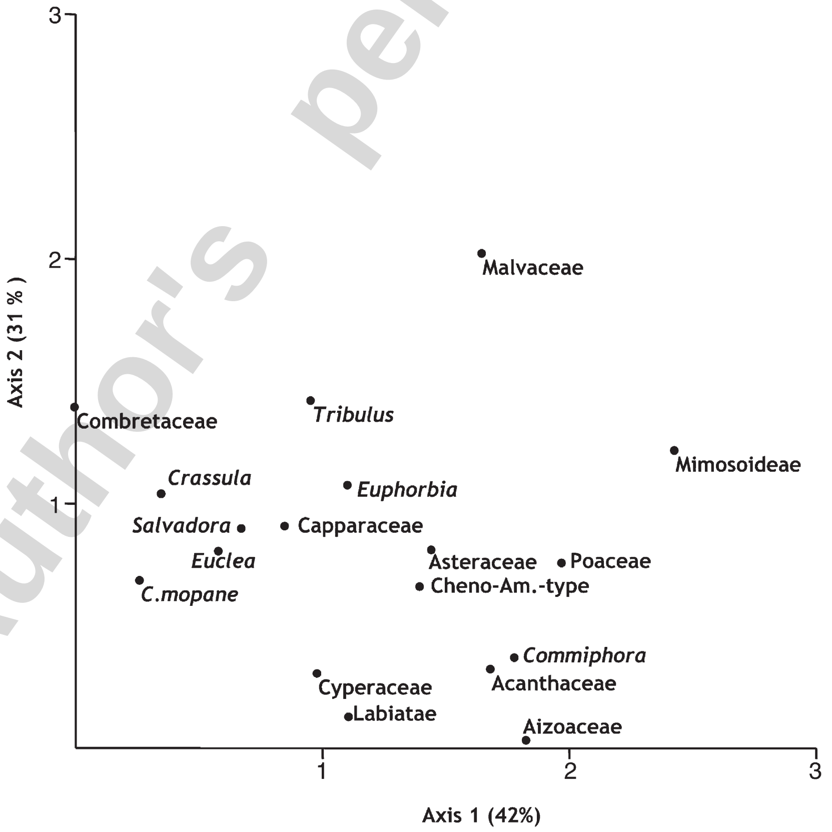

Fig. 6. Scatter diagram of axis one and two detrended correspondence analysis (DCA)values of selected taxa. The percentage variance for every axis is in brackets.

Table 3
DCA scores of every taxon in Axis 1 and 2

	Axis 1		Axis 2
Combretaceae	0.000	Aizoaceae	0.000
Colophospermum mopane	0.266	Labiatae	0.198
Crassula	0.351	Cyperaceae	0.298
Salvadora	0.671	Acanthaceae	0.319
Euclea	0.680	*Commiphora*	0.374
Capparaceae	0.849	Mopane	0.682
Tibulus	0.954	Poaceae	0.731
Cyperaceae	0.984	Cheno-Am	0.790
Euphorbia	1.106	Asteraceae	0.817
Labiatae	1.121	*Euclea*	0.855
Asteraceae	1.426	*Salvadora*	0.892
Cheno-Am	1.436	Capparaceae	0.905
Malvaceae	1.653	*Crassula*	1.036
Acanthaceae	1.682	*Euphorbia*	1.068
Commiphora	1.752	Mimosiodeae	1.209
Aizoaceae	1.835	Combretaceae	1.387
Poaceae	1.889	*Tribulus*	1.412
Mimosiodeae	2.433	Malvaceae	2.104

The values for each axis are arranged in ascending order.

despite retaining some hemicryptophytes and therophytes (*Tribulus* or Lamiaceae). The highest values in Axis 1 mainly correspond to chamaephytes and herbs (Poaceae, Acanthaceae, Aizoaceae or Chenopodiaceae–Amaranthaceae pollen types) as well as *Commiphora* and Mimosoideae which are phanerophytes. The second DC axis explains around 30% of the variation and it includes a complex group of taxa where the highest values correspond to Malvaceae, *Tribulus*, Combretaceae and Mimosoideae, while the lowest values include Aizoaceae, Lamiaceae, Cyperaceae, Acanthaceae and *Commiphora*. Thus, DC axis 1 can be read as a savanna gradient factor whose lower values are pointing towards either thicker savanna – *Colophospermum mopane*, Combretaceae, Capparaceae and phreatophytes such as *Euclea* and *Salvadora* – or to a decrease in cover of the herbaceous stratum. Although Mimosoideae suggests the spread of savanna, its high value in Axis 1, in contrast with other arboreal pollen, probably relates to its isolated appearance in Midden VI b where, in addition, it attains a high percentage due to the small pollen sum and diversity obtained in samples 15 to 18. Nevertheless, Mimosoideae seedpods are appreciated by large game and livestock and its sudden increment could be related to the presence of domestic animals spreading *Acacia* seeds in their dung or a natural establishment of such trees in the dry riverbed.

The taxa reflecting higher DC values are those indicating more desert-like conditions but with elements responding quickly to some rain, (e.g. Poaceae, Chenopodiaceae) or adapted to live and flower during long periods of drought with elements such as Acanthaceae, Aizoaceae, or *Commiphora* (Curtis and Mannheimer, 2005).

DC axis 2 is difficult to interpret in terms of an environmental gradient since the biological significance of the obtained grouping is not clear and it could be biased by the scattered presence of Malvaceae and Aizoaceae.

The DC axis 1 scores for every sample were plotted in the pollen diagram (Fig. 5) and seem to suggest a generally stable vegetation in the early part of the record, followed by erratic sharp oscillations later, which may be an indication of environmental perturbations or disturbance.

5. Discussion

In attempting to interpret the pollen diagram we encountered problems that can only be solved satisfactorily by a detailed modern pollen study of the wider region and this is planned as part of our continuing study of the area. At this stage, however, we investigate possible models and hypotheses applicable to our pollen sequence. Crucial to that interpretation is the understanding that the tree/grass pollen ratios are relative and that we do not know the actual cover of either (i.e., a decline in one my result in a higher percentage of the other even without recruitment). Although today the site appears to be within the Nama-Karoo biome, the fossil pollen spectra indicate a former greater ratio of tree pollen in the late Holocene, which reflects the presence of arid savanna elements. The floral landscape of part of the mid-Holocene (ca. 6000 to 4000 cal yr BP) could be viewed as either a more open savanna system or a tree covered Nama-Karoo system dominated by annual herbs and shrubs. Consequently, the observed variations in the vegetation cover could be partially understood in terms of savanna dynamics with consideration of the ecotone character of the site.

It is possible that some differences in pollen spectra are partially due to the different time lengths represented by the samples, for example in Midden VI b compared to Midden II (Fig. 4). The clearly defined fluctuations in the tree/grass ratio in Midden VI b may be showing inter-decadal variability, while changes through Midden II may show centennial fluctuations. The stochastical pattern of rainfall in this area, with a high inter-annual variability (ca. 70–90% after Mendelsohn et al., 2002), might promote changes in the tree and, especially, in the grass cover that might not be as prominent at a centennial scale. Thus, the constant percentages of trees between ca. 6000 and 4000 cal yr BP in Midden II, and the relatively high values in Midden VI b, might be ascribed, to some extent, to the different time resolution of the samples in these two middens. In addition, we have a poor chronological control on changes in plant communities from ca. 4000 to 1200 cal yr BP. This hiatus in the chronology could be as result of environmental changes, which would have prevented the midden formation during that time, e.g., extreme drought and lack of grazing in the basin. However, hyrax middens can be found in very different environments across the African subcontinent (Scott and Bousman, 1990; Carrión et al., 1999). Consequently, the temporal interruption in the chronology might be simply related to the sample size studied and further dating in new middens could help to fill the time gap.

Despite problems of age control and temporal resolution, the contrast in pollen between Midden II and the most recent deposits suggests that the general trend was a progressive decrease in the herbs to tree ratio over the last 1500 yr. This trend is clearly visible in Fig. 7, which shows the main taxa in every sample in relation to depth and age within the midden deposit. If we evaluate the results from Midden I to Midden VI b together as a chronologically ordered record, 1500 yr of change can be deduced. Samples #25 to 33 from Midden II clearly shows a lower tree and higher grass ratio from ca. 6000 to 4000 cal yr BP and the inverse trend from ca. 1200 cal BP to the present.

Thus, the data indicate a higher proportion of grasses relative to trees during the mid-Holocene but they cannot be used to estimate the actual tree or grass cover. More grasses relative to trees could indicate an improvement in moisture availability. As observed in modern times in desert-edge savannas, rainfall events suddenly generate new grasses but tree cover stay constant. Such a situation in the past could result from more frequent rainfall events rather than an increase in total rainfall. However, if conditions during the mid-Holocene were more humid we might also expect an increase in woody elements. If humidity increases significantly, however, we would expect the tree species composition to change as well. There are different possible reasons for the negative tree/grass correlation. The ecological basis for a more closed or more open landscape may be ascribed to diverse factors acting at different spatial and time scales. A brief analysis of determinants of tree to grass relationships in savannas is relevant as the study site is greatly influenced by savanna dynamics. Such features may be expressed in the fluctuation of the pollen spectra.

The coexistence of trees and grasses in the same environment is a topic of current debate and has stimulated much research. The tree/grass equilibrium has been explained frequently by the well known hypothesis of rooting-niche separation (Walter, 1971; Walker et al., 1981; Knoop and Walker, 1985). According to this view the trees are able to extract water from deeper soil layers while grasses exploit surface layers. In the context of this classical hypothesis, our record may indicate more frequent mid- to late-Holocene rains, providing better edaphic moisture to the root zone of grass. The low but constant presence of trees would be attributed to underground water. The later decrease in the Poaceae ratio against woody elements, especially *Colophospermum mopane*, either indicates decreasing grass cover or expanding woody elements. The former could be the result of drier conditions setting in, probably due to spatially more scattered rains or temporally fewer recurrent precipitation events. Trees would still be able to use phreatic water, especially after an upstream input during a cyclonic event, and therefore would appear more prominent in the last millennium.

However, the shallow soils in the study area could not have retained enough moisture to allow tree development. Recent studies have proposed new hypotheses about savanna structure, including among others demographic stages of trees, limiting factors for tree establishment, potential interactions between trees and grasses (see Sankaran et al., 2004 for a more complete review). This research observed great differences in the degree of edaphic moisture access, so rooting-niche separation is unlikely to be a general mechanism for explaining tree/grass coexistence (Scholes, 1997; Scholes and Archer, 1997; Ward, 2005; Wiegand et al., 2005). Furthermore, a number of spatio–temporal simulation models (Belsky, 1990; Jeltsch et al., 1996; Ward and Ngairorue, 2000; Ward, 2005; Wiegand et al., 2005) suggest that savannas may not represent a stable mixture of trees and grasses but an inherently unstable system which persists owing to disturbances as fire, hervibory and fluctuating rainfall (Sullivan, 1996, 1999).

Wiegand et al. (2006) proposed a patch-dynamic arid savanna hypothesis that allows for both tree/grass coexistence and bush encroachment to occur at the same time in an arid savanna mosaic landscape. Under this scenario woody plant encroachment, mature stands and open savanna are three states of a cyclical succession in the same system, and disturbances would cause exchangeable situations (Jeltsch et al., 1996). The primary determinants of savanna structure are water and soil nutrients, while fire and hervibory are secondary determinants (Scholes, 1997; Zeidler et al., 2002). In the particular case of arid savannas, where the main limiting

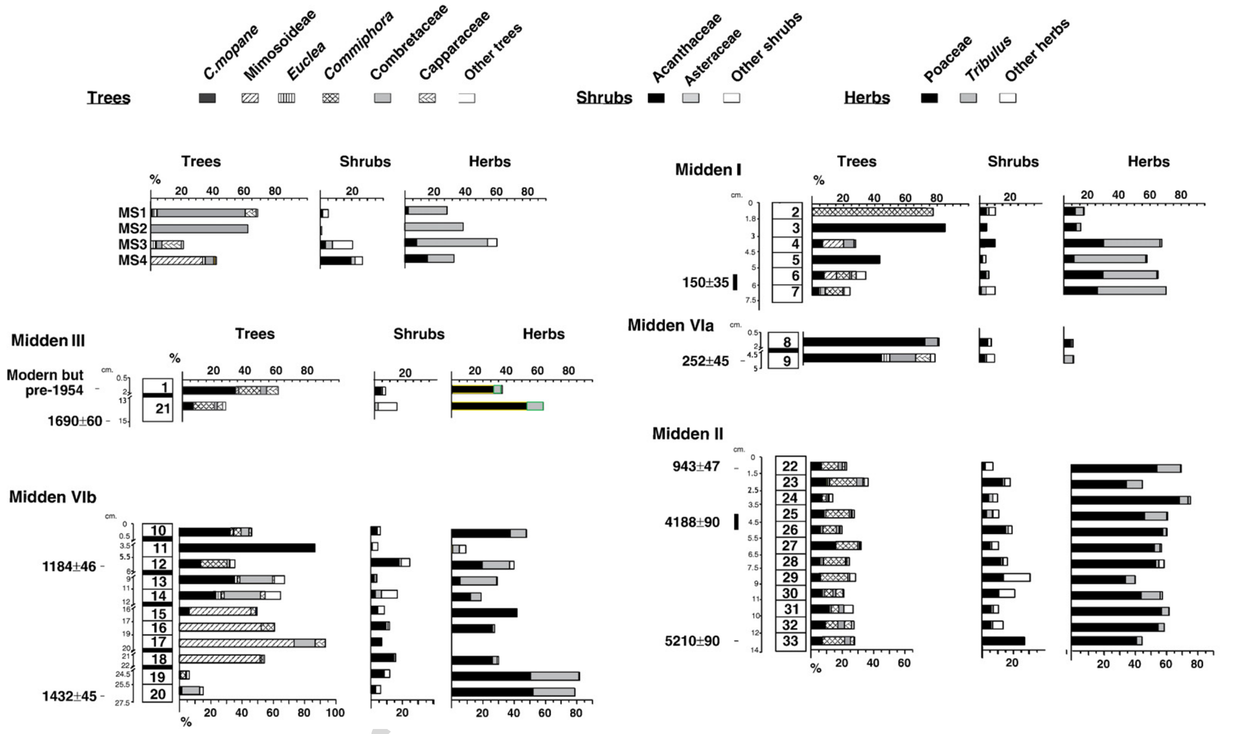

Fig. 7. Synthetic pollen diagram with percentages of selected taxa of trees, shrubs and herbs for all the samples. Uncalibrated radiocarbon ages and sample depth appear on the left for every midden (compare with Fig. 4). Note that black, white and grey are used in every composite histogram but refer to different taxa as indicated by the legend at top.

factor is the patchiness of rainfall, the conversion from an open savanna plot to a bush-encroached area is initiated by the spatial and temporal overlap of several rainfall events (Wiegand et al., 2005). After time and inter-tree competition, the thicket will become sparser and eventually revert to open savanna again. However, since rainfall in arid regions is very stochastically distributed in time and space, there is a low probability of several rainfall events in a single area. Eventually a mosaic structure, with very important spatial disparity amongst the three states will develop (Wiegand et al., 2005, 2006).

These hypotheses provide the conceptual context for explaining the changes from ca. 1300 cal yr BP. More frequent rains occurring from ca. 6000–4000 and 1400–1300 cal yr BP would have allowed a greater grass cover but not necessarily tree sprouting, especially in the case of mopane which has no tolerance to grass competition while establishing (Burke, 2006). This would explain the general low tree ratio throughout that time. Nevertheless, if such smoothly distributed, more frequent rainfall periods were long enough, a critical value would be reached where tree seedlings would have been able to develop. This might be an explanation for the general increase in tree percentage during the last millennium while Poaceae declines. The consequent enhancement in tree density would have changed the site from more grassy savanna into a sort of shrubland or woody encroached area, as is supported by the more negative scores reflected in DC axis 1 (Fig. 4). The higher tree/grass pollen ratio in the last millennium would be a consequence of the establishment of more mature trees in inter-specific competition with the grasses. Eventually, self-thinning of trees during drier periods and increasing human impact would have turned the landscape again into an open savanna or denser Nama-Karoo as is currently observed in the area.

Additional environmental factors could have affected, although not determined, the inherent ecosystem dynamics in decisive ways. Regional droughts during the last 1300 yr would have promoted the migration of herbivorous game. Consequently, the reduction in herb cover could be due to tree/grass competition as well as by grazing activities. Given its ruderal behaviour, the increase in percentages of *Tribulus* could be connected with grazers. In that sense, the erratic pollen composition of samples after 1500 cal yr BP, as is shown by the irregular values of factor scores in DC axis 1, is possibly due to livestock disturbance. Linked to these variations along the DC axis 1, it is important to indicate that the high scores reached in modern samples are mainly due to the abundance of Combretaceae pollen. This should not be understood as a real expansion of these trees in modern times; rather, as explained above, pollen in modern samples is determined by the season of deposition while pollen in fossil samples, deposited over decades or longer, presents average conditions over this time. The scarcity of studies related to intra-specific tree competition and recruitment in Namibian savannas, differences in pollen production, and the pollination ecology of trees restricts the possibility to separate individual causal factors and how variability in one component may impact on pollen representation.

The non-selective diet of hyraxes and the reduction of grasses due to drier conditions might have resulted in a foraging switch from predominantly grazer to more browsing, biasing for a greater presence of tree spectra. Depositional effects must also be considered; e.g., variations in pollen deposition amongst different middens could also explain the erratic spectra of some trees, although, in general terms, all except *Commiphora* increased during the last millennium.

Charcoal area analysis does not indicate major anthropogenic events since the values are constant, excluding Midden III where they are slightly higher. Though human presence as early as 4000 cal yr BP cannot be excluded (Albrecht et al., 2001; Eichhorn, 2004), the pollen spectra do not indicate any significant changes except the rise in *Tribulus*. Evidence for human occupation of northwestern Namibia during the Holocene is in general very poor, though with some evidence for early livestock from ca. 2000 years ago (Vogelsang et al., 2002).

In summary, it is reasonable to think that the pollen fluctuations observed are the result of several factors: the inherent ecosystem dynamics, drier conditions from ca. 1200 cal yr BP, subsequent overgrazing by pastoralists, depositional effects, and hyrax diet.

The area has always received summer rainfall since the only significant floristic element that would indicate winter rainfall is the succulents. Its modern presence and fossil fluctuation does not support changes in the seasonality of precipitation. This confirms the tropical character of the study site and suggests that any fluctuation in precipitation must be strongly related to tropical lows. Climatic causes explaining higher rainfall frequencies during the past could be linked to slight variations in the atmospheric circulation, resulting in wet spells or more regular rains. Wetter conditions may be explained by any of several mechanisms, e.g. changes in the Inter-tropical Convergence Zone (ITCZ), the Congo Air Boundary (CAB), or the subtropical jet (Tyson, 1986; Preston-Whyte and Tyson, 1988), as well as in ocean currents or sea surface temperature (see above).

There is other evidence that support wetter conditions during the mid-Holocene in northwestern Namibia (Kaokoland and Damaraland), even if quite diverse in terms of space and time. Nevertheless, a regional framework of environmental change is emerging.

The closest fossil pollen record is from the marine core sequence GeoB 1023, off the northern Namibian–southern Angolan coast, near the Cunene River mouth (17°09′ S 11°01′ E). It 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 the GeoB 1023 site is further north than our site, these findings seem to confirm humid conditions during the middle Holocene. In GeoB 1023, the grass spectrum fluctuates from 5000 cal BP with an eventual decrease during the last 1000 yr. Charcoal analysis from Omungunda 99/1 (Vogelsang et al., 2002; Eichhorn, 2004) and Oruwanje 95/1 (Albrecht et al., 2001) suggests stable, but not drier, conditions with short-duration wet spells in the more eastern woodlands during the mid- to late-Holocene to ca. 500 cal yr BP. The occurrence of *Colophospermum mopane* charcoal at site N 2000/1, west of Okandjombo, indicate more humid conditions around 2000 cal yr BP along the desert margin (Eichhorn, 2004).

The work of Rust and Vogel (1988), Vogel (1989), Eitel et al. (2005) and Srivastava et al. (2005) 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 loess accumulation in different basins of Kaokoland (Omungunda, Opuwo and Okaoraore) during the last 3 millennia, which seems to correspond with an increase in moisture and fluvial activity during the transition between the mid- and late-Holocene. Eitel et al. (2005, 2006) in their study on the Amspoort Silt terrace and the catchment of the Hoanib drainage system, conclude that the climate became significantly more humid at the eastern desert margin after ca. 3000 BP, when a fluvial phase developed, which was followed by arid conditions ca. 1000 yr BP. A Holocene marine clay mineral record from the GeoB 1023 marine core (Gingele, 1996) indicates a maximum fluvial signal between 6000 and 5000 cal yr BP. However, the same study points to less fluvial activity during the last 4000 yr. Despite the heterogeneity in the available records it becomes clear that wet conditions were widespread during the mid-Holocene in northwestern Namibia.

Alkenone-derived sea surface temperatures (SSTs) in GeoB 1023 show a decrease to the present values over the past 1000 yr (Dupont et al., 2004), while similar decreases in SSTs during the late Holocene have also been recorded in marine cores further south (Kirst et al., 1999). Several studies confirm that SSTs modulate rainfall by controlling moisture and stability in the lower atmosphere (Nicholson and Entekhabi, 1987; Nicholson, 2000). Thus, rainfall events over the southwestern African coastal areas are related to high SSTs (Kirst et al., 1999; Dupont and Behling, 2006). The SST reduction registered in GeoB 1023 during the last millennium would have produced higher pressures and therefore more arid conditions in the coastal strip. However, relationships between SSTs and rainfall in northern arid Namibia are still unclear (Nicholson and Entekhabi, 1987; Nicholson, 2000).

Alternatively, if we attribute more rainfall in the northern most areas of Namibia primarily to CAB input, i.e., tropical equatorial moisture from humid conditions in the Congo basin, it should have prevailed during the transition from mid- to late-Holocene. However, a well known extended dry event is registered by different paleoarchives in equatorial Africa during the late Holocene from ca. 4500 yr BP to to ca. 1300 yr BP yr BP (see Marchant and Hooghiemstra, 2004 for a detailed review). Different components of that climate system could lead to a reduction in the moisture contents of tropical rain-bearing systems and therefore to a late-Holocene equatorial arid episode, which is beyond the scope of this paper.

We could, however, consider an alternative scenario of a relatively arid event from 5200 to 1300 yr BP, in which conditions were possibly drier than those that were established subsequently, but not drier than today since the vegetation composition indicates mainly shrubs and herbs of the Nama-Karoo with high Poaceae proportions. Such a scenario would be purely hypothetical as our results only cover the early and late stages of equatorial African aridity. Such aridity could result in a weakening of southwestwards shifts in the CAB, thus reducing the rainfall input over northern Namibia. Since the occasional precipitation in the area is primarily ascribed to moisture input from Indian Ocean air masses, the absence of moisture from CAB shifts would lead to greater aridity, but not desert conditions. A potential dry period therefore does not preclude rainfall events, indeed, grasses in drylands flower quickly after modest amounts of rain (Günster, 1995). A subsequent wetter period, lasting several centuries after 1300 cal yr BP, would have allowed tree expansion in this ecotone area. The reduction in grass proportions after 1200 cal yr BP does not imply a real decrease in Poaceae cover as more frequent rains would allow grass growth. However, increased germination and the development of wooded savanna patches with more mature trees would result in increased tree pollen before inter-specific competition turned the landscape into an open savanna again (Wiegand et al., 2006).

The geographical position of Okandjombo near the southernmost boundary of the CAB system makes the latter interpretation possible, although, as explained earlier, paleoarchives from closer sites show the opposite. We lack of independent palaeoclimatic evidence nearer to the studied area, supporting for wet conditions during the last 1200 yr and more arid conditions before that, leads us to the conclusion that this alternative hypothesis is unlikely. Furthermore, in terms of moisture fluctuations the CAB system may not respond in the same way in the Congo as in northern Namibia. A better understanding of this question that flows from our study, about long-term interactions between these regions, will undoubtedly be useful in efforts to model tropical climate in Africa. Different studies related to the northern Namib environment, such as modern climate variations, plant community response to those fluctuations and modern and fossil pollen surveys, are therefore essential.

6. Conclusions

A record of vegetation changes in northwestern Namibia, on the margin of the Namib Desert, represents the period 6000 cal yr BP to the present but it has a major hiatus between ca. 4200 and 1690 cal yr BP. The study area is within an ecotone (Nama-Karoo) that favours the expression of structural properties of the adjacent biomes (Desert and Savanna). The pollen spectra from our non-continuous sequence match arid savanna vegetation, and do not indicate any significant expansion of desert conditions. Several hypotheses have been proposed to explain the tree/grass codominance in savannas; we conclude that those that include spatial–temporal factors in their interpretation explain the pollen spectra best. Tree pollen increases when overlapping rainfall events in the same patch of open savanna permit tree seedlings to develop. Thus, the arid savanna landscape becomes a mosaic with different phases of the same biome; open savanna (lower tree/grass ratio) or encroached savanna (higher tree/grass ratio).

The midden sequence records high values of grasses, indicating more frequent precipitation than currently, in two phases separated by a hiatus viz., around the mid-Holocene ca. 6000 to 4000 cal yr BP and from ca. 1690 to ca. 1200 cal yr BP. However, the rainfall was never sufficient to bring about a marked increase in tree sprouting within the savanna itself according to the available parts of our record. Instead, long periods of more frequent rains eventually resulted in an expansion of savanna woodlands, mainly *Colophospermum mopane* and Combretaceae. After ca. 1200 cal yr BP, there was an increase in the ratio of trees to grasses, suggesting progressively drier conditions in the area and poorer cover in the lower stratum. The more arid conditions in the region affected the trees (established during the earlier humid phase) less than the grasses, as the arboreal layer was able to tap deeper underground water. The current vegetation in the area is well represented in the modern control samples, although differences in Combretaceae pollen content amongst samples indicate that depositional effects may affect the pollen spectra.

This interpretation is consistent with other paleoarchives from northwestern Namibia that also suggest wetter conditions during the mid- to late-Holocene, replaced by progressively drier conditions during the last millennium. In particular marine core GeoB 1023 off the Cunene River mouth also shows high Poaceae percentages from the mid- to late-Holocene, while SSTs seem to indicate arid conditions during the last millennium in the southwestern African coastal zone.

An alternative, less likely, hypothesis to explain the observed change in the tree/grass ratio involves a mid–late-Holocene dry event due to a reduction in the moisture derived from equatorial CAB system, which may have resulted in greater aridity with more grass and a reduction in tree cover.

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References

Albrecht, M., Berke, H., Eichhorn, B., Frank, T., Kuper, R., Prill, S., Vogelsang, R., Wenzel, S., 2001. Oruwanje 95/1: a late Holocene stratigraphy in northwestern Namibia. Cimbebasia 17, 1–22.

Belsky, A.J., 1990. Tree/grass ratios in East African savannas; a comparison of existing models. Journal of Biogeography 17, 483–489.

Brunotte, E., Sander, H., 2000. Loess accumulation and soil formation in Kaokoland northern Namibia as indicators of Quaternary climatic change. Global and Planetary Change 26, 67–75.

Burke, A., 2006. Savanna trees in Namibia — factors controlling their distribution at the arid end of the spectrum. Flora 201, 189–201.

Carrión, J.S., Scott, L., Davis, O.K., 1997a. Interés de algunos depósitos biogénicos en la reconstrucción paleoambiental de zonas áridas. El caso de *Procavia, Petromus* y *Neotoma*. II. Datos palinológicos. Cuaternario y Geomorfología 11, 51–73.

Carrión, J.S., Scott, L., Davis, O.K., 1997b. Interés de algunos depósitos biogénicos en la reconstrucción paleoambiental de zonas áridas. El caso de *Procavia, Petromus* y *Neotoma*. I. Bases conceptuales y metodológicas. Cuaternario y Geomorfología 11, 45–50.

Carrión, J.S., Scott, L., Vogel, J.C., 1999. Twentieth century changes in montane vegetation in the eastern Free State, South Africa, derived from palynology of hyrax dung middens. Journal of Quaternary Science 14, 1–16.

Curtis, B., Mannheimer, C., 2005. Tree Atlas of Namibia. National Botanical Research Institute, Windhoek, Namibia.

du Plessis, W.P., 2001. Effective rainfall defined using measurements of grass growth in the Etosha National Park Namibia. Journal of Arid Environments 48, 397–417.

Dupont, L.M., Behling, H., 2006. Land-sea linkages during deglaciation: high resolution records from the eastern Atlantic off the coast of Namibia and Angola (ODP site 1078). Quaternary International 148, 19–28.

Dupont, L.M., Wyputta, U., 2003. Reconstructing pathways of aeolian pollen transport to the marine sediments along the coastline of SW Africa. Quaternary Science Review 22, 157–174.

Dupont, L.M., Kim, J.-H., Schneider, R.R., Shi, N., 2004. Southwestern African climate independent of Atlantic sea surface temperatures during the Younger Dryas. Quaternary Research 61, 318–324.

Eichhorn, B., 2004. Anthrakologische Untersuchungen zur Vegetationsgeschichte des Kaokolandes, Nordwest-Namibia. Ph.D. Dissertation, Universität zu Köln, Germany. http://kups.ub.uni-koeln.de/volltexte/2004/1178/.

Eitel, B., Blümel, W.D., Hüser, K., Mauz, B., 2001. Dust and loessic alluvial deposits in northwestern Namibia (Damaraland, Kaokoveld): sedimentology and palaeoclimatic evidence based on luminescence data. Quaternary International 76/77, 57–65.

Eitel, B., Blümel, W.D., Hüser, K., 2004. Palaeoenvironmental transitions between 22 ka and 8 ka in monsoonally influenced Namibia. In: Smykazt-Kloss, W., Felix-Henningsen, P. (Eds.), Palaeoecology of Quaternary drylands. Springer-Verlag, Heidelberg, pp. 167–194.

Eitel, B., Kadereit, A., Blümel, W.D., Hüser, K., Kromer, B., 2005. The Amspoort Silts, northern Namib Desert (Namibia): formation, age and palaeoclimatic evidence of river-end deposits. Geomorphology 64, 299–314.

Eitel, B., Kadereit, A., Blümel, W.D., Hüser, K., Lomax, J., Hilgers, A., 2006. Environmental changes at the eastern Namib Desert margin before and after the Last Glacial Maximum: new evidence from fluvial deposits in the upper Hoanib River catchment, northwestern Namibia. Palaeogeography, Palaeoclimatology, Palaeoecology 234, 201–222.

Faegri, K., Iversen, J., 1989. Textbook of Pollen Analysis. John Wiley & Sons, Chicester.

Fourie, L.J., Perrin, M.R., 1989. Quantitative and qualitative aspects of the diet of rock hyrax (*Procavia capensis* Pallas, 1766) in the Mountain Zebra National Park. Journal of African zoology 103, 361–370.

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

Gingele, F.X., 1996. Holocene climatic optimum in southwest Africa—evidence from the marine clay mineral record. Palaeogeography, Palaeoclimatology, Palaeoecology 127, 77–87.

Gosz, J.R., 1992. Ecological functions in a biome transition zone: translating local responses to broad-scale dynamics. In: Hansen, A.J., De Castri, F. (Eds.), Landscape Boundaries. Consequences for Biotic Diversity and Ecological Flows.). Springer Verlag, Heidelberg, pp. 55–75.

Günster, A., 1995. Grass cover distribution in the central Namib: a rapid method to assess regional and local rainfall patterns of arid regions? Journal of Arid Environments 29, 107–114.

Hachfeld, B., Jürgens, N., 2000. Climate patterns and their impact on the vegetation in a fog driven desert: the Central Namib Desert in Namibia. Phytocoenologia 30, 567–589.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica 4, 1–9.

Heine, K., 2004. Little Ice Age climatic fluctuations in the Namib Desert, Namibia, and adjacent areas: evidence of exceptionally large floods from slack water deposits and desert soil sequences. In: Smykazt-Kloss, W., Felix-Henningsen, P. (Eds.), Palaeoecology of Quaternary Drylands. Springer-Verlag, Heidelberg, pp. 137–165.

Holmgren, C., Betancourt, J.L., Rylander, K.A., 2006. A 36,000-yr history of the Peloncillo Mountains, southeastern Arizona, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 240, 405–422.

Horowitz, A., 1992. Palynology of Arid Lands. Elsevier, Amsterdam.

Irish, J., 1994. The biomes of Namibia as determined by objective categorisation. Navorsinge van die Nasionale Museum, Bloemfontein 10, 550–552.

Jackson, S.T., Betancourt, J.L., Lyford, M.E., Gray, S.E., Rylander, K.A., 2005. A 40,000-year woodrat-midden record of vegetational and biogeographic dynamics in northeastern Utah. Journal of Biogeography 32, 1085–1106.

Jeltsch, F., Milton, S., Dean, W.R.J., van Rooyen, N., 1996. Tree spacing and coexistence in semiarid savannas. Journal of Ecology 84, 583–595.

Jury, M.R., Engert, S., 1999. Teleconnections modulating inter-annual climate variability over northern Namibia. International Journal of Climatology 19, 1459–1475.

Kirst, G.J., Schneider, R.R., Müller, P.J., von Storch, I., Wefer, G., 1999. Late Quaternary temperature variability in the Benguela current system derived from alkenones. Quaternary Research 52, 92–103.

Knoop, W.T., Walker, B.H., 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. Journal of Ecology 73, 235–253.

Lancaster, N., Lancaster, J., Seely, M.K., 1984. Climate of the Central Namib Desert. Madoqua 14, 5–61.

Le Houérou, H.N., 1996. Climate change, drought and desertification. Journal of Arid Environments 34, 133–185.

Legget, K., Fennessy, J., Schneider, S., 2003. Seasonal vegetation changes in the Hoanib River catchment, north-western Namibia: a study of a non-equilibrium system. Journal of Arid Environments 53, 99–113.

Maldonado, A., Betancourt, J.L., Latorre, C., Villagran, C., 2005. Pollen analyses from a 50,000-yr rodent midden series in the southern Atacama Desert (25°30′S). Journal of Quaternary Science 20, 493–507.

Marchant, R., Hooghiemstra, H., 2004. Rapid environmental change in African and South American tropics around 4000 yr. BP: a review. Earth Science Reviews 66, 217–260.

Mendelsohn, J., Jarvis, A., Roberts, C., Robertson, T., 2002. Atlas of Namibia. David Philip, Cape Town. Available as digital data from http://www.uni-Neilson, R.P., 1993. Transient ecotone response to climatic change: some conceptual and modelling approaches. Ecological Applications 3, 385–395.

Neilson, R.P., 1993. Transient ecotone response to climatic change: some conceptual and modelling approaches. Ecological Applications 3, 385–395.

Nicholson, S.E., 2000. The nature of rainfall variability over Africa on time scales of decades to millennia. Global and Planetary Change 26, 137–158.

Nicholson, S.E., Entekhabi, D., 1987. Rainfall variability in equatorial southern Africa: relationships with sea surface temperatures along the southwestern coast of Africa. Journal of Climate and Applied Meteorology 26, 561–578.

Noble, I.R., 1993. A model for responses of ecotones to climate change. Ecological Applications 3, 396–403.

Preston-Whyte, R.A., Tyson, P.D., 1988. The Atmosphere and Weather of Southern Africa. Oxford University Press, Cape Town.

Richters, J., 2005. Biomass changes in north-western Namibia: first results from a remote sensing modelling approach. European Association of Remote Sensing Laboratories Proceedings 4, 157–170.

Rübsamen, K., Hume, I.D., Engelhardt, W.V., 1982. Physiology of the Rock Hyrax. Comparative Biochemistry and Physiology 72A, 271–277.

Rust, U., Vogel, J.C., 1988. Late Quaternary environmental changes in the northern Namib Desert as evidenced by fluvial landforms. Palaeocology of Africa 19, 127–137.

Rutherford, M.C., Westfall, R.H., 1994. Biomes of southern Africa: an objective categorization. Memoirs of the Botanical Survey of South Africa, vol. 63. National Botanical Institute, Pretoria.

Sankaran, M., Ratnam, J., Hanan, N.P., 2004. Tree–grass coexistence in savannas revisited — insights from an examination of assumptions and mechanisms invoked in existing models. Ecology Letters 7, 480–490.

Scholes, R.J., 1997. Savanna. In: Cowling, R.M., Richardson, D.M., Pierce, S.M. (Eds.), Vegetation of Southern Africa. Cambridge University Press, Cape Town, pp. 258–277.

Scholes, R.J., Archer, S.R., 1997. Tree–Grass interactions in savannas. Annual Review of Ecology and Systematics 28, 517–544.

Scholes, R.J., Gebauer, G., Zeigler, H., Lange, O.L., 2002. Trends in savanna structure and composition along an aridity gradient in the Kalahari. Journal of Vegetation Science 88, 451–459.

Scott, L., 1990. Hyrax (Procaviidea) and dassie-rat (Petromuridae) middens in palaeoenvironmental studies in Africa. In: Betancourt, J.L., van Devender, T.R., Martin, P.S. (Eds.), Packrat Middens: The Last 40,000 years of Biotic Change. University of Arizona Press, Tucson, pp. 398–407.

Scott, L., 1994. Palynology of Late Pleistocene hyrax middens, Southwestern Cape Province, South Africa: a preliminary report. Historical Biology 9, 71–81.

Scott, L., 1996. Palynology of hyrax middens: 2000 years of palaeoenvironmental history in Namibia. Quaternary International 33, 73–79.

Scott, L., Bousman, C.B., 1990. Palynological analysis of hyrax middens from southern Africa. Palaeogeography, Palaeoclimatology, Palaeoecology 76, 367–379.

Scott, L., Cooremans, B., 1992. Pollen in recent *Procavia* (Hyrax), *Petromus* (dassie rat) and bird dung in South Africa. Journal of Biogeography 19, 205–215.

Scott, L., Vogel, J.C., 2000. Evidence for environmental conditions during the last 20 000 years in southern Africa from 13C in fossil hyrax dung. Global and Planetary Change 26, 207–215.

Scott, L., Woodborne, S., in press. Pollen analysis and dating of Late Quaternary fecal deposits (*hyraceum*) in the Cederberg, Western Cape, South Africa. Review of Palaeobotany and Palynology. doi:10.1016/j.revpalbo.2006.07.004.

Scott, L., Cooremans, B., de Wet, J.S., Vogel, J.C., 1991. Holocene environmental changes in Namibia inferred from pollen analysis of swamp and lake deposits. The Holocene 1, 8–13.

Scott, L., Marais, E., Brook, G.A., 2004. Fossil hyrax dung and evidence of Late Pleistocene and Holocene vegetation types in the Namib Desert. Journal of Quaternary Science 19, 1–4.

Scott, L., Bousman, C.B., Nyakale, M., 2005. Holocene pollen from swamp, cave and hyrax dung deposits at Blydefontein (Kikovsberge), Karoo, South Africa. Quaternary International 129, 49–59.

Shi, N., Dupont, L.M., Beug, H.-J., Schneider, R., 1998. Vegetation and climate changes during the last 21000 years in S.W. Africa based on a marine pollen record. Vegetation History and Archaeobotany 7, 127–140.

Shi, N., Dupont, L.M., Beug, H.-J., Schneider, R.R., 2000. Correlation between vegetation in southwestern Africa and oceanic upwelling in the past 21000 years. Quaternary Research 54, 72–80.

Shi, N., Schneider, R.R., Beug, H.-J., Dupont, L.M., 2001. Southeast trade wind variations during the last 135 Kyr: evidence from pollen spectra in eastern south Atlantic sediments. Earth and Planetary Science Letters 187, 311–321.

Srivastava, P., Brook, G.A., Marais, E., 2005. Depositional environment and luminescence chronology of the Hoarusib river Clay Castles sediments, northern Namib Desert, Namibia. Catena 59, 187–204.

Stockmarr, J., 1973. Determination of spore concentration with an electronic particle counter. Danmarks Geologiske Undersogelse Arbog 1972, 87–89.

Stuut, J.-B.W., Lamy, F., 2004. Climate variability at the southern boundaries of the Namib (southwestern Africa) and Atacama (northern Chile) coastal deserts during the last 120,000 yr. Quaternary Research 62, 301–309.

Stuut, J.-B.W., Prins, M.A., Schneider, R., Weltje, G.J., Jansen, J.H.F., Postma, G., 2002. A 300-Kyr record of aridity and wind strength in southwestern Africa: inferences from grain-size distributions of sediments on Walvis ridge, SE Atlantic. Marine Geology 180, 221–233.

Sullivan, S., 1996. Towards a non-equilibrium ecology: perspectives from an arid land. Journal of Biogeography 23, 1–5.

Sullivan, S., 1999. The impacts of the people and livestock on topographically diverse open wood- and shrub-lands in arid northwest Namibia. Global Ecology and Biogeography 8, 257–277.

Thomas, D.S.G., Knight, M., Wiggs, G.F.S., 2005. Remobilization of southern African desert dunes by twenty-first century global warming. Nature 435, 1218–1221.

Tinner, W., Sheng Hu, F., 2003. Size parameters, size-class distribution and area-number relationship of microscopic charcoal: relevance for fire reconstruction. The Holocene 13, 499–505.

Tyson, P.D., 1986. Climatic Change and Variability in Southern Africa. Oxford University Press, Cape Town.

van Zinderen Bakker, E.M., 1975. The origin and palaeoenvironment of the Namib Desert biome. Journal of Biogeography 2, 65–73.

van Zinderen Bakker, E.M., 1984. A Late- and Post- Glacial pollen record form the Namib Desert. Palaeoecology of Africa 16, 421–428.

van Zinderen Bakker, E.M., Müller, M., 1987. Pollen Studies in the Namib Desert. Pollen et Spores 24, 185–206.

Vogel, J.C., 1989. Evidence of Past Climatic change in the Namib Desert. Palaeogeography, Palaeoclimatology, Palaeoecology 70, 355–366.

Vogel, J.C., Rust, U., 1987. Environmental changes in the Kaokoland Namib Desert during the present millennium. Madoqua 15, 5–16.

Vogelsang, R., Eichhorn, B., Ritcher, J., 2002. Holocene human occupation and vegetation history in northern Namibia. Die Erde 133, 113–132.

Walker, B.H., Ludwig, D., Holling, C.S., Peterman, R.S., 1981. Stability of semi-arid savanna grazing systems. Journal of Ecology 69, 473–498.

Walter, H., 1971. Ecology of tropical and subtropical vegetation. Oliver & Boyd, Edinburgh.

Ward, D., 2005. Do we understand the causes of bush encroachment in African savannas? African Journal of Range and Forage Science 22, 101–105.

Ward, D., Ngairorue, B.T., 2000. Are Namibian grasslands desertifying? Journal of Range Management 53, 138–144.

Wiegand, K., Ward, D., Saltz, D., 2005. Multi-scale patterns and bush encroachment in an arid savanna with a shallow soil layer. Journal of Vegetation Science 16, 311–320.

Wiegand, K., Saltz, D., Ward, D., 2006. A patch-dynamics approach to savanna dynamics and woody plant encroachment—Insights from an arid savanna. Perspectives in Plant Ecology, Evolution and Systematics 7, 229–242.

Zeidler, J., Hanrahan, S., Scholes, M., 2002. Land-use intensity affects range condition in arid to semi-arid Namibia. Journal of Arid Environments 52, 389–403.