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Evidence for environmental conditions during the last 20 000 years in Southern Africa from ^{13}C in fossil hyrax dung

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Abstract

$^{13}C/^{12}C$ ratios in plants depend on factors like temperature, evaporation or seasonal moisture distribution. Fluctuations of $^{13}C/^{12}C$ in *Procavia capensis* (hyrax) dung samples from different vegetation zones and various ages over the last 20 000 years indicate variations in the amounts of C4 and CAM, or C3 plants consumed by these herbivores. Potentially they also indicate vegetation changes that may have occurred. $^{13}C/^{12}C$ values for a series of hyrax middens of Late Pleistocene/Holocene age, from a variety of biomes across Southern Africa, show that hyraxes favour mainly C3 plants in their diets but they do incorporate CAM or C4 plants under certain circumstances. In the eastern mountainous summer-rain area around Clarens with C3 woodland and unpalatable "sour" grassland consisting mainly of C4 grasses and fewer of the C3 type, hyraxes seem to avoid at least the C4 component of grass and rely mainly on leaves of the woody plants. Isotopic data for hyrax dung in the western Cape Cederberg region indicate diets composed almost exclusively of C3 plants during the last 20 000 years. Slight shifts towards more enriched values occur, e.g., around 420 and 2100 years ago, which may indicate slight increase in CAM or C4 plants. Interestingly no enrichment occurs during the Last Glacial Maximum when a shortage of atmospheric CO_2 may have favoured C4 plants. During the late Holocene some CAM and/or C4-plant ingestion by hyraxes is suggested in the dry western and southern areas which receive more summer rains, probably reflecting the availability of some palatable (or "sweet") summer grasses. Although slight, a comparable pattern of isotope change is observed in three areas viz., the Cederberg, the Karoo and the Namib Desert, suggesting that plant cover is responding to regional climate mechanism ca. 2100 years BP. This does not necessarily imply similar seasonal rainfall shifts over the whole of this wide area.

Keywords: hyrax; dung deposits; stable carbon isotope; late Quaternary; vegetation change

1. Introduction

It has been shown that stable carbon isotope concentrations in plants are influenced by environmental factors such temperature, evaporation (salinity), moisture and seasonality of moisture which determines the temperature of the growing season in an area. Plants with different metabolic pathways like those that form initial molecules with three and four carbon atoms (C3 plants and C4 plants respectively), have specific carbon isotope signals in their tissue (Ehleringer et al., 1997). Some CAM (crassulacean acid metabolism) plants have isotope values ranging between those of C3 and C4 plants (Barbour et al., 1987, pp. 363–365). This paper aims to de-

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scribe the stable carbon isotope composition of hyrax (or dassie) diet reflected in their fossil dung, and to investigate the associated environmental conditions during the last 20 000 years in Southern Africa.

The ratio of grass to small-shrubs in the vegetation indicated by fossil pollen assemblages (Bousman et al., 1988; Scott, 1989, 1993). Stable carbon isotope ratio (i.e. δ^{13}C, the $^{13}C/^{12}C$ ratio per mil relative to an international standard) in fossil speleothems (Talma and Vogel, 1992), palaeosols (Botha et al., 1992; Bond et al., 1994), antelope tooth collagen (Vogel, 1983) and tooth enamel (Lee-Thorp and Beaumont, 1995), are useful in reconstructing seasonal variations of moisture distribution. Hyrax (*Procavia capensis*) dung-middens (Scott, 1990; Scott and Bousman, 1990) are residues of fossil diet of which the δ^{13}C content may also register past vegetation and environmental changes. Hyrax species are herbivores which select a wide range of plant species in their diets including grasses, leaves, barks, pods, etc., of herbs, shrubs and trees (Smithers, 1983; Lensing 1983; Fourie and Perrin, 1989). Not all hyrax species have the same dietary preferences, e.g., in East Africa, one species appears to browse and another to graze (De Niro and Epstein, 1978). Different preferences and habits may also account for different inclusions in hyrax dung, e.g., some from the Middle East (Fall et al., 1990) seem

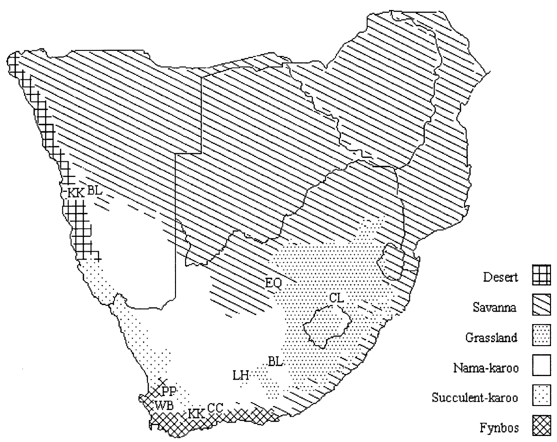

Fig. 1. Locality map of sites with stable carbon isotope data from hyrax dung and other sources. KU, Kuiseb River; BL, Blasskranz; EQ, Equus Cave; CL, Clarens (Rooiberg); BL, Blydefontein; LH, Leeuhoek; CC, Cango Caves; KK, Keerkloof; WB, Wolfberg; PP, Pakhuis Pass.

Table 1
Radiocarbon dates/concentrations and stable isotope ratios in hyrax dung samples from the Cederberg, South Africa

Site	Lab. No.	^{14}C date (years BP)	δ^{13}C (‰)
Pakhuis Pass	Pta-5295	19 700 ± 120	−26
	Pta-5881	19 300 ± 180	−26.3
	Pta-5501	19 300 ± 210	−26.3
	Pta-5733	18 700 ± 190	−25.9
	Pta-5499	16 900 ± 190	−26.2
	Pta-5744	16 200 ± 160	−25.9
	Pta-5882	15 800 ± 160	−26.2
	Pta-5895	15 200 ± 120	−26.4
	Pta-5897	14 470 ± 140	−26.3
	Pta-5737	13 850 ± 130	−26
	Pta-5896	13 000 ± 130	−26.6
	Pta-6041	11 390 ± 100	−25.7
	Pta-6923	9680 ± 100	−26.3
	Pta-7179	9050 ± 70	−26.5
	Pta-6040	8230 ± 80	−26.1
	Pta-5747	8180 ± 100	−27.1
	Pta-6035	7950 ± 80	−26.1
	Pta-7167	7930 ± 80	−26.2
	Pta-6037	7630 ± 80	−25.5
	Pta-6934	7250 ± 60	−25.6
	Pta-6044	4900 ± 70	−25.5
	Pta-5885	4690 ± 50	−27.3
	Pta-6036	4380 ± 60	−26.3
	Pta-6921	2600 ± 45	−25.7
	Pta-6919	2470 ± 45	−25.7
	Pta-6931	2110 ± 40	−25
	Pta-5735	1740 ± 50	−26.3
	Pta-5880	1650 ± 45	−26.3
	Pta-6924	1610 ± 50	−26.1
	Pta-5746	1370 ± 50	−26.7
	Pta-7164	1250 ± 40	−27.1
	Pta-7163	540 ± 50	−25.8
	Pta-6932	420 ± 40	−24.1
Wolfberg	Pta-6929	1190 ± 25	−26.9
	Pta-7165	1070 ± 50	−28.4
	Pta-6918	815 ± 20	−26.5
	Pta-6922	710 ± 40	−26.5

to contain relatively more macrofossils than those in South Africa (Scott, 1994).

Dating from the Quaternary period in Southern Africa, hyrax dung deposits which were presumably formed by *P. capensis*, are preserved in dry rock shelters (Scott, 1990, 1994), and contain fossil pollen spectra and other inclusions which give additional evidence of past changes in vegetation (Scott, 1996). Although the plant species that hyraxes consumed, can not be determined from the dung, variations in the ratio of plants with different metabolic pathways in their diet, may potentially be estimated by means of $\delta^{13}C$ values in their dung. It does not reflect vegetation directly, but the dietary selection of hyraxes. The stable isotope ratio depends on the ratio of C4 (mainly tropical grasses) and CAM plants (some succulents), to C3 plants (most other plant and certain grass species). Past variations in the C4, C3 and CAM plant availability as reflected in fossil remains were most likely caused by past changes in temperature and moisture conditions and seasonality of rainfall. These plants groups have different physiological adaptations to seasonal moisture and growth conditions and changes in moisture and temperature regimes can be expected to influence the ratio between them. This is demonstrated by the current distribution of grass subfamilies in Southern Africa. C3 grasses are present in the winter-rainfall area of the Western and Eastern Cape Provinces and along the cool high-lying eastern escarpment, while C4 grasses are dominant in the central summer-rain and warm dry regions of South Africa (Vogel, 1978; Vogel et al., 1978; Ellis et al., 1980). This distribution reflects the ability of C4 grasses to bind carbon effectively during warm growing seasons, while C3 grasses are successful in environments where moisture is available and growth takes place under relatively cool conditions. Plant material of C3 and C4 species and bones derived from C3 and C4 plant diets give different stable carbon isotope ($\delta^{13}C$) signals with C3-derived tissue being more depleted in ^{13}C (Vogel, 1978; Lee-Thorp and van der Merwe, 1987). Bond et al. (1994) showed that enrichment of $\delta^{13}C$ values of soil organic material in the Karoo area (corresponding with the Nama-Karoo biome, Fig. 1), increase towards the north-east, together with the amount of summer rain. Marked isotope depletion is recorded in soils from the Cape winter-rain area, corresponding with the Fynbos Biome (Fig. 1) (Stock et al., 1993). Similarly the isotope

Table 2
Radiocarbon dates/concentrations and stable isotope ratios in hyrax dung samples from sites in Karoo and Free State, South Africa

Site	Lab. No.	^{14}C date/concentration (years BP/%)	$\delta^{13}C$ (‰)
Anysberg Nature Reserve			
Keerkloof	Pta-5734	8420 ± 80	−24.1
	Pta-5883	7680 ± 50	−24.7
	Pta-5884	4250 ± 40	−25.1
	Pta-5742	(104.9 ± 0.6)%	−25.7
Leeuhoek	Pta-6322	120 ± 70	−25
	Pta-6324	(100.3 ± 0.8)%	−24.4
	Pta-6326	(123.3 ± 1.1)%	−24.1
Blydefontein (Noupoort)			
Oppermanskop	Pta-5003	1070 ± 50	−23
	Pta-4571	460 ± 45	−22.1
Meerkat	Pta-4403	300 ± 35	−23
	Pta-5026	200 ± 45	−22.7
Clarens			
Rooiberg I	Pta-4493	(141.5 ± 0.95)%	−28.4
	Pta-4232	(128)%	−27
Rooiberg IIa	Pta-5939	10 ± 50	−26.3
	Pta-7260	10 ± 45	−27
	Pta-5608	150 ± 45	−27
	Pta-5935	190 ± 60	−27.9
	Pta-5565	80 ± 40	−28.1
	Pta-7263	(137.6 ± 0.7)%	−29
	Pta-5938	(126.53 ± 0.62)%	−28.8
Rooiberg IIb	Pta-6099	90 ± 45	−26.7
	Pta-6092	0 ± 50	−26.9

ratio in fossil dung middens is expected to give an indication of variation in the amounts of C3 and C4 and CAM plants in hyrax diets, reflecting on the availability of these plants and environmental conditions. Hyraxes are likely to have changed the plants in their diets depending on what was available in local vegetation. If a change is recorded over a wide region it is reasonable to assume that it was driven by regional climate rather than by local factors.

In this paper $\delta^{13}C$ in fossil hyrax dung from areas receiving winter-rain like the Cederberg (Pakhuis Pass and Wolfberg sites) and Anysberg Nature Reserve (Keerkloof), are compared with those from summer rain-fall areas at Clarens (Rooiberg), Blydefontein (Meerkat and Oppermanskop) and the Namib desert (Kuiseb River and Blasskranz) (Fig. 1). The fossil dung samples are up to 20 000 years old and we intend to investigate how their isotope ratio can be related to changes in past environmental conditions and seasonality.

2. Materials and methods

Sub-samples of hyrax midden that were investigated date from different times in the Holocene and

Table 3
Radiocarbon dates/concentrations and stable isotope ratios in hyrax dung samples from sites in Namibia

Site	Lab. No.	^{14}C date/concentration (years BP/%)	$\delta^{13}C$ (‰)
Kuiseb River			
SA	Pta-5289	2080 ± 50	−19.3
D	Pta-5705	1840 ± 60	−22.9
SA	Pta-5568	1700 ± 80	−24.5
A1	Pta-5288	1680 ± 50	−23.7
A1	Pta-5571	1310 ± 40	−23.8
A2	Pta-5292	970 ± 50	−24.7
D	Pta-5700	950 ± 50	−24.7
A2	Pta-5294	930 ± 40	−24.6
A2	Pta-5572	620 ± 50	−22.1
H2	Pta-5301	580 ± 30	−24.4
H2	Pta-6238	380 ± 50	−24.5
H2	Pta-5573	190 ± 50	−25.5
D	Pta-5701	(131.4 ± 0.5)%	−26.4
H1	Pta-5177	120 ± 40	−23.4
SC	Pta-5169	50 ± 80	−21.4
Blasskranz			
	Pta-5164	1500 ± 45	−19.2

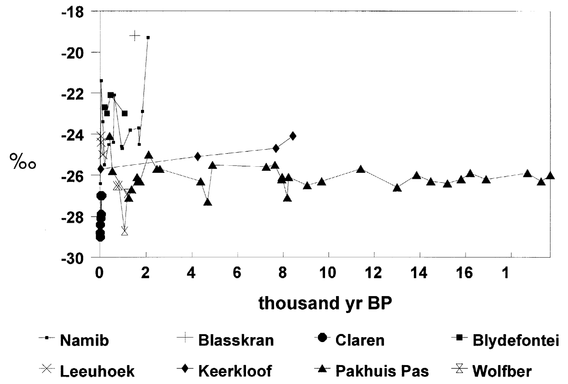

Fig. 2. $\delta^{13}C$ values in hyrax dung from different ages and sites in Southern Africa over the last 20 000 years.

Late Pleistocene as listed in Tables 1–3. The hyrax dung accumulated in local horizontally stratified heaps in dry rock shelters. Several radiocarbon-dated heaps from the same area can be used to build up a sequence for each. Samples from these midden deposits also contain pollen that provides independent environmental information (Scott, 1994; Scott 1996; Scott and Bousman, 1990; Scott and Vogel, 1992; Bousman and Scott, 1994). The data from the Cederberg mountains are from two sites in this almost exclusively winter-rain area viz.: the Pakhuis Pass Shelter on the low-lying (450 m), dry eastern side (Scott, 1994) and Wolfberg Shelter at a higher-altitude (ca. 1200 m) southern side of the range. According to Vogel et al. (1978), few C4 grasses occur in the Cederberg. The Anysberg Nature Reserve (Keerloof site) lies further to the south east in an area with winter-rain and very small amounts of summer rain. This falls in the area that supports intermediate amounts of C3 and C4 grasses (Vogel et al., 1978). The Noupoort sites at Blydefontein (Oppermanskop and Meerkat) fall in the summer-rain region and the vegetation consists of upland grassland and karoo shrubs (Scott and Bousman, 1990; Bousman and Scott, 1994). The Clarens (Rooiberg) area is also characterized by summer-rain but is surrounded by denser grassland with wooded slopes (Scott, 1989; Scott and Vogel, 1992). Both the latter areas fall in high lands, but Clarens receives a higher rainfall than Noupoort (ca. 700 mm versus ca. 400 mm). Both areas favour so-called “sour grass”, a term used by farmers to describe rigid unpalatable species of higher rainfall areas. These grasses, however, consist of a mixture of C4 and C3 species. The Kuiseb river sites fall in an area with less than 100 mm of mainly summer-rainfall, while Blasskranz lies further to the interior escarpment with slightly more rain, also of summer origin. The vegetation of the dry areas, like the Namib, include woody species and tasty "sweet grass" which are mainly C4 species. The δ^{13}C ratios of hyrax dung samples that were intended for pollen analysis, were measured at QUADRU during routine radiocarbon dating (Tables 1–3).

3. Results

The results of the ^{13}C measurements (Tables 1–3) are plotted against the respective un-calibrated radiocarbon dates in Figs. 2 and 3. The samples from the winter-rain Cederberg region (Pakhuis Pass and Wolfberg), gave negative values (depleted in ^{13}C), close to the generally accepted mean value for C3 plants (−26‰) consistent with the shrubby vegetation of the area, and a diet of almost exclusively of C3 plants. Peaks at the 2110 and 420 years BP levels of −25‰ and −24.1‰, respectively, are exceptions. A comparison between isotope sequences of the Cederberg and the apparently slightly drier Anysberg Nature Reserve (Keerkloof), indicates either that the Keerkloof diet included some C4 or CAM plants with mainly C3 plants, or that aridity influenced the values. Aridity and higher temperatures cause enrichment of C3 plants up to −24‰ (Tiezen, 1991). The samples from the summer-rain region of Noupoort in the Karoo and the dry Namib desert region gave slightly higher values (Fig. 3), indicating that small amounts of CAM plants or C4 plants were incorporated in hyrax diets in addition to C3 plants. The strongly negative δ^{13}C values from the Clarens area that receives summer rain, were not expected, and indicate a C3 diet in this area where C4 grasses are numerous. This shows that the hyraxes prefer C3 shrubs above grass.

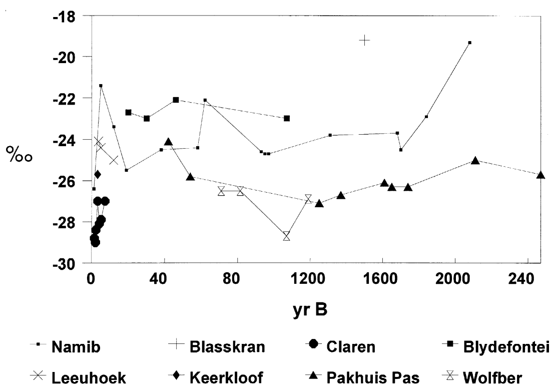

Fig. 3. δ^{13}C values in hyrax dung from different ages and sites in Southern Africa over the last 2000 years.

4. Discussion

With the exception of the δ^{13}C values from Clarens the regional isotope ratios seem to be slightly more enriched in areas receiving summer rain. The anomaly of Clarens suggests that δ^{13}C isotope in hyrax dung is not useful as indicator of seasonality at least in this area. A closer examination of the Clarens situation may help to find the reason for the anomaly. Town expansion at the site and grazing competition by live stock changed the vegetation of the studied mountain slopes from predominantly grassland to mountain woodland during the second half of the 20th century (Scott and Vogel 1992, L. Scott and J. Carrion, unpublished data). The δ^{13}C ratio in older samples (Pta-4232; Pta-5608) which contain mainly grass pollen indicates a C3 diet and the rejection of freely available C4 grasses which are mainly of the "sour" type, and suggests that the pollen composition is not influenced much by diet. The changing vegetation in the 20th century did not influence the isotope pattern markedly. If hyraxes in this area eat some grass, of which we are not sure, a contributing factor for low δ^{13}C values may be that almost half of grass species are of the C3 type. This was found in an unpublished survey by Johan du Preez at Fouriesburg, ca. 30 km to the west of the Rooiberg sites, in a similar environment. Further δ^{13}C values may be even lower than expected simply as result the cooler conditions and high moisture availability which are thought to influence these values in C3 plants (Tiezen, 1991). The δ^{13}C anomaly of the Clarens dung can be attributed therefore to a C3 diet and the exclusion of unpalatable "sour" grasses and the local climate. This may not be the case in other dry areas of Southern Africa where "sweet" grasses occur. The higher C4 indications in the drier Noupoort area may, e.g., be due to the greater availability of "sweet" grasses or other C4 plants, while more aridity could have influenced the $\delta^{13}C$ enrichment of C3 plants.

A salient feature of the whole set of $\delta^{13}C$ data of hyrax dung (Fig. 2) is that negative values of the Cederberg samples persisted throughout the last 20 000 years. This suggests that the region continually received winter rains over this interval or that plant growth happened under the cool conditions of winter or the Pleistocene. The pollen data from the same dung indicate the presence of vegetation of mainly the C3 type (fynbos and shrubs) in the region including, Asteraceae, Restionaceae, Cyperaceae, and *Dodonea*, and very little grass and Chenopodiaceae, throughout the last 20 000 years (Scott, 1994). Together with some C4 plants, succulents of the Aizoaceae and Mesembryanthemaceae types that possibly include some CAM species, could have been responsible for slight isotope enrichment at certain times. Although the summer rain ratio may have increased during these events, at the most the amounts must have been relatively small in comparison with the winter-rain contributions.

In general the long-term $\delta^{13}C$ record from the Cederberg dung, shows relatively small variations. Variability of $\delta^{13}C$ in samples from the Cederberg, is slightly greater in the Holocene than in the Late Pleistocene, possibly reflecting more unstable conditions in the Holocene. The constant values in the late Pleistocene may be due to the absence of a C4 component in the vegetation and to hyrax's dietary preference of C3 plants. It is interesting that a shortage of CO_2 in the atmosphere of the last glacial period as was suggested in the case of lake deposits in tropical regions (Ehleringer et al., 1997; Street-Perrott et al., 1997) did not seem to favour C4 plants in the Cape region. The Cederberg pattern is supported by stalagmite data from the Cango Caves (Talma and Vogel, 1992) and soil carbon data from Kwazulu/Natal (Botha et al., 1992). Tooth enamel samples from grazer remains in Equus Cave in the summer-rain region to the north (Lee-Thorp and Beaumont, 1995), may be closer to the tropical lakes pattern but dating resolution is not good enough for a certainty.

The contrast between Pleistocene and Holocene is not very marked in the Cederberg dung. In comparison, wider amplitudes are found in studies on other materials like the isotopes in a stalagmite from the Cango Caves (Talma and Vogel, 1992) and grazers in Equus Cave (Lee-Thorp and Beaumont, 1995). $\delta^{13}C$ values from early Holocene dung in the Cederberg show raised values, but have no counterparts in the Cango Caves because the stalagmite sequence is interrupted over this period. A general similarity of relatively more positive $\delta^{13}C$ (or enrichment in ^{13}C) values in the early Holocene and low values in terminal Pleistocene is manifested in the tooth-enamel sequence from Equus Cave. Unfortunately differences in time resolution rule out any close comparison. The generally low $\delta^{13}C$ in the Late Pleistocene samples of the Cederberg could be as result of cooler growing seasons. The preliminary pollen results (Scott, 1994) throw some light on vegetation changes of the late Holocene but further pollen analysis of the Cederberg dung is in progress.

Overall, the stalagmites from the Cango Caves (Talma and Vogel, 1992) and tooth-enamel from antelopes in Equus Cave (Lee-Thorp and Beaumont, 1995) give more positive $\delta^{13}C$ values than hyrax material. These differences confirm that hyraxes strongly rely on C3 plants, and that even when C4 plants are available they eat C3 plants. A $\delta^{13}C$ value of $-21.4‰$ of hyrax bones from Aspoort (on the east bank of the Doorn River, in the Doorn Karoo) support the indication of a strong C3 diet (Sealy, 1986, p. 109; Sealy and van der Merwe, 1986). In comparison grazers in Equus Cave, reflect a predominantly C4-grass area in their tooth enamel, which with periodic exceptions, remained as such during the Pleistocene (Lee-Thorp and Beaumont, 1995). The difference in isotope values between hyrax dung and the Cango stalagmite, is probably due to the effect of a general unbiased mixture of carbon sources in the vegetation on the stalagmite, while diet selection is reflected in the dung material. The stalagmite values (Talma and Vogel, 1992) are affected by admixture with parent rock carbonate material, but compare better with those in soil organic material in the Karoo which is slightly lower (Bond et al., 1994). Despite the large difference in the average $\delta^{13}C$ values in the Cango stalagmite and the Cederberg dung samples, trends in the sequences are partly comparable, and the significance of this, if any, should be investigated further.

A peak at just before 2000 years BP as recorded in the Cango stalagmite, is found not only in the Cederberg but also in the Namib (Kuiseb River) middens. Since the Cango Caves and the Cederberg are ca. 200 km apart and the Kuiseb River is ca. 800 km to the north, this points to a wide regional change. The cause may not be the same over the whole of this wide area. At the Cango Caves in the speleothem data and in the Namib in the dung data, this may be related to an increase in C4 plants. In the Cederberg dung, it may, however, also be due to a dry episode since the values are too low to be certain of the presence of any C4 component in the hyrax diet. The dung that formed later, between 2000 and ca. 800 years BP, shows low $\delta^{13}C$ values in the Cederberg, Noupoort, and Kuiseb sequences. In the former, the isotopic values of hyrax dung are the lowest at 1000 BP, and probably reflect the relatively high proportion of C3 plants and cooler or maybe wetter conditions in the Cape region although the position of the Wolfberg site may have exaggerated the decline. This trend is also noticed in the stalagmite data. One possibility is that this may indicate a relative decline in summer rain in the north with concomitant wetter winter-rain conditions in the fynbos area. A renewed rise of isotope ratio is recorded in the hyrax middens from ca. 800 years BP onward (Fig. 3), but is not noticeable in the Cango stalagmite samples (Talma and Vogel, 1992).

The $\delta^{13}C$ record from hyrax dung over the last 1000 years for the Karoo area is not complete enough to give a clear picture of vegetation change. However, pollen records from the dung at Noupoort (Scott and Bousman, 1990; Bousman and Scott, 1994) suggest that karroid shrub expanded considerably during the last 300 years, and the $\delta^{13}C$ values, although limited, do not contradict this. Undated stable isotope values from soils over a wide area of the Karoo support the indication of recent grass deterioration over the whole area (Bond et al., 1993). The lower $\delta^{13}C$ values for the recent midden at Leeuhoek in comparison with the older Noupoort (Blydefontein) values may either confirm indications of shrub expansion in recent centuries, or reflect the grassy environment at Noupoort.

In order to investigate the Kuiseb River isotope sequence over the last 2000 years it is useful to consider the pollen contents of the middens. The dry Kuiseb River bed contains mainly C3 trees and shrubs while the surrounding areas are barren or sparsely covered with C4 grass during moist events. High grass pollen ratios in the Kuiseb River middens are thought to indicate wet periods, while relatively high arboreal pollen ratios probably indicate dry periods when the grass cover deteriorated but trees remained (Scott, 1996). The raised $\delta^{13}C$ values just before 2000 years BP in the Kuiseb river can be attributed to a more grassy environment and therefore to more rainfall as is suggested by the pollen record. Other $\delta^{13}C$ increases are also associated with more grass pollen, except in one case with more arboreal pollen (Pta-5169, −21.4‰) in which the $\delta^{13}C$ peak is probably due to more easily available local C4 grass on the sand dunes at the particular site (Scott, 1996). However, since the Kuiseb is an extremely dry area where more that 90% of the grass is C4 (Ellis et al., 1980) it is possible that any rainfall, during winter or summer, will favour the relative C4 or CAM component. The palynological data (Scott, 1996) suggest that not only the grasses but other plants like Asteraceae and succulents were also prominent ca. 2000 years BP, and therefore speculations about the seasonality of rain are not possible. It is also premature to be more specific about the seasonal significance of the Namib isotope sequence. However, the area to the south of the Kuiseb, that receives more winter-rain and has more Asteraceous vegetation, is not more than 200 km away and a shift of this zone towards the Kuiseb is not improbable. More isotope and pollen data of recent dung along the summer to winter rain transition zone are necessary as control of past conditions in the area.

5. Conclusion

Carbon isotope ratios from middens which formed during the last 20 000 years, are associated with plant growth in the Cederberg during winter months, or under cool climates of the Pleistocene. Like at the Cango Caves C4 plants were generally not available at the Cederberg during the glacial phase, despite a CO_2 shortage in the atmosphere. Low temperatures helped to prevent them from flourishing during this phase. In the southern parts of South Africa, the influence of summer rains from the north was small during the Holocene, probably allowing only very limited C4 plant availability, e.g., at 2100 and 420 years BP.

From different parts of the country, the suggested C4 ratio during the last 2000 years in the studied hyrax middens, provide evidence that changes occurred on a regional scale. This is partly supported by the $\delta^{13}C$ sequences in stalagmite (Talma and Vogel, 1992).

In areas with summer-rains where "sweet" grass is likely to develop, $\delta^{13}C$ values of hyrax dung deposits are slightly enriched. Only in these areas may variations in isotope ratios during the Holocene be reflecting rainfall seasonality.

Depleted $\delta^{13}C$ values of this century from the Clarens dung material suggest that "sour" grasses of the C4 type are not included in hyrax diets in this upland grassland region. A longer fossil record of hyrax dung is required to determine if and any $\delta^{13}C$ enrichment by drought adapted C4 grasses occurred during the Holocene.

Closer time resolution of fossil isotope values, more modern controls, and palynological research are needed to make an accurate reconstruction of past vegetation changes possible. To be effective controls from the modern environment should take into account site peculiarities and biases imposed on isotope values by modern land-use practices or local site characteristics.

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