Short communication

Nocturnal water storage in plants having Crassulacean acid metabolism

U. Lütte
Institut für Botanik, Technische Hochschule Darmstadt, Schnittspahnstrasse 3, D-6100 Darmstadt, Federal Republic of Germany

Abstract. Measurements of water uptake and transpiration, during the dark period of plants having Crassulacean acid metabolism (CAM) allow calculation of leaf-volume changes (ΔV). Nocturnal leaf-volume changes of CAM plants have also been reported in the literature on the basis of water-displacement measurements. A third way of estimation is from measurements of turgor changes and cellular water-storage capacity using the pressure probe, cytromorphometry and the Scholander pressure chamber. An extension of the interpretation of results reported in the literature shows that for leaf succulent CAM plants the three different approaches give similar values of ΔV ranging between 2.3 and 10.7% (v/v). It is evident that nocturnal malic-acid accumulation osmotically drives significant water storage in CAM leaf tissue.

Key words: Crassulacean acid metabolism – Water storage (nocturnal).

Abbreviations and symbols: Cw = water-storage capacity; E = transpiration (evaporational water loss); P = turgor pressure; U = water uptake; V = cell volume; ε = cell-wall elastic modulus; π = osmotic pressure; CAM = Crassulacean acid metabolism (ΔV) is equal to the difference between water uptake (U) and transpirational (or "evaporational") water loss (E):

ΔV = U - E 

eqn. 1.

At the cellular level

ΔV ≈ V · ΔP/ε 

eqn. 2,

where V is the cell volume, ΔP the turgor-pressure change and ε the volumetric cell-wall elastic modulus (see Steudle et al. 1980). Hence, for a given period of time (Δt), e.g. for the dark period of CAM,

U - E = ΔV ≈ V · ΔP/ε 

eqn. 3.

Measurements of U can be made by potometry (Ruess and Eller 1985), those of E by porometry (e.g. Smith and Lütte 1985); ε and ΔP can be determined with the pressure probe (Steudle et al. 1980; Lütte and Nobel 1984). Changes in P can also be estimated from measurements of xylem tension with the Scholander pressure chamber and cryoscopic determinations of π (Smith and Lütte 1985). Cell dimensions are assessed by quantitative cytromorphometry.

Unfortunately, so far, simultaneous measurements of all parameters for a given species during the CAM rhythm are not available. For Senecio medley-woodii, U and E were measured carefully but ε, ΔP and cell dimensions have not been determined (Ruess and Eller 1985). With Kalanchoë daigremontiana these parameters were studied in detail but U was not measured (Steudle et al. 1980; Smith and Lütte 1985). However, using the information obtained with K. daigremontiana the data on S. medley-woodii recently published in this jour-
Table 1. Total water uptake ($U$), transpiration ($E$), volume changes ($AV$) and ratios of $AV$ to cell-wall elastic modulus ($e$) in *Senecio medley-woodii* calculated from experiments of Ruess and Eller (1985)

<table>
<thead>
<tr>
<th>Figure in Ruess and Eller 1985</th>
<th>$\Delta t$ (dark period) (h)</th>
<th>$U$ (kmol·m$^{-3}$)</th>
<th>$E$ (kmol·m$^{-3}$)</th>
<th>$AV$ (kmol·m$^{-3}$)</th>
<th>%</th>
<th>$\Delta P/e$</th>
</tr>
</thead>
<tbody>
<tr>
<td>3b</td>
<td>11</td>
<td>8.4</td>
<td>2.4</td>
<td>6.0</td>
<td>10.7</td>
<td>0.107</td>
</tr>
<tr>
<td>3c</td>
<td>11</td>
<td>6.0</td>
<td>2.4</td>
<td>3.6</td>
<td>6.4</td>
<td>0.064</td>
</tr>
<tr>
<td>4c</td>
<td>11</td>
<td>7.2</td>
<td>4.4</td>
<td>2.8</td>
<td>5.0</td>
<td>0.050</td>
</tr>
<tr>
<td>5a</td>
<td>10</td>
<td>4.7</td>
<td>1.6</td>
<td>3.1</td>
<td>5.5</td>
<td>0.055</td>
</tr>
<tr>
<td>5b</td>
<td>10</td>
<td>2.5</td>
<td>1.2</td>
<td>1.3</td>
<td>2.3</td>
<td>0.023</td>
</tr>
</tbody>
</table>

The percent values of $AV$ are in the same order of magnitude as the estimations of volume changes of various CAM plants of up to 2.7% obtained by Chen and Black (1983) with the water-displacement method. They can also be compared with the water-storage capacity ($C_c$) calculated for individual leaf cells of *K. daigremontiana*, where $C_c$ was $91 \cdot 10^3$ μm$^3$·MPa$^{-1}$·cell$^{-1}$ (Steudle et al. 1980). Since cell diameter was $90.9 \pm 14.1$ μm (SD, $n=266$), average cell volume was about $390\cdot10^3$ μm$^3$. Thus, for a pressure change of 0.2 MPa, as was observed with *K. daigremontiana* (Smith and Lüttge 1985), water-storage is about 4.6% of the cell volume. It has been noted in *K. daigremontiana* that the water-storage capacity of leaves is comparable with the total amount of water lost by transpiration during the entire dark period (Steudle et al. 1980). Table 1 shows that this also holds for *S. medley-woodii*; where $E$ and $AV$ are of the same order.

Furthermore, according to eqn. 2, $\Delta P/e$ can be obtained from $AV$ in Table 1. The ratio of $\Delta P/e$ for *S. medley-woodii* ranges between 0.023 and 0.107. As mentioned above, in *K. daigremontiana*, $\Delta P$ was up to 0.2 MPa. The average value of $e$, in this species was $4.24 \pm 2.77$ MPa (SD, $n=21$) (Steudle et al. 1980). This gives $\Delta P/e=0.047$, which is very close to the ratios in *S. medley-woodii* and indicates that similar values of $\Delta P$ and $e$ may pertain in *S. medley-woodii* as in *K. daigremontiana*.

Naturally, there are several simplifications in these comparisons. First, it is assumed that the tissue is very homogenous. To a fair extent this assumption is fulfilled in the species of *S. medley-woodii* and *K. daigremontiana* discussed here, where the succulent leaves have no separate water-storage tissue and are made up predominantly of one type of almost spherical green cells. Second, cellular water-storage capacity

$$C_c = V/(e + \pi)$$

and thus is very much determined by $e$. However, $e$ is pressure and volume dependent and changes during the dark period particularly as a consequence of the pressure changes noted above. Therefore, the $C_c$ value quoted above can only be taken as a rough average. Such relationships presumably are also the reason for the range of values of $AV$ and $\Delta P/e$ obtained from the experiments of Ruess and Eller (Table 1). The highest value ($\Delta P/e=0.107$) was from a plant which had only been in the potometer for 1 d and which showed high rates of water uptake ($U=8.4$ kmol m$^{-3}$). The lowest value ($\Delta P/e=0.023$) was from a plant under mild water stress caused by limited availability of $O_2$ in the root medium and a consequently low water uptake ($U=2.5$ kmol m$^{-3}$). Thus $\Delta P/e$ appears to depend on the actual water status of the plants. Third, we compare different CAM species.

Nevertheless, it is gratifying that three fundamentally different approaches for the estimation of nocturnal water storage in relation to total volume give closely similar results; namely in summary:

i) determination of $U$ and $E$ 2.3 to 10.7% (Table 1),

ii) determination of tissue volumes by water displacement 2.7%, and