Transpiration and water uptake of succulents in their natural habitat: Field determinations with a potometer

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Abstract

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An attempt was made to use potometric measurements to determine transpiration and water uptake of succulent plants in the field in South Africa. The results show that with some precautions taken, such measurements are feasible. The water uptake patterns of *Aloe marlothii, Aloe davyana* and *Portulaca quadrifida* are similar to those of the daytime transpiration water loss but shifted towards nighttime. The main driving force for water uptake of these plants is the water deficit in the plant tissues caused by daytime transpiration. Similar results were also obtained with *Lampranthus maximiliani*. Anatomical differences of succulent plants are discussed in relation to these results.

Key words: Aloe marlothii, Aloe davyana, Portulaca quadrifida, Lampranthus maximiliani, Crassulacean acid metabolism (CAM), potometer, transpiration, water uptake.

Introduction

The majority of plants exhibiting the Crassulacean acid metabolism (CAM) are succulents (Kluge and Ting 1978). Moreover, the expression of CAM depends upon the actual plant water status, which is correlated with the availability of water in the soil and the transpirational water loss (von Willert et al. 1985, Ting 1985). Succulents can override short or long term negative water budgets (water uptake – transpiration, for a given time period) by making use of their water storage capacity. However, water taken from the store must be replaced during periods when sufficient water is available from the soil. It has been shown that CAM can be involved in the enhancement of water uptake during the night (Ruess and Eller 1985, Eller and Ruess 1986).

The most direct way to measure water uptake rates of succulent plants is by potometry (Eller and Ruess 1982, Ruess 1983). Until now, potometric measurements were restricted to investigations in the laboratory and no attempt was made to use this technique in field experiments. It was the aim of this study to evaluate the feasibility of such measurements.
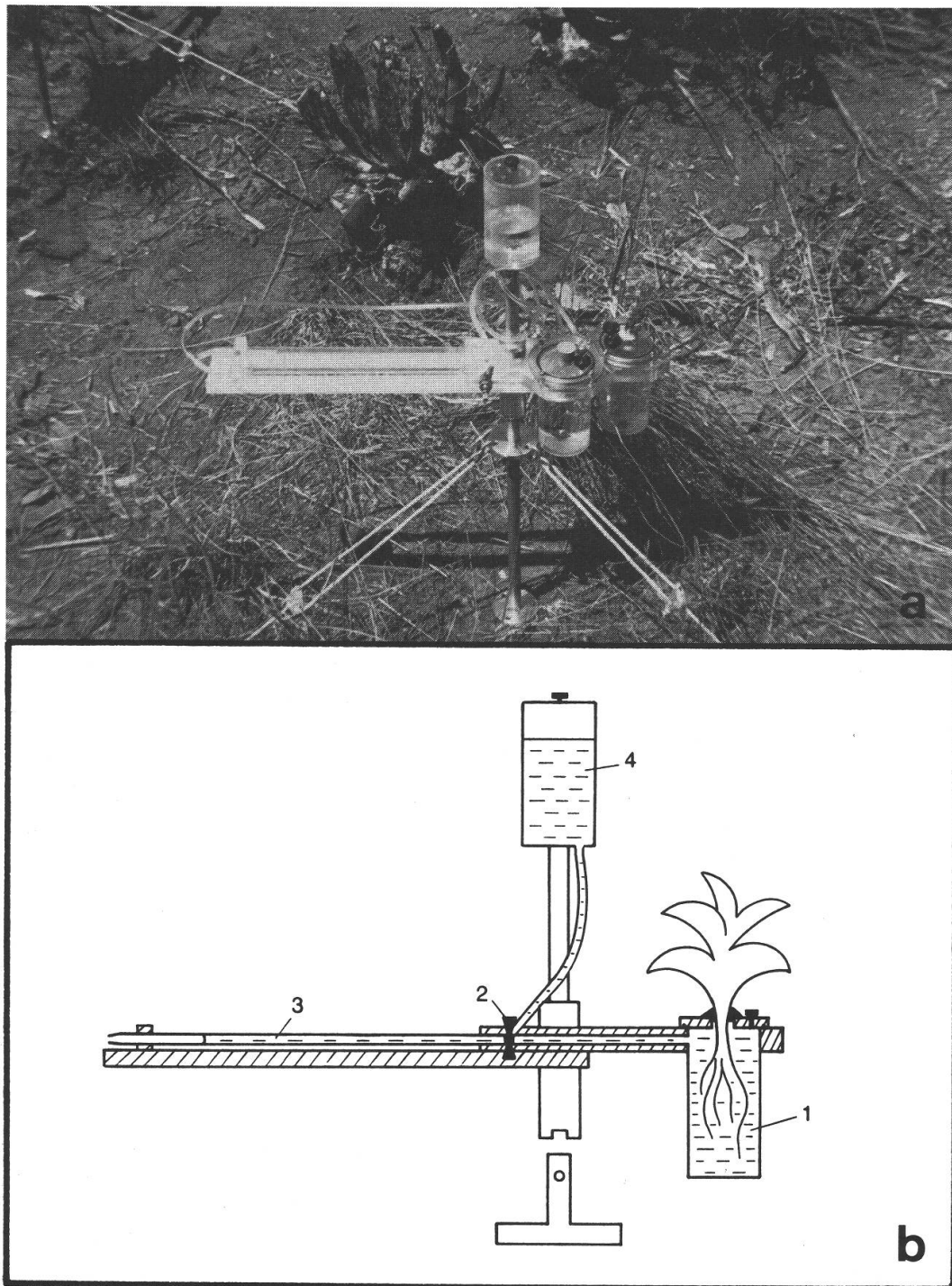
Fig. 1. Field potometer. a) Experimental set-up during measurements in the Roodeplaat Dam Nature Reserve. b) Schematic drawing of one set of the twin potometer: 1- Water container with plant, 2- Valve for refilling the pipette (3) from the water reservoir (4).

Material and methods

The measurements were made with a weighing potometer especially designed for this purpose. In such a potometer, transpiration is determined by weighing and water uptake by measuring the volumetric variation of the water in the container in which the root system of the plant is bathed. A pipette (2 ml) fixed to this container is used for evaluating the water uptake rates. Volumetric changes are not only caused by water uptake but can also result from temperature variations in parts of the measuring device and in the solution. To determine these variations, a second identical combination of water container and pipette without plant was attached to the first potometer, forming a twin potometer as shown in Fig. 1. The readings of the second set were used to calculate the proper value of the water uptake by the plant. To avoid water loss by evaporation from the pipettes, a capillary plastic tube 1 m long (causing a very high resistance against the diffusion of water vapour) was affixed to the ends of both pipettes (Fig. 1a).

Since only short-term measurements were performed, no precautions in regard to oxygen content of the solution, as needed for long term measurements (Ruess and Eller 1981, Ruess 1983), were taken. Readings were made once every hour. Weighing of the entire equipment was made with an electronic balance (Mettler, PL 1200-02, Greifensee, CH).

A first study was undertaken in the Roodeplaat Dam Nature Reserve near Pretoria (Tvl, Republic of South Africa). Detailled information on vegetation and climate is given by van Rooyen (1983) and von Rooyen et al. (1986). Measurements were made at the end of the rain period (January) with *Aloe marlothii* Berger, *A. davyana* Schonl. and *Portulaca quadrifida* L. A second study with *Lampranthus maximiliani* (Schltr. et Bgr.) L. Bol. was made on the escarpment west of Nieuwoudtville (Cp, Republic of South Africa) at the end of the drought period of this region (February).

Air temperature and relative air humidity were determined with an aspirated psychrometer (Hänny, Jegenstorf, CH) and solar irradiance with a solarimeter CM5 (Kipp & Zonen, Delft, NL). Leaf area was determined with a planimeter. Transpiration and water uptake were calculated for the projected (single) leaf area. Malate was determined enzymatically after Möllering (1974). For *A. marlothii* and *A. davyana* each value is the mean of 2–4 samples consisting of a leaf disc of 16 mm diameter. For *L. maximiliani* each sample (3) consisted of 10 leaves of different plants and for *P. quadrifida* each of the two samples consisted of 4–5 leaves.

Results

In the first study, the highest and the lowest temperature reached 29.3 °C and 16.4 °C, respectively (Fig. 2a). The measurements of transpiration had to be interrupted after 22 h because of the nocturnal formation of dew. The roots of the plants were placed in hydroculture 4 hours before starting the experiment. For the measurements with the *Aloes,* only small plants could be used whereas *Portulaca* was an old, established plant. The plant of *A. marlothii* had leaves of about 10 cm length. The age of the plant was estimated to about 10 years. *A. davyana* had leaves up to 14 cm long and was about 5 years old. The water uptake patterns of *A. marlothii, A. davyana* and *P. quadrifida* were similar but slightly higher than the transpiration patterns (Fig. 2). During nighttime, the water uptake rate remained quite high mainly as a consequence of the water deficit caused by daytime transpiration. The low morning transpiration rates (from 9.30 a.m. onward) are due to the cloudy weather, as can be seen from the irradiance, and subsequently from the temperature curve. The highest transpiration rate of *A. marlothii* reached 0.66 mmol $m^{-2} s^{-1}$. Similar values were measured with *S. medley-woodii* (Eller and Ruess 1986).

In the second study, air temperature varied between 28.6 and 14.8 °C (Fig. 3a). A small, adult plant of *L. maximiliani* was transferred to hydroculture 24 h before starting
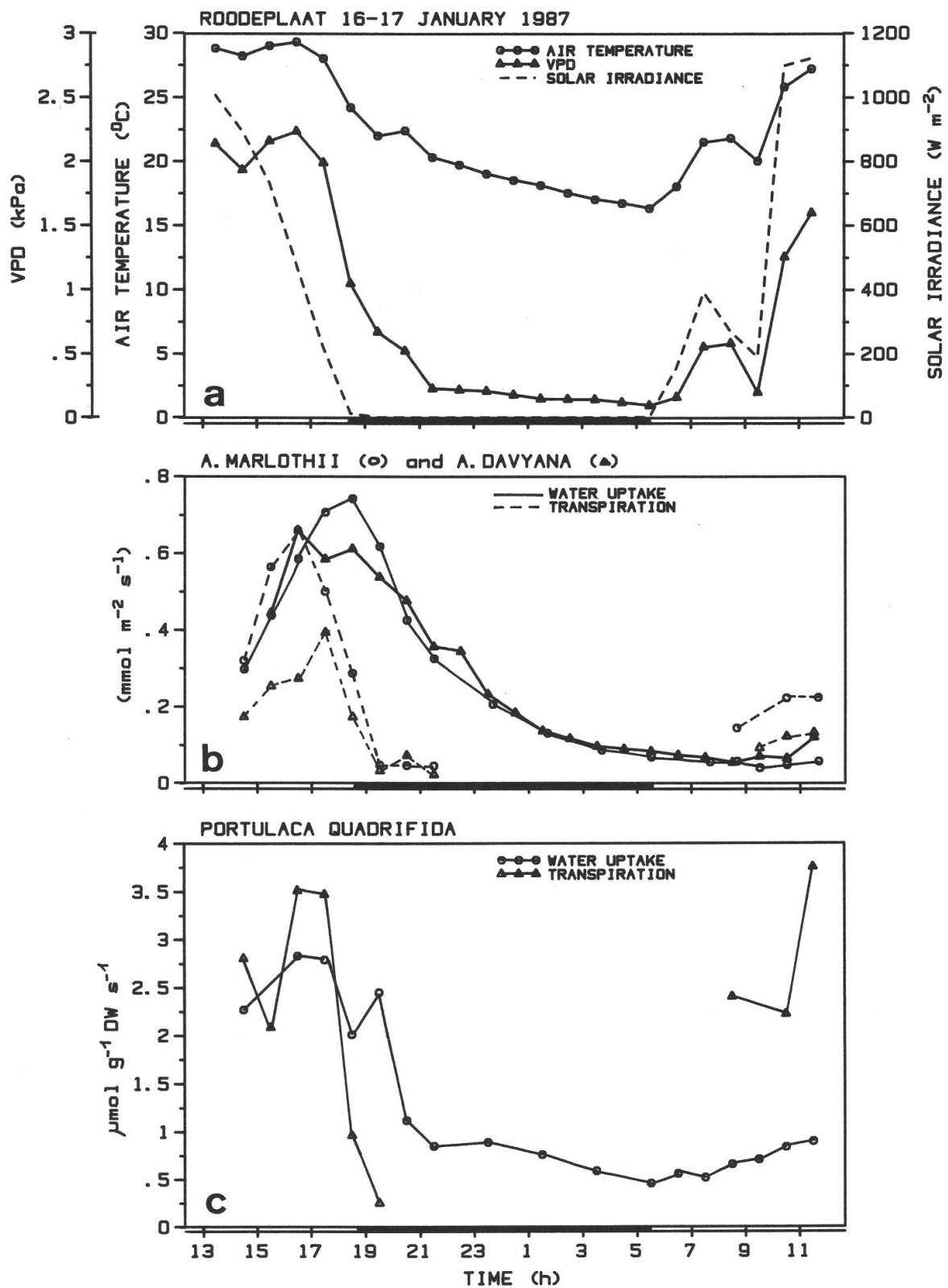
Fig. 2. Transpiration and water uptake of *Aloe marlothii, A. davyana* and *Portulaca quadrifida* as measured in their natural habitat. VPD = Water vapour pressure deficitl; DW = Dry weight.
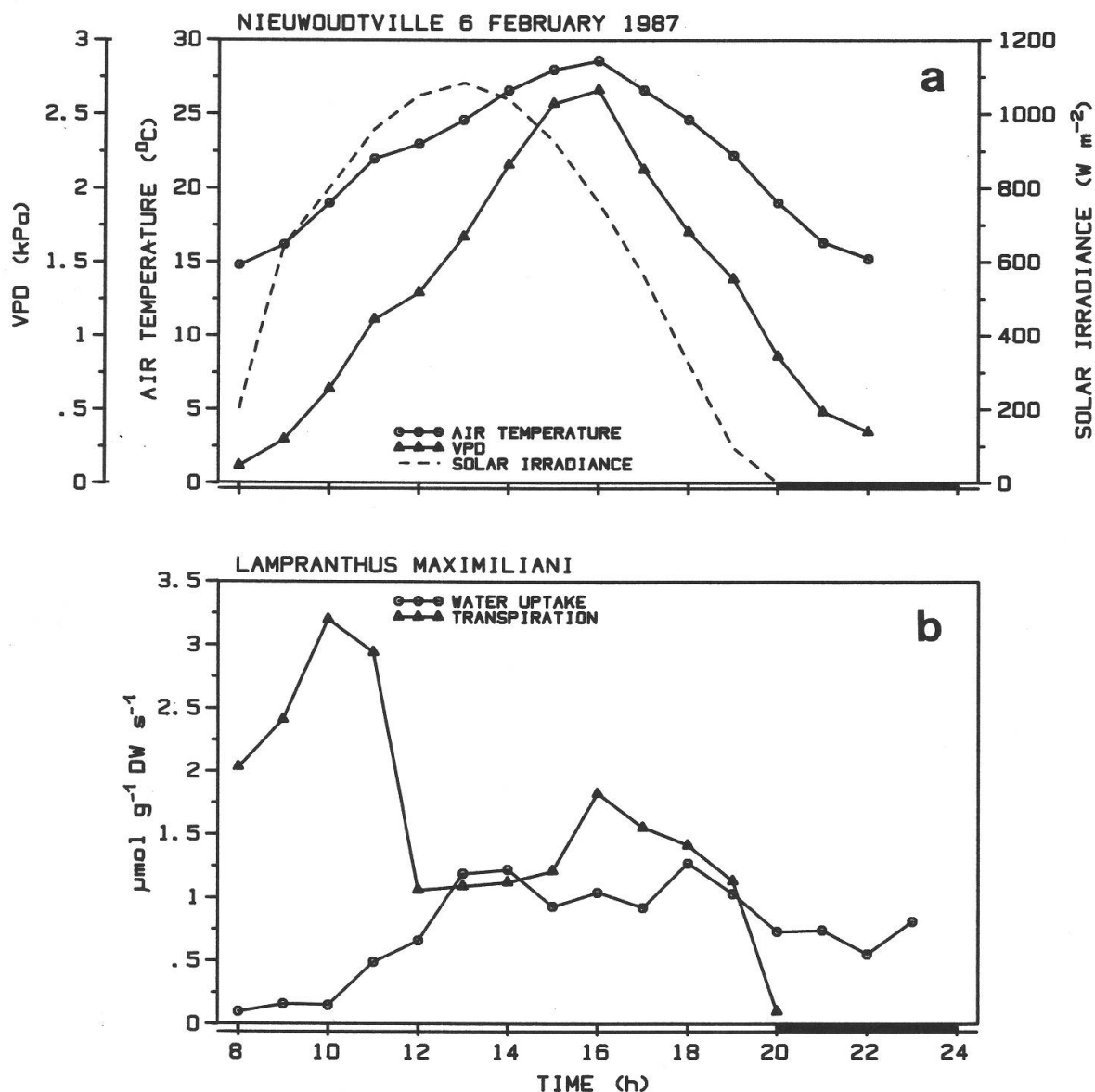
Fig. 3. Transpiration and water uptake of *Lampranthus maximiliani* as measured in the natural
habitat. VPD = Water vapour pressure deficit; DW = Dry weight.

the measurements. The daytime transpiration showed a characteristic midday depression
(Fig. 3b) with stomatal closure beginning at 11 a.m., when the VPD reached 1.11 kPa.
Thus, the plant was able to balance its water budget, transpiration and water uptake
being on the same level. At the beginning of the night, water uptake remained at a high
level and the daytime water deficit (mainly between 8 a.m. and 12 a.m.) was, therefore,
partly compensated for.

A. *marlothii*, A. *davyana* and probably also L. *maximiliani* are CAM plants with
diurnal variations of malate (Δ malate) whereas P. *quadrifida* showed no expression of
CAM. The day/night canges of malate of A. *marlothii* were 18 mol m^{-3} and
24.6 mol m^{-3} for small and big plants, respectively. For A. *davyana,* the corresponding
values were 30 mol m^{-3} and 50.3 mol m^{-3}, whereas L. *maximiliani* had a very low Δ
malate of 4 mol m^{-3}. These values were estimated from samples of whole leaves (*Lam-*

pranthus) or leaf discs (*Aloe*), representing the mean value of Δ malate for the chlorenchyma and the colourless hydrenchyma. With the *Aloes,* additional determinations of Δ malate were made separately for the chlorenchyma and the hydrenchyma. In both plants, the hydrenchyma showed no significant Δ malate. The values of Δ malate for the chlorenchyma were $55 \, mol \, m^{-3}$ and $99.2 \, mol \, m^{-3}$ for *A. marlothii* and *A. davyana,* respectively.

Discussion

From the results it is evident that potometric measurements are feasible, even under the varying environmental conditions in the field. However, some precautions and restrictions had to be observed. A check for insects, litter or sand deposition by wind was compulsory before each weighing. From the onset of rain or dew-fall, measurements were restricted to readings of water uptake. Moreover, hygroscopic water uptake by the plant can occur in a not clearly defined period before dew formation becomes observable.

The water economy of the four plants studied (Fig. 2, 3) was quite similar, although the plants are characterized by anatomical and physiological differences. The water uptake rate of *A. marlothii, A. davyana* and *P. quadrifida* is higher than the transpirational water loss. We assume that this is due to a water deficit prior to the potometric measurements. The water uptake pattern is similar to that of the transpirational water loss but shifted towards nighttime. This indicates that the main driving force for water uptake is the water deficit in the plant tissues caused by daytime transpiration, which is in contrast with the finding that nocturnal water uptake of *Senecio medley-woodii* is enhanced by malate accumulation (Ruess and Eller 1985, Eller and Ruess 1986). Smith and Lüttge (1985) also showed, with *Kalanchoe daigremontiana,* that the malate accumulation is paralled by an increase of the suction tension in the xylem. *S. medley-woodii* and *K. daigremontiana* are leaf succulents with a pigmented water storing mesophyll. Thus, the diurnal variations of malate occur over the entire cross section of the leaf.

However, the *Aloes* have a thin chlorenchyma (28% of leaf disc volume for *A. marlothii* and 48% for *A. davyana*) and with *L. maximiliani* the chlorenchyma is restricted to a thin layer of 0.2 mm (about 20% of total leaf volume). If in these cases the determination of Δ malate is made from whole leaf discs or leaves, the Δ malate is reduced as a consequence of the mixing of the chlorenchyma with the colourless water tissue which shows no Δ malate. This explains the low Δ malate of $24.6 \, mol \, m^{-3}$ measured for a leaf disc of *A. marlothii,* while the measured value for the chlorenchyma alone was $55 \, mol \, m^{-3}$. In the intact plant, the big water storage tissue buffers the osmotic effectiveness of malate accumulation in the chlorenchyma, with respect to water uptake by the roots. Therefore, in the plants characterized by a distinct separation of chlorenchyma and hydrenchyma and showing a high transpirational water loss, transpiration and not diurnal malate variation is the driving force for the water uptake by the roots (see also Smith et al. 1987). The same mechanism of water uptake with transpiration as driving force was also measured by *P. quadrifida* which shows no CAM. Therefore, apart from physiological differences, morphological and anatomical variations must also be considered in order to understand whether CAM (Δ malate) enhances water uptake from the roots or not. Further potometric research with different types of succulent plants are needed to elucidate the interrelationships between CAM and water economy of succulent plants.

References

Eller B. M. and Ruess B. R. 1982. Water relations of *Lithops* plants embedded into the soil and exposed to free air. Physiol. Plant. 55: 329–334.

Eller B. M. and Ruess B. R. 1986. Modulation of CAM and water balance of *Senecio medley-woodii* by environmental factors and age of leaf. J. Plant Physiol. 125: 295–309.

Kluge M. and Ting I. P. 1978. Crassulacean acid metabolism. Springer, Berlin Heidelberg New York, 29 pp.

Möllering H. 1974. L-(–)Malat-Bestimmung mit Malat-Dehydrogenase und Glutamat-Oxalacetat-Transaminase. In Methoden der enzymatischen Analyse (ed. H. W. Bergmeyer), Verlag Chemie, Weinheim, 1636 pp.

Ruess B. R. 1983. L'économie d'eau et le métabolisme acide des crassulacées chez *Senecio medley-woodii*. Adag Druck, Zürich, 33 pp.

Ruess B. R. and Eller B. M. 1981. Rétablissement de l'équilibre hydrique de *Mesembryanthemum crystallinum* L. suite à un traitement salin. Bot. Helv. 91: 81–88.

Ruess B. R. and Eller B. M. 1985. The correlation between crassulacean acid metabolism and water uptake in *Senecio medley-woodii*. Planta 166: 57–66.

Rooyen N. van 1983. Die plantegroei van die Roodeplaatdam-natuurreservaat. I. 'n Voorlopige plantspesielys. S. Afr. J. Bot. 2: 105–114.

Rooyen N. van, Thron G. K. and Grobbelaar N. 1986. The vegetation of the Roodeplaat Dam Nature Reserve. VI. Phenology and climate. S. Afr. J. Bot. 52: 159–166.

Smith J. A. C. and Lüttge U. 1985. Day-night changes in leaf water relations associated with the rhythm of crassulacean acid metabolism in *Kalanchoe daigremontiana*. Planta 163: 272–282.

Smith J. A. C., Schulte P. J. and Nobel P. S. 1987. Water flow and water storage in *Agave deserti:* Osmotic implications of crassulacean acid metabolism. Plant, Cell and Environ. 10: 639–648.

Ting I. P. 1985. Crassulacean acid metabolism. Annu. Rev. Plant Physiol. 36: 595–622.

Willert D. J. von, Brinckmann E., Scheitler B. and Eller B. M. 1985. Availability of water controls crassulacean acid metabolism in succulents of the Richtersveld (Namib desert, South Africa). Planta 164: 44–55.