

High Temperatures and Net CO₂ Uptake, Growth, and Stem Damage for the Hemiepiphytic Cactus *Hylocereus undatus*¹

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ABSTRACT

Hylocereus undatus, which is native to tropical forests experiencing moderate temperatures, would not be expected to tolerate the extremely high temperatures that can be tolerated by cacti native to deserts. Nevertheless, total daily net CO₂ uptake by this hemiepiphytic cactus, which is widely cultivated for its fruits, was optimal at day/night air temperatures of 30/20°C, temperatures that are higher than those optimal for daily net CO₂ uptake by cacti native to arid and semiarid areas. Exposure to 35/25°C for 30 weeks led to lower net CO₂ uptake than at 10 weeks; exposure to 40/30°C led to considerable necrosis visible on the stems at 6 weeks and nearly complete browning of the stems by 19 weeks. Dry mass gain over 31 weeks was greatest for plants at 30/20°C, with root growth being especially noteworthy and root dry mass gain representing an increasing percentage of plant dry mass gain as day/night air temperatures were increased. Viability of chlorenchyma cells, assayed by the uptake of the vital stain neutral red into the central vacuoles, was decreased 50 percent by a one-hour treatment at 55°C compared with an average of 64°C for 18 species of cacti native to deserts. The lower high-temperature tolerance for *H. undatus* reflected its low high-temperature acclimation of only 1.4°C as growth temperatures were raised by 10°C compared with an average acclimation of 5.3°C for the other 18 species of cacti. Thus, this tropical hemiepiphytic cactus is not adapted to day/night air temperatures above ca 40/30°C, although its net CO₂ uptake is optimal at the relatively high day/night air temperatures of 30/20°C.

RESUMEN

Cabe esperar que *Hylocereus undatus*, una especie nativa del bosque tropical expuesta a temperaturas moderadas, no sea capaz de tolerar las temperaturas extremadamente altas que toleran los cactus nativos del desierto. Sin embargo, la asimilación diaria neta óptima de CO₂ de esta cactácea hemiepífita, ampliamente cultivada por sus frutos, ocurrió a temperaturas ambiente de 30/20°C (diurna/nocturna); mismas que son mayores que las de los cactus nativos de zonas áridas y semiáridas. Un régimen de temperaturas de 35/25°C durante 30 semanas condujo a una asimilación neta de CO₂ menor que aquella registrada a las 10 semanas; un régimen de 40/30°C condujo a una necrosis considerable, visible en los tallos a partir de la sexta semana, que se extendió hasta cubrirlos casi totalmente a las 19 semanas. Después de 31 semanas el incremento en peso seco fue mayor en las plantas sometidas a 30/20°C, el crecimiento de la raíz fue especialmente notable y representó una proporción creciente del peso seco conforme las temperaturas diurna/nocturna se elevaron. La viabilidad de las células del clorénquima, determinada mediante la incorporación *in vivo* de la tinción rojo neutro en las vacuolas centrales, disminuyó 50 por ciento después de una hora a 55°C, comparada con el promedio de 64°C registrado para las otras 18 cactáceas nativas del desierto. La escasa tolerancia de *H. undatus* a temperaturas elevadas se reflejó en una aclimatación mínima de sólo 1.4°C, cuando la temperatura se elevó 10°C durante su crecimiento; las otras 18 especies de cactus presentaron una aclimatación promedio de 5.3°C. Por lo tanto, esta cactácea hemiepífita, no está adaptada a temperaturas diurna/nocturna superiores a los 40/30°C, a pesar de que su asimilación neta óptima de CO₂ ocurre a temperaturas relativamente altas de 30/20°C.

Key words: acclimation; cactus fruit; desert cacti; necrosis; neutral red; pitahaya; productivity; root growth; tropical forest; vine cactus.

HEMIEPIPHYTIC CACTI, such as *Hylocereus polyrhizus*, *H. undatus*, and *Selenicereus megalanthus*, are receiving increasing attention because of the commercial value of their fruits (Mizrahi *et al.* 1997, Jacobs 1999, Mizrahi & Nerd 1999, Nerd *et al.*

2002) in addition to the well-known ornamental value of their flowers. These climbing vine-like species have been cultivated for fruit in Cambodia, Colombia, Ecuador, Guatemala, Indonesia, Mexico, Nicaragua, Peru, Taiwan, and especially Vietnam (introduced ca 1860), with more recent cultivation in Australia, Israel, Japan, New Zealand, the Philippines, Spain, and the southwestern United States (Mizrahi & Nerd 1999, Nerd *et al.* 2002).

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Hemiepiphytic cacti are native to tropical forests of Mexico, the West Indies, Central America, and northern South America (Britton & Rose 1963, Backeberg 1966, Barthlott & Hunt 1993), where they occur in shaded habitats (Croat 1978, Lüttge 1997). Indeed, net CO₂ uptake by *H. undatus* is inhibited by full sunlight (Raveh *et al.* 1998); thus in Israel, it and other hemiepiphytic cacti are commercially grown under shade cloth that attenuates solar irradiation by 30 to 60 percent (Raveh *et al.* 1998, Mizrahi & Nerd 1999).

The tropical regions where hemiepiphytic cacti are native have warm temperatures that vary little seasonally (Croat 1978, Lüttge 1997), and yet little is known about the physiological responses of these cacti to temperature. It is hypothesized that *H. undatus*, the species chosen for the present study because it is the most widely cultivated hemiepiphytic cactus, will not survive the high temperatures that are readily tolerated by cacti native to deserts, where plants often receive full solar irradiation. In this regard, desert cacti are among the most tolerant of high temperatures among vascular plant species (Nobel 1988). When cacti are acclimated to high growth temperatures, the photosynthetically active chlorenchyma cells from all of the 18 species examined can tolerate one hour at 60°C and chlorenchyma cells from the barrel cacti *Ferocactus covillei* and *F. wislizenii* can tolerate one hour at 69°C, as assayed using the cellular uptake of a vital stain (Smith *et al.* 1984). The high temperature that can be tolerated is lower when the temperatures are maintained for longer periods. For example, these two species and another cactus native to the deserts of the southwestern United States and northwestern Mexico (Britton & Rose 1963, Benson 1982), *F. acanthodes*, cannot tolerate day/night air temperatures of 60/50°C maintained for one week, but all three species can survive one week at the lower but still high day/night air temperatures of 55/45°C (Smith *et al.* 1984).

Hylocereus undatus grows semi-wild in tropical countries worldwide, although Britton and Rose (1963) list its type locality as "China, evidently in cultivation." Maximal air temperatures in its native microhabitats generally do not exceed 35°C (Croat 1978, Freiberg 1997, Lüttge 1997, Benzing 1998). Recently, attempts have been made to extend the cultivation of *H. undatus* to hotter regions than where it is native, such as Israel, northern Africa, and the southwestern United States (Mizrahi & Nerd 1999; Nerd *et al.* 2002; P. S. Nobel, pers. obs.), where high temperatures may become a limitation that does not occur with other locally cul-

tivated cacti such as platyopuntias (prickly pear cacti; Nobel 1988). Data were therefore obtained on net CO₂ uptake, dry mass gain, and stem damage for *H. undatus* growing at various moderate to warm day/night air temperatures as well as on the high temperatures that can be lethal to chlorenchyma cells during one-hour treatments.

MATERIALS AND METHODS

Bare-root plants of *H. undatus* (Haworth) Britton and Rose (common names include pitahaya, red pitahaya, strawberry pear, dragon fruit, night-blooming cereus, and queen of the night) were obtained from the Cactus Trading Company, Jamul, California. The plants averaged 171 g in fresh mass (16 ± 1% contributed by the roots), and the mostly unbranched stems averaged 41 cm in length. Individual plants were placed in rectangular pots 13 × 15 cm that were filled to a depth of 10 cm with equal parts by volume of washed premium-grade plaster sand and vermiculite.

The plants were maintained in Conviron E-15 environmental chambers (Controlled Environments, Pembina, North Dakota) with 13 hour days/11 hour nights. The instantaneous photosynthetic photon flux (PPF, wavelengths of 400 to 700 nm; measured with a LI-190S quantum sensor, LI-COR, Lincoln, Nebraska) incident on the upper half of the plants averaged 340 μmol/m²/sec, which led to a total daily PPF of 16 mol/m²/d, and resulted in *ca* 95 percent of the maximal total daily net CO₂ uptake by *H. undatus* (Raveh *et al.* 1995). The day/night air temperatures were 25/15, 30/20, 35/25, or 40/30°C (air temperatures were controlled ±0.1°C). The dew point temperature (temperature to which air needs to be cooled for water vapor to condense) was determined with a Hygro-M1 optical dew point monitor (General Eastern, Watertown, Massachusetts); it averaged 9.6°C for plants at day/night air temperatures of 25/15°C (day/night relative humidities of 40/72%), increasing to 10.5°C at 40/30°C (day/night relative humidities of 19/32%). The plants weekly received a nutrient solution sufficient to keep the soil moist (soil water potential in the center of the root zone above -0.3 MPa; measured with PCT-55 thermocouple psychrometers, Wescor, Logan, Utah) that consisted of 0.2-strength Hoagland's solution supplemented with micronutrients (Hoagland & Arnon 1950).

Net CO₂ uptake by *H. undatus* was measured with a LI-COR LI-6200 portable photosynthesis system. Measurements were made every two hours

over 24-hour periods for plants under the different day/night air temperatures. The cuvette was adapted to the flat sides of the approximately triangular stems by replacing the lid with an acrylic plate having a rectangular extension with an opening of 1×3 cm, the margin of which was covered with a foam rubber gasket to help form an air-tight seal with the stem surface. At the same stem locations as used for measurements of net CO_2 uptake, the temperature near the middle of the *ca* 1.6-mm thick chlorenchyma was determined using copper-constantan thermocouples 0.51 mm in diameter connected to an HH-25TC digital thermometer (Omega Engineering, Stamford, Connecticut).

The sensitivity of chlorenchyma cells to high temperatures was assayed using the uptake into the central vacuole of the vital stain neutral red (3-amino-7-dimethylamino-2-methylphenazine hydrochloride; Onwueme 1979, Didden-Zopf & Nobel 1982, Nobel *et al.* 1995). High temperatures in 3 to 5°C intervals beginning at 25°C were created using a forced-draft oven. Approximately 2 g stem samples were removed during the daytime with a scalpel and placed in contact with a copper-constantan thermocouple 0.51 mm in diameter and wrapped in aluminum foil to prevent desiccation. To reach a particular high temperature, the samples were heated at 6°C/hour, similar to rates occurring for cacti in the field (Nobel 1988, Nobel *et al.* 1995). After the tissue samples were exposed to a particular high temperature $\pm 0.5^\circ\text{C}$ for one hour, they were sliced into sections *ca* 600 μm thick using a razor blade and then placed in 0.2 percent (w/w) neutral red in 0.25 M potassium phosphate (pH 7.8) for ten minutes to allow for stain uptake, which occurs for the central vacuoles of living cells only and indicates integrity of the plasma membrane and the tonoplast (Onwueme 1979, Nobel *et al.* 1995). The tissue samples were next placed in 0.25 M potassium phosphate (pH 7.8) for ten minutes, and then 200 to 240 chlorenchyma cells per sample were examined at 100 \times using a BH-2 phase-contrast microscope (Olympus, Lake Success, New York) to count stained (living) and unstained cells. Data are expressed relative to the value at 25°C, for which *ca* 80 percent of the chlorenchyma cells took up the stain. The high temperature that halves stain uptake is a reliable test for eventual tissue necrosis and death of half of the stems (Didden-Zopf & Nobel 1982, Nobel *et al.* 1995).

To determine organ dry weight, roots and the shoot were dried for 72 hours in a forced-draft oven at 80°C. To determine dry mass gain over 31

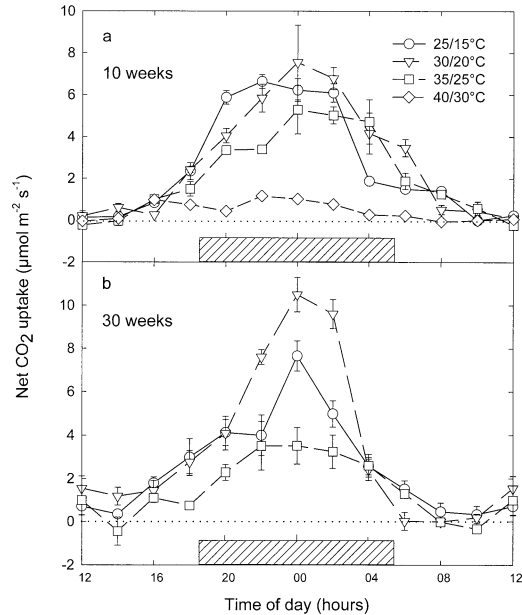


FIGURE 1. Net CO_2 uptake by *Hylocereus undatus* over 24-hour periods for plants maintained for (a) 10 weeks or (b) 30 weeks at the indicated day/night air temperatures. Hatched bars indicate nighttime. Data are means ± 1 SE ($N = 5$ plants).

weeks at various day/night air temperatures, the initial dry masses of roots and the shoot were estimated from the initial fresh mass of the bare-root plants, the proportion of fresh mass contributed by the roots, and the dry mass:fresh mass ratios of the organs. The latter initially averaged 0.133 for the shoots and 0.189 for the roots. The measured final dry mass minus the estimated initial dry mass for both organs was then calculated.

Data are presented as means ± 1 SE ($N =$ number of measurements). Statistical significance was tested using Student's *t*-test and one-way ANOVA followed by Tukey's test.

RESULTS

The pattern and the amount of daily net CO_2 uptake by *H. undatus* were influenced by the day/night air temperatures and the time at particular day/night air temperatures (Fig. 1). After plants had been in the environmental chambers for 10 weeks (Fig. 1a), substantial net CO_2 uptake began in the late afternoon. The maximal instantaneous rate of net CO_2 uptake was greatest at 30/20°C and least at 40/30°C ($P < 0.01$). The total daily net CO_2 uptake, obtained by integrating the in-

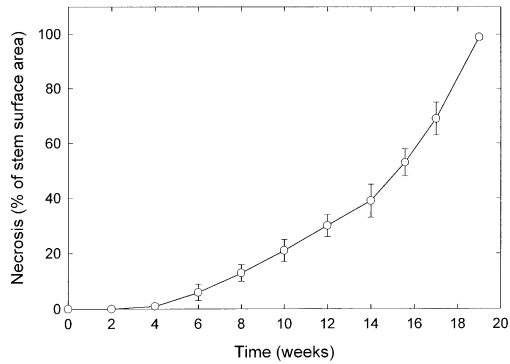


FIGURE 2. Development of necrosis on the stems of *Hylocereus undatus* maintained at day/night air temperatures of 40/30°C. Data are means \pm 1 SE ($N = 5$ plants).

stantaneous values over 24 hours (Fig. 1a), was 238 ± 8 mmol/m²/d at 25/15°C, 262 ± 14 mmol/m²/d at 30/20°C, 200 ± 11 mmol/m²/d at 35/25°C, and 40 ± 3 mmol/m²/d at 40/30°C ($N = 5$ plants at all temperatures). Near noon, the chlorenchyma temperatures for the stem surfaces where net CO₂ exchange was determined were $27.2 \pm 0.2^\circ\text{C}$ for plants at day/night air temperatures of 25/15°C, $32.0 \pm 0.2^\circ\text{C}$ at 30/20°C, $36.8 \pm 0.3^\circ\text{C}$ at 35/25°C, and $41.5 \pm 0.4^\circ\text{C}$ at 40/30°C, for an average of 1.9°C above air temperatures (measured in triplicate for $N = 5$ plants at all temperatures). Near midnight, these temperatures were 14.1 ± 0.1 , 18.4 ± 0.1 , 23.2 ± 0.2 , and $29.2 \pm 0.1^\circ\text{C}$, respectively, for an average of 1.3°C below air temperatures.

For plants maintained in the environmental chambers for 30 weeks (Fig. 1b), the daily patterns and the total daily amounts of net CO₂ uptake changed somewhat from the data at 10 weeks (Fig. 1a). In particular, maximal instantaneous net CO₂ uptake rates were considerably lower ($P < 0.01$) for 30 weeks at 35/25°C ($3.5 \mu\text{mol/m}^2/\text{sec}$) than at 25/15 or 30/20°C (average of $9.1 \mu\text{mol/m}^2/\text{sec}$; maximal rates among these three growth temperatures did not differ significantly at 10 weeks). The total daily net CO₂ uptake at 30 weeks was 226 ± 16 mmol/m²/d at 25/15°C and 294 ± 15 mmol/m²/d at 30/20°C, which were not statistically different than values at 10 weeks; however, the uptake was 126 ± 14 mmol/m²/d at 35/25°C, which was 37 percent less than at 10 weeks ($P < 0.05$).

Even though daily net CO₂ uptake by *H. undatus* was measurable after 10 weeks at day/night air temperatures of 40/30°C (Fig. 1a), such high

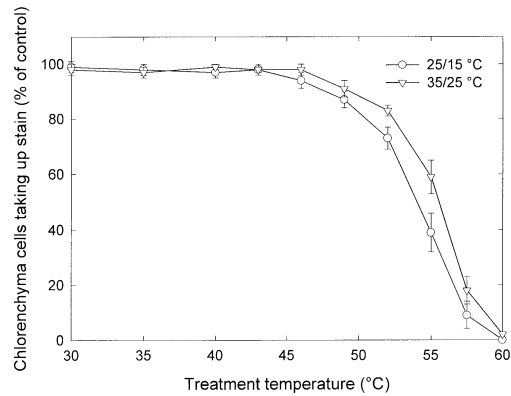


FIGURE 3. Influence of high temperatures on the accumulation of the vital stain neutral red by chlorenchyma cells following a one-hour treatment at the indicated temperatures compared with the control at 25°C for *Hylocereus undatus* growing at 25/15 or 35/25°C for 26 weeks. Data are means \pm 1 SE ($N = 5$ plants).

temperatures led to increasing visible damage to the stems (Fig. 2). In particular, at 6 weeks stem necrosis was clearly evident, as brown patches were avoided for CO₂ measurements; Fig. 1a). Necrosis increased to about half of the stem surface area at 15 weeks and nearly the entire stem surface area at 19 weeks (Fig. 2). The eight plants that were transferred from 40/30 to 25/15°C at 19 weeks did not show any evidence of recovery by 25 weeks, when the entire stem was brown and severely desiccated (stem fresh mass was then only 22% greater than stem dry mass).

Viability of chlorenchyma cells was determined for plants maintained at day/night air temperatures of 25/15 or 35/25°C for 26 weeks and exposed to a high-temperature treatment for one hour (Fig. 3). Uptake of neutral red by chlorenchyma cells was unaffected by high-temperature treatments up to 43°C for plants from both day/night air temperatures. Stain uptake was reduced at treatment temperatures of 49°C ($P < 0.05$) and 52°C ($P < 0.01$). Stain uptake was halved at 54.0°C for plants grown at 25/15°C and at 55.4°C for plants grown at 35/25°C (Fig. 3). Essentially no chlorenchyma cells survived one hour at 60°C.

New stems at least 2 mm in length were apparent at 16 weeks for plants at day/night air temperatures of 30/20°C but not until 20 weeks for plants at 25/15 or 35/25°C (no new stems were formed on plants at 40/30°C). The dry mass gain at 31 weeks was greatest for plants at 30/20°C (Table 1), which also had the highest daily net CO₂

TABLE 1. Dry mass gain for roots and shoots of *H. undatus* maintained at various day/night air temperatures for 31 weeks. Plants at 40/30°C were measured after 19 weeks at those temperatures followed by 12 weeks at 25/15°C. Data are means \pm 1 SE (N = 5 plants, except N = 8 plants at 40/30°C).

Day/ night air tem- peratures (°C)	Dry mass gain (g)		
	Roots	Shoots	Total
25/15	15.6 \pm 1.5	12.2 \pm 3.9	27.8 \pm 4.7
30/20	21.5 \pm 1.7	13.9 \pm 4.7	35.4 \pm 5.9
35/25	13.7 \pm 1.9	6.8 \pm 3.1	20.5 \pm 3.3
40/30	1.6 \pm 0.6	0.3 \pm 0.5	1.9 \pm 0.6

uptake. Roots made up a higher percentage of the plant dry mass gain as the day/night air temperatures increased ($P < 0.05$; Table 1).

DISCUSSION

Daily net CO₂ uptake by *H. undatus* was greatest at day/night air temperatures of 30/20°C, a refinement of previous results where the optimum was found to be between 25/15 and 35/25°C (Raveh *et al.* 1995). Such optimal temperatures are higher than for the other cacti that have been investigated; *e.g.*, optimal temperatures for daily net CO₂ uptake are 23/13°C for *F. acanthodes* and *Opuntia ficus-indica* (Nobel 1988) and *ca* 25/15°C for *Stenocereus queretaroensis* (Nobel & Pimienta-Barrios 1995). The tropical forests where *H. undatus* is native are wetter and more humid than the arid and semiarid regions where *F. acanthodes*, *O. ficus-indica*, and *S. queretaroensis* are native (Croat 1978, Benson 1982, Nobel 1988, Lüttge 1997). The greater water availability helps sustain transpiration, and the greater humidity helps mitigate against excessive transpirational water loss. Perhaps more important, the higher optimal temperatures for net CO₂ uptake by *H. undatus* are closer to the mean air temperatures in tropical forests (Croat 1978), which enhances net carbon gain and hence productivity. Indeed, lessening the dependence on erratic water availability and on maintaining a high water-use efficiency that is so important for cacti from arid and semiarid regions (Nobel 1988, 1999) may allow *H. undatus* and other hemiepiphytic cacti to be well-suited to the temperatures of their native environments with regard to net CO₂ uptake.

Extreme summer daytime temperatures of 45°C can greatly reduce flower production for *H.*

undatus, and brief exposure to 50°C can lead to stem necrosis (Mizrahi & Nerd 1999). Similarly, a one-hour treatment at 49°C led to a detectable decrease in cell membrane integrity for *H. undatus*, as assayed by a decrease in the uptake of neutral red into the central vacuoles of chlorenchyma cells. Damage is evident at lower temperatures if they are experienced for a longer period. For example, *H. undatus* maintained at day/night air temperatures of 45/35°C for one week showed some stem necrosis and daily net CO₂ uptake was then negative (Raveh *et al.* 1995), an obviously untenable condition for long-term survival. When *H. undatus* was maintained at 40/30°C, stem necrosis became evident at 6 weeks and covered nearly the entire stem at 19 weeks. Thus, *H. undatus* should not be cultivated where day/night air temperatures are occasionally 45/35°C or slightly higher or where they average 40/30°C for several weeks.

The detrimental influence of prolonged exposure to high temperatures for *H. undatus* was underscored by the decrease in maximal instantaneous net CO₂ uptake rates and total daily net CO₂ uptake at the warm day/night air temperatures of 35/25°C from 10 to 30 weeks. Specifically, the total daily net CO₂ uptake decreased 37 percent at 35/25°C from 10 to 30 weeks but was not significantly affected at 25/15 or 30/20°C over this period. The gain in plant dry mass over 31 weeks, which integrates the daily net CO₂ uptake by the stem over time, was 42 percent lower for plants at 35/25 than at 30/20°C; this was intermediate between the reductions for total daily net CO₂ uptake of 24 percent at 10 weeks and 57 percent at 30 weeks for plants at 35/25°C compared with 30/20°C. When *H. undatus* was maintained at 35/25°C for over six months, its net CO₂ uptake ability thus decreased substantially although visible damage to the stem was not evident, indicating that long periods of relatively warm temperatures can be harmful to this species. In its native habitats, *H. undatus* would most likely not experience air temperatures above *ca* 35°C (Croat 1978, Freiberg 1997, Lüttge 1997, Benzing 1998), suggesting that the lack of tolerance to high temperatures is genetically fixed.

For *H. undatus* growing for 31 weeks after planting bare-root plants, the average dry mass gain was partitioned more to the roots than to the shoots, whereas roots of mature cacti from arid and semiarid regions represent only *ca* 10 percent of plant dry mass (Nobel 1988). The high diversion of new dry mass gain to roots for *H. undatus* probably reflects the need to acquire water and nutrients before investing in new shoot growth; this did not

begin until 16 weeks and then only for the plants at 30/20°C, which had the greatest root dry mass gain. Root dry mass gain for *H. undatus* represented an increasing percentage of plant dry mass gain as the day/night air temperatures were increased. This may reflect a requirement for more water uptake to offset the decreasing water-use efficiency with increasing temperature (Nobel 1999). Another factor is that average soil temperatures for root growth tend to be high for cacti, averaging about 30°C, with maximal root elongation rates for *O. ficus-indica* occurring at day/night air temperatures of 35/25°C (Drennan & Nobel 1998); thus, the higher day/night air temperatures may simply favor greater root growth.

Vacuolar uptake of neutral red by chlorenchyma cells of *H. undatus* was halved at a tissue temperature of 55°C for plants at the highest day/night air temperatures not leading to stem necrosis, compared with an average of 64°C for 18 other species of cacti acclimated to high day/night air temperatures (Nobel 1988). Nearly all of the other species are native to desert regions where they occur in sparse vegetation and thus can be exposed to full sunlight. *Hylocereus undatus* is apparently the only cactus in tribe Hylocereae, one of the nine tribes in the subfamily Cactoideae (Gibson & Nobel 1986), for which high-temperature tolerance has been determined. Many species in this tribe occur as epiphytes and hemiepiphytes in tropical forests, where both temperatures and light levels are moderate (Croat 1978, Lüttge 1997). Although *H. undatus* in tropical forests may only rarely experience 35°C or higher air temperatures, such exposure is routine for cacti native to deserts. For example, soil temperatures can reach 70°C in the Chihuahuan Desert, where the native dwarf cactus *Ariocarpus fissuratus* reaches similar temperatures (Nobel *et al.* 1986, Nobel 1988). Also, because of the typically shaded microhabitat and relatively thin stems of *H. undatus*, its chlorenchyma temperatures are expected to rise only 1–2°C above air temperatures during the daytime, whereas temperatures of stems of the considerably more massive barrel and columnar cacti that are often exposed to full sunlight can be more than 10°C above air temperatures (Nobel

1988). Besides *H. undatus*, another cactus with a low high-temperature tolerance is the ancestral leafy cactus *Pereskia columbiana* from Colombia, in which leaves have visible damage following 30 minutes at 54°C (Schnetter 1971). Thus, species tolerance to high temperatures varies substantially within the Cactaceae.

A key for tolerating high temperatures is substantial high-temperature acclimation, which is defined here as the increase in the high temperature that halves the vacuolar uptake of neutral red by chlorenchyma cells as the day/night air temperatures are raised by 10°C. For the 18 species of cacti from arid and semiarid regions, the high-temperature acclimation averages 5.3°C (Nobel 1988) compared with only 1.4°C for *H. undatus*. Although the mechanism is not understood, high-temperature acclimation for cacti is accompanied by the accumulation of 26 kilodalton and other proteins (Kee & Nobel 1986). Also, photosystem I and II electron transport reactions for *O. ficus-indica* acclimate when plants are transferred to higher growth temperatures (Chetti & Nobel 1987). The relatively small degree of high-temperature acclimation for *H. undatus* compared with the other cacti examined so far helps explain its intolerance of high temperatures and may reflect its native habitat in tropical forests, which experiences little seasonal change in temperature (Croat 1978, Lüttge 1997). Also, the meager high-temperature acclimation of *H. undatus* may provide a comparison species for future research that investigates why cacti from other habitats acclimate so well, a topic of great potential importance with respect to rising air temperatures accompanying global climate change.

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