

Zeitschrift:	Botanica Helvetica
Herausgeber:	Schweizerische Botanische Gesellschaft
Band:	103 (1993)
Heft:	2
Artikel:	Influence of transpiration and photosynthetic pathway on water uptake of <i>Cotyledon orbiculata</i> (CAM) and <i>Othonna opima</i> (C3)
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DOI:	https://doi.org/10.5169/seals-71339

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Influence of transpiration and photosynthetic pathway on water uptake of *Cotyledon orbiculata* (CAM) and *Othonna opima* (C₃)

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Manuscript accepted September 21, 1993

Abstract

Eller B. M., Egli A. and Flach B. M.-T. 1993. Influence of transpiration and photosynthetic pathway on water uptake of *Cotyledon orbiculata* (CAM) and *Othonna opima* (C₃). Bot Helv. 103: 207–221.

The water fluxes and the CO₂ exchange of two leaf succulents, *Cotyledon orbiculata* and *Othonna opima* with similar growth form but different CO₂ fixation pathways CAM (Crassulacean acid metabolism) and C₃, respectively, were monitored with a gas exchange cuvette combined with a potometric system to quantify water uptake. Measurements, which are primarily valid for plants with a sufficient water supply, were made during 4 to 14 consecutive days under constant experimental conditions (Air temperature 20 °C, dewpoint temperature 13 °C, 12/12 h light/dark photoperiod at 400 to 500 µmol m⁻² s⁻¹ photon irradiance). All plants for most days showed a water gain quotient for 24 h (= water uptake/transpiration) close to unity indicating stable plant water relations. Water uptake of the C₃-plant *O. opima* increased during the light period when transpiration increased or was high, and decreased after transpiration was reduced during the dark period with the lowest water uptake rates at the end of the dark period. The young and expanding leaves of the CAM-plant *C. orbiculata* had not yet established the CAM and thus showed a daily CO₂ exchange, transpiration and water uptake pattern like the C₃-plant *O. opima*. Plants of *C. orbiculata* with a number of old, mature leaves exceeding that of young leaves had the typical diurnal CO₂ gas exchange and transpiration of a CAM-plant, and the pattern of water uptake differed from that of a C₃-plant with a similar growth form and water storage volume such as *O. opima*. If nocturnal CO₂ fixation was high and water loss by transpiration moderate then water uptake during the dark period was enhanced, which must be attributed to the osmotically active products of the CO₂ dark fixation as was already postulated for other CAM-succulents. Water uptake of the *C. orbiculata* plants decreased during the light period or varied little at a high level. Only when water loss by transpiration was high and CO₂ dark fixation was at moderate levels, did water uptake display variations which could be attributed to changes in water loss by transpiration. However, these variations were delayed in time and much smaller compared with transpiration changes. If the water storage tissue is

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pigmented and thus identical with the photosynthetically active tissue then one can suppose that the diurnal course of water uptake rates is primarily modulated by cyclic production and consumption of CO_2 dark fixation products and only secondarily by the diurnal course of water loss by transpiration as was demonstrated with *C. orbiculata*.

Key words: Water uptake, water budget, plant water relations, Crassulacean acid metabolism, CAM.

Introduction

The plant water status is described by the water potential, and the water potential gradients control the water fluxes at the different organisation levels (cell, tissue, organs) in the plant and also in the soil – plant – atmosphere continuum. In which way physical and osmotic properties of plants act on water fluxes at the level of cells or tissues is quite well known but there are gaps of how the linkage between water relations and plant metabolism occurs (Steudle 1989, 1992). The same is valid for water fluxes at higher organisational levels (plant organ or intact plant). Every plant has a certain water storage capacity which enables it to buffer for a short time period water loss by transpiration which exceeds water gain from the substrate. Plants with large water storage volumes, e.g. large trees (Milne 1989) or succulents (von Willert et al. 1992), can buffer high water loss by transpiration during longer periods of drought. In plants with small buffer volumes and with little changing osmotic potential, the water potential varies concomitant with transpiration and water gain by uptake is directly linked to loss by transpiration. The diurnal variation of water uptake follows transpiration with a timeshift dependent on the amount of the actual internal water reserves of that plant and the availability of water from the substrate. If a larger water store buffers diurnal water loss then water uptake via the roots is to some extent unlinked from actual transpiration rates, i.e. transpiration peaks are not repeated in the pattern of diurnal water uptake or are shifted in time and smoothed (see e.g. Ruess et al. 1988). If osmotically effective metabolic specializations like the Crassulacean acid metabolism (CAM) exist, then the CAM not only modulates transpiration but can also interfere with water uptake (Ruess and Eller 1985; Eller and Ruess 1986; Eller et al. 1992). That CAM has an impact on the water gain of succulents (Ruess and Eller, 1985) has been questioned (Smith et al. 1987), and more experimental evidence of this interaction is needed (Lütte 1987; Griffiths 1988). Such determinations also could validate models proposed for simulation of water uptake fluxes of succulents (e.g. Smith et al. 1987; Schulte et al. 1989).

The aim of this investigation was to improve knowledge of impacts on water uptake resulting from transpiration and caused by different CO_2 fixation pathways, CAM and C_3 , respectively. Determinations of water uptake by the roots were made with a potometric setup. One can argue that water budgets (gain minus loss) of succulents determined in a potometer are not significant for succulents subject to severe drought-stress in their habitat, but unquestionable such investigations provide valuable information of plant water relations in general and also on the water budget of succulents if water is abundantly available from the soil. Moreover, only water uptake rates measured by a direct way as with a potometer can give evidence to what extent CAM influences water uptake and how different types of water stores buffer transpiration and modulate the diurnal pattern of transpiration and water uptake.

Material and methods

Plant material

Two leaf succulents, *Cotyledon orbiculata* var. *orbiculata* L. (Crassulaceae), a constitutive CAM-plant and *Othonna opima* Merxm. (Asteraceae) with the C₃ pathway of photosynthesis, were used for the investigations. Plants were propagated from specimens collected in their habitat in the southern Namib desert (Namaqualand, Cp., Rep. South Africa). Both species are shrublets with similar growth forms, with succulent, linear lanceolate, terete leaves in a more or less upright position. The leaves of *C. orbiculata* are all-cell succulent, i.e. the entire cross-section of the leaf contains chlorophyll and there is no differentiation between assimilatory and water storing tissue but the density of pigmentation decreases towards the center of leaf cross-section. *Othonna opima* leaves have a peripheral chlorenchyma which accounts for about 30% of the cross-section and a central achlorophyllous hydrenchyma. Plants were cultivated in plant growth cabinets at 20 °C air and 13 °C dewpoint temperature of the ambient air. The light/dark photoperiod was 12/12 hours with a photon irradiance of about 400 to 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ determined with a quantum sensor (LICOR Ltd., Lincoln, USA). Environmental conditions were not changed during measurements. The surface of the terete leaves was determined by covering the harvested leaves with 'peel off' nail laquer. The dry cover of laquer was cut into stripes, peeled off the leaf surface and the area of the stripes determined with a planimeter.

Water fluxes

Two water fluxes, water gain (J_{wg}) through uptake by the roots and/or other surfaces, and water loss (J_{wl}), predominantly by transpiration, link the plant with its environment. Gain minus loss is the water budget J_w (net) of the whole plant which is equal to the amount of water that is put into or taken out from the internal water reserves of a plant. For a given time period the input or output of water into or from a plant's water reserves is the water balance.

$$\text{Water balance} = \int_{\Delta t} J_{wg} \cdot dt - \int_{\Delta t} J_{wl} \cdot dt.$$

If the balance is positive then the plant's water status improves and the water gained is stored as utilizable water or becomes structural water (von Willert et al. 1992). A negative balance indicates drought, either short term drought if the balance is negative for some hours during a day or long term drought if a negative balance persists for days or months. The quotient gain/loss for a time period is the water gain quotient WGQ (WGQ24h for a 24 hour period)

$$\text{Water gain quotient} = \text{WDQ} = \frac{\int_{\Delta t} J_{wg} \cdot dt}{\int_{\Delta t} J_{wl} \cdot dt}$$

which reveals quickly if the plant has gained ($\text{WGQ} > 1$) or lost ($\text{WGQ} < 1$) water during the observed time period.

Gas-exchange cuvette

CO₂ gas-exchange and transpiration were monitored with a climatized gas-exchange cuvette after Koch et al. (1968) (GWK8; Walz, Effeltrich, FRG). The original cuvette was modified for combined use with the potometer. CO₂ gas-exchange was determined differentially with an infrared gas analyzer UNOR4 (Maihak, Hamburg, FRG) and air humidities with dewpoint mirrors TS3 (Walz, Effeltrich, FRG). Flows were measured with electronic mass-flow meters FM-360 (TYLAN, Eching, FRG). To determine the accuracy of transpiration measurements, water loss was simulated by a device similar to a PICHE-evaporimeter (Steubing and Fangmeier, 1992), which was mounted into the empty cuvette. Transpiration was estimated by readings from the graduated glass tube of the evaporimeter (resolution 50 μl), and measured simultaneously by the gas exchange equipment.

Water loss from the evaporimeter tube and the same evaporation measured in the cuvette like a plant's transpiration differed, at evaporation/transpiration rates of about 300 mmol per day, by less than 3%.

The cuvette was installed in a plant growth cabinet operated with the same environmental parameters as prevailed during precultivation of the plants. Online computer control was performed with a multitasking computer based on the VME-Bus (CPU: E3-121/68k, ELTEC, Mainz, FRG) in a configuration realized at our institute. Data aquisition, realtime dataprocessing, the automatic control of the gas-exchange cuvette and a partial control of the plant growth cabinet was achieved in the combination of the computing system with a data-logger ORION 3530 (Solartron/Schlumberger, Farnborough, UK). Data aquisition for automatic control and control was at a 6 s-cycle. Every 2 min a set of ecophysiological data and calculated results were registered and from 5 sets mean values for 10 min were calculated for final results. Software for this application was written by the first author.

The potometer

The plants were mounted into the gas-exchange cuvette with their roots bathing in the water container of a potometric system as described and illustrated in detail by Ruess and Eller (1985). Some mechanical and physical alterations were made but without changing the basic principle. To improve e.g. the mechanical stability the platform for the balance and the gas exchange cuvette with the attached upper part (control unit) of the potometer was connected with steel rods of low thermal expansion coefficient. Figure 1 shows the cuvette/potometer setup as it was used for this investigation. Water uptake was measured as the loss of weight of the container filled with a hydroculture solution. The solution was temperature controlled and its oxygen concentration continuously adjusted to $7-8 \text{ g m}^{-3}$ (near saturation). The water container was fixed on a balance PL 1200 (Mettler, Greifensee, Switzerland). Weight changes were corrected for buoyancy.

The plant growth cabinet generated vibration which interfered with the weighing procedure. To minimize errors caused by such sources they were switched off during weighing by computer control. The accuracy of water uptake measurements was estimated with a test. A stainless steel tube filled with SiO_2 -powder was fixed between potometer container and cuvette. This tube acted like a wick causing a water flux between water container and cuvette. Water uptake and evaporation of this tube was measured like water uptake and transpiration of a plant. Flow rates were of the same magnitude as with the plants. The uptake- and the "transpiration"-values determined with this SiO_2 -filled tube differed less than 4% (in most cases less than 2%) from each other.

Abbreviations: CAM = Crassulacean acid metabolism, WGQ = Water gain quotient, WGQ24h = WGQ for 24 h

Results and discussion

CO_2 exchange, transpiration and water uptake of *Othonna opima* and *Cotyledon orbiculata* plants were measured in the potometer/gas-exchange cuvette for time periods of 4 to 14 consecutive days. Investigations were made with 6 plants of *C. orbiculata* and 6 of *O. opima*, all of which were in the vegetative phase with expanding young leaves. Data from plants (1 *C. orbiculata*, 3 *O. opima*) that in the potometer displayed disturbed physiological reactions (e.g. caused by injuries or infections on the roots) were excluded from results presented below. For the other plants CO_2 gas exchange and water relations at day 1 in the potometer are summarized in Tab. 1. There are differences in the absolute values e.g. between plant number 2 and 10 even though they had about the same leaf surface (but different number of young leaves). However, the water gain quotients (WGQ24h) were about unity for all plants, if determination errors were considered indicating that water loss and uptake were balanced and thus the plants in a stable

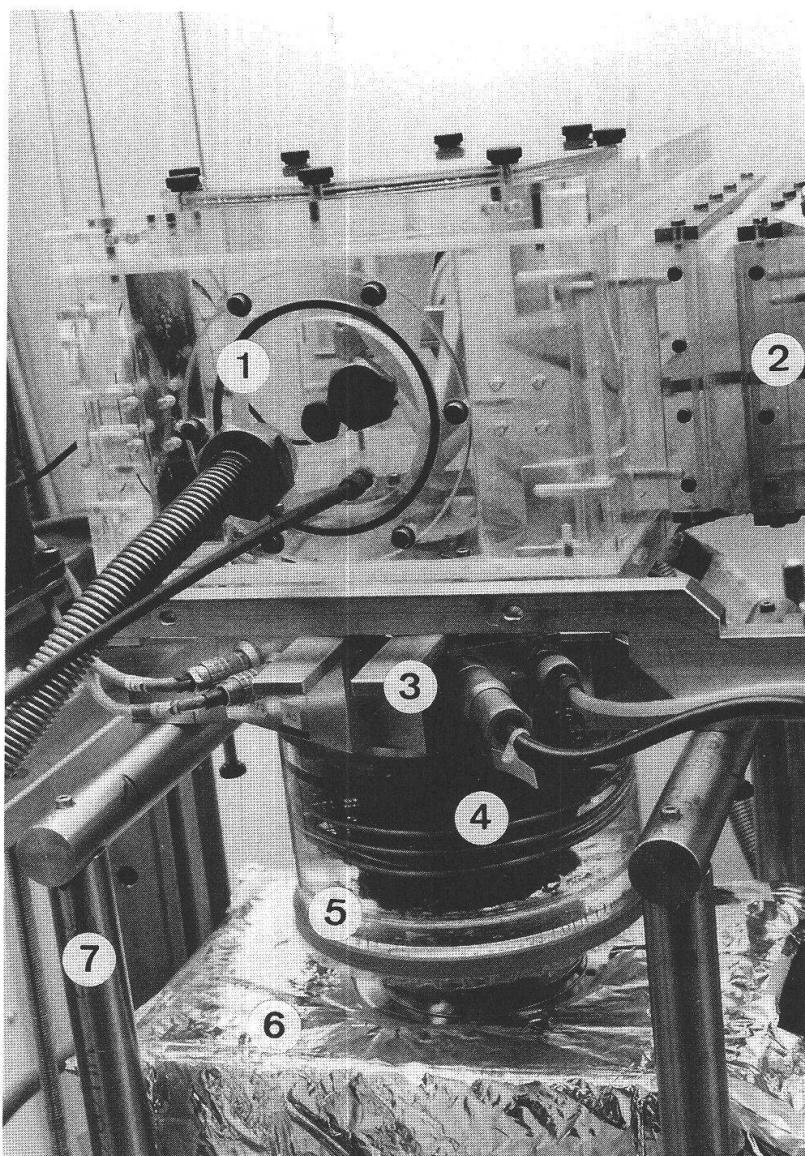


Fig. 1. Gas-exchange cuvette with photometer. 1: Cuvette, 2: Peltier cooling-unit for the climatization of the cuvette, 3: Photometer-head (control unit) connected to the gas-exchange cuvette, 4: Upper part or photometer (with plexiglas-basket attached to the photometer control unit, prevents soil particles from falling into the hydroculture-container) with cooling and O₂ supplying tubing, O₂-electrode and stirrer, 5: Photometer-container for hydroculture solution positioned on balance (the part of the hydroculture solution in contact with ambient air is sealed with oil), 6: Balance, 7: Cage of steel-rods with low thermal expansion coefficient connecting the balance platform with cuvette and photometer-head (wind and radiation shields not shown).

condition of plant water relations. The diurnal pattern of CO₂ exchange, transpiration and water uptake were similar for all plants of both species. The results of two individuals of *C. orbiculata* and of one of *O. opima* are presented below, and are characteristic for *C. orbiculata* and *O. opima*, respectively.

The typical diurnal course of CO₂ gas exchange, transpiration and water uptake of an *O. opima* (plant # 12 of Tab. 1) in stable conditions in respect to plant water relations and CO₂ fixation is shown in Fig. 2. The CO₂ gas exchange expressed the C₃ pathway

Table 1. CO_2 -exchange, transpiration, water uptake by the roots and water gain quotient (WGQ 24 h = uptake/transpiration) of 5 plants of *Cotyledon orbiculata* and 3 plants of *Othonna opima*. Values for a 24 hour time period with a 12/12 h light/dark photoperiod. Environmental conditions: Air temperature (24 h) 20 °C, dewpoint temperature of ambient air (24 h) 13 °C, photon irradiance 400 to 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Plant	Num- ber	Number of leaves		Leaf- surface [m^2]	CO_2 - exchange [mmol m^{-2}]	Transpira- tion [mol m^{-2}]	Uptake* [mol m^{-2}]	WGQ 24 h
		old	young					
<i>Cotyledon</i> <i>orbiculata</i>	2	8	0	$14.6 \cdot 10^{-3}$	189.98	26.89	27.87	1.04
	3	10	6	$17.9 \cdot 10^{-3}$	152.11	13.19	13.32	1.01
	8	10	6	$20.5 \cdot 10^{-3}$	169.80	18.82	19.54	1.04
	10	10	4	$14.8 \cdot 10^{-3}$	161.51	16.55	17.97	1.09
	13	10	4	$17.2 \cdot 10^{-3}$	131.98	12.97	12.27	0.95
<i>Othonna</i> <i>opima</i>	6	11	0	$17.0 \cdot 10^{-3}$	130.45	13.96	13.80	0.99
	9	8	1	$13.3 \cdot 10^{-3}$	94.37	23.76	24.08	1.01
	12	9	2	$20.4 \cdot 10^{-3}$	82.31	12.72	12.82	1.01

* Water uptake on a leaf surface basis

of photosynthesis. Transpiration was high during the light period and was reduced to a lower level in the dark period as could be expected for a plant supplied abundantly with water. If transpiration exceeds water gain by uptake then the plant's turgor decreases and the water potential of the plant's roots eventually will drop to more negative values. This enhances uptake via the roots provided that water is available. Increases of the uptake rates for *O. opima* were high at the start of the light period when transpiration also increased drastically (Fig. 2) but later increases were much smaller. The uptake remained at lower level than transpiration during the whole light period. The water budget (uptake minus transpiration) was, after a sharp decrease to negative values early in the light period, negative and nearly constant. This constancy could indicate, together with the fact that after about 10H00 the water uptake increased only little, that uptake capacity was limited. An insufficient conductivity of the hydraulic system between root and leaves could be the cause for this limitation. As a consequence, the balance became negative and the plant's water reserves decreased gradually during the light period. The daily balance had its most negative value (-86.8 mmol) at the end of the light period. This value represented that amount of water taken from the stored water reserves to buffer transpiration exceeding uptake but does certainly not quantify the maximal amount of water on which the plant could rely to buffer long term drought.

Transpiration decreased sharply at the onset of the dark period. At about 19H00 transpiration became smaller than uptake rates and thus the water budget became positive. The balance value at the end of the 24 h period differed not significantly from zero (Fig. 2) and uptake at the beginning of the next light period was the same as 24 h earlier. Transpiration and uptake for the light, the dark and the 24 h period are summarized together with the 24h-balance and the water gain quotients in Tab. 2. It was known from preliminary investigations with *O. opima* that inspite of the plants being well watered during precultivation they had a small water deficit when they were transferred to the potometric system. This deficit for the first day always caused a positive water balance. Also the plant used in this investigation had for day 1 a water gain quotient for

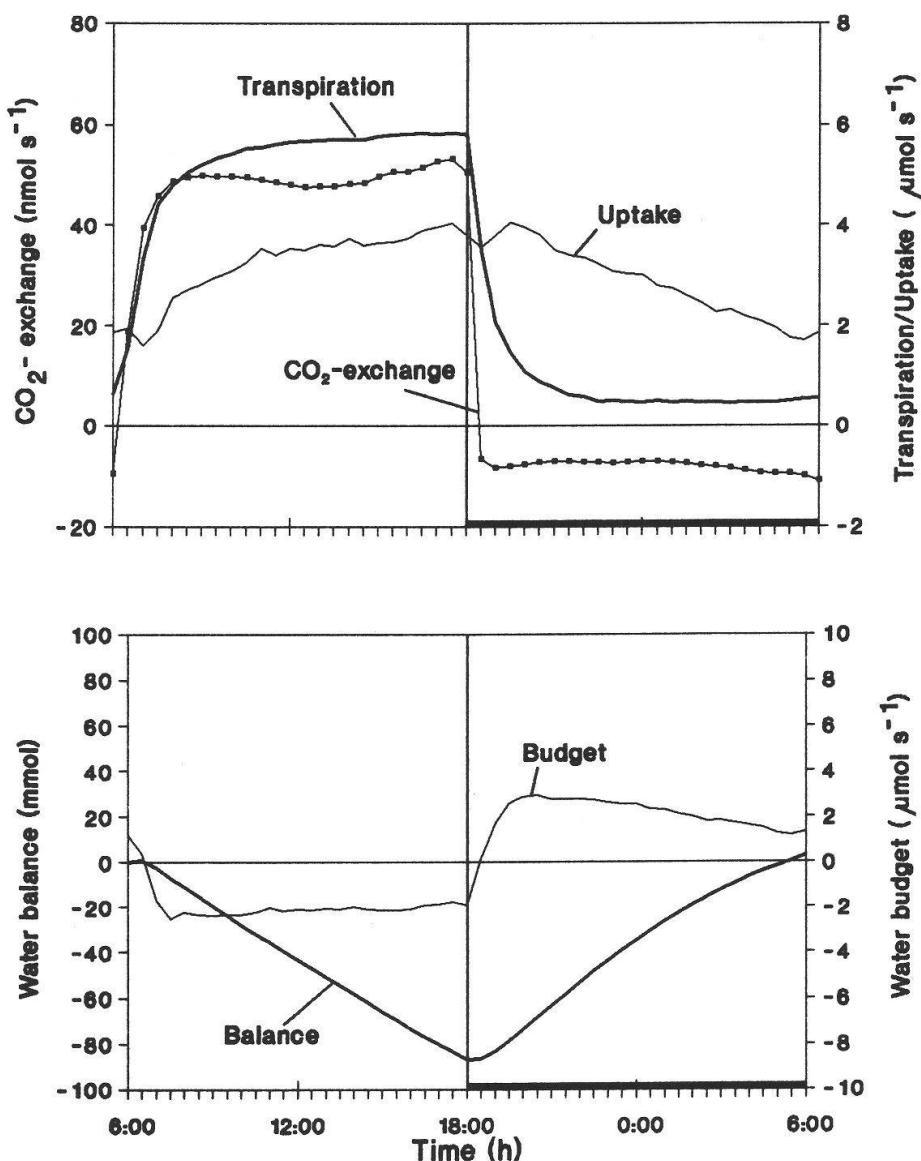


Fig. 2. Diurnal pattern of CO₂-exchange and water relations of an *Othonna opima* plant (9 old and 2 young leaves) in the photometer. Ambient conditions: Air temperature (24 h) 20°C, dewpoint temperature (24 h) 13°C, 12/12 h day/night photoperiod at a photon irradiance of $470 \pm 30 \mu\text{mol m}^{-2} \text{s}^{-1}$. Data of day 5 of Tab. 2.

24 h (WGQ24h) of 1.48 (Tab. 2) but on the subsequent days the WGQ24h dropped to about 1. Water uptake from day 1 through day 3 exceeded transpiration by 75.4 mmol (= 1358 mg) or by an average of 123 μl per leaf (not considering water consumed or stored in the stem or the roots). It was impossible to determine leaf volumes on the intact plant but measured leaf diameter in the abaxial/adaxial direction at the start of the experiment and at day 4 showed a mean increase of 1.6 mm (span = 1.0 to 2.2 mm) per leaf. Increases or decreases determined at day 7 and day 11 were not significant since the inaccuracy of the determinations exceeded values measured (0.1 to 0.4 mm). Between day 4 and day 7 the WGQ24h was about 1 and therefore no increase in leaf volume could be expected. Between day 8, when the young and growing leaves were cut off, and day 11 the water balance was positive (+ 81.6 mmol) and even exceeded the balance value

Table 2. Transpiration, water uptake, water balance for 24 h (uptake minus transpiration) and water gain quotient of an *Othonna opima* plant with 9 old and 2 young (immature) leaves (=plant number 12 of Tab. 1). Environmental conditions: Air temperature (24 h) 20 °C, dewpoint temperature of the ambient air (24 h) 13 °C, 12/12 h light/dark-period with photon irradiance values between 400 and 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Day 1 is the first day after the plant was transferred to the photometer.

Day	Leaf-age classes	Transpiration			Water Uptake			24 h Balance	Water Gain Quotient		
		Day	Night	24 h	Day	Night	24 h		Day	Night	24 h
1	y + o	86.2	27.6	113.8	97.4	71.4	168.8	54.8	1.13	2.59	1.48
2	y + o	163.5	31.0	194.5	125.9	87.0	212.9	18.3	0.77	2.8	1.09
3	y + o	200.3	34.4	234.7	132.4	104.6	237	2.3	0.66	3.04	1.01
4	Determination of leaf dimensions										
5	y + o	225.0	34.7	259.7	140.0	121.7	261.7	2.0	0.62	3.51	1.01
6	y + o	226.5	34.7	261.2	153.5	113.3	266.8	5.6	0.68	3.26	1.02
7	Determination of leaf dimensions										
8	Young leaves removed										
9	o	215.7	30.0	245.7	155.2	115.0	270.2	24.5	0.72	3.84	1.10
10	o	223.4	30.7	245.1	172.1	139.1	311.2	57.1	0.77	4.53	1.22
11	Determination of leaf dimensions										
12	o	218.9	34.7	253.6	130.9	110.4	241.3	-12.3	0.60	3.19	0.95

Values for transpiration, water uptake and water balance are in mmol.

between the start and day 4 but only very small and not significant increases of the leaf diameters were measured. These results, a positive water balance with a concomitant increase of leaf diameters between day 1 and 4, and also a positive balance of the same magnitude between day 8 and 11 but with none or only small increases in leaf diameter, seem to be contradictory. However, a surplus of water must not implicitly increase the volume of mature or expanding leaves, but could also be consumed by root growth or could be stored in the stem. In fact substantial root growth was observed at that time period. At day 7 the two immature and slowly growing leaves were removed. CO_2 gas exchange, water fluxes and budget and also the diurnal course of the water balance remained very similar (Fig. 3) to those for the plant with young and old leaves (Fig. 2). Measurements with *O. opima* plants with only young leaves showed also similar diurnal patterns in the variations of the CO_2 exchange and the water fluxes but with a positive water balance for the 24 h period (unpublished results).

Cotyledon orbiculata displayed the diurnal course of transpiration and CO_2 fixation of a CAM-plant only when the number of mature leaves (performing CAM) exceeded that of the young leaves (unpublished results). The daily course of the CO_2 exchange of young leaves varied with leaf age in a similar manner as was determined by Eller et al. (1988) for the CAM-succulent *Senecio medley-woodii*. For the 24 hour period the smallest of the young leaves had a negative CO_2 balance, more expanded leaves showed a CO_2 exchange like a C_3 -plant and then the growing but still immature leaves showed all transitions from a CO_2 exchange characteristic for the C_3 -pathway of photosynthesis to a CO_2 exchange typical for CAM-plants.

Transpiration, water uptake by the roots and the CO_2 exchange of a *C. orbiculata* (plant #13 of Tab. 1) are given in Fig. 4. The diurnal course of CO_2 fixation and the water loss by transpiration were typical for a CAM-plant with a high CO_2 dark fixation. The diurnal course of water uptake rates of this *C. orbiculata* was like a mirror-image of

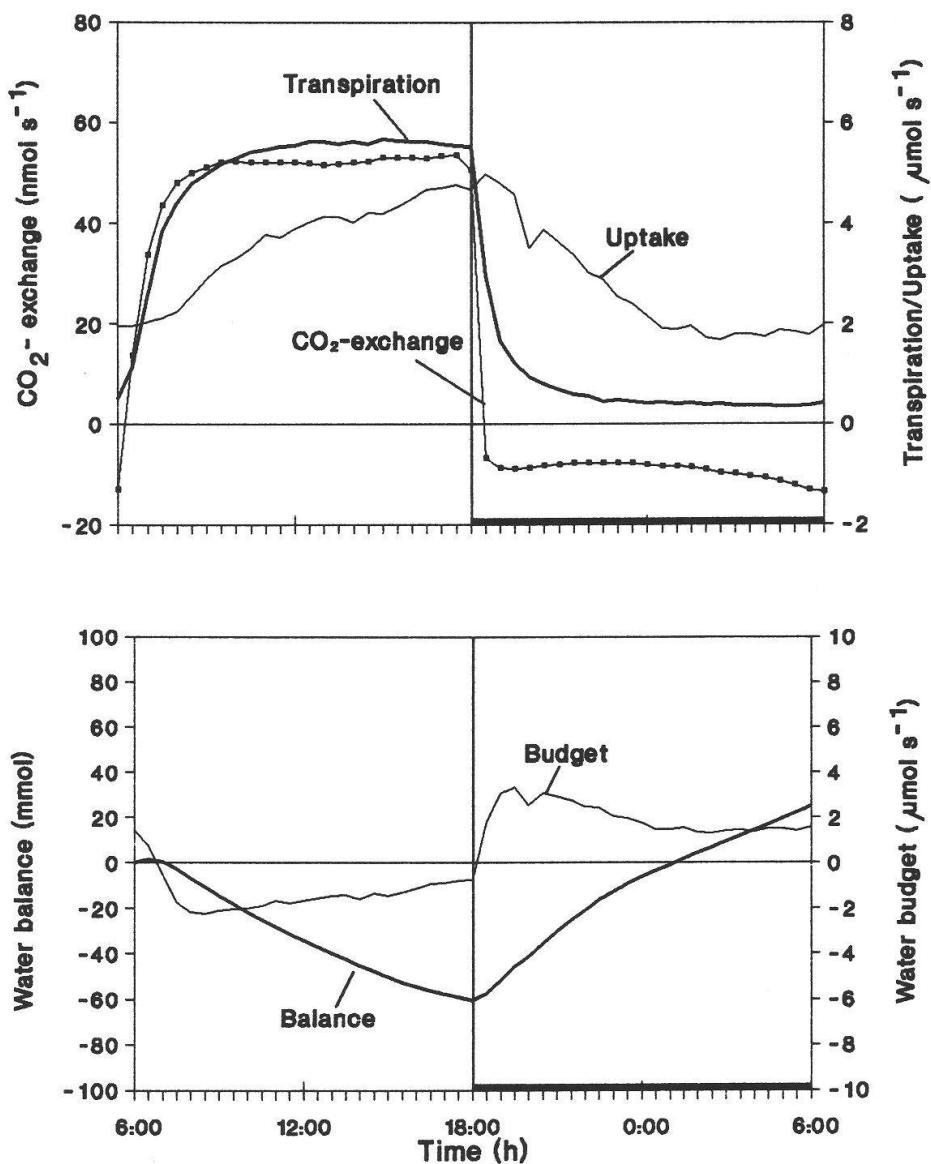


Fig. 3. Diurnal pattern of CO_2 -exchange and water relations of the same *Othonna opima* plant as in Fig. 2 but with the young leaves removed. Ambient conditions: Air temperature (24 h) 20°C, dewpoint temperature (24 h) 13°C, 12/12 h day/night photoperiod at a photon irradiance of $470 \pm 30 \mu\text{mol m}^{-2} \text{ s}^{-1}$. Data of day 9 of Tab. 2.

that of the C_3 -plant *O. opima* (Fig. 2). In the case of *O. opima* the uptake rates were highest when transpiration was highest at the end of the light period or shortly thereafter (Fig. 2) but uptake for this *C. orbiculata* at about the same time was at its minimum. Maximal values of uptake rates for *C. orbiculata* occurred towards the end of the night and shortly after the beginning of the light period when uptake of *O. opima* was at its lowest. After about 20H00 transpiration was constant or decreased but water uptake increased. This is in contrast to the reaction of *O. opima* where a decrease in transpiration initiated almost immediately a decrease in uptake. One must assume that the enhancement of the water uptake of *C. orbiculata* is caused by the osmotically active organic acids from CO_2 dark fixation as has been demonstrated for the CAM-plant *Senecio medley-woodii* (Ruess and Eller 1985; Ruess et al. 1988). Because the transpiration between

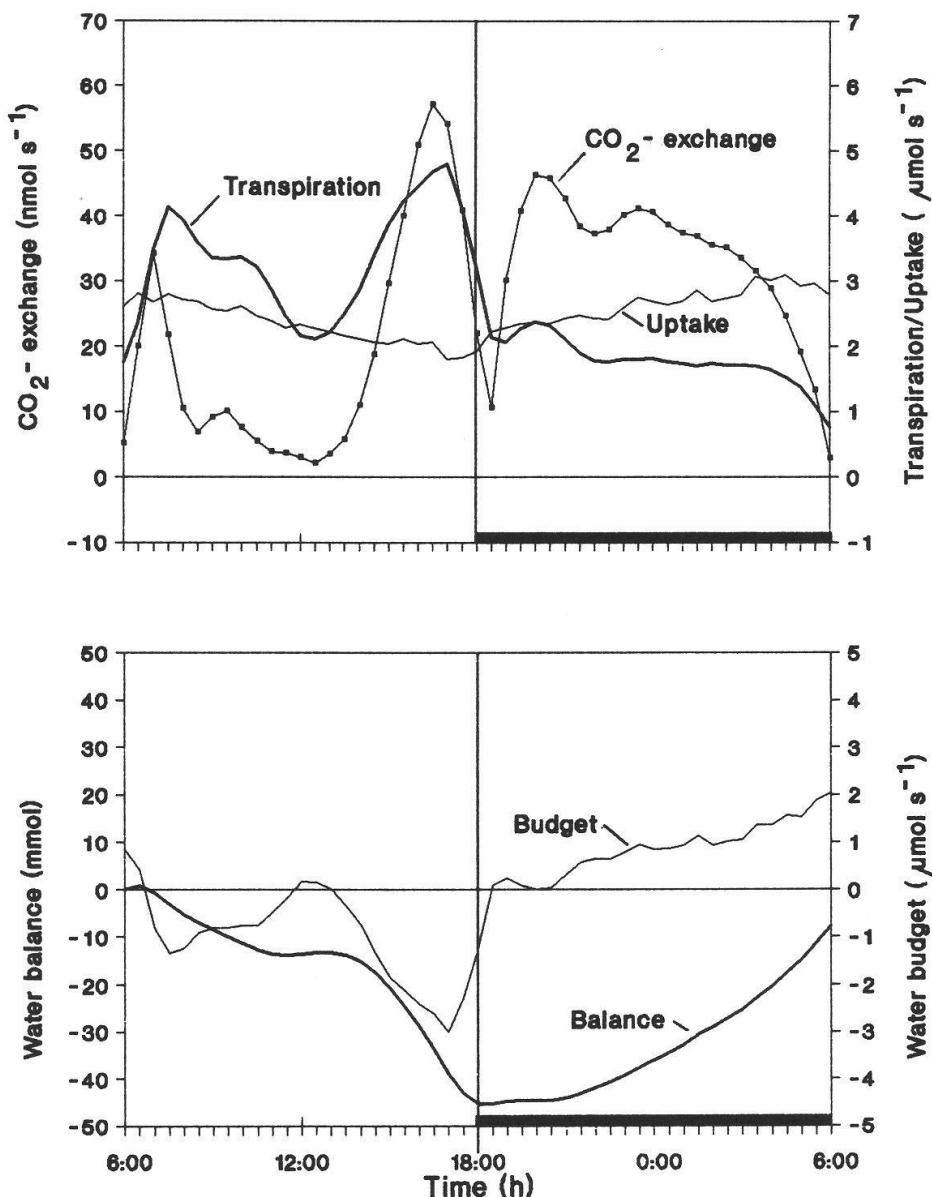


Fig. 4. Diurnal pattern of CO_2 -exchange and water relations of a *Cotyledon orbiculata* plant (10 old and 4 young leaves) in the photometer. Ambient conditions: Air temperature (24 h) 20 °C, dewpoint temperature (24 h) 13 °C, 12/12 h day/night photoperiod at a photon irradiance of $400 \pm 30 \mu\text{mol m}^{-2} \text{s}^{-1}$. Data of day 1 after the transfer to the photometer.

23H00 and 04H00 varied for both species only little (Fig. 2, 4) the nocturnal water budget varied concomitantly with the values of water uptake. The water balance of both species decreased during the light period with most negative values around 18H00. Thereafter the water deficit (negative balance) from the light period was nearly compensated by the nocturnal surplus in uptake (positive budget). However, there were different gradients in the nocturnal course of the balance curve, increasing for the CAM-plant *C. orbiculata* and decreasing for the C_3 -plant *O. opima*.

For the CAM-plants *S. medley-woodii* (Ruess et al. 1988) and *C. orbiculata* (Ferrari 1991) is known that their highest dark fixation rates occur when water availability is slightly reduced, e.g. at the onset of drought. The 24 hour data given for plant #13 in

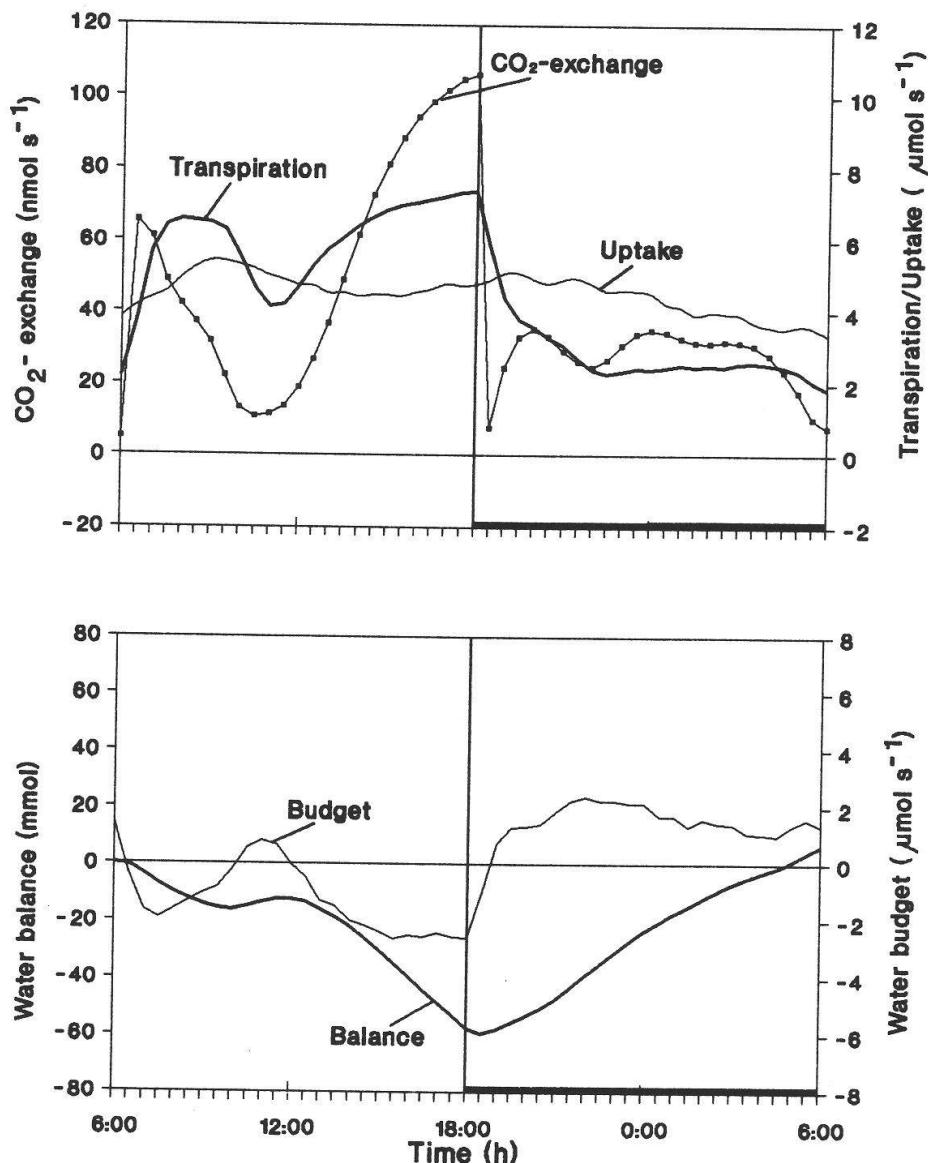


Fig. 5. Diurnal pattern of CO_2 -exchange and water relations of a *Cotyledon orbiculata* plant (10 old and 6 young leaves) in the photometer. Ambient conditions: Air temperature (24 h) 20 °C, dewpoint temperature (24 h) 13 °C, 12/12 h day/night photoperiod at a photon irradiance of $450 \pm 30 \mu\text{mol m}^{-2} \text{s}^{-1}$. Data of day 1 of Tab. 3.

Tab. 1 are those for the *C. orbiculata* of Fig. 4 and they reveal that transpiration exceeded water uptake ($\text{WGQ24h} = 0.95$) slightly but significantly indicating a shortage in water supply causing moderate drought. Therefore, the results for *C. orbiculata* with an optimal water status and suboptimal CO_2 dark fixation might show variations as outlined below. Fig. 5 and 6 illustrate the diurnal performance in CO_2 fixation and also the diurnal changes in water fluxes and plant water relations of another *C. orbiculata* plant (plant # 8 of Tab. 1) with old and immature leaves (Fig. 5), and, after the old leaves had been harvested (Fig. 6). Transpiration rates and the values for uptake, budget, balance and WGQ24h for the whole investigation period are summarized in Tab. 3. The WGQ24h -values of the first 4 days did not significantly differ from unity and one must assume that during this time period the plant was in an optimal plant water status. The young leaves

Table 3. Transpiration, water uptake, water balance for 24 h (uptake minus transpiration) and water gain quotient of an *Cotyledon orbiculata* plant with 10 old and 6 young (immature) leaves (=plant number 8 of Tab. 1). Environmental conditions: Air temperature (24 h) 20 °C, dewpoint temperature of the ambient air (24 h) 13 °C, 12/12 h light/dark-period with photon irradiance values between 400 and 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Day 1 is the first day after the plant was transferred to the photometer.

Day	Leaf-age classes	Transpiration			Water Uptake			24 h Balance	Water Gain Quotient		
		Day	Night	24 h	Day	Night	24 h		Day	Night	24 h
1	y+o	261.0	123.9	384.9	207.8	192.1	399.9	14.9	0.80	1.55	1.04
2	Old leaves removed										
3	y	114.5	34.7	149.2	101.6	54.2	155.8	6.6	0.89	1.56	1.04
4	y	107.8	34.3	142.1	95.0	50.4	145.4	3.3	0.88	1.47	1.02
5	y	112.4	29.5	141.9	102.1	50.6	152.7	10.9	0.91	1.71	1.08
6	Three of 6 young leaves removed										
7	y	64.3	12.3	76.6	59.6	27.2	86.7	10.1	0.93	2.21	1.13

Values for transpiration, water uptake and water balance are in mmol.

(Fig. 6) had a diurnal CO_2 gas exchange, transpiration and water uptake pattern like an *O. opima* as illustrated in the Fig. 2 and 3. The same also holds for the water budget and the daily water balance and one can assume that leaf succulents with a CO_2 gas exchange pattern of the C_3 pathway of photosynthesis have a similar pattern in the diurnal variations of the water budget and the 24 hour water balance. A comparison with the results from *C. orbiculata* with the prevailing CAM-feature of the old leaves (Fig. 4) supports such an assumption. However, one can also argue that the water uptake curve of the other *C. orbiculata* (Fig. 5) matches better that of the C_3 -plant *O. opima* (Fig. 2) than that of the *C. orbiculata* of Fig. 4. The water uptake curve (Fig. 5) had two maxima, one early in the morning and one after the onset of the dark period. These maxima could match the two transpiration peaks but only early in the light period did water uptake increase when transpiration increased and did uptake decrease (with some time lag) when the water loss by transpiration was reduced after about 08H30 (Fig. 5). However, in contrast to a marked increase of transpiration after 11H30 water uptake rates hardly changed. The uptake curve even declined further and only in the late afternoon a very small increase was noticed but not of a magnitude which would be in relation to the high transpiration rates in the afternoon. Nevertheless one can assume that the two maxima in the curve for uptake correspond somehow to the two maxima in transpiration but shifted in time. Moreover one can argue that an interaction from the CO_2 dark fixation as assumed from the results presented in Fig. 4 for a different individual of *C. orbiculata* does not exist in this plant or is small and masked by the influence of water loss by transpiration. Comparing the results illustrated in the Fig. 4 (plant #13 of Tab. 1) and Fig. 5 (plant #8 of Tab. 1) reveals that the second assumption is the more likely. The CO_2 fixation during the dark period had, on a leaf surface basis, for plant #8 a value of $57.96 \text{ mmol m}^{-2}$ compared with $83.14 \text{ mmol m}^{-2}$ for plant #13 (or 143% of the value of plant #8). Diurnal water losses by transpiration were $18.82 \text{ mmol m}^{-2}$, and $12.97 \text{ mmol m}^{-2}$ (or 66% of that of plant #8), respectively. Plant #8 transpires much more than #13 and has a much smaller CO_2 dark fixation. There is no doubt that for *C. orbiculata* these results prove that the diurnal modulation of water uptake results from the two features, water loss by transpiration and changes in the osmotic potential

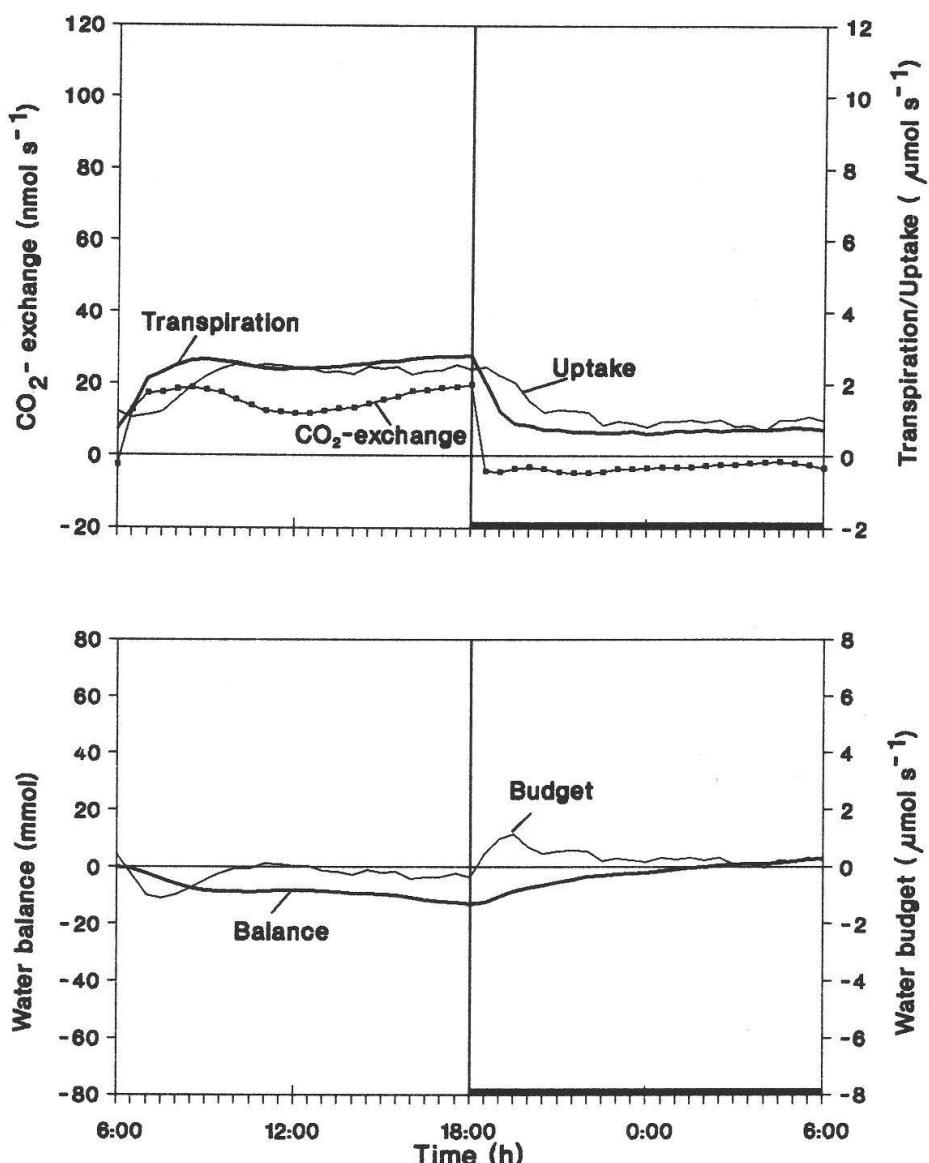


Fig. 6. Diurnal pattern of CO_2 -exchange and water relations of a *Cotyledon orbiculata* plant as in Fig. 5 but with the old leaves removed. Ambient conditions: Air temperature (24 h) 20°C, dewpoint temperature (24 h) 13°C, 12/12 h day/night photoperiod at a photon irradiance of $450 \pm 30 \mu\text{mol m}^{-2} \text{s}^{-1}$. Data of day 4 of Tab. 3.

resulting from CO_2 dark fixation, and only if the influence of the nocturnal CO_2 fixation prevails then water uptake is enhanced as for plant #13 (Fig. 4).

Concluding remarks

By not considering growth or reproduction one can certainly argue that eventually only the plant's water loss by transpiration produces a need for water uptake and, therefore, generally the diurnal course of water uptake should match water loss by transpiration. However, this would be an oversimplification since buffering of water loss by stored water, limitations in the conductivity of the substrate, the hydraulics of the

plant, and changes in tissue osmolalities also determine and modulate the pattern of the diurnal course of water uptake. If one intends to compare the water management of species with different physiological features, e.g. the C₃-pathway of photosynthesis versus the CAM, one must ascertain that species are compared which have very similar growth forms. Moreover, the individuals used for the determinations must be in a stable physiological state with only minor changes on consecutive days. The presented investigation did comply with these prerequisites.

Othonna opima with the C₃-pathway of photosynthesis and the CAM-plant *C. orbiculata* have similar growth forms and equally large water storage volumes in their terete leaves. In both species water uptake depends on water loss by transpiration but the water uptake of *C. orbiculata* also depends on CO₂ dark fixation. A high nocturnal carbon gain of *C. orbiculata* combined with a moderate water loss by transpiration results in a diurnal modulation of uptake (Fig. 4) that must be considered characteristic for leaf succulents of the all-cell type of succulence (von Willert et al. 1992). Water uptake of *C. orbiculata* is enhanced by the osmotically active products of CO₂ dark fixation as demonstrated by Ruess and Eller (1985) for *S. medley-woodii*. However, if CO₂ dark fixation of *C. orbiculata* is small then the impact of the diurnal course of water loss by transpiration on the diurnal course of water gain by uptake becomes clearly visible (Fig. 5) and one can assume that with further decreasing rates of nocturnal carbon gain the diurnal pattern of water uptake becomes gradually like that of the C₃-plant *O. opima*. If CO₂ fixation is restricted to a peripheral chlorenchyma with only small water storage volume, and water is stored predominantly in a central achlorophyllous hydrenchyma, then an impact of the nocturnal carbon gain on the modulation of the diurnal water might not exist as has been shown by Smith et al. (1987) for *Agave deserti*. Therefore one must assume that the nocturnal CO₂ fixation of CAM-plants enhances nocturnal water uptake provided CO₂ fixation is high and the main water store of leaf succulents is the photosynthetically active tissue and not primarily an achlorophyllous hydrenchyma.

The investigations were supported by grants of the Swiss National Science Foundation (Grants 31-9463.88, 31-30895.91) and the Stiftung für Wissenschaftliche Forschung an der Universität Zürich.

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