Ecological significance of South-West African grass leaf phytoliths: A climatic response of vegetation biomes to modern aridification trends

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Abstract

Recent advances in autecology and plant physiology on the effects of aridity stress conditions on the micro-morphology of plant epidermal short-cell silica bodies (phytoliths) provide a new tool for evaluating subtle change in precipitation. An on-going, integrated project concerning the modern phytoliths/vegetation/climate relationships of the Namibian area is outlined. The photosynthetic pathway appears to be the major factor determining how successful plant species are under different climates. Contemporary grass phytoliths clearly illustrate how the chorology of species with C_3 or C_4 photosynthetic pathways depends on the mean annual rainfall. The photosynthetic pathway of grass species can be determined by examining the shape of the silica bodies formed in the short-cells of the grass leaf epidermis. The differences in these shapes can be used to show how the relative abundance of species varies with the annual rainfall. Therefore modern grass leaf phytoliths are physiologically informative, and can easily be distinguished from those of other parts of the plant (and from non-grasses). It is demonstrated that African grass phytoliths have to be used as a proxy for aridity to improve the resolution of fossil records, in that changes in the total phytolith assemblages provide information about phytoclimatic shifts of the deciduous open vegetation in response to past rainfall events. Phytoliths offer a powerful addition to conventional palynology in arid areas. Since their biogenic signal can also be recovered from sediments, this approach: (1) can contribute to explain the functional patterns of the past vegetation, and (2) can help to predict future trends of the biomes of arid lands.

Key words: C_4 (four-carbon chain fixation); K (Kranz anatomy); me (malate enzyme); NAD (nicotinamideadeninedinucleotide); NADP (nicotinamideadeninedinucleotidephosphate); PCK (phosphoenolpyruvatecarboxykinase); Okavango; silica bodies; annual rainfall; vegetation biomes.

Introduction

The sensitivity of present-day plant species and plant communities for climate can be assessed in different ways, at a taxonomic level (biogeography of specific taxa) and at the level of the plant formation (Box 1981), but the real behaviour of an ecosystem cannot be predicted from lower levels (Weiner 1996). Since the extrapolation at a short-term time course often fails to predict the functional patterns of the vegetation (Prentice *et al.* 1992), long-term field experiments on the response of plant specimens, plant populations and plant communities are necessary in predicting the ecological effects of climate.

Prognostic models of the response of the vegetation to climatic changes are mainly focused on the ecophysiological constraints of the plant functional types (Claussen 1994; Haxeltine and Prentice 1996). However, present-day field measurements and modern data sets often do not agree with the simulation, for instance failing to distinguish between natural and potential vegetation. According to Prentice *et al.* (1998), the vegetation-atmosphere interaction has been disregarded in most prognostic models. The arid scenario of South-West Africa provides evidence of the weakness of any implementation of the biome reconstruction models based only on the (scarce) pollen records so far available. Especially in Namibia, an interpretation of still supposed Quaternary biome shifts cannot rely on any terrestrial pollen-based evidence (Heine 1998). Tarasov *et al.* (1998) suggested that an objective assessment of the biophysical feedback of arid landscapes have to lay on the statistical weight of the herba-

ceous taxa. The ecological information supplied by herbs and grasses growing under extreme environmental conditions is critical in the prediction of the aridity effects (which will otherwise be overestimated in most simulations).

In using a realistic global vegetation-climate coupling to evaluate the vegetation distribution in arid and semi-arid zones of Africa, we have to take the carbon storage into account. In southern Africa (an area still critical for all the BIOME-models mentioned before), the present-day desert is an important source of carbon to the atmosphere (cf. Lioubimtseva *et al.* 1998). The Kalahari and the Namib-Naukluft deserts are contrasted offshore by the Benguela Upwelling System. The Benguela Current in the SE Atlantic Ocean is regarded as a carbon sink and a major component in the equatorial circulation across the South- and the North Atlantic (Wefer *et al.* 1996). This land-sea coupling contributed during the Quaternary to both short- and long-term desertification trends. However, the magnitude of simulated changes in Africa during the Late Quaternary shows some persistent mismatches with the fossil pollen records (Jolly *et al.* 1998). A much larger modern data set is necessary to test correctly the lateral expansion of the distribution of the xerophytic plant associations.

The photosynthetic pathway has been chosen as the main factor in vegetation response to climatic changes. In the study of marine or lacustrine Quaternary sediments, the commonly used tool to unravel physiologic trends of the vegetation is the signal of the C_3/C_4 ratio derived from land plants (recovered offshore as terrigenous organic matter), as this terrestrial ratio provides an evaluation of the stable isotope signal from bulk organic material (Kelly *et al.* 1991). However, even subtle differences in grass physiology can be inferred from morphological evidence and quantified by LM observations of the epidermal cells (Ellis 1979, 1988).

Cumulative interactions between CO_2, temperature and precipitation in the past have been recognised in several parts of the world, but palynological sequences and independent sedimentological records are difficult to correlate in time with temperature and rainfall trends. According to Ehleringer *et al.* (1997), Cerling *et al.* (1998), Collatz *et al.* (1998) and Mulder (1999), the low atmospheric CO_2 content and the low temperatures during the last glacial maximum (18,000 yr B.P.) enabled C_4-dominated biomes to expand their global distribution, but actually to what extent? Although it is known that the plant available moisture is important in determining the distribution of present-day plants (Ellery *et al.* 1991; Rutherford and Westfall 1994), the temporal changes along the NE-SW African rainfall gradient (related to the upwelling variations of the Benguela Current) remain unclear because of the lack of an unambiguous aridity/humidity signal on land (cf. Partridge *et al.* 1990). Stokes *et al.* (1997) suggested that several significant short-lived (5-20,000 yr long) episodes of aridity in the Kalahari are related to changes in the sea-surface temperature (SST) gradient across southern Africa. However, the low resolution of most proxy data available in Africa makes the timing of the Holocene Climatic Optimum (hypsithermal) uncertain (Cohen and Tyson 1995).

This pilot study is designed to assess whether present-day leaf phytoliths (mainly epidermal short-cell silica bodies) can be used to quantify the degree of aridity and its rate of change in the past. Phytoliths are produced by passive silica up-take and deposition in the epidermal cells. Present-day phytoliths were studied under different environmental conditions throughout the modern vegetation patterns of southern Africa. In tracing such present-day patterns, the study of taxonomically identified phytoliths provides an assessment of the biotic response of the flora. Spatial ecological constraints change the degree of occurrence of individual species (competitivity), which may be recognised in temporal trends of the total percentage of the phytolith types occurring in the sediments (fossil phytolith assemblage).

Fossil plant phytoliths have already been recovered from continental (Fredlund and Tieszen 1997a; Lu *et al.* 1998) and from marine sediments (Jansen and van Iperen 1991; Romero *et al.*, 1998). The phytolith dispersal is linked to vegetation (canopy cover, clearings, and fires), autecology (plant tissue desiccation, water stress), and geomorphology (surface run-off, soil erosion, wind threshold velocity). This study focuses on the grass phytoliths because the distribution of many species in the flora of Namibia is ecologically dependent from the precipitation thresholds (Ellis *et al.* 1980).

STUDY AREA

The study area of about 1,000,000 km^2 is south of the Cunene River (18°S) and ranges from the coastal Namib Desert up to the fringes of the Kalahari desert, where the Okavango River discharges into a seismically active extension of the East African Rift Valley System (Fig. 1). Even though some geological records are available (Rust and Vogel 1988; Thomas and Shaw 1991; Heine 1992), the palaeobiological record of the study area is still hardly explored, mainly because of the lack of knowledge on the ecology of the desert plant species involved and on the dynamics of the plant populations (Jürgens *et al.* 1997).

Throughout Namibia only a small variation in the biogenic signal of *[13]C values has been measured in spite of a steep SW-NE-rainfall gradient (50 up to 600 mm/yr in Schulze *et al.* 1996) and a dominant ecological gradient running in a WSW-ENE direction (Jürgens *et al.* 1997). The regional rainfall variations can be easily recognised (Fig. 1). In most of Namibia complicating factors such as soils, herbivore and/or human disturbance, and surface fire regime do not obscure the biogenic signal. The local physiological competition (Werger and Ellis 1981) and to the lack of secondary variation in air humidity make the chosen area ideal for temporal aridification studies.

Up to now, the phases of aridity can be judged merely from gaps in time in lacustrine and fluvial deposits (Thomas *et al.* 1997), or from randomised pollen recovered from fossil middens (Scott 1996). Phytoliths are often preserved in large amounts in several sediments of the study area, such as in Okavango peats (where up to 70% biogenic silica occurs according to McCarthy *et al.* 1989), in the Ncamasere Valley (Meadows, pers. comm.), and in some calcretes and river terraces of the Kuiseb and the Tsondab drainage basins related to past erosive events (van der Wateren, pers. comm.). We assume that these deposits contain also less severe dry phases (apart from the gaps), that can be checked by the analyses of phytolith assemblages.
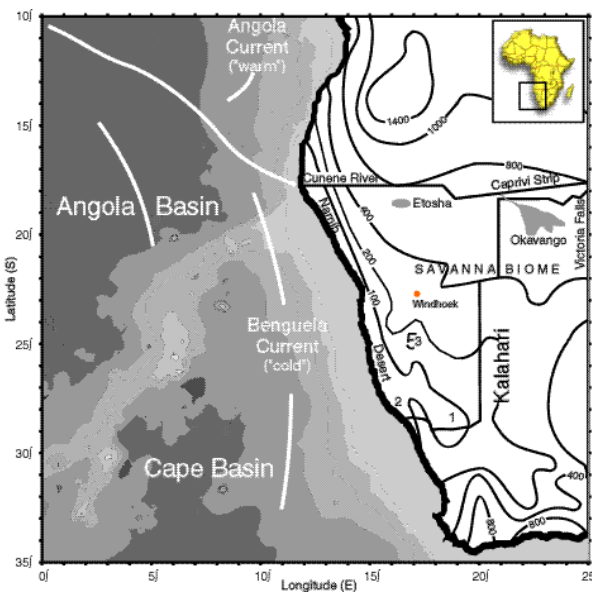
Fig. 1. The boundaries of the selected biomes in the study area depend on the mean annual precipitation (the rainfall is indicated in mm/yr by dotted lines). Grass samples were collected in the Okavango Fan (Botswana), along the Caprivi Strip (Namibian border) and near the Victoria Falls (Zambezi River, Zimbabwe). The vegetation of the savanna is the most variable of the biomes. This is evident in NW Botswana, where the Okavango sedimentation processes strongly affect the local vegetation succession. Relevès were taken for the dominant grass species in: the Namib Desert (**1.**), the Succulent Karoo Biome (**2.**), and the Nama-Karoo (**3.**), and compared with minimum -, mean -, and maximum annual rainfall, and the distribution area of the investigated herbaria specimens (reference vouchers in the Appendix).

MATERIALS AND METHODS

Laboratory treatment.

Grass samples of 68 locally common species belonging to 37 genera were collected during two expeditions (September-October 1997, and July-August 1998). For each taxon at least 10 leaves were sampled under different environmental conditions. The leaves from field specimens (mainly from the Okavango area) and from the Namibian herbarium vouchers (J, PRE) were ashed in an oven at 280°C for 1 hour to extract the phytoliths. At the same time, a reference collection of Light Microscopy (LM) and Scanning Electron Microscopy (SEM) photographs according to the method suggested by Theunissen (1994) was established in order to facilitate identification of phytoliths from other sources. Phytoliths were described and identified respectively at a 1,000 x or 500 x magnification with an Olympus BH-2 microscope (objectives: SPlan100 1.25 Oil and DPlan50 0.90 Oil).

In addition, some surface samples ('litter' from monospecific populations) were prepared for palynological treatment by flotation and decanted supernatant (Kondo *et al.* 1994). HCl and HNO_3 were added to remove carbonates and organic matter. The phytoliths were transferred to test tubes by centrifugation after heavy liquid flotation ($ZnCl_2$ at a specific gravity of 2.2). Phytoliths and cuticula remains were mounted in silicone oil 2000CS or in glycerine jelly after drying by Acetone.

Statistical approaches.

The reliability of palaeoenvironmental reconstructions depends on a complete assessment of the modern analogues. The high-resolution study of present-day flora and vegetation patterns is always a contribution towards a better interpretation of past environmental trends. Several grass-phytolith keys are available for archaeobotanical purposes (Mulholland and Rapp Jr 1992; Piperno and Pearsall 1998), but the nomenclature followed in Watson and Dallwitz (1994) has been chosen for our purpose.

This pilot study is the first assessment of the response to climate of modern grass leaves involving their physiology and the phytolith morphology. To avoid possible spurious relationships in the resulting ordination, the taxonomical species-matrix deserves close scrutiny. The non-diagnostic phytoliths are excluded from Table 1, as they have been downweighted at this stage. The total variance of all the phytolith types taken into account is set to 100%.

PCA (indirect gradient approach). The Principal Component Analysis (PCA) of the grass phytolith types (based on SEM observations of leaves from the herbarium reference vouchers given in the Appendix) has been performed with the PrinComp program (SYN-TAX 5.0 package of Podani 1993). The statistics of the phytolith variables are given in Table 1, while in the Appendix the percentages of variance of objects accounted for by each component are given. A graphical synthesis of the principal components of the investigated species (Appendix) weighted by the phytolith types taken into account (Table 1) is shown in Fig. 2.

CCA (direct gradient approach). The Canonical Correspondence Analysis (CCA) developed by ter Braak (1987) was carried out to integrate the indirect approach of the PrinComp program. CCA incorporates both correlation and regression between floristic data and environmental factors; in this way, an integrated direct ordination is obtained (Kent and Coker 1992). The input parameters have to be of high quality and restricted in number. A too large number of environmental variables would support any pattern and would give misleading results in the direct gradient analysis (McCune 1997). The important underlying variables have been measured or taken from the literature. Each grass species was plotted against its ^{13}C value, the minimum and maximum annual rainfall of the growing-area (Schulze et al. 1996), the tribe, the Kranz anatomy of the leaves (as defined in Ellis 1988), and the biomes within which it occurs viz. Savanna, Nama-Karoo, Succulent Karoo, and Desert (Gibbs Russell et al. 1991). The latter chorological variables were weighted against the relevés and the mean annual precipitation. The floristic (principal) input was also defined by plotting the same grass species against the phytolith types (based on LM observations of specimens growing under different environmental conditions). The biplot was performed with the CANOCO 3.10 program (ter Braak 1991) for a canonical correspondence between the local environmental variables and the biogenic silica forms occurring in the leaf sections of the dominant grasses of each biome (Fig. 3c).

RESULTS AND DISCUSSION

A strong linear relation between the leaf characters and a combination of climate variables has been known for decades (Raunkiaer 1934; Dolph and Dilcher 1979), and even the seasonality in the rainfall is reflected in the foliar physiognomy of perennial plants (Werger and Morris 1991; Jacobs 1999). According to Tieszen *et al.* (1979) and Twiss (1992), the prediction capacity

Table 1. Principal Component Analysis of the Namibian grass phytolith types. Data set of the observed frequencies of the different phytolith types, established for each phytolith (sub) type of each grass species as an average value of the J or PRE herbarium vouchers, the specimens collected on the field and/or the samples from the plots where the taxa have been relevéd. Pooled variance = 90.2607

| PHYTOLITH STANDARDIZED CORRELATION (PrinComp)						
Phytolith type	Mean	Standard Deviation	Variance	Variance as Percentage	Eigenvalues	Eigenvalues as Percentage
Pooid type	0.3857	1.8360	3.3708	3.735 %	3.896	32.47 %
Smooth type	0.6286	1.9424	3.7731	4.180 %	1.650	13.75 %
Round type	1.1000	2.6438	6.9899	7.744 %	1.108	9.23 %
Saddle type	1.8714	3.3705	11.3600	12.586 %	1.023	8.52 %
Tall-and-Narrow type	0.6429	1.8730	3.5083	3.887 %	0.954	7.95 %
Crenate type	1.0714	2.4573	6.0383	6.690 %	0.894	7.45 %
Oryzoid type	0.3429	1.5778	2.4894	2.758 %	0.827	6.89 %
Panicoid type	5.4857	4.3330	18.7752	20.801 %	0.599	4.99 %
Cross-Shaped subtype	2.1143	3.2372	10.4795	11.610 %	0.475	3.96 %
Butterfly-Shaped subtype	1.7143	2.9740	8.8447	9.799 %	0.323	2.69 %
Dumb-bell subtype	2.2143	2.9971	8.9824	9.952 %	0.161	1.34 %
Nodular subtype	1.2143	2.3768	5.6491	6.259 %	0.091	0.76 %
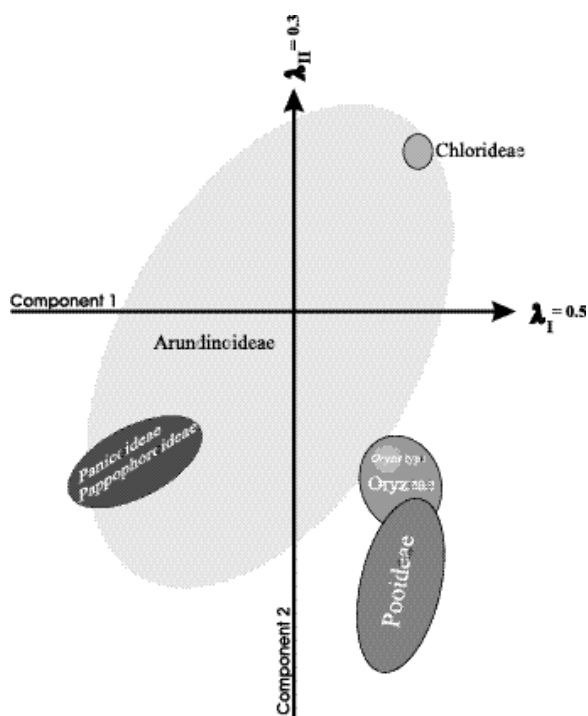
Fig. 2. Standardized Principal Component Analysis (PCA) of the phytolith types found in the herbarium vouchers weighted by the plant available moisture. In a PCA the eigenvalues measure the importance of each axis. λ_I and λ_{II} are the eigenvalues of axes I and II, respectively. These eigenvalues indicate that the axes account for 49.78% and 32.03%, respectively, of the total variation in the data set. Axis III is not shown (λ_{III} = .18). The total variance of the phytoliths is set to 1 (100%). To avoid crowding on the plot the position of the 68 Namibian grass species is not shown on this diagram, but their PCA values are given in Appendix.

of the response to climate of the functional types occurring within a flora in Africa suggested a different environmental scenario from that occurring in the mid-latitudes, where the productivity of arido-active plants is controlled by a combination of temperature and rainfall (Epstein *et al.* 1997; Fredlund and

Tieszen 1997b). Since the rainfall is the dominant controlling factor in arid lands, the climatic balance between C_3 grasses (the usual metabolism of plants growing in temperate and moist areas) and C_4 grasses (the dominant metabolism of plants growing in semi-desertic biomes) provides more information if the C_4 metabolism is split up in the various physiotypes (Fig. 3a). Our preliminary results in SW Africa show to what extent this can in true be achieved.

The occurrence of phytoliths infilling the cell lumina of the leaves of most taxa points to strong links between the morphology of biogenic silica bodies and the Kranz anatomy typical for the C_4 metabolism (small substomatal spaces, dense mesophyll, and large bundle sheath cells). Short-cell phytoliths clearly reflect the grass physiology in response to climate. Table 1 shows that the highest eigenvalue of the phytolith types comes from the C_3 Pooid phytolith type (3.896, covering 32.47 % of the total ecological significance of grass phytoliths), while the typical nodular subtype, only present in C_4 grasses, has the lowest eigenvalue of the whole set. Since all the panicoid-like phytolith (sub) types score together only 14.01 % of the total variance, it becomes evident that variously shaped elongate phytoliths (like those occurring in intercostal long cells, in cell walls or in extracellular spaces) are even less significant than the latter subtype due to the lack of a distinctive micromorphology (i.e., taxonomically or physiologically not diagnostic).

A clear link between taxonomy and phytolith morphology is not evident in Fig. 2. In fact, the principal component analysis (PCA) shows that a potentially misleading noise is due to overlap of the phytolith types belonging to the Oryzeae (Bambusoideae) with the physiologically variable Arundinoideae. In Appendix the statistically significant values of the first two components are marked in bold, and show taxa of high ecological significance for future applications. For instance, the occurrence and the physiology of facultative perennials like *Stipagrostis* are put into evidence by a high significance of both the 1st and 2nd component values, since a particular kind of C_4 NAD-me metabolism enables this genus to respond opportunistically to the minimal rainfall (Seely

Table 2. Canonical Correspondence Analysis of the Namibian grasses. Autecological intraset of $*^{13}C$ (reflecting the actual physiology, from Schulze *et al.* 1996), minimum and maximum annual rainfall from the plots where the specimens were collected, where the J or PRE vouchers have been sampled, or where the taxa were relevéd (according to Müller 1982), tribe (according to Watson and Dallwitz, 1994), and leaf transectional anatomy (the anatomical types of Ellis 1988) vs. Synecological intraset, defined by the biomes where the selected species occur (according to Gibbs Russell *et al.* 1991). Wilks 8 for the full set = .24233.

Roots Removed	Canonical R	R–Squared	χ^2	Degrees of Freedom	λ Prime
Full set	.7748	.600	90.01	25	.2423
I removed	.5583	.312	31.78	16	.6063
2 removed	.2810	.079	8.06	9	.8808
3 removed	.2087	.044	2.83	4	.9564
4 removed	.0080	.000	.00	I	.9999

1990). We would also assume a high ecological significance of the Oryzeae, since all C_3 species show an extremely low 2nd component value. However, if we compare the Appendix with Table 1, we can see that even if the phytoliths produced by *Oryza* belong always to the Oryzoid type and the species occurring in NW Botswana is statistically very significant (–2.983), the phytolith morphology scores only 0.827 (Table 1). Also the ecology of *Leersia* is statistically significant (-3.039), but no diagnostic phytolith types mark the occurrence of this species.

The Chloridoideae include species with either C_4 NAD-me or C_4 PCK metabolism in various degrees. However, the Chlorideae even include one species of *Eragrostis* (described as a C_3 plant by Ellis, 1984) which is the only non-Kranz species where also the 1st component value is statistically significant. Furthermore, *Eragrostis walteri* shows the lowest 1st component value of the whole Appendix (-5.46, surely due to extreme environmental conditions!). Within the Panicoideae the same C_3 metabolism occurs in *Sacciolepis* (2nd component value always significant throughout the genus), while otherwise most Panicoideae species have a C_4 NADP-me or C_4 PCK metabolism.

The correlation between the photosynthetic pathway and the annual precipitation (grouped into 6 clusters) is demonstrated in Fig. 3b, where the percentage of the total physiological types recognised in the transectional anatomy of the collected leaves and/or the herbarium vouchers is plotted against the mean annual precipitation of each study site where the samples were collected. Moisture availability during the growth season was obtained from an assessment of the climate at a biome-scale. Among the C_4 species, the pyruvate-formers show a clear negative correlation with the annual rainfall only within the C_4 NAD-me metabolic type, while the malate formers (C_4 NADP-me) show a positive correlation with annual rainfall. The C_4 PCK grasses were not taken into further account, but their percentage can be evinced from Fig. 3b as difference [C_4 PCK % = (100 – total shown percentages)]. The canonical correspondence analysis (CCA) of the phytoliths in the biplot of Fig. 3c provides evidence for an implementation of the prognostic models mentioned before, and enhances the temporal interpretation of environmental records in showing phytoclimatic shifts of biomes. As explained by ter Braak (1987), this kind of output clarifies the (present-day) floristic response to environmental conditions.

A multiple regression for each phytolith type on each axis selected the independent variable that best explains its variation of occurrence in any biome. The component scores in any R analysis are different from the eigenvector scores on the first two axes (phytolith loadings, compare Table 2). The biome scores and the phytolith type scores are computed at different scales on the same graph (Fig. 3c). Direction and length of the arrows indicate the rate of spatial change of each biome: the short arrow of the Desert biome indicates an extremely rapid change, and the long arrow of the Nama-Karoo biome indicates a gradual change. Furthermore, the position of each arrow indicates its degree of correlation with each CANOCO axis.

This implies that the boundaries of the Nama-Karoo biome are the most closely rainfall-related (its arrow is almost parallel to the second axis), while the Succulent Karoo and the Desert are almost equally related to both axes. The Savanna biome is even more related to the first axis, corresponding to an increase of temperature (and CO_2, as suggested from a C_4 grass enrichment in the hyrax diet during the Namibian Holocene by Scott, 1996). This different vegetation response pointed out by the grass phytolith morphology of modern southern African grasses is a reliable reflection of their physiology.

According to Low and Rebelo (1996) the Succulent Karoo has few C_3 grasses, the Nama-Karoo is dominated by C_4 grasses, and the Savanna grass layer consists mostly of C_4 grasses in areas where the growing season is hot, but in the region with winter rainfall C_3 grasses are dominant. The biome arrows in the biplot of Fig. 3c show this climatic threshold, since the winter rainfall boundary can be related to the minimum annual rainfall. Both the Savanna and the Succulent Karoo are linked to an area of (very) low winter rainfall, where the (primary) moisture availability is increased by the continuous effects of the coastal fog in the latter biome.

Some C_3-type phytolith assemblages recovered from the Okavango Savanna ecotones suggest a higher amount of water, available at the seasonal-scale. In most regional time sequences in the Okavango channels the development of the cross-sectional area (with its decline in current velocity and the debris blockages) plays an important role (Ellery *et al.* 1992). At the scale of a biome the relative abundance of C_3-type phytoliths points to changes in the rate of precipitation, useful for long-term correlations (especially the statistically significant Pooid phytolith type of Table 1).
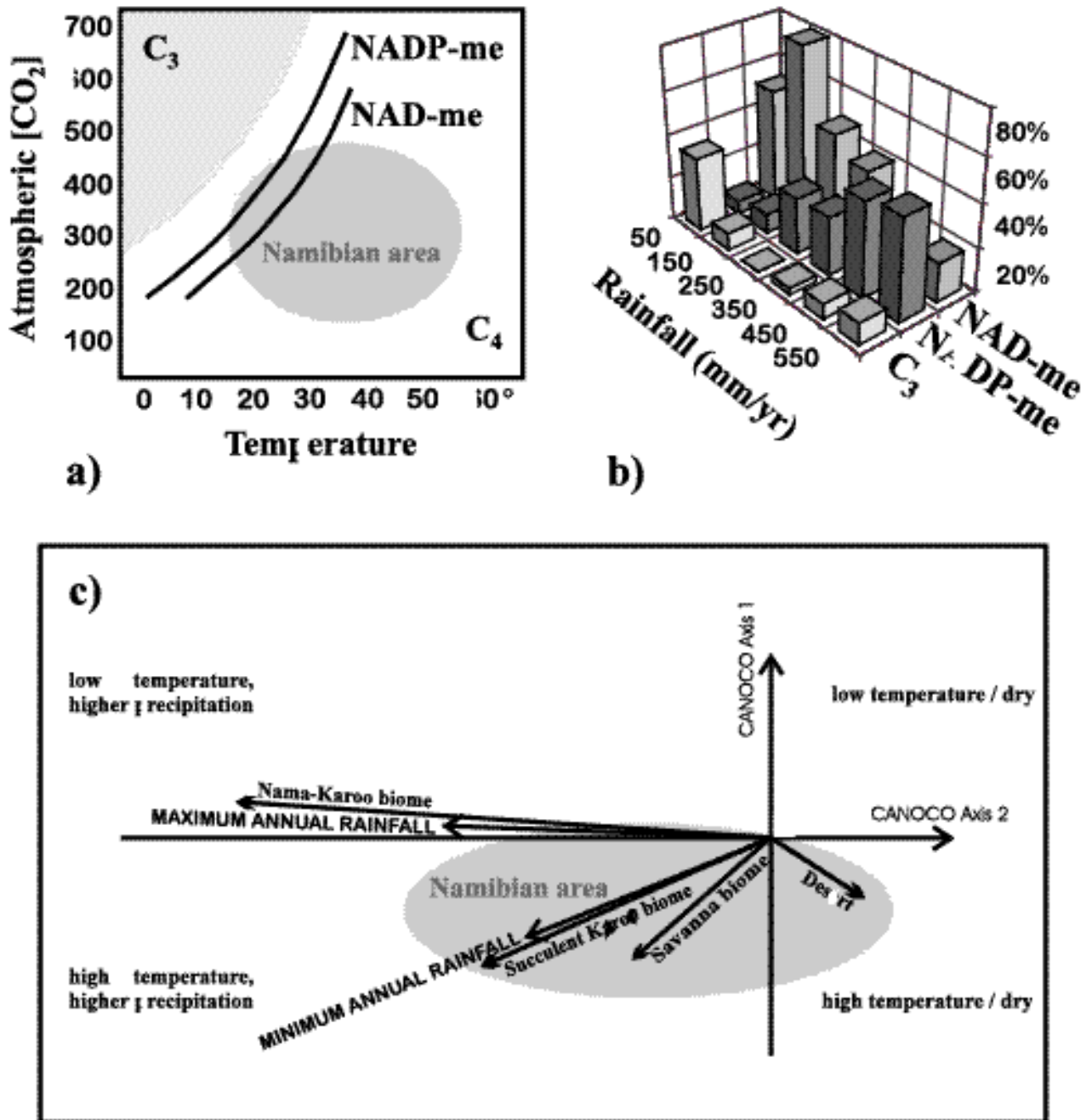
a)

b)

c)

Fig. 3. *a)*. Crossover daytime temperatures during the growing-season of the correspondent CO_2-uptake quantum yield as a function of atmospheric CO_2 (concentration in ppmv). Changes in the CO_2-uptake quantum yield mainly due to photorespiration; average temperature in Celsius degrees of the different CO_2-uptakes equivalent for both the C_3 and C_4 monocots (modified from Ehleringer *et al.* 1997). Estimated (palaeo) climatic boundaries of the study area given by the shaded area (cf. Müller 1982; Lioubimtseva *et al.* 1998). *b)*. Relationships between the annual precipitation and the share of metabolic types of the Namibian grass species [%C_3 + %C_4 PCK + %C_4 NAD-me + %C_4 NADP-me = 100 %]. Specimens were collected from the Okavango, throughout Caprivi and Etosha, up to the littoral. Please see the text for further explanations. *c)*. Environmental co-ordinates for a CANOCO t-value biplot (no transformation). The vertical Axis 1 corresponds to a temperature diminishing during the wet season. The horizontal Axis 2 corresponds to a fall in precipitation, reflecting the gradient of plant moisture availability (with the moist biomes on the left of the CCA). Estimated vegetation boundaries of the study area given by the shaded area. The superimposed length of the arrows representing each environmental variable (vegetation biome and rainfall) indicates the direction to which the variability of grass species (magnitude of change) increases more rapidly. The longer arrows (maximal rainfall and Nama-Karoo) are more closely related to the ordinates since they indicate a gradual magnitude of spatial change, while the short arrow (Desert) represents abrupt spatial changes. The rate of change is bidimensional (spatial patterns), as no time factor was taken into account.

The zonal distribution of the C_4 grasses, and the relative abundance of their phytoliths, reflect at the regional scale the water stress variation of the plant community. Aridification trends in southern Africa can be inferred at the biome-scale from C_4 grass phytoliths (especially in the karroid vegetation assemblages). The use of this tool after additional investigations will help us in the future to integrate the marine records offshore Namibia.

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Appendix. Percentage of variance of objects (phytoliths) accounted for by each component (grass species). Autecological intraset of *δ¹³C (Schulze *et al.* 1996), minimum and maximum annual rainfall (according to Müller 1982), tribe (according to Watson and Dallwitz, 1994), and leaf transectional anatomy (types in Ellis 1988). Reference vouchers from the herbaria of J and PRE. Statistical significant values are marked in **bold**, and the relevant species (highest or lowest scores) in *CAPITALS*.

Reference Vouchers		Min. mm/yr	Max. mm/yr	δ^{13}C	First Perc. Var.	Second Perc. Var.	Third Perc. Var.	Mean	First Comp.	Second Comp.	Third Comp.	Phytochem
Andropogon eucomus Ellery 53904, J; Ellis 1357, PRE	A N	400	600	-11.55	81.646	14.925	3.429	600	0.684	0.292	-0.140	NADP-me
Andropogon schirensis Ellis 970, PRE	A N	400	600	-11.41	79.422	17.046	3.532	600	0.694	0.322	-0.146	NADP-me
Aristida congesta Dye 60148, J	A R	200	500	-12.91	62.163	35.236	2.601	400	-1.065	0.802	-0.218	NADP-me
Aristida stipoides Smith 1954, PRE; s.n. 1, J	A R	500	600	-12.49	78.406	1.385	20.21	600	1.027	-0.137	-0.522	NADP-me
Brachiaria deflexa Smook 1138, PRE	P A	200	500	-13.98	90.778	8.262	0.960	300	-1.216	0.367	-0.125	PCK
Brachiaria humidicola Ellery 57600, J; Ellis 343, PRE	P A	400	600	-11.69	83.878	12.808	3.314	600	0.674	0.263	-0.134	PCK
Cenchrus ciliaris Balkwill 85016, J; Ellis 4603, PRE	P A	100	600	-12.26	14.925	29.465	55.610	500	-0.601	0.845	1.161	NADP-me
Chloris gayana Ellery 331, J; Ellis 3746, PRE	C H	500	600	-11.58	78.951	0.184	20.864	600	1.093	0.053	-0.562	PCK
Cymbopogon excavatus Ellis 99, PRE; Maguire 67135, J	A N	300	600	-11.70	17.266	61.613	21.122	600	0.262	0.495	0.290	NADP-me
Cynodon dactylon Dye 20, J; Ellis 332, PRE	C H	100	600	-15.60	29.049	0.919	70.032	450	-0.843	0.150	1.309	NAD-me
Dactyloctenium giganteum Baines&Parry 74962, J; Ellis 3847, PRE	C H	500	600	-11.63	79.024	0.120	20.857	600	1.090	0.042	-0.560	PCK
Digitaria brazzae Ellis 1338, PRE	P A	500	600	-10.41	74.910	4.739	20.351	600	1.178	0.296	-0.614	NADP-me
Digitaria debilis Dye 9, J; Ellis 1545, PRE	P A	400	600	-11.35	78.476	17.951	3.574	600	0.698	0.334	-0.149	NADP-me
Digitaria eylesii Ellis 2081, PRE	P A	500	600	-10.21	73.902	5.934	20.163	600	1.192	0.338	-0.623	NADP-me
Digitaria milanjiana Voster 2779, PRE	P A	400	600	-11.25	76.914	19.448	3.638	600	0.706	0.355	-0.153	NADP-me
Echinochloa colona Ellis 2908, PRE	P A	300	600	-12.58	16.068	39.720	44.212	600	0.198	0.312	0.329	NADP-me
Echinochloa crus-galli Smook 5871, PRE	P A	400	600	-11.08	74.312	21.950	3.738	600	0.718	0.390	-0.161	NADP-me
Echinochloa pyramidalis Ellery 54479, J; Ellis 1892, PRE	P A	300	600	-13.41	11.086	11.211	77.703	600	0.138	0.139	0.366	NADP-me
Echinochloa stagnina Cohen 23353, J; Jacobsen 2978, PRE	P A	300	600	-10.63	16.727	74.756	8.517	600	0.339	0.717	0.242	NADP-me
Enteropogon macrostachyus Bainer&Parry 75022, J; Ellis 2078, PRE	C H	400	600	-13.60	93.364	5.850	0.786	600	0.536	-0.134	-0.049	NAD-me
Eragrostis aspera Killick 1714, PRE	C H	300	500	-12.41	44.599	19.766	35.635	400	-0.691	0.460	-0.618	NAD-me
Eragrostis cilianensis Ellery 58261, J; Ellis 888, PRE	C H	100	500	-14.32	87.822	9.023	3.156	400	-1.652	0.530	0.313	NAD-me
Eragrostis echinochloidea De Winter&Wiss 4427, Retief 1530, PRE	C H	100	600	-12.61	16.553	25.126	58.321	300	-0.627	0.772	1.176	NAD-me
Eragrostis lappula Ellis 2014, PRE; Henning 77512, J	C H	500	600	-12.65	77.853	2.176	19.972	600	1.016	-0.170	-0.514	PCK
Eragrostis pilosa Smook 1765, PRE	C H	500	600	-15.04	53.725	33.662	12.613	600	0.843	-0.667	-0.408	NAD-me

Appendix. Percentage of variance of objects (phytoliths) accounted for by each component (grass species). Autecological intraset of *^{13}C (Schulze *et al.* 1996), minimum and maximum annual rainfall (according to Müller 1982), tribe (according to Watson and Dallwitz, 1994), and leaf transectional anatomy (types in Ellis 1988). Reference vouchers from the herbaria of J and PRE. Statistical significant values are marked in **bold**, and the relevant species (highest or lowest scores) in *CAPITALS*. *(Continued)*

Reference Vouchers		Min. mm/yr	Max. mm/yr	δ^{13}C	First Perc. Var.	Second Perc. Var.	Third Perc. Var.	Mean	First Comp.	Second Comp.	Third Comp.	Phytochem
Eragrostis porosa De Winter&Codd 284, PRE	C H	100	500	-12.64	73.844	24.362	1.794	400	-1.531	0.879	0.239	NAD-me
Eragrostis superba Ellery 52841, J	C H	300	600	-12.47	16.392	43.154	40.455	600	0.206	0.334	0.324	NAD-me
Eragrostis viscosa Ellis 530, PRE; Witkowski s.n., J	C H	300	600	-13.94	6.132	0.504	93.364	500	0.100	0.029	0.389	NAD-me
ERAGROSTIS WALTERI Ellis 4344, 4346, PRE; Giess 8104, PRE	C H	50	200	-26.71	84.258	7.163	8.579	100	-5.460	-1.592	-1.742	n-K
Eriochrysis pallida Killick 251,PRE	P A	400	400	-11.84	23.507	3.803	72.691	400	-1.140	0.459	-2.005	NADP-me
Heteropogon contortus Ellery&Ellery 78945, J; Ellis 52, PRE	A N	200	600	-12.10	3.245	42.372	54.383	600	-0.178	0.645	0.730	NADP-me
Hyparrhenia filipendula Codd 6880, PRE	A N	500	600	-12.00	79.214	0.084	20.703	600	1.063	-0.035	-0.543	NADP-me
Hyparrhenia hirta Ellis 4772, PRE	A N	100	600	-13.03	18.542	20.134	61.323	500	-0.657	0.685	1.195	NADP-me
Hyparrhenia rufa Ellis 3715, PRE; Williamson&Payet 84896, J	A N	600	600	-11.18	69.846	0.281	29.873	600	1.533	-0.097	-1.003	NADP-me
Hyperthelia dissoluta Ellis 340, PRE	A N	500	600	-11.44	78.695	0.434	20.871	600	1.103	0.082	-0.568	NADP-me
Imperata cylindrica Ellis 320, PRE; Henning 321, J	A N	300	600	-12.19	16.947	50.993	32.06	600	0.226	0.393	0.311	NADP-me
LEERSIA HEXANDRA Ellery 269, J; Ellis 3713, PRE	B A	500	600	-26.44	0.003	99.893	0.104	500	0.018	-3.039	0.098	n-K
Miscanthus junceus Ellery 54480, J; Ellis 317, PRE	A N	400	600	-12.76	97.498	0.454	2.048	600	0.596	0.041	-0.086	NADP-me
ORYZA LONGISTAMINATA Ellery 300, J; Ellis 3677, PRE	B A	500	600	-26.17	0.015	99.902	0.083	600	0.037	-2.983	0.086	n-K
Panicum maximum Ellery 257, J; Ellis 3850, PRE	P A	300	600	-12.83	15.063	31.294	53.643	600	0.180	0.260	0.340	PCK
Panicum repens Ellery 53905, J; Smook 4211, PRE	P A	300	600	-12.50	16.310	42.236	41.454	600	0.204	0.328	0.325	PCK
Paspalidium geminatum Giess 3132, PRE	P A	200	600	-12.68	5.427	30.686	63.887	600	-0.220	0.524	0.756	NADP-me
Paspalum scrobiculatum Smook 1006, PRE	P A	300	600	-12.31	16.751	47.796	35.453	600	0.218	0.368	0.317	NADP-me
PASPALUM VAGINATUM Ellis 276, PRE	P A	100	300	-12.82	74.656	7.605	17.739	100	-3.347	1.068	-1.631	NADP-me
Pennisetum glaucocladum Ellis 2922, PRE; Maguire 75405, J	P A	500	600	-10.94	77.215	2.057	20.728	600	1.139	0.186	-0.590	NADP-me
Perotis patens Balkwill 80940, J; Ellis 1926, PRE	C H	400	600	-13.03	98.292	0.071	1.637	600	0.577	-0.015	-0.074	NAD-me
PHRAGMITES AUSTRALIS Ellis 187, PRE; Maguire 68446, J	A R	100	600	-25.62	26.506	40.342	33.152	600	-1.568	-1.935	1.754	n-K
Pogonarthria squarrosa Baines&Parry 75285, J; Ellis 2089, PRE	C H	300	600	-13.04	13.892	23.811	62.298	600	0.165	0.216	0.349	NAD-me
SACCIOLEPIS AFRICANA De Winter&Marais 4528, PRE	P A	400	600	-26.92	2.058	94.644	3.297	600	-0.428	-2.905	0.542	n-K
SACCIOLEPIS HUILLENSIS Johnstone 356, PRE	P A	400	600	-27.71	2.360	94.304	3.336	600	-0.486	-3.070	0.577	n-K

Appendix. Percentage of variance of objects (phytoliths) accounted for by each component (grass species). Autecological intraset of $*^{13}$C (Schulze *et al.* 1996), minimum and maximum annual rainfall (according to Müller 1982), tribe (according to Watson and Dallwitz, 1994), and leaf transectional anatomy (types in Ellis 1988). Reference vouchers from the herbaria of J and PRE. Statistical significant values are marked in **bold**, and the relevant species (highest or lowest scores) in *CAPITALS*. *(Continued)*

Reference Vouchers		Min. mm/yr	Max. mm/yr	δ^{13}C	First Perc. Var.	Second Perc. Var.	Third Perc. Var.	Mean	First Comp.	Second Comp.	Third Comp.	Phytochem
SACCIOLEPIS TYPHURA Ellery 58278, J; Ellis 1527, PRE	P A	500	600	-26.08	0.022	99.902	0.076	600	0.044	-2.964	0.082	n-K
Schmidtia pappophoroides Dye 12, J; Ellis 929, PRE	C H	100	600	-12.57	16.365	25.616	58.019	500	-0.624	0.780	1.174	PCK
Setaria sagittifolia Ellery 241, J; Ellis 2085, PRE	P A	400	600	-12.07	89.761	7.294	2.945	600	0.646	0.184	-0.117	NADP-me
Setaria sphacelata Ellery 312, J; Ellis 329, PRE	P A	500	600	-11.92	79.227	0.022	20.751	600	1.069	-0.018	-0.547	NADP-me
SETARIA VERTICILLATA Ellery 58288, J; Ellis 764, PRE	P A	100	600	-11.63	12.137	37.435	50.427	500	-0.556	0.976	1.133	NADP-me
SORGHASTRUM FRIESII Ellery 334, J; Ellis 3695, PRE	A N	600	600	-12.54	66.597	4.677	28.726	600	1.435	-0.380	-0.942	NADP-me
SPOROBOLUS AFRICANUS Smook 5456, PRE	C H	600	600	-13.05	64.355	7.790	27.855	600	1.398	-0.486	-0.920	PCK
Sporobolus fimbriatus Dye 19, J; Ellis 4074, PRE	C H	300	600	-13.35	11.599	13.096	75.304	600	0.142	0.151	0.363	PCK
Sporobolus ioclados De Winter&Codd 340, PRE; Traill 61140, J	C H	200	600	-13.23	8.013	19.863	72.124	500	-0.260	0.410	0.781	NAD-me
Sporobolus pyramidalis Smook 5043, PRE	C H	300	600	-11.78	17.254	60.128	22.618	600	0.256	0.478	0.293	PCK
Sporobolus spicatus Ellery 244, J; Ellis 3706, PRE	C H	200	600	-13.15	7.612	21.373	71.015	600	-0.254	0.426	0.777	NAD-me
STIPAGROSTIS CILIATA Maguire 74002, J	A R	50	300	-13.54	81.254	6.700	12.046	300	-3.605	1.035	-1.388	NAD-me
Themeda triandra Ellis 295, 371, 2023, PRE	A N	300	600	-11.59	17.263	63.513	19.225	600	0.270	0.518	0.285	NADP-me
Trachypogon spicatus Ellery 58304, J; Ellis 143, PRE	A N	500	600	-13.15	75.149	5.873	18.978	600	0.980	-0.274	-0.492	NADP-me
Tragus berteronianus Ellery 243, J; Ellis 2021, PRE	C H	100	500	-15.07	91.816	4.399	3.785	500	-1.706	0.374	0.346	NAD-me
Tragus racemosus Smook 2774, PRE	C H	200	600	-12.32	3.999	37.988	58.013	500	-0.194	0.599	0.740	NAD-me
Vetiveria nigritana Davidson 41756, J; Ellis 342, PRE	A N	400	600	-12.14	90.777	6.356	2.867	600	0.641	0.170	-0.114	NADP-me
VOSSIA CUSPIDATA Ellis 3708, PRE; Henning 77475, J	A N	600	600	-10.56	70.097	0.028	29.875	600	1.578	0.032	-1.030	NADP-me