

Occurrence of C-4 plants in the Central Namib Desert

by

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ABSTRACT

A survey of the carbon isotope composition ($^{13}\text{C}/^{12}\text{C}$) of plants in the Central Namib Desert has been undertaken to ascertain the significance of the C-4 photosynthetic pathway to the desert flora. Using this criterion it is found that all the grasses and some sedges are of the C-4 type, while the majority of the other species are C-3. Of the latter group *Trianthema*, *Salsola*, *Gisekia* and *Blepharis* show the high ^{13}C -content characteristic of "Kranz" or strong CAM plants. The C-4 pathway is thus an efficient, but by no means an obligatory adaptive condition for survival in a hot desert environment.

1 INTRODUCTION

The 4-carbon (C-4) or Hatch-Slack mode of photosynthesis is an evolutionary adaptation to hot dry climates. This is evidenced in the fact that C-4 plants have the ability to photosynthesize at high temperatures and a high degree of water-use efficiency. They are thus, in general, more drought tolerant than plants that utilize the more widespread 3-carbon or Calvin cycle of CO_2 fixation (cf. Björkman & Berry, 1973). Several hundred C-4 species belonging to at least thirteen different families of the *Angiosperms* have been identified to date (Downton, 1975). They all exhibit the Kranz syndrome, i.e. their vascular bundles are surrounded by a sheath ('Kranz') of cells containing large specialized chloroplasts in which 4-carbon molecules such as malic and aspartic acid, initially formed in the mesophyll cells, are decarboxylated and the resulting CO_2 converted to sugars and starch via the normal Calvin cycle. The syndrome is especially common in the grass family, but is also present among the *Cyperaceae*, *Chenopodiaceae*, *Aizoaceae*, *Amaranthaceae* and others.

In addition to these 'Kranz' plants many succulents which exhibit the Crassulacean acid metabolism (CAM) also utilize the C-4 pathway, but they do this by night (Nuerenbergk, 1961; Sutton & Osmond, 1972). Malic acid is stored until the following day when it is decarboxylated, providing CO_2 for photosynthetic carbon reduction. The plants therefore can keep their stomata closed during the hot dry daytime and so minimize water loss. CAM thus also represents an adaptation for some species occupying a xerophytic niche (Neales *et al.*, 1968).

2 METHODOLOGY

In view of the obvious significance of the C-4 photosynthetic pathway for the ecology of arid zones, a survey has been made of the C-4 status of plants in the different ecosystems of the Namib desert. This represents a first attempt to evaluate the significance of the C-4 physiological process for the biomass of a region. A convenient means of doing this is to measure the $^{13}\text{C}/^{12}\text{C}$ ratios in the plants. 'Kranz' and C-3 plants show different degrees of isotope fractionation during the assimilation of CO_2 from the air (Bender, 1971; Smith & Epstein, 1971). As a result the relative ^{13}C con-

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tent, δ^{13} , of the former ranges from -10 to -16‰ (parts per thousand deviation from PDB standard carbon) while that of the latter group lies between -22 and -32‰ . Thus both modes of photosynthesis produce a slight depletion in the heavy ^{13}C isotope as compared with atmospheric CO_2 ($\delta^{13} = -7\text{‰}$) but ranges do not overlap.

CAM plants, on the other hand, reveal δ^{13} -values over the whole range from -10‰ to -26‰ (Osmond *et al.*, 1973), depending on the ratio of nocturnal C-4-type assimilation to direct daily C-3 photosynthesis. This ratio is partially controlled by environmental conditions, notably by water stress, but it appears that the tendency to utilize CAM differs between species. While some species can be induced to revert to the CAM mode only with difficulty and thus show δ^{13} -values in the C-3 range when growing in their natural habitat, others mainly assimilate CO_2 at night even under favourable conditions and always have δ^{13} -values in the C-4 range (Vogel, unpubl.). Isotope ratio measurements can thus only distinguish plants with an appreciable tendency to CAM from C-3 plants and not ones that are merely capable of CAM. ^{13}C analyses have the advantage that small dried samples can be used and it is not necessary to have physiologically active material to hand.

3 RESULTS AND DISCUSSION

The survey thus far has been confined mainly to the coastal tract in the vicinity of Sandwich Harbour (fog desert) and the sand desert further inland. The gravel plains north of the Kuiseb river and the Inselberge protruding from them harbour a much larger variety of species, the analysis of which is still under way. All three of these regions represent extremely arid habitats.

Rainfall along the coast amounts to less than 15 mm a year on average. An additional 40 mm of (saline) moisture is derived from the frequent early-morning fogs that are caused by advection from the adjacent cold sea (Goudie, 1972). In this adverse environment the limited plant communities are mainly restricted to such places where groundwater surfaces from below the desert floor. Inland from the coast average maximum temperatures rise rapidly from 19°C to 30°C while the precipitation increases only gradually to reach 100 mm annually on the inner margin of the desert. The very sparse vegetation in the sand desert and on the gravel plains is subject to extreme heat, high light intensities and long periods of aridity between the episodic showers. These conditions are somewhat tempered by the advective fogs which extend to the inner edge of the Namib several times each year and occur more frequently towards the coast (70 to 100 days per year 50 km inland).

Practically all the species occurring in the sand desert and along the coast are listed in Table 1 together with their relative δ^{13} contents. Some of the more common plants on the gravel plains are also included. The results show that all the grasses

are of the C-4 type. In fact, of the 56 grass species listed for the entire region, including the inner desert margin, only three are 'Nonkranz' — two *Phragmites* and one *Polypogon* species, which are restricted to the river beds. This is in contrast to the findings for the coastal desert south of the Orange River where 95% of the grass species are 'Nonkranz' (Vogel *et al.*, 1977). Of the three sedges found on the coast one is Kranz and two 'Nonkranz'. Six of the seven other sedges on the regional check list are also Kranz so that, here too, the Kranz types predominate.

Most of the other plants in Table 1 are of the C-3 type. The only exceptions are the two species of *Trianthema* and those of *Salsola*, *Gisekia* and *Blepharis*. Microscopic examination of the small succulent leaves of *T. hereroensis* showed no sign of a bundle sheath so that it must be a strong utilizer of CAM. The other species referred to with high ^{13}C contents (-11 to -15‰) may either be CAM or 'Kranz' plants. It would be necessary to obtain fresh material of these plants to distinguish between the two possibilities. Two further samples, viz. *Mesembreanthemum querichianum* and *Welwitschia mirabilis* fall just outside the range for C-3 plants and are therefore probably weak utilizers of CAM in their natural habitat. In fact, *Welwitschia* has been reported to possess the necessary enzymes for CAM and to assimilate carbon dioxide at night (Dittrich & Huber, 1974). On the other hand experiments conducted by one of us (JSV) on a fresh leaf showed no nocturnal carbon dioxide fixation. Assimilation only took place in the early morning and late afternoon, in accordance with the findings of Bornman (1972). These observations together with the relatively low ^{13}C content of specimens collected in the Namib desert suggest that, although the species is capable of CAM, it predominantly utilizes the Calvin mode of photosynthesis in its natural environment.

The rest of the plants listed in Table 1 are classified as C-3 species on the basis of their low δ^{13} values. It cannot be excluded that some of them are also capable of exhibiting CAM, but this is clearly not their normal mode of photosynthesis. We observe that only ten (four genera) of the nearly fifty dicots thus far investigated from the Central Namib desert (20%) have adapted one of the two C-4 modes of carbon dioxide fixation.

4 CONCLUSIONS

The surprisingly low frequency of C-4 species encountered in this survey as well as the fact that several of the C-3 species are endemic to the Namib desert, suggest that the C-4 pathway may constitute an effectual but not an obligatory adaptive condition for survival in a hot desert environment. During prolonged isolation the endemic species have evolved satisfactory mechanisms of withstanding the dry heat of their habitat without converting to C-4. The high frequency of C-4 grasses, on the other hand, merely reflects the general situation in the interior of Southern Africa (Vogel *et al.*, 1977) and is not specific to the Namib desert.

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Table 1. Flora of the Central Namib Desert

A: Dune fields south of the Kuiseb River

Family ¹	Species ²	Collector Specimen No. ³	Locality	Sa No M-	Anal. MC-	$\delta^{13}\text{C}$ ‰
26. Molluginaceae	Limeum fenestratum	Seely & Vogel	NW of Tsondab	608	850	-22,6
	do.	Ward 166	Natab, W of Gobabeb	699	984	-23,5
	do.	Ward 213	12 km E of Tsondab	689	995	-23,9
27. Aizoaceae	*Trianthema hereroensis	Giess 9841	16 km S of Gobabeb	616	879	-14,5
	do.	Seely & Vogel	NW of Tsondab	605	853	-12,5
	T. triquetra var. parvifolia	Jensen 276	S of Gobabeb	618	878	-11,7
47. Capparaceae	Cleome paxii	Ward 214	12 1/2 km E of Tsondab	688	985	-24,2
64. Geraniaceae	*Monsonia ignorata	Seely & Vogel	NW of Tsondab	607	857	-24,5
84. Sterculiaceae	Hermannia minimifolia	Ward 210	10 km E of Tsondab	691	993	-25,6
115. Rubiaceae	*Kohautia ramosissima	Seely & Vogel	NW of Tsondab	604	852	-23,4
	do.	Ward 211	10 km E of Tsondab	690	994	-21,8
131. Pedaliaceae	*Sesamum abbreviatum	Seely & Vogel	NW of Tsondab	609	859	-25,0
139. Asteraceae	Helichrysum fleckii	Ward 216	6 km S of Hudaob	687	983	-27,3
147. Liliaceae	Hexacyrtis dickiana	Seely & Vogel	NW of Tsondab	606	856	-24,0
	do.	Strey 2590	S of Hudaob	611	874	-26,6
160. Gramineae	Asthenatherum glaucum	Seely & Vogel	near Tsondab	602	854	-12,8
	do.	Ward 161	Natab, W of Gobabeb	686	981	-15,1
	Eragrostis spinosa	Seely & Vogel	near Tsondab	599	847	-14,9
	Stipagrostis ciliata	do.	do.	601	851	-13,4
	*S. gonatostachys	do.	NW of Tsondab	596	846	-13,1
	*S. lutescens	do.	do.	598	844	-14,1
	S. namaquensis	do.	near Tsondab	600	848	-13,6
	*S. sabulicola	do.	NW of Tsondab	597	845	-13,2

B: Coastal Area

Family ¹	Species ²	Collector Specimen No. ³	Locality	Sa No M-	Anal. MC-	$\delta^{13}\text{C}$ ‰
32. Chenopodiaceae	Arthrocnemum affine	Ward 197	Sandwich harbour	695	987	-26,4
	Salsola nollothensis	Ward 203	10 km N of Sandwich ha.	693	989	-12,8
47. Capparaceae	*Capparis hereroensis	Ward 202	10 km N of Sandwich ha.	694	988	-26,2
119. Heliotropiaceae	Heliotropium curassavicum	Ward 195	Sandwich harbour	696	986	-24,6
124. Solanaceae	Lycium tetrandrum	Ward 193	4 km S of Sandwich ha.	698	1007	-24,1
160. Gramineae	Dactyloctenium aegyptium	Vogel	Spencer Bay N	654		-14,4
	Eragrostis cyperoides	Vogel	Spencer Bay N	674	628	-13,1
	do.	Ward 190	9 1/2 km S of Sandwich ha.	692	991	-12,7
	Sporobolus virginicus	Ward 194	Sandwich harbour	697	997	-13,2
165. Cyperaceae	Juncellus laevigatus	Rodin 2147	near Swakop ri.	628	906	-10,6
	Scirpus dioicus	De Winter 3442	Aroab, dunes	619	896	-22,4
	S. littoralis	Giess 3872	Kaokoveld	620	897	-23,5

C: Plains North of the Kuiseb river and the Inselberge

Family ¹	Species	Collector Specimen No. ³	Locality	Sa No M-	Anal. MC-	$\delta^{13}\text{C}$ ‰
13. Welwitschiaceae	Welwitschia mirabilis	Bornman	Central Namib	C406	—	-19,9
	do.	Herre	near Swakopmund	C647	695	-22,4
25. Nyctaginaceae	Commicarpus squarrosus	Jensen 32	Arechadamab hills	764	1098	-24,5
26. Molluginaceae	Gisekia africana	Jensen 72	Hotsas hills	758	1108	-11,9
	G. pharnaceiodes	Tälken & Hardey 845	Outjo	753	1114	-12,1
	Limeum argute-coronatum	Jensen 138	near Ganab	754	1112	-24,8
27. Aizoaceae	Aizoanthemum dinteri	Ihlenfeldt & de Winter 3249	Twyfelfontein	755	1111	-22,9
	Galenia africana	Jensen	Hamilton range	756	1110	-25,9
	Mesembryanthemum guericchianum	Merxmüller & Giess 28713	Lüderitz-Süd	757	1109	-20,1
	Trianthema triquetra	Jensen 130	near Ganab	613	880	-12,2
32. Chenopodiaceae	Salsola aphylla	Jensen 9	W of Welwitschia	760	1105	-13,9
	S. tuberculata	de Winter & Giess 6223	Lüderitz	759	1107	-13,0
33. Amaranthaceae	Arthraerua leubnitziae	Jensen 46	Swartbank	752	1097	-24,4
	Calicorema capitata	Jensen 340	Gobabeb	751	1096	-25,6
65. Zygophyllaceae	Zygophyllum stapfii	Vogel	S of Swartbank	749	1094	-25,1
84. Sterculiaceae	Hermannia elliotiana	Jensen 453	Onanis	788	1141	-24,6
	H. modesta	Ihlenfeldt, de Winter & Hardey 3223	30 km from Torra bay	790	1143	-27,8
94. Cucurbitaceae	Citrullus ecirrhosus	de Winter 3193	Swakop-Usakos road	786	1139	-26,1
105. Plumbaginaceae	Dyerophytum africanum	Jensen 50	Hope Mine	789	1142	-24,4
114. Asclepiadaceae	Asclepias buchenaviana	Koch A13	Swakopmund	787	1140	-22,1
120. Boraginaceae	Trichodesma africanum			783	1136	-24,3
126. Scrophulariaceae	Sutera maxii	Jensen 155	N of Gobabeb	782	1134	-24,1
130. Acanthaceae	Blepharis bossii	Ihlenfeldt 1932	Kleinnabib ri.	776	1127	-11,6
	B. obmitrata	Jensen 147	Namib Desert Park	780	1131	-12,9
	Monechma arenicola	Tälken & Hardey 867	Swakopmund	781	1132	-24,6
	M. desertorum	Jensen 180	Kriesserus	779	1130	-23,5
	Petalidium setosum	Kinges 2409	Lüderitz	775	1126	-24,1
	Ruellia diversifolia	Jensen 197	Ojab farm	778	1129	-25,8
131. Pedaliaceae	Rogeria longiflora	Ihlenfeldt 1780	5 km N of Vioolsdrif	777	1128	-23,0
139. Asteraceae	Gnaphalium luteoalbum	Res. Sta. Gobabeb 00068	Gobabeb	774	1125	-28,5
	Helichrysum roseo-niveum	Pearson	Welwitschia	768	1118	-26,5
	Osteospermum microcarpum ssp. septentrionale	Barnard 102	Omaruru	767	1116	-23,7
	Pechuel-Loeschea leubnitziae	Keets 1230	Swakopmund	773	1124	-22,3
160. Gramineae	Eragrostis porosa	Kinges 2136	Lüderitz	761	1102	-12,9
	Sporobolus robustus	Jensen 523	Hudaob	762	1101	-13,9
	Stipagrostis obtusa	Jensen 181	6 km S of Kriesserus	763	1099	-12,8
	Triraphis ramosissima	Giess 3002	near Usakos	650	926	-13,8

¹ The numbering of the families is according to Merxmüller: Prodrum einer Flora von Südwestafrika.² Endemic species are designated by an asterisk.³ The unnumbered samples were collected specifically for this investigation. In addition, J. D. Ward collected a number of specimens for us. These will be housed in the National Herbarium, Pretoria for possible future reference. The rest are samples taken from specimens in the National Herbarium.

In some cases the plants are not actually from the area under consideration, but only from the general region. In our experience the locality can only influence the isotopic composition insignificantly so that this procedure is acceptable. It has the advantage that the specimens are available to other investigators.