

Variability of CAM in leaf-deciduous succulents from the Succulent Karoo (South Africa)

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Abstract

Seasonal or drought-induced deciduousness is a common adaptational strategy in aboveground persistent succulent species native to the Succulent Karoo (South Africa). This feature may appear together with crassulacean acid metabolism (CAM) in stems and/or leaves. Due to differences in morphology or life cycle, different species may exhibit different degrees of flexibility in the expression of CAM. The potential for CAM plasticity has not been investigated in leaf-deciduous succulents of the Succulent Karoo. Diurnal gas exchange and nocturnal organic acid accumulation were measured to investigate whether the expression of CAM may vary in *Tylecodon paniculatus* (L.F.) Toelken (Crassulaceae), *Monilaria moniliformis* (Mesembryanthemaceae) and *Ceraria fruticulosa* H. Pearson & Stephens (Portulacaceae), a selection of leaf-deciduous succulents. These species differ both in leaf and stem morphology. In the seasonal deciduous *Tylecodon paniculatus* only obligate CAM was found, regardless of the plant water status. When droughted *Monilaria moniliformis* switches directly from CAM-cycling (C_3 -like diurnal gas exchange patterns combined with nocturnal acid accumulation) to CAM-idling (gas exchange completely ceased while acid accumulation still continued). This seasonal deciduous species has also both succulent leaves and stem. A highly flexible CAM expression (CAM-cycling, full-CAM and CAM-idling) was observed in the drought deciduous *Ceraria fruticulosa* (non-succulent stem showing no CAM) in response to changes in water availability. The ecological significance of the observed diversity in the flexibility of CAM expression was discussed in terms of morphological traits, and the relative ecological significance of both metabolic adaptation and leaf-deciduousness.

Saisonal oder durch Trockenstress induzierter Blattwurf ist eine relativ häufige Überlebensstrategie in oberirdisch überdauernden Sukkulente der Sukkulente Karoo in Süd Afrika. Diese Eigenschaft kann in Kombination mit einem Crassulaceen Säurestoffwechsel (CAM) im Sproß und/oder in den Blättern auftreten. Der CAM gilt allgemein als ein physiologischer Anpassungsmechanismus an Trockenheit. In Arten mit unterschiedlicher Morphologie oder Lebenszyklen kann er unterschiedlich flexibel auftreten. Diurnaler Gaswechsel und nächtliche Akkumulation von Apfel- und Zitronensäure wurden in den saisonal bzw. durch Trockenstress induziert laubwerfenden Arten *Tylecodon paniculatus* (L.F.) Toelken (Crassulaceae), *Monilaria moniliformis* (Mesembryanthemaceae) und *Ceraria fruticulosa* H. Pearson & Stephens (Portulacaceae) gemessen, um deren

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CAM-Ausprägung zu charakterisieren. *Tylecodon paniculatus* zeigte unabhängig vom Blattwasserzustand ausschließlich obligaten CAM. Im Gegensatz dazu wechselte *Monilaria moniliformis* bei Trockenstress von typischem CAM-cycling (C_3 -typisches Gaswechsellmuster, aber nächtliche Akkumulation organischer Säuren) direkt zu CAM-idling. Der diurnale Gasaustausch ist dann bei dieser saisonal laubwerfenden Art nahezu vollständig unterbunden, die nächtliche Säureakkumulation bleibt aber bestehen. Hohe CAM-Flexibilität konnte auch bei *Ceraria fruticulosa* gezeigt werden. In Abhängigkeit von der Wasserversorgung traten bei dieser trockenstress-induziert laubwerfenden, blattsukkulenter Art (nicht-sukkulenter Stamm ohne CAM) hier alle bisher beschriebenen Formen des CAM (CAM-cycling, obligater CAM und CAM-idling) auf. Diese Variabilität in der CAM-Flexibilität der unterschiedlichen laubwerfenden Blattsukkulenten wird im Hinblick auf mögliche morphologische Einflüsse, sowie die relative ökologische Relevanz beider Anpassungsstrategien (CAM, Sukkulenz) diskutiert.

Key words: Adaptational strategies – CAM flexibility – night-time organic acid accumulation – photosynthesis – Succulent Karoo.

Introduction

The Succulent Karoo, a winter-rainfall desert of north-western South Africa, is characterised by a high biodiversity and a large number of succulent species, in particular taxa in the families of the Mesembryanthemaceae and the Crassulaceae (Jürgens 1986, Milton et al. 1997). These succulents have developed various integrated and co-adapted morphological and ecophysiological features that maximise their chances of surviving the detrimental conditions in arid habitats. From the results of numerous long-termed field investigations on the ecophysiology of plants of the Namib desert and the Karoo, von Willert et al. (1990) proposed a hierarchical ranking of the importance of the different adaptational strategies found in these succulents. Based on the duration of the respective life-cycles, they distinguished ephemerals, annuals, paucennial and perennials. Among the latter, a relatively common strategy in various genera of the southern African flora (von Willert et al. 1992) is above-ground persistent perennialism. Many species, with or without succulent stems, have deciduous succulent leaves. In contrast to leaf shedding, CAM is more widespread although it is assumed to be of relatively low importance in the proposed hierarchy of adaptational strategies in these desert plants (von Willert et al. 1990).

On the other hand, CAM can be expressed in various ways. Its expression may range from a C_3 -type pattern of photosynthesis to nearly exclusive night-time CO_2 uptake. This range of extremes may be found within one species during progressing plant development and/or as a response to changes in environmental conditions (De Santo & Bartoli 1996, Herppich et al. 1998). This variability in the expression of CAM may also be recognised within different species of a single genus (Lüttge 1996, Herppich & Herppich 1996). CAM plasticity is assumed to be of particular

adaptive value (Lüttge 1996). For example, it may explain the great range of adaptability of species in the genus *Kalanchoë* (Kluge & Brulfert 1996).

To our knowledge, no information is available to what degree CAM expression may vary in deciduous leaf-succulent shrubs from the Succulent Karoo. We were, therefore, interested whether CAM plasticity also occurs in deciduous plants, collected from this region and grown under controlled conditions. In order to include different ecological and morphological elements of the life strategies found in above-ground perennial succulents with deciduous leaves we selected *Tylecodon paniculatus* (Crassulaceae, seasonal deciduous, succulent shoot), *Monilaria moniliformis* (Mesembryanthemaceae, seasonal deciduous, non-succulent shoot) and *Ceraria fruticulosa* (Portulacaceae, drought deciduous, succulent shoot) for our investigations.

Material and methods

Plant material and growth conditions

The seasonal deciduous Botterboom *Tylecodon paniculatus* (L.F.) Toelken (Crassulaceae) is widespread in the Western Cape Province and Namibia (Court 1981). The shrubs can reach heights of up to 2 m. Their succulent stems are covered with a yellowish bark which is photosynthetically active (CAM, von Willert et al. 1992). The large fleshy leaves (degree of succulence $S \geq 3 \text{ g cm}^{-2}$) abscise before the brick-red nodding flowers appear.

Monilaria moniliformis (Thunb.) Ihlenf. & Jörg. (Mesembryanthemaceae) is a small shrublet which grows up to 20 cm (Ihlenfeldt & Jörgensen 1971, Smith et al. 1998). Each year it develops two types of leaf pairs per season (Smith et al. 1998). The first leaves are small (length 0.3–1 cm), and the second

cylindrical leaves ($S \geq 8 \text{ g cm}^{-2}$) are up to 10 cm long. The genus is found from Vanrhynsdorp northwards into Namaqualand.

Ceraria fruticulosa H. Pearson & Stephens (Portulacaceae) is a dwarf shrub between 5 and 50 cm (Jürgens 1990) with small (4 to 6 mm) more or less cylindrical ($S \geq 4 \text{ g cm}^{-2}$) leaves. This species is native to Namaqualand, Bushmanland and the area south of Lüderitz, Warmbad and Keetmanshoop (Court 1981).

T. paniculatus and *C. fruticulosa* were collected in Numees, in the Richtersveld, and *M. moniliformis* in the Knersvlakte (for closer information, c.f. von Willert et al. 1992). *T. paniculatus* and *Ceraria* are normally found in open habitats on northwest-facing rocky slopes (Jürgens 1986). *M. moniliformis* grows fully exposed, mostly on clay and quartzitic soils (Schmiedel & Jürgens 1999).

The plants were grown in the greenhouse of the Dept. of Plant Ecology (Münster) under semi-controlled conditions for several years. Typically, temperature ranged between 18 °C and 25 °C during the day and 12 °C and 15 °C during the night. Natural light was supplemented by high-pressure mercury lamps (Power Star W/D, Osram, München, Germany) to provide photosynthetic photon fluence rates (PFR) of 350–450 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at plant level.

Gas exchange measurements and determination of malic and citric acid

At least one week before the start of the experiments, plants were transferred into a growth chamber (Eco-phyt Model VEPHQ 5/1350, Heraeus-Voetsch, Balingen, Germany) and grown at 25 °C/15 °C day/night air temperature, a dew point of 12 °C, and photon fluence rates of 450–500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at plant level (light period: 12 h; Osram HQI-R 250W/NDL, Osram, München, Germany). Using fully developed, non-senescent leaves (*T. paniculatus* and *M. moniliformis*) or whole twigs with at least 10 leaves (*C. fruticulosa*) CO_2 exchange was measured with a differential infrared gas analyser (BINOS 4b.2, Fisher-Rosemount GmbH u. Co., Hanau, Germany) in an open system (Minicuvette, H. Walz GmbH, Effeltrich, Germany). Dew point mirrors (H. Walz GmbH, Effeltrich, Germany) monitored the humidity of the air entering and leaving the temperature-controlled gas exchange chambers. Gas exchange parameters, calculated from data continuously recorded by a computer at 5 min intervals, were based on the total leaf surface. Approximately 1 h and 9 h after illumination, leaf samples were taken, their shape immediately drawn on paper, weighed and dried to constant weight at 85 °C. The areas of the paper traces were obtained with an area

meter (Delta T Devices, Cambridge, UK). Leaf surface area was estimated as twice the projected area in *T. paniculatum*. Leaves of *M. moniliformis* and *C. fruticulosa* were treated as cylinders in order to calculate areas. In hot-water extracts of the dried leaf material the contents of malic and citric acid were determined by means of a gas chromatograph (Varian aerograph, series 3600; Varian, Walnut Creek, USA).

During the experiments plants were well watered for 3 days, then drought stress was induced by withholding watering for 12 d. Afterwards, plants were well watered again. Each cycle was at least repeated once. Two plants (*M. moniliformis* and *C. fruticulosa*) were used for each study.

Results

Diurnal patterns of gas exchange of *Tylecodon paniculatus* were typically the same as those of an obligate CAM plant. In well-watered plants atmospheric CO_2 was taken up during night and day. On the other hand, daytime carbon gain rapidly ceased during drought while it remained more or less unaffected at night (Fig. 1). This was always accompanied by a substantial night-time accumulation of both citric and malic acid (data not shown).

In contrast, night-time CO_2 uptake never occurred in *Monilaria moniliformis*, regardless of the water status of the plants. In this species, gas exchanges ceased day and night when water was withheld (Fig. 2). The considerable night-time malic (137 $\text{mmol kg}^{-1} \text{DM}$) and citric acid (52 $\text{mmol kg}^{-1} \text{DM}$) accumulation was found to be only slightly affected by water availability.

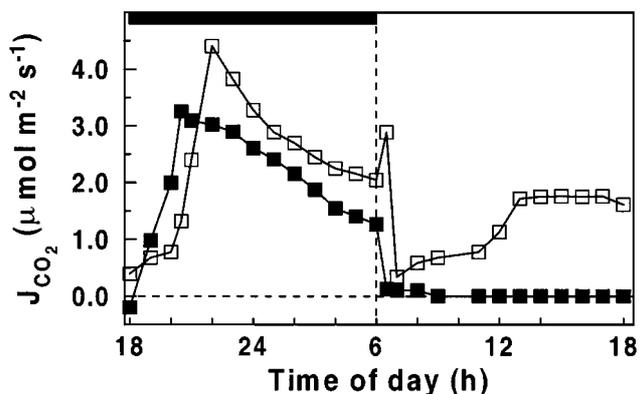


Fig. 1. Patterns of diurnal net CO_2 exchange rates (J_{CO_2}) of well-watered (open symbols) and drought stressed (closed symbols) plants of *Tylecodon paniculatus* as measured under controlled environmental conditions in a growth chamber. The black bar denotes night-time hours.

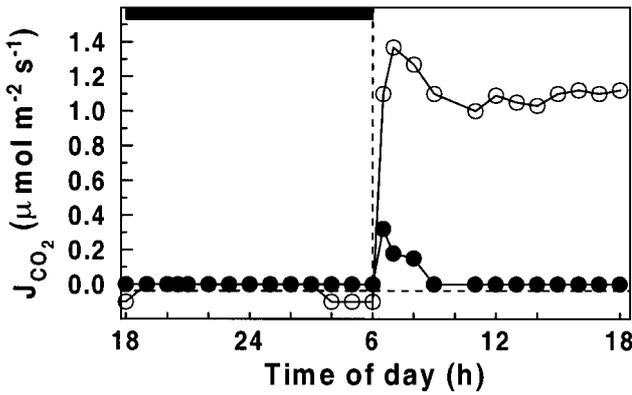


Fig. 2. Diurnal patterns of net CO₂ exchange of well-watered (open symbols) and drought stressed (closed symbols) plants of *Monilaria moniliformis* as measured under controlled environmental conditions in a growth chamber. The black bar denotes night-time hours.

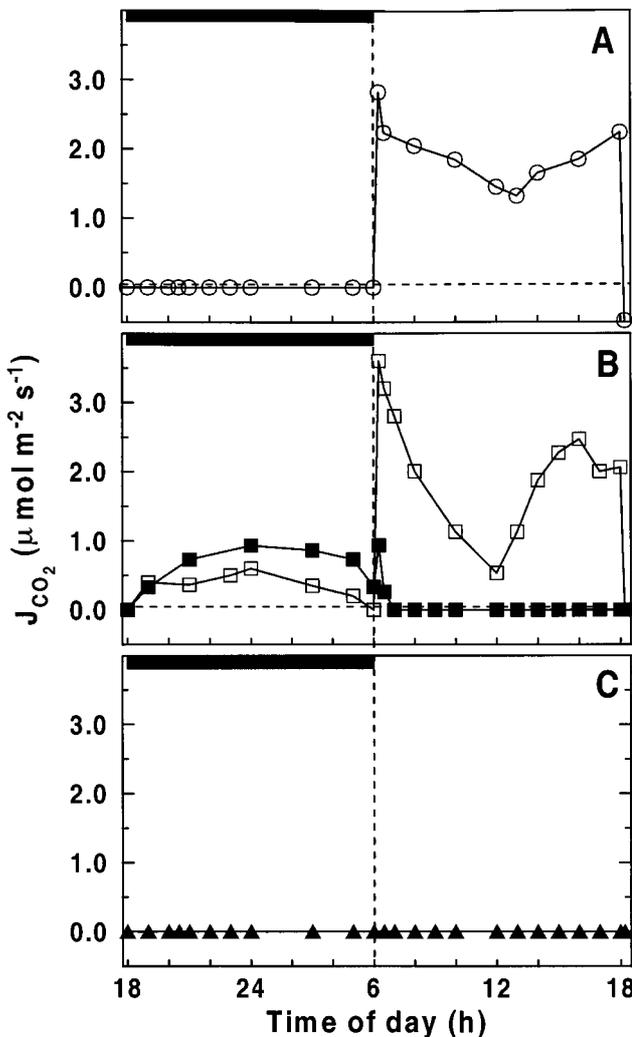


Fig. 3. Diurnal patterns of net CO₂ exchange determined in plants of *Ceraria fruticulosa* that have been watered daily (A), 3 (open symbols) and 9 (closed symbols) days after withholding watering (B), and after 12 days of drought (C). The black bar denotes night-time hours.

A distinct plasticity of CAM features was found in *Ceraria fruticulosa*. When well watered only daytime CO₂ uptake was observed (Fig. 3A). Nevertheless, this was accompanied by a pronounced night-time accumulation of organic acids (malic acid: 78 mmol kg⁻¹_{DM}; citric acid: 28 mmol kg⁻¹_{DM}). This means that *Ceraria fruticulosa* utilizes CAM-cycling (Martin 1996) under this condition. A reduced or irregular water supply stimulated CO₂ uptake during the night, while daytime uptake was reduced (Fig. 3B). Nocturnal acid accumulation increased concomitantly (malic acid: 220 mmol kg⁻¹_{DM}; citric acid: 101 mmol kg⁻¹_{DM}). During prolonged drought closed stomata prevented any CO₂ uptake throughout the day/night period (Fig. 3C) and plants showed pattern of CAM-idling (Rayder & Ting 1981; malic acid: 54 mmol kg⁻¹_{DM}; citric acid: 34 mmol kg⁻¹_{DM}). Watering the plants reversed these changes, and the stomata opened again at daytime.

Discussion

Monilaria moniliformis exhibited all features of a typical CAM-cycling plant (Martin 1996). The amount of nocturnally accumulated malic acid (c. 250 mmol kg⁻¹_{DM}) was well within the range observed for *Delosperma tradescantioides* (200 to 380 mmol kg⁻¹_{DM}; Herppich et al. 1996); however, the degree of photosynthetic plasticity was lower in *Monilaria moniliformis* when compared with other Mesembryanthemaceae. For example, in *Delosperma tradescantioides* (Herppich et al. 1996) and *Aptenia cordifolia* (Herppich & Peckmann 1997) all modes of CAM could be observed.

On the other hand, *Ceraria fruticulosa* reversibly switches from CAM cycling to “full-CAM” (Kluge & Ting 1978) and to CAM-idling (Rayder & Ting 1981), depending on water supply. This high flexibility in the expression of CAM and the large degree of daytime CO₂ uptake clearly corresponds with the finding of Rundel et al. (1999). Their analysis of carbon isotope discrimination showed that this shrubby species largely relies on C₃ photosynthesis in the field. In addition, CAM plasticity and a pronounced ability to utilize the CAM-cycling mode of photosynthesis is also well known for other species of the Portulacaceae native to North America (Martin et al. 1988b). A highly flexible CAM-expression is known for several succulent species native to the Succulent Karoo (Rundel et al. 1999). The leaf-succulents *Drosanthemum hispidum* (Martin et al. 1988a) and *Delosperma tradescantioides* (Herppich et al. 1996), both being South African species of the Mesembryanthemaceae, may also exhibit similar pronounced flexibility in the expression of CAM.

Table 1. Examples of aboveground perennial plants having succulent, deciduous leaves that grow in the Succulent Karoo and that exhibit different combinations of leaf and stem features and shoot photosynthetic metabolisms. The data of *Brownanthus schlichtianus* were taken from von Willert et al. (1992).

| Species | Type of deciduousness | Shoot type | Shoot metabolism | CAM mode of leaves |
|----------------------------------|-----------------------|---------------|------------------|--------------------|
| <i>Ceraria fruticulosa</i> | Drought | Non-succulent | C ₃ | Flexible CAM |
| <i>Brownanthus schlichtianus</i> | Drought | Succulent | CAM | Low obligate CAM |
| <i>Monilaria globosa</i> | Seasonal | Succulent | CAM | CAM-cycling |
| <i>Tylecodon paniculatus</i> | Seasonal | Succulent | CAM | Obligate CAM |

In contrast to *Monilaria moniliformis* and *Ceraria fruticulosa*, *Tylecodon paniculatus* exhibited a very limited flexibility in its mode of carbon metabolism. This species always utilized strict CAM, virtually independent of plant water status and environmental temperature or air humidity conditions (Herppich & von Willert, unpublished results).

Overall, the results indicate that deciduous succulent species from the Succulent Karoo utilize all CAM modes previously described in the literature (Winter & Smith 1996, Herppich et al. 1998). The reason(s) for this diversity in the metabolic plasticity among species from this arid region is/are not clear. Different life histories, i.e. whether the plants shed or retain their leaves throughout the year, has been identified as one possible reason for the divergent flexibility in the expression of this carbon metabolism in perennials species. The importance of life history as well as life form as an essential determinant of the mode of CAM has been emphasized by Kluge & Brulfert (1996), based on their comparative investigations on many species of the genus *Kalanchoë* native to Madagascar. In contrast, the species examined in the present study are true deciduous perennials (von Willert et al. 1992), thus certainly having the same life history. As a result of leaf shedding, all species might be considered as "quasi-annuals" (Kluge & Brulfert 1996) avoiding the "dangerous months of the dry season by behaving analogously to geophytes" (Kluge & Brulfert 1996). Nevertheless, they showed a pronounced difference in their degree of CAM flexibility.

Hence, the variability in CAM expression may result from differences in the degree of leaf succulence. This parameter seems to exhibit a strong negative effect on the plasticity of the CAM mode. Among Malagasy *Kalanchoë* species Kluge and Brulfert (1996) observed a "clear correlation between the expression of CAM and plant morphology". These authors recognised that those species showing a high degree of CO₂ fixation during the day (i.e. a high flexibility) had relatively thin leaves. However, in the present study all three species had succulent leaves. Furthermore, *Tylecodon paniculatus*, showing the least flexibility, had less succulent leaves than the other species. Thus, dif-

ferences in leaf morphology cannot explain the differences in CAM expression.

According to Lüttge (1996) plasticity (or flexibility) of CAM should be of particular adaptive value when interacting stress factors are not extreme or when stresses are highly variable over time. In contrast, extreme levels of stresses result in the evolution of specialist behavior. All plants investigated here grow in the winter rain region of the Succulent Karoo and were found in comparable microhabitats with similar mean environmental conditions, and lacking extreme stress (von Willert et al. 1992). Thus, the extent of stress, experienced by these plants in their natural environment does not seem to be the decisive element determining the degree of CAM plasticity in these species.

Comparing the diverse levels of life strategies of the species investigated (as summarised in Table 1), CAM flexibility did also not depend on whether deciduousness was drought or seasonally induced. For example, the seasonal deciduous species *Tylecodon paniculatus* exhibited exclusively obligate CAM, i.e. virtually no metabolic plasticity was observed. On the other hand, in *Monilaria moniliformis* only CAM-cycling was detected. Very similar behaviour could be found in the drought deciduous species *Brownanthus schlichtianus* (von Willert et al. 1992). This species performs only obligate CAM (von Willert et al. 1992). In contrast to *Ceraria*, *Brownanthus schlichtianus* possesses a succulent, CAM-utilising stem. Thus, it might be assumed that flexibility was restricted to species having a succulent stem that also utilizes the CAM pathway of photosynthesis, however, *Monilaria moniliformis* clearly shows both features and exhibits CAM cycling.

For *Delosperma tradescantioides*, a leaf-succulent perennial (Herppich et al. 1996), it has been assumed that CAM-cycling may be ecologically relevant in that it provides the ability to rapidly switch between fast growth due to unrestricted C₃ photosynthesis when well-watered and reduced water loss due to CAM-idling when drought-stressed. This conclusion may also be valid for *Ceraria*, which has a non-succulent stem, and hence no additional water reserves during drought. In this species, leaf shedding is rather flexible

and depends on water availability. When growing well-watered in a greenhouse, *Ceraria* shows a regular yearly growth without any leaf shedding, a situation rarely observed in the field (Jürgens 1990). The above-mentioned ecological relevance of CAM cycling may, however, not apply for *Monilaria moniliformis* with its succulent, CAM-performing stem.

In conclusion, the results presented above clearly indicate, that all modes of CAM have evolved in deciduous South African succulents. Within species of the same life form, yet different morphological adaptations, a highly flexible physiological diversity exists. However, the differences in the respective CAM modes cannot be explained by differences in morphology or life-history strategies.

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