



Microhabitat and Diel Tissue Acidity Changes for Two Sympatric Cactus Species Differing in Growth Habit

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MICROHABITAT AND DIEL TISSUE ACIDITY CHANGES FOR TWO SYMPATRIC CACTUS SPECIES DIFFERING IN GROWTH HABIT

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SUMMARY

(1) Of two cactus species occurring sympatrically in the north-western Sonoran Desert, *Echinocereus engelmannii* has short stems occurring in tightly packed clumps, whereas *Opuntia acanthocarpa* has stems that freely branch, producing a taller and more open canopy; the stems of *E. engelmannii* are also much more spinose, being shaded 62% by spines compared with only 10% for *O. acanthocarpa*.

(2) Because of differences in height, the mean daily wind speed was 2.4-fold higher and the daytime air temperature 5°C lower at the top of *O. acanthocarpa* than at the top of *E. engelmannii*; similar root depths for the two species led to similar soil water potentials, CO₂ levels and temperatures in the root zone.

(3) Nocturnal increases in stem acidity and osmotic pressure in the field were about twice as high for *O. acanthocarpa* as for *E. engelmannii*, as was the nocturnal CO₂ uptake in the laboratory, consistent with the higher photosynthetic photon flux density on the stem surface of the former species.

(4) Root length and the ground area explored by roots per unit shoot area were about threefold higher for *O. acanthocarpa*, consistent with a threefold higher daily transpiration per unit shoot area, than for *E. engelmannii*.

(5) Thus, *O. acanthocarpa* apparently has distinct advantages over *E. engelmannii* with respect to water acquisition and net CO₂ uptake.

INTRODUCTION

The establishment, survival and growth of desert succulents are affected by the microhabitat, where plant morphology also influences the physiological responses (McAuliffe & Janzen 1986; Yeaton & Manzanares 1986; Nobel 1988). For instance, low air temperatures dictate the distributional limits of various columnar cacti in the Sonoran Desert (Turnage & Hinckley 1938; Steenbergh & Lowe 1983), yet the limits are also affected by ecotypic variations in stem diameter and apical spine coverage (Nobel 1980). The photosynthetic photon flux density (PPFD) absorbed by photosynthetic tissues is influenced by shoot morphology, including shading by spines (Geller & Nobel 1987). Removal of the spines increases the total daily PPFD incident on stems of *Opuntia bigelovii* by about 47%, resulting in a corresponding increase in nocturnal acid accumulation and in growth (Nobel 1983). The roots of some desert succulents occur at greater densities under rocks, where water may collect or persist, than in adjacent soil without rocks (Rowley 1978). The germination

and establishment of seedlings of *Agave deserti* occur most frequently in conjunction with a nurse plant, such as the bunchgrass *Hilaria rigida* (Nobel 1984; Franco & Nobel 1988). The reduction of maximal temperatures by the nurse plant allows for seedling survival, and the increase in soil nitrogen levels under the canopy of *H. rigida* favours growth of *A. deserti*, partially offsetting the reduced CO₂ uptake due to competition for water and PPFD.

The hedgehog cactus, *Echinocereus engelmannii*, and the buckhorn cholla cactus, *Opuntia acanthocarpa*, are two sympatric desert cacti that differ considerably in growth form (Benson 1982). Stems of *E. engelmannii* are unbranched and occur closely spaced in a clump, whereas stems of *O. acanthocarpa* are taller and freely branching, leading to a more open canopy. Such differences affect the wind speed and air temperature at the top of the plants. Moreover, *E. engelmannii* is more densely covered by spines than is *O. acanthocarpa*, which affects the PPFD reaching the stem surface. PPFD interception should influence nocturnal acid accumulation for these species, both of which have previously been shown to be Crassulacean-acid-metabolism (CAM) plants based on CAM-like carbon isotope ratios (Mooney, Troughton & Berry 1974; Sutton, Ting & Troughton 1976) and nocturnal acid accumulation (Ting & Dugger 1968; Ting 1976) as well as some nocturnal net CO₂ uptake for *O. acanthocarpa* (Patten & Dinger 1969). The microhabitat of these two species has not previously been described quantitatively, nor have root distribution and shoot morphology been related to physiological responses. Besides addressing these objectives, nocturnal acid accumulation was measured in the field for north-facing and for south-facing stems of each species in the present study and was related to the PPFD incident on the stem surface. Diel patterns of net CO₂ uptake and water loss were also determined in the laboratory. Water loss was related to the water uptake ability surmised for the root distributions observed in the field.

METHODS

Plant material

Echinocereus engelmannii (Parry) Lem. (Cactaceae) and *Opuntia acanthocarpa* Engelm. & Bigel. (Cactaceae) were studied in the north-western Sonoran Desert at the Philip L. Boyd Deep Canyon Desert Research Center about 8 km south of Palm Desert, California (33°38'N, 116°24'W, 850 m a.s.l.). *Echinocereus engelmannii* is cespitose, the strongly ribbed stems occurring in small mounds, whereas the conspicuously tuberculate stems of *O. acanthocarpa* have numerous branches ascending at acute angles. Most measurements were made on randomly chosen plants on 2–3 March 1990 (the preceding few days had been similar with respect to air temperature and incident radiation), approximately 2 weeks after a rainfall of 12 mm. Additional morphological measurements were made in the field on 17–18 March 1990; four excavated plants of each species were transferred to the laboratory for gas-exchange studies in an environmental chamber.

Morphological parameters measured were the number of stems per plant, stem branching order, stem dimensions, and the stem area index (SAI). Stem surface area was based on mean stem length and mean stem diameter, assuming a stem to be cylindrical with a hemispherical distal end. Roots were carefully excavated to their termini; root surface area was based on mean diameter and length, again assuming a cylindrical shape (Böhm 1979; Sattelmacher & Klotz 1983).

Microclimate

The microclimate of the two species was characterized for the root (soil water potential, temperature and CO₂ level) and the shoot (photosynthetic photon flux density, air temperature and wind speed). The soil at the field site is of granitic origin with a relatively high gravel content (24% of the soil by weight) and a relatively high sand content (77% of the non-gravel fraction); small rock outcrops and patches of bare soil are common, as the total vegetation cover typically is only about 21% (Nobel 1976). Soil water potential in the root zone at a depth of 0.10 m was determined at dawn using soil psychrometers (Wescor PCT-55-15-SF; Wescor, Logan, UT) and a microvoltmeter (Wescor HR-33T) in the psychrometric mode. Temperatures were recorded hourly with a Campbell Scientific CR-5 datalogger (Campbell Scientific, Logan, UT) using 0.5-mm-diameter copper–constantan thermocouples placed near the centre of the root zone at a depth of 0.10 m in the soil and at the soil surface; suspended at 0.16 m, 0.87 m (the tops of the two species) and at 1.50 m above the ground on a mast; and inserted 0.5 mm into the chlorenchyma of vertical stems in each of the four cardinal directions. Readings from three thermocouples, which generally agreed to within $\pm 0.3^\circ\text{C}$, were averaged for each location.

Wind speeds were monitored for 10 min each hour at 0.16, 0.87 and 1.50 m above the ground using Thornthwaite cup anemometers. Wind direction was determined with a weather vane and air pressure was determined with a Thommen altimeter. The soil gas phase at depths of 0.05, 0.10 and 0.20 m in the root zone of *O. acanthocarpa* was sampled using cylindrical airstones (used for aeration of aquaria; 24 mm long and 15 mm in diameter) attached to Tygon tubing leading to the soil surface; 5 ml of soil gas was removed with a syringe and injected into the closed loop of a closed-circuit portable gas-exchange system (LI-COR LI-6200; LI-COR, Lincoln, NB) to determine CO₂ levels (Nobel & Palta 1989). The readings, which were made approximately every 3 h, generally differed by less than $\pm 20\ \mu\text{mol mol}^{-1}$ (here equivalent to ± 20 p.p.m. by volume) for the three replicates that were averaged. PPFD (wavelengths of 400–700 nm) was measured hourly during the daytime for north-facing and south-facing sides of stems at the top of the canopy of each species using a quantum sensor (LI-COR LI-190S). Four to six readings, which took into consideration the local orientations of the stem surface, were averaged. Short-wave radiation was determined with a Moll–Gorczynski solarimeter.

Physiological variables

The percentage shading of the stems by spines for PPFD perpendicular to the stem surface was determined visually by comparing individual stems to a graded series of prepared standards with known fractions of surface area shaded by spines (Nobel 1983). Short-wave and PPFD absorptances of the stems were measured with an integrating sphere radiometer (Smith & Nobel 1977). Chlorophyll was determined after extracting tissue in 80% acetone/20% water by volume (Arnon 1949). Freehand sections were examined with a phase-contrast microscope at 100 \times to determine the area of chlorenchyma cells per unit stem surface area, $A_{\text{chlorenchyma}}/A$ (Nobel 1991). Stomatal frequency was determined using stem surface impressions made with an acrylic polymer and examined at 100 \times . Tissue osmolality was measured with a thermocouple psychrometer (Decagon SC-10; Decagon Devices, Pullman, WA) for cell sap expressed from tissue samples excised with a cork borer 10 mm in diameter

and then crushed between acrylic plates in a vice; the demarcation between the chlorenchyma and the water-storage parenchyma, which was judged visually based on chlorophyll content, resulted in a thickness of 2.8–3.2 mm for the chlorenchyma of *E. engelmannii* and 2.5–2.9 mm for *O. acanthocarpa*. Osmotic pressure was calculated from the measured osmolality using the van't Hoff relation (Nobel 1991) and the stem temperatures measured in the field. The water potential of excised roots was determined with a Scholander-type pressure chamber (PMS 600; PMS Instrument, Corvallis, OR).

Chlorenchyma acidity levels, which reflect the content of organic acids such as malate, were determined for tissue samples excised with a cork borer 10 mm in diameter ($7.85 \times 10^{-5} \text{ m}^2$ surface area). After adding 20 ml of distilled water, the samples were ground with a pestle and mortar and were titrated to pH 7.4 with 0.005 mol l^{-1} NaOH dispensed with a burette graduated in 0.1-ml increments. The duplicate readings generally agreed to within $\pm 15 \text{ mmol H}^+ \text{ m}^{-2}$.

Gas exchange was determined in the laboratory with the LI-COR LI-6200 for well-watered plants that had been excavated in the field and placed in an environmental chamber with a 12-h photoperiod for 3–4 weeks (sufficient time for new roots to appear). The stem temperatures were within 2°C of the average field values during the day and within 1°C during the night. Four General Electric cool-beam 300-W PAR lamps at 60° above the horizontal on one side of the plants were used to supplement the warm-white fluorescent lamps and to simulate the prevailing direction of solar irradiation at the field site in early spring; the average total daily PPFD on the stems used for gas exchange was within 3% of the field values. A cylindrical lucite chamber lined with transparent Teflon (to minimize water adsorption and desorption) was sealed to the upper 50 mm of the stem of each species with mastic and then fitted to the LI-COR LI-6200 gas-exchange system.

RESULTS

Plant morphology

Although the stem diameters were similar (31–39 mm), shoot morphology of the two species differed considerably (Table 1). *Echinocereus engelmannii* consisted of a clump of closely spaced, unbranched, vertical stems averaging nineteen per plant and 0.19 m in height. *Opuntia acanthocarpa* had an average of eight primary stems per plant 0.53 m in length from which branched an average of twenty-seven secondary stems 0.17 m long, which in turn had an average of eleven tertiary stems, 0.08 m in length (0.6 quaternary stems per plant were included with the tertiary stems; the lowermost 10–30 mm at the base of the primary stems had an outer region that was brown and necrotic, which was not included in the stem length nor used in calculating SAI). The ten plants of *O. acanthocarpa* averaged $0.87 \pm 0.11 \text{ m}$ in height. The primary and secondary stems of *O. acanthocarpa* had approximately equal total surface areas and the tertiary stems had about one-quarter as much (Table 1). Based on a polygon circumscribing the vertical projections of the stems on to the ground to obtain the ground area, the stem area index was over twice as high in *E. engelmannii* as in *O. acanthocarpa*.

The root distributions of each species were quite shallow with regard to both the root length and the percentage of total root surface area at various depths (Table 2). The mean root depth was 0.110 m for *E. engelmannii* and 0.079 m for

TABLE 1. Shoot morphology of *Echinocereus engelmannii* and *Opuntia acanthocarpa*. Figures are means \pm 1 S.D. ($n = 10$); where mean stem properties are indicated, four stems per plant were measured. The shoot ground area per plant and stem area index (SAI) were based on a polygon circumscribing the stems.

Variable	Mean \pm 1 S.D.
<i>E. engelmannii</i>	
Stems per plant	19.3 \pm 13.6
Mean stem height (m)	0.186 \pm 0.019
Mean stem diameter (mm)	38.6 \pm 1.5
Total stem area per plant (m ²)	0.401 \pm 0.255
Shoot ground area per plant (m ²)	0.0630 \pm 0.0388
SAI	6.88 \pm 1.15
<i>O. acanthocarpa</i>	
Primary stems per plant	8.1 \pm 4.3
Mean primary stem length (m)	0.527 \pm 0.159
Mean primary stem diameter (mm)	32.6 \pm 2.1
Total area of primary stems (m ²)	0.450 \pm 0.291
Secondary stems per plant	26.6 \pm 16.1
Mean secondary stem length (m)	0.170 \pm 0.071
Mean secondary stem diameter (mm)	32.1 \pm 1.8
Total area of secondary stems (m ²)	0.421 \pm 0.318
Tertiary stems per plant	10.8 \pm 8.6
Mean tertiary stem length (m)	0.075 \pm 0.036
Mean tertiary stem diameter (mm)	31.1 \pm 1.7
Total area of tertiary stems (m ²)	0.100 \pm 0.107
Total stem area per plant (m ²)	0.971 \pm 0.581
Shoot ground area per plant (m ²)	0.295 \pm 0.256
SAI	2.84 \pm 0.73

TABLE 2. Root properties of *Echinocereus engelmannii* and *Opuntia acanthocarpa*. Figures are means \pm 1 S.D. ($n = 4$). Stem diameters and lengths are similar to the averages in Table 1; total stem area per plant averaged 0.117 \pm 0.019 m² for *E. engelmannii* and 0.150 \pm 0.032 m² for *O. acanthocarpa*. The root ground area per plant was assumed to extend 10 mm horizontally on either side of each individual root. Water potential was determined for roots about 2 mm in diameter from the centre of the root zone.

	<i>E. engelmannii</i>	<i>O. acanthocarpa</i>
Total length (m)	6.5 \pm 1.2	27.3 \pm 2.9
Length at various depths (% of total)		
0.00 – 0.05 m	13 \pm 10	34 \pm 12
0.05 – 0.10 m	30 \pm 19	35 \pm 9
0.10 – 0.15 m	36 \pm 11	21 \pm 12
0.15 – 0.20 m	18 \pm 19	9 \pm 8
> 0.20 m	3 \pm 5	1 \pm 2
Total surface area (m ²)	0.039 \pm 0.005	0.297 \pm 0.045
Surface area at various depths (% of total)		
0.00 – 0.05 m	26 \pm 17	38 \pm 13
0.05 – 0.10 m	33 \pm 13	35 \pm 9
0.10 – 0.15 m	33 \pm 9	20 \pm 13
0.15 – 0.20 m	7 \pm 5	6 \pm 5
> 0.20 m	1 \pm 2	1 \pm 2
Root ground area per plant (m ²)	0.17 \pm 0.03	0.73 \pm 0.13
Root water potential (MPa)	-0.48 \pm 0.05	-0.39 \pm 0.06

O. acanthocarpa based on root length and 0.087 m and 0.074 m, respectively, based on root surface area. *Opuntia acanthocarpa* had 29% more shoot surface area than *E. engelmannii*, a 4.2-fold greater total length of roots and a 7.6-fold greater total root surface area (Table 2). The root ground area explored per plant was 4.3-fold higher for *O. acanthocarpa* than for *E. engelmannii*. The average water potential of the roots was about -0.5 MPa for *E. engelmannii* and -0.4 MPa for *O. acanthocarpa* (Table 2).

Very few roots from other species were found to overlap with the roots of the four excavated plants of each cactus species. None of the plants examined (Tables 1 and 2) occurred in obvious association with a nurse plant but two of eleven seedlings of *E. engelmannii* and six of thirteen seedlings of *O. acanthocarpa* were under the canopies of the subshrub *Encelia farinosa* or the bunchgrass *Hilaria rigida* (the rest were usually at least partially shaded by rocks). Nets or mats of fine roots of *O. acanthocarpa* occurred preferentially next to the upper and the lower surfaces of rocks in the soil, and the finer roots of *E. engelmannii* were also more common adjacent to rocks. In both cases, fine roots branching from the primary roots emanating from the stem were much less common in rock-free portions of the soil. Such primary roots extended up to 1.8 m from the plant base for *O. acanthocarpa* and up to 0.9 m for *E. engelmannii*. Although the species were often adjacent at the field site, *E. engelmannii* had a greater tendency to be associated with rock outcrops.

Microclimate

The PPFD on the south-facing or the north-facing sides of exposed stems was similar for each species, but air temperature and wind speed differed considerably (Fig. 1). The total daily PPFD was $26.3 \text{ mol m}^{-2} \text{ day}^{-1}$ for the south-facing side of *O. acanthocarpa* and $6.5 \text{ mol m}^{-2} \text{ day}^{-1}$ for the north-facing side (Fig. 1a). On an unshaded horizontal surface the total daily PPFD was $29.8 \text{ mol m}^{-2} \text{ day}^{-1}$ and the total daily short-wave irradiation was $18.6 \text{ MJ m}^{-2} \text{ day}^{-1}$.

Although air temperatures at night were similar for the two species, from solar times of 10.00–15.00 hours the air temperature at the top of the canopy averaged 4.9°C higher for the shorter species, *E. engelmannii* (Fig. 1b). At 1.50 m above the ground, which is often used for weather shelter data, the air temperature had a similar daily pattern and similar values to those at the top of the canopy of *O. acanthocarpa* (Fig. 1b), averaging 0.2°C higher at night and 0.5°C lower during the daytime. From 20.00 to 05.00 hours (night-time) the hourly stem surface temperatures of *E. engelmannii* averaged 0.6°C below its ambient air temperature (Fig. 1b) and that of *O. acanthocarpa* averaged 0.7°C below its ambient air temperature. From 10.00 to 15.00 hours (day-time) the hourly stem surface temperatures of *E. engelmannii* averaged 5.3°C above its ambient air temperature and that of *O. acanthocarpa* averaged 3.2°C above its ambient air temperature (Fig. 1b).

Wind speed over the 24-h period averaged 0.64 m s^{-1} at the top of *E. engelmannii*, 1.52 m s^{-1} at the top of *O. acanthocarpa* (Fig. 1c), and 2.21 m s^{-1} at 1.50 m above the ground. Besides hourly changes in wind speed, wind direction changed near dusk and near dawn. In particular, the average prevailing wind direction was from 58° east of north during the daytime (09.00–18.00 hours), rotating by 167° clockwise during the nighttime. The air pressure averaged 0.18 kPa higher near the middle of the day (10.00–15.00 hours) than during the night (19.00–07.00 hours).

The daily variations in soil temperature were greater and the extreme values

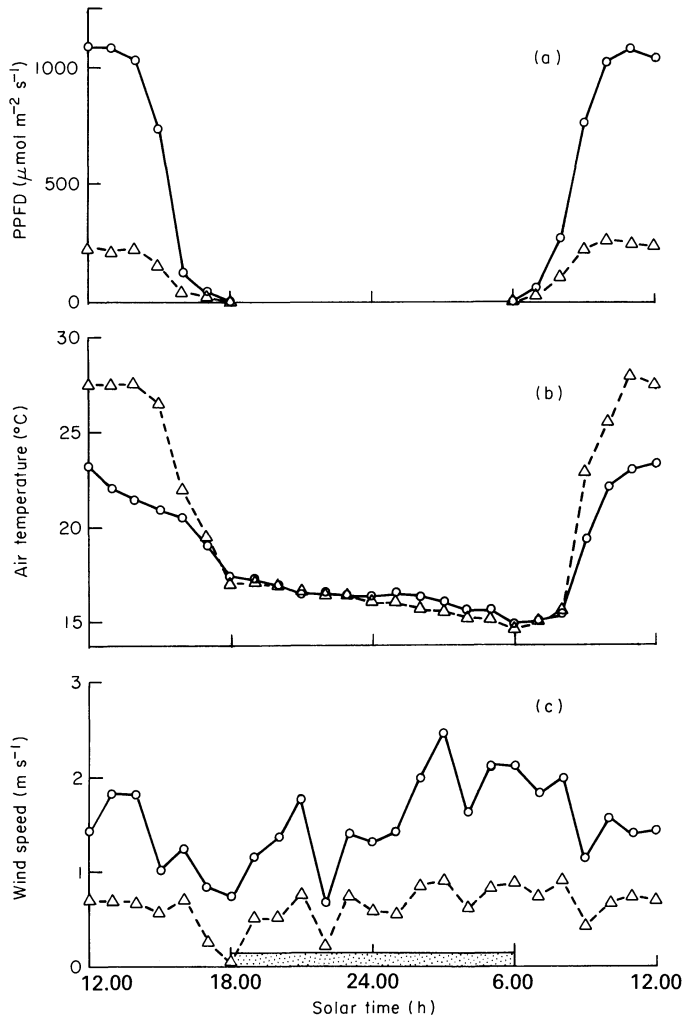


FIG. 1. Shoot microclimate for two cactus species in the Sonoran Desert: (a) photosynthetic photon flux density incident on north-facing (Δ) and south-facing (\circ) stems of *Opuntia acanthocarpa* (essentially identical patterns occurred for *Echinocereus engelmannii*); (b) air temperature for *E. engelmannii* (Δ) and *O. acanthocarpa* (\circ); and (c) wind speed for *E. engelmannii* (Δ) and *O. acanthocarpa* (\circ). All measurements were made at the top of the canopy at a height of 0.16 m for *E. engelmannii* and 0.87 m for *O. acanthocarpa*. The stippled bar indicates night.

occurred sooner at the soil surface than near the centre of the root zone at 0.10 m below the soil surface (Fig. 2). Specifically, the daily variations were 18.1°C at the surface and 9.9°C at a soil depth of 0.10 m. The maximum temperatures occurred at 12.00 hours at the surface and at 15.00 hours at a depth of 0.10 m, and the minimum temperatures were at 05.00 and 08.00 hours, respectively (Fig. 2a). At any time of day, the CO_2 level in the soil gas phase increased with depth, averaging $505 \mu\text{mol mol}^{-1}$ at 0.05 m, $621 \mu\text{mol mol}^{-1}$ at 0.10 m, and $718 \mu\text{mol mol}^{-1}$ at 0.20 m (Fig. 2b). At

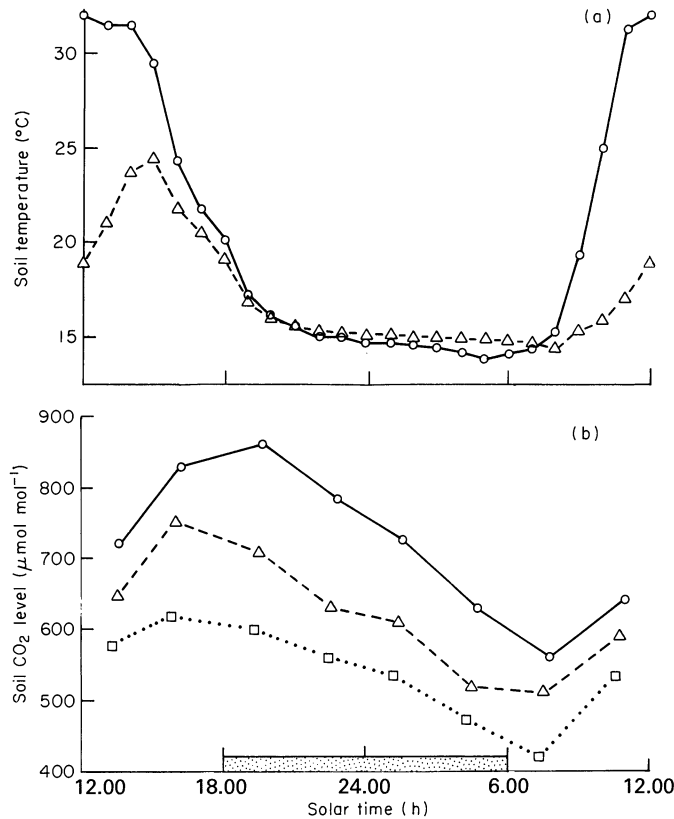


FIG. 2. Root microclimate for two cactus species in the Sonoran Desert: (a) soil temperature at the surface in the centre of *Echinocereus engelmannii* (○) and at a depth of 0.10 m (△) (essentially identical patterns occurred for *Opuntia acanthocarpa*); and (b) soil CO₂ concentrations at depths of 0.05 m (□), 0.10 m, (△) and 0.20 m (○) in the root zone of *O. acanthocarpa*. The stippled bar indicates night.

0.10 m, the maximum CO₂ level coincided in time with the maximal soil temperature, and the minimum CO₂ level coincided with the minimum temperature (Fig. 2). The maximum soil CO₂ level at 0.20 m occurred near 20.00 hours, which was later than for shallower depths in the soil. The soil water potential at a depth of 0.10 m was -0.25 ± 0.03 MPa (S.D. for $n = 4$) in the root zone of *E. engelmannii* and -0.27 ± 0.04 ($n = 4$) for *O. acanthocarpa*.

Physiological variables

Although many properties related to radiation absorption by the stems of the two species were similar, spines reduced the PPFD reaching the stem surface by 62% for *E. engelmannii* but by only 10% for *O. acanthocarpa* (Table 3). The short-wave and PPFD absorbances, the chlorophyll per unit stem area, and the area of chlorenchyma cells per unit stem area were similar for the two species. These four variables were not significantly different for north-facing compared with south-facing sides of the

TABLE 3. Stem physiological variables for *Echinocereus engelmannii* and *Opuntia acanthocarpa*. Figures are means \pm 1 S.D. ($n = 5$). Measurements were made for north-facing and south-facing stem surfaces at the top of the canopy.

	North	South
<i>E. engelmannii</i>		
Spine shading (%)	61 \pm 7	63 \pm 6
Short-wave absorptance	0.63 \pm 0.03	0.62 \pm 0.02
PPFD absorptance	0.83 \pm 0.02	0.82 \pm 0.02
Chlorophyll (g m ⁻²)	0.65 \pm 0.07	0.56 \pm 0.09
A _{chlrenchyma} /A	67 \pm 6	64 \pm 5
Stomatal frequency (number mm ⁻²)	46 \pm 4	47 \pm 3
Osmotic pressure (MPa)		
parenchyma		
dusk	0.61 \pm 0.03	0.63 \pm 0.03
dawn	0.62 \pm 0.03	0.64 \pm 0.02
chlrenchyma		
dusk	0.65 \pm 0.02	0.76 \pm 0.03
dawn	0.71 \pm 0.04	0.93 \pm 0.05
<i>O. acanthocarpa</i>		
Spine shading (%)	10 \pm 2	10 \pm 1
Short-wave absorptance	0.59 \pm 0.02	0.58 \pm 0.02
PPFD absorptance	0.79 \pm 0.03	0.79 \pm 0.02
Chlorophyll (g m ⁻²)	0.63 \pm 0.03	0.64 \pm 0.06
A _{chlrenchyma} /A	68 \pm 4	69 \pm 7
Stomatal frequency (number mm ⁻²)	79 \pm 5	83 \pm 4
Osmotic pressure (MPa)		
parenchyma		
dusk	0.93 \pm 0.03	0.99 \pm 0.04
dawn	0.95 \pm 0.04	0.98 \pm 0.03
chlrenchyma		
dusk	0.98 \pm 0.05	1.18 \pm 0.06
dawn	1.12 \pm 0.06	1.52 \pm 0.11

stem (Table 3). Stomatal frequency was 74% higher for *O. acanthocarpa* than for *E. engelmannii* (Table 3).

For both species, the osmotic pressure in the parenchyma was similar for north-facing and south-facing sides of the stem and did not increase from dusk to dawn (Table 3). In contrast, the osmotic pressure in the chlrenchyma was higher for south-facing than for north-facing sides of both species and increased from dusk to dawn. The nocturnal increase in osmotic pressure averaged 0.06 MPa and 0.14 MPa for the north-facing sides of *E. engelmannii* and *O. acanthocarpa*, respectively, and 0.17 MPa and 0.34 MPa for their south-facing sides (Table 3).

The nocturnal increases (dawn values minus dusk values) in osmotic pressure were accompanied by nocturnal increases in titratable acidity per unit stem surface area (Fig. 3). The nocturnal acidity increases were higher for the south-facing side of the stem compared with the north-facing side for each species and were higher for *O. acanthocarpa* than for *E. engelmannii*. Specifically, the nocturnal increases were 169 mmol m⁻² and 296 mmol m⁻² for the north-facing sides of *E. engelmannii* and *O. acanthocarpa*, respectively, and 399 mmol m⁻² and 610 mmol m⁻² for their south-facing sides. The nocturnal increases in chlrenchyma acidity were reversed during the daytime for both species (Fig. 3).

For plants examined in the laboratory under conditions similar to those in the

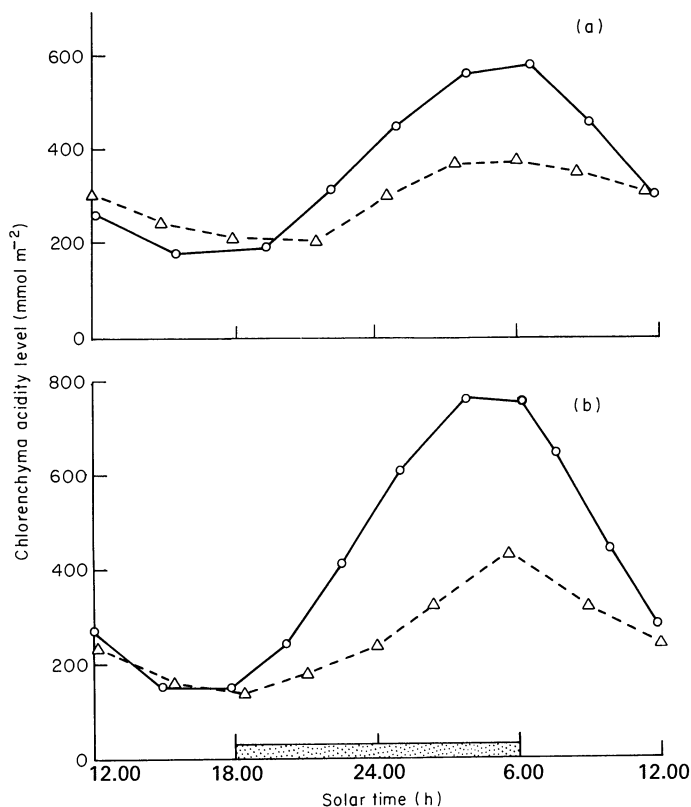


FIG. 3. Chlorenchyma acidity levels for (a) *Echinocereus engelmannii* and (b) *Opuntia acanthocarpa* in the Sonoran Desert. Data were obtained for north-facing (Δ) and south-facing (\circ) stems at the top of the canopy (see Fig. 1). The stippled bar indicates night.

field, net CO_2 uptake, acid accumulation and water loss were greater at night in *O. acanthocarpa* than in *E. engelmannii*. The maximum rates of net CO_2 uptake were $5.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ in *O. acanthocarpa* and 2.9 in *E. engelmannii*; the total nocturnal CO_2 uptake was 203 and 101 mmol m^{-2} , respectively, for these two species (Fig. 4). Over the 24-h period, net CO_2 uptake was 187 mmol m^{-2} in *O. acanthocarpa* and 98 in *E. engelmannii*. The nocturnal increases in acidity averaged for the high and the low PPFD sides of the stem were 479 mmol m^{-2} in *O. acanthocarpa* and 236 mmol m^{-2} in *E. engelmannii*. Stomatal conductance and transpiration exhibited a diel pattern similar to that of net CO_2 uptake. The maximum water vapour conductance was $119 \text{ mmol m}^{-2} \text{s}^{-1}$ in *O. acanthocarpa* and 44 in *E. engelmannii*; the total water loss over the 24-h period was 17.2 and 5.4 mol m^{-2} , respectively, for these two species.

DISCUSSION

The different root and shoot morphologies of *Echinocereus engelmannii* and *Opuntia acanthocarpa* result in different water uptake abilities, different photosynthetic photon

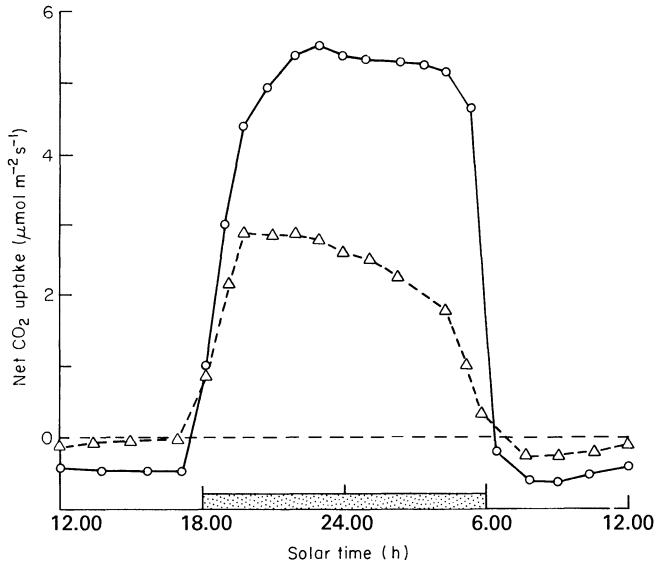


FIG. 4. Net CO₂ uptake in the laboratory, under conditions similar to those in the field, in *Echinocereus engelmannii* (Δ) and *Opuntia acanthocarpa* (○), from the Sonoran Desert. The stippled bar indicates night.

flux densities intercepted by the stem surface, and hence different rates of gas exchange. Spine shading of the stem averaged 62% for *E. engelmannii* but only 10% for *O. acanthocarpa*. Indeed, *E. engelmannii* is among the most spinose of the forty-four species of *Echinocereus* (Taylor 1985). The 2.4-fold lower stem area index for *O. acanthocarpa*, combined with its 4.7-fold greater height, leads to a much more open canopy than that of *E. engelmannii*. Yet many individual stem properties are similar, such as diameter, short-wave absorptance, PPFD absorptance, chlorophyll per unit area, and the area of chlorenchyma cells per unit stem surface area. The values for $A_{\text{chlorenchyma}}/A$ of 64–69 for *E. engelmannii* and *O. acanthocarpa* are lower than values observed for other desert succulents, such as 82 for *Agave deserti* and 137 for *Ferocactus acanthodes*, but much higher than values of 10–30 typically observed for C₃ and C₄ plants (Nobel 1988, 1991).

The nearly fivefold greater height of *O. acanthocarpa* led to higher wind speeds near the top of its canopy, enhancing convective heat exchange (Nobel 1991) and thereby causing the stem temperature during the daytime to be closer to ambient air temperature than for *E. engelmannii*. During the night, transpiration contributed to the lowering of stem temperatures below ambient air temperature. The greater transpiration by *O. acanthocarpa* than *E. engelmannii* together with the higher windspeeds for the former caused the lowering to be about the same for the two species. Because of the heating of the ground by short-wave irradiation during the daytime, the upper part of stems of *E. engelmannii* averaged 7°C warmer than those of *O. acanthocarpa* near midday. In this regard, *O. acanthocarpa* at day/night air temperatures of 50°C/40°C is the least tolerant of high temperatures of the eighteen species of cacti tested so far, including four other species occurring at the field site

(Nobel 1988). In contrast to *E. engelmannii*, in which no brown stem areas were observed, necrotic outer tissue occurred at the base of many plants of *O. acanthocarpa*, presumably as a consequence of the high soil-surface temperatures at the field site (Jordan & Nobel 1984; Nobel *et al.* 1986) and the greater vulnerability of the latter species to high temperatures.

The mean ambient wind speeds were high, reflecting the influence of local topographical features on air movement. Specifically, the field site experienced a mountain-valley wind system, characterized by heating of air on the valley floor during the daytime, leading to uphill flow of this buoyant air, followed by downhill drainage of cool air at night (Fleagle 1950; Schwoegler & McClintock 1981). The times of wind reversal (09.00 and 18.00 hours) corresponded to times of local minima in wind speeds (except for a calm period at night) following changes in heating of the valley floor. The local air pressure tended to increase shortly after dawn and to decrease near dusk, indicating that the field site was closer to the valley than the mountain part of the wind system, in agreement with the local topography (altitudes of 240 m for the local valley floor, 850 m for the field site, and 2460 to 2660 m for local mountain peaks).

The distributions of root length and surface area with depth were similar for the two species, although thicker roots tended to be somewhat more superficial than finer roots for *E. engelmannii*. The roots of both species were shallow, averaging 0.09 m in depth, based on length, and 0.08 m based on root surface area. The finer roots were associated with the surfaces of rocks for each species; the presence of new root growth adjacent to rocks and the absence of branches on the primary roots in soil regions devoid of rocks implies plant uptake of channelled and trapped rain water before it percolates to lower soil depths. Also, the occurrence of root nets of *O. acanthocarpa* on the lower surfaces of flat rocks, which has also been observed for other species of cacti (Rowley 1978), may enable this species to obtain water seeping around the rocks as well as water moving upward in the soil by capillarity during drought periods. The shallowness of the root systems of both species is advantageous with respect to harvesting of water, as the water availability (soil-to-plant drop in water potential integrated over a year) for succulent plants at the field site in an average rainfall year is highest in the uppermost soil layer (Nobel 1989a). Also, levels of nutrients such as nitrogen and potassium are higher in the more superficial layers; sodium increases and hence becomes more inhibitory with depth (Nobel 1989a, b). Thus, comparing the uppermost (0.00–0.05 m) and the lowermost (0.15–0.20 m) soil layers having appreciable representation of roots for each species, the water and nutrient conditions of the upper soil layer lead to just over twice the predicted growth rate compared with the lower layer.

Maximum soil temperatures tend to exclude roots of desert succulents from the upper 20 mm or so, except directly under the stems or in other shaded locations (Jordan & Nobel 1984; Nobel 1988). The attenuation of surface temperatures is described by the damping depth, where the soil temperature variation decreases to 37% of the value at the soil surface, which is about 0.10 m for the field site (Nobel & Geller 1987). The slightly lower attenuation observed in the present study was a consequence of the shading of the soil surface by the cactus canopies, which reduced the daily excursion of the soil surface temperature about its mean compared with the case for bare soil. The lag of 3.7 h predicted for the maximum and the minimum soil temperatures to reach a depth of 0.10 m agrees well with observed values of 3 h.

The time of day for maximum CO_2 level at a depth of 0.20 m coincides with the time for maximum soil temperature at that depth. Also, the soil CO_2 level is expected to increase with depth, as was observed. The highest soil CO_2 level observed, $860 \mu\text{mol mol}^{-1}$, is less than the CO_2 level ($2000 \mu\text{mol mol}^{-1}$) leading to deleterious effects on the roots of other desert succulents (Nobel & Palta 1989; Nobel 1990).

Nocturnal increases in the concentration of malic acid in CAM plants can cause substantial increases in the osmotic pressure of the chlorenchyma (Lüttge & Nobel 1984; Rygol, Winter & Zimmermann 1987). The nocturnal increase in H^+ averaged 284 mmol m^{-2} for the north-facing plus south-facing sides of *E. engelmannii*, and 453 mmol m^{-2} for *O. acanthocarpa*. Because two H^+ are involved per malic acid molecule (Nobel 1988), this corresponds to 142 and $227 \text{ mmol malic acid m}^{-2}$, respectively. For the two stem surfaces, the nocturnal osmotic pressure increases in the chlorenchyma averaged 0.12 MPa for *E. engelmannii* and 0.24 MPa for *O. acanthocarpa*. Using the van't Hoff relation (Nobel 1991) as well as osmotic responses observed for *Cereus validus* (Lüttge & Nobel 1984), these osmotic pressure increases correspond to malic acid concentrations of 50 mmol l^{-1} for *E. engelmannii* and 100 mmol l^{-1} for *O. acanthocarpa*. To account for the measured increases in acidity per unit stem surface area, the chlorenchyma would have to correspond to a liquid thickness of $(142 \text{ mmol m}^{-2}) / (50 \times 10^3 \text{ mmol m}^{-3})$ or 2.8 mm for *E. engelmannii* and $(227 / 100 \times 10^3)$ or 2.3 mm for *O. acanthocarpa*. This is in excellent agreement with the thicknesses of the chlorenchyma samples used for the osmotic pressure and acidity determinations of about 3.0 mm for *E. engelmannii* and 2.7 mm for *O. acanthocarpa*, thicknesses that include intercellular air spaces and cell wall material.

The large values for nocturnal increases in osmotic pressure and in acidity are consistent with values for other desert succulents under ideal conditions (Lüttge & Nobel 1984; Nobel 1988). Moreover, the conditions could have been close to ideal in the field. Nocturnal acidity increases tend to be maximal for nighttime air temperatures near 15°C (Nobel 1988), similar to the values observed. The mean soil water potential (-0.26 MPa) was higher than the mean root water potential (-0.44 MPa), a condition necessary for water uptake by the plants.

For many well-watered CAM plants at ideal temperatures, the maximum nocturnal increase in acidity at saturating PPFD (about $30 \text{ mol m}^{-2} \text{ day}^{-1}$) is approximately $600 \text{ mmol H}^+ \text{ m}^{-2}$ (Nobel 1988). For a PPFD of $23.7 \text{ mol m}^{-2} \text{ day}^{-1}$ incident on a south-facing exposed stem, *O. acanthocarpa* had a nocturnal acidity increase of $610 \text{ mmol m}^{-2} \text{ day}^{-1}$, consistent with observations on other cacti under ideal conditions (Nobel 1988). For the total PPFD of $5.9 \text{ mol m}^{-2} \text{ day}^{-1}$ incident on a north-facing stem of *O. acanthocarpa*, the predicted nocturnal acidity increase was within 3% of the measured value. Assuming that nocturnal acidity increases by *E. engelmannii* respond to PPFD, as for *O. acanthocarpa* and other cacti, the predicted nocturnal acidity increase for a PPFD of $10.0 \text{ mol m}^{-2} \text{ day}^{-1}$ for the south-facing stem surface was $401 \text{ mmol m}^{-2} \text{ day}^{-1}$, essentially identical to the observed value. Furthermore, the north-facing surface, where the total daily PPFD reaching the stem was only $2.5 \text{ mol m}^{-2} \text{ day}^{-1}$, had a nocturnal acidity increase within 4% of the predicted value. Thus, the effects on PPFD of stem orientation and of spine shading of the stem surface fully account for the fourfold variations in nocturnal acidity increases observed in the field for two species of cacti differing greatly in spine coverage. The observed PPFD levels were for unshaded stems at the top of the canopy. The incident PPFD would be less at lower levels in the canopy, as has been observed in

the field for *E. engelmannii* and *Opuntia echinocarpa* (Geller & Nobel 1987), a cylindropuntia that is morphologically similar to *O. acanthocarpa* (Benson 1982).

Nocturnal CO_2 uptake for the upper stem segments in the laboratory amounted to 101 mmol m^{-2} for *E. engelmannii* and 203 mmol m^{-2} for *O. acanthocarpa*. Assuming that each CO_2 molecule taken up is incorporated into malate, yielding 2 H^+ (Nobel 1988), the acidity increase expected is 202 and $406 \text{ mmol H}^+ \text{ m}^{-2}$, respectively. The measured acidity increases in the laboratory averaged 17% higher than these values, apparently reflecting the fixation of some CO_2 released by respiration. Nocturnal increases in acidity averaged for north-facing and south-facing stems in the field were similar to the average nocturnal increases determined in the laboratory, indicating that the similar conditions of temperature, PPFD and water status led to similar physiological responses. In this regard, the twofold higher net CO_2 uptake and more than threefold higher water loss per unit area for *O. acanthocarpa* observed in the laboratory suggests that it should have a lower water-use efficiency (Nobel 1991) than does *E. engelmannii*. Consistent with the higher transpiration rate, *O. acanthocarpa* has a higher stomatal frequency (81 mm^{-2}) than does *E. engelmannii* (47 mm^{-2}), whose stomatal frequency is similar to that of other CAM plants (Nobel 1988). For instance, the mean stomatal frequency ranges from 30 to 50 mm^{-2} for twenty-three taxa of agaves (Gentry & Sauck 1978) and from 30 to 62 mm^{-2} for five species of *Opuntia* (Conde 1975), which is considerably less than the $100\text{--}300 \text{ mm}^{-2}$ observed for both sides of most monocotyledonous leaves and the lower surfaces of most dicotyledonous leaves (Esau 1977).

Because *O. acanthocarpa* has much less spine shading of the stem, a lower stem area index, and a more open canopy than *E. engelmannii*, it has a higher PPFD averaged over its shoot. Higher incident PPFD results in greater nocturnal acid accumulation, as the responses of nocturnal acid accumulation to PPFD on the stem surface are similar for the two species. Because of the higher levels of PPFD, *O. acanthocarpa* should have a greater stomatal conductance and hence should require more water per unit stem surface area than does *E. engelmannii*, as was observed. The total root length, total root surface area and root ground area, per unit stem surface area, were 3.3, 5.9 and 3.3 times higher, respectively, in *O. acanthocarpa* than in *E. engelmannii*. Consistent with this, the water loss per unit shoot area over a 24-h period was more than three times greater in *O. acanthocarpa* than in *E. engelmannii* under laboratory conditions similar to those observed in the field. Although knowledge of stomatal conductance and root hydraulic conductance in the field are necessary for unambiguous interpretation of such correlations, *O. acanthocarpa* apparently uses more water per unit stem surface area than *E. engelmannii*. Thus, *O. acanthocarpa* can obtain more soil water and because of its taller canopy and lower spine coverage can have a higher PPFD intercepted by the stem, leading to more net CO_2 uptake, than for the sympatric *E. engelmannii*.

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REFERENCES

- Arnon, D. I. (1949). Copper enzymes in isolated chloroplasts. Polyphenoloxidase in *Beta vulgaris*. *Plant Physiology*, **24**, 1–15.
- Benson, L. (1982). *The Cacti of the United States and Canada*. Stanford University Press, Stanford, CA.
- Böhm, W. (1979). *Methods of Studying Root Systems*. Springer Verlag, Berlin.
- Conde, L. F. (1975). Anatomical parameters of five species of *Opuntia* (Cactaceae). *Annals of the Missouri Botanical Garden*, **62**, 263–284.
- Esau, K. (1977). *Anatomy of Seed Plants*, 2nd edn. Wiley, New York.
- Fleagle, R. G. (1950). A theory of air drainage. *Journal of Meteorology*, **7**, 227–232.
- Franco, A. C. & Nobel, P. S. (1988). Interactions between seedlings of *Agave deserti* and the nurse plant *Hilaria rigida*. *Ecology*, **69**, 1731–1740.
- Geller, G. N. & Nobel, P. S. (1987). Comparative cactus architecture and PAR interception. *American Journal of Botany*, **74**, 998–1005.
- Gentry, H. S. & Sauck, J. R. (1978). The stomatal complex in *Agave*: groups Deserticolae, Campaniflorae, Umbelliflorae. *Proceedings of the California Academy of Sciences*, **41**, 371–387.
- Jordan, P. W. & Nobel, P. S. (1984). Thermal and water relations of desert succulents. *Annals of Botany*, **54**, 705–717.
- Lüttge, U. & Nobel, P. S. (1984). Day–night variations in malate concentration, osmotic pressure, and hydrostatic pressure in *Cereus validus*. *Plant Physiology*, **75**, 804–807.
- McAuliffe, J. R. & Janzen, F. J. (1986). Effects of intraspecific crowding on water uptake, water storage, apical growth and reproductive potential in the sahuaro cactus, *Carnegiea gigantea*. *Botanical Gazette*, **147**, 334–341.
- Mooney, H., Troughton, J. H. & Berry, J. A. (1974). Arid climates and photosynthetic systems. *Carnegie Institution Year Book*, **73**, 793–805.
- Nobel, P. S. (1976). Water relations and photosynthesis of a desert CAM plant, *Agave deserti*. *Plant Physiology*, **58**, 576–582.
- Nobel, P. S. (1980). Morphology, surface temperatures, and northern limits of columnar cacti in the Sonoran Desert. *Ecology*, **61**, 1–7.
- Nobel, P. S. (1983). Spine influences on PAR interception, stem temperature, and nocturnal acid accumulation by cacti. *Plant, Cell and Environment*, **6**, 153–159.
- Nobel, P. S. (1984). Extreme temperatures and the thermal tolerances for seedlings of desert succulents. *Oecologia*, **62**, 310–317.
- Nobel, P. S. (1988). *Environmental Biology of Agaves and Cacti*. Cambridge University Press, New York.
- Nobel, P. S. (1989a). Temperature, water availability, and nutrient levels at various soil depths—consequences for shallow-rooted desert succulents, including nurse plant effects. *American Journal of Botany*, **76**, 1486–1492.
- Nobel, P. S. (1989b). A nutrient index quantifying productivity of agaves and cacti. *Journal of Applied Ecology*, **26**, 635–645.
- Nobel, P. S. (1990). Soil O₂ and CO₂ effects on apparent cell viability for roots of desert succulents. *Journal of Experimental Botany*, **41**, 1031–1038.
- Nobel, P. S. (1991). *Physicochemical and Environmental Plant Physiology*. Academic Press, San Diego.
- Nobel, P. S. & Geller, G. N. (1987). Temperature modelling of wet and dry desert soils. *Journal of Ecology*, **75**, 247–258.
- Nobel, P. S., Geller, G. N., Kee, S. C. & Zimmerman, A. D. (1986). Temperatures and thermal tolerances for cacti exposed to high temperatures near the soil surface. *Plant, Cell and Environment*, **9**, 279–287.
- Nobel, P. S. & Palta, J. A. (1989). Soil O₂ and CO₂ effects on root respiration of cacti. *Plant and Soil*, **120**, 263–271.
- Patten, D. T. & Dinger, B. E. (1969). Carbon dioxide exchange patterns of cacti from different environments. *Ecology*, **50**, 686–688.
- Rowley, G. G. (1978). *Illustrated Encyclopedia of Succulent Plants*. Crown Publishers, New York.
- Rygel, J., Winter, K. & Zimmermann, U. (1987). The relationship between turgor pressure and titratable acidity in mesophyll cells of intact leaves of a crassulacean-acid-metabolism plant, *Kalanchoe daigremontiana* Hamet et Perr. *Planta*, **172**, 487–493.
- Sattelmacher, B. & Klotz, F. (1983). Bestimmung von Wurzeloberflächen mit Hilfe von Schnellmethoden. *Wurzelökologie und ihre Nutzenanwendung: Ein Beitrag zur Erforschung der Gesamtpflanze* (Ed by W. Böhm, L. Kutschera & E. Lichtenegger), pp. 95–98. Bundesanstalt für alpenländische Landwirtschaft, Irtding, Austria.
- Schwoegler, B. & McClintock, M. (1981). *Weather and Energy*. McGraw Hill, New York.
- Smith, W. K. & Nobel, P. S. (1977). Temperature and water relations for sun and shade leaves of a desert broadleaf, *Hyptis emoryi*. *Journal of Experimental Botany*, **28**, 169–183.
- Steenbergh, W. F. & Lowe, C. H. (1983). *Ecology of the Saguaro: III. Growth and Demography*. National Park Service Scientific Monograph Series 17, Washington, DC.
- Sutton, B. G., Ting, I. P. & Troughton, J. H. (1976). Seasonal effects on carbon isotope composition of

- cactus in a desert environment. *Nature*, **261**, 42–43.
- Taylor, N. P. (1985).** *The Genus Echinocereus*. Timber Press, Portland, OR.
- Ting, I. P. (1976).** Crassulacean acid metabolism in natural ecosystems in relation to annual CO₂ uptake patterns and water utilization. *Metabolism and Plant Productivity* (Ed by R. H. Burris & C. C. Black), pp. 251–268. University Park Press, Baltimore, MD.
- Ting, I. P. & Dugger, W. M. Jr (1968).** Non-autotrophic carbon dioxide metabolism in cacti. *Botanical Gazette*, **129**, 9–15.
- Turnage, W. V. & Hinckley, A. L. (1938).** Freezing weather in relation to plant distribution in the Sonoran Desert. *Ecological Monographs*, **8**, 529–550.
- Yeaton, R. I. & Manzanares, A. R. (1986).** Organization of vegetation mosaics in the *Acacia schaffneri*–*Opuntia streptacantha* association, southern Chihuahuan Desert, Mexico. *Journal of Ecology*, **74**, 211–217.

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