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Nitrogen relations for net CO_2 uptake by the cultivated hemiepiphytic cactus, *Hylocereus undatus*

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Abstract

The net CO_2 uptake ability of a vine-like cactus native to shaded habitats, *Hylocereus undatus*, was hypothesized to adjust more rapidly to changes in the applied nitrogen concentration, which can have major impacts on fruiting, than the more massive cactus most widely cultivated for fruit, *Opuntia ficus-indica*. Specific objectives were to examine the effects of applied N on stem N concentrations and chlorophyll levels, which can affect net CO_2 uptake ability and hence growth. After 9 weeks, the total daily net CO_2 uptake for *H. undatus* was only 26% less for the relatively low N concentration of 0.32 mM than for 8 mM N (the N concentration in 0.5-strength Hoagland solution; all other nutrients were maintained at their concentration in 0.2-strength Hoagland solution), compared with 2 weeks for major changes for *O. ficus-indica* in response to changing applied N. Based on the maximal net CO_2 uptake rates at night for the Crassulacean acid metabolism *H. undatus*, the half-time for the shift in response to seven different N concentrations applied for 22 weeks was 12–13 weeks; the half-time for the attainment of the highest net CO_2 uptake rate of 10 μmol m^{-2} s^{-1} in response to subsequent application of 16 mM N for 11 weeks was 8–9 weeks. After 22 weeks, the stem N level in response to 0.16 mM N was 0.9% by dry mass and the chlorophyll content per unit stem area was 0.30 g m^{-2} compared with 2.5% and 0.63 g m^{-2} for 16 mM N. Subsequent application of 16 mM N for 11 weeks reversed the observable stem bleaching and raised the chlorophyll toward the highest levels. Both the chlorophyll content and the N level per unit stem area are highly correlated with the net CO_2 uptake ability of *H. undatus* and either could help assess the physiological status of this cactus.

Keywords: Chlorophyll; Crassulacean acid metabolism; Hoagland solution; Maximal net CO_2 uptake rate; Nitrogen content; Pitahaya

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1. Introduction

Various species of cacti are becoming increasingly important worldwide as sources of fruits, vegetables, and fodder (Russell and Felker, 1987; Barbera et al., 1995; Mizrahi et al., 1997; Nerd et al., 2002). Utilization of Crassulacean acid metabolism leading to nocturnal CO_2 uptake and tolerance of arid and semiarid conditions are important attributes of cacti for such agronomic purposes (Nobel, 1988, 1994). Currently, most of the commercially harvested cactus fruits come from *Opuntia ficus-indica*, which is cultivated for such use as ‘‘cactus pears’’ on about 100,000 hectares worldwide, 70% of which are in Mexico (Nobel, 1994; Inglese et al., 2002). Commercially, cactus pears have two disadvantages: glochids (small spines) on their surface and many relatively large seeds (similar in size to those in grapes). In contrast, fruits of hemiepiphytic cacti in the genera *Hylocereus* and *Selenicereus* have no surface spines and have small, readily swallowed seeds (similar in size to those in kiwi fruit; Mizrahi and Nerd, 1999; Nerd et al., 2002). Yet, except for *O. ficus-indica*, relatively little is known about the most advantageous growth conditions for cacti bearing commercially important fruit (Raveh et al., 1993; Barbera et al., 1995; Castillo Martínez et al., 1996; Mizrahi et al., 1997).

Hylocereus undatus was chosen for this study because it is the most widely cultivated hemiepiphytic cactus. It occurs naturally in shaded habitats of tropical forests of Mexico, the West Indies, Central America, and northern South America, where it acquires water via roots in the ground and adventitious roots along its slender, three-flanged stems (Britton and Rose, 1963; Backeberg, 1966; Benzing, 1990; Barthlott and Hunt, 1993; Castillo Martínez et al., 1996). It has various common names, including pitaya, red pitaya, strawberry pear, and increasingly pitahaya in Latin America, night-blooming cereus and queen of the night in North America (the species is also cultivated for its large flowers), and red dragon fruit and fire dragon fruit in Asia. This species is currently grown for fruit in Australia, Cambodia, Colombia, Ecuador, Guatemala, Indonesia, Israel, Japan, New Zealand, Nicaragua, Mexico, Peru, the Philippines, Spain, Taiwan, Thailand, the United States, and Vietnam (Mizrahi and Nerd, 1999; Nerd et al., 2002; Nobel, personal observations).

As for other hemiepiphytes (Lüttge, 1997), relatively little is known about the responses of net CO_2 uptake to nutrient concentrations for *H. undatus*, and yet nutrients strongly influence the net CO_2 uptake ability of other cacti (Nobel, 1989). Nocturnal acidity and CO_2 uptake by *O. ficus-indica* increase as the tissue nitrogen level increases (Nobel, 1983, 1988). Application of nitrogen supplied as NH_4NO_3 (120 kg ha^{-1}) to *O. ficus-indica* in the field raises the cladode N level and induces floral buds within 2 weeks (Nerd et al., 1993). Similarly, for detached cladodes of *O. ficus-indica* placed in pots, applying 16 mM N (the N concentration in full-strength Hoagland solution; Hoagland and Arnon, 1950) substantially raises its cladode N content in 2 weeks (Nerd and Nobel, 1995). Because the stems of *H. undatus* are much less massive than are those of *O. ficus-indica* (an average thickness of only 3–4 mm compared with 12 to over 20 mm for *O. ficus-indica*), responses of *H. undatus* to changes in the applied N concentration are hypothesized to occur more quickly than in 2 weeks. For example, shoot responses to changes in N fertilization for C_3 and C_4 agronomic plants occur in a few days (Mengel and Kirkby, 1987; Marschner, 1995). Rapid responses to N application may have important implications for the cultivation of *H. undatus*, because fruiting can be manipulated by N application, as for *O. ficus-indica* (Nerd et al., 1993), and extending the season for fruit production by *H. undatus* is highly desirable commercially (Mizrahi and Nerd, 1999). Because of N already present in the stems of *H. undatus*, changes in the rate of net CO_2 uptake associated with decreased applied N concentrations are further hypothesized to be slower than changes with increasing applied N concentrations. Also, low applied N should lead to a loss of chlorophyll and stem bleaching, which should be reversible by application of high N concentrations.

2. Materials and methods

2.1. Plant material

Thirty-five bare-root plants of *H. undatus* (Haworth) Britton and Rose (Cactaceae) averaging 164 g in fresh mass and 45 cm in stem length were obtained from a commercial vendor and randomly selected in groups of five for the seven nitrogen concentrations applied. Single plants were placed in rectangular pots that were 13 cm × 15 cm and that were filled to a depth of 10 cm with equal parts by volume of washed premium-grade plaster sand and vermiculite (2.0 l soil per pot). The plants were maintained approximately 0.3 m apart 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 CO_2 uptake by *H. undatus* (Nobel and De la Barrera, 2002). The day/night relative humidities averaged 40/71%, similar to values in its native habitats (Benzing, 1990; Castillo Martínez et al., 1996). The instantaneous photosynthetic photon flux (PPF, wavelengths of 400–700 nm; measured with an LI-190S quantum sensor, LI-COR, Lincoln, Nebraska) incident on the upper half of the stems used for net CO_2 uptake measurements averaged 340 μmol m^{-2} s^{-1}; this led to a total daily PPF of 16 mol m^{-2} per day, which results in about 95% of the maximal total daily net CO_2 uptake by *H. undatus* (Raveh et al., 1995) and is similar to the PPF levels in the shaded habitats where this species occurs naturally (Benzing, 1990; Barthlott and Hunt, 1993).

2.2. Nutrient solution

Every week each plant received 400 ml of a nutrient solution that was sufficient to keep the soil moist (water potential in the center of the root zone was greater than −0.3 MPa; measured with PCT-55 thermocouple psychrometers, Wescor, Logan, Utah). The solution consisted of 0.2-strength Hoagland solution no. 2 supplemented with micronutrients devised by Hoagland and Arnon (1950) and modified by Johnson et al. (1957) and Epstein (1972) and contained various concentrations of nitrogen (all solutions were prepared using distilled water). Specifically, NH_4NO_3, KNO_3, and $Ca(NO_3)_2$ were varied proportionally in seven steps from the N concentrations in 0.01-strength to that in full-strength Hoagland solution (the concentrations were 0.4, 0.8, and 0.8 mM, respectively, for 0.2-strength

Hoagland solution). For the other macronutrients, $MgSO_4$ was kept at 0.2 mM, 0.4 mM $NH_4H_2PO_4$ was replaced by 0.4 mM KH_2PO_4, and 0.8 mM KCl and 0.8 mM $CaCl_2$ were added to maintain K^+ and Ca^{2+} at least at their concentrations for 0.2-strength Hoagland solution (micronutrient concentrations were not varied).

2.3. Net CO_2 uptake

Net CO_2 uptake by stems of *H. undatus* was measured using an LI-COR LI-6200 portable photosynthesis system in the environmental chambers. Measurements were made every 2 h over 24 h periods or at times for maximal net CO_2 uptake rates (0:00 and 2:00 h) for plants receiving various N concentrations for 22 weeks. Subsequently, all plants received 16 mM N for 11 weeks. The cuvette was fitted to the flat sides of the three-flanged stems by replacing the lid with a transparent acrylic plate having a rectangular extension with an opening of 1 cm $\times$ 3 cm with the margin covered by a foam rubber gasket to form an air-tight seal with the stem surface. Data are expressed based on the stem area exposed to the cuvette, not on the projected area that is conventionally used for flat leaves; similarly, the area used for expressing chlorophyll data is the total area of both sides of the core taken through portions of the relatively thin stems.

2.4. Nitrogen, chlorophyll

To determine levels of N in the stems after 22 weeks of a specific applied N concentration, approximately 20 g fresh mass was obtained from the upper parts of plants (avoiding any new growth) and then dried in a forced-draft oven at 80 °C until no further mass change occurred (48–72 h). The entire dried tissue was ground to a fine powder using a Mini-Beadbeater homogenizer (BioSpec Products, Bartlesville, Oklahoma), seived through a no. 60 mesh screen (pore size of 90 μm), and then submitted to the DANR Analytical Laboratory (University of California, Davis, California) for determination of total N on a dry mass basis. For determination of the chlorophyll content per unit stem area after 23 weeks at a specific applied N concentration or a subsequent application of 16 mM N for 11 weeks, samples through the stem were removed from the same regions as used to measure net CO_2 uptake using a cork borer 13 mm in diameter. After removing the cuticle from both sides of the tissue cylinder using a razor blade, the tissue was ground with a mortar and pestle, and chlorophyll was extracted using 95% (v/v) ethanol and then analyzed spectrophotometrically at 643 and 662 nm (Lichtenthaler, 1987) using a DU-60 spectrophotometer (Beckman Instruments, Fullerton, California).

Data are presented as means $\pm$ 1S.E. ($n =$ number of plants). Statistical analyses were performed with SigmaStat (SPSS Science, Chicago, Illinois), using Student's *t*-test or one-way ANOVA followed by Tukey's test for significance (Sokal and Rohlf, 1995).

3. Results

Differences in the instantaneous rate of net CO_2 uptake and the total daily net CO_2 uptake were apparent for plants of *H. undatus* maintained for 9 weeks under different

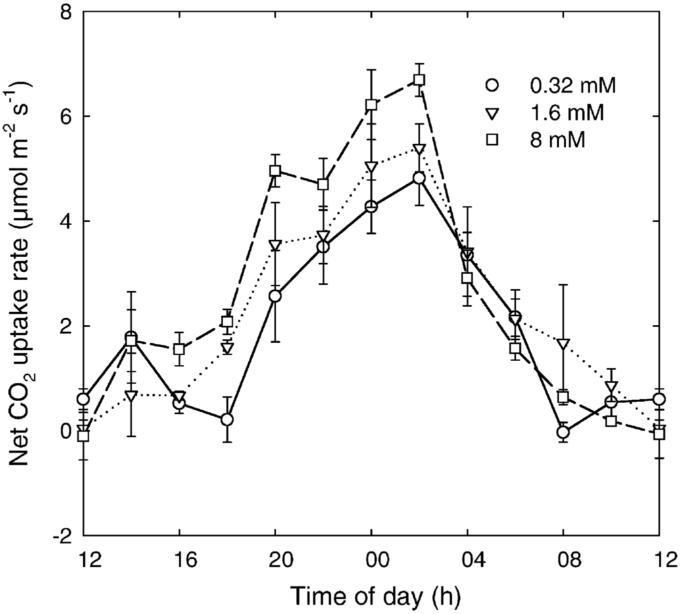

Fig. 1. Net CO_2 uptake by *H. undatus* over 24-h periods for plants maintained for 9 weeks at an applied nitrogen concentration of 0.32, 1.6, or 8 mM. The hatched bar indicates nighttime. Data are means ± 1S.E. ($n = 5$ plants).

applied concentrations of nitrogen (Fig. 1); N application for 6 weeks had no statistically significant effect on maximal rates ($P > 0.4$). The maximal rate of net CO_2 uptake was greater for 8 mM N compared with 0.32 mM N ($P < 0.05$). The total daily net CO_2 uptake, obtained by integrating the instantaneous values over 24 h (Fig. 1), increased steadily with the logarithm of the applied nitrogen concentration ($P < 0.01$ by ANOVA); it was 148 ± 8 mmol m^{-2} per day for 0.32 mM N, 181 ± 10 mmol m^{-2} per day for 1.6 mM N, and 201 ± 11 mmol m^{-2} per day for 8 mM N.

Compared with the maximal net CO_2 uptake rates at 9 weeks, maximal rates became lower at low applied N concentrations and higher at high concentrations at 16 and 22 weeks (Fig. 2). Indeed, the curves for maximal net CO_2 uptake ability at different application times appeared to pivot about values for 1.6 mM N. The maximal rates at 9 weeks averaged 4.17 µmol m^{-2} s^{-1} at 0.16 and 0.32 mM N, 4.91 µmol m^{-2} s^{-1} for 0.8–3.2 mM N, and 6.13 µmol m^{-2} s^{-1} for 8 and 16 mM N. At 16 weeks, these values were 2.83 µmol m^{-2} s^{-1} ($P < 0.05$ compared with 9 weeks), 5.55 and 9.82 µmol m^{-2} s^{-1} ($P < 0.05$), respectively, and at 22 weeks they were 2.51, 5.93, and 9.98 µmol m^{-2} s^{-1}, respectively (not statistically different from 16 weeks, $P > 0.6$).

Applying 16 mM N beginning at 23 weeks to plants from all seven initial N concentrations led to maximal net CO_2 uptake rates after 2 and 4 weeks (Fig. 3) that were similar to those after 22 weeks of the initial concentrations (Fig. 2). However, by 8 weeks (Fig. 3) stimulation occurred for maximal net CO_2 uptake rates at N concentrations that formerly

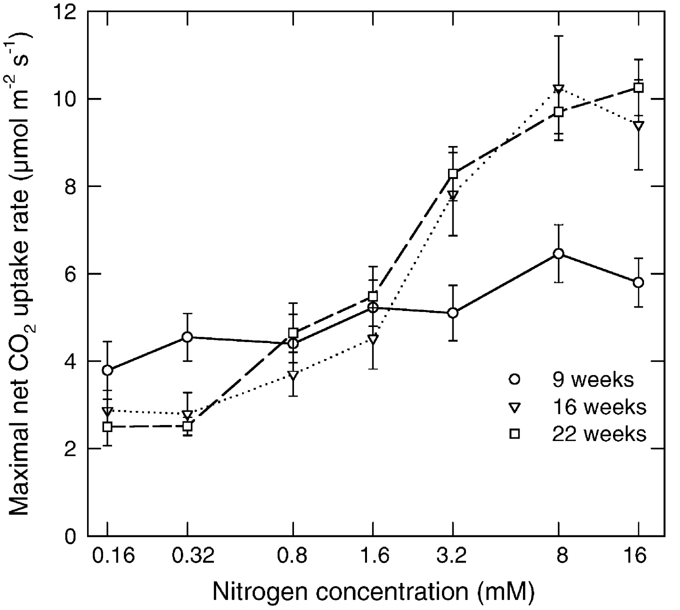

Fig. 2. Maximal net CO_2 uptake rates for *H. undatus* maintained for 9, 16, or 22 weeks at the indicated N concentration. Data are means of net CO_2 uptake rates at 0:00 and 2:00 h ± 1S.E. ($n = 5$ plants) and for this and subsequent figures are presented with a logarithmic scale on the abscissa.

were 0.8 mM or lower ($P < 0.05$). At 11 weeks of 16 mM N, the maximal net CO_2 uptake rates were similar for all seven initial N concentrations (Fig. 3).

New stems at least 1 mm in length were first visible at 13 weeks for plants treated with 16 mM N, 1 week later for 8 mM N, 3 weeks later for 3.2 mM N, and 7 weeks later (at 20 weeks) for 0.8 mM N. The accumulated stem length per plant after 22 weeks for the five plants examined under a particular N concentration averaged 2 mm at 0.8 mM N, 6 mm at 3.2 mM, 22 mm at 8 mM, and 85 mm at 16 mM N.

The N level in the stems at 22 weeks increased as the N concentration in the nutrient solution increased (Fig. 4). The stem N level on a dry mass basis averaged 0.99% for the lowest two N concentrations, 1.58% for the intermediate three, and 2.18% for the highest two ($P < 0.05$). The greatest individual increase in stem N occurred from 8 to 16 mM N, the latter leading to a stem level of 2.5% N (Fig. 4).

After 22 weeks at the lower concentrations of applied N, bleaching of the entire stem occurred that was subsequently reversed by the application of 16 mM N for 11 weeks. Consistent with this, the amount of chlorophyll per unit stem area was only about 0.30 g m^{-2} after 22 weeks for the three lowest applied N concentrations (0.16–0.8 mM N), increasing steadily from 1.6 to 16 mM N, the latter leading to 0.63 g chlorophyll m^{-2} ($P < 0.01$; Fig. 5). After 11 weeks of application of 16 mM N, the chlorophyll content per unit stem area was similar for the seven initial N concentrations (Fig. 5).

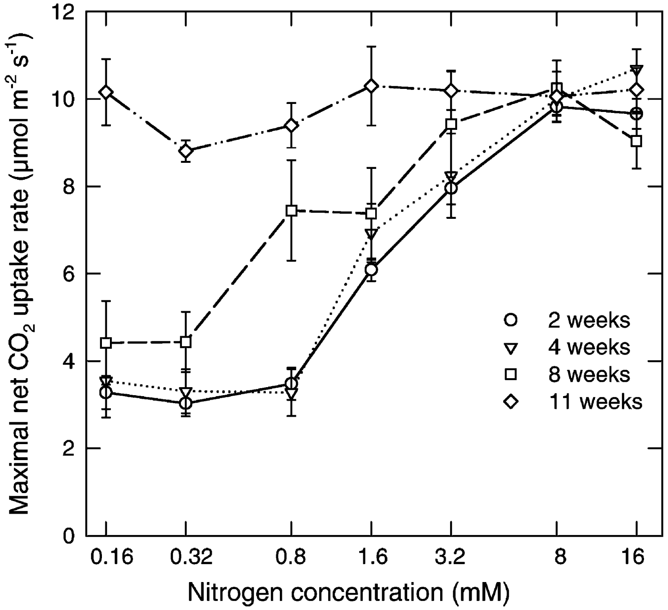

Fig. 3. Maximal net CO_2 uptake rates for *H. undatus* maintained for 23 weeks at the indicated N concentrations and then given 16 mM N for 2, 4, 8, or 11 weeks. Data are means of instantaneous net CO_2 uptake rates at 0:00 and 2:00 h $\pm$ 1S.E. ($n = 5$ plants).

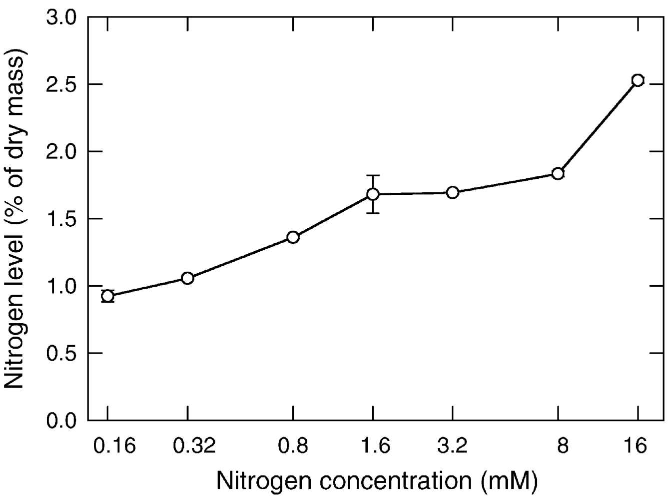

Fig. 4. Variation in stem nitrogen for *H. undatus* maintained for 22 weeks at the indicated N concentration. Data are means $\pm$ 1S.E. ($n = 5$ plants).

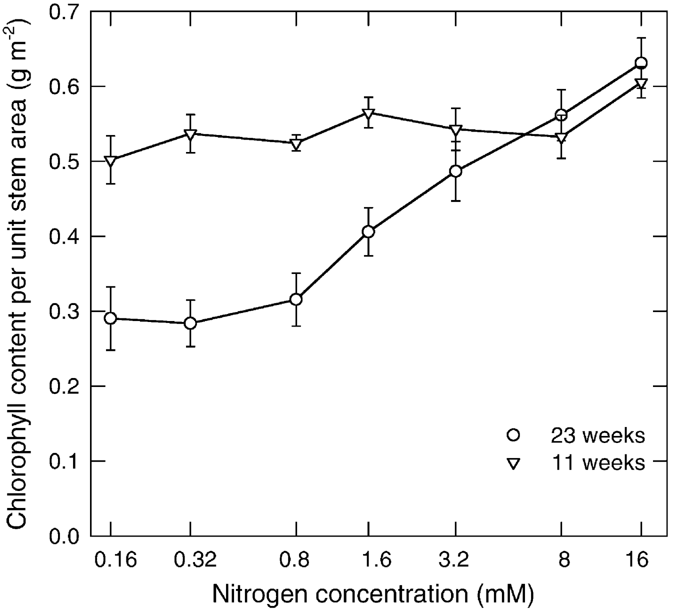

Fig. 5. Variation in amount of chlorophyll per unit stem area for *H. undatus* maintained for 23 weeks at the indicated N concentrations (○) or subsequently subjected to 16 mM N for 11 weeks (▽). Data are means ± 1S.E. ($n = 5$ plants).

4. Discussion

As previously demonstrated (Raveh et al., 1995), *H. undatus* exhibits Crassulacean acid metabolism, with most net CO_2 uptake occurring at night. Of the total daily net CO_2 uptake of 201 mmol m^{-2} per day occurring after 9 weeks with an applied nitrogen concentration of 8 mM (equivalent to that in 0.5-strength Hoagland solution), 76% of the net CO_2 uptake occurred at night. The total daily net CO_2 uptake for *H. undatus* is considerably less than the approximately 600 mmol m^{-2} per day for *O. ficus-indica* under near optimal conditions (Nobel, 1988; Nobel and Israel, 1994). The lower value for *H. undatus* may reflect its adaptation to shaded habitats (Britton and Rose, 1963; Backeberg, 1966; Barthlott and Hunt, 1993). Indeed, in Israel maximal growth for *H. undatus* and other hemiepiphytic cacti occurs under shade cloth that attenuates solar irradiation by 30–60% (Raveh et al., 1998; Mizrahi and Nerd, 1999).

A response of net CO_2 uptake rates for *H. undatus* to the different applied N concentrations was evident at 9 weeks, but the total daily net CO_2 uptake was then only 26% less for the relatively low nitrogen concentration of 0.32 mM compared with the relatively high 8 mM N. Such high concentrations are common for intensive horticultural systems, such as greenhouse crops and field-grown vegetables and ornamentals (Moorby and Besford, 1983; Huett, 1996; Langhans and Tibbitts, 1997). Based on maximal rates of nocturnal net CO_2 uptake at 9, 16, and 22 weeks, the half-time for the shift from the initial condition, when all plants should have the same net CO_2 uptake rate, to the final condition reflecting long-term responses to the applied N concentration was 12 or 13 weeks. This is a much slower response than expected based on responses of *O. ficus-indica* to changing N application, for which 2 weeks leads to substantial changes (Nerd et al., 1993; Nerd and Nobel, 1995), and the even more rapid responses of C_3 and C_4 agronomic plants (Mengel and Kirkby, 1987; Marschner, 1995). Similarly, when all plants received 16 mM N after 22 weeks at different concentrations, the upward shift in maximal net CO_2 uptake rates was approximately half complete in 8 weeks at intermediate N concentrations (0.8–3.2 mM) and at 11 weeks all had reached essentially the maximal value. Thus the half-times for net CO_2 uptake responses to lowered applied N concentration were 12–13 weeks and somewhat shorter, 8–9 weeks, in response to increased N concentrations, but both responses were relatively slow compared with responses of *O. ficus-indica*, contrary to the initial hypothesis. The slow responses for *H. undatus* may reflect the relatively low adaptability of a species only recently selected for cultivation (Mizrahi and Nerd, 1999; Nerd et al., 2002) and which is native to regions that fluctuate relatively little seasonally with respect to resource availability (Benzing, 1990; Lüttge, 1997).

The maximal rate of net CO_2 uptake for plants receiving 1.6 mM N changed little over 22 weeks, whereas those receiving lower applied N concentrations had decreasing maximal rates after 9 weeks and those receiving higher concentrations had increasing rates. Thus the plants responded as if they were initially acclimated to this N concentration. The maximal net CO_2 uptake rate nearly doubled when 16 mM N was applied for 11 weeks following 23 weeks at 1.6 mM, reaching the same value as for plants receiving 16 mM N for 34 weeks. This maximal net CO_2 uptake rate of 10 μmol m^{-2} s^{-1} occurs under well-watered conditions, a high applied N concentration, optimal day/night air temperatures of 30/20 °C, and essentially saturating PPF. Also, this net CO_2 uptake rate is higher than the maximal rate of 6 μmol m^{-2} s^{-1} reported for *H. undatus* under optimal water, temperature, and PPF conditions but 1.6 mM N (Raveh et al., 1995). In comparison, the maximal net CO_2 uptake rate for *O. ficus-indica* under optimal conditions is 15–20 μmol m^{-2} s^{-1} (Cui and Nobel, 1994; Nobel and Israel, 1994).

The maximal nocturnal net CO_2 uptake rate of *H. undatus* reflects the N level in its stem tissue. After 22 weeks under the two lowest applied N concentrations (0.16 and 0.32 mM), the stem N level averaged 1.0% by dry mass, which is similar to the N levels in the relatively slow growing cacti *Opuntia basilaris*, *O. bigelovii*, *O. phaeacantha*, *Stenocereus queretaroensis*, and *Trichocereus chilensis* under arid and semiarid conditions in the field (Nobel, 1988; Nobel and Pimienta-Barrios, 1995). After 22 weeks under the two highest applied N concentrations for *H. undatus*, the mean stem N level of 2.2% is near the average level for cultivated agronomic plants of about 2% N by dry mass (Mengel and Kirkby, 1987; Nobel, 1988; Marschner, 1995). Only a few cacti have stem N levels higher than 2.0%, such as *Opuntia engelmannii* in the field trials in Kingsville, Texas (Nobel et al., 1987) and *O. ficus-indica* raised as a vegetable in Fillmore, California (Nobel, 1988). In any case, stem N levels for *H. undatus* are correlated with its maximal net CO_2 ability, the latter rising 3-fold from 3 to 10 μmol m^{-2} s^{-1} as the tissue N level increases 3-fold from 0.9 to 2.5% N by dry mass ($P < 0.01$). Similarly, the maximal nocturnal acid accumulation for 10 species of cacti increases 3-fold as the chlorenchyma N level increases from 1.0 to 2.6% by dry mass ($P < 0.01$; Nobel, 1983).

Experiments with *O. ficus-indica* (Nerd and Nobel, 1995) indicate that 0.8 mM N may be near a deficit level with respect to N, and 16 mM N may cause a luxury consumption of N (Chapin et al., 1990). In particular, application of 16 mM N leads to accumulation of nitrate in the stems without more growth than for 4 mM N (Nerd and Nobel, 1995). For *H. undatus*, the maximal net CO_2 uptake rate was the same at 8 and 16 mM N, although the N level was 36% higher at the higher N concentration, again suggesting luxury consumption at the highest applied N concentration.

Applying 0.8 mM N or less for 22 weeks led to a visible bleaching of the stems and a reduction in the chlorophyll content per unit area to 0.30 g m^{-2}, whereas 16 mM N raised the chlorophyll to 0.63 g m^{-2} at 22 weeks. Similarly, the chlorophyll content per unit area for *O. ficus-indica* is 0.39 g m^{-2} for cladodes treated with 0.8 mM N for 6 weeks, 0.45 g m^{-2} for 4 mM, and 0.54 g m^{-2} for 16 mM N (Nerd and Nobel, 1995). *H. undatus* provided with 1.6 mM N for about 8 weeks has a chlorophyll content per unit area of 0.49 g m^{-2} (Raveh et al., 1995) compared with 0.41 g m^{-2} for 22 weeks at that N concentration in the present experiments, and *Hylocereus polyrhizus* has about 0.45 g chlorophyll m^{-2} under comparable conditions (Raveh et al., 1998). Such chlorophyll contents per unit area for *H. undatus* and *O. ficus-indica* are similar to typical values of 0.4–0.5 g m^{-2} for leaves of C_3 and C_4 plants (Nobel, 1999), although the latter are for projected area (summed for both sides of the leaves), whereas values for cacti are for each side of the essentially opaque stems.

In conclusion, both the net CO_2 uptake ability of *H. undatus* and its growth, as evidenced by the timing and extent of new stem growth, responded to the N concentration in the nutrient solution, although the responses required a few months for substantial differences to be evident. Ease of measurement makes chlorophyll determination a recommended assay to assess the general physiological status of *H. undatus* with respect to its net CO_2 uptake ability ($P < 0.001$). Moreover, color charts similar to those available for other plants (Munsell, Ben Meadow, Canton, Georgia) could be developed for visual assessment of chlorophyll content per unit stem area in the field, such content responding to N, other nutrients, and light levels. As for correlations with the leaf N level for C_3 and C_4 species (Field and Mooney, 1986; Taub and Lerdau, 2000), the stem N level of *H. undatus* also correlates well with its net CO_2 uptake ability ($P < 0.01$). In any case, maximal net CO_2 uptake ability and, by extension, maximal growth of *H. undatus* required substantial N concentrations in the nutrient solution, such as 8 mM, as is also the case for 1-year-old seedlings of the cacti *C. gigantea*, *Ferocactus acanthodes*, and *T. chilensis* (Nobel, 1983) as well as for intensively managed crops (Moorby and Besford, 1983; Huett, 1996; Langhans and Tibbitts, 1997). The quantifiable responses of *H. undatus* to the N concentration in the nutrient solution underscore the importance of this element for its net CO_2 uptake ability and general physiological status and allow prediction of the conditions maximizing its growth.

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