



Plant form and function

Ecological and phylogenetic patterns of carbon isotope discrimination in the winter-rainfall flora of the Richtersveld, South Africa

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Abstract

Leaf tissues of vascular plant species from the arid Richtersveld of northern Namaqualand (Succulent Karoo), South Africa, show a great range of variation in carbon isotope discrimination. Analyses of Δ values for species with obligate C₃ metabolism demonstrated that the water use efficiency indicated by these values varies between species and within a species population both between seedlings and mature shrubs and between sites along an aridity gradient. An expected pattern of increasing water use efficiency with greater longevity in these species was not present, however. Only among ephemerals were there taxa with high Δ values associated with low water use efficiency, but these high values were balanced by other ephemeral species with low Δ values comparable to those typical of moderate to long-lived shrubs. The extent to which putative CAM species in the succulent flora rely entirely on nocturnal carbon fixation is highly variable. Species of Crassulaceae and *Aloe* (Asphodelaceae) relied almost exclusively on CAM photosynthesis, although Crassulaceae from more mesic environments may be CAM-flexible. Succulent-leaved species of *Senecio* and leaves of stem-succulent *Euphorbia* were CAM-flexible in their Δ values, while shrubby species of *Ceraria* (Portulacaceae) appeared to rely primarily on C₃ photosynthesis. Variable patterns of reliance on CAM photosynthesis were present in the ecologically dominant Mesembryanthema of the Aizoaceae. Shrubby species of the subfamily Mesembryanthemoideae, although capable of CAM-flexibility in less xeric habitats, relied largely on CAM fixation of carbon in our field sites. Within the subfamily Ruschioideae, there was a wide range of Δ values indicating species with CAM, CAM flexibility, and primary reliance on C₃ photosynthesis. Low Δ values indicative of typical CAM fixation were associated with species with greater longevity, suggesting that a positive correlation may exist between the degree of reliance on CAM photosynthesis and plant life span.

Introduction

The flora of Namaqualand, a winter-rainfall desert region (Cowling et al. 1999), is characterized by remarkable plant diversity at all scales (Cowling et al. 1998), particularly among leaf succulent species (Van Jaarsveld 1987). This diversity, combined with the steep environmental gradients in the area (Jürgens 1986; Desmet & Cowling 1999), offers interesting opportunities for studying the physiological ecology of desert plants (Von Willert et al. 1992). Although

succulent-leaved shrubs and subshrubs form a dominant component of vegetation cover (Cowling et al. 1994), relatively little is known about the possible significance of differential strategies of water use efficiency and photosynthetic assimilation in relation to community structure and diversity within these communities. Previous studies have established that growth-form diversity in the Succulent Karoo of Namaqualand is lower than that of comparable North American desert regions despite the far higher species diversity in Namaqualand (Esler & Rundel 1999; Es-

ler et al. 1999). Low growth-form diversity with high species diversity might be possible if there is a functional niche separation in ecophysiological traits among coexisting species.

Research in recent years has demonstrated that carbon isotope fractionation in C_3 species can be used as an integrated indicator of relative water use efficiency (Farquhar et al. 1982; Rundel et al. 1989; Ehleringer et al. 1993b,c). Absolute water efficiency in desert plants is influenced during the growing season by changes in water availability and leaf-to-air water vapor gradient, and thus changes significantly between seasons (Ehleringer et al. 1992). These changes affect all plant species in a community, however, and therefore the relative ranking of Δ values among species provides insight into fitness components related to water use efficiency since the relative rankings of Δ values among plants grown under common conditions remain constant over time (Johnson et al. 1990; Ehleringer 1993b,c).

In addition to its value in assessing relative water use efficiency among C_3 species, carbon isotope discrimination allows a means of identifying the relative use of Crassulacean acid metabolism (CAM) among putative CAM taxa. Such measurements allow a separation of species with pure CAM, CAM-flexibility, and primary reliance on C_3 metabolism (Kluge & Ting 1978; Brulfert et al. 1996).

In this paper we report on a three-year study of carbon isotope discrimination in the vascular plant flora of the arid Richtersveld region of northern Namaqualand. We collected samples from this species-rich area to test hypotheses about the relationship between carbon isotope discrimination, and thus water use efficiency, and such traits as plant longevity, growth form, and leaf morphology and phenology (Ehleringer & Cooper 1988; Ehleringer 1993b,c; Brooks et al. 1997). Moreover, we had a further objective to evaluate the significance of CAM photosynthesis within the Mesembryanthema of the Aizoaceae (sensu Bittrich & Hartmann 1988), the most ecologically and floristically diverse and dominant family in this region (Ihlenfeldt 1994; Chesselet et al. 1995).

Materials and methods

Study sites and sampling protocols

A series of arid field sites in northern Namaqualand were used in the collection of data for this study (Figure 1). Two sites were located in the Richtersveld

National Park. The first site was at Akkerdisdraai (28°14' S lat, 17°05' E long) in the Swartpoort area of the park (Rundel et al. 1995), and it was here that the largest number of species were sampled. Leaf samples were collected from species growing in a diverse community of stem and leaf succulent perennials on a south-southwest facing granite slope, and from a wash woodland community below, which formed the drainage for this slope. This site lies at about 300 m elevation and receives a mean annual rainfall of about 50 mm. Also sampled were leaf succulents growing at Hellskloof in the park (28°23' S lat, 16°58' E long; 800 m elevation, 80 mm mean annual precipitation). These sites fall within the upland Succulent Karoo of Low & Rebelo (1996). A small number of species were sampled in riparian habitats and low rock outcrops along the Orange (Gariiep) River near Brandkaros (28°29' S lat, 16°40' E long; 100 m elevation, 40 mm mean annual precipitation), a site just outside of the Richtersveld National Park. Additional study sites, not part of the primary survey but serving as less xeric comparisons, were located at: (a) McDougall's Bay (29°16' S lat, 16°53' E long) at an elevation of about 5 m (mean annual precipitation of 80 mm); and (b) 300 m elevation at Augrabies Mountain (29°16' S lat, 17°5' E long) near Port Nolloth where coastal fogs bring somewhat more moderate conditions and a mean annual rainfall of about 100 mm (Desmet & Cowling 1999b). Collections were made in Strandveld Succulent Karoo around the former site, and at Augrabies on alluvial slopes dominated by a mixed assemblage of leaf succulents (particularly Mesembryanthema) and *Euphorbia ephedroides*, and on steep rocky slopes of the mountain itself. The Augrabies site is classified as lowland Succulent Karoo (Low & Rebelo 1996). Only selected data from these additional sites is presented here.

Tissue samples for carbon isotope and nitrogen analyses were collected on four field expeditions carried out in July 1993, July 1995, February and July 1996. Mature leaf tissues from a minimum of three individuals of common species at each sample site were collected, and these samples were pooled for analysis.

Each species was identified and classified into one of four growth-forms: ephemerals (annuals), short-lived herbaceous perennials, and geophytes, moderate-lived subshrubs, long-lived woody shrubs, and long-lived wash woodland phreatophytes. Moderate-lived subshrubs include those species thought to have an average longevity of 5–20 years, while long-lived shrubs and phreatophytes

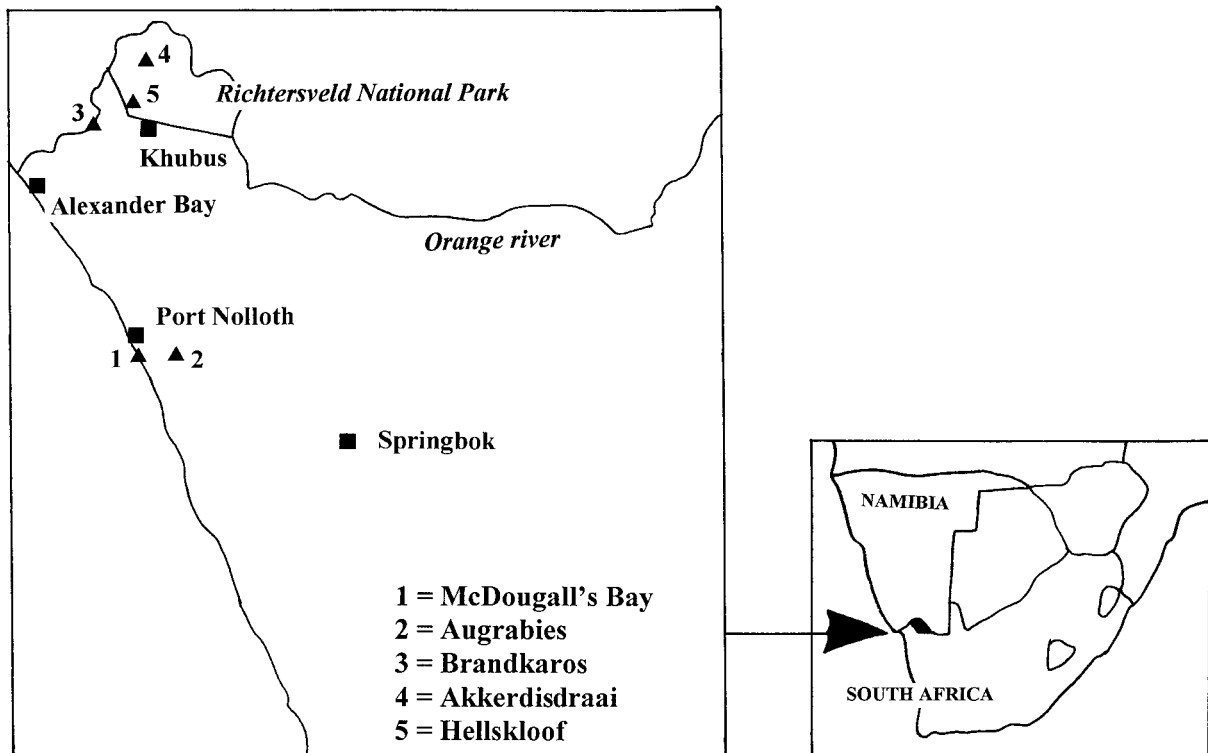


Figure 1. Field sites (indicated by ▲) in Namaqualand.

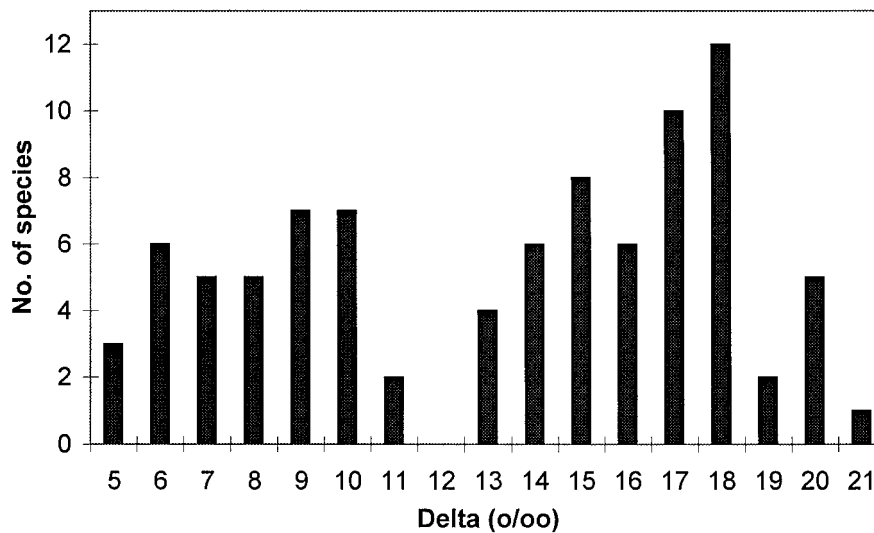


Figure 2. Carbon isotope discrimination (Δ) in leaf tissues of 89 species of vascular plants from the Richtersveld and adjacent areas. C_4 species are not included in this graph. See Table 1 for individual data. A mean value is shown for two species sampled in two populations.

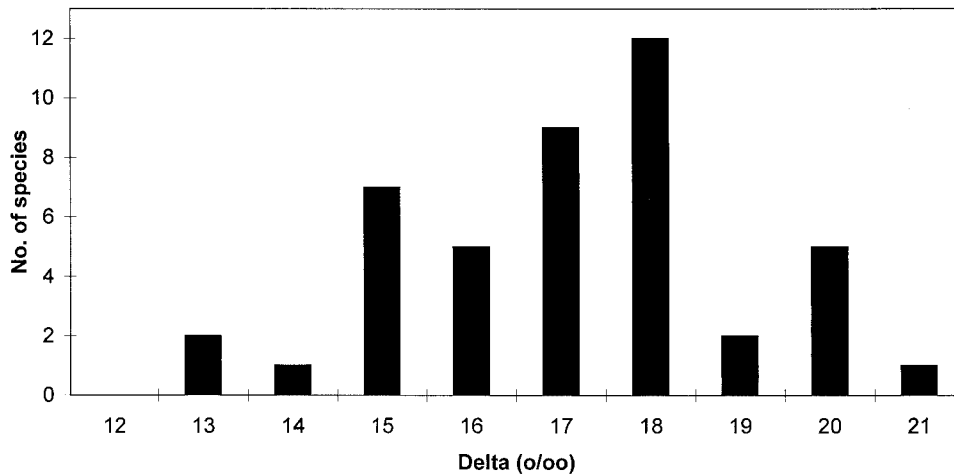


Figure 3. Carbon isotope discrimination (Δ) in leaf tissues of plants with obligate C_3 metabolism from the Richtersveld.

are those thought to survive for well over 20 years. Many species in this latter category probably live for 100 years or more. Nomenclature used in this paper follows that of Arnold & De Wet (1993).

Isotopic analyses

Natural ^{13}C ratios were measured at the Duke University Phytotron (Durham, North Carolina) on a SIRA Series II isotope ratio mass spectrometer (VG Isotech, Middlewich, United Kingdom) operated in automatic trapping mode after combustion of samples in an elemental analyzer (NA1500, Carlo Erba Instrumentation, Milan, Italy). The reference CO_2 , calibrated against standard Pee Dee belemnite (PDB), was obtained from Oztech (Dallas, Texas). Carbon isotope discrimination (Δ) was calculated for each species on the basis of the following formula:

$$\Delta = \frac{\delta_a - \delta_p}{1 + \delta_p},$$

where δ_a is the carbon isotope ratio of the atmosphere, here assumed to be -7.8‰ , and δ_p is the carbon isotope ratio of plant leaf tissues.

Although Δ values were calculated to 0.1‰ , the accepted accuracy of carbon isotope analyses, summary graphs of carbon isotope discrimination were rounded to the lower whole integer to show patterns of distribution among and within taxa.

Surveys of midday leaf temperatures were carried out in a variety of species, particularly those with succulent leaves, using an Erickson infrared thermometer calibrated with an emissivity of 0.98 and a precision of $0.1\text{ }^\circ\text{C}$.

Results

Carbon isotope analyses of 103 plant species (105 collections) from the Richtersveld and nearby areas provided a broad range of discrimination values (Δ) from 5 to 21‰ (Table 1). A histogram of these data (Figure 2) suggested two distinct arrays of values, with one from 5– 11‰ and the second from 13– 21‰ . Since the lower range likely represented species with Crassulacean acid metabolism (CAM) or C_4 metabolism, we separated species in genera that have been previously reported to be CAM (Mooney et al. 1977, Kluge & Ting 1978, Von Willert et al. 1992). This allowed us to analyze the range of carbon isotope discrimination present in taxa expected to possess normal Calvin cycle (C_3) metabolism. Putative CAM genera separated for independent analysis were Asclepiadaceae (*Sarcostemma*), Asphodelaceae (*Aloe*), Asteraceae (*Senecio*), Crassulaceae (all genera), Euphorbiaceae (*Euphorbia*), Mesembryanthema (all genera), and Portulacaceae (*Ceraria*). Five C_4 taxa were also excluded from further analysis – the shrubs *Atriplex cinerea* ssp. *bolusii* and *Salsola nollothensis* (Chenopodiaceae) and grasses *Cladoraphis cyperoides*, *Karoochloa* and *Stipagrostis* (Poaceae).

Carbon isotope discrimination in C_3 species

Eliminating putative CAM taxa and C_4 taxa gave us carbon isotope discrimination data on 44 species, all in the range of 13– 21‰ (Figure 3, Table 1). The modal carbon isotope discrimination in these C_3 taxa was 17‰ , and 75% of these taxa had Δ values in the range of 15– 18‰ . Among these taxa, there was no

Table 1. Taxonomic listing with ecological classification of growth form and estimated life span of plant species sampled for carbon isotope discrimination in the Richtersveld area of Namaqualand. Discrimination values (D) are means of pooled samples of tissue from three individuals. See text for discussion.

Species	Site	Growth-form*	Tissue sampled	Discrimination (%)	Estimated life span
Acanthaceae					
<i>Acanthopsis disperma</i> Nees	Akkerdisdraai	A	leaf	20.4	annual
<i>Blepharis capensis</i> (L.f.) Pers.	Akkerdisdraai	ES	leaf	14.5	moderate
<i>Monochma mollissimum</i> (Nees) P.G. Mey.	Akkerdisdraai	ES	leaf	15.7	moderate
Aizoaceae – Tetragonioideae					
<i>Galenia sarcophylla</i> Fenzl.	Akkerdisdraai	ES	leaf	18.7	moderate
<i>Hypertelis salsoloides</i> (Burch.) Adamson var. <i>salsoloides</i>	Akkerdisdraai	ES	leaf	15.3	moderate
<i>Tetragonia spicata</i> L.f.	Akkerdisdraai	LS	leaf	15.9	moderate
Aizoaceae (Mesembryanthea) – Mesembryanthemoidea					
<i>Brownanthus neglectus</i> Pierce & Gerbaulet	Brandkaros	LS/SS	stem	9.4	moderate
<i>Brownanthus nucifer</i> (Hltenf. & Bitterich) Pierce & Gerbaulet	Akkerdisdraai	LS	leaf	7.1	long
<i>Brownanthus pseudoschlichtianus</i> Pierce & Gerbaulet	Hellskloof	LS/SS	stem	6.2	moderate
<i>Mesembryanthemum hypertrophicum</i> (Dinter) Gerbaulet	Brandkaros	LS	leaf	5.0	annual
<i>Mesembryanthemum</i> sp.	Akkerdisdraai	LS	leaf	9.3	annual
<i>Mesembryanthemum</i> sp.	Hellskloof	LS	leaf	9.5	annual
<i>Psilocaulon</i> sp.	Hellskloof	LS	leaf	7.4	moderate
<i>Phyllobolus sinuosus</i> (L. Bol.) Gerbaulet	Akkerdisdraai	LS	leaf	13.6	moderate
<i>Phyllobolus</i> sp.	Hellskloof	LS	leaf	6.0	short
Aizoaceae (Mesembryanthea) – Ruschioideae					
<i>Antimima</i> sp.	Hellskloof	LS	leaf	11.9	moderate
<i>Astridia</i> cf. <i>hallii</i>	Hellskloof	LS	leaf	10.6	moderate
<i>Astridia longifolia</i> (L. Bol.) L. Bol.	Akkerdisdraai	LS	leaf	8.7	moderate
<i>Cephalophyllum</i> sp.	Akkerdisdraai	LS	leaf	10.6	moderate
<i>Cheiridopsis robusta</i> (Haw.) N.E. Br.	Akkerdisdraai	LS	leaf	11.1	moderate
<i>Conophytum saxetanum</i> (N.E. Br.) N.E. Br.	Brandkaros	LS	leaf	6.4	long
<i>Conophytum</i> sp.	Akkerdisdraai	LS	leaf	7.4	long
<i>Dracophilus dealbatus</i> (N.E. Br.) Walg.	Brandkaros	LS	leaf	8.9	moderate
<i>Drosanthemum uniflorum</i> L. Bol.	Hellskloof	LS	leaf	8.1	moderate
<i>Drosanthemum</i> sp. 1	Hellskloof	LS	leaf	10.7	short
<i>Drosanthemum</i> sp. 2	Hellskloof	LS	leaf	14.7	short
<i>Eberlanzia stylosa</i> (L. Bol.) L. Bol.	Akkerdisdraai	LS	leaf	15.0	moderate
<i>Leipoldtia weingangiana</i> (Dinter) Dinter & Schwant.	Akkerdisdraai	LS	leaf	18.1	moderate
<i>Leipoldtia schultzei</i> (Schltr. & Diels) Friedr.	Akkerdisdraai	LS	leaf	14.9	moderate
<i>Leipoldtia schultzei</i> (Schltr. & Diels) Friedr.	Hellskloof	LS	leaf	16.2	moderate
<i>Mitrophyllum</i> sp.	Hellskloof	LS	leaf	14.0	moderate
<i>Psammophora modesta</i> (Dinter & Berger) Dinter & Schwant.	Brandkaros	LS	leaf	8.3	long
<i>Ruschia schneideriana</i> (Berger) L. Bol.	Akkerdisdraai	LS	leaf	7.9	moderate

Table 1 (continued).

Species	Site	Growth-form*	Tissue sampled	Discrimination (%)	Estimated life span
<i>Ruschia</i> sp.	Akkerdisdraai	LS	leaf	10.7	moderate
<i>Ruschia</i> sp.	Akkerdisdraai	LS	leaf	10.3	moderate
<i>Ruschia</i> sp.	Hellskloof	LS	leaf	9.7	moderate
<i>Stoeberia arborescens</i> Van Jaarsveld	Hellskloof	LS	leaf	10.6	long
<i>Stoeberia frutescens</i> (L. Bol.) Van Jaarsveld	Akkerdisdraai	LS	leaf	6.3	long
<i>Synaptophyllum juttae</i> (Dinter & Berger) N.E. Br.	Hellskloof	LS	leaf	9.1	short
Unknown sp.	Hellskloof	LS	leaf	8.4	long
Anacardiaceae					
<i>Ozoroa concolor</i> (Presl ex Sond.) De Winter	Akkerdisdraai	RT	leaf	14.8	long
<i>Rhus populifolia</i> E. Mey. ex Sond.	Akkerdisdraai	RS	leaf	16.8	long
<i>Rhus undulata</i> Jacq.	Akkerdisdraai	RT	leaf	15.2	long
Apocynaceae					
<i>Pachypodium namaquanum</i> (Wyley ex Harv.) Welw.	Akkerdisdraai	SS	leaf	15.8	long
Asclepiadaceae					
<i>Sarcostemma viminalis</i> (L.) R. Br.	Augrabies	SS	stem	5.5	long
Asphodelaceae (Part A)					
<i>Trachyandra</i> sp.	Akkerdisdraai	HP-G	leaf	20.3	short
Asphodelaceae (Part B)					
<i>Aloe ramosissima</i> Pillans	Akkerdisdraai	LS	leaf	6.5	long
Asteraceae					
<i>Berkheya fruticosa</i> (L.) Ehrh.	Akkerdisdraai	ES	leaf	18.2	moderate
<i>Didelta carnosus</i> (L.f.) Ait. var <i>carnosus</i>	Akkerdisdraai	HP	leaf	18.4	short
<i>Didelta spinosa</i> (L.f.) Ait.	Akkerdisdraai	DS	leaf	17.5	moderate
<i>Gazania lichtensteinii</i> Less.	Akkerdisdraai	A	leaf	18.0	annual
<i>Osteospermum polycephalum</i> (DC.) T. Norl.	Akkerdisdraai	A	leaf	18.3	annual/biennial
<i>Othonna opima</i> Merxm.	Akkerdisdraai	LS	leaf	16.9	moderate
<i>Othonna</i> sp.	Akkerdisdraai	LS	leaf	18.4	moderate
<i>Senecio corymbiferus</i> DC.	Akkerdisdraai	LS	leaf	14.7	moderate
<i>Senecio longiflorus</i> (DC.) Sch. Bip.	Akkerdisdraai	LS	leaf	9.9	moderate
<i>Ursinia</i> sp.	Akkerdisdraai	A	leaf	20.9	annual
Brassicaceae					
<i>Heliophila</i> sp.	Akkerdisdraai	A	leaf	21.0	annual
Burseraceae					
<i>Commiphora capensis</i> (Sond.) Engl.	Akkerdisdraai	SS	leaf	18.1	long
Capparaceae					
<i>Boschia albitrunca</i> (Burch.) Gilg. & Ben.	Akkerdisdraai	RT	leaf	18.9	long
Chenopodiaceae					
<i>Atriplex cinerea</i> Poir subsp. <i>bolusii</i> (C.H. Wr.) Aell.	McDougall's Bay	ES	leaf	5.9	moderate
<i>Salsola nollothensis</i> Aell.	McDougall's Bay	ES	leaf	3.9	moderate

Table 1 (continued).

Species	Site	Growth-form*	Tissue sampled	Discrimination (%)	Estimated life span
Crassulaceae					
<i>Crassula deceptor</i> Schonl. & Bak. f.	Akkerdisdraai	LS	leaf	6.8	moderate
<i>Crassula subacaulis</i> Schonl. & Bak. f. subsp. <i>erosula</i> (N.E. Br.) Tolken	Akkerdisdraai	LS	leaf	7.7	moderate
<i>Crassula fusca</i> Herre	Akkerdisdraai	LS	leaf	6.5	moderate
<i>Crassula muscosa</i> L.	Akkerdisdraai	LS	leaf	10.6	moderate
<i>Crassula rupestris</i> Thunb.	Akkerdisdraai	LS	leaf	7.4	moderate
<i>Crassula sericea</i> Schonl. var. <i>velutina</i> (Friedr.) Tolken	Akkerdisdraai	LS	leaf	5.6	moderate
<i>Crassula</i> sp.	Akkerdisdraai	LS	leaf	7.0	moderate
<i>Tylecodon bucholzianus</i> (Schuldt & Stephens) Tolken	Akkerdisdraai	LS	leaf	8.6	moderate
<i>Tylecodon paniculatus</i> (L.f.) Tolken	Akkerdisdraai	LS	leaf	5.5	long
<i>Tylecodon rubrovenosus</i> (Dinter) Tolken	Akkerdisdraai	LS	leaf	5.5	moderate
Ebenaceae					
<i>Euclea pseudebenus</i> E. Mey. ex A. DC.	Akkerdisdraai	RT	leaf	17.8	long
Euphorbiaceae					
<i>Euphorbia decussata</i> E. Mey. ex Boiss.	Akkerdisdraai	SS	leaf	12.2	long
<i>Euphorbia dregeana</i> E. Mey. ex Boiss.	Akkerdisdraai	SS	leaf	6.3	long
<i>Euphorbia hamata</i> (Haw.) Sweet	Akkerdisdraai	SS	leaf	11.2	long
<i>Jatropha orangeana</i> Dinter ex P.G. Mey.	Akkerdisdraai	LS	leaf	16.9	long
Fabaceae					
<i>Acacia</i> cf. <i>karoo</i>	Brandkaros	RT	leaf	20.5	long
<i>Indigofera</i> sp.	Akkerdisdraai	A	leaf	15.2	annual
<i>Schotia afra</i> (L.) Thunb.	Akkerdisdraai	RT	leaf	15.4	long
Geraniaceae					
<i>Pelargonium crithmifolium</i> J.E. Sm.	Akkerdisdraai	LS	leaf	17.5	moderate
<i>Pelargonium klinghardtense</i> Knuth	Akkerdisdraai	LS	leaf	17.5	moderate
<i>Sarcocaulon crassicaule</i> Rehm	Akkerdisdraai	SS	leaf	18.3	moderate
Hyacinthaceae					
<i>Lachenalia</i> sp.	Akkerdisdraai	HP-G	leaf	18.1	short
Moraceae					
<i>Ficus cordata</i> Thunb.	Akkerdisdraai	ET	leaf	15.8	long
Oxalidaceae					
<i>Oxalis</i> sp.	Akkerdisdraai	A	leaf	20.7	annual
Poaceae					
<i>Cladoraphis cyperoides</i> (Thunb.) S.M. Philips	McDougall's Bay	HP	leaf	5.1	short
<i>Karoochloa</i> sp.	Akkerdisdraai	HP	leaf	5.6	short
<i>Stipagrostis</i> sp.	Akkerdisdraai	HP	leaf	5.5	short

Table 1 (continued).

Species	Site	Growth-form*	Tissue sampled	Discrimination (‰)	Estimated life span
Portulacaceae					
<i>Anacampseros</i> cf. <i>papyracea</i>	Brandkaros	LS	leaf	9.2	long
<i>Ceraria fruticulosa</i> Pearson & Stephens	Akkerdisdraai	LS	leaf	13.6	long
<i>Ceraria fruticulosa</i> Pearson & Stephens	Brandkaros	LS	leaf	13.3	long
<i>Ceraria namaquensis</i> (Sond.) Pearson & Stephens	Akkerdisdraai	LS	leaf	14.3	long
Scrophulariaceae					
<i>Aptosimum spinescens</i> (Thunb.) Weber	Akkerdisdraai	ES	leaf	18.1	moderate
<i>Heibenstretitia</i> sp.	Akkerdisdraai	A	leaf	19.7	annual
<i>Hyperia</i> sp.	Akkerdisdraai	A	leaf	16.8	annual
<i>Nemesia</i> sp.	Akkerdisdraai	A	leaf	17.9	annual
<i>Sutera tomentosa</i> (Thunb.) Hiern	Akkerdisdraai	ES	leaf	17.1	moderate
Solanaceae					
<i>Solanum</i> sp.	Akkerdisdraai	RS	leaf	19.2	long
Tamaricaceae					
<i>Tamarix usneoides</i> E. Mey. ex Bunge	Brandkaros	RT	leaf	17.8	long
Urticaceae					
<i>Forsskaolea candida</i> L.f.	Akkerdisdraai	ES	leaf	13.8	moderate
Verbenaceae					
<i>Plexipus garipensis</i> (E. Mey.) R. Fernandes	Akkerdisdraai	A	leaf	16.6	annual
Zygophyllaceae					
<i>Zygophyllum cordifolium</i> L.f.	Akkerdisdraai	ES	leaf	17.5	long
<i>Zygophyllum</i> cf. <i>macrocarpum</i>	Akkerdisdraai	ES	leaf	17.1	long
<i>Zygophyllum prismatocarpum</i> E. Mey. ex Sond.	Akkerdisdraai	ES	leaf	15.5	long

*A = annual, ES = evergreen shrub/subshrub, DS = deciduous shrub/subshrub, RT = riparian tree, RS = riparian shrub, LS = leaf succulent, SS = stem succulent; HP = herbaceous perennial, G = geophyte.

significant correlation of leaf morphology (succulent or non-succulent) or phenology (evergreen or deciduous) with carbon isotope discrimination and thus water use efficiency. The great majority of woody shrubs and subshrubs, however, were characterized by the presence of evergreen succulent leaves.

To provide an assessment of the range of variability of carbon isotope fractionation present in a given species at a specific site, we collected and individually analyzed leaf samples from 41 individuals of *Pachypodium namaquanum* (Apocynaceae) at the Akkerdisdraai site in the Richtersveld. Although nearly half of all individuals had a Δ value of 16‰, single individuals tailed out to values of 14 and 18‰ (Figure 4). This

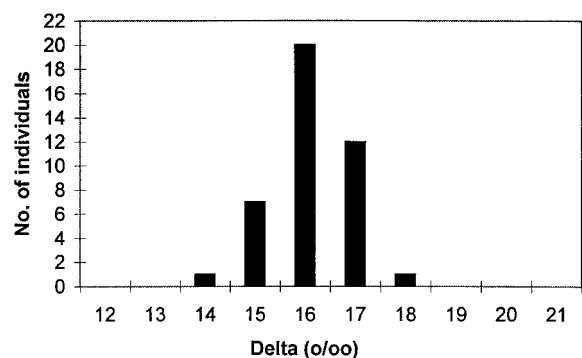


Figure 4. Distribution of carbon isotope discrimination (Δ) in leaf tissues from 41 individuals of *Pachypodium namaquanum* (Apocynaceae) from Akkerdisdraai, Richtersveld National Park.

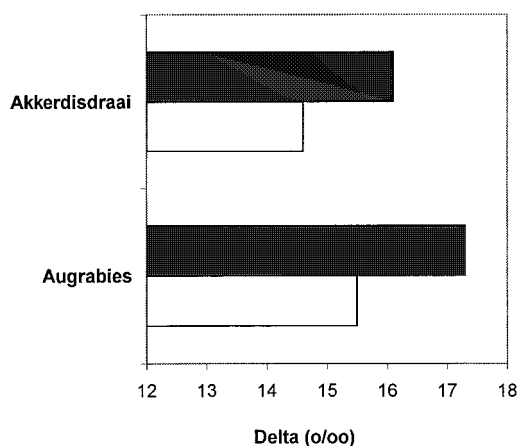


Figure 5. Comparative carbon isotope discrimination (Δ) in leaf tissues from first-year seedlings (dark bars) and mature shrubs (open bars) of *Zygophyllum prismatocarpum* (Zygophyllaceae) at Akkerdisdraai and Augrabies.

range showed some inverse correlation with age of the plant (data not shown).

To better assess the significance of shrub age and site conditions on discrimination, we compared analyses of leaf tissues of mature shrubs and seedlings of the evergreen shrub *Zygophyllum prismatocarpum* (Zygophyllaceae) at each of two sites. At both Akkerdisdraai and Augrabies there was a large difference in Δ , with seedlings exhibiting 1.5 and 1.8‰ more positive discrimination, respectively (Figure 5). There was also a strong difference between sites for discrimination in this species. Mature shrubs and seedlings had Δ values 0.9 and 1.2‰ higher, respectively, at Augrabies, demonstrating thereby lower average water use efficiency.

Since new leaf tissues are generally formed annually in the Richtersveld species studied, we compared analyses for eight species (including both C_3 and CAM flexible species) collected at Akkerdisdraai in both 1995, a relatively dry year, and 1996, a relatively wet year. These data showed no pattern of difference in discrimination between the two years (Figure 6).

The relationship between growth form and/or species longevity and water use efficiency in Richtersveld species was assessed by dividing 44 C_3 species into four categories of growth form. Six species of long-lived shrubs had a relatively tight distribution of Δ ranging from 15–18‰ (Figure 7). The lowest value, indicating higher water use efficiency, was found in *Zygophyllum prismatocarpum*, while the highest Δ value occurred in the deciduous stem succulent *Commiphora capensis* (Bursaceae). There was a

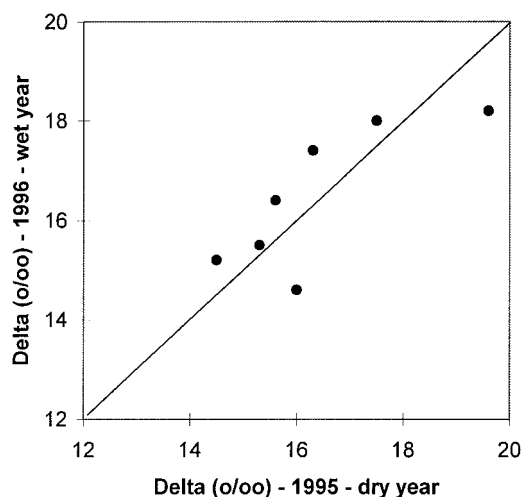


Figure 6. Comparative carbon isotope discrimination (Δ) between the relatively dry year of 1995 and relatively wet year of 1996 for leaf tissues of individual species at Akkerdisdraai, Richtersveld National Park. Both obligate C_3 and CAM-flexible species are included.

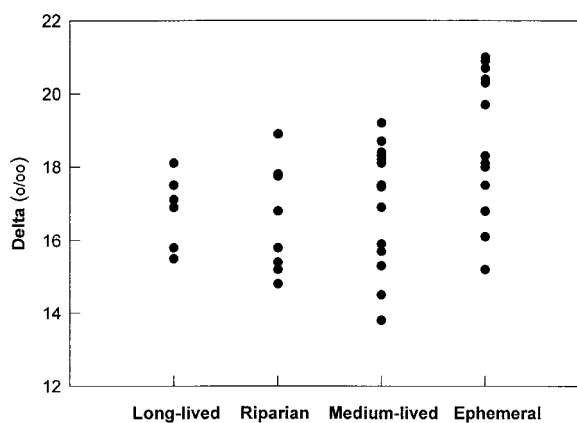


Figure 7. Distribution of values of carbon isotope discrimination (Δ) among leaf tissues in species representing four growth forms in the Richtersveld. Growth forms included in this analysis are long-lived shrubs surviving to well over 20 years (often 100 years or more), long-lived riparian trees of wash woodland habitats, moderate-lived small shrubs surviving an estimated 5–20 years, and ephemeral species including annuals and geophytes.

much broader range of Δ , however, in riparian species at Akkerdisdraai with discrimination values of 14–19‰. The lowest value was found in the deciduous *Ozoroa concolor* (Anacardiaceae), and the highest in the evergreen *Boscia albitrunca* (Capparaceae).

A broad range of carbon isotope discrimination was found in the 16 species of moderate-lived subshrubs sampled in this survey, ranging from 13–19‰ (Figure 7). Two species, *Forsskaolea candida* (Urticaceae) and *Blepharis capensis* (Acanthaceae), had

the lowest value, while the highest value was found in a semi-woody *Solanum* species growing along sandy washes.

Although the highest values of carbon isotope discrimination found in our survey were present in ephemeral species at Akkerdisdraai, the range of Δ values was nevertheless broad (15–21‰), and not significantly different overall from that of any other growth form (Figure 7). The lowest value of 15‰ was found in a species of *Indigofera* (Fabaceae), and a Δ value of 16‰ occurred in species of *Sutera* (Scrophulariaceae) and *Plexipus garipiensis* (Verbenaceae). The highest Δ value of 21‰, and thus lowest water use efficiency, was present in a species of *Heliophila* (Brassicaceae), with four other taxa having values of 20‰. These were species of *Ursinea* (Asteraceae), *Oxalis* (Oxalidaceae), *Trachyandra* (Aspodelaceae) and *Acanthopsis disperma* (Acanthaceae).

Carbon isotope discrimination in CAM species

Putative species with CAM metabolism were compared with C_3 plants to investigate their relative levels of carbon isotope discrimination. Although no C_3 species had Δ values lower than 13‰, the majority of putative CAM species had Δ values of 5–11‰, indicating a strong reliance on CAM (Figure 8, Table 1). There were 10 putative CAM species, however, that had Δ values from 13–17‰.

The largest number of putative CAM species sampled were members of the Mesembryanthema. Taxa sampled in this family at Richtersveld sites covered a surprisingly broad range of Δ values from 5 to 17‰ (Figure 9, Table 1). At the low end of this range was the annual *Mesembryanthemum hypertrophicum* (5.0‰) which was particularly abundant on sandy flats in the western Richtersveld in February 1996. Also with low Δ values of 6–7‰ in our analyses were the shrubby *Stoeberia frutescens*, subshrubs *Brownanthus nucifer*, *Brownanthus pseudoschlichtianus*, *Phyllobolus* sp., *Psilocaulon* sp., and *Ruschia schneideriana*, and small dwarf succulents in the genus *Conophytum*.

Mesembryanthema with high values for carbon isotope discrimination more typical of C_3 species included *Leipoldtia weigangiana* (18.1‰), *Leipoldtia schultzei* (14.9, 16.2‰), *Eberlanzia stylosa* (15.0‰), *Drosanthemum* sp. (14.7‰) and *Mitrophyllum* sp. (14.0‰). In order to establish the potential variability of carbon isotope discrimination within individuals of a species of Mesembryanthema at a specific site, we sampled leaf tissues from 11 individuals of *Mitrophyll-*

lum clivorum at Augrabies. All individuals were found to have Δ values from 13–15‰ (Figure 10).

Most species of Crassulaceae in the genera *Crassula* and *Tylecodon* had low Δ values indicative of regular use of CAM. Analyzing data on 14 collections of Crassulaceae from Akkerdisdraai, Augrabies and McDougall's Bay (data from these last two sites not included here), we found that all but two collections had Δ values of 4–8‰ (Figure 11). One species of *Crassula*, *C. muscosa*, was an outlier with Δ values of 10‰ at both Akkerdisdraai and Augrabies. Among leaf succulent species of Portulacaceae (*Ceraria fruticulosa*, *C. namaquensis*), Δ values were higher at 14‰ in both species. Three species of stem succulent euphorbias sampled at Akkerdisdraai (*E. dregeana*, *E. hamata*, and *E. decussata*) had Δ values of 6.3 to 12.2‰.

Discussion

Diurnal patterns of carbon assimilation and related measurements of organic acid concentrations have been studied in a variety of perennial species from the Richtersveld, under both field and controlled growth conditions, and these measurements have provided a wealth of information about contrasting patterns of carbon fixation (Von Willert et al. 1985, 1992; Eller & Ferrari 1997). The use of carbon isotope analyses in leaf tissues, as we discuss here, offers an expanded seasonal assessment of the relative significance of CAM in succulent species over the time in which their leaves were formed and matured, as well as providing a comparative assessment of water use efficiency.

C_3 photosynthesis

Low values of discrimination in C_3 species are directly related to high water use efficiency, while high values indicate lower water use efficiency (Farquhar et al. 1982; Rundel et al. 1989; Ehleringer et al. 1993b,c). The C_3 species described here have Δ values ranging from 13 to 21‰, with the largest number of species falling in the 17–18‰ range. This distribution of Δ values among C_3 species in the Richtersveld flora is broadly comparable with values reported for other desert floras.

Surveys of desert plants from India, Saudi Arabia and Egypt reported a range of Δ from 14 to 22‰ (Winter & Troughton 1978a; Ziegler et al. 1981), while Sonoran Desert studies of woody species have

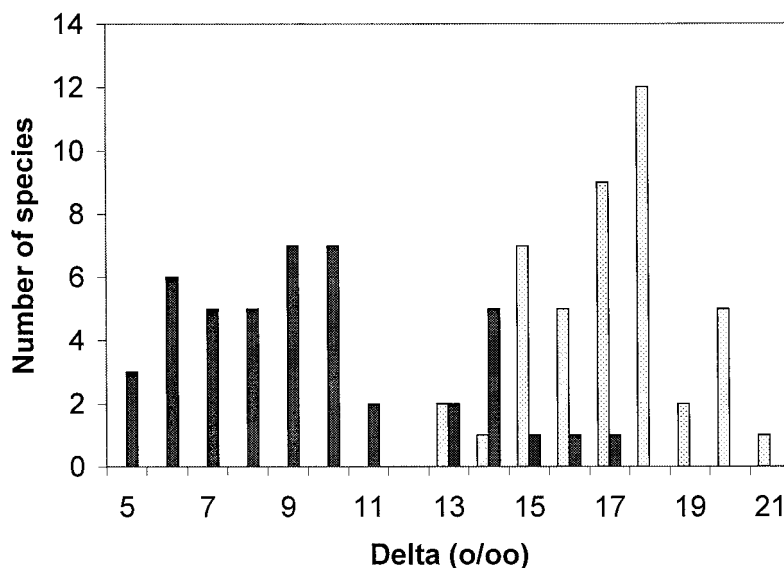


Figure 8. Comparative carbon isotope discrimination (Δ) leaf tissues of obligate C_3 species (stippled bars) and putative CAM species (solid bars) from the Richtersveld.

reported a Δ range of 15–20‰ (Ehleringer et al. 1987; Ehleringer & Cooper 1988). The hyperarid Atacama Desert in northern Chile has a flora with a similar range of Δ values from 11 to 20‰ (Ehleringer et al. 1998). However, the Atacama Desert exhibits somewhat higher water use efficiencies in a group of long-lived shrubs with discrimination values of 11–14‰, which are lower than those of comparable species in the Richtersveld. All of these desert regions exhibit Δ values which are generally lower than the mean global averages of about 20‰ for vascular plant species (Farquhar et al. 1982; O’Leary 1988). This pattern reinforces the significance of high water use efficiencies in the adaptive strategies of desert plants.

Comparative studies of carbon isotope fractionation between species are subject to a number of cautions (Kelly & Woodward 1995). The predictive models of relating water use efficiency and carbon isotope discrimination (Farquhar et al. 1982) assume a common vapor pressure gradient and leaf-air temperature differential for all species. By confining our analysis to Richtersveld species, we are able to minimize any impact of differential VPD environment on our results. Our observed differences in mean Δ between both mature shrubs and seedlings of *Zygo-phyllum prismatocarpum* between our primary study site at Akkerdisdraai and Augrabies (Figure 5) point out changes in Δ that can occur with only slightly

less xeric conditions caused by closer proximity to the coast.

The great majority of our study species have small leaf sizes, and therefore closely tracked ambient air temperatures. Ehleringer et al. (1992) have investigated the significance of leaf temperature differentials in impacting estimations of comparative water use efficiency. They found that temperature differentials of 2.5 °C or less caused no more than a 1‰ difference in Δ , allowing them to unambiguously rank desert plants with respect to comparative water use efficiency. We encountered species with leaf temperature differentials greater than this amount only in small succulents near ground level (e.g. *Psammophora*, *Anacampseros*, *Dracophilus*) and in *Aloe*.

Our data support the fact that plant age and genetics may impact carbon isotope discrimination within a species. The range of Δ of 4‰ reported here in a study of 41 individuals of *Pachypodium namaquanum* is comparable to ranges of variation reported for North American desert species within and between habitats (Ehleringer & Cooper 1988; Ehleringer 1993a; Rundel & Sharifi 1993). These ranges of variation may relate both to genetic polymorphisms for water use efficiency within the population (Donovan & Ehleringer 1994; Schuster et al. 1994) and to age-related differences in developmental plasticity of the phenotype (Sandquist et al. 1993).

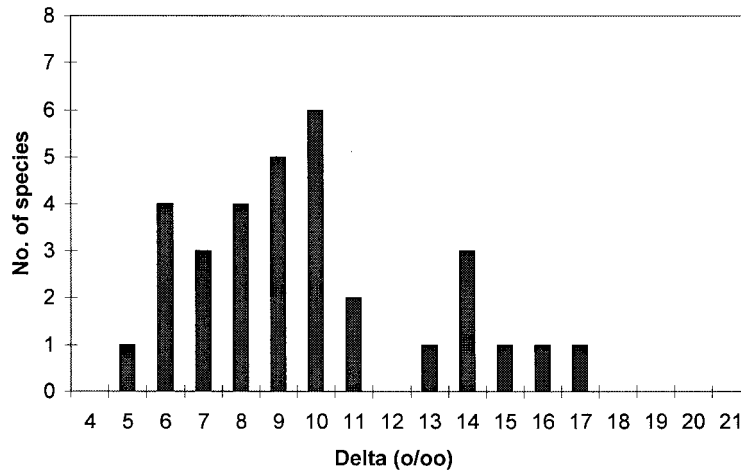


Figure 9. Comparative carbon isotope discrimination (Δ) in leaf tissues of 31 species *Mesembryanthema* (Aizoaceae) from the Richtersveld and adjacent areas.

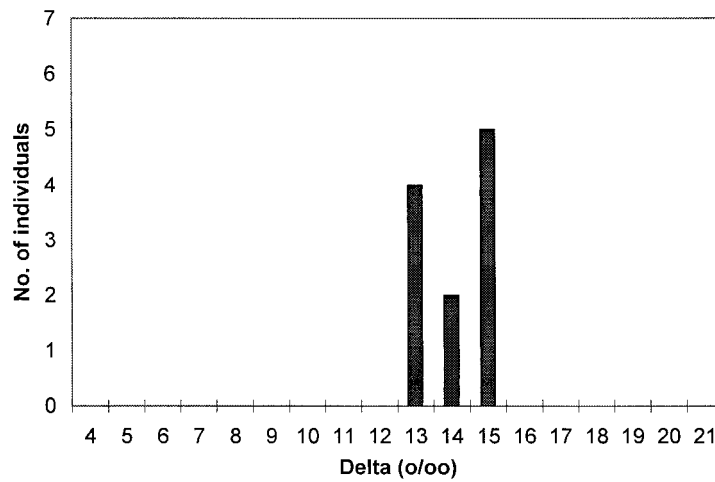


Figure 10. Distribution of carbon isotope discrimination (Δ) in leaf tissues from 11 individuals of *Mitrophyllum clivorum* (Mesembryanthema, Aizoaceae) from Augrabies.

Studies in the Sonoran Desert of North America have suggested that a pattern exists in which the carbon isotope discrimination at the species level is inversely related to plant life span (Ehleringer & Cooper 1988; Schuster et al. 1992). It was found that species with life span longer than 50 years had the lowest Δ values, while short-lived perennials with life spans of 2–5 years had the highest values. Medium-lived shrubs with a life span of 10–40 years were intermediate in Δ value. This pattern does not exist, however, in our data set of Richtersveld species (Figure 7). There was no statistically significant pattern of difference in the distribution of Δ values among long-lived shrubs, wash woodland trees, and moderate-lived shrubs in our samples. The lowest Δ values measured were

in two subshrubs with relatively moderate live spans, rather than occurring as expected in long-lived woody species.

Ephemeral species from the Richtersveld showed a very broad pattern of distribution, with a group of five species having higher Δ values of (20–21‰) than any longer-lived species (Figure 7). Low Δ values were also present in this group, however. This range of Δ values present in ephemeral species clearly suggests that there are very different patterns of water use efficiency among these taxa and thus multiple strategies of adaptation to the arid Richtersveld environment. Annual plants in North American warm deserts have been shown to utilize a variety of phenological, morpho-

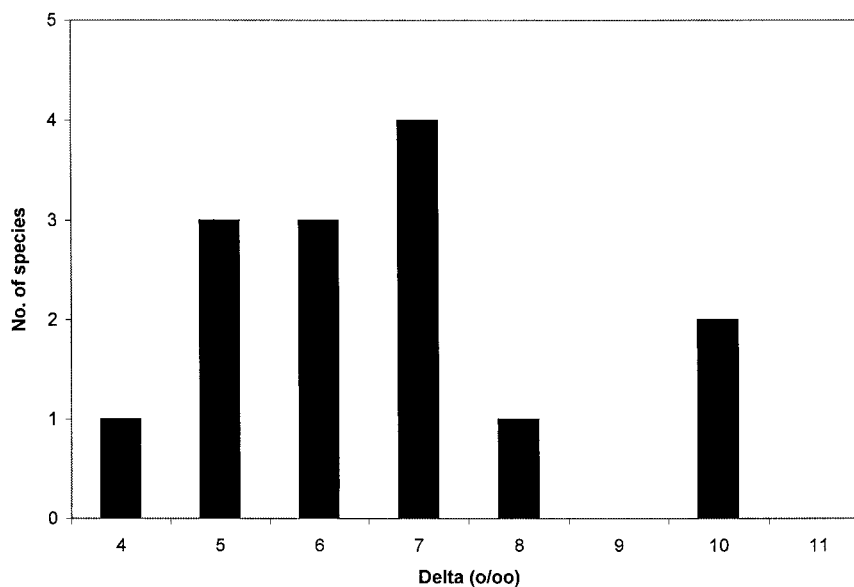


Figure 11. Distribution of carbon isotope discrimination (Δ) in leaf tissues of 14 collections of Crassulaceae from the Richtersveld area, Augrabies and McDougall's Bay.

logical and ecophysiological strategies of adaptation (Mulroy & Rundel 1977).

The absence of a clear pattern of inverse correlation between carbon isotope discrimination, and thus water use efficiency, and species longevity in the Richtersveld flora may well relate to the relative predictability of annual precipitation in the Succulent Karoo (Esler et al. 1999; Esler & Rundel 1999). A low coefficient of variation in patterns of annual precipitation means that extreme drought conditions in the Succulent Karoo are neither as frequent nor as severe as in North American deserts. It is extreme drought conditions that would select for the higher water use efficiency in long-lived shrubs as a strategy to maximize the potential for survival over the life span of the plant.

CAM photosynthesis

The widespread presence of CAM in the succulent flora of Namaqualand was demonstrated by Mooney et al. (1977) in a broad isotopic survey of South African and Namibian arid lands. Excluding C_4 species from consideration, carbon isotope discrimination values of 4–8‰ are generally indicative of a fixed reliance on CAM, while values of 14‰ or above point to reliance on or exclusive use of C_3 metabolism. Intermediate values suggest that CAM flexibility is present. The range of Δ values found among putative

CAM species in our survey strongly demonstrates that there is a wide variation in the degree to which these taxa utilize CAM.

Among the Crassulaceae and genus *Aloe* (Asphodelaceae), the great majority of species have Δ values within the range suggesting obligate use of CAM. It is impossible without further study to establish whether this condition represents a genetic trait or rather a phenotypic response to the arid Namaqualand environment. *Crassula muscosa* was an exception to this pattern, exhibiting indications of CAM-flexibility at two sites where it was sampled, and we have found Δ values indicative of CAM-flexibility and reliance on C_3 metabolism in species of *Crassula* and *Tylecodon* collected from less xeric areas of fynbos vegetation (data not shown).

Studies with organic acid cycles in three species of *Ceraria* from the Richtersveld suggest that significant CAM is present (Von Willert et al. 1992), and CAM flexibility is well known in the related genus *Portulacaria* (Lee & Assman 1992; Guralnick et al. 1992). The Δ values of 14‰ in *C. fruticulosa* and *C. namaquensis* indicate that there is a primary reliance on C_3 metabolism in these species. Our data further suggest strong CAM-flexibility in succulent-leaved *Senecio*, with a greater reliance on C_3 metabolism in *S. corymbosa* than in *S. longiflorus*, and in leaves of stem-succulent *Euphorbia*.

The physiology of CAM activity in species of *Mesembryanthema* has been investigated in a series of laboratory and field ecophysiological studies of succulent species native to the Richtersveld and other parts of the Succulent Karoo (Martin et al. 1988; Von Willert et al. 1992; Herppich et al. 1996). CAM-flexible patterns of carbon assimilation were found in most of the species studied, suggesting that photosynthetic modes are plastic in all subfamilies and subtribes of the *Mesembryanthema*. Our data support this suggestion, but moreover clearly point to a wide variation in the degree to which CAM species utilize a mode of photosynthetic plasticity between CAM and C₃ metabolism.

Several patterns of variation present in the range of Δ values exhibited among Aizoaceae in our survey may be related to phylogenetic and life history characteristics. One pattern is that Richtersveld samples of species within the subfamily Mesembryanthemoideae commonly had low Δ values indicative of complete reliance on CAM for carbon fixation. This group includes annual species of *Mesembryanthemum* which are known to exhibit irreversible shift to CAM photosynthesis with development (Winter & Von Willert 1972; Winter & Troughton 1978b; Herppich et al. 1992), but also shrubby species of *Phyllobolus* (in part), *Psilocaulon* and *Brownanthus*. As with the Crasulaceae, this trait in the latter shrubby species may be more environmentally induced than a fixed genetic trait. We have measured higher Δ values indicative of CAM-flexibility in samples of these genera from less xeric sites further south in Namaqualand (data not shown).

Low Δ values suggesting primary reliance on CAM photosynthesis were also present in a number of species within the subfamily Ruschioideae. This group of species with Δ values of 6–8‰ include woody shrubs (*Stoeberia* and *Ruschia*, in part) and miniature succulents (*Conophytum* and *Psammophora*) which share the characteristic of long life spans. Thus, it is possible that although carbon isotope discrimination and life span are not inversely related among C₃ species in the Richtersveld, this pattern may exist among the *Mesembryanthema* in the subgenus Ruschioideae. More study is necessary to adequately test this hypothesis.

From the data presented in this study, it can be seen that desert plants in the flora of the Richtersveld utilize a wide array of patterns of photosynthetic carbon assimilation, from C₃ to flexible CAM to pure CAM to C₄ metabolism. Among C₃ plants there is a range

of water use efficiency from high to relatively low, particularly in ephemeral species. Among the *Mesembryanthema*, there are clear indications that habitat conditions, phylogenetic relationships and longevity may all be factors in explaining the degree to which CAM is used in carbon assimilation. These data suggest that descriptions of functional plant niches should be based not only on traditional measures of plant morphology and phenology, but also on quantitative characterizations of ecophysiological traits in an arid-land environment such as this. With increasing data collection on the comparative water relations and photosynthetic plasticity of Namaqualand plant species, a better understanding of the evolution of community structure and species diversity in this region will certainly result.

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