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Diversity, metabolic types and $\delta^{13}\text{C}$ carbon isotope ratios in the grass flora of Namibia in relation to growth form, precipitation and habitat conditions

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Abstract The grass flora of Namibia (374 species in 110 genera) shows surprisingly little variation in $\delta^{13}\text{C}$ values along a rainfall gradient (50–600 mm) and in different habitat conditions. However, there are significant differences in the $\delta^{13}\text{C}$ values between the metabolic types of the C4 photosynthetic pathway. NADP-ME-type C4 species exhibit the highest $\delta^{13}\text{C}$ values (–11.7 ‰) and occur mainly in regions with high rainfall. NAD-ME-type C4 species have significantly lower $\delta^{13}\text{C}$ values (–13.4 ‰) and dominate in the most arid part of the precipitation regime. PCK-type C4 species play an intermediate role (–12.5 ‰) and reach a maximum abundance in areas of intermediate precipitation. This pattern is also evident in genera containing species of different metabolic types. Within the same genus NAD species reach more negative $\delta^{13}\text{C}$ values than PCK species and $\delta^{13}\text{C}$ values decreased with rainfall. Also in *Aristida*, with NADP-ME-type photosynthesis, $\delta^{13}\text{C}$ values decreased from –11 ‰ in the inland region (600 mm precipitation) to –15 ‰ near the coast (150 mm precipitation), which is a change in discrimination which is otherwise associated by a change in metabolism. The exceptional C3 species *Eragrostis walteri* and *Panicum heterostachyum* are coastal species experiencing 50 mm precipitation only. Many of the rare species and monotypic genera grow in moist habitats rather than in the desert, and they are not different in their carbon isotope ratios from the more common flora. The role of species diversity with respect to habitat occupation and carbon metabolism is discussed.

Key words C4 photosynthesis · $\delta^{13}\text{C}$ values · Grass flora of Namibia · Poaceae · Geographic distribution

Introduction

Does the number of species make any difference to the functioning of an ecological system or a region? This is one of the key questions addressed by the Global Biodiversity Assessment of UNEP (Mooney 1995), but there are very few data to clarify this issue (Schulze and Mooney 1994). In this paper we use an apparently “simple” system, namely the Namib desert and its transition to subtropical grasslands and savannas, in order to investigate whether the unusual diversity of grasses in this region (374 species in 110 genera) has led to a broader occupation of habitats and if this is related to the carbon metabolism. The precipitation gradient in Namibia from about 50 mm of rain and fog at the coast to more than 600 mm inland, gives rise to the hypothesis that without differentiation into species exhibiting different physiology grasses would not have been able to adapt to these habitats. This would have left large areas as barren desert along this climatic gradient.

The grass flora of Namibia is dominated by C4 grasses, represented by different physiological types (Ellis 1977a; Watson and Dallwitz 1989), and it has been shown (Ellis et al. 1980) that an increasing rainfall is associated with an increasing contribution of the NADP-malic-enzyme (NADP-ME) type of C4 photosynthesis, while the contribution of the NAD-malic-enzyme (NAD-ME type) type decreases, and the phosphoenolpyruvate-carboxykinase (PCK) type shows a maximum contribution to the local grass flora at intermediate rainfall. Similar patterns were documented for South Africa (Vogel et al. 1978), North America (Teeri and Stowe 1976), and Australia (Hattersley 1983).

Despite knowledge about the general distribution of photosynthetic types, it remains unclear whether this change in physiology is associated with an ecological change in functioning, such as habitat occupation and

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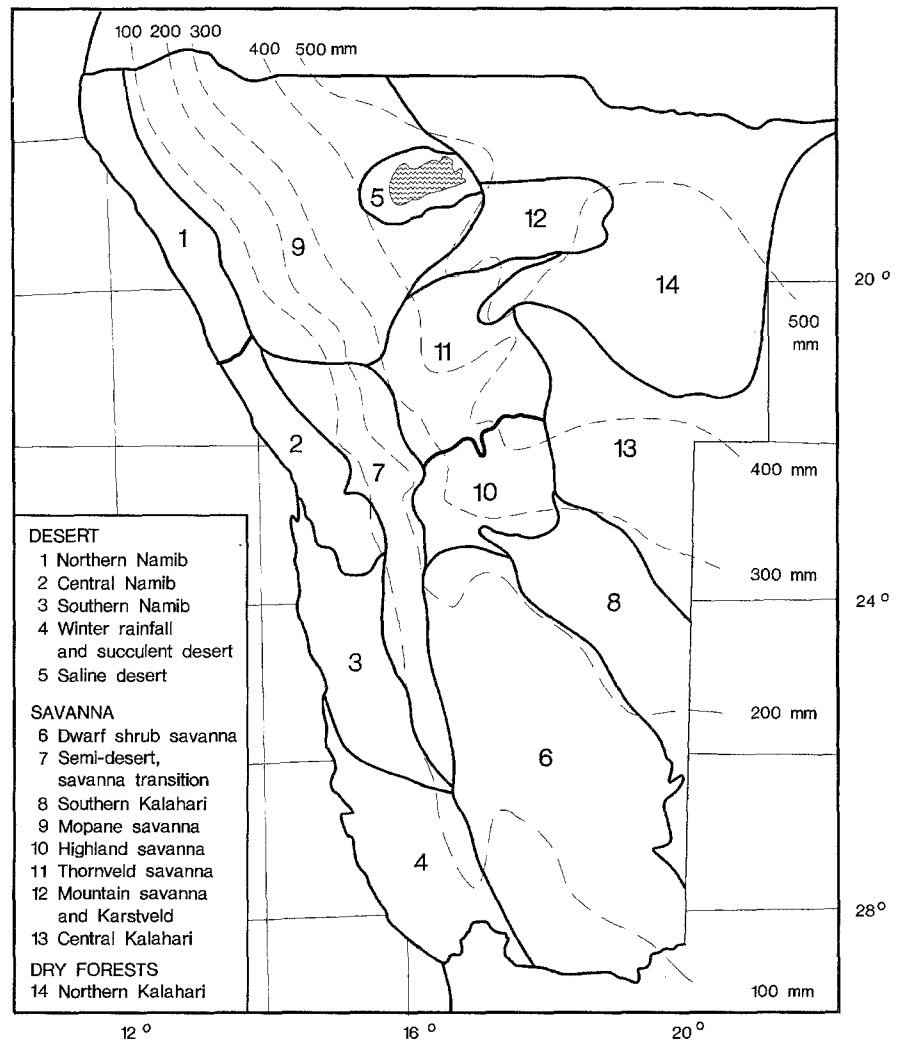
competition. We do not know to what extent differentiation of species is associated with a temporal or spatial replacement (Ehleringer and Monson 1993) of species exhibiting differences in carbon assimilation along a climatic gradient. A change in metabolic pathways may also act in maintaining assimilation and transpiration at a constant level even though environmental conditions change from the coast, which is dry with respect to rainfall but humid with respect to air humidity, to the interior of Namibia, which is moist with respect to seasonal rainfall but dry with respect to air humidity (Schulze and Schulze 1976).

The NADP type of C4 photosynthesis has the highest quantum yield (Ehleringer and Pearcy 1983) and structures of the bundle sheath which lead to the lowest rate of CO₂ leakage when compared to the NAD and PCK type (Farquhar 1983). Nevertheless it is unclear to what extent these differences become apparent in the carbon isotope ratios, the $\delta^{13}\text{C}$ values, which respond also to stomatal closure and environmental stress (Farquhar and Lloyd 1993). In contrast to C3 plants the $\delta^{13}\text{C}$ values of C4 subtypes result from a change of several factors, including (i) overcycling of the C4 pathway relative to RuBP carboxylation in the C3 pathway, (ii) incomplete

compartmentation of the C3 and C4 pathway between mesophyll and bundle sheath cells, and (iii) properties of the bundle sheath cell wall (e.g. by suberization). The net result of any of these factors is a back-diffusion of CO₂ from the bundle sheath to the intercellular spaces (leakiness) which results in a lower efficiency of CO₂ assimilation in NAD and PCK species as compared to the NADP type (Ehleringer and Pearcy 1983). Thus CO₂ leakiness overlays the relation between $\delta^{13}\text{C}$ values and stomatal conductance because it may change the $\delta^{13}\text{C}$ value without a change in conductance (Farquhar 1982). Leakiness may (Buchmann et al. 1995) or may not (Evans et al. 1986) change with stress. In addition, post-gas exchange effects on $\delta^{13}\text{C}$ values need to be considered (G. Farquhar, personal communication).

Based on these considerations, we (1) measure carbon isotope ratios and correlate these with species related traits (such as C4 type and growth form) and environmental parameters (such as precipitation and soil conditions) for all species of the Namibian grass flora, and (2) investigate the strategies of speciation and site occupation in different environments for selected genera that contain large or small numbers of species of contrasting physiotypes.

Fig. 1 Vegetation and rainfall map of Namibia (after Besler 1972; Müller 1985)



The Namib desert

The Namib desert is one of the most extreme deserts in the world (Fig. 1; Walter 1964). There is almost no rain and only fog at the coast with maximum daily summer temperatures of 19°C, the upper range of temperatures where C3 plants contribute to a mixed C3/C4 flora (Hattersley 1983), and where effects of minimum temperature (10°C at the coast) on C4 metabolism cannot be excluded (Ellis et al. 1980). Although total precipitation is low at the coast (about 50 mm), there is moisture available throughout the year due to fog precipitation and vapour pressure deficits are generally low (Walter 1964). Inland temperatures increase and reach about 30°C maximum summer temperatures about 50 km from the coast. In this region temperatures are well within the range reported by Hattersley (1982) for dominance of a C4 flora. Total precipitation initially decreases with distance from the coast to about 20 mm due to decreasing contribution of fog and very high vapour pressure deficits (Besler 1972). Adjoining this coastal desert, there is a fringe of subtropical semi-desert grassland (100–300 mm rainfall) which exhibits a seasonal climate with a distinct dry and wet season, and great variability in yearly rainfall. Years with no rain may alternate with relatively high precipitation. Rainfall progressively increases eastwards with elevation of the escarpment and vegetation changes into a savanna (300–600 mm rainfall) and a deciduous forest (>600 mm rainfall; Giess 1971; Ellis et al. 1980; Schulze et al. 1991). The increase in rainfall is associated with constant or decreasing summer temperatures at increasing elevation in the hinterland to almost 2000 m above sea level. At the same time, the inland climate is characterized by one or two distinct dry seasons. While the north of Namibia has a typical subtropical summer rainfall climate with bimodal rainfall distribution, the south extends into the winter rainfall region (Walter 1964).

Namibia is noted for its diverse flora, with numerous endemics in most plant families (Merxmüller 1970; Müller 1985). The grass flora is especially diverse containing 374 species in 110 genera in an area of about 800 000 km² (Gibbs Russell et al. 1990). There are only seven genera which contain more than 10 species, with *Eragrostis* containing 53 species, and with *Stipagrostis*, *Sporobolus* and *Panicum* containing between 20 and 25 species each. In contrast to these species-rich genera there are 58 genera with only one species present.

The anatomy of these grass species has been documented by Ellis (1977a,b, 1984a,b, 1988). The distribution of the different species in the floral regions of Namibia is documented in Merxmüller (1970), Ellis et al. (1980), and Müller (1985). The ecological requirements of most species has been studied for farm management purposes (Walter and Volk 1954; Volk 1974; Müller 1985). For rare species the information is still very limited. This study completes these data sets from our own observations and summarizes the diverse sources of information concerning the physiology and ecology of this unique grass flora (see Appendix).

Materials and methods

It is not possible to characterize each of the 374 grass species with respect to geographical variation of its carbon isotope $\delta^{13}\text{C}$ ratios in combination with local climatic and edaphic conditions. It is known that the $\delta^{13}\text{C}$ value may change within a species by about $\pm 2\text{‰}$ due to local growing conditions (Ehleringer et al. 1993). In contrast to studies which focus on few species, we analyse only one or a few $\delta^{13}\text{C}$ samples per species, and compare species with respect to growth form and typical distribution.

Grass samples were collected during an expedition to Namibia in 1975 (about 50% of the species, including multiple samples per species). Additional grass samples were taken from herbarium specimens from the "Bayerische Staatsherbar" in Munich and from the South African National Herbarium in Pretoria. The samples taken in the field and in the herbarium represent typical growth sites of the species in Namibia. Repeated samples taken for widely distributed common species from different locations exhibit a standard deviation of $\pm 0.63\text{‰}$ ($n = 15$ species with 2–7 samples per species). The absolute range of $\delta^{13}\text{C}$ per species was between -12.82‰ and -13.68‰ in *Stipagrostis uniplumis* ($n = 7$ habitats), -12.01‰ and -12.75‰ for *S. hirtigluma* ($n = 5$ habitats), and -11.88‰ and -14.43‰ for *Melinis repens* ($n = 5$ habitats). Since the main emphasis of the study is a comparison of species traits (annuals vs perennials), growth conditions (rainfall dependency, soil type), and successional stage (pioneer, late successional "climax" species) in most cases a single measurement per species was used. Thus, in this paper, each data point represents an individual species, and averages of $\delta^{13}\text{C}$ values refer to averages of $\delta^{13}\text{C}$ values found in different species.

Nomenclature of the grass species follows Gibbs Russell et al. (1990). Habitat conditions for each species were characterized from the literature (e.g. Merxmüller 1970; Ellis 1977; Ellis et al. 1980; Vogel et al. 1978; Müller 1985) and personal knowledge of the Namibian grass flora (R.P. Ellis). We distinguish the following criteria for the area of distribution of all species:

1. Minimum, maximum and common rainfall
2. Summer and winter rainfall
3. Rain dependence (dependent/independent i.e. growth only in wet or also in dry season)
4. Edaphic conditions (sand, clay, rock, moisture, salt)
5. Early, intermediate, and late successional species
6. The vegetation type
7. The growth form (annual, perennial)

The species were classified according to different physiological types of C4 photosynthesis following Ellis (1977a,b, 1984a,b, 1988) and Watson and Dallwitz (1989). The present classification is based on anatomical and physiological features (see Hattersley 1992). We distinguish between:

1. The NADP-malic enzyme physiology with a single Kranz type bundle sheath and no suberine lamella (referred to as NADP species).
2. The NADP-malic enzyme physiology in the genus *Aristida* (referred to as *Aristida* NADP), which exhibits a double layer of bundle sheath cells in contrast to other NADP species.
3. The NAD-malic enzyme physiology with a double bundle sheath (the outer being the Kranz) and centripetal arrangement of chloroplasts in Kranz sheath cells (referred to as NAD species), and a suberine lamella on the mestome sheath separating bundle sheath and vascular system.
4. The phosphoenolpyruvate carboxylase (PCK)-type physiology with a double bundle sheath, the outer Kranz with centrifugal arrangement of chloroplasts (referred to as PCK species), and two suberine lamellas on both sides of the bundle sheath and a mestome sheath separating the bundle sheath from the vascular system.
5. C3 physiology without Kranz anatomy.

It is known that the anatomical differentiation does not correlate with the physiological classification in all cases of NAD and PCK type species (Prendergast and Hattersley 1987; Prendergast et al. 1987). This was also true in this study in the genera *Chloris*, *Diandrichloa*, *Enneapogon*, *Eragrostis*, *Microchloa*, *Panicum*, and

Triraphis (see Appendix). Pendergast et al. (1986) report that in most of these cases the physiology follows the NAD type. For the large number of species investigated in this study these "exceptions" do not change the overall interpretation (see also Table 1). We will use our own anatomical observations in cases of discrepancies with Watson and Dallwitz (1989).

The carbon isotope ratios ($\delta^{13}\text{C}$ values relative to PDB standard) were determined according to Osmond et al. (1975) using a Heraeus CHN rapid elemental analyser coupled on-line to a trapping-box-gas-isotope-mass spectrometer system (Finnigan MAT Delta S). The error of determinations is $\pm 0.1\%$ external precision.

For data analysis the tabulation programme Excel and for statistical analyses (one-way ANOVA) SPSS statistical programs were used. A complete list of the primary data of isotope measurements, the photosynthetic types and the habitat conditions is summarized in the Appendix. In cases where repeated measurements were made for samples from different locations but using the same species, average values are listed in the Appendix.

Results

Comparisons based on the whole grasses flora

The different types of CO_2 fixation resulted in significant differences in the $\delta^{13}\text{C}$ values between C3 and C4 as well as within C4 species (Table 1). C3 plants exhibited about 14‰ lower $\delta^{13}\text{C}$ values than C4 species. The lowest C3 $\delta^{13}\text{C}$ value (-30.6%) was found in *Oplismenus burmanii*, a rain-dependent annual (Paniceae) growing in shade habitats in the 500 mm rainfall region, while the highest C3- $\delta^{13}\text{C}$ value (-23.3%) was found in *Ehrharta thunbergii*, a rain-dependent annual (Bambusoideae) growing on sand in the 50 mm rainfall region.

Within the C4 species the $\delta^{13}\text{C}$ values differed significantly ($P < 0.05$) between the different physiological types. The average $\delta^{13}\text{C}$ value was lowest (most negative) in NAD species. Within this group the lowest $\delta^{13}\text{C}$ value (-16.3%) was found in *Tripogon minimus*, a rain-

dependent perennial (Chloridoideae) growing on rocks at 100 mm rainfall, while the highest value (-11.2%) was observed for *Enteropogon prieurii*, a rain-dependent annual (Chloridoideae) growing in moist habitats at 600 mm rainfall.

The $\delta^{13}\text{C}$ values of NADP species were on average 1.6‰ higher than in NAD species. The lowest value (-13.9%) was found in *Bothriochloa radicans*, a rain-dependent late successional perennial (Andropogoneae) in the 500 mm rainfall region, while the highest $\delta^{13}\text{C}$ value (-10.0%) was found in *Digitaria eriantha*, a rain-dependent late successional perennial (Panicoideae) in the 400 mm rainfall region.

The $\delta^{13}\text{C}$ values of PCK species were intermediate between NAD- and the NADP-type photosynthesis. The lowest value (-14.6%) was found in *Chloris virgata*, a rain-dependent annual of disturbed habitats at high rainfall, while the highest value (-11.1%) was found in *Brachiaria dictyoneura*, a rain-dependent late successional perennial at high rainfall (Panicoideae).

Aristida forms a morphologically and anatomically distinct group within the NADP species (Clayton 1981; Watson and Dallwitz 1989), which exhibited $\delta^{13}\text{C}$ values that were on average 1.1‰ lower (more negative) than the "normal" NADP species. The $\delta^{13}\text{C}$ values of *Aristida* covered the whole range between the NAD and the NADP type with lowest values matching NAD species (-15.1%) in the rain-dependent annual *Aristida parvula* at 100 mm rainfall, and maximum values similar to "normal" NADP species (-11.0%) in *A. junciformis* a perennial of wet habitats at high rainfall.

The total number of grass species increased almost exponentially with rainfall ($r^2 0.77$, $a = 2.66$ for $y = e^{ax}$; Fig. 2A). The increase in species numbers with rainfall was mainly caused by an increase in grass genera, rather than species per genus (Ellis et al. 1980). For instance, the 61 rain-dependent NADP species, which were found at more than 400 mm rainfall, belonged to 43 genera. Species composition representing different anatomical types of C4 photosynthesis changed dramatically with precipitation (Ellis et al. 1980). C3 species occurred in the coastal winter rainfall area (40% of the coastal flora). They were absent in the 200 mm rainfall area of subtropical grasslands, and they contributed about 10% of the inland summer rainfall flora (Fig. 2B).

The NADP-type grasses, which reached the highest $\delta^{13}\text{C}$ values, were absent at the coast and very poorly represented in the very hot and dry grassland at 200 mm rainfall, but contributed up to 40% of the flora inland at higher rainfall. In contrast, the NAD-type species with the lowest $\delta^{13}\text{C}$ values contributed the largest fraction of the coastal grass flora and dominate in the extremely hot and dry subtropical grasslands of the desert fringe. The relative proportion of NAD species reached more than 60% of the flora between 200 and 300 mm rainfall. The absolute number of NAD species increased up to 450 mm rainfall, but decreased further inland when the NADP species reached a maximum (Fig. 2A). The PCK type was similar to the NADP type except that it contrib-

Table 1 Average values of $\delta^{13}\text{C}$ values ‰ PDB carbon discrimination, standard deviation (SD) and number of investigated species (n). The C4 types were classified according to anatomical and physiological criteria into NADP-, NAD- and PCK-type species with Kranz (K) anatomy of pyruvate species (PS) or malate species (MS) and C3 species. *Aristida* was treated separately because of its anatomy. Letters indicate significant differences ($P < 0.05$, t -test)

Photosynthesis type	$\delta^{13}\text{C}$ value	SD	n	maximum	minimum
C3 type	-26.6^a	1.7	40	-22.7	-30.6
C4 Anatomy					
K-PS-NAD	-13.4^b	0.9	130	-11.2	-16.3
K- <i>Aristida</i> -NADP	-12.8^c	0.9	16	-11.0	-15.1
K-PS-PCK	-12.5^c	0.8	81	-11.1	-14.6
K-MS-NADP	-11.7^d	0.9	104	-10.0	-13.9
C4 Physiology					
NAD-ME	-13.3^b	1.0	147	-11.2	-16.3
PCK	-12.5^c	0.8	60	-11.1	-14.6
NADP-ME	-11.8^d	1.0	119	-10.0	-13.9
Type unknown			3		
Total			374		

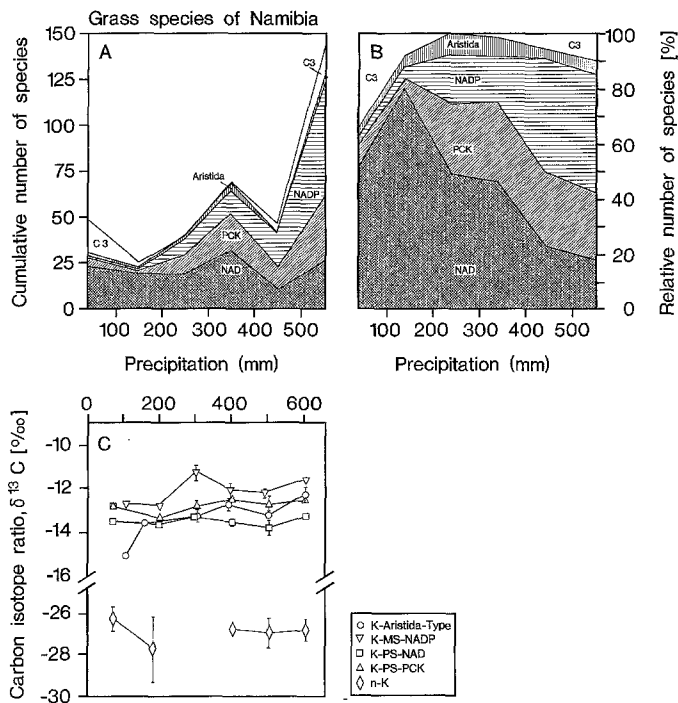


Fig. 2 **A** Cumulative number and **B** relative number of species of different metabolic types as related to precipitation. The total number of species at each level of precipitation is set as 100%. **C** Carbon isotope ratios, $\delta^{13}C$ values in ‰, as related to precipitation. (Vertical bars are standard errors)

uted a larger fraction of the coastal grass flora than the NADP type and the PCK type was also less diverse than the NADP type in the inland region. The distribution of physiological types was similar to the distribution of C4 grasses in Australia (Hattersley 1993; Henderson et al. 1994), except that the contribution of the NAD type was higher in the Namib, and the increase of NAD at low rainfall (50–200 mm rain) was not observed in Australia.

The average $\delta^{13}C$ values (Fig. 2C) within each physiological type showed only a minor trend of an increase with rainfall although the differences between physiological types were obvious. Only the NADP *Aristida* type showed a marked increase of $\delta^{13}C$ values with rainfall.

C3 species at the coast experience not only low precipitation but also lower temperatures and evaporative demand, and winter rainfall. The fraction of C3/C4 plants at the coast matched the fraction reported by Hattersley (1983) at 19°C. The increasing number of C3 species at high rainfall was due to weedy species on sites of disturbance by grazing, and due to species occupying wet and shady habitats.

The relative small response in $\delta^{13}C$ values for all three C4-types along such a broad range of precipitation might have resulted from averaging of different habitats and growth attributes. We therefore investigated the variation in $\delta^{13}C$ values along the rainfall gradient in greater detail by distinguishing between annual and perennial species. Effects of habitat conditions were also considered (Table 2).

About half of the C3 species occurred in the coastal desert (Table 2). There were slightly more annual than perennial C3 species, and more than half of the C3 species were rain independent (i.e. growing on wet sites), especially at higher precipitation. The largest number of the Namibian grasses are of the NAD type with annuals contributing to about 34% of the NAD-type flora; 25% of the NAD species were rain-independent. The PCK flora contribution contained more annuals (43% of total PCK species number), and a higher proportion which was rain-independent (40%). In contrast, in the NADP-type flora annuals contributed less than 30%, but also 40% of the NADP species were rain-independent. The difference in species number between NAD and NADP species (131 vs 103 species) was mainly due to 25 NAD species occurring only at less than 100 mm rainfall where NADP species failed.

In all physiological types no interaction of $\delta^{13}C$ values between rainfall and rain-dependence was found. All rain-independent annuals and perennials grew in moist or wet habitats, explaining their insensitivity to rainfall. However, the rain-dependent annuals also did not show a response in $\delta^{13}C$ values to rainfall except for rain-dependent C3 species which had slightly ($P = 0.07$ for annuals) or significantly ($P = 0.01$ for perennials) higher $\delta^{13}C$ values than rain-independent species (+0.64 ‰). In PCK species an interaction between rainfall and growth form was also significant ($P = 0.04$) with lower $\delta^{13}C$ values in rain-dependent annuals at high rainfall. In general, the rain-dependent annuals grew in sheltered or disturbed habitats or on sand whenever moisture was available. This may explain a lack of significant differences of $\delta^{13}C$ values between these rain-dependent and rain-independent annuals or perennials.

Since growth form and rain dependence did not show significant variation along the rainfall gradient, we investigated the effect of substrate and of successional stage on $\delta^{13}C$ values (Table 3) and species numbers. NAD species reached a maximum of species number on sandy soils. PCK and C3 species reached highest numbers in moist habitats. This also held for NADP species which reached highest numbers in moist habitats or in late successional types of vegetation. However, there was no significant effect of habitat or successional stage on the $\delta^{13}C$ value of NAD or NADP species (Table 2). Only in PCK species, there were significantly higher $\delta^{13}C$ values in species growing on clay as compared to species growing on disturbed sites. The variation was greater in C3 species, where species on sand had significantly more negative $\delta^{13}C$ values in wet habitats than in disturbed or shady sites.

Effects of variation in photosynthetic types within grass genera on $\delta^{13}C$ values

There were no grass genera in which C4 photosynthesis varied between NADP and non-NADP types. The NADP type of C4 photosynthesis was thus very conservative

Table 2 Carbon isotope ratios of annual and perennial grass species at different precipitations for different metabolic types of C4 metabolism (NADP-ME, NAD-ME, PCK) and for C3 grass. The first column shows the average for all species for a given metabolic type or a given rainfall. Annual and perennial species are divided again into rain-dependent and rain-independent species. The

first column summarizes the rain-dependent plus the independent types. Only in the PCK type was the effect of growth form on $\delta^{13}\text{C}$ significant (ANOVA). $\delta^{13}\text{C}$ values in ‰, av average values, n number of observations. For a few species the available information on photosynthetic type (3), or on growth form or habitat preference (7 species) remains unknown, although the $\delta^{13}\text{C}$ values were measured. These data are listed as "incomplete"

Type	Precipitation (mm)	Total average			Annual						Perennial											
		Annual and perennial			Total rain Dependent and independent			Rain dependent			Rain independent			Total rain Dependent and independent			Rain dependent			Rain independent		
		av.	SD	n	av.	SD	n	av.	n	av.	n	av.	SD	n	av.	n	av.	n				
C3	av.	-26.6	1.7	40	-27.1	2.0	22	-26.8	12	-27.5	8	-26.0	1.0	18	-25.6	7	-26.3	11				
	50	-26.2	2.0	18	-26.5	2.2	12	-26.0	9	-28.1	3	-25.6	1.4	6	-25.4	5	-26.7	1				
	150	-29.2		1	-29.2		1			-29.2	1				0			0				
	250			0			0		0					0		0		0				
	350	-26.7		1	-26.7		1		0	-26.7	1			0		0		0				
	450	-26.8	1.2	3	-27.0	1.6	2	-28.1	1	-25.9	1	-26.4		1			-26.4	1				
	550	-26.8	1.4	15	-28.4	1.8	4	-29.7	2	-27.1	2	-26.2	0.8	11	-26.0	2	-26.2	9				
Incomplete			2	-27.4		2																
NAD	av.	-13.4	0.9	131	-13.3	1.1	45	-13.4	35	-13.1	10	-13.4	0.8	84	-13.3	59	-13.6	23				
	50	-13.4	0.6	25	-13.3	0.5	8	-13.1	6	-13.8	2	-13.5	0.7	17	-13.4	15	-13.8	2				
	150	-13.6	0.8	18	-13.5	0.5	7	-13.5	7		0	-13.6	1.0	11	-13.7	8	-13.4	3				
	250	-13.2	0.9	21	-12.8	1.3	4	-13.8	2	-11.8	2	-13.2	0.8	17	-13.2	15	-13.5	2				
	350	-13.6	1.1	29	-13.4	1.3	16	-13.5	12	-13.2	4	-13.8	0.9	13	-13.7	7	-13.8	6				
	450	-13.5	0.9	9	-13.5	1.4	3	-13.5	3		0	-13.5	0.7	6	-12.9	3	-14.0	3				
	550	-13.2	0.9	25	-13.3	1.3	7	-13.1	5	-13.8	2	-13.2	0.7	18	-13.1	11	-13.2	7				
Incomplete			4	-15.0		2					-12.7		2									
PCK	av.	-12.5	0.8	81	-12.7	0.9	35	-12.9	20	-12.5	15	-12.3	0.6	46	-12.4	28	-12.2	18				
	50	-12.8	0.4	4	-13.1	0.4	2	-13.1	2		0	-12.6	0.2	2	-12.5	1	-12.7	1				
	150	-13.3		1			0		0		-13.3		1	-13.3	1		0					
	250	-12.8	0.8	11	-13.0	0.8	6	-13.2	3	-12.8	3	-12.6	0.8	5	-12.6	5		0				
	350	-12.4	0.5	19	-12.4	0.6	13	-12.7	6	-12.1	7	-12.4	0.4	6	-12.4	3	-12.3	3				
	450	-12.6	1.1	12	-13.2	1.4	6	-13.7	4	-12.1	2	-12.1	0.5	6	-12.2	5	-11.5	1				
	550	-12.4	0.7	34	-12.7	0.9	8	-12.5	5	-13.2	3	-12.3	0.6	26	-12.3	13	-12.2	13				
NADP	av.	-11.7	0.9	103	-11.6	0.7	25	-11.7	18	-11.5	7	-11.7	0.9	78	-11.7	43	-11.7	34				
	50	-12.8		1		0		0		0	-12.8		1		0		-12.8	1				
	150	-12.5		1		0		0		0	-12.5		1	-12.5	1			0				
	250	-11.4	0.9	8	-10.8	1.2	2	-10.8	2		0	-11.6	0.8	6	-11.6	6		0				
	350	-11.9	1.0	15	-11.8	1.5	5	-11.8	5		0	-11.9	1.2	10	-11.7	8	-13.0	2				
	450	-12.2	0.8	13	-12.3	0.4	6	-12.2	5	-12.7	1	-12.2	1.0	7	-12.4	6	-11.2	1				
	550	-11.5	0.8	64	-11.3	0.6	12	-11.4	6	-11.3	6	-11.6	0.9	52	-11.5	23	-11.6	29				
Incomplete			1																			
NADP <i>Aristida</i>	av.	-12.8	0.9	16	-13.2	0.9	8	-13.2	6	-13.2	2	-12.5	0.9	8	-12.6	6	-12.0	2				
	50	-14.3	1.1	2	-15.1		1	-15.1	1		0	-13.5		1	-13.5	1		0				
	150			0					0					0		0		0				
	250	-13.1	0.6	4	-13.2	0.7	3	-13.2	3		0	-12.8		1	-12.8	1		0				
	350	-12.7	0.8	4	-13.0	0.8	2	-13.0	2		0	-12.3	0.9	2		2		0				
	450	-13.1		1			0		0		-13.1		1		0	-13.1	1					
	550	-12.1	0.7	5	-12.5		2	-12.5	2		0	-11.9	0.9	3	-11.9	3		0				
Incomplete			3																			

(Hattersley 1992). In contrast, there were several genera in which species within the same genus are either of NAD- or PCK-type anatomy, and there were a few cases where NAD and PCK genera contain rare C3-type species. These exceptions were *Panicum heterostachyum* and *Eragrostis walteri* which were previously recognized as C3 species (Ellis 1984a).

In *Eragrostis* (53 species) 80% of the species were of the NAD type and about 20% PCK type (see Appendix).

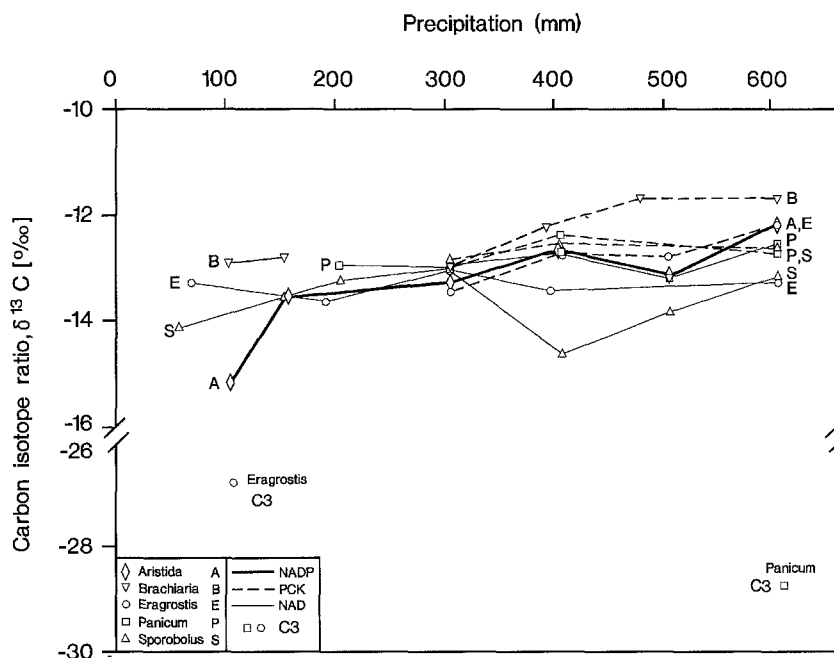
In *Sporobolus* (23 species) and *Panicum* (21 species) about half of the species were either NAD or PCK type. We investigated the conditions under which species exhibited this change in photosynthetic type. In all three genera PCK metabolism was restricted to more than 200 mm precipitation (Fig. 3), although PCK species occurred in other genera along the whole rainfall gradient. Independent of the metabolic type, there was a general increase in $\delta^{13}\text{C}$ values with increasing precipitation es-

Table 3 Carbon isotope ratios ($\delta^{13}\text{C}$ values in ‰) related to habitat conditions and successional stage for the different metabolic types of C4 metabolism (NADP-ME, NAD-ME, PCK) and for C3

grasses. [Significant differences (*t*-test) within a column and for a metabolic type are indicated by different letters, *av.* average values, *n* number of observations]

Habitat	NAD				PCK				NADP				NADP-Aristida				C3 species			
	av.	SD	n	%	av.	SD	n	%	av.	SD	n	%	av.	SD	n	%	av.	SD	n	%
Sand	-13.37	0.74	47	36	-12.64	0.62	12	16	-11.38	0.66	7	7	-11.93		1	6	-25.12 ^a	1.30	7	18
Clay	-12.93	0.01	2	2	-11.88 ^a	0.52	6	8			0				0					0
Rock, gravel	-13.36	0.98	17	14	-12.64	0.50	9	12	-11.80	1.13	5	5			0		-26.96		1	2
Moist	-13.14	1.15	23	18	-12.31	0.52	23	30	-11.74	0.97	36	36	-12.63	1.14	4	25	-26.85 ^b	1.23	17	40
Salt	-13.61	0.92	14	11	-12.69		1	1			0				0					0
Disturbed	-13.64	1.24	9	7	-13.16 ^b	1.25	8	10	-11.63	0.70	6	6	-12.82	0.58	6	38	-28.84 ^{bc}	0.94	2	5
Late succession	-13.28	0.86	3	2	-12.05	0.69	8	10	-11.94	0.79	29	29	-12.81	0.04	2	13				0
Shade	-13.29	0.45	2	2	-13.70		1	1	-11.79	0.36	5	5			0		-29.28 ^c	1.17	4	9
Incomplete	-13.06			11	-13.01		9	5	-11.78	0.71	15		-13.42	1.69	4		-25.25	1.94	4	18

Fig. 3 Carbon isotope ratios ($\delta^{13}\text{C}$ values in ‰) of different grass genera which contain species of different metabolic types related to precipitation



pecially for PCK species and for *Aristida*. The differences between species of PCK and NAD metabolism were largest at high rainfall.

The ecology of monospecific Namibian grass genera

There are 58 genera in the Namibian grass flora which are monospecific, i.e. they are represented by just one species in Namibia (see Appendix). This fraction was largest in C3 species (33% of the C3 species), and became smaller in NADP (19%), PCK (12%) and NAD species (11%). Some of these genera are not only monospecific in the Namibian flora but contain only one species in the whole genus (*Entoplocamia*, *Leptocarydion*, *Vossia*, *Tarigidia*, *Kaokochloa*, *Oryzidium*). In fact, the majority of the monospecific Namibian genera were species-poor genera. About half of these monospecific genera occurred in moist or saline habitats (30 species) in the high rainfall range above 400 mm rain. Only 5 out of 44 monospecific C4 genera, but 8 of the 14 monospecific

C3 genera were found in the coastal desert. Despite the relative preference for moist habitats in the high rainfall region, in C4 genera there was no obvious difference in the $\delta^{13}\text{C}$ values between these monospecific genera and the rest of the species of the respective metabolic type.

Discussion

The results show that (1) there are inherent differences in $\delta^{13}\text{C}$ values between metabolic types of C4 photosynthesis (Table 1, and Farquhar 1982), (2) $\delta^{13}\text{C}$ values of different metabolic types and species sampled from their central range of distribution were quite insensitive to precipitation and habitat conditions including soil type, salinity and drought, (3) species exhibiting C4 metabolism with lowest leakiness (NADP type) occurred in the high and not in the low rainfall regimes, (4) genera switching between metabolic types changed towards C4 types with higher leakiness at low rainfall, and (5) endemism was centred in the high rainfall area on moist

soils where competition would be expected to be largest (this contrasts with the findings of Pate and Hopper 1994). The observed increase in species diversity with increasing rainfall in Namibia was not a result of increasing disturbance by grazing, but an inherent property of this grass flora (Ellis et al. 1980).

The differences in carbon isotope ratios of the C4 types result from differences in leakiness for CO₂ due to imbalances between CO₂ assimilation by PEP-carboxylase (C4 cycle) and the photosynthetic carbon reduction by RubP-carboxylase (C3 cycle), and the cellular differentiation and compartmentation between mesophyll, bundle sheath and vascular system (Hattersley 1992). In the NAD type, decarboxylation of the organic acid takes place in the cytoplasm of the bundle sheath cells. In this case by back diffusion the CO₂ enrichment in the chloroplast seems not to be as high as in the case of a chloroplastic NADP-type decarboxylation. The PCK decarboxylation plays an intermediate role for unknown reasons. Any of these factors will cause a decrease in assimilation efficiency, e.g. as measured by quantum yield (Ehleringer and Pearcy 1983). Stomata may compensate a potential change in intercellular CO₂ by opening or closure. Thus, the $\delta^{13}\text{C}$ value in C4 plants results from both changes in leakiness and stomatal response. An apparent insensitivity of the $\delta^{13}\text{C}$ values to rainfall was predicted by Farquhar (1982) for a leakiness of 0.4. Thus, the interpretation of changes in $\delta^{13}\text{C}$ values with rainfall will depend on the absolute range at which these changes take place. If we take into account the $\delta^{13}\text{C}$ values of the atmosphere (-7.8 ‰) and the fractionation by diffusion of CO₂ in air (-4.4 ‰), then only for $\delta^{13}\text{C}$ values that are more negative than -12 ‰ and at constant high leakiness (>0.4), would stomatal closure result in an increase in the $\delta^{13}\text{C}$ value (similar to C3 plants). In contrast, for $\delta^{13}\text{C}$ values more positive than -12 ‰ and an associated leakiness of <0.4, stomatal closure would result in more negative $\delta^{13}\text{C}$ values (opposite to C3 plants). We also have to consider post-gas exchange effects, such as lignification of woody tissues in perennial grasses. However, most processes in secondary plant metabolism would increase rather than decrease the $\delta^{13}\text{C}$ value. Gebauer and Schulze (1991) show for trees that needles had 1–2 ‰ lower $\delta^{13}\text{C}$ values than twigs. Thus if post-gas exchange effects have taken place, then the “real” $\delta^{13}\text{C}$ value of photosynthesis is most likely even more negative than measured in leaf tissue.

The average $\delta^{13}\text{C}$ values of the Namibian NAD, PCK, and *Aristida* species were more negative than -12 ‰. Only NADP species reached values less negative than -12 ‰. Leakiness was 0.2–0.3 in NADP species (Farquhar 1983), but reached values of 0.45 (sun leaves) and 0.75 (shade leaves) in NAD species (Buchmann et al. 1995). Considering the range of $\delta^{13}\text{C}$ value and the leakiness of NADP species, and the fact that leakiness may increase by 0.1 due to water stress affecting the $\delta^{13}\text{C}$ value by 0.7 ‰ (Buchmann et al. 1995), the slight decrease in $\delta^{13}\text{C}$ values of NADP species at low rainfall may indicate stomatal closure by stress, possibly due to salinity in

wet habitats (Fig. 2, Table 2). This appears to contrast with the other metabolic types, which operate at $\delta^{13}\text{C}$ values more negative than -12 ‰. In this case the $\delta^{13}\text{C}$ values become more negative at low rainfall, which would either indicate increased leakiness with stress at constant stomatal opening, or that stomata are more open at the coast than inland. We cannot distinguish between these possibilities without further measurements.

It seems useful to inspect the habitats and growth conditions more closely for further interpretation. We compared species in their “typical” habitat, which may be the optimum of the range of distribution for that species. One possible explanation for the small response in the $\delta^{13}\text{C}$ value may be that the active phase of growth for each species is restricted to a period whenever water is sufficiently available. This is quite obvious for rain-dependent annuals, and for rain-independent species in moist habitats. The $\delta^{13}\text{C}$ values seem to suggest that the rain-dependent perennials generally escape drought in some dormant state, and restrict the active phase of carbon fixation to a period whenever water is available. This does not exclude the possibility that within a species, favourable and unfavourable conditions of more or less extreme habitats may result in a variation of $\delta^{13}\text{C}$ values. A remarkable insensitivity to rainfall was described for C3/C4 shrubs on Hawaii (Robichaux and Pearcy 1984).

In the inland region rains occur as summer rains when temperatures and vapour pressure deficits are high. Even at bimodal precipitation of more than 400 mm, the vegetation will experience short-term dry periods (days), which may cause stomata to close. In addition, the summer rain periods are separated by distinct dry periods. Disturbances and local habitat conditions will modify water availability. Conditions are different in the coastal desert. Although rainfall is low, the temperature and vapour pressure deficit is lower than inland, and there may be little but continuous moisture available at all seasons due to fog and winter rain. The most extreme situation, however, is found in the subtropical grassland, where rainfall is low and variable, and temperatures and vapour deficits are high.

The NADP species with their most effective CO₂-capturing system are found only at high rainfall. They seem to maintain stomata more open under these conditions than at low rainfall. The NADP species are late successional species which may extend their physiological activity into the dry season. They also use nitrogen more effectively (Ehleringer and Monson 1993). In contrast, species with high intrinsic leakiness (NAD, PCK type) are restricted to disturbed habitats or to niches of high local water availability, such as sand, or rock, or shade, where they successfully compete against the dominant NADP flora. The NAD and PCK type is more dominant at low rainfall; however, under these conditions the majority of these species are rain dependent. With lower vapour deficits these species would possibly have stomata more open at the coast than in the inland savanna. Also the C3 species gain dominance in the coastal region exhibiting $\delta^{13}\text{C}$ values which would be typical for fairly

open stomata. This interpretation, however, does not explain why the NADP species are not dominant in the 200–300 mm rainfall region of subtropical grassland, which is a hot and dry transition zone between coast and inland dominated by NAD-type grass cover.

The *Aristida* NADP type seems to be an exception from the general NADP pattern, in that *Aristida* exhibited very low $\delta^{13}\text{C}$ values close to the coast. This genus occurs at lower rainfall than any other NADP species. It may be that this C4 type, which has been classified only by leaf anatomy, does not perform NADP-type photosynthesis along the whole rainfall gradient. The anatomical feature of a double layer of bundle sheath cells in *Aristida* (Watson and Dalwitz 1989) may point at a physiological transition in this genus. *Aristida* seems thus to represent a case of adaptive radiation of NADP-type species into the coastal low rainfall and temperature regime, which would conform with the evolutionary history of this genus, which is distinct from the other NADP species (Clayton 1981). The behaviour of *Aristida* could indicate that NAD-type metabolism is of advantage in coastal climates.

With respect to the endemic monospecific genera it is surprising to see that they do not occupy extreme habitats, or exhibit extreme $\delta^{13}\text{C}$ values. The majority of these species seem to have retreated to the few moist habitats in an otherwise dry landscape despite obvious competition in this niche (effects of salt cannot be excluded for moist habitats in a semi-arid climate). These species seem to indicate a more favourable climate in the vegetation history, rather than an adaptation to the present conditions of drought. The conditions are different for the coastal C3 species, which are unique to this fog desert.

It appears that the NAD-type speciation reflects a radiation to the low rainfall part of this transect as a result of the "lost" competition at high rainfall. With lower nitrogen requirements (Penning de Vries and Djitéye 1982), higher quantum yield and a more efficient internal carbon economy, and higher contents of tannin-like substances in leaves (Ellis 1990), the NADP-type species dominate the high rainfall area where these species compete with the woody vegetation in forming the typical facies of a savanna (Ehleringer and Monson 1993). It is possible that there is a trade-off between low rainfall and high air humidity which favours the NAD-type metabolism in coastal regions. Since speciation took place in rain-dependent and rain-independent NAD species, it is not just drought tolerance which determines this segregation of habitats. The utilization of short rain events would require more open stomata and this would be more likely in the coastal desert.

With regard to the initial question as to whether it matters how many species occur, we present evidence that species diversity is important for this region. First of all the moist habitats maintain a reservoir of species that seem to have evolved in and that are adapted to more humid conditions, and it would be this reservoir of presently rare species that could gain dominance if climate

changed to wetter conditions. Secondly, with respect to the fog desert, there are 29 new NAD-type species and a unique group of C3 species which only occur in the dry coastal desert, which do not extend inland, and which are an essential basis for the Namib desert ecosystems. Thirdly, the subtropical grassland is occupied by a very small number of grasses as sole vegetation cover. The geographical distribution of grasses in Namibia demonstrates that species do matter in ecosystem functioning. Without C4 species parts of this country would be barren desert (the present sub-tropical grasslands), other parts would have a cover of woody species if the grasses were absent, and the cover of woody species would probably increase if the NADP-type species were replaced by NAD species.

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Appendix Tabulation of the grass species of Namibia. The following data are listed for each species: *column 1* Species with nomenclature following Gibbs Russell et al. (1990); *column 2* carbon isotope ratio, $\delta^{13}C$ value in ‰; *column 3* anatomy (*n-K* no Kranz type bundle sheath, *K* Kranz type bundle sheath, *PS* pyruvate species, *MS* malate species with NADP, NAD or PCK-dependent decarboxylation according to the bundle sheath anatomy (Ellis 1977a, b, 1984a, b, 1986, 1988; Watson and Dallwitz 1989) and new observations; *column 4* physiology according to Watson and Dallwitz (1989); *C3* C3-type photosynthesis; *C4* C4-type photosynthesis, *NADP-ME*: NADP-malic-enzyme type; *NAD-ME*: NAD-malic-enzyme type, *PCK*: phosphoenolpyruvate-carboxylase type of carboxylation; *column 5*, 6, 7 minimum, maximum, and common rainfall; *column 8* season of rainfall (*s* summer, *w* winter); *column 9* rainfall dependence (*d* dependent, *i* independent); *col-*

umn 10 growth form (annual, perennial); *column 11* vegetation types (see Fig. 1) according to Müller (1983) with desert (1) Northern Namib, (2) Central Namib, (3) Southern Namib, (4) winter rainfall desert and succulent steppe, (5) saline desert with dwarf shrub and savanna, (6) dwarf shrub savanna, (7) semi-desert - savanna transition, (8) Southern Kalahari - mixed tree and shrub savanna, (9) Mopane savanna, (10) highland savanna, (11) Thornveld savanna - tree and shrub savanna, (12) mountain savanna and Karstveld, (13) Central Kalahari - Cameldom savanna, (14) Northern Kalahari dry forest; *column 12* habitat or successional stage. Fields remain blank whenever information is missing. In those cases where the anatomical and physiological classification differ, the anatomical evidence was used in the comparative analysis of the data

Species	$\delta^{13}C$	Anatomy	Physiology	Rainfall		Common	Season	Dependence	Growth form	Vegetation type	Habitat
				Min	Max						
<i>Acrachne racemosa</i>	-13.25	K-PS-NAD	C4-NAD-ME	100	300	250	s	d	annual	9, 7	moist shade
<i>Acroceras macrum</i>	-27.37	n-K	C3	400	600	600	s	i	perennial	12, 4	hydrophyte
<i>Agrostis lachnantha</i>	-26.24	n-K	C3	200	600	600	s	i	perennial	10-12	hydrophyte
<i>Allotropis cimbicina</i>	-13.20	K-PS-PCK	C4-PCK			600	s	i	annual	14	moist sand
<i>Andropogon brazzae</i>	-12.11	K-MS-NADP	C4-NADP-ME			600	s	i	perennial	14	hydrophyte
<i>Andropogon chinensis</i>	-12.16	K-MS-NADP	C4-NADP-ME	400	600	500	s	d	perennial	8, 9, 12-14	rocks, late succession
<i>Andropogon eucomis</i>	-11.55	K-MS-NADP	C4-NADP-ME	400	600	600	s	i	perennial	11, 12, 14	hydrophyte
<i>Andropogon gayanus</i>	-11.84	K-MS-NADP	C4-NADP-ME	400	600	600	s	d	perennial	12-14	dry soil, late succession
<i>Andropogon huillensis</i>	-11.78	K-MS-NADP	C4-NADP-ME			600	s	i	perennial	14	hydrophyte
<i>Andropogon schirensis</i>	-11.41	K-MS-NADP	C4-NADP-ME	400	600	600	s	d	perennial	12, 14	loam, late succession
<i>Antheophora argentea</i>	-12.31	K-MS-NADP	C4-NADP-ME	200	400	300	s	d	perennial	8, 13	sand, late succession
<i>Antheophora pubescens</i>	-12.22	K-MS-NADP	C4-NADP-ME	200	600	450	s	d	perennial	8-14	sand, late succession
<i>Antheophora ramosa</i>	-10.88	K-MS-NADP	C4-NADP-ME	200	300	300	s	d	perennial	5-7	sand, late succession
<i>Antheophora schinzii</i>	-11.45	K-MS-NADP	C4-NADP-ME	200	500	400	s	d	perennial	7-9, 11	disturbance
<i>Aristida adscensionis</i>	-13.93	K-Aristida	C4-NADP-ME	100	500	300	s, w	d	annual	4, 6-13	disturbance
<i>Aristida congesta</i>	-12.91	K-Aristida	C4-NADP-ME	200	500	400	s	d	perennial	6, 7, 10-14	disturbance
<i>Aristida effusa</i>	-12.41	K-Aristida	C4-NADP-ME	300	500	400	s	d	annual	9-14	pioneer
<i>Aristida engleri</i>	-13.50	K-Aristida	C4-NADP-ME	100	200	150	s, w	d, i	perennial	4, 6	rocks
<i>Aristida hordeacea</i>	-13.59	K-Aristida	C4-NADP-ME	100	600	400	s	d, i	annual	9, 12, 14	moist, depressions
<i>Aristida hubbardiana</i>	-12.85	K-Aristida	C4-NADP-ME	300	400	300	s	d, i	annual	5, 12	moist, depressions
<i>Aristida junciformis</i>	-10.98	K-Aristida	C4-NADP-ME			600	s	d, i	perennial	14	damp habitats
<i>Aristida meridionalis</i>	-12.79	K-Aristida	C4-NADP-ME	200	600	300	s	d	perennial	8, 10, 11, 13, 14	sand, late succession
<i>Aristida mollissima</i>	-12.84	K-Aristida	C4-NADP-ME			600	s	d	perennial	14	sand, late succession
<i>Aristida parvula</i>	-15.06	K-Aristida	C4-NADP-ME	50	200	100	s, w	d	annual	1-4, 6	gravel plains
<i>Aristida pilgeri</i>	-13.10	K-Aristida	C4-NADP-ME	400	600	500	s	d, i	perennial	13, 14	moist habitats
<i>Aristida rhinichloa</i>	-12.70	K-Aristida	C4-NADP-ME	200	500	350	s	d	annual	9, 11, 12, 14	sand
<i>Aristida scabrivalvis</i>	-12.47	K-Aristida	C4-NADP-ME			600	s	d	annual	14	disturbance
<i>Aristida stipitata</i>	-11.93	K-Aristida	C4-NADP-ME	300	600	600	s	d	perennial	12-14	sand
<i>Aristida stipoides</i>	-12.49	K-Aristida	C4-NADP-ME	300	500	600	s	d	annual	13, 14	sand
<i>Aristida vestita</i>	-11.69	K-Aristida	C4-NADP-ME	300	600	400	s	d	perennial	11	stony soil
<i>Arundo donax</i>	-24.86	n-K	C3	300	600	600	s, w	i	perennial	10	hydrophyte
<i>Bothriochloa bladhii</i>	-13.43	K-MS-NADP	C4-NADP-ME			600	s	i	perennial	14	most habitats
<i>Bothriochloa insculpta</i>	-11.76	K-MS-NADP	C4-NADP-ME	300	600	600	s	d	perennial	9, 12, 14	clay, late succession
<i>Bothriochloa radicans</i>	-13.85	K-MS-NADP	C4-NADP-ME	200	500	500	s	d	perennial	6, 8, 11, 12, 14	clay, late succession
<i>Brachiaria arrecta</i>	-11.65	K-PS-PCK	C4-PCK			600	s	i	perennial	14	hydrophyte
<i>Brachiaria brizantha</i>	-11.65	K-PS-PCK	C4-PCK			600	s	d	perennial	14	sand, late succession
<i>Brachiaria flexa</i>	-13.98	K-PS-PCK	C4-PCK	200	500	300	s	d	annual	6, 10-14	shade, pioneer

Appendix (continued)

Species	$\delta^{13}C$	Anatomy	Physiology	Rainfall		Common	Season	Dependence	Growth form	Vegetation type	Habitat
				Min	Max						
<i>Brachiaria dictyonera</i>	-11.05	K-PS-PCK	C4-PCK			600	s	d	perennial	14	late succession
<i>Brachiaria dura</i>	-12.12	K-PS-PCK	C4-PCK			600	s	d, i	perennial	14	sand riverbed
<i>Brachiaria eruciformis</i>	-11.09	K-PS-PCK	C4-PCK	300	500	400	s	d, i	annual	9, 11, 12, 14	moist clay
<i>Brachiaria glomerata</i>	-12.76	K-PS-NAD	C4-PCK	50	200	150	s, w	d	annual	2-4, 6, 8	sand
<i>Brachiaria grossa</i>	-11.84	K-PS-PCK	C4-PCK	200	400	300	s	d	annual	7, 10, 11, 12	rocks, shade
<i>Brachiaria humiticola</i>	-11.69	K-PS-PCK	C4-PCK			600	s	i	perennial	14	hydrophyte
<i>Brachiaria malacodes</i>	-13.20	K-PS-PCK	C4-PCK	200	500	350	s	i	annual	9, 12, 14	pans, disturbance
<i>Brachiaria marlothii</i>	-12.34	K-PS-PCK	C4-PCK	300	400	400	s	i	annual	10, 11, 14	moist depressions
<i>Brachiaria nigropedata</i>	-12.37	K-PS-PCK	C4-PCK	300	500	400	s	d	perennial	10-14	dry soil, late succession
<i>Brachiaria psammophila</i>	-12.86	K-PS-NAD	C4-PCK			100	s	d	annual	1	sand
<i>Brachiaria schoenfelderi</i>	-11.74	K-PS-PCK	C4-PCK	400	500	450	s	i	annual	5, 9, 12	moist depressions
<i>Brachiaria serrata</i>	-11.49	K-PS-PCK	C4-PCK	400	500	500	s	d	perennial	10, 11	dry soil, late succession
<i>Brachiaria xantholeuca</i>	-11.80	K-PS-PCK	C4-PCK	300	500	400	s	d	annual	9	clay, disturbance
<i>Brachyachne patentiflora</i>	-12.39	K-PS-PCK	C4-PCK (?)			600	s	d	perennial	14	lithophyte
<i>Bromus catharticus</i>	-26.85	n-K	C3	400	600	600	s	d	perennial	10	weed
<i>Bromus diandrus</i>	-28.17	n-K	C3	400	600	500	s	d	annual	10	weed
<i>Cenchrus biflorus</i>	-11.08	K-MS-NADP	C4-NADP-ME			600	s	d	annual	14	sand
<i>Cenchrus ciliaris</i>	-12.26	K-MS-NADP	C4-NADP-ME	100	600	500	s	d	perennial	4, 6-14	sand, late succession
<i>Centropodia glauca</i>	-14.22	K-PS-NAD	C4-NAD-ME	50	300	200	s, w	d	annual/	1-4, 6, 7	sand dunes
<i>Centropodia mossamedensis</i>	-12.88	K-PS-NAD	C4-NAD-ME	50	500	250	s	d	perennial	1, 2, 7, 9	dry riverbeds
<i>Chaetobromus involucreatus</i>	-24.94	n-K	C3			50	w	d	perennial	4	sand
<i>Chloris flabellata</i>	-13.53	K-PS-NAD	C4-PCK (?)			50	s	i	perennial	1	halophyte
<i>Chloris gayana</i>	-11.58	K-PS-PCK	C4-PCK			600	s	d	perennial	14	loam, late succession
<i>Chloris pycnothrix</i>	-14.33	K-PS-PCK	C4-PCK	400	500	500	s	d	annual	12	disturbance
<i>Chloris virgata</i>	-14.56	K-PS-PCK	C4-PCK	100	600	500	s	d	annual	6-14	disturbance
<i>Cladoraphis cyperoides</i>	-13.04	K-PS-NAD	C4-NAD-ME (?)			50	s, w	d	perennial	1-4	costal dunes
<i>Cladoraphis spinosa</i>	-13.79	K-PS-NAD	C4-NAD-ME (?)	50	200	100	s, w	d	perennial	2-4	sand
<i>Coelachyrum yemenicum</i>	-12.95	K-PS-NAD	C4-NAD-ME (?)			600	s	d	perennial	14	limestone, shade
<i>Craspedorhachis rhodesiana</i>	-13.05	K-PS-NAD	C4-NAD-ME			600	s	d, i	perennial	14	pan margins
<i>Cymbopogon dieterlenii</i>	-13.40	K-MS-NADP	C4-NADP-ME	200	400	400	s	d	perennial	10, 11	rocky soil, late succession
<i>Cymbopogon excavatus</i>	-11.70	K-MS-NADP	C4-NADP-ME	300	600	600	s	d	perennial	9-12, 14	rocky soil, late succession
<i>Cymbopogon plurinodis</i>	-11.56	K-MS-NADP	C4-NADP-ME	200	400	300	s	d	perennial	6, 7, 9-11	loam, late succession
<i>Cynodon dactylon</i>	-15.60	K-PS-NAD	C4-NAD-ME	100	600	450	s	d	perennial	6, 7, 9-11, 14	saline soil
<i>Dactyloctenium aegyptium</i>	-11.32	K-PS-PCK	C4-PCK	100	600	500	s	d, i	annual	6-14	disturbance, moist
<i>Dactyloctenium giganteum</i>	-11.63	K-PS-PCK	C4-PCK			600	s	d	annual	14	disturbance, sand
<i>Danthoniopsis dinteri</i>	-10.02	K-MS-NADP	C4-NADP-ME	200	400	300	s	d	annual	9, 11	rocky soil
<i>Danthoniopsis ramosa</i>	-12.80	K-MS-NADP	C4-NADP-ME	200	400	350	s	d	perennial	7, 10-12	rocks
<i>Diandrochloa namaquensis</i>	-12.91	K-PS-PCK	C4-NADP-ME	200	400	400	s	i	annual	7, 9-12	hydrophyte
<i>Diandrochloa pusilla</i>	-12.22	K-PS-PCK	C4-NAD-ME	200	500	500	s	i	annual	6, 10-14	hydrophyte
<i>Dianthanthium annulatum</i>	-13.67	K-MS-NADP	C4-NADP-ME	100	500	400	s	i	perennial	6, 8, 10-13	moist habitats
<i>Digitaria brazzae</i>	-10.41	K-MS-NADP	C4-NADP-ME			600	s	d	perennial	14	sandy soil
<i>Digitaria debilis</i>	-11.35	K-MS-NADP	C4-NADP-ME			600	s	i	annual	14	moist habitats
<i>Digitaria diagonalis</i>	-10.57	K-MS-NADP	C4-NADP-ME			600	s	d, i	perennial	14	moist habitats
<i>Digitaria eriantha</i>	-9.96	K-MS-NADP	C4-NADP-ME	200	500	450	s	d	perennial	6, 7, 10, 11	late successional
<i>Digitaria eylesii</i>	-10.21	K-MS-NADP	C4-NADP-ME			600	s	i	perennial	14	hydrophyte

<i>Digitaria gayana</i>	-10.49	K-MS-NADP	C4-NADP-ME	600	s	d	annual	14	disturbance
<i>Digitaria gazensis</i>	-10.48	K-MS-NADP	C4-NADP-ME	600	s	d	perennial	14	sand
<i>Digitaria longiflora</i>	-11.84	K-MS-NADP	C4-NADP-ME	600	s	d	perennial	14	sand
<i>Digitaria maniculata</i>	-11.35	K-MS-NADP	C4-NADP-ME	600	s	i	annual	14	moist habitats
<i>Digitaria milanijana</i>	-11.25	K-MS-NADP	C4-NADP-ME	600	s	d	perennial	14	late successional
<i>Digitaria monodactyla</i>	-11.34	K-MS-NADP	C4-NADP-ME	600	s	d	perennial	14	late successional
<i>Digitaria nuda</i>	-11.84	K-MS-NADP	C4-NADP-ME	400	s	d	annual	12	disturbance
<i>Digitaria perrottetii</i>	-12.08	K-MS-NADP	C4-NADP-ME	600	s	d	annual	14	sand, shade
<i>Digitaria perrotigluma</i>	-10.55	K-MS-NADP	C4-NADP-ME	600	s	i	annual	14	hydrophyte
<i>Digitaria sanguinalis</i>	-11.89	K-MS-NADP	C4-NADP-ME	400	s	d	annual	6, 10, 14	disturbance
<i>Digitaria seritata</i>	-12.24	K-MS-NADP	C4-NADP-ME	500	s	d	perennial	8, 13, 14	sand
<i>Digitaria velutina</i>	-10.92	K-MS-NADP	C4-NADP-ME	600	s	i	annual	14	moist habitats
<i>Digitaria velutina</i>	-10.99	K-MS-NADP	C4-NADP-ME	600	s	d	annual	10, 11, 13, 14	disturbance
<i>Diheteropogon filifolius</i>	-11.88	K-MS-NADP	C4-NADP-ME	400	s	d	perennial	10	late successional
<i>Dinebra retroflexa</i>	-12.92	K-PS-PCK	C4-PCK (?)	400	s	d	annual	14	clay, moist
<i>Diplachne cuspidata</i>	-13.21	K-PS-NAD	C4-NAD-ME	400	s	i	perennial	9	hydrophyte
<i>Diplachne eleusine</i>	-14.25	K-PS-NAD	C4-NAD-ME	100	s	d	perennial	9	sand, late succession
<i>Diplachne fusca</i>	-14.08	K-PS-NAD	C4-NAD-ME	100	s	i	perennial	5-7, 10-12, 14	hydrophyte
<i>Diplachne gigantea</i>	-15.55	K-PS-NAD	C4-NAD-ME	600	s	i	perennial	14	hydrophyte
<i>Dregeochloa pumila</i>	-26.96	n-K	C3	50	w	d	perennial	4	rocks
<i>Echinochloa colona</i>	-12.58	K-MS-NADP	C4-NADP-ME	600	s	i	annual	10-12, 14	hydrophyte
<i>Echinochloa crus-galli</i>	-11.08	K-MS-NADP	C4-NADP-ME	600	s	i	annual	14	hydrophyte
<i>Echinochloa holubii</i>	-12.30	K-MS-NADP	C4-NADP-ME	600	s	i	perennial	12-14	hydrophyte
<i>Echinochloa pyramidalis</i>	-13.41	K-MS-NADP	C4-NADP-ME	600	s	i	perennial	14	hydrophyte
<i>Echinochloa stagnina</i>	-10.63	K-MS-NADP	C4-NADP-ME	600	s	i	perennial	9, 14	hydrophyte
<i>Ehrharta brevifolia</i>	-24.51	n-K	C3	50	w	d	annual	4	sand
<i>Ehrharta calycina</i>	-25.54	n-K	C3	50	w	d	perennial	4	sand
<i>Ehrharta delicatula</i>	-27.83	n-K	C3	100	w	d	annual	4, 6	shade
<i>Ehrharta longiflora</i>	-25.40	n-K	C3	50	w	d	annual	4	shade
<i>Ehrharta pusilla</i>	-23.90	n-K	C3	50	w	d	annual	3, 4, 6	sand
<i>Ehrharta thunbergii</i>	-23.25	n-K	C3	50	w	d	perennial	4	sand
<i>Ehrharta tritandra</i>	-29.71	n-K	C3	50	w	d	annual	4	shade
<i>Eleusine coracana africana</i>	-12.53	K-PS-NAD	C4-NAD-ME	400	s	d	annual	10, 11, 14	ruderal
<i>Eleusine indica</i>	-16.27	K-PS-NAD	C4-NAD-ME	400	s	d	annual	10, 11	ruderal
<i>Elionurus muticus</i>	-11.59	K-MS-NADP	C4-NADP-ME	600	s	d	perennial	10, 11, 14	loam, late succession
<i>Elionurus tripsacoides</i>	-11.06	K-MS-NADP	C4-NADP-ME	600	s	d	perennial	14	late succession
<i>Elymandra grillata</i>	-11.42	K-MS-NADP	C4-NADP-ME	600	s	d	perennial	14	sand
<i>Elytrophorus globularis</i>	-25.90	n-K	C3	50	s	i	annual	2, 9, 11, 12, 14	hydrophyte
<i>Elytrophorus spicatus</i>	-26.42	n-K	C3	600	s	i	annual	14	hydrophyte
<i>Enneapogon cenchroides</i>	-14.95	K-PS-NAD	C4-NAD-ME	400	s	d	annual	3, 6, 7, 9-14	sand
<i>Enneapogon desvauxii</i>	-14.01	K-PS-NAD	C4-NAD-ME	300	s, w	d	annual	1-4, 6, 7, 9-11, 13, 14	shallow soil^
<i>Enneapogon scaber</i>	-13.25	K-PS-PCK	C4-NAD-ME	200	s, w	d	perennial	2, 4, 6, 7	rocks
<i>Enneapogon scoparius</i>	-13.45	K-PS-PCK	C4-NAD-ME	300	s	d	perennial	1, 2, 7, 9, 11	rocks
<i>Enteropogon macrostachyus</i>	-13.60	K-PS-NAD	C4-NAD-ME	600	s	d	perennial	12, 14	shade
<i>Enteropogon prieurii</i>	-11.24	K-PS-NAD	C4-NAD-ME	400	s	d	perennial	5	sand
<i>Enteropogon rupestris</i>	-12.93	K-PS-NAD	C4-NAD-ME	500	s	d	perennial	9, 12	clay
<i>Entollocamia aristulata</i>	-14.31	K-PS-NAD	C4-NAD-ME	200	s	d	annual	2, 6, 7, 9-11	brack soils
<i>Eragrostis annulata</i>	-13.27	K-PS-NAD	C4-NAD-ME	300	s	d	annual	2, 6, 7, 9-12	sand, disturbance
<i>Eragrostis aristata</i>	-13.03	K-PS-NAD	C4-NAD-ME	200	s	d	annual	1, 2	moist habitats
<i>Eragrostis aspera</i>	-12.41	K-PS-NAD	C4-NAD-ME	50	s	i	annual	1, 2	disturbance
<i>Eragrostis bergiana</i>	-13.07	K-PS-PCK	C4-NAD-ME	400	s	d	perennial	9, 12, 14	disturbance
				300	s	d	perennial	10, 11	limestone

<i>Eragrostis trichophora</i>	-13.53	K-PS-NAD	C4-NAD-ME	200	600	400	s	d	perennial	6, 7, 9-12, 14	sand
<i>Eragrostis truncata</i>	-14.04	K-PS-NAD	C4-NAD-ME	100	400	350	s	d	perennial	7, 11-13	limestone
<i>Eragrostis viscosa</i>	-13.94	K-PS-PCK	C4-NAD-ME	300	600	500	s	d	annual	10, 11, 13, 14	disturbance
<i>Eragrostis walteri</i>	-26.71	n-K	C3	50	200	100	s	i	perennial	1, 2, 6, 7	hydrophyte
<i>Eriochloa fatimensis</i>	-12.30	K-PS-PCK	C4-PCK	100	400	400	s	i	annual	6, 9	hydrophyte
<i>Eulalia aurea</i>	-11.78	K-MS-NADP	C4-NADP-ME			600	s	i	perennial	14	hydrophyte
<i>Eustachys paspaloides</i>	-12.56	K-PS-PCK	C4-NADP-ME			600	s	d	perennial	14	sand, late succession
<i>Fingerhuthia africana</i>	-13.21	K-PS-NAD	C4-NAD-ME	50	600	600	s, w	d	perennial	1, 3, 4, 6, 7, 9-12, 14	dry soil
<i>Hemarthria altissima</i>	-12.43	K-MS-NADP	C4-NADP-ME			600	s	i	perennial	14	hydrophyte
<i>Heteropogon contortus</i>	-12.10	K-MS-NADP	C4-NADP-ME	200	600	600	s	d	perennial	6, 7, 9, 11-14	late successional
<i>Heteropogon melanocarpus</i>	-12.62	K-MS-NADP	C4-NADP-ME			500	s	d	annual	12, 14	well drained soil
<i>Hyparrhenia dichroa</i>	-10.77	K-MS-NADP	C4-NADP-ME			600	s	i	perennial	14	moist habitats
<i>Hyparrhenia filipendula</i>	-12.00	K-MS-NADP	C4-NADP-ME			600	s	d	perennial	14	late successional
<i>Hyparrhenia hirta</i>	-13.03	K-MS-NADP	C4-NADP-ME	100	600	500	s	d	perennial	6, 7, 9-11, 14	late successional
<i>Hyparrhenia pocilotricha</i>	-10.77	K-MS-NADP	C4-NADP-ME			500	s, w	d	perennial	14	late successional
<i>Hyparrhenia rufa</i>	-11.18	K-MS-NADP	C4-NADP-ME			600	s	d, i	perennial	14	moist, disturbed
<i>Hyperthelia dissoluta</i>	-11.44	K-MS-NADP	C4-NADP-ME			600	s	d	perennial	14	sand, late succession
<i>Imperata cylindrica</i>	-12.19	K-MS-NADP	C4-NADP-ME	300	600	600	s	i	perennial	11, 14	moist habitats
<i>Ischaemum afrum</i>	-12.13	K-MS-NADP	C4-NADP-ME			600	s	i	perennial	14	moist habitats
<i>Ischaemum fasciculatum</i>	-10.75	K-MS-NADP	C4-NADP-ME			600	s	i	perennial	14	hydrophyte
<i>Kaokochoa nigrirostris</i>	-13.34	K-PS-PCK	C4-PCK			50	s	d	annual	1	rocky soil
<i>Karochloa schismoides</i>	-26.20	n-K	C3			50	w	d	annual	4	sandy soil
<i>Leersia friesii</i>	-26.58	n-K	C3			600	s	i	perennial	14	hydrophyte
<i>Leersia hexandra</i>	-26.44	n-K	C3			500	s	i	perennial	11, 14	hydrophyte
<i>Leptocarydion vulpiastrum</i>	-13.34	K-PS-NAD	C4-NAD-ME			600	s	d	annual	14	sand
<i>Leptochloa uniflora</i>	-14.69	K-PS-NAD	C4-NAD-ME			600	s	d	annual	14	shade
<i>Leucophrys mesocoma</i>	-12.46	K-PS-PCK	C4-PCK			100	s, w	d	perennial	1, 4, 6	sand
<i>Lolium rigidum</i>	-26.81	n-K	C3			50	s	d	annual	3	weed
<i>Loudetia lanata</i>	-12.78	K-MS-NADP	C4-NADP-ME			600	s	i	perennial	14	moist habitats
<i>Megaloptrotachne albescens</i>	-12.14	K-MS-NADP	C4-NADP-ME	300	600	500	s	d	annual	8, 14	sand
<i>Megaloptrotachne glabrescens</i>	-12.00	K-MS-NADP	C4-NADP-ME	300	600	500	s	d	annual	9, 14	sand
<i>Melinis kallimorpha</i>	-13.49	K-PS-PCK	C4-PCK	400	600	600	s	d	annual	11, 14	sand, shade
<i>Melinis longiseta</i>	-12.55	K-PS-PCK	C4-PCK	300	500	600	s	d	perennial	9, 11, 12	rocky cervices
<i>Melinis nerviglamis</i>	-12.03	K-PS-PCK	C4-PCK	300	400	600	s	d	perennial	11	rocky soil
<i>Melinis repens</i>	-13.00	K-PS-PCK	C4-PCK	200	600	400	s	d	annual	6-14	disturbance
<i>Melinis subglabra</i>	-13.48	K-PS-PCK	C4-PCK			600	s	d	annual	14	shade
<i>Merxmuellera rangei</i>	-26.24	n-K	C3			50	w	d	perennial	4	sand
<i>Microchloa caffra</i>	-12.48	K-PS-NAD	C4-PCK (?)	200	400	300	s	d	perennial	6, 7, 10, 11, 14	lithophyte
<i>Microchloa indica</i>	-12.40	K-PS-PCK	C4-PCK (?)	300	400	400	s	d	annual	12	lithophyte
<i>Microchloa kunthii</i>	-12.26	K-PS-PCK	C4-PCK (?)	300	600	400	s	d	perennial	9-11, 14	hydrophyte
<i>Miscanthus junceum</i>	-12.76	K-MS-NADP	C4-NADP-ME			600	s	i	perennial	14	hydrophyte
<i>Monechlytrum luederitzianum</i>	-14.02	K-PS-NAD	C4-NAD-ME	200	400	300	s	d	annual/	9, 11, 12	rocks, calcrete
<i>Monocymbium cerasiiforme</i>	-11.72	K-MS-NADP	C4-NADP-ME			600	s	d	perennial	14	loam, late succession
<i>Odyssa paucinervis</i>	-13.62	K-PS-NAD	C4-NAD-ME	50	600	250	s	i	perennial	1, 2, 4-6, 8	halophyte
<i>Oplismenus burmannii</i>	-30.66	n-K	C3			600	s	d	annual	14	shade
<i>Oropetium capense</i>	-13.03	K-PS-NAD	C4-NAD-ME	200	600	400	s	d	perennial	4, 7, 9-11, 14	lithophyte
<i>Oryza longistaminata</i>	-26.17	n-K	C3			600	s	i	perennial	14	hydrophyte
<i>Oryzidium barnardii</i>	-11.67	K-PS-PCK	C4-PCK	300	600	400	s	i	perennial	9, 11	hydrophyte
<i>Panicum arbusculum</i>	-12.98	K-PS-NAD	C4-NAD-ME	100	200	200	s	d	perennial	6, 7	rocks
<i>Panicum arcuameum</i>	-12.77	K-PS-NAD	C4-NAD-ME	100	200	200	s	d	perennial	6	clay soil
<i>Panicum coloratum</i>	-12.59	K-PS-NAD	C4-NAD-ME	250	600	500	s	d	perennial	6, 7, 9, 11, 14	clay soil, late succession
<i>Panicum fluvicola</i>	-12.41	K-PS-PCK	C4-PCK			600	s	i	perennial	14	wet habitat
<i>Panicum gilyvum</i>	-14.05	K-PS-PCK	C4-PCK			600	s	i	annual	9	hydrophyte

Appendix (continued)

Species	$\delta^{13}\text{C}$	Anatomy	Physiology	Rainfall		Common	Season	Dependence	Growth form	Vegetation type	Habitat
				Min	Max						
<i>Panicum heterostachyum</i>	-28.73	n-K	C3			600	s	d	annual	14	shade
<i>Panicum impectium</i>	-12.93	K-PS-PCK	C4-PCK	200	300	300	s	i	annual	6, 7	wet habitat
<i>Panicum kalaharensense</i>	-12.85	K-PS-NAD	C4-NAD-ME	300	600	600	s	d	perennial	8, 13, 14	sand, late succession
<i>Panicum lanipes</i>	-12.52	K-PS-NAD	C4-NAD-ME	200	500	400	s	d	perennial	6, 8, 9-11	sand calcarete
<i>Panicum maximum</i>	-12.83	K-PS-PCK	C4-PCK	300	600	600	s	d	perennial	6, 9, 10, 11, 13, 14	shade, late succession
<i>Panicum novemnerve</i>	-12.49	K-PS-NAD		300	400	400	s	i	annual	12	moist habitats
<i>Panicum pansum</i>	-12.04								annual		
<i>Panicum pilgerianum</i>	-12.12	K-PS-PCK	C4-PCK	300	500	400	s	i	annual	11, 12	hydrophyte
<i>Panicum repens</i>	-12.50	K-PS-PCK	C4-PCK	300	600	600	s	i	perennial	11, 12, 14	hydrophyte
<i>Panicum repentellum</i>	-12.71	K-PS-NAD	C4-NAD-ME	300	600	600	s	i	perennial	14	hydrophyte
<i>Panicum schinzii</i>	-12.51	K-PS-PCK	C4-NAD-ME	300	400	400	s	i	annual	9	hydrophyte
<i>Panicum simulans</i>	-13.23	K-PS-NAD	C4-NAD-ME	100	400	400	s	i	annual	9, 12	moist habitats
<i>Panicum stapfianum</i>	-13.71	K-PS-NAD	C4-NAD-ME	300	600	500	s	i	perennial	9, 11, 12	rocky soils
<i>Panicum subalbidum</i>	-11.87	K-PS-PCK	C4-PCK			600	s	i	annual	14	hydrophyte
<i>Panicum trichonode</i>	-11.86	K-PS-NAD	C4-NAD-ME	300	600	600	s	i	perennial	12, 14	moist habitats
<i>Parathertia prostrata</i>	-11.18	K-MS-NADP	C4-NADP-ME			600	s	i	perennial	14	hydrophyte
<i>Paspalidium geminatum</i>	-12.68	K-MS-NADP	C4-NADP-ME	200	600	600	s	i	perennial	9, 14	hydrophyte
<i>Paspalidium scribuculatum</i>	-12.31	K-MS-NADP	C4-NADP-ME	300	600	600	s	i	perennial	11, 12, 14	hydrophyte
<i>Paspalum vaginatum</i>	-12.82	K-MS-NADP	C4-NADP-ME	100	300	100	s	i	perennial	2, 6	halophyte
<i>Pennisetum foermerianum</i>	-10.84	K-MS-NADP	C4-NADP-ME	100	400	300	s	d	perennial	7, 10-12	sand, late succession
<i>Pennisetum glaucocladum</i>	-10.94	K-MS-NADP	C4-NADP-ME			600	s	i	perennial	14	hydrophyte
<i>Pennisetum mezanum</i>	-12.54	K-MS-NADP	C4-NADP-ME	100	300	200	s	d	perennial	6, 9	gravel plains
<i>Pennisetum purpureum</i>	-10.07	K-MS-NADP	C4-NADP-ME			600	s	i	perennial		moist habitats
<i>Pennisetum thunbergii</i>	-11.25	K-MS-NADP	C4-NADP-ME			600	s	i	perennial		moist habitats
<i>Pentastichis airoides</i>	-22.69	n-K	C3			50	w	d	annual	4	sand
<i>Perotis leptopus</i>	-13.27	K-PS-NAD	C4-NAD-ME			600	s	d	annual	14	sand
<i>Perotis patens</i>	-13.03	K-PS-NAD	C4-NAD-ME	400	600	600	s	d	perennial	12, 14	sand
<i>Perotis vaginata</i>	-12.99	K-PS-NAD	C4-NAD-ME	400	600	600	s	d	annual	9, 14	sand
<i>Phragmites australis</i>	-25.62	n-K	C3	100	600	600	s	i	perennial	2, 9, 11, 12, 14	hydrophyte
<i>Phragmites mauritianus</i>	-26.07	n-K	C3	100	600	600	s	i	perennial	2, 8, 9, 14	hydrophyte
<i>Poa annua</i>	-26.66	n-K	C3	300	400	400	s	i	annual	10, 11	moist habitats
<i>Poa binata</i>	-27.15	n-K	C3								
<i>Pogonarthria fleckii</i>	-13.11	K-PS-NAD	C4-NAD-ME	200	600	500	s	d	annual	1, 2, 10, 11-14	sand
<i>Pogonarthria leiarthra</i>	-13.98	K-PS-NAD	C4-NAD-ME	200	400	400	s	d	annual	11, 12	sand
<i>Pogonarthria squarrosa</i>	-13.04	K-PS-NAD	C4-NAD-ME	300	600	600	s	d	perennial	11-14	sand
<i>Polyopogon griquensis</i>	-26.10	n-K	C3	100	200	150	s	i	annual	7	moist habitats
<i>Polyopogon monspeliensis</i>	-29.22	n-K	C3	100	200	200	s, w	i	annual	1, 2, 4, 7	moist habitats
<i>Polyopogon viridis</i>	-29.48	n-K	C3	100	200	200	s, w	i	annual	2-4	moist habitats
<i>Puccinellia angusta</i>	-28.60	n-K	C3			50	s	i	annual	2	moist habitats
<i>Rhynchacme robusta</i>	-10.75	K-MS-NADP	C4-NADP-ME			600	s	i	perennial	14	moist habitats
<i>Rothboellia cochinchinensis</i>	-12.65	K-MS-NADP	C4-NADP-ME	400	600	500	s	i	annual	12, 14	moist habitats
<i>Sacciolepis africana</i>	-26.92	n-K	C3			600	s	i	perennial	9, 14	hydrophyte
<i>Sacciolepis huillensis</i>	-27.71	n-K	C3			600	s	i	annual	14	hydrophyte
<i>Sacciolepis indica</i>	-27.55	n-K	C3			600	s	i	annual		hydrophyte
<i>Sacciolepis typhura</i>	-26.08	n-K	C3			600	s	i	annual	14	hydrophyte
<i>Sartidia angolensis</i>	-25.14	n-K	C3	400	600	600	s	d	perennial	12, 14	hydrophyte
<i>Schismus barbatus</i>	-26.69	n-K	C3			100	s, w	d	annual	4, 6	sand

<i>Schizachyrium exile</i>	-12.64	K-MS-NADP	C4-NADP-ME	300	500	s	d	9, 11, 14	shallow soil
<i>Schizachyrium jeffreysii</i>	-11.60	K-MS-NADP	C4-NADP-ME	300	600	s	d	11, 14	loam, late succession
<i>Schizachyrium sanguineum</i>	-11.80	K-MS-NADP	C4-NADP-ME	300	600	s	d	11, 12, 14	loam, late succession
<i>Schizachyrium ursulus</i>	-12.74	K-MS-NADP	C4-NADP-ME	400	500	s	d	12	clay, late succession
<i>Schmidia kalihariensis</i>	-12.75	K-PS-PCK	C4-PCK	100	500	s	d	6, 7, 9-11	sandy soil
<i>Schmidia pappohoroides</i>	-12.57	K-PS-PCK	C4-PCK	100	600	s	d	1, 6, 7, 10, 11, 13, 14	late succession
<i>Setaria ischaemoides</i>	-12.45	K-MS-NADP	C4-NADP-ME	300	400	s	d	12	dry soils
<i>Setaria appendiculata</i>	-11.39	K-MS-NADP	C4-NADP-ME	100	300	s	d	6, 7, 10, 11	rocks
<i>Setaria finita</i>	-11.64	K-MS-NADP	C4-NADP-ME	100	300	s	d	9-11	shade
<i>Setaria homonyma</i>	-11.63	K-MS-NADP	C4-NADP-ME	200	600	s	d	14	shade
<i>Setaria incrassata</i>	-10.61	K-MS-NADP	C4-NADP-ME	200	600	s	i	6, 7, 9-11, 14	moist clay
<i>Setaria pallide-fusca</i>	-10.35	K-MS-NADP	C4-NADP-ME	400	500	s	i	11, 12, 14	moist habitats
<i>Setaria sagittifolia</i>	-12.07	K-MS-NADP	C4-NADP-ME	400	600	s	d	9, 12, 14	shade
<i>Setaria sphacelata</i>	-11.92	K-MS-NADP	C4-NADP-ME	600	600	s	d	14	loam, late succession
<i>Setaria ustulata</i>	-11.24	K-MS-NADP	C4-NADP-ME	300	400	s	d	11, 14	shade
<i>Setaria verticillata</i>	-11.63	K-MS-NADP	C4-NADP-ME	100	600	s	d	6, 11, 12, 14	shade
<i>Sorghastrum friesii</i>	-12.54	K-MS-NADP	C4-NADP-ME	600	500	s	i	14	moist habitats
<i>Sorghum bicolor</i>	-12.40	K-MS-NADP	C4-NADP-ME	200	600	s	d, i	9, 11, 14	moist habitats
<i>Sorghum halepense</i>	-12.03	K-MS-NADP	C4-NADP-ME	300	500	s	d	11, 12	disturbed
<i>Sorghum versicolor</i>	-11.17	K-MS-NADP	C4-NADP-ME	300	500	s	i	9, 12	moist habitats
<i>Spartina maritima</i>	-12.69	K-PS-PCK	C4-PCK	50	50	w	i	3	halophyte
<i>Sporobolus acinifolius</i>	-14.30	K-PS-NAD	C4-NAD-ME	200	600	s	i	6, 9, 12	moist saline
<i>Sporobolus africanus</i>	-13.05	K-PS-PCK	C4-PCK	600	600	s	i	14	moist habitats
<i>Sporobolus albicans</i>	-13.32	K-PS-NAD	C4-NAD-ME	600	600	s	d	14	rocks
<i>Sporobolus conrathii</i>	-12.46	K-PS-PCK	C4-PCK	100	300	s	i	1, 2, 7, 9	moist saline
<i>Sporobolus consimilis</i>	-13.63	K-PS-NAD	C4-NAD-ME	300	500	s	i	6, 8, 9	moist saline
<i>Sporobolus coromandelianus</i>	-15.41	K-PS-NAD	C4-NAD-ME	100	300	s	d	1, 2, 6, 8, 9	sand
<i>Sporobolus engleri</i>	-13.65	K-PS-PCK	C4-PCK	200	600	s	d	7, 9-11, 14	lithophyte
<i>Sporobolus festivus</i>	-12.49	K-PS-PCK	C4-PCK	300	600	s	d	6, 9, 11, 13, 14	sandy soil
<i>Sporobolus fimbriatus</i>	-13.35	K-PS-PCK	C4-PCK	200	600	s	d	14	sand, disturbance
<i>Sporobolus iocladius</i>	-13.23	K-PS-NAD	C4-NAD-ME	200	600	s	d	6, 8, 9	sand
<i>Sporobolus natalensis</i>	-11.55	K-PS-PCK	C4-PCK	50	300	s	d	14	sand
<i>Sporobolus nebulosus</i>	-12.97	K-PS-NAD	C4-NAD-ME	200	300	s	d	2, 7, 9, 11	sand
<i>Sporobolus nervosus</i>	-12.75	K-PS-PCK	C4-PCK	200	300	s	d	6, 7, 9-11	sand
<i>Sporobolus panicoides</i>	-13.05	K-PS-PCK	C4-PCK	400	600	s	d	12, 14	sand
<i>Sporobolus pellucidus</i>	-12.33	K-PS-NAD	C4-NAD-ME	200	300	s	d	5	saline calcrete
<i>Sporobolus pyramidalis</i>	-11.78	K-PS-PCK	C4-PCK	300	600	s	d	8, 11, 14	moist habitats
<i>Sporobolus rangei</i>	-13.38	K-PS-NAD	C4-NAD-ME	200	400	s	i	6, 8, 11	pan margins
<i>Sporobolus salsus</i>	-15.02	K-PS-NAD	C4-NAD-ME	300	600	s	i	6, 9, 14	halophyte
<i>Sporobolus spicatus</i>	-13.15	K-PS-NAD	C4-NAD-ME	200	600	s	i	5, 9, 14	halophyte
<i>Sporobolus stapfianus</i>	-12.69	K-PS-PCK	C4-PCK	300	600	s	d	14	lithophyte
<i>Sporobolus tenellus</i>	-13.26	K-PS-NAD	C4-NAD-ME	300	400	s	i	5, 8, 9, 11	halophyte
<i>Sporobolus virginicus</i>	-14.08	K-PS-NAD	C4-NAD-ME	300	400	s, w	i	1-4	halophyte
<i>Sporobolus welwitschii</i>	-12.38	K-PS-NAD	C4-NAD-ME	100	300	s	i	14	pan margins
<i>Stipagrostis amabilis</i>	-11.91	K-PS-NAD	C4-NAD-ME	100	300	s	d	6, 8	dune crests
<i>Stipagrostis anomala</i>	-13.72	K-PS-NAD	C4-NAD-ME	50	200	s, w	d	4, 6	shallow soil
<i>Stipagrostis brevifolia</i>	-13.74	K-PS-NAD	C4-NAD-ME	50	200	s, w	d	4, 6	sand
<i>Stipagrostis ciliata</i>	-13.54	K-PS-NAD	C4-NAD-ME	50	300	s, w	d	2-4, 6-8	sand gravel
<i>Stipagrostis damarensis</i>	-13.05	K-PS-NAD	C4-NAD-ME	50	200	s	d	1, 2, 7	sand
<i>Stipagrostis dinteri</i>	-14.23	K-PS-NAD	C4-NAD-ME	50	50	s	d	1, 2	sand
<i>Stipagrostis dregeana</i>	-12.17	K-PS-NAD	C4-NAD-ME	100	50	w	d	4	sand
<i>Stipagrostis fastigiata</i>	-14.77	K-PS-NAD	C4-NAD-ME	50	200	s	d	3, 6	sand
<i>Stipagrostis garubensis</i>	-13.61	K-PS-NAD	C4-NAD-ME	50	50	s, w	d	3, 4	rocks

Appendix (continued)

Species	$\delta^{13}\text{C}$	Anatomy	Physiology	Rainfall		Common	Season	Dependence	Growth form	Vegetation type	Habitat
				Min	Max						
<i>Stipagrostis geminifolia</i>	-13.52	K-PS-NAD	C4-NAD-ME			50	w	d	perennial	4	sand
<i>Stipagrostis giesii</i>	-13.79	K-PS-NAD	C4-NAD-ME	50	300	200	s	d	perennial	1, 2, 9	gravel
<i>Stipagrostis gonatostachys</i>	-13.41	K-PS-NAD	C4-NAD-ME			50	s, w	d	perennial	2-4	sand
<i>Stipagrostis hermannii</i>	-13.86	K-PS-NAD	C4-NAD-ME			50	s	d	perennial	1-3	sand
<i>Stipagrostis hirtigluma</i>	-12.43	K-PS-NAD	C4-NAD-ME	50	600	300	s	d	annual/	1, 2, 6-9, 11, 13, 14	sand gravel
<i>Stipagrostis hochstetteriana</i>	-12.93	K-PS-NAD	C4-NAD-ME	50	400	200	s	d	perennial	1, 2, 6, 8, 9, 11	clay, sand rocks
<i>Stipagrostis lanipes</i>	-13.43	K-PS-NAD	C4-NAD-ME			50	w	d	perennial	4	sand
<i>Stipagrostis lutescens</i>	-14.14	K-PS-NAD	C4-NAD-ME			50	w	d	perennial	4	sand
<i>Stipagrostis namaquensis</i>	-13.90	K-PS-NAD	C4-NAD-ME	50	400	200	s, w	d	perennial	2-4, 6-8, 11	sand
<i>Stipagrostis namibensis</i>	-13.41	K-PS-NAD	C4-NAD-ME			50	s	d	annual	2	sand
<i>Stipagrostis obtusa</i>	-13.35	K-PS-NAD	C4-NAD-ME	50	400	200	s, w	d	perennial	2-4, 6-9, 13	sand
<i>Stipagrostis ramulosa</i>	-12.95	K-PS-NAD	C4-NAD-ME			50	s	d	perennial	1	sand
<i>Stipagrostis sabulicola</i>	-12.70	K-PS-NAD	C4-NAD-ME			50	s, w	d	perennial	2-4	dunes
<i>Stipagrostis schaeferi</i>	-12.53	K-PS-NAD	C4-NAD-ME			50	s, w	d	perennial	3, 4	gravel
<i>Stipagrostis subcaulis</i>	-13.20	K-PS-NAD	C4-NAD-ME			50	s, w	d	annual	1-4	sand
<i>Stipagrostis uniplumis</i>	-13.33	K-PS-NAD	C4-NAD-ME	50	600	300	s	d	perennial	1-3, 6-11, 13, 14	sand gravel
<i>Tarigidia aequiglumis</i>	-10.79	K-MS-NADP	C4-NADP-ME	300	400	400	s	d	perennial	8, 9, 12	rocky soil, late succession
<i>Tetragodon tenellus</i>	-12.97	K-PS-NAD	C4-NAD-ME	300	400	400	s	d	perennial	12	shade
<i>Themeda triandra</i>	-11.59	K-MS-NADP	C4-NADP-ME	300	600	600	s	d	perennial	6, 10, 11, 14	loam, late succession
<i>Trachypogon spicatus</i>	-13.15	K-MS-NADP	C4-NADP-ME			600	s	d	perennial	14	loam, late succession
<i>Tragus berteronianus</i>	-15.07	K-PS-NAD	C4-NAD-ME	100	500	500	s	d	annual	2, 6, 7, 9-11, 14	disturbed
<i>Tragus koelerioides</i>	-12.01	K-PS-NAD	C4-NAD-ME					9	perennial		
<i>Tragus pedunculatus</i>	-11.53	K-PS-NAD	C4-NAD-ME	400	500	400	s	d	annual	12	sand
<i>Tragus racemosus</i>	-12.32	K-PS-NAD	C4-NAD-ME	200	600	500	s	d	annual	6, 7, 9-11, 14	sand
<i>Tricholaena capensis</i>	-12.22	K-PS-PCK	C4-PCK	200	300	300	s	d	perennial	6, 7	sand
<i>Tricholaena monachne</i>	-12.55	K-PS-PCK	C4-PCK	100	600	500	s	d	perennial	1, 2, 7-11, 14	sand
<i>Trichoneura eleusinoides</i>	-13.28	K-PS-NAD	C4-NAD-ME	100	300	200	s	d	annual	2, 7, 9	rocks
<i>Tripogon grandiglumis</i>	-13.70	K-PS-NAD	C4-NAD-ME	300	600	600	s	d	perennial	10, 14	sand
<i>Tripogon minimus</i>	-16.25	K-PS-NAD	C4-NAD-ME	100	200	200	s	d	perennial	4	lithophyte
<i>Triraphis pumilo</i>	-12.80	K-PS-PCK	C4-NAD-ME			50	s, w	d	annual	1-4	sand
<i>Triraphis purpurea</i>	-13.14	K-PS-PCK	C4-NAD-ME	100	600	400	s	d	annual	6-11, 14	sand
<i>Triraphis ramosissima</i>	-11.43	K-PS-PCK	C4-NAD-ME	100	600	300	s	d	perennial	1, 2, 6, 7, 9-11	rocks, sand
<i>Triraphis schinzii</i>	-12.56	K-PS-PCK	C4-NAD-ME	400	600	500	s	d	perennial	11, 13, 14	sand
<i>Tristachya nodiglumis</i>	-10.77	K-MS-NADP	C4-NADP-ME			600	s	i	perennial	14	moist habitats
<i>Tristachya superba</i>	-11.14	K-MS-NADP	C4-NADP-ME			600	s	d	perennial	14	sand
<i>Urelytrum agropyroides</i>	-10.86	K-MS-NADP	C4-NADP-ME			600	s	d	perennial	14	sand
<i>Urochloa brachyura</i>	-12.57	K-PS-PCK	C4-PCK	200	600	400	s	d	annual	6, 9, 10, 11, 9-11	clay
<i>Urochloa oligotricha</i>	-11.76	K-PS-PCK	C4-PCK	300	600	500	s	d	perennial	9, 11, 14	clay
<i>Urochloa panicoides</i>	-12.34	K-PS-PCK	C4-PCK	200	400	400	s	d	annual	6, 9, 10, 11	weed
<i>Urochloa trichopus</i>	-12.75	K-PS-PCK	C4-PCK	300	600	600	s	d	annual	11, 14	sand
<i>Vetiveria nigriflora</i>	-12.14	K-MS-NADP	C4-NADP-ME			600	s	i	perennial	14	hydrophyte
<i>Vossia cuspidata</i>	-10.56	K-MS-NADP	C4-NADP-ME			600	s	i	perennial	14 hydrophyte	
<i>Willkommia sarmentosa</i>	-12.62	K-PS-NAD	C4-NAD-ME	300	600	600	s	i	perennial	9, 14	halophyte

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