

## The adaptive significance of growth form, leaf morphology, and CAM in the genus *Sansevieria*

AMALIA VIRZO DE SANTO, ANTONIETTA FIORETTO, ANNA ALFANI

Istituto di Botanica dell'Università di Napoli, Via Foria 223,  
I - 80139 Napoli, Italy.

### Riassunto

Sono state studiate le caratteristiche anatomiche e fisiologiche connesse con l'adattamento all'aridità di cinque specie del genere *Sansevieria*. La fotosintesi CAM, riscontrata in tutte le specie studiate, svolge un ruolo essenziale nella tolleranza all'aridità. Inoltre in tutte le specie esaminate è risultata molto elevata la resistenza alla perdita dell'acqua, grazie soprattutto al ridotto numero di stomi e all'elevato spessore della cuticola. Sulla base dei risultati sono state riconosciute come importanti strategie nell'adattamento all'aridità 1) la riduzione dell'interfaccia foglia-aria che si manifesta con la tendenza della foglia alla chiusura per saldatura dei margini e con la tendenza alla succulenza; 2) l'orientamento delle foglie parallelo ai raggi incidenti; 3) la riduzione del numero delle foglie per pianta. Le specie degli ambienti estremamente aridi presentano tutte e tre le caratteristiche, quelle degli ambienti meno xerici hanno, invece, foglie piatte, numerose e non erette. Tutte le possibili situazioni intermedie si possono riconoscere nelle specie di ambienti moderatamente aridi. Viene presentato uno schema delle possibili relazioni evolutive tra specie del genere *Sansevieria* con differente grado di adattamento all'aridità.

### INTRODUCTION

The genus *Sansevieria* Thunb. is chiefly confined to the tropical regions of the African continent, where most of the members are inhabiting semiarid and arid environments. The

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*Key Words:* Drought adaptation — Growth form — Leaf morphology — CAM — *Sansevieria*.

high degree of interspecific variability in leaf characteristics and growth form, within the genus *Sansevieria* (BROWN, 1915; PFENNIG, 1979), suggests that the species differ in their ability, and/or in the way adopted, to cope with different degree of environmental drought. Leaves range from fleshy to fleshy coriaceous and may be flat, channelled, half cylindrical or cylindrical indicating large differences in the surface/volume ratio; leaves also differ considerably for size, length ranging from 0.1 up to nearly 3 m, and for number per shoot that varies from only one, some two or three, up to fifteen and more. Because surface/volume ratio and leaf area affect carbon dioxide uptake and water loss (GIVNISH, 1979), the wide variation in leaf characteristics among the species of *Sansevieria* should be paralleled by a wide variation in water economy and carbon gaining efficiency.

Crassulacean Acid Metabolism (CAM) a biochemical variant of photosynthesis, which is regarded as an adaptive mechanism to conserve water in arid environments, has been documented in three species of *Sansevieria*, *S. trifasciata* (NUERNBERGK, 1961), *S. liberica* (MILBURN, 1968) and *S. thyrsiflora* (MOONEY *et al.*, 1977) and, as will be discussed later on, it has been found by the authors in other seven species of the genus.

This paper is a contribution to an understanding of the adaptive biology of the genus *Sansevieria*. Attention has been focused to the identification of the main functional and structural traits which enhance performance under low water supply.

#### MATERIALS AND METHODS

Five species of *Sansevieria* differing for leaf characteristics and growth form (Table 1) were obtained from the Orto Botanico, della Facoltà di Scienze, Università di Napoli. The specimens of all taxa were grown in the greenhouse under uniform environmental conditions.

Succulence (S) was determined according to DELF (1912):  
 $S = \text{water content (g)} / \text{surface (dm}^2\text{)}$ .

Table 1 - Leaf characteristic features and growth form of the study species

	Leaf form	Leaf dimensions (cm)			Leaf transection	Leaf orientation	Growth form
		Lenght	Width	Thickness			
<b>S. dooneri</b> N. E. Brown	linear-lanceolate	10-45	1.7-3	0.25 (at the middle)	slightly convex abaxially	recurved spreading from an erect basal part	lax rosette of 6-8 up to 20 leaves; thin creeping root- stock
<b>S. grandis</b> Hook var. <b>zuluensis</b>	elliptic	30-60	6-10	0.21-0.32	abaxially convex	ascending or ascending-spreading	rosette of 4-5 leaves; thick creep- ing rootstock
<b>S. aethiopica</b> Thumb.	linear, linear-lanceolate	13-43	1-1.4	0.37-0.58 (at the middle)	very convex ab- axially	ascending-spreading	rosette of 13-30 leaves; creeping rootstock
<b>S. gracilis</b> N. E. Brown	terete from a keeled base	23-60	0.6-0.9 (diameter at the top of the sheath, then gradually tapering)		at the base, for 5-13 cm, concave- chanelled adaxial- ly; above circular	ascending or spreading	8-12 leaves on a short stem (2.5-7 cm) often branched
<b>S. cylindrica</b> Bojer	cylindric	75-150	2-3 (diameter)		circular	stiffly erect	stemless with a stout creeping rootstock; 3-5 leaves two-ranked

Surface expansion (SE) was determined according to WALTER (1926):  $SE = \text{surface (cm}^2) / \text{fresh weight (g)}$ .

Transverse sections of fresh leaves from each species were observed at light microscope confining the attention on cuticular thickness, mesophyll characteristics and cell size. All measurements were made with an optical micrometer.

Chlorophyll content was determined after BRUINSMA (1963) by spectrophotometry (Zeiss PMQ II).

Malate content was measured enzymatically (HOHORST, 1970) in aqueous extracts (DE Luca *et al.*, 1977). Determinations were made on homogeneous samples collected at the end and at the beginning of the light period from plants which were normally watered. The measures were taken almost three weeks after transferring the plants from the greenhouse into a growth chamber (12 h light  $180 \text{ W m}^{-2}$  at the top of the leaves,  $27^\circ\text{C}$ , 54% RH; 12 h dark,  $15^\circ\text{C}$ , 84% RH).

To estimate water retentiveness leaves from each species, removed from the plants, were allowed to dry on a laboratory banch and the weight was recorded at intervals.

## RESULTS

Among the examined *Sansevierias* the species with bifacial leaves show lower succulence and higher surface expansion than the species with circular leaves (Table 2). Nevertheless, despite the remarkable leaf thickness, the degree of succulence is unexpectedly low in circular leaves, falling below the range (5-15 g  $\text{dm}^{-2}$ ) of typical succulents.

Leaf cross section evidences the same basic design in all study species. The mesophyll is differentiated outwardly into a tightly packed chlorenchyma and inwardly into a peculiar parenchyma; the latter consists of relatively large cells, containing few or no chloroplasts, interspersed among dead cells that we have named « hyalocysts ». Hyalocysts likely play an important role in water storage and transport (ALFANI *et al.*, 1983). The thickness of the chlorenchyma varies among the species. When

Table 2 - Leaf characteristics which influence water conserving ability and gas - exchange, chlorophyll content and CAM activity of 4 species of *Sansevieria*. Values are mean  $\pm$  one standard error.

		<i>S. dooneri</i>	<i>S. grandis</i> var. <i>zuluensis</i>	<i>S. aethiopica</i>	<i>S. gracilis</i>
Succulence (H <sub>2</sub> O mg/dm <sup>2</sup> )		0.59 $\pm$ 0.05	0.89 $\pm$ 0.09	0.97 $\pm$ 0.20	2.11 $\pm$ 0.26
Surface expansion (cm <sup>2</sup> /g f.wt.)		15.91 $\pm$ 1.29	9.33 $\pm$ 1.33	10.32 $\pm$ 1.62	4.62 $\pm$ 0.62
Thickness of cuticle and wax wall complex ( $\mu$ m)	adaxial	7.60 $\pm$ 0.035	12.90 $\pm$ 0.016	8.70 $\pm$ 0.006	8.50 $\pm$ 0.008
	abaxial	7.20 $\pm$ 0.004	10.90 $\pm$ 0.020	9.10 $\pm$ 0.008	
Stomatal density on leaf surface no/mm <sup>2</sup>	adaxial	8.60 $\pm$ 0.142	19.90 $\pm$ 0.261	20.50 $\pm$ 0.298	11.30 $\pm$ 0.235
	abaxial	10.30 $\pm$ 0.168	18.30 $\pm$ 0.285	18.70 $\pm$ 0.246	
Chlorophyll a+b (mg/g f.wt.)		0.482 $\pm$ 0.03	0.283 $\pm$ 0.02	0.395 $\pm$ 0.06	0.232 $\pm$ 0.03
Malic acid accumulation ( $\mu$ eq/g f.wt.)		146.50 $\pm$ 64.02	74.21 $\pm$ 24.62	108.64 $\pm$ 8.88	38.40 $\pm$ 13.61

measuring the thickness of chlorenchyma the occurrence of hyalocysts served as a base for defining the outer boundary of the inner parenchyma. The species with the thickest chlorenchyma are *S. aethiopica* (adaxial + abaxial band: to 1200  $\mu\text{m}$ ) and *S. gracilis* (the circular band of chlorenchyma is to 620  $\mu\text{m}$  thick); however, in *S. gracilis*, chloroplasts are very abundant in the outermost 2-3 cell layers and diminish very rapidly in

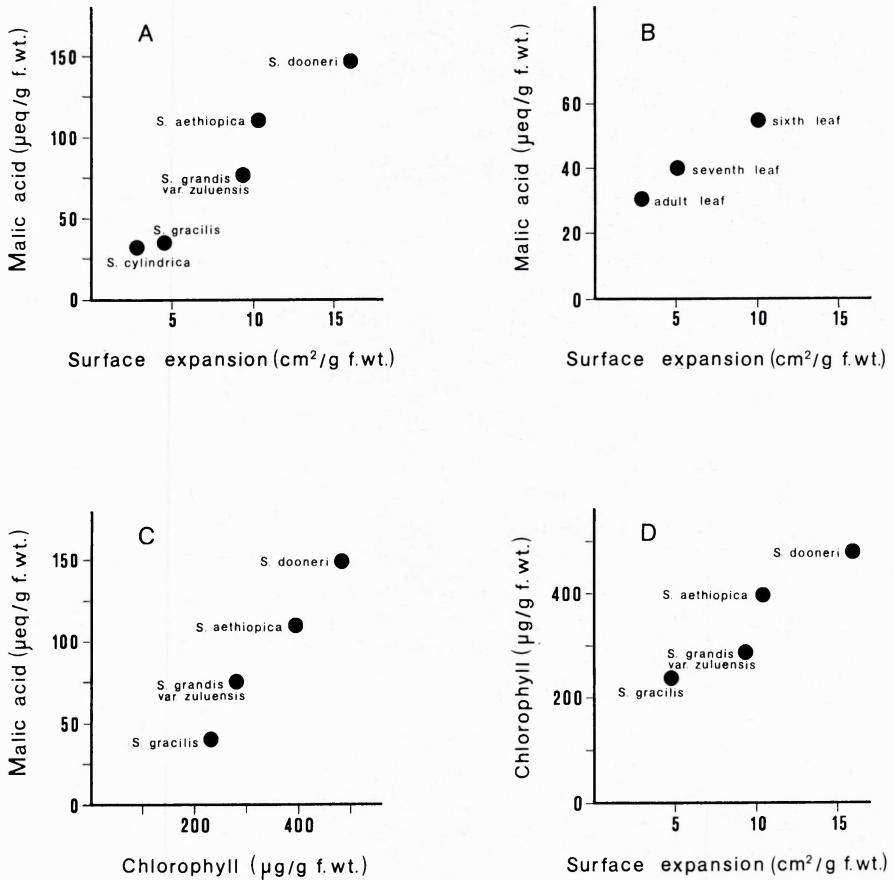


Fig. 1. - A: Relation between overnight malic acid accumulation and surface expansion in five species of *Sansevieria* and B: in adult and young (sixth and seventh leaves were used for determinations) specimens of *S. cylindrica*. C: relation between overnight malic acid accumulation and leaf chlorophyll content in four species of *Sansevieria*. D: relation between chlorophyll content and surface expansion in four species of *Sansevieria*.

the deeper chlorenchyma layers. *S. dooneri* has chlorenchyma (adaxial + abaxial band) to 680  $\mu\text{m}$  thick; *S. grandis* var. *zuluensis* has the thinnest chlorenchyma (adaxial + abaxial band: to 402  $\mu\text{m}$ ) among the studied species, but numerous cells with few chloroplasts also occur deeply in the inner parenchyma. All the values refer to measurements taken at the middle of leaf length.

The largest chlorenchymatous cells have been found in *S. dooneri* (mean diameter 60  $\mu\text{m}$ ), while the smallest ones are those of *S. aethiopica* (mean diameter 33  $\mu\text{m}$ ); in *S. grandis* var. *zuluensis* cell dimensions are two times larger on the adaxial (mean diameter 44  $\mu\text{m}$ ) than on the abaxial (mean diameter 22  $\mu\text{m}$ ) leaf side. Chlorenchymatous cells of *S. gracilis* are a little smaller (mean diameter 50  $\mu\text{m}$ ) than those of *S. dooneri*.

The thickness of the inner parenchyma increases from *S. dooneri* to *S. grandis* var. *zuluensis* and even more considerably to *S. aethiopica* and *S. gracilis*.

Vascular bundles, enclosed by a bundle sheath of cells bearing chloroplasts, are evenly scattered throughout the inner parenchyma; very numerous bundle fibers penetrate both the

Table 3 - Leaf succulence, surface expansion, chlorophyll content and CAM activity of *S. cylindrica* in the adult and in the juvenile stage. Individual measurements.

	adult stage	juvenile stage	
		VII *	VI *
Succulence (H <sub>2</sub> O mg/dm <sup>2</sup> )	3.03	1.71	0.67
Surface expansion (cm <sup>2</sup> /g f.wt.)	2.87	5.21	10.08
Chlorophyll a+b (mg/g f.wt.)	0.523	0.434	0.524
Malic acid accumulation ( $\mu\text{eq/g}$ f.wt.)	29.73	39.54	53.84

\* sixth and seventh leaves

chlrenchima and the inner parenchyma. The relatively low values found for the degree of succulence likely depend on the abundance of fibers. Raphides are common in all species.

The epidermis is one layered and shows a well developed cuticle (Table 2). Stomata occur on the whole surface of circular leaves; bifacial leaves are amphistomatic. Stomatal density is very low (Table 2) and falls in the range of CAM succulents (KLUGE & TING, 1978) which averagely show values ten times lower than  $C_3$  and  $C_4$  plants. Among the examined species the highest number of stomata per unit leaf area has been found in *S. aethiopica* and in *S. grandis* var. *zuluensis*, the lowest in *S. dooneri*. Guard cells are barely sunken in *S. dooneri* and *S. grandis* var. *zuluensis* and tend to be somewhat deeper in *S. gracilis* and *S. aethiopica*.

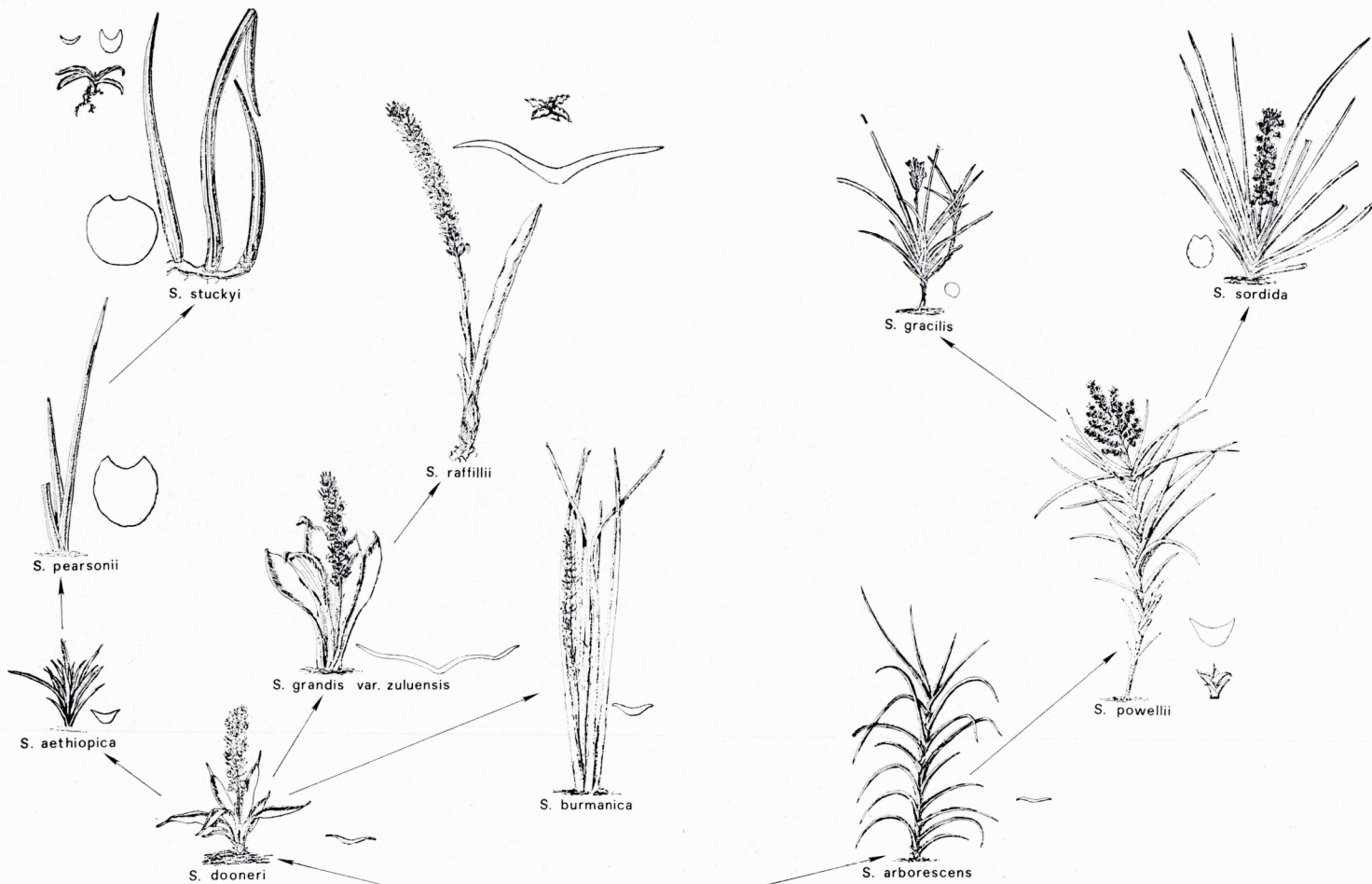
Chlorophyll content varies considerably among the species (Table 2). The highest content has been found in *S. dooneri*, the lowest in *S. gracilis*. Chlorophyll content and surface expansion are positively and significantly (Spearman's  $r = 1$ ) correlated (Fig. 1 D).

Overnight malate accumulation was measured during spring and late summer throughout two years; determinations were repeated four times on *S. grandis* var. *zuluensis* and *S. gracilis* and three times on *S. dooneri* and *S. aethiopica* with two replicates for each species. The results (mean and standard error) are reported in Table 2. Despite all measurements were made under the same controlled conditions, the degree of variation within each species is high likely because the tested leaves differed for age, or because of seasonal changes in their physiolo-

Fig. 2. - Model of the possible evolutionary relationship of growth forms and leaf morphology in the genus *Sansevieria* exemplified through species exhibiting different degree of adaptation to aridity. The configuration of the juvenile stage is reported for some species. For *S. stuckyi* leaf sections of juvenile stage are shown. All leaf transverse sections are in scale. Plant size are in scale with the only exception of *S. stuckyi*, which is about 1.3 times more reduced than the other species. Young plant of *S. stuckyi* in scale with the adult plant. Young plant of *S. powellii* 6 times less reduced than the adult plant.



VARIATIONS ASSOCIATED WITH ADAPTATION TO ARIDITY



ANCESTRAL FORM (ROSETTE WITH THIN BIFACIAL LEAVES)

gical activity. Among the study species *S. dooneri* shows the highest malate accumulation and *S. gracilis* the lowest, with values almost four times as low as those measured for *S. dooneri*. In *S. grandis* var. *zuluensis* malate accumulation is almost two times as low as that of *S. dooneri*, while a much smaller difference has been found between *S. dooneri* and *S. aethiopica*.

In the study species CAM activity seems to be not related to cell dimensions; in fact the highest values of malate accumulation have been observed in *S. dooneri*, that exhibits the largest chlorenchymatous cells, and in *S. aethiopica* with the smallest chlorenchymatous cells; besides malate accumulation is low in *S. gracilis* that shows relatively large chlorenchymatous cells. It is apparent in Table 2 that the species with higher surface expansion show higher CAM activity. Indeed malate accumulation and surface expansion, a leaf factor that affects gas exchange, are positively and significantly (Spearman's  $r = 1$ ) correlated (Fig. 1 A). More generally malate accumulation is lower in cylindric leaves, with lower surface expansion, than in bifacial leaves, as it is evident by comparing *S. gracilis* and *S. cylindrica* with *S. dooneri*, *S. grandis* var. *zuluensis* and *S. aethiopica* (Table 2 and 3).

In the genus *Sansevieria* the species having cylindric leaves exhibit a remarkable variability in the form of the leaf according to plant age (Fig. 2); seedlings, as well as young plants from cuttings, have moderately thin, flattened or concave leaves which are gradually succeeded by other leaves that are thicker, less flat, more ascending, and finally by more and more cylindric, erect leaves. A pattern of variation for surface expansion and malate accumulation similar to that observed between species with flat leaves and species with cylindric leaves can also be recognized within the same species between leaves of adult and leaves of young plants. Thus in *S. cylindrica* (Table 3) the thin and flat leaves of the young plant show lower succulence and higher surface expansion than the cylindric leaves of the adult plant; besides CAM activity is higher in the flat leaves of the juvenile stage (Fig. 1 B).

Chlorophyll content is very high in *S. cylindrica* both in adult and in young plants (Table 3) and seems to be unrelated to

malate accumulation. On the contrary there is a strong correlation (Spearman's  $r = 1$ ) between chlorophyll content and malate accumulation for *S. dooneri*, *S. grandis* var. *zuluensis*, *S. aethiopica* and *S. gracilis* (Fig. 1 C).

Cylindric leaves show higher water retentiveness than flat leaves (Fig. 3); the data support a strong relation of water loss with surface expansion and cuticle thickness. When excised, the slightly succulent leaves of *S. dooneri*, exhibiting high surface expansion and relatively thin cuticle (Table 2), lost 4% of their fresh weight during the first day and 11% during 12 days (Fig. 3).

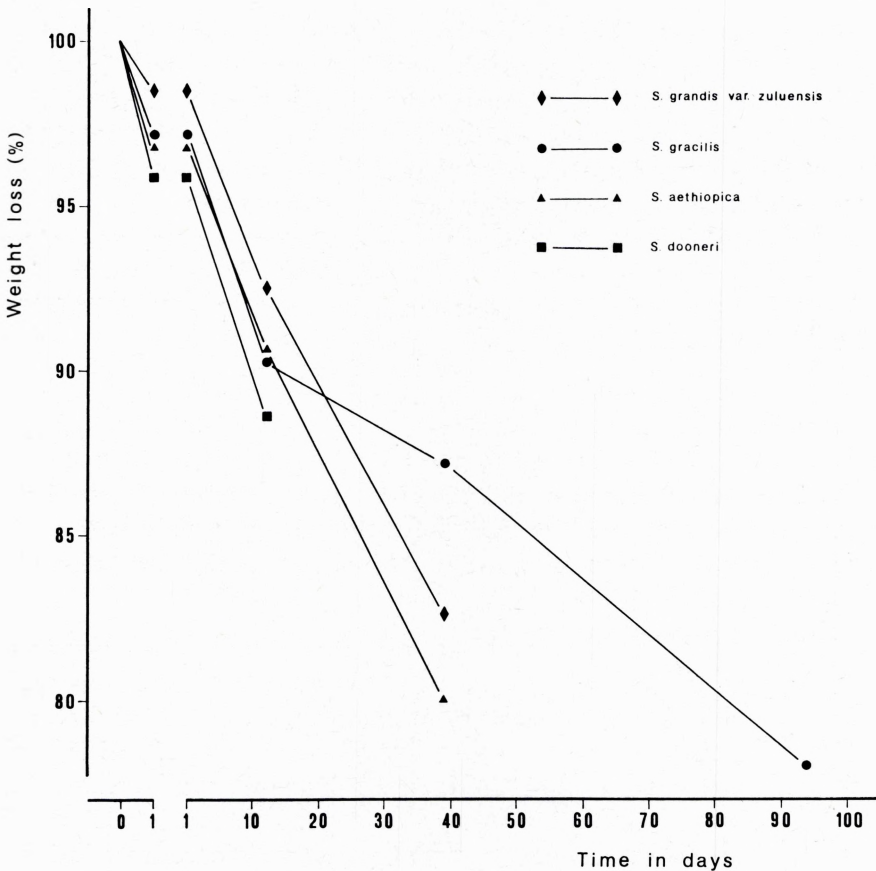


Fig. 3. - Water retentiveness of four species of *Sansevieria* expressed as weight loss of excised leaves versus time. Initial leaf weight put equal 100.

Under the same conditions, the more succulent leaves of *S. aethiopica* showing a thicker cuticle and a relatively lower surface expansion, lost 3% of their fresh weight during the first day, 9,5% during 12 days and 20% during 39 days. The leaves of *S. grandis* var. *zuluensis*, that exhibit the thickest cuticle among the study species and the lowest surface expansion among the species with flat leaves, showed the greatest water conserving ability losing 1,5% of their fresh weight during the first day, 7,5% during 12 days and 17,4% during 39 days. The leaves of *S. dooneri* did not tolerate high water loss and died two weeks after excision, while *S. aethiopica* and *S. grandis* var. *zuluensis* survived as long as six weeks. The leaves of *S. gracilis*, with a relatively thin cuticle but a very low surface expansion (Table 2) lost 3% of the fresh weight during the first day and 9,7% during 12 days; thereafter the fresh weight showed the least decline over time, losing only 13% in 39 days and 22% in 94 days; this would suggest that cuticle and/or leaf resistance to water loss increase by drying. Moreover *S. gracilis* appears to be capable of tolerating high water loss, the leaves being still alive after 94 days from excision; besides, as shown by ALFANI *et al.* (1983), moderate drought increases CAM activity in this species.

## DISCUSSION

The data presented indicate that the species of *Sansevieria* with flat leaves are less suited for life in extremely dry environments when compared with the species exhibiting cylindrical leaves.

The study species and, as reported above, *S. trifasciata*, *S. liberica* and *S. thyrsiflora*, all with flat erect leaves, as well as *S. canaliculata* with solitary erect cylindrical leaves and *S. rorida* with two ranked cylindrical leaves (ALFANI *et al.*, 1983 and unpublished data) exhibit CAM; in all probability all the species of *Sansevieria* perform CAM. CAM is a biochemical variant of photosynthesis that enhances water conserving because of night-time CO<sub>2</sub> fixation; moreover CAM plants are able to maintain a functional photosynthetic apparatus through periods of severe environmental drought allowing CO<sub>2</sub> fixation to commence al-

most immediately when water is again available (OSMOND, 1982).

The values measured for stomatal density (Table 2) are among the lowest found for xerophytes as reported in KRAMER (1969) and in KLUGE & TING (1978). Thus it can be assumed that minimum stomatal resistance, that depends primarily on stomatal number (BANNISTER, 1976), is large in the study species. Moreover the thick cuticle undoubtedly plays an important role in lowering water loss. Among the examined species the lowest values for stomatal density and for cuticle thickness have been found in *S. dooneri* and in *S. gracilis* (Table 2); nevertheless the two species greatly differ for water retentiveness (Fig. 3) and for CAM activity (Table 2). In fact when comparing *S. dooneri* with *S. gracilis* the rate of water loss and the rate of night carbon fixation are lower in *S. gracilis* which exhibits a very low surface expansion. As also confirmed by the data concerning *S. grandis* and *S. aethiopica* (Table 2, Fig. 3) and by the data concerning young and adult plants of *S. cylindrica*, the extent of leaf-air interface is the most effective feature controlling gas exchange. The cost of the adaptive marked reduction of water loss results in a lower carbon gaining ability. Really *S. dooneri* grows more fast than *S. gracilis* and other species with cylindric leaves.

Morphological adaptations represent primary means for plant to cope with environmental conditions. Anatomical features such as succulence, thick cuticle, low stomatal density, dense clorenchyma, low surface/volume ratio, few or only one leaf per plant that reduces the whole plant surface, leaf orientation parallel or nearly parallel to incident light rays that reduces the absorption of radiant energy, all are interpreted as adaptations enhancing water conservation and/or retarding water loss from the plant.

A better understanding of plant adaptive biology is possible if the morphological features are considered in the context of plant life history, physiology, and ecology.

The juvenile stage of all species of *Sansevieria* is a rosette with flat leaves while the adult stage may show different growth form and different form of leaves within the species of the genus (Fig. 2). The rosette form occurs in many plants. Rosette

with a leaf divergence of about  $138^\circ$  is considered the most effective configuration for radiation interception (EHLERINGER *et al.*, 1979). The adult stage of *S. dooneri* and of others among the less xeric species of *Sansevieria* is a rosette of many thin leaves recurved spreading from an erect basal part.

The presented physiological data (Table 2 and 3; Fig. 1 and 3) are consistent with the significance attributed to the anatomical features.

Under the ecological point of view, it must be remarked that in tropical Africa the species of the genus *Sansevieria* are common to different plant communities (SCHNELL, 1976; PFENNIG, 1979) as xeric wood (*S. suffruticosa*), savannah (*S. liberica*) and subdesertic steppe (*S. stuckyi*, *S. singularis*); they occur on sandy (*S. raffillii*) as well as on rocky substrate (*S. volkensis*) usually in sunny microhabitats (*S. gracilis*) and sometimes under light shade (*S. parva*). Mean annual precipitation and rainfall regime in the habitats of the different species of *Sansevieria* are quite different; rainfall can be evenly distributed throughout the year or concentrated in one period; but in any case such habitats are characterized by low water availability. Moreover water availability in sandy and in rocky substrates may be limiting due to rapid drainage and to high evaporation potential especially in open sites.

The species from environments with scanty rainfall (as for instance *S. stuckyi* of the subdesertic steppe), the species living in soil where water is available only for a short time following rainfall (as for instance *S. raffillii* of sandy soil), and those from open dry habitats characterized by high evaporative demand (as for instance *S. gracilis*), are really those showing all or several of the most xeromorphic features above mentioned (Fig. 2).

Let the juvenile stage of all the *Sansevieria* is a rosette, let the more mesic species of *Sansevieria* show a rosette configuration also in the adult stage, it is plausible that the xeromorphic *Sansevieria* have evolved from a mesomorphic ancestor whose growth form was a rosette with thin bifacial leaves (Fig. 2). The main evolutionary events would have been a) the reduction of surface/volume ratio, that decreases the extent of the leaf-air interface and implicates the increase of leaf succu-

lence; b) the reduction of the leaf area of the whole plant; and c) leaf orientation reducing radiation interception. Some species of *Sansevieria* (as for instance *S. gracilis*, *S. aethiopica*, *S. grandis*, *S. burmanica*) have experienced only one of the three main events in their evolutionary history, other species two events (as for instance *S. raffillii*, *S. sordida*), others finally all the three events (*S. stuckyi*). Moreover the ability to perform CAM was undoubtedly an useful feature in the adaptation to arid environments.

Further outdoor and laboratory studies are needed to provide much experimental support for the relationships among growth form, water economy and productivity, as well as to determine the ultrastructural and physiological basis of drought resistance in the genus *Sansevieria*.

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#### SUMMARY

Anatomical and physiological features related to drought adaptation were analyzed for five species of *Sansevieria*. All the species perform CAM and show thick cuticle and low stomatal density. In the less xeric species flat leaves with relatively high surface/volume ratio, are present; in the species adapted to the most extreme aridity, erect cylindrical leaves with low surface/volume ratio are produced that exhibit extraordinary capacity for water retention but a low carbon gaining capacity. The evolutionary trends of growth form and leaf morphology are suggested on the basis of their adaptive significance.

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