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NUTRIENT LEVELS IN CACTI—RELATION TO NOCTURNAL ACID ACCUMULATION AND GROWTH[1]

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ABSTRACT

The levels of ten essential nutrients and Na in the chlorenchyma and subjacent parenchyma of ten species of cacti were measured along with the maximal rates of nocturnal acid accumulation. Nutrient levels varied considerably among species; also, soil differences between sites affected levels within *Opuntia ficus-indica* and *O. chlorotica.* Compared to most agronomic plants, chlorenchyma levels of Ca, Mg, and Mn in cacti tended to be higher and Na lower. Moreover, Ca tended to accumulate in the chlorenchyma with age. The strongest correlation between nutrient level and a metabolic process for the 11 elements tested was with N, where nocturnal acid accumulation tended to be greater when the N level in the chlorenchyma was higher ($r^2 = 0.39$). Hydroponically grown seedlings of *Carnegiea gigantea, Ferocactus acanthodes,* and *Trichocereus chilensis* responded to N fertilization, reaching about 90% of their maximal growth rates when provided with N at 0.25× that in Hoagland's solution (namely, 4 mM nitrate). Nocturnal acid accumulation was negatively correlated with the chlorenchyma Na ($r^2 = 0.32$), which averaged only 28 ppm for *O. ficus-indica* (the root contained considerably more) and 234 ppm for the other species. Growth of seedlings was 50% reduced at about 100 mM NaCl for *F. acanthodes, T. chilensis,* and *C. gigantea,* while variations in P had a relatively small effect.

THE MINERAL NUTRIENT STATUS of plants, which affects their metabolic activity in many ways, has been studied in detail for C_3 and C_4 plants (e.g., Epstein, 1972; Hewitt and Smith, 1974; Clarkson and Hanson, 1980), but relatively little attention has been paid to Crassulacean acid metabolism (CAM) plants. Carbon dioxide uptake by CAM plants occurs primarily at night, when CO_2 is incorporated into phosphoenolpyruvate leading to four-carbon organic acids that are stored in the vacuoles of the chlorenchyma cells (Kluge and Ting, 1978). Such nocturnal acid accumulation is affected by plant water status, temperature, and light regime (see, e.g., Ting and Gibbs, 1982). A few studies have revealed effects of mineral ions on CAM plants, e.g., NaCl stress can induce CAM in certain plants (Kluge and Ting, 1978). Sodium has been implicated as essential for growth of the CAM plant *Kalanchoe tubiflora* (syn. *Bryophyllum tubiflorum*) when this species exhibits nocturnal CO_2 uptake (Brownell and Crossland, 1974). For *K. tubiflora, Sedum telephium,* and *S. telephoides,* Ca/K averaged 0.77 when the plants exhibited CAM metabolism and increased to 1.23 under environmental conditions which prevented CAM metabolism (Mathur, Natarella and Vines, 1978). Calcium can be high in certain CAM plants, being 1.5 to 3.5 times the level of K (on a mass basis) for *K. daigremontiana* (Phillips and Jennings, 1976).

The present study examines the levels of N, P, and K plus seven other essential nutrients and Na in ten species of cacti. Since very little is known about nutrient levels of cacti, such information is useful in determining possible differences between cacti and other plant groups. Indeed, cacti differ from most other plants both morphologically and physiologically, which could affect their mineral relations. For instance, cacti tend to have shallow root systems and thus would obtain minerals only from the upper part of the soil; they do not shed photosynthetic organs and so certain elements might accumulate; and their CAM nature leads to a high water-use efficiency (mass of CO_2 fixed/mass of H_2O transpired), so a relatively large fraction of the water taken up from the soil is retained in the stem (over 6% for *Ferocactus acanthodes*; Nobel, 1977).

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TABLE 1. *Summary of cacti examined. Nomenclature is according to Backeberg (1966) for South America and Shreve and Wiggins (1964) for North America, except Beatley (1976) for* Coryphantha

Species	Site location
Carnegiea gigantea (Engelm.) Britton & Rose	near Buckeye, Arizona (33°46′N, 112°41′W, 500 m)
Coryphantha vivipara (Nutt.) Britton & Rose var. *deserti* (Engelm.) W. T. Marshall	near Mercury, Nevada (36°40′N, 116°1′W, 110 m)
Ferocactus acanthodes (Lem.) Britton & Rose var. *lecontei* (Engelm.) Lindsay	at the Philip L. Boyd Deep Canyon Desert Research Center near Palm Desert, California (33°38′N, 116°24′W, 840 m)
F. wislizenii (Englem.) Britton & Rose var. *wislizenii*	near Tucson, Arizona (32°21′N, 111°2′W, 850 m)
Opuntia basilaris Engelm. & Bigel. var. *basilaris*	at the Philip L. Boyd Deep Canyon Desert Research Center (33°39′N, 116°22′W, 300 m)
O. bigelovii Engelm.	at the Philip L. Boyd Deep Canyon Desert Research Center (33°38′N, 116°24′W, 850 m)
O. chlorotica Engelm. & Bigel.	in the Granite Mountains, California (34°47′N, 115°39′W, 1,340 m)
O. echios Howell var. *gigantea* Howell	Santa Cruz Island, Galápagos Islands, Ecuador (0°44′S, 90°17′W, 10 m)
O. ficus-indica (L.) Miller	cultivated plantation near Fillmore, California (34°24′N, 118°53′W, 90 m)
	cultivated plantations at Til Til, Chile (33°3′S, 70°55′W, 660 m)
Trichocereus chilensis (Colla) Britton & Rose	near Cuesta la Dormida, Chile (33°3′S, 71°6′W, 1,250 m)

The major objective of the present study was to relate tissue elemental levels to an important metabolic process, the nocturnal increase in acidity, which is a convenient index of net CO_2 uptake by these CAM plants. Such findings could help identify deficiency, sufficiency, and perhaps even toxicity levels of various mineral nutrients for cacti. Since much of the interest in this study centered on a metabolic process taking place in the chlorenchyma, elemental levels were determined for the chlorenchyma at the same location as used for acidity measurements. Emphasis was on the general trends between nocturnal acid accumulation and levels of individual nutrients for cacti as a group, although intraspecific variation in tissue nutrient levels between sites provided important additional information.

MATERIALS AND METHODS—*Plant material*—Nutrient levels and diurnal acidity changes were examined for ten species of cacti from North and South America (Table 1). With the exception of the cultivated *Opuntia ficus-indica,* all were mature plants in natural populations. The *O. ficus-indica* were irrigated and the California site was also fertilized [approximately 500 kg/ha of $(NH_4)_2SO_4$ applied twice annually].

Growth was studied using commercially obtained seedlings approximately 1 yr of age. They were maintained hydroponically in 0.25× Hoagland's solution no. 1 supplemented with micronutrients (Hoagland and Arnon, 1950), except when modified as indicated. Stem growth over a 6-month period (January to July 1982) was monitored in a greenhouse. Growth was defined as the fractional increase in volume, calculated from the height times the diameter squared. The initial heights and diameters at midheight were respectively 2.2 ± 0.2 cm and 2.5 ± 0.2 cm for *Carnegiea gigantea,* 2.5 ± 0.2 cm and 3.1 ± 0.1 cm for *Ferocactus acanthodes,* and 2.6 ± 0.2 cm and 3.1 ± 0.2 cm for *Trichocereus chilensis* (data are presented as mean ± standard deviation for at least 20 measurements in each case). Chlorophyll was extracted and assayed in 80% acetone/20% water (v/v); data are expressed on a total stem area basis.

Elemental analysis—Stem tissue sections used for nutrient analysis were dried for 24 hr at 80 C and then ground to a fine powder using a Spex mill. Except for N, elemental analyses were done spectrographically (Alexander and McAnulty, 1981) using 10 mg (dry weight) samples. Total N determinations were performed on 200 mg (dry weight) samples using an Orion ammonia electrode following Kjeldahl digestion. Data are expressed as % (0.01 g g^{-1}) or ppm (μg g^{-1}) of the tissue dry weight. The samples for nutrient analysis were collected from the same location on the same

stems as used for acidity studies, generally a terminal cladode for the *Opuntias* and at mid-height for the other species. The clay, silt, and sand fraction (particle size under 2 mm) of 20-g (dry weight) soil samples was extracted with 1 N ammonium acetate to obtain material for elemental analysis, except for soil N, which was assayed similarly to tissue N but using 10-g (dry weight) samples; data are expressed as μg of element per g of dried soil.

Nocturnal acid accumulation—Diurnal changes in tissue acidity were previously determined in the field for *O. basilaris* (Nobel, 1980), *O. chlorotica* (Nobel, 1980), *O. echios* (Nobel, 1981), *O. ficus-indica* (Nobel, 1982, plus additional data reported here), and *T. chilensis* (Nobel, 1981). Measurements for other species were made on plants transferred from the field in native soil and maintained in environmental chambers with a 12-hr day at 25 ± 1 C and a night at 15 ± 1 C. Photosynthetically active radiation (PAR, 400 to 700 nm) of 600 μmol m^{-2} s^{-1} (26 mol m^{-2} day^{-1}) was provided 60% by warm-white fluorescent lamps and 40% by cool-beam tungsten lamps. Plants were irrigated weekly with 0.1× Hoagland's solution no. 1 supplemented with micronutrients such that the soil water potential near the roots was −0.2 ± 0.1 MPa.

Tissue acidity was measured on samples removed at dawn or dusk with a cork borer, immediately ground with sand in 30-ml distilled water, and then titrated to an endpoint of pH 6.8 using 0.010 N NaOH. Reported laboratory and field values represent the maximum nocturnal acid accumulation (dawn level minus dusk level) occurring near saturating PAR (26 to 30 mol m^{-2} day^{-1}) for well-watered conditions and optimal nocturnal temperatures (near 15 C). To facilitate comparisons among species and to be consistent with PAR determinations, such maximum acid accumulation determined graphically from measurements at various PAR levels (e.g., Nobel, 1980, 1981, 1982) was expressed per unit stem surface area. Moreover, since no daytime stomatal opening (except briefly at dawn) or CO_2 uptake was observed for the specific plants sampled, nocturnal acid accumulation as measured here should be a reliable index of net carbon gain.

RESULTS AND DISCUSSION—*Element levels and growth characteristics of Opuntia ficus-indica*—The levels of ten essential elements plus Na in various tissues of *Opuntia ficus-indica* from three different sets of plants are summarized in Table 2. Compared to mature 2-yr-old cladodes, 2-wk-old cladodes had substantially higher N, K, and Mn, but lower Na, Ca, and Fe (Table 2). The higher N level is consistent with higher metabolic activity in young cladodes. Since neither Ca nor Fe is very mobile in plants (Epstein, 1972), both would be expected to accumulate in older tissues, which helps explain the lower levels of these elements in young cladodes. Sodium levels were low for mature cladodes, but were even lower for the young cladodes. Compared with the (non-chlorophyllous) parenchyma,the chlorenchyma had much lower Na and Cu levels but a higher Ca level for the mature cladodes from California (similar results were obtained for the plants from Chile). Table 2 also indicates that the California plants had a higher rate of nocturnal acid accumulation than the Chile plants.

The growth of *O. ficus-indica* differed considerably between field sites. Terminal cladodes were harvested approximately every 6 wk from the California plants, limiting the height of the plants to about 130 cm. The Chile plants, which were not harvested, had a similar height, the 5-yr-old ones being 149 ± 19 cm tall (with 61 ± 10 cladodes) and the 12-yr-old ones being 126 ± 10 cm tall (with 63 ± 8 cladodes; 20 plants measured in each case). Since the soil texture (clay, silt, and sand content of the non-rock fraction), soil organic matter, the irrigation schedule, and climate were similar for the two nearby fields in Chile, the much lower growth rate of the 12-yr-old plants may reflect a poorer soil nutrient status. Indeed, the soil for the faster growing plants had more N (0.33 ± 0.09% vs. 0.06 ± 0.02%), more Mn (20 ± 3 ppm vs. 8 ± 3 ppm), more Fe (2.2 ± 0.3 ppm vs. 0.3 ± 0.2 ppm), and less Cu (0.5 ± 0.1 ppm vs. 7.2 ± 3.4 ppm) than the soil for the slower growing plants (six samples in each case; means for the other elements were within 40% of each other for the two cases). Chlorenchyma K, P, Mg, Ca, Zn, and B were similar (within 20% of each other), while N and Mn were higher in the faster growing (5-yr-old) plants and Na, Cu, and Fe were higher in the slower growing (12-yr-old) ones (Table 2). Compared to the *O. ficus-indica* growing in California, the Chile plants had lower N, P, Ca, and B, higher K and Mn, and similar (within 20%) Na, Mg, Zn, and Fe (Table 2).

Certain trends exist between element levels in *O. ficus-indica* and various indices of metabolism. This became apparent upon comparing 1) young vs. mature stems, where the young stems are presumably more active metabolically; 2) California vs. Chile plants, where the California plants had a higher rate of nocturnal acid accumulation; and 3) fast vs. slow

TABLE 2. *Nutrient levels in* Opuntia ficus-indica. *Samples were collected from 12-yr-old plants from Fillmore, California in April 1981 (Calif), and from 5-yr-old plants (Chile-5) and 12-yr-old plants (Chile-12) from Til Til, Chile in May 1981. All samples were from 1- to 2-yr-old cladodes that were 37 ± 3 cm long, except for the "young stems" from Fillmore, which were 2 wk old and 7 ± 1 cm long. Nutrient levels are presented as % dry weight or parts per million of dry weight. Data are for eight cladodes in each case and are given as mean ± standard deviation*

Sample	Maximum nocturnal acid accumulation (mol m^{-2})	N (%)	K (%)	Na (ppm)	P (ppm)	Ca (%)	Mg (%)	Mn (ppm)	Cu (ppm)	Zn (ppm)	Fe (ppm)	B (ppm)
Chlor-enchyma—Calif.	0.81	2.61 ± 0.14	1.18 ± 0.19	31 ± 14	3,320 ± 430	6.33 ± 0.93	1.43 ± 0.20	54 ± 14	15 ± 7	52 ± 11	88 ± 30	109 ± 21
Parenchyma—Calif.		2.19 ± 0.26	1.50 ± 0.19	70 ± 15	2,710 ± 410	2.44 ± 0.81	1.63 ± 0.30	42 ± 18	25 ± 9	59 ± 12	90 ± 14	90 ± 17
Entire stem—Calif.		2.45 ± 0.15	1.42 ± 0.10	59 ± 15	3,000 ± 160	4.67 ± 0.34	1.44 ± 0.10	51 ± 16	22 ± 10	56 ± 6	92 ± 5	102 ± 18
Young stem (entire)—Calif.		3.56 ± 0.35	2.16 ± 0.29	21 ± 4	3,420 ± 280	2.24 ± 0.37	1.21 ± 0.06	186 ± 26	16 ± 1	55 ± 8	58 ± 6	92 ± 17
Chlor-enchyma—Chile-5	0.65	1.53 ± 0.10	1.97 ± 0.12	30 ± 11	1,160 ± 250	3.90 ± 0.44	1.31 ± 0.21	371 ± 110	13 ± 9	52 ± 6	79 ± 14	35 ± 6
Chlor-enchyma—Chile-12	0.44	1.25 ± 0.19	2.01 ± 0.16	22 ± 12	990 ± 270	3.61 ± 0.62	1.16 ± 0.13	183 ± 44	38 ± 18	63 ± 4	112 ± 21	29 ± 10

growing Chile plants. Specifically, metabolic activity tended to be higher with higher levels of N ($P < 0.05$) and possibly with lower levels of Cu, while the other elements had little consistent effect for this species.

Survey of element levels in cacti—The maximum nocturnal acid accumulation and the levels of 11 elements in the chlorenchyma for nine species of cacti are summarized in Table 3. (In all cases, including *O. ficus-indica,* the essential element Mo was below the detection sensitivity of 0.2 ppm.) The range in levels differed widely between species, amounting to more than 10-fold for Na, P, and Mn. The 2- to 3-fold range found for N, K, Mg, Ca, and Fe represented the least variation.

In some cases the cause of the large range in nutrient levels could be identified. For instance, the chlorenchyma B level of the *O. ficus-indica* from California was about 3-fold higher than for the *O. ficus-indica* from Chile (Table 2) and nearly twice as high as that for the species with the next highest level (Table 3), probably because of the substantial B level in the irrigation water used at the California site (0.71 ± 0.03 ppm). Correlations were also found between the nutrient levels in *O. chlorotica* and those in the soil. For three specimens of *O. chlorotica* growing within 100 m of each other on a rocky, east-facing, 30° slope (Table 4), the relative levels in the chlorenchyma for 6 of the 7 elements that varied substantially (N, K, Na, P, Zn, and Fe) paralleled the variation of these elements in the respective soil samples ($r^2 > 0.86$ in each case, Table 4). Thus, soil differences can account for some of the element differences found for the cacti (Table 3).

The large regions of chlorenchyma (usually 2 to 3 mm thick) and underlying parenchyma (from about 5 to over 30 mm) in mature stems allowed the nutrient levels in these two tissues to be determined separately. In nearly all cases the chlorenchyma had higher levels of Ca, Mn, and B but lower levels of K, Na, Cu, and Fe than the parenchyma (Table 5). For *O. ficus-indica,* N averaged 17% ± 4% higher in the chlorenchyma than the parenchyma.

The levels of elements in cacti observed here (Tables 2 and 3) show some marked differences from other plants. Representative element levels in agronomic plants are about 2% for N, 2% for K, 1,000 ppm for Na, 3,000 ppm for P, 2% for Ca, 0.4% for Mg, 70 ppm for Mn, 8 ppm for Cu, 40 ppm for Zn, 150 ppm for Fe, and 30 ppm for B (Epstein, 1972; Larcher, 1980; W. L. Berry, pers. commun.). Based on these values, Ca, Mg, and Mn average at least

TABLE 3. *Summary of nutrient levels in the chlorenchyma of various cacti. The data are averages for 6 to 8 samples in each case*

Species	Maximum nocturnal acid accumulation (mol m^{-2})	N (%)	K (%)	Na (ppm)	P (ppm)	Ca (%)	Mg (%)	Mn (ppm)	Cu (ppm)	Zn (ppm)	Fe (ppm)	B (ppm)
Carnegiea gigantea	0.46	2.48 ± 0.20	1.18 ± 0.04	332 ± 27	1,180 ± 80	1.69 ± 0.30	0.60 ± 0.03	26 ± 2	4 ± 1	21 ± 2	117 ± 5	23 ± 8
Coryphantha vivipara	0.24	1.52 ± 0.09	1.02 ± 0.06	92 ± 10	3,820 ± 230	1.92 ± 0.02	0.58 ± 0.04	134 ± 12	3 ± 0	33 ± 6	178 ± 5	54 ± 3
Ferocactus acanthodes	0.38	1.62 ± 0.14	1.95 ± 0.09	315 ± 18	1,700 ± 150	4.62 ± 0.11	0.62 ± 0.03	122 ± 6	9 ± 1	22 ± 2	161 ± 5	62 ± 2
F. wislizenii	0.56	1.92 ± 0.15	1.68 ± 0.04	248 ± 35	1,830 ± 120	2.58 ± 0.15	0.60 ± 0.03	242 ± 37	9 ± 1	29 ± 4	155 ± 16	32 ± 5
Opuntia basilaris	0.58	1.19 ± 0.07	1.70 ± 0.16	121 ± 24	444 ± 39	3.10 ± 0.12	1.25 ± 0.04	31 ± 2	2 ± 1	7 ± 1	133 ± 13	13 ± 2
O. bigelovii	0.19	1.00 ± 0.05	1.52 ± 0.10	282 ± 36	1,220 ± 190	4.98 ± 0.15	1.34 ± 0.08	46 ± 11	6 ± 1	14 ± 5	219 ± 58	35 ± 1
O. chlorotica	0.76	2.06 ± 0.16	0.63 ± 0.04	18 ± 8	292 ± 65	6.10 ± 0.49	1.75 ± 0.09	498 ± 72	5 ± 1	28 ± 4	204 ± 35	52 ± 7
O. echios	0.32	1.58 ± 0.26	1.58 ± 0.16	484 ± 15	1,720 ± 280	3.14 ± 0.68	1.68 ± 0.32	209 ± 58	3 ± 1	25 ± 5	102 ± 44	18 ± 4
Trichocereus chilensis	0.26	1.23 ± 0.31	1.67 ± 0.25	215 ± 70	2,620 ± 480	5.92 ± 1.24	0.78 ± 0.16	478 ± 63	14 ± 6	44 ± 12	203 ± 78	44 ± 10
Nutrient average		1.63	1.44	234	1,650	3.78	1.02	208	6	25	164	37

TABLE 4. *Variation of element content with soil for* O. chlorotica. *Data are averages for the chlorenchyma of six cladodes or for extracts of eight soil samples taken from the root zone for single plants at three sites within 100 m of each other. Only those elements whose average for some site differed by at least 20% from their average for* O. chlorotica *in Table 3 are presented*

Site—sample	N (%)	K (ppm)	Na (ppm)	P (ppm)	Mn (ppm)	Zn (ppm)	Fe (ppm)
1—plant	2.01 ± 0.20	5,900 ± 700	16 ± 6	348 ± 140	530 ± 134	38 ± 6	219 ± 16
1—soil	0.141 ± 0.012	95 ± 7	3.3 ± 0.7	10 ± 9	6 ± 1	1.0 ± 0.1	0.26 ± 0.26
2—plant	1.29 ± 0.10	9,800 ± 900	40 ± 7	940 ± 240	102 ± 34	29 ± 2	323 ± 41
2—soil	0.068 ± 0.005	237 ± 4	5.1 ± 1.1	19 ± 6	4 ± 1	0.9 ± 0.1	0.30 ± 0.19
3—plant	1.65 ± 0.17	10,900 ± 1,600	88 ± 34	1,460 ± 520	441 ± 126	49 ± 6	511 ± 42
3—soil	0.090 ± 0.006	257 ± 10	9.6 ± 2.0	35 ± 9	16 ± 2	1.8 ± 0.2	0.86 ± 0.28

50% higher in the chlorenchyma of cacti, while Na averages about 80% lower. In some cases (*O. basilaris* and *O. chlorotica*), P is only about one-tenth the level representative of other plants, which would be expected to be a deficiency level in other plants (Berry, 1971). Based on data from other plants, Zn may also be approaching deficiency levels in *O. basilaris*. The high level for Ca may reflect the accumulation of calcium oxalate, which is known to occur in cacti (e.g., Bailey, 1965; Darling, 1976). A study on *Zygocactus truncatus* and five other CAM species (Mathur et al., 1978) indicated considerably higher levels for K, Na, P, Zn, and B than found here for cacti, e.g., *Z. truncatus* had 12% K, 1,720 ppm Na, 7,700 ppm P, 206 ppm Zn, and 417 ppm B.

Nocturnal acid accumulation and element levels—The wide range in tissue nutrient levels and the 4-fold range in the magnitude of the nocturnal acid accumulation (Table 3) should facilitate identification of relationships indicating elemental deficiency or toxicity. Such relationships between nutrient level and metabolic activity are often non-linear (e.g., Berry, 1971; Epstein, 1972). Nevertheless, linear regressions may be helpful in discerning general trends for cacti, and thus they were performed between each nutrient and the diurnal acid changes of the nine species in Table 3 plus the three different *O. ficus-indica* in Table 2. In addition, multiple linear regressions were performed (r = simple correlation coefficient; R = multiple correlation coefficient).

The correlations between maximal nocturnal acid accumulation and element level were generally slight, r^2 being less than 0.20 in all cases except for N ($r^2 = 0.39$) and Na ($r^2 = 0.32$). For two elements the multiple linear regression gave the best fit for N plus Na ($R^2 = 0.67$), indicating that they accounted for two-thirds of the observed variation in nocturnal acid accumulation. The next element to be added by the multiple regression analysis was P (leading to $R^2 = 0.81$), followed by Fe ($R^2 = 0.88$), and then Ca ($R^2 = 0.92$). Since the P level in the chlorenchyma was only slightly correlated with the maximal nocturnal acid accumulation ($r^2 = 0.07$), and the correlation was in fact negative, primary attention was focused on N and Na.

The maximal nocturnal acid accumulation increased approximately 4-fold as the chloren-

TABLE 5. *Summary of element levels in the chlorenchyma divided by those in the parenchyma for various species of cacti. At least five measurements in each tissue are included*

Species	Chlorenchyma/parenchyma ratio									
	K	Na	P	Ca	Mg	Mn	Cu	Zn	Fe	B
Carnegiea gigantea	0.39	0.23	1.21	2.14	0.77	4.45	0.41	0.90	0.64	1.00
Coryphantha vivipara	0.94	0.30	0.87	0.57	0.98	1.79	0.59	1.81	0.43	1.64
Ferocactus acanthodes	0.81	0.27	2.15	1.02	0.76	3.60	0.92	1.00	0.96	1.46
F. wislizenii	0.54	0.16	0.96	0.98	1.33	5.01	0.57	0.88	0.92	0.93
Opuntia basilaris	0.96	0.51	1.05	0.63	1.45	1.51	1.15	0.79	0.75	1.51
O. bigelovii	0.86	0.80	0.47	1.08	1.06	1.39	0.90	1.53	0.86	1.38
O. chlorotica	1.12	0.63	0.68	1.51	1.28	1.23	0.52	1.31	1.94	1.78
O. echios	0.32	0.14	2.28	2.42	1.35	7.79	0.25	0.91	0.59	1.00
O. ficus-indica (Calif.)	0.79	0.44	1.07	2.59	0.88	1.29	0.60	0.88	0.98	1.21
Trichocereus chilensis	0.52	0.17	0.49	2.40	0.66	7.15	0.82	2.04	0.96	1.28
Average	0.73	0.37	1.12	1.53	1.05	3.52	0.67	1.21	0.90	1.32

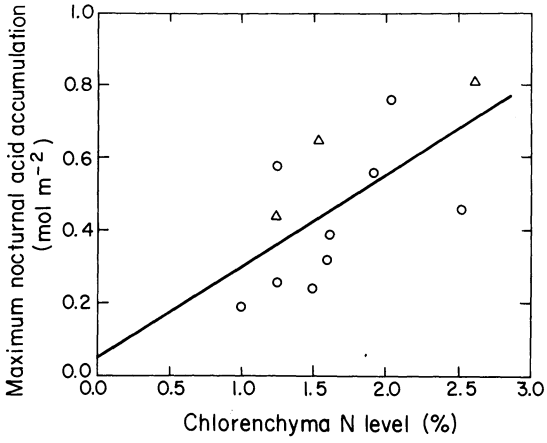

Fig. 1. Relationship between N level in the chlorenchyma and the maximum diurnal acidity change. Data are for the nine species in Table 3 (○) and the three mature *O. ficus-indica* in Table 2 (△). The indicated line represents the following regression equation: $y = 0.250x + 0.054$ ($r^2 = 0.39$).

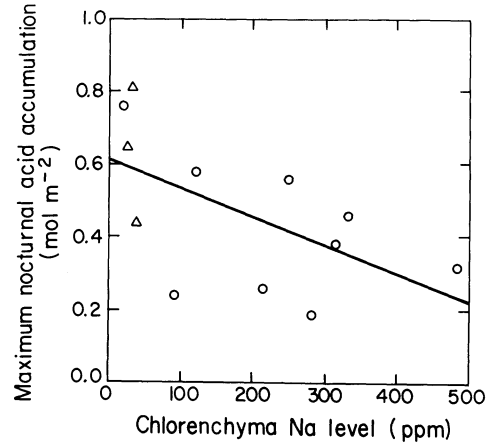

Fig. 2. Relationship between Na level in the chlorenchyma and the maximum diurnal acidity change. Data analyzed as for Fig. 1, with the following regression equation: $y = -0.00076x + 0.609$ ($r^2 = 0.32$).

chyma N increased 3-fold (Fig. 1). Indeed, N may commonly be the limiting nutrient for cacti under both natural and cultivated conditions, similar to observations on other vascular plants.

The nocturnal acid accumulation is negatively correlated with the Na level (Fig. 2), which suggests an inhibitory effect by Na, or, alternatively, that higher Na levels are associated with some stress. For *O. ficus-indica* in California, the Na level in the soil was 52 ± 2 ppm, the level in the roots was 608 ± 33 ppm, and the level in the chlorenchyma of the cladode nearest the base averaged only 47 ± 13 ppm, similar or slightly lower levels occurring for the chlorenchyma in the next four mature cladodes in sequence up to the top of the plant. For all five mature cladodes the Na level in the chlorenchyma was less than half of that in the parenchyma. Similarly, the Na level in the chlorenchyma for the other nine species studied was only 37% of the level in the parenchyma. This is the lowest average ratio for the elements compared, and also Na had the lowest individual values for the chlorenchyma/parenchyma ratio (Table 5). Thus, Na may be excluded from or actively transported out of chlorenchyma cells. The relatively high Na level in the roots but not in the stem suggests that Na may be excluded from the root xylem and thus not move in the transpiration stream to the stem. Plants showing higher metabolic activity might be expected to actively transport more Na out of chlorenchyma cells or perhaps not allow as much Na to move from the root to the stem, leading to the negative correlation between the magnitude of diurnal acid changes and the chlorenchyma Na levels (Fig. 2).

Effect of N and Na on growth of cactus seedlings—To investigate the effects of N and Na on cacti more fully, seedlings of three species were grown hydroponically over a wide concentration range of these elements. Figure 3 indicates that very little growth occurred for *Carnegiea gigantea, Ferocactus acanthodes,* and *Trichocereus chilensis* when the N level was 1% of that in Hoagland's solution, which contains 15 mM nitrate. At the N level for 0.25× Hoagland's solution, growth averaged 90% of the maximal, which occurred near full strength Hoagland's for all three species (Fig. 3). Such maximal growth caused the stem volume of *C. gigantea* to quadruple in 6 months, while the volumes of the other two species nearly doubled. Similarly, the dry weight of *Mammillaria elegans* increased about 30% more over a 3-month period at the N level in 0.5× Hoagland's compared to no added N (Stefanis and Langhans, 1980).

An increased N level in the hydroponic solution caused the N level in the stem tissue to increase (Fig. 4), similar to the response of *O. chlorotica* to varying element levels in the soil (Table 4). The higher N levels in the tissue occurred together with a greater amount of chlorophyll per unit surface area for *C. gigantea, F. acanthodes,* and *T. chilensis* (Fig. 4). In addition to leading to the higher growth rates (Fig. 3), the higher N levels in the hydroponic solutions led to greater amounts of nocturnal

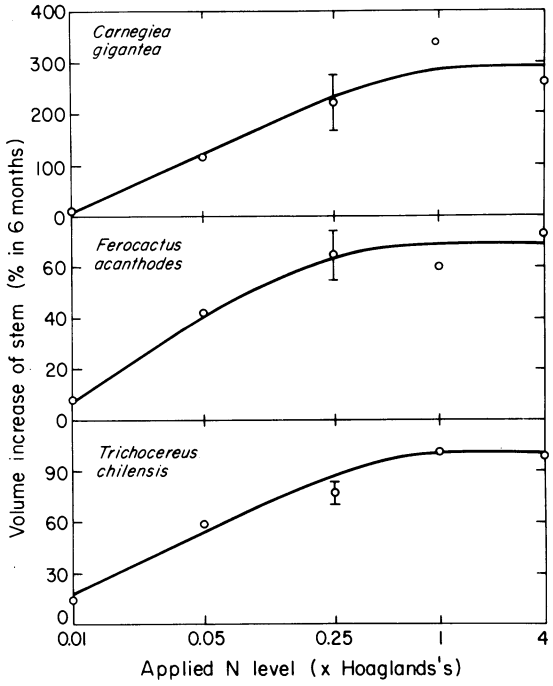

Fig. 3. Influence of N level in a hydroponic solution on the growth rate of cactus seedlings. The concentration of KNO_3 was varied to change the N level (15 mM NO_3^- in full strength Hoagland's solution); other nutrients were at the levels in 0.25× Hoagland's. Data are averages for six seedlings grown for 6 months under each condition, representative standard deviations being indicated.

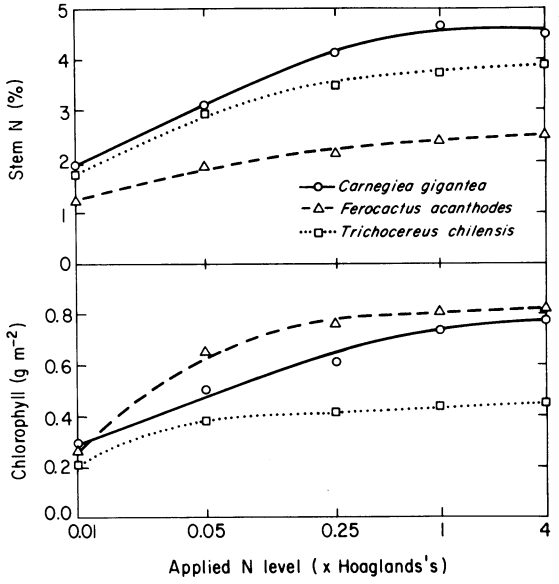

Fig. 4. Influence of N level in a hydroponic solution on tissue nitrogen and chlorophyll levels. Measurements done in duplicate for seedlings grown for 6 months as for Fig. 3.

acid accumulation. For instance, for seedlings of *F. acanthodes* the nocturnal acid accumulation at saturating PAR went from 0.01 mol m^{-2} for an N level of 0.01× Hoagland's, to 0.35 mol m^{-2} at 0.05×, to 0.54 mol m^{-2} at 0.25×, with very little further increase at higher N levels, similar to the N effect on growth (Fig. 3). Nitrogen availability has also been found to be critical for the growth of *O. polyacantha* (Dodd and Lauenroth, 1975). Thus, cacti can respond to nitrogen fertilization in a fashion similar to that for other plants.

As the NaCl level in the hydroponic solution was raised from the Na occurring as contamination in 0.25× Hoagland's solution (about 0.1 mM), growth of *F. acanthodes* became noticeably decreased at 50 mM (Fig. 5). Growth was inhibited 50% near 100 mM NaCl for *F. acanthodes* and *T. chilensis,* and 130 mM for *C. gigantea.* Since many species in other families can tolerate 50 mM NaCl with very little inhibitory effect (Gale, 1975; Longstreth and Nobel, 1979), at least some species of cacti may be moderately sensitive to salinity. As Na increased in the hydroponic solution, the Na level in the stem increased and achieved levels much higher than found here for the cacti growing in soil. At 100 mM NaCl, stem Na increased 8.2-fold for *C. gigantea,* 2.6-fold for *F. acanthodes,* and 2.9-fold for *T. chilensis* compared to the control, eventually reaching levels of over 6% for *C. gigantea* (Fig. 5). Increasing the Na level in the hydroponic solution decreased the chlorophyll per unit stem surface area. Compared to the control (0.1 mM Na^+ in 0.25× Hoagland's solution, see Fig. 4), 100 mM NaCl reduced chlorophyll by 11% for *C. gigantea,* 10% for *F. acanthodes,* and 39% for *T. chilensis,* and 200 mM NaCl reduced it by 26%, 22%, and 58%, respectively.

Since the third most important element in explaining the observed variation in maximal nocturnal acid accumulation was P, seedlings were also grown hydroponically in solutions containing various concentrations of this element. Two seedlings of each of the three species were exposed to 0.01, 0.05, 0.25, 1, and 4 times the P concentration in Hoagland's solution (2 mM phosphate). Very little variation in volume increase and no trend with P concentration occurred over a 6-month growth period for *C. gigantea* and *T. chilensis* (mean volume increases had standard deviations of 21% in both cases; see Fig. 3 for the volume increase in 0.25× Hoagland's). The seedling volume increase for *F. acanthodes* decreased slightly with

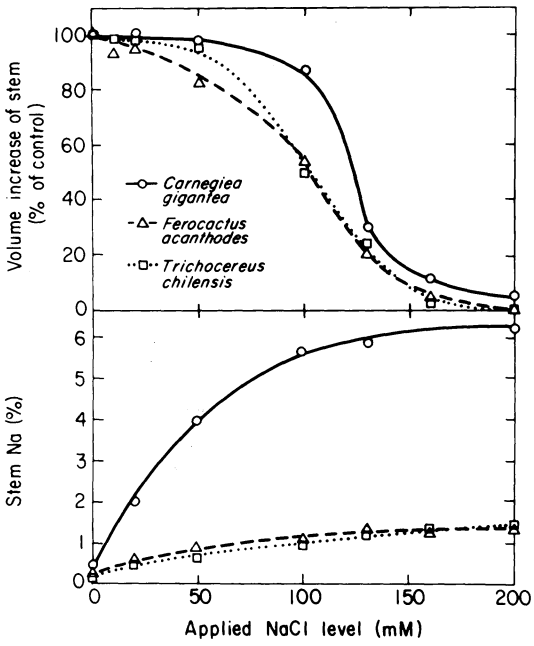

Fig. 5. Influence of NaCl level in a hydroponic solution on the growth rate and chlorenchyma Na level for seedlings of three species of cacti. Nutrients were at the levels in 0.25× Hoagland's (the "Control"), which had about 0.1 mM Na as contamination in addition to 2.5 mM Cl. Measurements were done in duplicate for seedlings grown for 6 months.

increasing P concentration, from 119% of its mean for the lowest two concentrations to 80% for the highest two. Thus, P had less effect on seedling growth for these three species than did N or Na, which is consistent with its lower correlation coefficient with the nocturnal acid accumulation for the cacti tested here.

CONCLUSIONS—Cacti represent very interesting plants for the study of nutrient levels and their effects on carbon gain, since the chlorenchyma can be readily separated from the underlying parenchyma and also since the photosynthetic organs are not periodically shed. In fact, cactus chlorenchyma can function for over 100 years, as has been observed for *C. gigantea* and *O. ficus-indica* (P. S. Nobel, personal observations of activity vs. estimated plant age). The higher level of Ca in cacti compared to other plants may represent the accumulation of calcium oxalate with age, while the lower Na level suggests that Na may be excluded from the chlorenchyma cells. Indeed, the Na level was higher in the root than the stem of *O. ficus-indica* and higher in the parenchyma than the chlorenchyma for all ten species of cacti examined. In hydroponic solutions containing 100 mM NaCl, which markedly reduced the growth of seedlings of *C. gigantea, F. acanthodes,* and *T. chilensis,* the chlorenchyma Na had increased at least 2.6-fold. As for other plants, the most critical nutrient appears to be N. The amount of acid accumulated in the tissue at night for the ten species examined was positively and most significantly correlated with the tissue N level. Also, raising the N level in hydroponic solutions substantially increased the rate of seedling growth. Thus, soil N may be the most limiting nutrient in the field for cacti.

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