



Stem water relations and net CO₂ uptake for a hemiepiphytic cactus during short-term drought

Park S. Nobel *, Erick De la Barrera

Department of Organismic Biology, Ecology and Evolution, University of California, Los Angeles, CA 90095-1606, USA

Received 16 January 2002; received in revised form 28 February 2002; accepted 1 March 2002

Abstract

Hylocereus undatus is widely distributed naturally and is currently cultivated in 19 countries for fruit. Because of its relatively thin stems, *H. undatus* was hypothesized to respond to drought more rapidly than other cacti. Stem water potential, water content and thickness were monitored during drought to provide easily measured parameters to be correlated with net CO₂ uptake ability, allowing the development of irrigation schedules to optimize water-use efficiency. *H. undatus* exhibited Crassulacean acid metabolism, as maximal stomatal opening and net CO₂ uptake occurred at night. Although the soil water potential decreased to -4.2 MPa during 12 days without watering, the stem water status parameters remained near their values under wet conditions (Ψ_{stem} of -0.67 MPa, water content of 90.8%, thickness of 4.48 mm). The drought was accompanied by a 63% decrease in the maximal water vapor conductance and a 57% decrease in the maximal net CO₂ uptake rate, but when the roots were excised for plants under wet conditions, neither parameter decreased appreciably over a comparable time period. Injection of 100 μM abscisic acid into attached stems and placing cut ends of detached stems in such a solution substantially reduced gas exchange 1 day later; at 2 days after injecting the hormone, the maximal water vapor conductance was similar to the minimal daytime values under wet conditions and the net CO₂ uptake rate was inhibited by 97%. Abscisic acid produced in the roots apparently leads to stomatal closure for this hemiepiphyte—whose roots can occur in very limited soil volumes—as soon as the water supply starts to deplete rather than after a large fraction of its stem water is transpired. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Abscisic acid; Crassulacean acid metabolism; *Hylocereus undatus*; Roots; Water potential; Water-use efficiency

1. Introduction

Responses of plants to short-term droughts of days to weeks can involve both sensitivity of plants to soil and leaf water potentials as well as

capacitance effects relying on water stored in the shoots or roots (Bray, 1997; Taiz and Zeiger, 1998; Nobel, 1999; Fitter and Hay, 2002). For isohydric species, decreases in soil water potential (Ψ_{soil}) during drought are accompanied by little initial change in leaf water content, which can be mediated by hormones such as abscisic acid travelling from the roots to the shoots leading to stomatal closure (Davies and Zhang, 1991;

* Corresponding author. Tel.: +1-310-206-3903; fax: +1-310-825-9433.

E-mail address: psnobel@biology.ucla.edu (P.S. Nobel).

Tardieu et al., 1996; Ali et al., 1999). For anisohydric plants, leaf water potential and stomatal conductance both decrease as Ψ_{soil} decreases, suggesting that stomatal opening is responding to leaf water content, not to a hormonal signal moving from the roots to the shoot. Capacitance effects that delay responses to drought are particularly apparent for cacti, where the volume (V , m^3) for shoot water storage is relatively large compared with the area (A , m^2) across which transpiration can occur. For instance, V/A is 9 mm for the photosynthetic stems of the prickly pear cactus *Opuntia ficus-indica* (L.) Miller, 25 mm for the columnar cactus *Stenocereus queretaroensis* (F.A.C. Weber) Buxbaum (Nobel et al., 2002) and 63 mm for the barrel cactus *Ferocactus acanthodes* (Lemaire) Britton and Rose (Nobel, 1988) but only ≈ 0.2 mm for leaves of C_3 plants (Nobel, 1999). The time required for drought to halve the total daily net CO_2 uptake under comparable field conditions is 20 days for *O. ficus-indica*, 33 days for *S. queretaroensis* and 45 days for *F. acanthodes* (Nobel, 1988; Nobel and Pimienta-Barrios, 1995), suggesting that a higher V/A and hence greater water-storage capacitance leads to longer periods during which stem water can support gas exchange.

The species examined, the hemiepiphyte *Hylocereus undatus* (Haworth) Britton and Rose, is a widely distributed cactus occurring naturally in tropical forests of Mexico, the West Indies, Central America and northern South America (Britton and Rose, 1963; Backeberg, 1966; Barthlott and Hunt, 1993). It typically occurs as a vine, with its numerous adventitious roots acquiring moisture and nutrients at microsites along the trees that it 'climbs' (Benzing, 1990; Castillo Martínez et al., 1996). It often maintains roots in the ground and can readily be propagated by placing detached stem segments in soil. Because its three-flanged stems are relatively thin, it is hypothesized that *H. undatus* will respond to drought more rapidly than the prickly pear, columnar and barrel cacti that have been examined. In any case, epiphytes and hemiepiphytes, which constitute $\approx 10\%$ of vascular plant species (Benzing, 1990; Lüttge, 1997), periodically face rapid changes in water content in their root zones, which often

occupy only a small volume of soil. Indeed, such species can frequently be subjected to short-term drought in a tropical forest, as the limited volume of substrate in the microsites along tree trunks where the roots of *H. undatus* might anchor can become extremely dry within a few days after a rainfall event (Croat, 1978; Freiberg, 1997; Lüttge, 1997; Benzing, 1998). Thus, abscisic acid from the roots may be necessary to help net CO_2 uptake by this species respond rapidly to drought. With regard to photosynthetic pathway, *H. undatus* appears to be an obligate Crassulacean acid metabolism (CAM) species (Raveh et al., 1995; Nobel and De la Barrera, 2002a), whereas *Chusia witana* Pittier, a common hemiepiphyte in tropical moist forests of Panama, switches from C_3 photosynthesis during wet periods to CAM during drought (Zotz and Winter, 1996). Indeed, $\approx 60\%$ of epiphyte and hemiepiphyte species obligately or facultatively exhibit CAM (Lüttge, 1997).

Although it has long been recognized horticulturally for its unusual growth form and attractive flowers, which are extremely large (up to 30 cm in length) and of short duration (usually only 1 night), *H. undatus* is also of interest because it is widely and increasingly cultivated for its fruit (Raveh et al., 1993; Mizrahi et al., 1997; Mizrahi and Nerd, 1999; Nerd et al., 2002). Currently, *H. undatus* is being cultivated for fruit in Australia, Cambodia, Colombia, Ecuador, Guatemala, Indonesia, Israel, Japan, Laos, Mexico, New Zealand, Nicaragua, Peru, the Philippines, Spain, Taiwan, Thailand, the southwestern US and Vietnam (Mizrahi and Nerd, 1999; Nerd et al., 2002; Nobel, personal observations). Many of the regions where this species has recently been brought into cultivation are arid or semiarid, quite different from its native tropical forests, so water relations responses to rainfall and drought are crucial for monitoring the vegetative biomass production of *H. undatus*; moreover, water for irrigation is an increasingly expensive resource. If changes in stem water potential, stem water content or stem thickness could be correlated with a decrease in stomatal conductance and resulted in a decrease in net CO_2 uptake, monitoring of such easily measured parameters would help growers make informed

management decisions, such as sporadically applying irrigation compared with continual irrigation, as is currently done. Allowing a short-term drought to reduce net CO₂ uptake by at most 50% and then irrigating should lead to a much higher biomass productivity per unit of water applied (one definition of water-use efficiency) than maintaining the plants continually under wet conditions. Hence, developing a relationship between stem water status parameters and plant productivity, as demonstrated by net CO₂ uptake, would be of economic advantage for such a new crop and of value in interpreting the responses of CAM hemiepiphytes ecologically.

2. Materials and methods

Bare-root plants of *H. undatus* (Haworth) Britton and Rose (Cactaceae) were provided by a commercial vendor. They were placed in individual pots filled to a depth of 10 cm with 2.0 l of 1:1 by volume of uncompacted washed premium-grade plaster sand and vermiculite. The plants were maintained for 1 year in Conviron E-15 environmental chambers (Controlled Environments, Pembina, North Dakota) with 13-h days at 30 °C and 11-h nights at 20 °C, day/night air temperatures that are optimal for net CO₂ uptake by this species (Nobel and De la Barrera, 2002a). The day/night relative humidities averaged 40/70%, similar to values in their native habitats (Benzing, 1990; Castillo Martínez et al., 1996). The photosynthetic photon flux (PPF, wavelengths of 400–700 nm; measured with a LI-188S integrating quantum sensor, LI-COR, Lincoln, NE) incident on the upper half of the stems averaged 320 μmol m⁻² s⁻¹; this leads to a total daily PPF of 15 mol m⁻² per day, resulting in >90% of the maximal total daily net CO₂ uptake by *H. undatus* (Raveh et al., 1995).

At the initiation of the experiments, the plants averaged ≈195 g in total fresh mass and 48 ± 3 cm in length for the main stems that were used for all measurements (new stem growth occurred on some plants). Three times per week in the early afternoon, each plant received 200 ml of 0.2-strength Hoagland solution no. 2 supplemented

with micronutrients but with the nitrogen level as in 0.5-strength Hoagland solution (Hoagland and Arnon, 1950; Epstein, 1972), which leads to maximal total daily net CO₂ uptake by *H. undatus* (Nobel and De la Barrera, 2002b).

Drought was imposed by withholding water, leading to a reduction in the soil water potential (Ψ_{soil} , MPa) in the center of the root zone, which was measured with PCT-55 thermocouple psychrometers whose output was monitored with an HR-33T dew point microvoltmeter (Wescor, Logan, UT). After 12 days of withholding water, the plants were again watered three times per week. The stem water potential (Ψ_{stem} , MPa) within 30 min of midnight was determined using cores through the flat parts of the stems at midstem (≈4.5 mm in thickness) obtained with a cork borer 13 mm in inside diameter; the cores were sliced paradermally at mid tissue with a razor blade and allowed to equilibrate for 3 h in a SC10C TruPsi thermocouple psychrometer (Decagon Devices, Pullman, WA). Water content on a mass basis for similar stem cores also split in half paradermally was determined after drying at 80 °C until no further mass change occurred (generally in 24 h).

The net CO₂ uptake rates (μmol m⁻² s⁻¹) by stems of *H. undatus* were measured using a LI-COR LI-6200 portable photosynthesis system. Measurements were routinely made every 2 h over a 24-h period (measurements required a total time of 40 min) or twice per stem from 00:00 to 02:00 h (a period when the net CO₂ uptake rate tended to be maximal) on stem locations receiving a PPF of ≈320 μmol m⁻² s⁻¹. Concomitant measurements of the transpiration rates (mmol m⁻² s⁻¹) at the same stem locations were made with a LI-COR LI-1600 steady-state porometer; the water vapor conductance (mmol m⁻² s⁻¹) was obtained by dividing the transpiration rate by the decrease in the mole fraction of water vapor from the stem to the ambient air (Nobel, 1999). For both instruments, the cuvette was fitted to a flat side of the three-flanged stems of *H. undatus* by replacing the lid of the cuvette with an acrylic plate having a rectangular extension with an opening of 10 × 30 mm whose margin was covered by a foam-rubber gasket to form an air-tight

seal with the stem surface. Gas exchange data are expressed based on the area of the stem side exposed to the inside of the cuvette.

Synthetic abscisic acid [ABA; 2-*cis*, 4-*trans*-abscisic acid; 5-(1-hydroxy-2,6,6-trimethyl-4-oxo-2-cyclohexen-1-yl)-3-methyl-2,4-pentadienoic acid] was purchased from Sigma-Aldrich, St. Louis, MI. Data are based on the biologically active + isomer (Tardieu et al., 1996; Taiz and Zeiger, 1998). Stem segments on intact plants were injected with distilled water or with 100 μM + ABA at three locations within 2 cm of their proximal region using a fine needle (external diameter of 0.5 mm, 16 mm in length); steady pressure was slowly applied to the syringe plunger so that all of the injected solution, which corresponded in mass to $\approx 1\%$ of the mass of the injected stem segments, remained within the stems (solution entry caused immediate darkening of the stem for a region extending ≈ 4 cm axially). Mature stems were also detached from plants at intersegment junctions that were maintained wet (to prevent cavitation); the stems were placed under distilled water and then recut, leading to a 20-cm segment that was placed in distilled water or in 100 μM + ABA in beakers so that the solution covered the proximal 6 cm of the segments (the beakers were covered with aluminum foil to prevent the entry of light, to which ABA is sensitive; Tardieu et al., 1996). Gas exchange measurements were subsequently made 6–8 cm distal to the injection sites for attached stems or the solution level for detached stems, all maintained in the environmental chambers with a PPF of $\approx 320 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Data are presented as means ± 1 S.E. (n = number of plants). Statistical significance was tested using Student's *t*-test or one-way ANOVA followed by Tukey's test.

3. Results

When water was withheld, the soil water potential (Ψ_{soil}) in the center of the root zone steadily decreased from -0.1 MPa ≈ 10 h after watering to -4.2 MPa at 12 days after watering ($P < 0.001$; Fig. 1A). On the other hand, neither the stem water potential (Ψ_{stem} ; Fig. 1B) nor the

percentage stem water content of *H. undatus* (Fig. 1B) decreased significantly during the 12 days after water was withheld. Specifically, Ψ_{stem} averaged -0.67 MPa at 10 h after watering and -0.68 MPa after water was withheld for 12 days and stem water content averaged 90.8% at 10 h after watering and 90.3% after water was withheld for 12 days. The thickness of cores near the stem margin of *H. undatus* was $4.48 \pm 0.17 \text{ mm}$ (n = ten plants) at 10 h after watering and $4.31 \pm 0.16 \text{ mm}$ (n = 10) after water was withheld for 12 days.

Gas exchange by *H. undatus* was consistent with it being a CAM species. Both the water vapor conductance and the net CO_2 uptake rate were higher at night, reaching a maximum from 00:00 to 02:00 h (Fig. 2). The maximal values under wet soil conditions were $81 \text{ mmol m}^{-2} \text{s}^{-1}$ for the water vapor conductance and $6.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the net CO_2 uptake rate. The minimal values during the daytime were 16 mmol m^{-2}

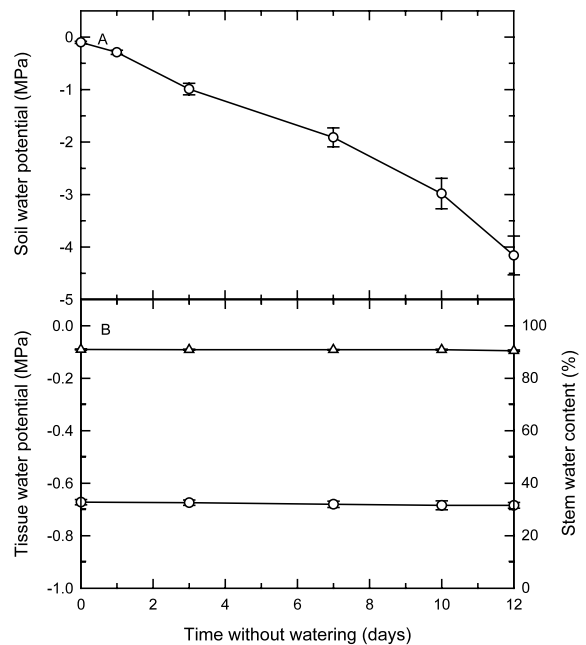


Fig. 1. Water relations parameters for *H. undatus* during soil drying: (A) Soil water potential in the center of the root zone ≈ 6 cm below the soil surface and (B) stem water potential (left ordinate, \circ) and stem percent water content (right ordinate, \triangle). Data are means \pm S.E. (unless the S.E. was smaller than the symbol; n = six plants).

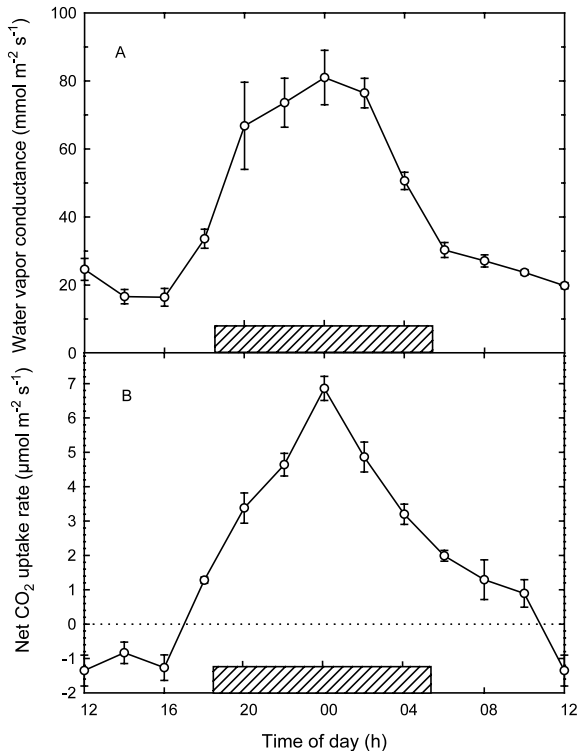


Fig. 2. Gas exchange parameters for *H. undatus* under wet conditions over a 24-h period: (A) water vapor conductance and (B) net CO₂ uptake rate. Hatched bars indicate nighttime. Data are means \pm S.E. ($n =$ five plants).

s⁻¹ for the water vapor conductance and $-1.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the net CO₂ uptake rate (Fig. 2). The total net CO₂ uptake over the 24-h period under wet conditions was 182 ± 10 ($n = 6$) mmol m⁻² per day.

When water was withheld, the maximal water vapor conductance decreased by 33% at 7 days ($P < 0.01$) and by 63% at 12 days ($P < 0.001$; Fig. 3A). Substantial recovery was observed at 1 day after rewatering ($P < 0.05$), half recovery at 2 days and full recovery to the same maximal water vapor conductance as under wet conditions occurred at 7 days after rewatering (Fig. 3A). The maximal net CO₂ uptake rate decreased by 17% at 7 days after water was withheld ($P < 0.05$) and decreased by 57% at 12 days ($P < 0.01$; Fig. 3B). Rewatering caused a recovery of half of the maximal net CO₂ uptake rate at 3 days and full recovery at 7 days after rewatering (Fig. 3B).

When all the roots were excised from well-watered plants, the maximal water vapor conductance and the maximal net CO₂ uptake rate did not change significantly for the next 10 days ($P > 0.3$; Fig. 4). After 10 days, both values decreased. For instance, at 20 days after root excision, the water vapor conductance decreased by 62% ($P < 0.01$; Fig. 4A) and the net CO₂ uptake rate decreased by 57% ($P < 0.01$; Fig. 4B). The stem water potential was -0.98 ± 0.02 ($n = 6$) MPa at 10 days after root excision ($P < 0.01$ compared with well-watered plants) and -1.17 ± 0.04 ($n = 6$) MPa at 20 days ($P < 0.01$ compared with at 10 days); the stem water content was 89.6 ± 0.3 ($n = 6$)% at 10 days ($P < 0.05$) after root excision and 88.9 ± 0.2 ($n = 6$)% at 20 days ($P < 0.05$).

The influences of 100 μM exogenous ABA could be seen within 1 day of application (Table

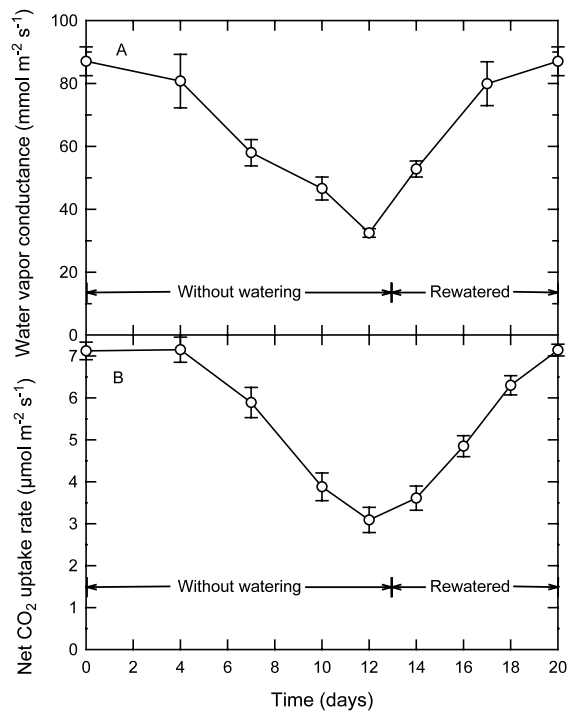


Fig. 3. Maximal gas exchange parameters for *H. undatus* during a 12-day period without watering and during subsequent routine watering (beginning on day 13) for 7 days: (A) water vapor conductance and (B) net CO₂ uptake rate. Data were obtained from 00:00 to 02:00 h and are means \pm S.E. ($n =$ five plants; two measurements were averaged for each plant).

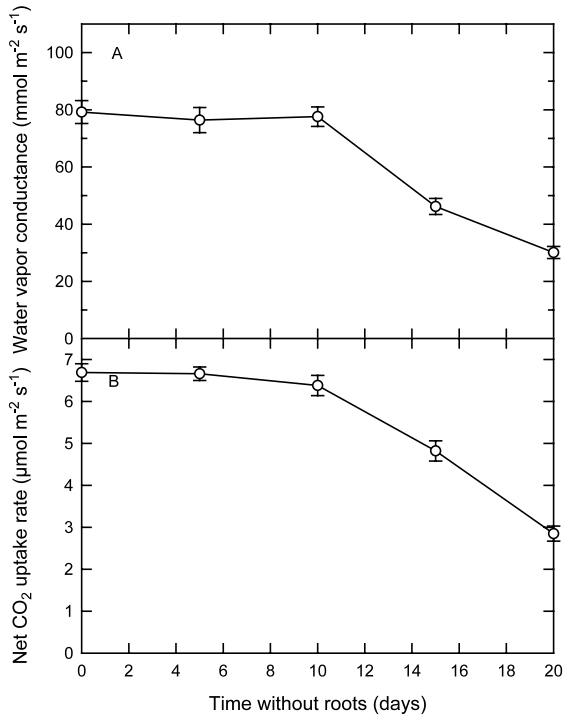


Fig. 4. Maximal gas exchange parameters for *H. undatus* whose roots were excised: (A) water vapor conductance and (B) net CO₂ uptake rate. Data were obtained from 00:00 to 02:00 h and are means \pm S.E. ($n =$ five plants; two measurements were averaged for each plant).

1). The water vapor conductance and the nocturnal rate of net CO₂ uptake 1 or 2 days later were not affected by the injection of distilled water into attached stems or by the immersion of the proxi-

mal part of detached stems into distilled water versus the values at the same times of the day for untreated plants under wet conditions (Fig. 2). However, 1 day after the ABA injections or placing in the ABA solutions, the water vapor conductance at various times of the night decreased by an average of 62% and it decreased by 74% at 2 days ($P < 0.01$; Table 1). Injection of 100 μ M ABA reduced the maximal rate of net CO₂ uptake by 83% at 1 day and by 97% at 2 days ($P < 0.01$); immersing excised stems in 100 μ M ABA similarly reduced the maximal rate of net CO₂ uptake by 78% at 1 day and by 84% at 2 days ($P < 0.01$; Table 1).

4. Discussion

The stems of *H. undatus* had a smaller volume for water storage relative to the area for transpiration (V/A of 2.2 mm for the portions used for the gas exchange measurements) than *F. acanthodes*, *O. ficus-indica* and *S. queretaroensis*. Also, the net CO₂ uptake ability decreased more rapidly during drought than for the other three cactus species (Nobel, 1988; Nobel and Pimienta-Barrios, 1995). The maximal net CO₂ uptake rate for *H. undatus* was halved at 11 days after water was withheld, slightly earlier than previously observed for this species (Raveh et al., 1995); the half-time corresponds to 9 days after Ψ_{soil} became less than Ψ_{stem} , compared with 20–45 days for the three cactus species with much thicker stems (No-

Table 1
Influences of abscisic acid (ABA) on gas exchange by *H. undatus*

Treatment	Time after treatment (h)	Water vapor conductance (mmol m ⁻² s ⁻¹)		Net CO ₂ uptake (μmol m ⁻² s ⁻¹)	
		Control	ABA	Control	ABA
Injection of attached stems	22	72 (2)	21 \pm 10 (4)	5.48 (2)	0.95 \pm 0.57 (4)
	42	77 \pm 8 (6)	10 \pm 1 (6)	5.71 \pm 0.35 (6)	0.16 \pm 0.12 (6)
Detached stems in solution	26	75 \pm 6 (6)	32 \pm 6 (6)	5.87 \pm 0.48 (6)	1.30 \pm 0.14 (6)
	48	82 \pm 10 (6)	32 \pm 4 (6)	4.49 \pm 0.25 (6)	0.70 \pm 0.16 (6)

The proximal ends of stems (attached to the root system) were injected with distilled water or with 100 μ M ABA equivalent to \approx 1% of their mass at 04:00 h or detached stem segments \approx 20 cm in length were placed in distilled water or in 100 μ M ABA at 22:00 h. Data are means \pm S.E. (number of plants sampled in parentheses).

bel, 1988; Nobel and Pimienta-Barrios, 1995). However, the halving of net CO₂ uptake and water vapor conductance during short-term drought for *H. undatus* was not accompanied by significant decreases in Ψ_{stem} , stem water content or stem thickness, indicating that *H. undatus* is an isohydric species (Tardieu et al., 1996; Ali et al., 1999); i.e. gas exchange decreased before obvious morphological stem changes occurred. Thus, monitoring stem water status, including stem thickness, is not a sensitive means for determining when water should be applied to maintain net CO₂ uptake ability and would not aid in developing an optimal irrigation strategy for this hemiepiphytic cactus with regard to vegetative biomass productivity. Also, as is the case for other cacti, the relationship between vegetative growth and reproductive growth is not known for *H. undatus*, although nitrogen application can differentially affect fruiting for certain species, such as *O. ficus-indica* (Nobel, 1988; Nerd et al., 1993; Nobel and De la Barrera, 2002b).

The soil used here drained quickly, reflecting its high sand content (50%) and relatively uncompacted nature. If the water-holding capacity of the soil were greater, such as due to compaction or greater fractions of silt, clay or organic matter, then Ψ_{soil} would not decrease below -0.67 MPa, the value for Ψ_{stem} under wet soil conditions, in just 2 days after watering. In any case, based on the kinetics of the decline in the maximal rate of net CO₂ uptake during drought in the well-drained soil used and its recovery during rewatering (half-time of 3 days), watering approximately every 2 weeks would lead to 77% of the maximal net CO₂ uptake rate. Thus, such intermittent irrigation apparently would not decrease net CO₂ uptake appreciably for *H. undatus* but would require much less irrigation water than for continuous irrigation and the resulting continual maintenance of wet conditions. The rapid responses of *H. undatus* to rewatering is consistent with the responses of young and older roots (ages of 4–6 weeks and 5–6 months, respectively) of the epiphytic cacti *Epiphyllum phyllanthus* (L.) Haworth and *Rhipsalis baccifera* (J.S. Miller) Stearn, whose hydraulic conductivity decreases during drought but fully recovers to the values

under wet conditions at 3 days after rewatering (North and Nobel, 1994).

Values of the water vapor conductance closely paralleled values of the net CO₂ uptake rate over the course of a day as well as during drought and the subsequent recovery following rewatering, suggesting that the stomates exert a major influence on gas exchange for *H. undatus*. Also, CAM leads to a relatively high water-use efficiency for this species. Under the day/night temperatures of 30/20 °C and day/night relative humidities of 40/70%, the total daily water loss for stem locations receiving a PPF of 15 mol m⁻² per day was 42.5 mol m⁻² per day and the total daily net CO₂ uptake was 182 mmol m⁻² per day. This corresponds to a water-use efficiency of 0.0043 CO₂/H₂O, which is characteristic of CAM species and 2- to 5-fold higher than is typical for C₃ and C₄ species under comparable conditions (Nobel, 1999). The water-use efficiency for stems of *H. undatus* is lower than for stems of *O. ficus-indica*, which is ≈ 0.0074 CO₂/H₂O under similar field conditions except with 50% higher PPF levels (Nobel, 1988; Goldstein et al., 1991; Nobel and Israel, 1994). The lower value for *H. undatus* reflects a lower maximal rate of net CO₂ uptake and a lower total daily net CO₂ uptake for the hemiepiphyte, which is adapted to shaded habitats (Britton and Rose, 1963; Backeberg, 1966; Barthlott and Hunt, 1993) and which achieves maximal growth in Israel under shade cloth that attenuates solar irradiation by at least 30% (Raveh et al., 1995, 1998; Mizrahi and Nerd, 1999). Also, daytime stomatal closure for *H. undatus* is not as complete as for *O. ficus-indica*, whose daytime water vapor conductance can decrease to 10 mmol m⁻² s⁻¹ (Goldstein et al., 1991), presumably reflecting the more humid habitat of the hemiepiphyte.

Although the maximal net CO₂ uptake rate by *H. undatus* was halved at 9 days after Ψ_{soil} for rooted plants became less than Ψ_{stem} , no significant decrease in this rate occurred at 10 days after its roots were excised. Apparently, a chemical message was sent from the roots in drying soil to the shoots, the most logical candidate being ABA (Davies and Zhang, 1991; Taiz and Zeiger, 1998; Fitter and Hay, 2002). In agreement with this

conjecture, injection of 100 μM ABA into the stems or placing detached stem segments in 100 μM ABA led to major decreases in the water vapor conductance and in the maximal rate of net CO_2 uptake in 22–26 h. At 42 h after ABA injection, the maximal water vapor conductance was lower than its typical minimum daytime value, indicating essentially complete stomatal closure and the maximal net CO_2 uptake rate decreased by 97%.

The relatively rapid decrease in water vapor conductance by *H. undatus* during short-term drought, apparently induced by the chemical messenger ABA produced in the roots, ensures that this species will conserve stem water. Thus, roots of this hemiepiphyte that occur in a microsite with a very limited soil volume (Lüttge, 1989; Benzing, 1990), such as a tree crotch, can send a message to the stem as soon as the local water supply begins to be depleted. A small rainfall event leading to a high Ψ_{soil} but only for a short period would then not lead to a sustained period of stomatal opening that could deplete a large fraction of the stem water, which is especially relevant taking into consideration the thin stems of *H. undatus* with their low A/V compared with other cacti. Without roots and hence without the purported chemical signal produced during drought, the stems lost $\approx 13\%$ of their water in 10 days and 19% in 20 days (assuming for the calculation that no change in dry mass occurred). Such major water losses could threaten the viability of this hemiepiphyte under natural conditions. Thus, in addition to the widespread occurrence of CAM among epiphytes and hemiepiphytes (Lüttge, 1997), leading to high water-use efficiencies, such species may rely on ABA produced in the roots in response to a decreasing Ψ_{soil} to limit loss of shoot water during drought instead of using a decreasing Ψ_{stem} to lead to stomatal closure.

Acknowledgements

We thank Kevin Coniff for generously providing the plant material. This research was supported by the US–Israel Binational Agricultural Research and Development Fund, Grant No. IS-3282-01.

References

- Ali, M., Jensen, C.R., Mogensen, V.O., Andersen, M.N., Henson, I.E., 1999. Root signalling and osmotic adjustment during intermittent soil drying sustain grain yield of field grown wheat. *Field Crops Res.* 62, 35–52.
- Backeberg, C., 1966. *Das Kakteenlexikon*. Gustav Fischer, Jena, Germany.
- Barthlott, W., Hunt, D.R., 1993. Cactaceae. In: Kubitzki, K. (Ed.), *The Families and Genera of Vascular Plants*, vol. 2. Springer-Verlag, Berlin, pp. 161–196.
- Benzing, D.H., 1990. *Vascular Epiphytes: General Biology and Related Biota*. Cambridge University Press, Cambridge, UK.
- Benzing, D.H., 1998. Vulnerabilities of tropical forests to climate change: the significance of resident epiphytes. *Climate Change* 39, 519–540.
- Bray, E.A., 1997. Plant responses to water deficit. *Trends Plant Sci.* 2, 48–54.
- Britton, N.L., Rose, J.N., 1963. *The Cactaceae: Descriptions and Illustrations of Plants of the Cactus Family*, vol. 2. Dover, New York.
- Castillo Martínez, R., Cáliz De Dios, H., Rodríguez Canto, A., 1996. *Guía Técnica para el Cultivo de Pitahaya*. Universidad de Quintana Roo, Chetumal, Quintana Roo, Mexico.
- Croat, T.B., 1978. *Flora of Barro Colorado Island*. Stanford University Press, Stanford, CA.
- Davies, W.J., Zhang, J., 1991. Root signals and the regulation of growth and development of plants in drying soil. *Ann. Rev. Plant. Physiol. Mol. Biol.* 42, 55–76.
- Epstein, E., 1972. *Mineral Nutrition of Plants: Principles and Perspectives*. Wiley, New York.
- Fitter, A.H., Hay, R.K.M., 2002. *Environmental Physiology of Plants*, third ed. Academic Press, London.
- Freiberg, M., 1997. Spatial and temporal pattern of temperature and humidity of a tropical premontane rain forest tree in Costa Rica. *Selbyana* 18, 77–84.
- Goldstein, G., Ortega, J.K.E., Nerd, A., Nobel, P.S., 1991. Diel patterns of water potential components for the Crasulacean acid metabolism plant *Opuntia ficus-indica* when well-watered or droughted. *Plant Physiol.* 95, 274–280.
- Hoagland, D.R., Arnon, D.I., 1950. The water-culture method for growing plants without soil. *Calif. Agric. Exp. Station Circ.* 347, 1–32.
- Lüttge, U. (Ed.), 1989. *Vascular plants as epiphytes. Evolution and Ecophysiology*. Ecological Studies Series, vol. 76, Springer-Verlag, Berlin.
- Lüttge, U., 1997. *Physiological Ecology of Tropical Plant*. Springer-Verlag, Berlin.
- Mizrahi, Y., Nerd, A., 1999. Climbing and columnar cacti: new arid land fruit crops. In: Janick, J. (Ed.), *Perspectives on New Crops and New Uses*. ASHS Press, Alexandria, VI, pp. 358–366.
- Mizrahi, Y., Nerd, A., Nobel, P.S., 1997. Cacti as crops. *Hort. Rev.* 18, 291–319.

- Nerd, A., Mesika, R., Mizrahi, Y., 1993. Effect of N fertilizer on autumn floral flush and cladode N in prickly pear (*Opuntia ficus-indica* (L.) Mill.). *J. Hort. Sci.* 68, 337–342.
- Nerd, A., Tel-Zur, N., Mizrahi, Y., 2002. Fruits of vine and columnar cacti. In: Nobel, P.S. (Ed.), *Cacti: Biology and Uses*. University of California Press, Berkeley, CA, pp. 185–197.
- Nobel, P.S., 1988. *Environmental Biology of Agaves and Cacti*. Cambridge University Press, New York.
- Nobel, P.S., 1999. *Physicochemical and Environmental Plant Physiology*, second ed. Academic Press, San Diego, CA.
- Nobel, P.S., Israel, A., 1994. Cladode development, environmental responses of CO₂ uptake, and productivity for *Opuntia ficus-indica* under elevated CO₂. *J. Exp. Bot.* 45, 295–303.
- Nobel, P.S., Pimienta-Barrios, E., 1995. Monthly stem elongation for *Stenocereus queretaroensis*: relationships to environmental conditions, net CO₂ uptake and seasonal variations in sugar content. *Environ. Exp. Bot.* 35, 17–24.
- Nobel, P.S., De la Barrera, E., 2002a. High temperatures and net CO₂ uptake, growth, and stem damage for the hemiepiphytic cactus *Hylocereus undatus*. *Biotropica* (in press).
- Nobel, P.S., De la Barrera, E., 2002b. Nitrogen relations for net CO₂ uptake by the cultivated hemiepiphytic cactus, *Hylocereus undatus*. *Sci. Hort.* (in press).
- Nobel, P.S., Pimienta-Barrios, E., Zañudo Hernández, J., Ramírez-Hernández, B.C., 2002. Historical aspects and net CO₂ uptake for cultivated CAM plants in Mexico. *Ann. Appl. Biol.* (in press).
- North, G.B., Nobel, P.S., 1994. Changes in root hydraulic conductivity for two tropical epiphytic cacti as soil moisture varies. *Am. J. Bot.* 81, 46–53.
- Raveh, E., Weiss, J., Nerd, A., Mizrahi, Y., 1993. Pitayas (Genus *Hylocereus*): a new fruit crop for the Negev Desert of Israel. In: Janick, J., Simons, J.E. (Eds.), *New Crops*. Wiley, New York, pp. 491–495.
- Raveh, E., Gersani, M., Nobel, P.S., 1995. CO₂ uptake and fluorescence responses for a shade-tolerant cactus *Hylocereus undatus* under current and doubled CO₂ concentrations. *Physiol. Plant* 93, 505–511.
- Raveh, E., Nerd, A., Mizrahi, Y., 1998. Responses of two hemiepiphytic fruit-crop cacti to different degrees of shade. *Sci. Hort.* 73, 151–164.
- Taiz, L., Zeiger, E., 1998. *Plants Physiology*, second ed. Sinauer Associates, Sunderland, MA.
- Tardieu, F., Lafarge, T., Simonneau, Th., 1996. Stomatal control by fed or endogenous xylem ABA in sunflower: interpretation of correlations between leaf water potential and stomatal conductance in anisohydric species. *Plant Cell Environ.* 19, 75–84.
- Zotz, G., Winter, K., 1996. Seasonal changes in daytime versus nighttime CO₂ fixation of *Clusia uvitana* in situ. In: Winter, K., Smith, J.A.C. (Eds.), *Crassulacean Acid Metabolism: Biochemistry, Ecophysiology and Evolution*. Springer-Verlag, Berlin, pp. 312–323.