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Objektyp: **Article**

Zeitschrift: **Botanica Helvetica**

Band (Jahr): **102 (1992)**

Heft 2

PDF erstellt am: **18.07.2024**

Persistenter Link: <https://doi.org/10.5169/seals-70941>

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Spatial and diel variations of water relations in leaves of the CAM-plant *Senecio medley-woodii*

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Manuscript accepted September 9, 1992.

Abstract

Eller B. M., Ferrari S. and Ruess B. R. 1992. Spatial and diel variations of water relations in leaves of the CAM-Plant *Senecio medley-woodii*. Bot. Helv. 102: 193–200.

Plants of *Senecio medley-woodii* Hutchins. with a crassulacean acid metabolism (CAM) for CO₂ fixation, were used to investigate the diel (diurnal) variations in plant water relations and their relationship with the features of CAM. Plants were well supplied with water and cultivated at 17°C air temperature, 80% relative air humidity, 450 µmol m⁻² s⁻¹ photon irradiance and a 12/12 h day/night period. The diurnal changes in leaf water relations result mainly from the day/night changes of the malic acid content resulting from CO₂ dark fixation. A comparison with earlier determinations of CO₂ exchange, transpiration and water uptake by the roots is made and the possibility that transpirational water loss also can enhance water uptake during phases 2 and 4 of CAM is discussed.

Key words: Crassulacean acid metabolism, CAM, *Senecio medley-woodii*, water budget, water uptake, water relations.

Introduction

The characteristic feature of plants with crassulacean acid metabolism (CAM) is the nocturnal fixation of CO₂ when ambient air temperatures usually are lower than during the light period. Open stomata during the night and more or less closed stomata during the light period minimize transpirational water loss and as a consequence a better water budget (water uptake minus transpiration) for 24 hours results for the plant. However, CAM plants can also open the stomata during the light period or at least in the late afternoon, if sufficient water is available from the soil (Osmond 1978).

The other and perhaps even more important characteristic feature of CAM is the day/night fluctuation of acid levels, mainly malic acid (Kluge and Ting, 1978). This acidification in the dark and deacidification in the light can have an impact on the water relations of CAM-plants (Lüttge and Ball 1977, Lüttge and Nobel 1984, Ruess and Eller 1985, Rygol et al. 1987, Smith et al. 1987). Water uptake from the roots and transpirational water losses cause day/night variations in leaf water relations (Lüttge and Nobel 1984, Smith and Lüttge 1985, Ruess and Eller 1985, von Willert et al. 1992). The aim of

the present study was to investigate the relationships between the daily course of leaf water relations and the CAM in *Senecio medley-woodii* for conditions with a good water availability from the soil.

Material and methods

The investigated plant, *Senecio medley-woodii* Hutchins. (Asteraceae), is a leaf succulent with obovate bifacial leaves. Its natural habitat is the Province of Natal, Republic of South Africa. Plants were raised from cuttings and grown in the greenhouse. At the age of 6 to 10 months they were transferred to a plant growth chamber one week before the measurements. Air temperature was held constant ($17^{\circ}\text{C} \pm 0.5 \text{ K}$), relative air humidity was $80\% \pm 5\%$ (water vapour pressure deficit $0.388 \text{ kPa} \pm 0.096 \text{ kPa}$) and photon irradiance was $450 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (120 W/m^2) with a 12/12 h light/dark period. All plants used in the experiments were well watered and therefore in a good plant water status.

Leaf water potential (Ψ_L) was determined with a pressure chamber according to Scholander et al. (1965) with an adaptor specially designed for an airtight fixation of the soft succulent leaves of *S. medley-woodii* in the pressure chamber. The leaf morphology of *S. medley-woodii* does not allow the distinction between the leaf blade and the petiole so that an "overpressure" above the balance pressure during the measurements would result in xylem sap mixed with the leaf blade cell sap. This would lead to an overestimate of the xylem sap osmotic potential. On the other hand, an overpressure of 0.2 MPa already damaged the soft succulent tissue. Therefore, no correction was made for the solute potential of the xylem sap and the leaf water potentials given in this paper are the negative values of the balance pressures measured at the base of the leaves.

Immediately after the excision of the leaf its fresh weight (FW) and the leaf water potential were determined. Then the excised leaf was boiled at about 90°C for 10 minutes, the leaf crushed in a vial and the sap osmolality estimated using an osmometer (Mod. 3B, Vogel, Giessen, FRG). Tissue dry weight (DW) was determined after drying the crushed tissue and the leaf sap at 80°C for 72 h. Malate was estimated enzymatically after Möllering (1974). CO_2 gas exchange and transpiration were measured with a fully climatized cuvette system as used by Ruess and Eller (1985). Water uptake was determined with a potometric system presented in detail earlier (Ruess and Eller, 1985). Values given for CO_2 gas exchange, transpiration and water uptake are given for the projected (single) leaf area determined with a planimeter.

The osmotic pressure (π) of the leaf was calculated using the Van't Hoff relation. The leaf turgor pressure (P) was calculated from π and Ψ_L . Leaf water content was calculated as fraction (in %) of FW and per unit leaf area (WCA). For comparisons dry and fresh weight were also calculated per unit leaf area (DWA and FWA, respectively).

Abbreviations: CAM = Crassulacean acid metabolism, DW = Dry weight, DWA = Dry weight per unit leaf area, FW = Fresh weight, FWA = Fresh weight per unit leaf area, WC = Leaf water content in % of FW, WCA = Leaf water content per unit leaf area, WUE = Water use efficiency.

Results

The aim of the investigation was to determine diel (diurnal) changes of leaf water parameters by sampling leaves every two hours for a time period of 24 h. To get reliable data from such a sampling one has to ascertain that the sampled leaves of a branch had at least comparable parameters when the sampling was started or that only leaves were sampled which comply with that criterion. To get this information all leaves of branches were sampled at about the same time. Leaf number one was the topmost leaf of the branch that could be used to determine Ψ_L with the pressure chamber. Sampling was done during late afternoon (phase 4 of CAM; Osmond 1987) and the results of such a

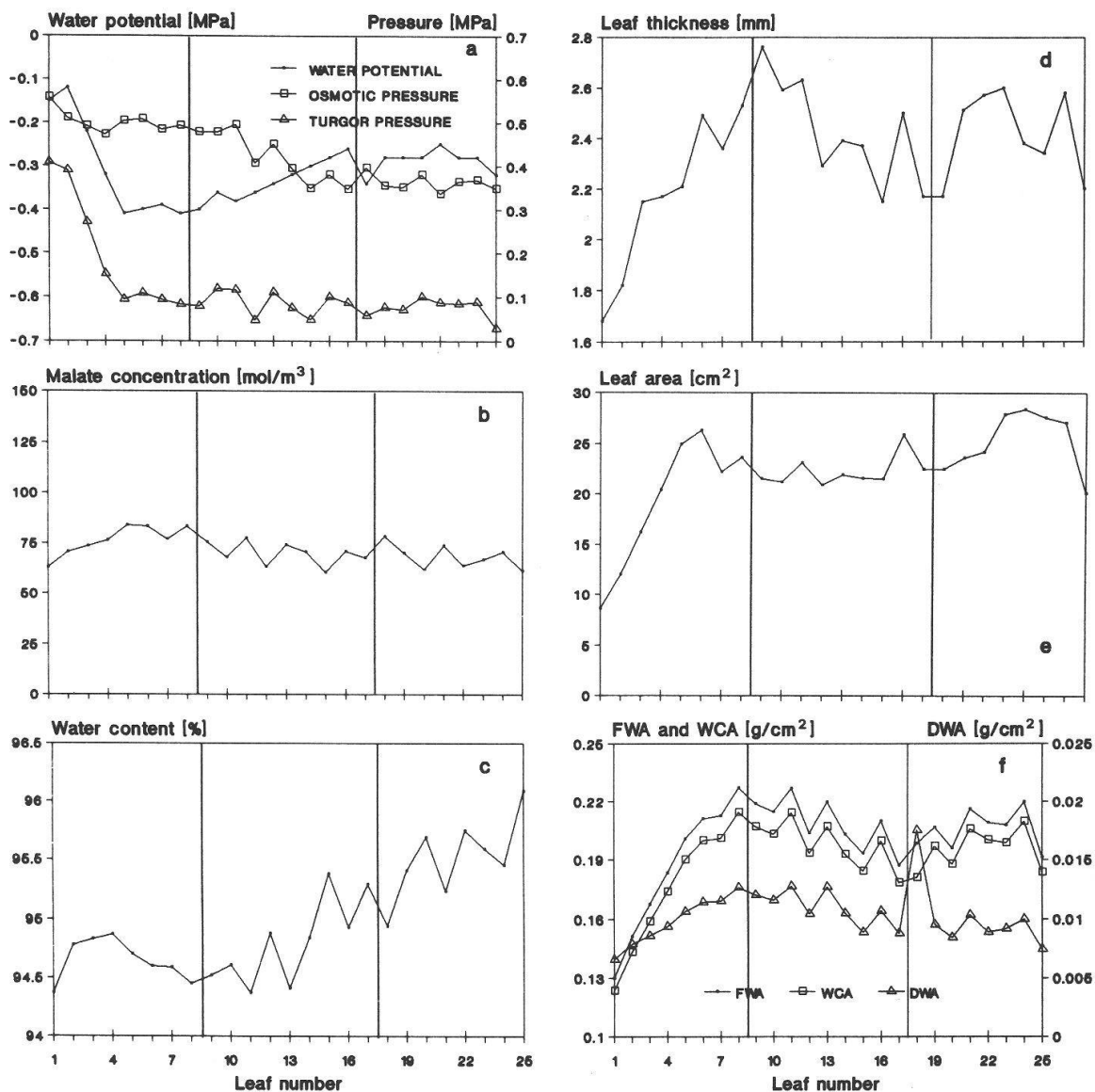


Fig. 1. Water relations, malate concentration and geometric parameters for the 25 leaves of one branch of a well-watered plant of *Senecio medley-woodii*. Determinations were made between 14h00 and 16h00 Phase 4 of CAM). FWA, WCA and DWA are the values calculated per leaf area for fresh weight, water content and dry weight, respectively. Leaf number one is the topmost leaf of the branch that could be used for the determination of all the parameters. Cultivation at 17°C air temperature, 80% relative air humidity, 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photon irradiance and 12/12 h day/night period.

determination of leaf parameters are presented in Fig. 1. Additional samplings from other branches resulted in similar spatial distributions of values but at different mean levels of some parameters.

Leaf parameters within one branch were not entirely homogeneous. Malate (Fig. 1 b) showed only small variations with leaf age, with a mean value of about 75 mol m^{-3} . On the other hand, the other parameters showed clear differences with increasing leaf age. The first 6 leaves were thinner and smaller than the adult ones (Fig. 1 d and 1 e), which had about the same size (from 22 cm^2 to 28 cm^2) but varied in thickness from 2.17 mm to 2.76 mm. π and Ψ_L showed the opposite behaviour from leaf 5 to leaf 17 (Fig. 1 a). Ψ_L

increased to less negative values (from -0.41 MPa of leaf 5 to -0.26 MPa of leaf 17), whereas π decreased for the same leaf numbers from 0.503 MPa to 0.347 MPa, respectively. For the leaves 17 to 25 the variations were very small. The course of Ψ_L and π results in an approximately constant value of the turgor (P) from leaf 5 to leaf 25 (Fig. 1 a). For the first 5 leaves Ψ_L showed decreasing values with big differences, π on the other hand varied little, therefore P decreased rapidly from 0.41 MPa of the first to 0.09 MPa of the fifth leaf.

Water content (WC) in % of fresh weight differed between the first 8 and the other leaves (Fig. 1 c). It increased from 94.52% of leaf 9 to 96.04% of leaf 25. Among the young leaves the water content was quite constant (94.37% – 94.87%), with slightly decreasing values after leaf 4. The course of the water content per unit leaf area (WCA, Fig. 1 f) was different from that of the WC (Fig. 1 c). The first 5 leaves showed clearly smaller values for the WCA than the following ones (from 0.1234 g/cm² to 0.1739 g/cm²). The WCA increased from leaf 1 to leaf 8, then decreased slightly to leaf 17, and increased again to leaf 25.

From these results we deduce that young leaves (the first 5 to 7) were in a physiological condition differing from adult leaves (leaves 8 to 25). Similar conclusions resulted from the same type of measurements with samplings in the morning (phase 2 of CAM) and at midnight (phase 1 of CAM). For the determinations over a 24 h period (Fig. 2) we decided, therefore, to sample only leaves with numbers greater than 7.

The diel course of π , Ψ_L and P (Fig. 2 a, 2 b) of three different plants was very similar. The leaf water potential (Fig. 2 a) decreased during night, reaching its minimum between 02h00 and 04h00 (mean value at 04h00 = -0.45 MPa), increased thereafter and during the light period till 14h00 (mean value at 14h00 = -0.273 MPa), and decreased again in the late afternoon. The osmotic pressure (Fig. 2 b) had its maximum between 04h00 and 08h00 (mean value at 08h00 = 0.532 MPa) and then decreased to its minimum in the late afternoon. The diel course of the turgor pressure (Fig. 2 b) was characterised by three phases. In the night it increased, reaching its maximum at dawn (mean value = 0.14 MPa), in a second phase it stayed at a high and nearly constant level (from 08h00 until midday), while during the afternoon it decreased again to its minimum (0.03 MPa at 20h00).

The diel course of the malate (Fig. 2 c) was typical for that of CAM-plants. Increasing night values were followed by decreasing ones during the light period, with a minimum in the afternoon. In the late afternoon the values increased again. The values ranged from 70 mol/m³ in the afternoon to 125 mol/m³ in the early morning. The water content per leaf area (WCA, Fig. 2 d) did not show marked changes over the 24 hour period. All the plants displayed a small increase during the night, followed by a small decrease till afternoon, and showed a tendency to increase during the last hours of the light period. The variation for the period of 24 hours did not exceed 0.03 g/cm², and ranged from 0.018 g/cm² for the plant 1 to 0.024 g/cm² for plant 2 and 0.028 g/cm² for plant 3. Data of the water content (WC) per unit FW are not shown, since the water content per unit leaf area basis better characterizes the absolute leaf water content.

Discussion

In the dark the malate concentration in well watered plants of *Senecio medley-woodii* (Fig. 2 c) increase as a consequence of the dark fixation of CO₂ and is typical for CAM-plants (Osmond 1978, Kluge and Ting 1978) and led to a concomitant increase of

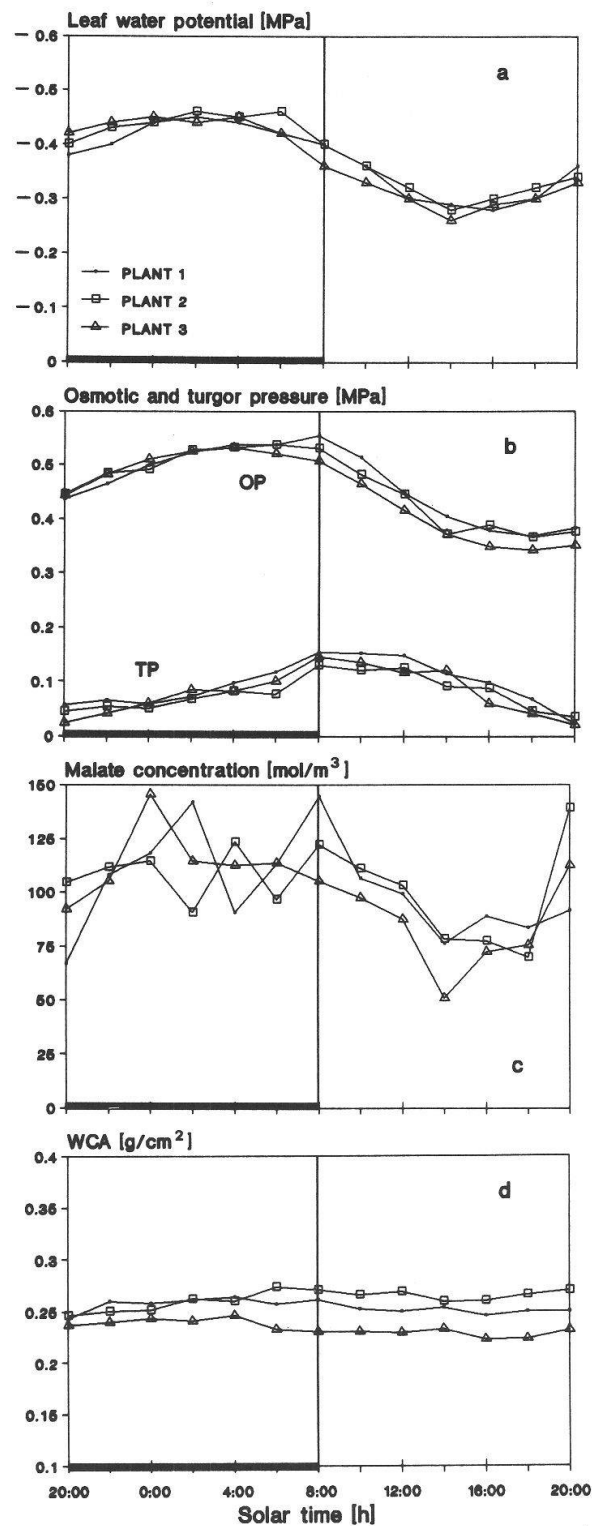


Fig. 2. Diel variations of water relations, malate concentration and leaf water content per unit leaf area (WCA) of three *Senecio medley-woodii* plants with good water supply from the soil. Cultivation at 17°C air temperature, 80% relative air humidity, 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photon irradiance and 12/12 h day/night period.

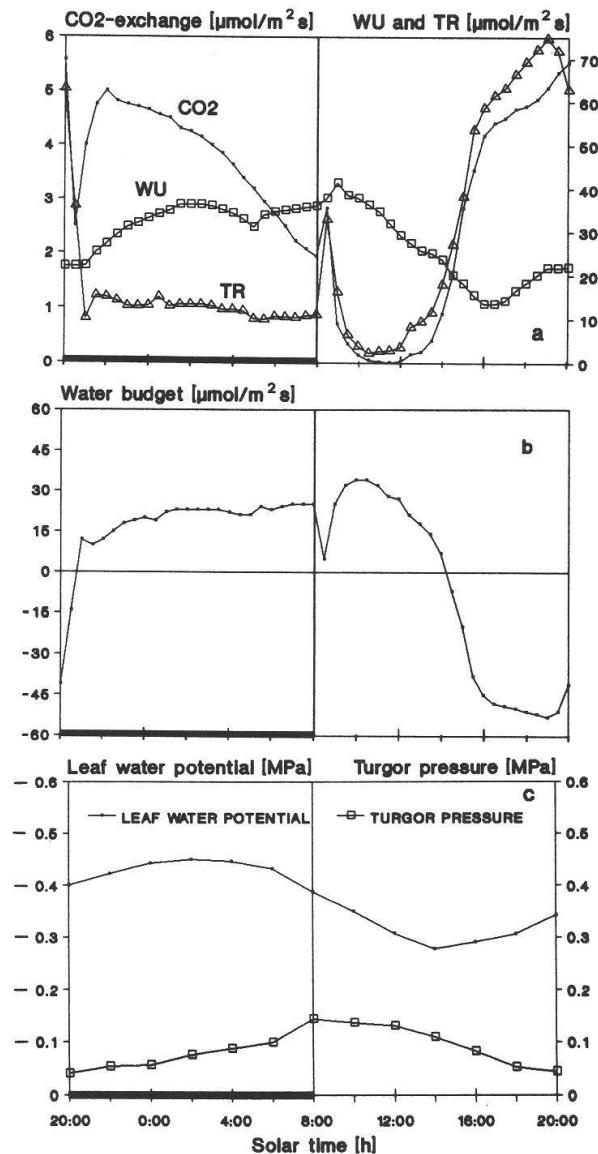


Fig. 3. CO₂ exchange, transpiration (TR), water uptake (WU) and water budget (uptake minus transpiration) of plant of *Senecio medley-woodii* as estimated with a potometer combined with a gas exchange cuvette (data from Ruess 1983, environmental data are similar to those of fig. 2). The values for turgor pressure and leaf water potential (c) are the mean values taken from fig. 2.

the osmotic pressure (Fig. 2b). In the light period that followed the malate concentration decreased (Fig. 2c), because CO₂ was liberated by the plants from malate for the photosynthetic processes and as a consequence the osmotic pressure also decreased (Fig. 2b).

In order to understand the relationships between the variation of the daily course of π and P more clearly, it would be advantageous to know the daily course of water uptake and transpiration of well watered plants of *S. medley-woodii*. Such measurements had already been made with the help of a potometer (determination of the water uptake) combined with a gas exchange cuvette (measurement of transpiration and of CO₂ uptake) by Ruess (1983) and Ruess and Eller (1985). In Fig. 3 the data from such a determination are given together with the daily water budget (absorbed minus transpired water). Included into Fig. 3 are also the mean values of Ψ_L and P of the data shown in Fig. 2.

Well watered plants of *S. medley-woodii* can take up water 24 h a day (Fig. 3 a). Transpiration is reduced in the dark period and in the late morning (between 09h30 and 12h30). Turgor pressure is at its highest (0.154 MPa) during the morning hours (Fig. 3 c) since the water budget in the morning is always positive (Fig. 3 b). *S. medley-woodii* takes up water during this time period (09h00 to 12h00) although the transpiration decreases to about zero (Fig. 3 a). Water uptake is at its highest after the morning peak of CO₂ uptake which is paralleled by a transpiration peak. As leaf water potential already increases one could argue that for this period (phase 2 of CAM, Osmond 1978) uptake is enhanced by transpirational water loss.

In the afternoon, transpiration exceeded water uptake and the water budget became negative (Fig. 3 a, 3 b). The turgor pressure decreased steadily and reached its minimum at the end of the light period (Fig. 3 c). At the same time the increasing transpiration caused a decrease of the leaf water potential to more negative values (Fig. 3 c). Opening of stomata in the afternoon, and, as a consequence, higher transpiration and decreasing turgor are typical for well watered CAM plants (Osmond 1978, Smith and Lüttge 1985, Rygol et al. 1987). We presume that in this time period turgor pressure decrease (Fig. 3 c) resulting from transpirational water loss more likely causes the decrease of Ψ_L than changes of the osmotic pressure (Fig. 2 b). Most probably, the high transpiration causes to a greater extent the increase of the water uptake rate after about 16h00 than osmotically active primary products from photosynthesis. This assumption is supported by the fact that after the transpiration is reduced at dawn the water uptake is not further enhanced.

If transpiration alone is the driving force for water uptake, then uptake rates could not increase continuously after the onset of the night. The high water uptake persists throughout the night and is only reduced when the consumption of malate starts in phase 3 of CAM. The steep increase of CO₂ dark fixation (Fig. 3 a, after about 21h00) was paralleled by increasing osmotic pressure (Fig. 2 b) and a decreasing leaf water potential. As a consequence the water uptake (Fig. 3 a) is enhanced and results in an increase of turgor (Fig. 3 c). Parallel increases of Ψ_L (to less negative values) and of the turgor during nocturnal acidification are well known from earlier investigations with different CAM-plants (Lüttge and Ball 1977, Lüttge and Nobel 1984, Smith and Lüttge 1985), but in our results the leaf water potential increases only in the first part of the night (until about 02h), thereafter the leaf water potential decreases. We can only propose that this results from a change in cell elasticity with increasing cell volume. In fact, the turgor pressure increases much more after about 02h (Fig. 3 c) than the water uptake rate (Fig. 3 a). If the tissue elasticity increases, a further increase in volume ΔV would result in a higher increase of turgor (ΔP) since $\Delta P \approx \varepsilon \cdot \Delta V / V$ (Steudle et al. 1980).

One could argue that water uptake increases during the night only as a consequence of the high transpiration during the afternoon as increases uptake after about 16 h which is evidently caused (with a time lag of about 4 h) by the onset of high transpirational water loss afternoon. However, the water uptake is stabilized at a constant value when transpiration decreases after about 19 h and there is no reason why uptake should suddenly increase again during the night when transpiration is low. This sharp increase after about 21 h matches only with the steep increase of the CO₂ dark fixation at about the same time of the night.

In summary, we conclude that there is clear evidence that the diel fluctuation of malate (and perhaps other acids resulting from CO₂ dark fixation) is the major cause for the diel pattern of water uptake and the corresponding parameters of the water status of *Senecio medley-woodii*. However, as stated above, during phase 4 of CAM (and perhaps

also phase 2) the high transpiration rates of *S. medley-woodii* plants with a very good water supply can also enhance water uptake, but much less than the diel fluctuations of the acidification in the dark. However, we must emphasize that these conclusions only hold for CAM-succulents such as *Senecio medley-woodii* with leaf tissues that are not (or not entirely) differentiated into a not water storing chlorenchyma and an achlorophyllous water storage tissue. In leaf succulents with distinctly differentiated chlorenchyma and water storage tissues the relationships between water relations and CAM are distinctly different as has been shown earlier (Smith et al. 1987, Ruess et al. 1988, 1988a).

This work was supported by the Swiss National Science Foundation (Grants 31-9463.88, 31-30895.91) and the Stiftung Jubiläumsspende für die Universität Zürich.

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