

CO₂ uptake by the cultivated hemiepiphytic cactus, *Hylocereus undatus*

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Summary

The climate of the native tropical forest habitats of *Hylocereus undatus*, a hemiepiphytic cactus cultivated in 20 countries for its fruit, can help explain the response of its net CO₂ uptake to environmental factors. Under wet conditions, about 85% of the total daily net CO₂ uptake occurs at night via Crassulacean acid metabolism, leading to a high water-use efficiency. Total daily net CO₂ uptake is reduced 57% by only 10 days of drought, possibly involving stomatal closure induced by abscisic acid produced in the roots, which typically occupy a small substrate volume. Total daily net CO₂ uptake for *H. undatus* is maximal at day/night air temperatures of 30/20°C, optimal temperatures that are higher than those for desert cacti but representative of ambient temperatures in the tropics; its total daily net CO₂ uptake becomes zero at day/night air temperatures of 42/32°C. Stem damage occurs at 45°C for *H. undatus*, whose photosynthetic cells show little acclimation to high temperatures compared with other cacti and are also sensitive to low temperatures, -1.5°C killing half of these cells. Consistent with its shaded habitat, total daily net CO₂ uptake is appreciable at a total daily PPF of only 2 mol m⁻² day⁻¹ and is maximal at 20 mol m⁻² day⁻¹, above which photoinhibition reduces net CO₂ uptake. Net CO₂ uptake ability, which is highly correlated with stem nitrogen and chlorophyll contents, changes only gradually (halftimes of 2-3 months) as the concentration of applied N is changed. Doubling the atmospheric CO₂ concentration raises the total daily net CO₂ uptake of *H. undatus* by 34% under optimal conditions and by even larger percentages under adverse environmental conditions.

Key words: Abscisic acid, nitrogen relations, photosynthesis, pitahaya, temperature tolerance, tropical forest, water-use efficiency

Introduction

Epiphytic and hemiepiphytic cacti with edible fruits, commonly known as pitahayas, are native to Mexico, the Caribbean, Central America, and northern South America (Fig. 1). These species occur mainly in two genera of the tribe Hylocereeae of subfamily Cactoideae (Anderson, 2001): *Hylocereus* Britton & Rose [18 species; edible fruits are obtained from *H. costaricensis* (F.A.C. Weber) Britton & Rose, *H. polyrhizus* (F.A.C. Weber) Britton & Rose, *H. triangularis* (L.) Britton & Rose, and especially *H. undatus* (Haworth) Britton & Rose] and *Selenicereus* (Berger) Britton & Rose [28 species; *S. megalanthus* (K. Schumann ex Vaupel) Moran is the best known edible one, with fruits also consumed from *S. setaceus* (A.P. de Candolle) Werdermann]. Fruits of a few epiphytic cacti in other genera are also edible, such as those of *Epiphyllum anguliger* (Lemaire) D. Don. Most of these vine-like cacti are native to tropical forests ("hyle" in *Hylocereus* is the Greek for forest), where they tend to climb or clamber on trees. They produce aerial roots, which facilitate anchoring along the trunks, and have large

flowers and large fruits. The climate of the native habitats of such epiphytes (plants living on other plants) and hemiepiphytes (epiphytes that can secondarily develop roots in the ground) is characterised by moderate temperatures with little annual variation, high rainfall leading to high relative humidity, and reduced light levels at the canopy locations where these cacti occur (Croat, 1978; Benzing, 1990; Castillo Martínez *et al.*, 1996; Lüttge, 1997; Ortíz, 1999).

This review focuses on how the net CO₂ uptake of pitahaya-bearing cacti responds to climate, specifically to temperature, drought, and light, the latter represented by wavelengths that can be absorbed by photosynthetic pigments—400 to 700 nm, the photosynthetic photon flux (PPF). The most widely cultivated such vine-like cactus is *H. undatus*, which currently is grown in 20 countries (Fig. 1), and it is also the one most studied in terms of gas exchange. Its net CO₂ uptake ability has been determined with respect to temperature, drought, and photosynthetic photon flux (PPF) as well as applied nitrogen concentration and elevated atmospheric CO₂ concentrations.

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Fig. 1. Countries where *Hylocereus undatus* is currently being cultivated for fruit (back slanted hatching) and where it as well as other cacti bearing pitahayas are native (forward slanted hatching). Data are from Britton & Rose (1963), Bravo (1978), Backeberg (1966), Barthlott & Hunt (1993), Mizrahi & Nerd (1999), Nerd *et al.* (2002), Ortíz (1999), and P S Nobel (unpublished observations).

The native distribution of pitahayas (Fig. 1) is mostly restricted to tropical dry forests (Barbeau, 1990), where mean daily air temperature is near 24°C, ranging from 21°C to 26°C (Fig. 2A). Rainfall is usually more than 600 mm year⁻¹ (Rzedowski, 1983), most of which occurs during the summer, while the spring is essentially dry (Fig. 2B). Such seasonality for water availability leads to seasonal differences in canopy foliage. For instance, the leaf area index (LAI, the ratio of total leaf area to unit ground surface area; Norman & Campbell, 1989) for the upper canopy is three-fold greater during the wet season than at the end of the dry season (Fig. 2C), averaging 1.9 throughout the year. A seasonally varying PPF occurs under the upper canopy, reflecting the changes in water availability and hence LAI; instantaneous PPF under the canopy is 50% of the maximum during the dry season but only about 25% of the maximum during the wet season (Fig. 2C).

Crassulacean Acid Metabolism

The net CO₂ uptake patterns by the stems of *Hylocereus undatus* over 24-h periods are characteristic of plants employing the Crassulacean acid metabolism (CAM) pathway of photosynthesis, a pathway used by 7% of the nearly 300 000 species of vascular plants (Nobel, 1991; Winter & Smith, 1996). As for other CAM species, net CO₂ uptake by *H. undatus* occurs mainly at night (Fig. 3). In particular, under wet conditions and moderate temperatures, about 85% of its net CO₂ uptake is at

night, which is the major period for its stomatal opening (Fig. 3; Ortíz *et al.*, 1996; Ortíz, 1999). This day/night inversion of the CO₂ uptake pattern compared with the majority of plants minimises water loss by CAM plants. About 92% of plant species use the C₃ pathway (initial fixation of CO₂ catalysed by ribulose-1,5-bisphosphate carboxylase/oxygenase, leading to the formation of a three-carbon compound) and 1% use the C₄ pathway (initial fixation of CO₂ catalysed by phosphoenolpyruvate carboxylase, leading to the formation of a four-carbon compound); such plants take up CO₂ only during the daytime. CO₂ uptake at night (Phase I for CAM plants; Osmond, 1978; Nobel, 1988, 1999) involves a binding of CO₂ to a three-carbon compound catalysed by phosphoenolpyruvate carboxylase, leading to the accumulation of organic acids that are stored in the vacuoles of photosynthetic cells. Some net CO₂ uptake generally occurs early in the morning for *H. undatus* (Fig. 3; Phase II) and involves the binding of CO₂ by ribulose-1,5-bisphosphate carboxylase/oxygenase and also in the late afternoon (Phase IV), whereas CO₂ tends to be released during the middle of the daytime (Phase III) when the organic acids formed during the previous night are decarboxylated, leading to a high CO₂ concentration within the stem.

Air and stem temperatures tend to be lower at night, which is the key to appreciating the water-conserving aspects of CAM. Lower temperatures lead to less water loss, because air in the intercellular air spaces of the stems is essentially saturated with water vapour, the saturation water vapour pressure

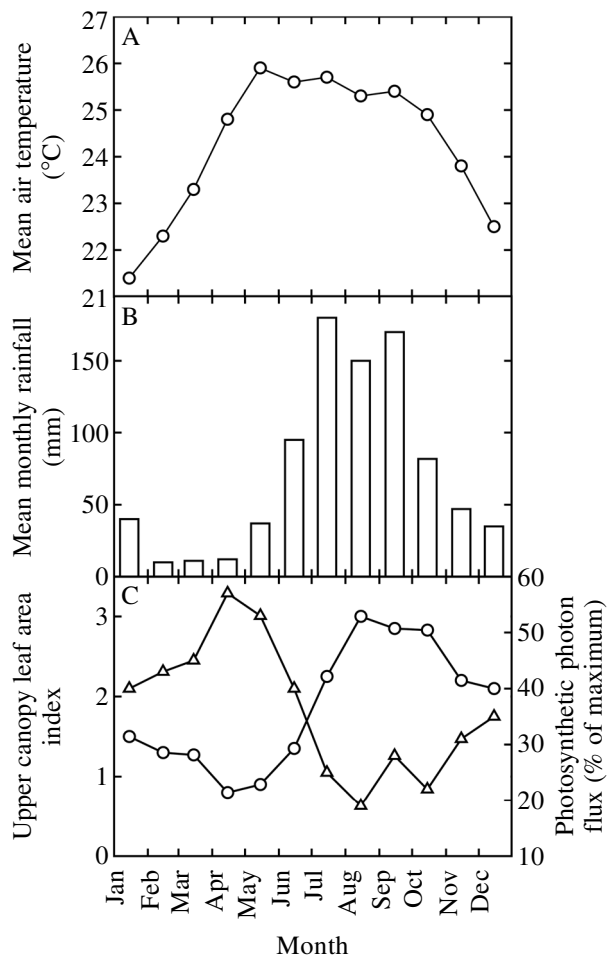


Fig. 2. Representative climate for tropical dry forests in North and South America where *H. undatus* is native: (A) mean daily air temperature, (B) mean monthly rainfall, and (C) upper canopy leaf area index (○) and understorey available PPF (Δ). Data were synthesised from Bullock (1986), Maas *et al.* (1995), Vázquez *et al.* (1995), and Pimienta *et al.* (1998).

increases nearly exponentially with temperature, and, for a given degree of stomatal opening, the transpiration rate depends on the difference in water vapour pressure from the stem to the surrounding air. For example, the saturation water vapour pressure is 2.34 kPa at 20°C and 4.25 kPa at 30°C (Nobel, 1999). If the ambient air had a water vapour pressure of 1.23 kPa (dewpoint temperature of 10°C), the force leading to water loss would be three times greater at 30°C compared with 20°C [(4.25 – 1.23)/(2.34 – 1.23) = 3.0], leading to three times more transpirational water loss at 30°C than at 20°C for the same degree of stomatal opening.

Because of predominantly nocturnal stomatal opening and hence predominantly nocturnal net CO₂ uptake, the water-use efficiency (ratio of CO₂ fixed to water transpired) is typically higher for CAM plants than for C₃ or C₄ plants. In particular, the total daily net CO₂ uptake for *H. undatus* under wet conditions can be 232 mmol m⁻² day⁻¹ (Fig. 3). This

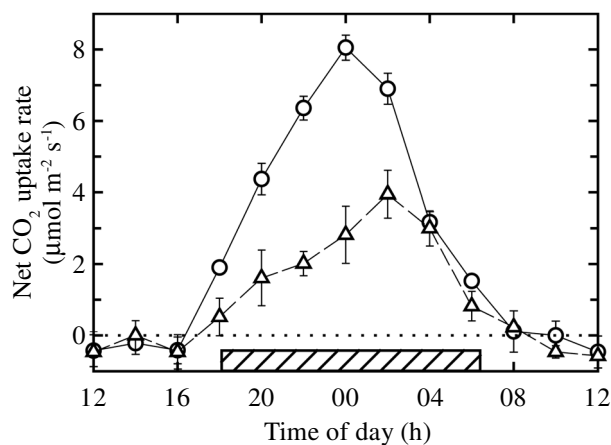


Fig. 3. Net CO₂ uptake by *H. undatus* over 24-h periods under wet conditions (○) or after 10 days of drought (Δ). The soil water potential at the centre of the rooting zone was -0.2 MPa under wet conditions and -3.2 MPa after 10 days of drought. Day/night air temperatures were 30/20°C, and the total daily PPF incident on the 1-yr-old stem surfaces considered was 10 mol m⁻² day⁻¹. Data are means ± SE (*n* = 5 plants; P S Nobel & E De la Barrera, unpublished measurements).

is accompanied by a total daily water loss of 53 mol m⁻² day⁻¹ (Nobel & De la Barrera, 2002a), leading to a water-use efficiency of 232 mmol CO₂ m⁻² day⁻¹ / 53 mol H₂O m⁻² day⁻¹, or 0.0044 CO₂/H₂O. Such a water-use efficiency for *H. undatus* is characteristic of CAM plants but is two- to five-fold higher than for C₃ or C₄ species under comparable conditions (Nobel, 1988, 1999).

Water Relations

Why does *H. undatus* employ the water-conserving CAM when it is native to moist regions? Actually, the microsites occupied by its roots in trees are relatively small and are subject to rapid drying (Andrade & Nobel, 1997). The substrate for an epiphyte growing in the crotch of a tree can become dry a few days after a rainfall event (Croat, 1978; Freiberg, 1997; Lüttge, 1997; Benzing, 1998). Thus most epiphytes are presumably CAM species with their roots occupying a small substrate volume that has little water holding capacity and consequently dries rapidly; for example, most of the approximately 20 000 species of orchids probably employ CAM (Winter & Smith, 1996; Lüttge, 1997; Zotz & Hietz, 2002). Many of the regions where *H. undatus* is cultivated for fruit (Fig. 1) are arid or semiarid, which are climatically quite different from the tropical forests where it is native, so knowledge of its water relations are also important horticulturally.

Drought commences when the water potential of the soil in the root zone becomes less than the water potential of the roots so that water uptake is thermodynamically not possible. For *H. undatus*

rooted in silica sand, the total daily net CO₂ uptake does not change appreciably for the first 7 days of drought but decreases by 78% at 17 days (Raveh *et al.*, 1995). For *H. undatus* rooted in a sand/vermiculite mixture, the net CO₂ uptake ability decreases by 57% at 10 days of drought (Fig. 3). Also, the maximal rate of net CO₂ uptake during drought tends to occur later in the night (Fig. 3), when stem temperatures generally are lower and hence transpiration is lower for a given degree of stomatal opening.

The water vapour conductance for *H. undatus* decreases during 10 days of drought, indicating stomatal closure, but the stem water potential does not decrease significantly (Nobel & De la Barrera, 2002a). A chemical message, probably abscisic acid, is apparently sent from the roots in the drying soil to the shoots, leading to stomatal closure as a means for conserving water. Moreover, the stomatal response to this water-stress hormone prevents the loss of stem water, which may be crucial for epiphytic and hemiepiphytic cacti whose roots explore only a relatively small soil volume. When the roots of *H. undatus* are excised so that no abscisic acid can move from the roots to the shoot during drought, the decline in net CO₂ uptake is much slower (50% inhibition is delayed by approximately 8 days compared with plants with their roots intact), emphasising the importance of this hormone for conserving stem water during drought (Nobel & De la Barrera, 2002a).

When *H. undatus* that has been droughted for 10 days is rewatered, a significant increase in net CO₂ uptake occurs in 1 day, the CO₂ uptake ability is half restored in only 2 days, and full recovery occurs in 7 days (P S Nobel and E De la Barrera, unpublished observations). Thus this cactus can respond rapidly to rainfall events, which may be crucial for its growth in tropical regions with frequent rainfalls (Freiberg, 1997; Lüttge, 1997) as well as of importance in developing irrigation schedules when it is cultivated as a crop (Mizrahi & Nerd, 1999; Nerd *et al.*, 2002). Similarly, the hydraulic conductivity of the roots (a direct measure of plant water uptake ability) of two epiphytic cacti, *Epiphyllum phyllanthus* and *Rhipsalis baccifera*, decreases during drought but increases to the values under wet conditions only 3 days after rewatering (North & Nobel, 1994).

Temperature

Temperature influences nearly every plant process, including net CO₂ uptake and hence growth. The optimal day/night air temperatures for total daily net CO₂ uptake by *Hylocereus undatus* are 30/20°C (Fig. 4), which are relatively high compared with temperatures optimal for other CAM plants. Because

most net CO₂ uptake occurs at night, the nighttime temperatures are more crucial for total daily net CO₂ uptake than are the daytime ones. The optimal nighttime temperatures for total daily net CO₂ uptake by cacti native to arid or semiarid regions are from 10°C to 15°C (Nobel, 1988). Apparently, the higher optimal nighttime temperatures for *H. undatus* reflect temperatures characteristic of the primarily tropical regions where it is native (Fig. 1). The total daily net CO₂ uptake is half of the maximal value at low day/night temperatures of 18/8°C and at high day/night temperatures of 38/28°C (Fig. 4). Above day/night air temperatures of 42/32°C, a net loss of CO₂ occurs over a 24-h period (Fig. 4), indicating that this species is not adapted to such high temperatures.

Temperature also affects the survival of cacti, and *H. undatus* is more sensitive to temperature extremes than are most other cacti. Based on an assay using the uptake of the vital dye neutral red into the central vacuole of a cell (Onweume, 1979; Nobel *et al.*, 1995), half of the photosynthetic (chlorenchyma) cells are killed by a 1-h low-temperature treatment at -1.5°C for *H. undatus* maintained at day/night temperatures of 20/10°C and half are killed at -1.3°C for plants maintained at 30/20°C (Nobel *et al.*, 2002). For 19 other species of cacti, half of the photosynthetic cells are killed at an average temperature of -10.2°C for plants maintained at 20/10°C, and the low-temperature acclimation or hardening (decrease in lethal temperatures as the day/night temperatures are reduced) averages 0.7°C as the day/night temperatures are reduced by 10°C (Nobel, 1988), much greater than the 0.2°C observed for *H. undatus*. Again using the uptake of neutral red into the cell central vacuoles as the assay, half of the photosynthetic cells of *H. undatus* are killed by a 1-h high-temperature treatment at 54.0°C for plants at 25/15°C and at 55.4°C for plants at 35/25°C (Nobel & De la Barrera, 2002b). For 18 other species of cacti, half of the photosynthetic cells are killed at an average temperature of 57.0°C for plants maintained at 35/25°C, and the high temperature acclimation (as the day/night temperatures are raised by 10°C) averages 5.3°C (Nobel, 1988) compared with only 1.4°C for *H. undatus*. Thus both the low-temperature and the high-temperature acclimations, which are the crucial factors for the tolerance of extreme temperatures (Nobel, 1988; Nobel & De la Barrera, 2002b), are less than one-third as great for *H. undatus* as is the average for other cacti.

Time of exposure to extreme temperatures is also crucial when examining tolerances, especially for high temperatures. For instance, *H. undatus* is not expected to tolerate day/night air temperatures above 42/32°C on a prolonged basis, as the total daily net CO₂ uptake would then be negative (Fig. 4). In this regard, the maximal temperatures in the native

habitats of *H. undatus* generally do not exceed 35°C (Croat, 1978; Freiberg, 1997; Lüttge, 1997; Benzing, 1998). Maintaining *H. undatus* at 40/30°C gradually leads to visible damage of the stems, which first becomes evident at 6 wk (Nobel & De la Barrera, 2002b). Necrosis increases to about half of the stem surface area at 15 wk and no new stem growth is observed at such temperatures. Also, daytime temperatures of 45°C in the field greatly reduce flower production by *H. undatus*, and brief exposure to 50°C leads to stem necrosis (Mizrahi & Nerd, 1999). Thus this species cannot be cultivated where daytime maximal temperatures average 40°C for several weeks or occasionally exceed 45°C. Indeed, total daily net CO₂ uptake by *H. undatus* is 37% lower after 30 wk at 35/25°C compared with at 10 wk (Nobel & De la Barrera, 2002b), suggesting that *H. undatus* does not have phenotypic plasticity to tolerate temperatures exceeding those in its native habitat for prolonged periods.

Photosynthetic Photon Flux

Hylocereus undatus has considerable net CO₂ uptake at a total daily PPF of only 2 mol m⁻² day⁻¹ (Fig. 5), indicating that it is well adapted to the low-light conditions of a tropical forest (total daily net CO₂ uptake is negative for desert CAM species at this PPF; Nobel, 1988). [Net CO₂ uptake responses to PPF for CAM plants are not expressed versus the instantaneous level of such light, as is conventional for C₃ and C₄ plants, but rather versus the total daily PPF, as most CO₂ uptake occurs at night in Phase I (Fig. 3), when no light is available.] Total daily net CO₂ uptake by *H. undatus* increases as the total daily PPF increases to about 20 mol m⁻² day⁻¹, above which net CO₂ uptake decreases with increasing PPF (Fig. 5), indicating that high PPF levels damage the

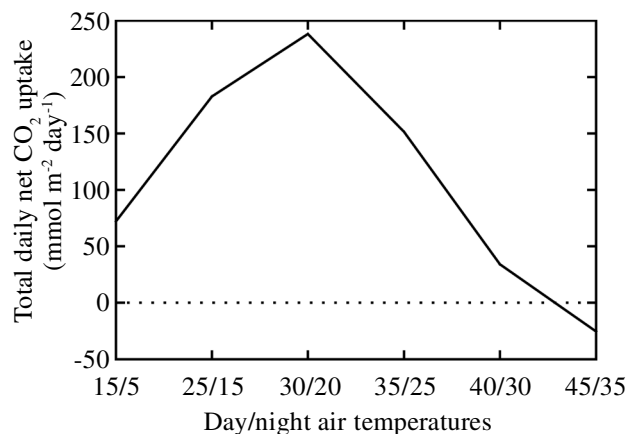


Fig. 4. Total daily net CO₂ uptake by *H. undatus* at the indicated day/night air temperatures. Plants were growing under wet conditions and the PPF was 10 mol m⁻² day⁻¹. Data are from Raveh *et al.* (1995) and Nobel & De la Barrera (2002b).

photosynthetic apparatus. Total daily net CO₂ uptake for *H. undatus* is about 90% of maximal at only 10 mol m⁻² day⁻¹ (Fig. 5). For CAM plants such as barrel cacti (e.g., *Ferocactus acanthodes*) and platyopuntias (e.g., *Opuntia ficus-indica*), a total daily PPF of 10 mol m⁻² day⁻¹ leads to about 40% of the maximal total daily net CO₂ uptake; maximal uptake for such cacti generally occurs from 30–40 mol m⁻² day⁻¹ (Nobel, 1988), levels attained by surfaces facing east or west on clear days in the summer.

Photoinhibition leading to a reduction in total daily net CO₂ uptake sets in at a total daily PPF of 20 mol m⁻² day⁻¹ for *H. undatus* (Fig. 5) compared with above 40 mol m⁻² day⁻¹ for desert CAM species (Nobel, 1988). Measurement of chlorophyll fluorescence for *H. undatus* indicates that photosynthetic efficiency (total daily net CO₂ uptake divided by PPF) actually begins to decrease at a relatively low total daily PPF of 5 mol m⁻² day⁻¹ (Raveh *et al.*, 1995). To avoid exceeding a total daily PPF of 20 mol m⁻² day⁻¹, a vertical climbing or clambering stem of *H. undatus* would need to be shaded by nearly 40% on a clear day for stem surfaces facing east or west (north- or south-facing surfaces would need no shading). In this regard, *H. undatus*, *H. polyrhizus*, and *Selenicereus megalanthus* are commercially grown in Israel under shade cloth that attenuates solar irradiation by 30–60% (Raveh *et al.*, 1993, 1998; Mizrahi & Nerd, 1999). Such shading is comparable to that in the forests where such species are native (Benzing, 1990; Barthlott & Hunt, 1993; Lüttge, 1997). When exposed to full sun on clear days, *H. undatus* in

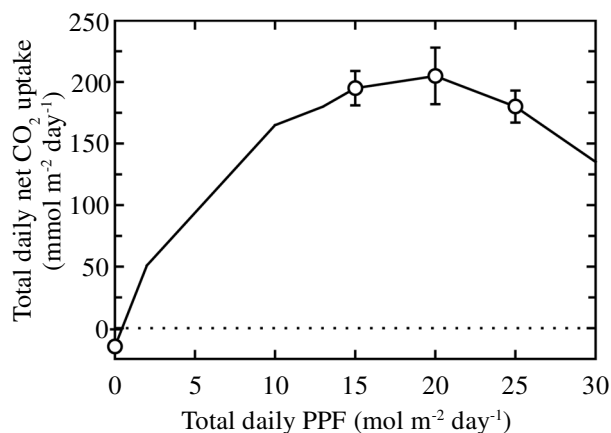


Fig. 5. Total daily net CO₂ uptake by *H. undatus* at the indicated total daily PPF incident on the stem surface. Plants were growing under wet conditions, and the day/night temperatures were 25/15°C. Data are from Raveh *et al.* (1995) and P S Nobel & E De la Barrera (unpublished measurements for 1-yr-old stems with data indicated by means ± SE for *n* = 5 plants and normalised to the previous measurements at a total daily PPF of 20 mol m⁻² day⁻¹).

Mexico (Ortíz, 1999) and 23 genotypes of *Hylocereus* in Israel (Nerd *et al.*, 1990) develop visible necrosis on the stems. However, *H. undatus* is cultivated in southeast Asia, such as in the Mekong Delta of Vietnam, without shading (Nerd *et al.*, 2002; P S Nobel, personal observations). Evidently the prevalent cloud cover in such regions reduces the total daily PPF to values that do not lead to stem bleaching and necrosis.

Nutrients

The effects of soil nutrients on net CO₂ uptake of cacti bearing pitahayas have received little attention (Castillo Martínez *et al.*, 1996; Ortíz, 1999), although nutrients are known to have substantial effects on other cacti (Nobel, 1988, 1989). For instance, application of nutrients such as nitrogen can alter the timing of fruiting for *Opuntia ficus-indica* (Mizrahi & Nerd, 1999). Application of boron and zinc can increase the number of fruits for *H. undatus*, and foliar application of magnesium can increase fruit size (Castillo Martínez *et al.*, 1996). Variations in the applied nitrogen concentration for *H. undatus* rooted in a sand/vermiculite mixture for 22 wk affects its net CO₂ uptake ability as measured by the maximal nocturnal net CO₂ uptake rate: 0.16 mM N leads to a maximal nocturnal net CO₂ uptake rate of 2.5 μmol m⁻² s⁻¹, 1.6 mM N leads to 5.6 μmol m⁻² s⁻¹, and 16 mM N leads to 9.8 μmol m⁻² s⁻¹ (Fig. 6), the latter being the N concentration in full-strength Hoagland solution (Hoagland & Arnon, 1950; Johnson *et al.*, 1957; Epstein, 1972). Thus net CO₂ uptake for *H. undatus* is highest under a relatively high applied N concentration (8–16 mM; Fig. 6), as is the case for intensively managed greenhouse crops

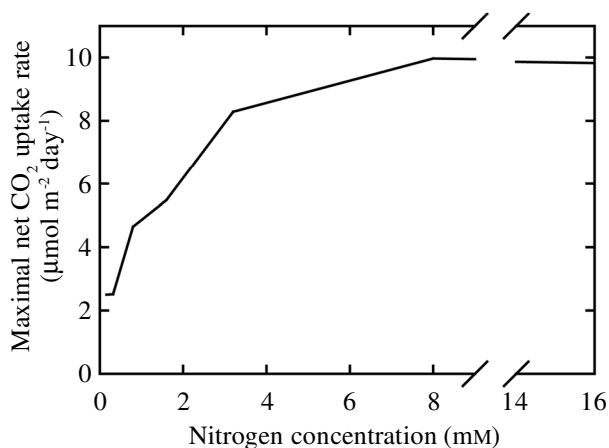


Fig. 6. Maximal net CO₂ uptake rate at night for *H. undatus* maintained for 22 wk at the indicated nitrogen concentration. Plants were growing under wet conditions, the day/night air temperatures were 30/20°C, and the total daily PPF was 10 mol m⁻² day⁻¹. The maximal rate occurred between 22:00 h and 02:00 h. Data are from Nobel & De la Barrera (2002c).

and field-grown vegetables and ornamentals (Huett, 1996; Langhans & Tibbitts, 1997). A maximal nocturnal net CO₂ uptake rate of 10 μmol m⁻² s⁻¹ (Fig. 6) places *H. undatus* fourth highest among the 28 species of cacti whose maximal net CO₂ uptake rates have been reported (Nobel & Bobich, 2002). Thus this species has a high potential growth rate under high-nutrient conditions.

Shifts in stem properties of *H. undatus* as the applied nitrogen concentration is changed are relatively slow. For instance, the half-time for the shift in net CO₂ uptake ability in response to applied N is 12–13 wk (Nobel & De la Barrera, 2002c). After 22 wk at 0.16 mM applied N, the stem N level on a dry mass basis decreases to only 0.9% (Nobel & De la Barrera, 2002c). After 22 wk at an applied N concentration of 16 mM, stem N is 2.5%, comparable to values in the shoots of cultivated C₃ and C₄ plants under high-nutrient conditions (Mengel & Kirkby, 1987; Marschner, 1995). Also, the chlorophyll level of *H. undatus* at an applied N concentration of 0.16 mM for 23 wk is only 0.29 g m⁻² compared with 0.63 g m⁻² at 16 mM N (Nobel & De la Barrera, 2002c); *H. undatus* supplied with 1.6 mM N for 8 wk has a stem chlorophyll level of 0.49 g m⁻² (Raveh *et al.*, 1998) and *H. polyrhizus* has 0.45 g chlorophyll m⁻² under comparable conditions (Raveh *et al.*, 1998). Following 23 wk at low N levels, the stem net CO₂ uptake ability and chlorophyll level both increase to maximal values when 16 mM N is applied to *H. undatus* for 11 wk with a half-time for the increase of 8 wk (Nobel & De la Barrera, 2002c). Thus responses of *H. undatus* to changes in the applied N concentration are slower than for most C₃ and C₄ crops and other cacti, for which major responses can occur in 2 wk (Mengel & Kirkby, 1987; Nerd *et al.*, 1993; Marschner, 1995; Nerd & Nobel, 1995), suggesting lack of genetic plasticity in this recently domesticated cactus, or relatively slow nutrient uptake by the roots. Because the maximal net CO₂ uptake rates for *H. undatus* are similar at applied N concentrations of 8 and 16 mM (Fig. 6), the latter level may lead to luxury (excess) N consumption, as the tissue level after 22 wk is 36% higher at 16 mM than at 8 mM applied N (Nobel & De la Barrera, 2002c).

Elevated Atmospheric CO₂

Another environmental variable influencing net CO₂ uptake by cacti is the atmospheric CO₂ concentration, which currently is increasing by nearly 3 parts per million (0.9%) per year (Schimel *et al.*, 1996; Stitt & Krapp, 1999). For all 20 CAM species studied, biomass productivity increases for a doubled atmospheric CO₂ concentration compared to the current atmospheric CO₂ concentration (Drennan & Nobel, 2000). The increase averages

35% at 700 ppm (700 μ litre litre⁻¹ or 70 kPa) compared with 350 ppm, which represents an approximately 1% increase in growth per 10 ppm increase in atmospheric CO₂ concentration for CAM plants (Nobel, 1991). Data for *H. undatus* are consistent with the results for other CAM plants, as a doubled atmospheric CO₂ concentration increases the total daily net CO₂ uptake by 34% (Raveh *et al.*, 1995). Most of the increase occurs during the daytime in Phases II and IV. Moreover, increases in total daily net CO₂ uptake under a doubled atmospheric CO₂ concentration compared with the current atmospheric CO₂ concentration are more prominent under less favorable or even stressful climatic conditions. For instance, the increase in total daily net CO₂ uptake for *H. undatus* due to a doubled atmospheric CO₂ concentration is 63% higher at 35/25°C versus 25/15°C, 90% higher at 24 days of drought versus 14 days, and 120% higher at a PPF of 30 mol m⁻² day⁻¹ versus 20 mol m⁻² day⁻¹ (Raveh *et al.*, 1995). Thus the responses to atmospheric CO₂ increases will not only lead to greater total daily net CO₂ uptake but also will lead to proportionally greater net CO₂ uptake under adverse environmental conditions.

Conclusions and Future Prospects

A striking feature of *H. undatus* is how rapidly nocturnal stomatal opening and net CO₂ uptake ability decrease during drought. Such rapid responses, which undoubtedly are related to the often small substrate volume that is occupied by its roots, may be mediated by abscisic acid. Other root properties, such as the apparently low nutrient uptake rate and the influence of mycorrhizae, also need investigation. Another striking ecophysiological feature of *H. undatus* compared with barrel and columnar cacti, which is especially pertinent to its cultivation outside its native regions, is its poor tolerance of high temperatures, such as those above 40°C. Indeed, its photosynthetic cells do not show much acclimation as the day/night air temperatures are gradually raised over a period of weeks, contrary to the case for other cacti. Comparisons at a molecular level between *H. undatus* and other cacti showing substantial high-temperature acclimation could help elucidate the mechanisms involved for the latter group. The intolerance of *H. undatus* to high PPF presumably relates to its shaded natural habitat. Levels of stem nitrogen and chlorophyll correlate well with the net CO₂ uptake ability of *H. undatus*, providing relatively simple assays for the physiological status of its stems, which change relatively slowly in response to changes in the concentration of applied nitrogen. Indeed, understanding how climatic factors in general and hormonal factors in particular affect the gas

exchange of *H. undatus* and related species will be interesting ecologically and extremely important horticulturally for the expanding cultivation of pitahayas.

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